PHYLOGENY OF NORTH AMERICAN *DICHANTHELIUM* (PANICOIDEAE, POACEAE): TESTING SPECIES LIMITS IN ONE OF THE MOST TAXONOMICALLY COMPLICATED GROUPS OF GRASSES

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Premise of research. *Dichanthelium* extends from Canada to Argentina and is most species rich in eastern North America. These C_3 panicoid grasses, which are mixed mating and flower two or three times per year, displaying different vegetative growth forms over that time, are renowned for their taxonomic complexity. Thus, there are drastically differing taxonomic treatments; however, no well-sampled phylogenetic perspective is yet available to further explore relationships among species or species complexes.

Methodology. We developed the first broadly sampled phylogeny of *Dichanthelium*, covering the entire range of the genus, but with a focus on the species-rich eastern North American distribution. We sampled 72 taxa (290 accessions), including all currently recognized taxa in the recent Flora of North America treatment. Our dataset consisted of the plastid locus *rpl32-trnL* and the nuclear loci internal transcribed spacer (ITS) and granule-bound starch synthase I (GBSSI) and was analyzed using maximum likelihood. We calibrated our phylogeny to test the divergence time of the North American clade and likewise used ITS data to explore putative hybridization.

Pivotal results. South American species of *Dichanthelium* formed a grade of successive sisters to the North American clade, which we recovered as originating in the late Miocene–early Pliocene. We recovered 27 subclades, most of these representing species complexes or morphologically similar species. Numerous taxa were resolved outside of their putative species groups and are apparently morphologically cryptic species. We show several cases of putative hybridization in eastern North American and Hawaiian species.

Conclusions. Our phylogeny provides a foundation for understanding this taxonomically complicated group of grasses, which will need detailed future studies into species complexes to provide greater taxonomic resolution and understanding of biological processes driving the evolution and diversification of the clade. This should include further study of autogamy and its evolutionary consequences in North American taxa. We propose an adjusted taxonomic treatment of specific members of the genus based mostly on our phylogenetic results.

Keywords: autogamy, cryptic species, Dichantheliinae, Paniceae, *Panicum*, Poales.

Online enhancements: appendix figures.

Introduction

The cosmopolitan Poaceae are one of the best-known families of angiosperms, with an estimated 11,783 species (Stevens 2001–; Soreng et al. 2022). Phylogenetic relationships are relatively well understood among subclades within the family (although see Duvall et al. 2020), consisting of roughly 12 currently recognized subfamilies (Soreng et al. 2022). Likewise, relationships among subfamilies have been studied moderately well, especially within the second-largest subfamily, Panicoideae (ca. 3325 species; Soreng et al. 2022), primarily using the plastid gene *ndhF* (Alisconi et al. 2003; Morrone et al. 2012; Zuloaga et al.

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2014, 2018) or, more recently, plastomes (Burke et al. 2016). Approximately 25 subclades have been recovered in those analyses (these are generally recognized as subtribes in tribe Paniceae; see Zuloaga et al. 2018), and the traditionally recognized (and highly polyphyletic) large genus *Panicum* s.l. has subsequently been separated into 13 genera based on those phylogenetic analyses and suites of morphological characters (Alisconi et al. 2003; Morrone et al. 2012; Zuloaga et al. 2014, 2018; Nicola et al. 2015). Many traditionally recognized genera within this clade have been maintained, such as *Cenchrus* s.l., *Echinochloa*, *Lasiacis*, *Oplismenus*, and *Sacciolepis*. Recent research suggests that even more genera should likely be recognized from the polyphyletic *Panicum* s.l. (Zuloaga et al. 2018). Among those subclades within Paniceae, the subtribe Dichantheliinae is a well-supported clade sister to Neurachninae (Burke et al. 2016) and consists of the two sister C_3 (non-Kranz-anatomy-containing) clades, *Adenochloa* and *Dichanthelium* (Zuloaga et al. 2014), two of the generic segregates of *Panicum* s.l. *Adenochloa* consists of ca. 14 African species, whereas the more diverse *Dichanthelium* consists of ca. 62–120 taxa of the Western Hemisphere, including Hawaii (Hitchcock 1950; Freckmann and Lelong 2003; Soreng et al. 2017, 2022). *Adenochloa* and *Dichanthelium* are distinguished by a combination of hair types (pedicellate, multicellular hairs in *Adenochloa* and the lack thereof in *Dichanthelium*) and the presence of foliar dimorphism and cleistogamous flowers in *Dichanthelium* (both lacking in *Adenochloa*; Zuloaga et al. 2014).

The genus *Dichanthelium*, formerly a subgenus of *Panicum* (Hitchcock and Chase 1910) but raised to generic rank by Gould (1974), is a group of mostly rosette-forming grasses (Brown and Smith 1975) inhabiting diverse habitats, from wet to xeric communities. The genus appears to be relatively young, with a putative origin dating to the early Pliocene (Huang et al. 2022). The bulk of the species richness in *Dichanthelium* occurs in eastern North America (Hitchcock 1935, 1950; Freckmann and Lelong 2003), with the center of diversity being the southeastern United States (Gould and Clark 1978). However, the genus inhabits the Americas from Argentina to Canada (including the Antilles), and new species are still being described (Zuloaga and Morrone 1991; LeBlond et al. 2020; Matos et al. 2020). A number of species found in the southeastern United States are also shared with the Antilles, Central America, and northern South America, such as *D. aciculare* (Desv. ex Poir.) Gould & C.A.Clark (Zuloaga et al. 1993); thus, several species have very large distributions. In contrast, some species are endemic to the southeastern United States or, more broadly, to the coastal plain of the eastern United States. In general, most species of *Dichanthelium* are restricted to specific habitats and thus presumably are ecological niche specialists; *D. erectifolium* (Nash) Gould & C.A.Clark, for example, is found in the moist, sandy, and nutrient-poor soils of pine savannas in the southeastern United States, western Cuba, and Belize.

Linnaeus (1753) was the first to describe species now recognized as *Dichanthelium* with the publication of *D. clandestinum* (L.) Gould, *D. dichotomum* (L.) Gould, and *D. latifolium* (L.) Harvill (all described under *Panicum*). Many other workers followed him (e.g., Vasey 1885; Nash 1895, 1899; Beal 1896; Ashe 1898; Lamson-Scribner and Merrill 1901; Hitchcock and Chase 1910), eventually publishing several hundred names for this taxonomically complicated group, many of which were relegated to synonymy in later treatments (Hitchcock and Chase 1910; Gould and Clark 1978; Freckmann and Lelong 2003). Merrill (1900) greatly criticized the many new species put forth by Ashe (1898) during this time for what he perceived to be a lack of systematic judgment for such a complicated group of grasses. Hitchcock and Chase (1910) recognized a total of 109 species of *Dichanthelium* for North America, and Gould and Clark (1978) recognized 26 species (45 taxa). More recently, Freckmann and Lelong (2003) recognized 34 species in their treatment for the Flora of North America North of Mexico, albeit with many infraspecific taxa recognized based on morphology. However, more recent assessments of species limits have included recognizing many of these formerly unrecognized taxa or infraspecific taxa at the species level, doubling the number of recognized species ($n = 68$) for eastern North American *Dichanthelium* alone (see LeBlond 2020).

Species limits in *Dichanthelium* have long been considered problematic, and the genus is considered taxonomically very difficult, which can be seen from the vastly different taxonomic treatments of the group and the deluge of species names proposed for the genus (reviewed in Gould and Clark 1978). Species of *Dichanthelium* flower at least twice a year, with the spring/early summer flowers in broad, open panicles (vernal culms) from basal rosettes, producing chasmogamous flowers, and the summer/late summer/fall flowers produced along secondary branches borne from the original flowering culm (i.e., autumnal culms), producing mostly cleistogamous flowers (although this is not always strictly the case; see Hitchcock and Chase 1910; Bell and Quinn 1985; LeBlond 2016). This has been defined as dimorphic cleistogamy by Culley and Klooster (2007). Given the annual production of large numbers of cleistogamous flowers in autumnal culms, the genus has been found to be predominantly autogamous (Spellenberg 1975), and high levels of homozygosity result from this reproductive mode (Hammer et al. 2012). South American species are less prone to autogamy than their North American relatives, according to Morrone and Zuloaga (1991). The size of leaves and inflorescences is much reduced in these secondary (autumnal) culms, and in general, most species look very different, being highly ramified, from their initial flowering phase (vernal culms), although most diagnostic morphological features are essentially the same (e.g., ligules, leaf and spikelet indumentum, spikelet dimensions). Another confounding factor is that many species of *Dichanthelium* are sympatric and syntopic; it is not uncommon to find five to 10 or more species growing together in the southeastern United States. Thus, spikelet size and shape, leaf color, and plant body indumentum, as well as numerous other features, are necessary for proper identification. As a consequence of morphological variation across what have been presumed to be closely related morphotypes, many species were represented by numerous proposed infraspecific taxa at either varietal levels or subspecific levels (Lelong 1984; Freckmann and Lelong 2003), or in some cases, many of those putative infraspecific taxa have been raised to the level of species (e.g., LeBlond 2020).

Last, species of *Dichanthelium* are very well known to hybridize (Church 1929; Lelong 1965; Spellenberg 1970, 1975; Freckmann and Lelong 2003; Hammer et al. 2012; L. C. Majure, R. F. C. Naczi, and B. Budach, personal observation), which may further confuse species identification or potentially lead to the overdescription of species based on F_1 hybrids. However, and in contrast to other North American grasses, only a handful of polyploids (tetraploids, 2n = 36) are known (i.e., *D. boscii*, *D. clandestinum*, *D. latifolium*, and *D. xanthophysum* (A.Gray) Freckmann; Gould and Clark 1978; Freckmann and Lelong 2003). Likewise, only two Central-South American species of *Dichanthelium* are known to be tetraploids (*D. sabulorum* (Lam.) Gould & C.A.Clark and *D. viscidellum* (Scribn.) Gould), and *D. davidsei* (Zuloaga & Morrone) Zuloaga has been recorded as an octoploid (2n = 72; Dubcovsky and Zuloaga 1991). Thus, most hybridization is apparently at the homoploid level and has not led to extensive polyploidy, although chromosome studies are greatly lacking in this group.

To date, all species-level classifications and treatments of *Dichanthelium* have been based solely on morphological characters, and the range of species recognized varies greatly depending on the treatment (Zuloaga et al. 1993; Freckmann and Lelong 2003; Zuloaga and Morrone 2003; LeBlond 2020). Only a handful of species have been included in phylogenetic analyses, and these are based on Sanger data (Alisconi et al. 2003) or plastome data (Pischl et al. 2020; Gallaher et al. 2022). In this study, our goal was to develop a species-level phylogeny based on DNA sequence data, with a focus on North American taxa, to test species limits and provide a preliminary hypothesis of species relationships.

Material and Methods

Taxon Sampling

We sampled broadly across *Dichanthelium*, with a focus on North American taxa (where applicable, all taxon labels presented in the subsequent trees are based on Freckmann and Lelong 2003), for a total of 72 taxa (62 mostly North American, six South American, and four Hawaiian) and 290 samples altogether in our phylogenetic analysis. Multiple accessions per taxon were included across their distribution where possible to test for clade formation. Most samples were fresh collected and preserved in silica gel (especially from the collectors Abbott, Majure, and Naczi) and otherwise were sampled from existing herbarium specimens, when fresh material was unavailable. Outgroups were chosen based on their relationships within tribe Paniceae and included *Adenochloa adenophora*, *Coleataenia anceps*, *Echinochloa* sp., *Panicum dichotomiflorum*, *Panicum miliaceum*, *Panicum trichoides*, and *Setaria italica* (data for *Echinochloa*, *P. miliaceum*, and *S. italica* were downloaded from GenBank), and the tree was rooted with *Coleataenia* (tribe Paspaleae) based on previous phylogenetic work (Alisconi et al. 2003; Zuloaga et al. 2014).

Extractions, Amplification, and Sequencing

Genomic DNA was extracted using a modified cetyltrimethylammonium bromide (CTAB) technique (Doyle and Doyle 1987), scaled to a 1.5-mL volume reaction. Approximately 10 mg of dried tissue was pulverized and then suspended in 1.5 mL of CTAB 2× buffer and 100 μg of proteinase K. After incubating at 50°C for 1–3 h, samples were purified by mixing with a 24 : 1 ratio of chloroform to isoamyl alcohol. The supernatant was then mixed with a binding buffer and placed in a silica column, followed by purification with a wash buffer and then elution with 150 μL of 1× TE (for full details, see Neubig et al. 2014).

Amplifications were performed using a Biometra TGradient or Eppendorf Mastercycler EpGradient S thermocycler and reagents in ~25-μL volumes using GoTaq reagents. Loci were chosen based on previous evidence demonstrating relatively high nucleotide variation.

nrITS (ITS 1 + 5.8S rDNA + ITS 2). This region was amplified with a protocol using the parameters of 98°C for 2 min; 35 cycles of 95°C for 15 s, 55°C for 15 s, and 72°C for 1 min; and 72°C for 2 min with the primers F (TAG AGG AAG GAG AAG TCG TAA CAA) and R (CCC GCC TGA CCT GGG GTC GC; Hoshi et al. 2008) and the following reaction components: 1.0 μL of template DNA (~10–100 ng), 16.5 μL of water, 5 μL of 5× buffer, 0.75 μL of $MgCl_2$ (50 mM), 0.5 μL of 10 mM dNTPs, 0.5 μL each of 10-μM primers, and 0.5 units of Taq.

GBSSI. This region was amplified with a protocol using the parameters of 94°C for 3 min; 36 cycles of 94°C for 20 s, 65°C for 30 s, and 72°C for 1 min; and 72°C for 3 min with the primers L1-for (GCA AGA CCG GGT TCC ACA TGG) and M-bac (GGC GAG CGG CGC GAT CCC TCG CC; Mason-Gamer 2004) and the following reaction components: 1.0 μL of template DNA (~10–100 ng), 16.5 μL of water, 5 μL of 5× buffer, 0.5 μL of $MgCl_2$ (50 mM), 0.5 μL of 10 mM dNTPs, 0.5 μL each of 10-μM primers, and 0.5 units of Taq.

rpl32-trnL. This region was amplified with a touchdown protocol using the parameters of 94°C for 3 min; 8 cycles of 94°C for 30 s, 60°C for 45 s but reducing 1°C per cycle, and 72°C for 1 min 30 s; 30 cycles of 94°C for 30 s, 50°C for 45 s and holding at the same temperature, and 72°C for 1 min 30 s; and 72°C for 3 min with the primers *trnL*(UAG) (CTG CTT CCT AAG AGC AGC GT) and *rpl32-F* (CAG TTC CAA AAA AAC GTA CTT C; Shaw et al. 2007) and the following reaction components: 1.0 μL of template DNA (~10–100 ng), 16.5 μL of water, 5 μL of 5× buffer, 1.5 μL of $MgCl_2$ (25 mM), 0.5 μL of 10 mM dNTPs, 0.5 μL each of 10-μM primers, and 0.5 units of Taq.

Raw uncleaned polymerase chain reaction products were run on 1% agarose gel to visualize quality and determine the degree of necessary dilution. Polymerase chain reaction products were cleaned and diluted with water to approximately equivalent concentrations, cycle sequenced, and sequenced by Eurofins Genomics on an ABI3730xl.

While most data were obtained through Sanger sequencing, some samples were sequenced with Illumina technology as part of ongoing genomic-level study of *Dichanthelium* and included here in our existing Sanger dataset to supplement taxon sampling. Unenriched total DNAs, extracted using the above protocol, were sent to Rapid Genomics for sequencing. DNA libraries were prepped with 500-bp inserts and sequenced (paired end) on Illumina HiSeq or HiSeqX, resulting in reads of 100–150 bp in length, with adapter sequences removed.

Data Editing and Phylogenetic Analyses

Sanger sequence data were edited in Geneious versions R10 and Prime (Kearse et al. 2012). Forward and reverse sequences were edited to trim low-quality ends and checked for improper base calls and polymorphisms for all loci; ends of the loci were trimmed to exclude primer sequences. Four samples showed a putative hybrid signal in our sequence data and were removed from further analyses (see "Results").

For Illumina data, raw data were processed using the GetOrganelle pipeline (Jin et al. 2020), implemented on the Southern Illinois University (SIU) high-performance computing cluster (HPCC; BigDawg). Resultant assembled plastomes were annotated in Geneious, and the *rpl32-trnL* region was exported and combined with the aforementioned Sanger data. For internal transcribed spacer (ITS), raw Illumina data were imported into Geneious, paired, and then trimmed using default Geneious settings. Those data were reference assembled against various Sanger data produced in this study; used reads were de novo assembled, and the final contigs were produced with a 75% mismatch setting to capture any latent polymorphisms. We could not assemble granule-bound starch synthase I (GBSSI) from these data, due to no/partial recovery and/or low coverage across the locus.

All data from these assemblies were included in the following analyses, except for a small portion of seven nucleotides in the *rpl32-trnL* region. This region is a homopolymer nucleotide sequence that was prone to a homoplasious inversion and therefore removed. Phylogenetic analysis was implemented in IQ-TREE (ver. 2.2.0.3; Minh et al. 2020), implemented on the SIU HPCC (BigDawg). A test of data partitioning was implemented in PartitionFinder 2 (Guindon et al. 2010; Lanfear et al. 2016) using the greedy algorithm (Lanfear et al. 2012). Models were determined using the corrected Akaike information criterion: TNe+I+Γ (for GBSSI), SYM+I+Γ (for ITS), and TVM+I+Γ (for *rpl32-trnL*). Thus, they were implemented in the following maximum likelihood (ML) and Bayesian methods. The combined concatenated dataset was partitioned by the three separate regions. A best tree search and ultrafast bootstrap (BS) were performed with 408 iterations, and each gene region was analyzed separately for topological comparison. Given that no hard incongruences were uncovered in resulting topologies of individual loci (figs. S1–S3; figs. S1–S7 are available online), we used the concatenated dataset for all further analyses. Bayesian phylogenetic estimation was performed in MrBayes (ver. 3.2.7; Ronquist et al. 2012) and implemented on the CIPRES Science Gateway (Miller et al. 2010).

Divergence Time Estimation

Divergence time estimation was performed in BEAST (ver. 2.7.3; Bouckaert et al. 2014), implemented on the SIU HPCC (BigDawg). The three-gene data matrix from above was imported into BEAUTi. Again, PartitionFinder 2 was used to test for models of DNA evolution but constrained only to the models that can be implemented in BEAST. Three partitions were selected with the following settings: TNe+I+Γ (for GBSSI), GTR+I+Γ (for ITS), GTR+I+Γ (for *rpl32-trnL*), estimate proportion invariant sites, relaxed clock log normal clock model, a Yule prior, and a prior to constrain the crown age of the Paniceae (all taxa, excluding *Coleataenia*) at 29.96 Myr old (95% confidence interval: 26.8–34.3 Myr old; Gallaher et al. 2022). Despite many comparative analyses, we used a Yule prior (instead of a birth-death prior) because it always gave better effective sample size estimations. Trees were set to link under these three partitions. Under these parameters, four independent runs with a chain length of 100 million were performed. The resultant trees from the four independent analyses were significantly better effective sample size values in one of these analyses, so results from that analysis are presented here, with 10% of the burn-in trees removed, as stationarity was confirmed using Tracer (ver. 1.7.1). A maximum clade credibility tree with common ancestor heights was produced from these trees using TreeAnnotator.

Biogeography

Biogeographic reconstruction was carried out in RASP (Yu et al. 2015), and we implemented DIVALIKE (Yu et al. 2015), as well as the dispersal, local extinction, and cladogenesis (DEC) model (Ree and Smith 2008), on our calibrated phylogeny from the BEAST analysis. Biogeographic areas were designated as South America (*a*), North America (including Central America and the Caribbean; *b*), Hawaii (*c*), and Old World (*d*). No biogeographic constraints were implemented in either analysis, and maximum areas were set to 2.

Results

Phylogeny, Divergence Time Estimation, and Biogeography

Data from both Sanger sequencing and genome skimming data placed taxa in comparable parts of the topology. DNA sequence data statistics can be found in table 1. Analysis of individual gene regions for topological comparisons can be seen in figures S1–S3. Additionally, Bayesian inference of the combined dataset can be seen in figure S4. Based on our maximum likelihood phylogenetic reconstruction of our combined dataset, *Dichanthelium* formed a well-supported clade (BS = 100) composed of ca. 27 subclades (figs. 1–7), representing currently recognized species, species complexes, or closely related species. Our BEAST topology was comparable to our ML topology, resolving essentially the same clades (fig. S5).

South American taxa included in our dataset formed a grade and were successive sisters to a mostly North American clade (fig. 1). Divergence time estimation indicated that *Dichanthelium*

Table 1

Information on the Individual and Combined DNA Matrices Used in Phylogenetic Analyses in This Study

DNA region	Aligned length	Total variable sites	Parsimony-informative sites	Sequencing method
GBSSI	570	259	120	Sanger
ITS	651	240	158	Sanger and Illumina
rpl32-trnL	708	141	63	Sanger and Illumina
Combined	1929	636	340	Sanger and Illumina

Note. GBSSI = granule-bound starch synthase I; ITS = internal transcribed spacer.

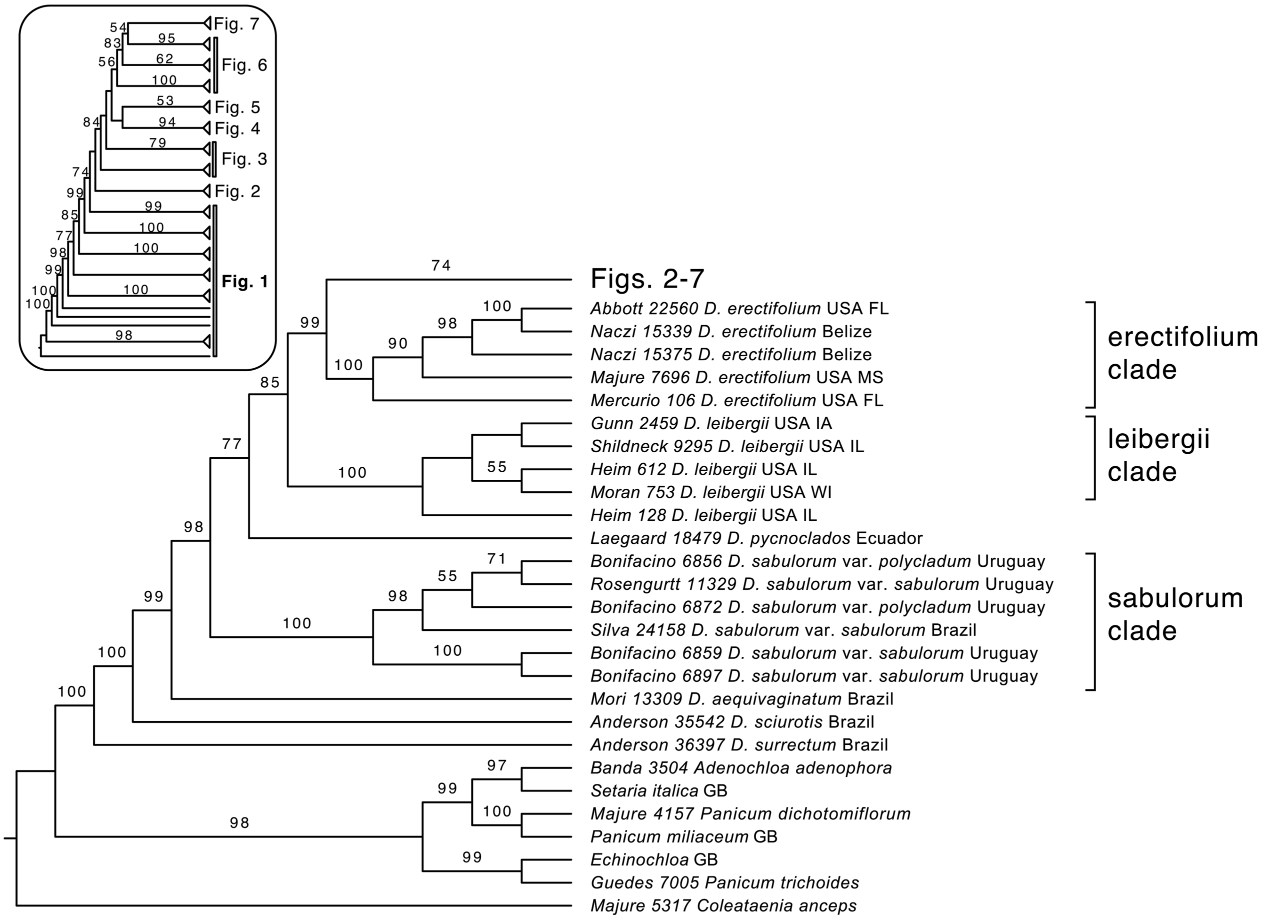

Fig. 1 Maximum likelihood phylogenetic tree based on a combined dataset of three DNA regions of *Dichanthelium*, with *Adenochloa*, *Coleataenia*, *Echinochloa*, *Panicum dichotomiflorum*, *Panicum miliaceum*, *Panicum trichoides*, and *Setaria* used as outgroups. Ultrafast bootstrap values are given above the branches. The South American species of *Dichanthelium*, represented by *D. aequivaginatum*, *D. pycnoclados*, *D. sciurotis*, *D. surrectum*, and the *D. sabulorum* clade, were successive sisters to the well-supported North American clade. *Dichanthelium leibergii* of the midwestern United States and *D. erectifolium* of the southeastern United States and Central America were well supported as successive sisters to the rest of the North American species. GB = data obtained from GenBank.

had an early Miocene origin (~17.4 mya) in South America and that the North American *Dichanthelium* clade (including a Hawaiian subclade) arose in the late Miocene–early Pliocene (~4.9 mya; fig. S5). DIVALIKE supported a South American origin of *Dichanthelium* with subsequent movement into North America. There was then one dispersal event into Hawaii (Hawaiian clade, see below) from North America (fig. S6). The DEC model recovered a South American/North American origin for the clade (fig. S7).

Based on our ML analysis, *D. leibergii* (Vasey) Freckmann was sister to the rest of the North American clade, followed by *D. erectifolium*. However, the backbone of the phylogeny was mostly unresolved within the rest of the North American clade. The majority of species/species complexes sampled in our phylogenetic analysis were resolved as clades, and these were generally recovered as Pleistocene in age (fig. S5). We further outline relationships within these subclades below.

The South American *D. sabulorum* formed a well-supported clade (BS = 100). Multiple accessions of *D. sabulorum* var. *polycladum* were interdigitated within *D. sabulorum* var. *sabulorum*.

Dichanthelium portoricense s.l. (=*D. lancearium* (Trin.) Greuter & R.Rankin, see treatment), including infraspecific taxa, was recovered as a well-supported clade but otherwise was mostly unresolved based on infraspecific-level delimitations (this also included material referable to *D. webberianum* (Nash) LeBlond). The sister clade *D. chamaelonche* contained the taxon *D. chamaelonche* ssp. *breve* deeply nested within other accessions of *D. chamaelonche* ssp. *chamaelonche*. The (*D. chamaelonche* + *D. portoricense*) clade was sister to a (*D. nudicaule* + (*D. tenue* + (*D. acuminatum* ssp. *leucothrix*/*longiligulatum* + *D. wrightianum*))) clade, with *D. commutatum* ssp. *equilaterale* and *D. ensifolium* nested within that larger clade (fig. 2).

Dichanthelium nudicaule formed a well-supported clade unsupported as sister to a clade containing *D. acuminatum* ssp. *leucothrix*, *D. ensifolium* s.l., *D. tenue*, and *D. wrightianum* (fig. 2). *Dichanthelium acuminatum* ssp. *longiligulatum* was nested within *D. acuminatum* ssp. *leucothrix*, and *D. tenue* and *D. wrightianum* formed well-supported clades. *Dichanthelium ensifolium* s.l. was nested within this clade in two positions: with

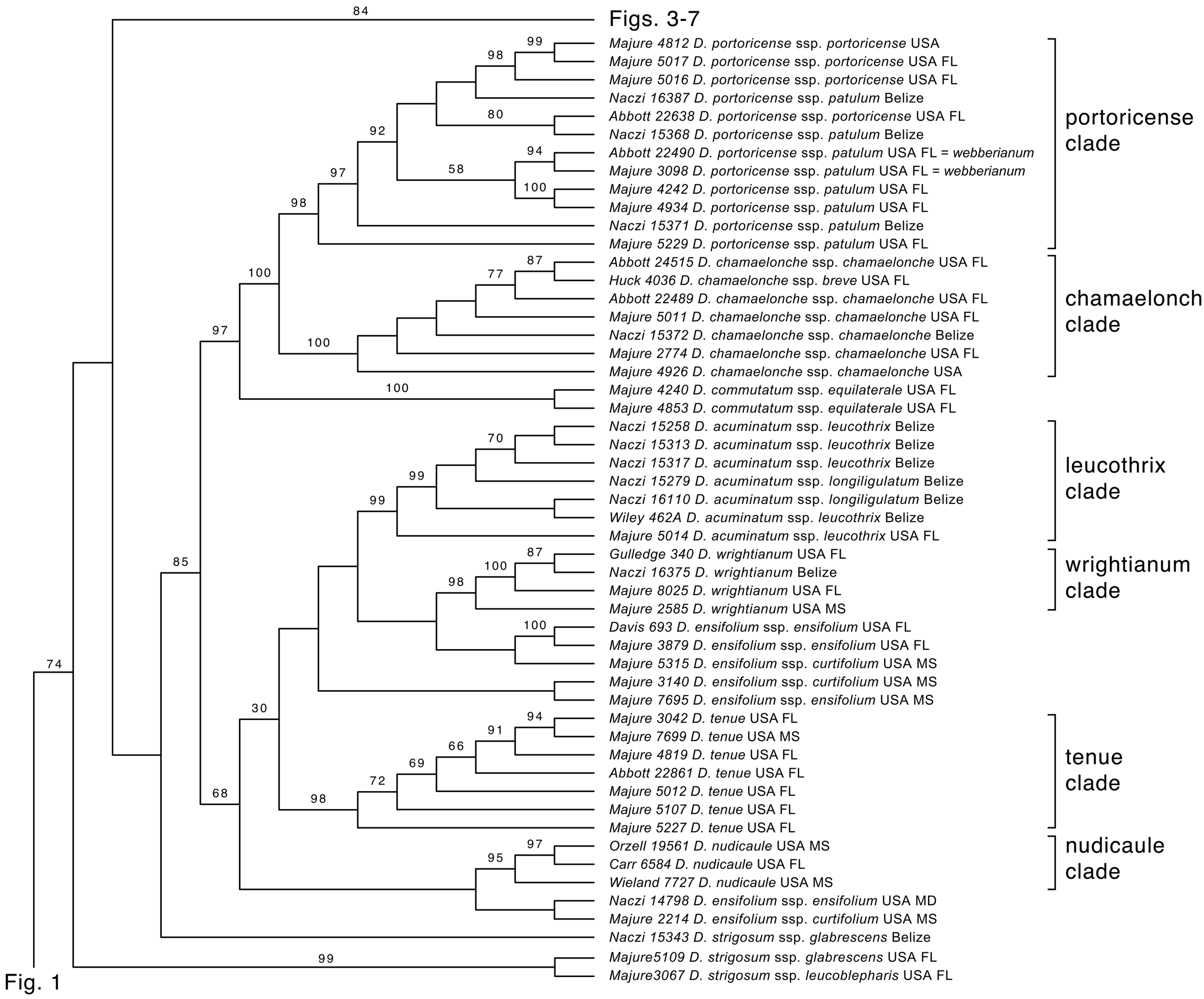

Fig. 2 Maximum likelihood phylogenetic tree continued. The *Dichanthelium portoricense* and *D. chamaelonche* clades were well supported as sisters, and *D. commutatum* ssp. *equilaterale* was sister to that clade. The *D. leucothrix* clade was well supported, as were the *D. wrightianum*, *D. tenue*, and *D. nudicaule* clades, all of which were nested within a clade containing the unresolved *D. ensifolium* s.l. *Dichanthelium strigosum* was mostly sister to that larger clade.

D. ensifolium ssp. *curtifolium* nested within *D. ensifolium* s.s. and then as successive sister to the *D. acuminatum* ssp. *leucothrix* + *D. wrightianum* + *D. tenue* clade.

The *D. aciculare* complex formed a clade that was well supported and included all previously recognized infraspecific taxa within the species based on Freckmann and Lelong (2003; fig. 3). No infraspecific taxa were resolved as monophyletic in the clade when more than one accession per taxon was analyzed. We sampled two accessions of the taxon that is sometimes referred to as *D. pinetorum* (Swallen) LeBlond (but given here as *D. aciculare* ssp. *neuranthum* (Griseb.) Freckmann & Lelong, *Harriman 13566*, *Workman* s.n.), which were also nested within *D. aciculare*, with one of those accessions recovered as sister (BS = 100) to *D. aciculare* ssp. *neuranthum* s.s. (*Majure 3060*). *Dichanthelium filiramum*, which is recognized by some authors (LeBlond 2020), was deeply nested within *D. aciculare* ssp. *aciculare* (as *D. aciculare* ssp. *angustifolium*, *Naczi 14785*). *Dichanthelium consanguineum* (Kunth) Gould & C.A.Clark was likewise nested within this clade. However, in general, relationships within the clade were poorly resolved.

The *D. dichotomum* complex formed a clade consisting of all currently recognized infraspecific taxa based on Freckmann and Lelong (2003), other than *D. dichotomum* ssp. *lucidum*, which was not resolved as part of the clade (*D. dichotomum* ssp. *lucidum* was resolved as sister to the *D. commutatum* + *D. clandestinum* + *D. boscii*/*D. latifolium* clade, see below; fig. 4). *Dichanthelium acuminatum* ssp. *spretum* (Schult.) Freckmann & Lelong (two accessions), *D. boreale* (Nash) Freckmann, and *D. hirstii* were nested within *D. dichotomum* s.l. Most accessions of *D. dichotomum* ssp. *microcarpon* (Muhl. ex Elliott) Freckmann & Lelong formed a well-supported clade within *D. dichotomum* s.l. However, all other taxa with more

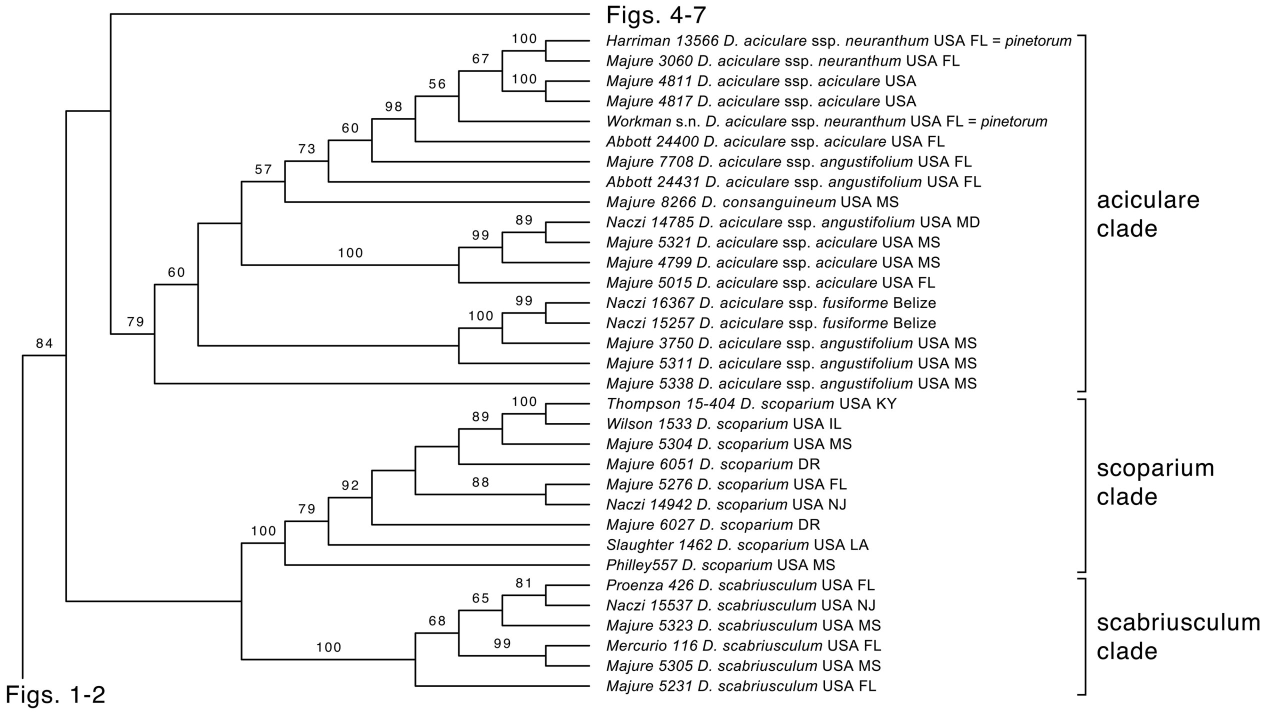

Fig. 3 Maximum likelihood phylogenetic tree continued. The *Dichanthelium scabriusculum*, *D. scoparium*, and *D. aciculare* clades were mostly well supported. Infraspecific taxa of *D. aciculare* were interdigitated within the species complex, and resolution was lacking within that clade. *Dichanthelium consanguineum* was also nested within that clade.

than one accession were not monophyletic. *Dichanthelium hirstii* was sister to the phenetically very similar *D. dichotomum* ssp. *roanokense* (Ashe) Freckmann & Lelong.

The *D. commutatum* complex was resolved in different subclades (figs. 2, 4, 5); one subclade consisted of *D. commutatum* ssp. *commutatum* and *D. commutatum* ssp. *joorii* (Vasey) Feckmann & Lelong, both of which were unresolved in a clade sister to the mostly tetraploid *D. clandestinum* clade and the *D. boscii*/*D. latifolium* clade (fig. 5). *Dichanthelium commutatum* ssp. *ashei* was resolved outside of the *D. commutatum* complex as sister to a member of *D. commutatum* s.l., as currently circumscribed but recognized traditionally as *Panicum mutabile* Scribn. & J.G.Sm. and recently transferred to *D. mutabile* (Scribn. & J.G.Sm.) Wipff (2020; fig. 4). Finally, *D. commutatum* ssp. *equilaterale* was resolved as well supported (BS = 97) as sister to the *D. portoricense* + *D. chamaelonche* clade (fig. 2).

The four Hawaiian taxa formed a well-supported clade (BS = 100; including *D. cynodon* (Reichardt) C.A.Clark & Gould, *D. hillebrandianum* (Hitchc.) C.A.Clark & Gould, *D. isachnoides* (Munro ex Hillebrand) C.A.Clark & Gould, and *D. koolauense* (H.St.John & Hosaka) C.A.Clark & Gould), the Hawaiian clade, which was resolved (albeit poorly supported; BS = 53) as sister to the well-supported clade (BS = 91) that included *D. boscii*/*D. latifolium*, *D. clandestinum*, *D. commutatum*, and *D. dichotomum* ssp. *lucidum* (fig. 5). We removed *D. hillebrandianum* of the Hawaiian clade from our final analysis, given the polymorphic ITS sequences recovered for the two accessions included of that taxon that suggested a hybrid origin for the species as a result of shared polymorphisms in ITS data (fig. 8*A*) between *D. isachnoides* and either *D. cynodon* or *D. koolauense*, which had indistinguishable genotypes. The *D. lucidum* clade consisted solely of *D. dichotomom* ssp. *lucidum* and was sister to the *D. boscii*/*D. latifolium* + *D. clandestinum* + *D. commutatum* clade. *Dichanthelium latifolium* formed a grade with *D. boscii* nested within it.

Two accessions of the tetraploid *D. xanthophysum* formed a well-supported clade (BS = 100), which was sister to the rest of the eastern North American *Dichanthelium* clade (figs. 6, 7). The *D. oligosanthes* clade was poorly supported (BS = 62) as sister to the *D. polyanthes* and *D. sphaerocarpon* sister clades. The *Panicum helleri* Nash form of what is currently circumscribed as *D. oligosanthes* ssp. *scribnerianum* (Nash) Freckmann & Lelong s.l. was sister to the rest of the clade, which consisted of (*D. oligosanthes* ssp. *oligosanthes* + *D. oligosanthes* ssp. *scribnerianum* s.s.) + *D. pedicellatum* (fig. 6). *Dichanthelium sphaerocarpon* was moderately supported (BS = 74) as sister to the morphologically very similar *D. polyanthes*, and *D. laxiflorum* (accessions from Alabama, Florida, Illinois, Kentucky, Missouri, Texas, and Haiti) formed a well-supported clade (BS = 95).

The *D. acuminatum* complex (excluding *D. acuminatum* ssp. *leucothrix*, *D. acuminatum* ssp. *longiligulatum*, and *D. acuminatum* ssp. *spretum*, see above) formed a series of subclades, which were poorly or well supported with other taxa nested within. However, the backbone of this part of the tree was not well

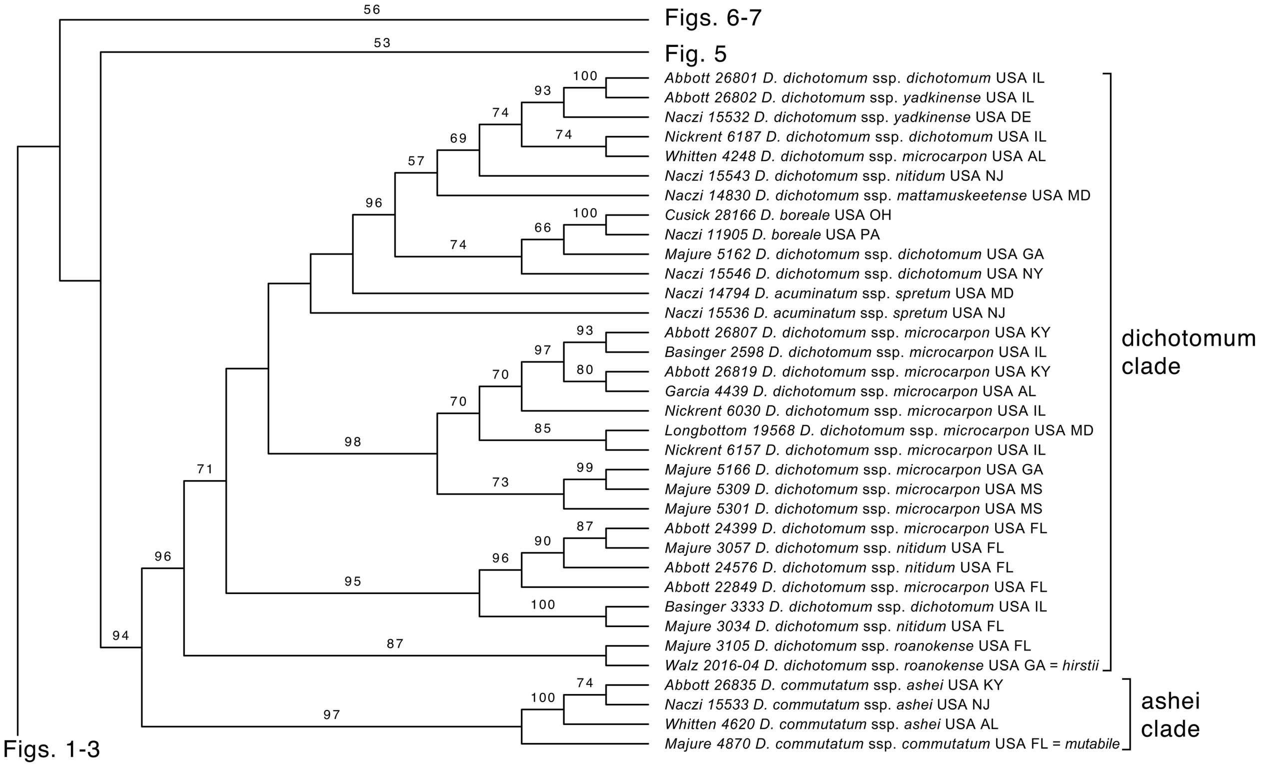

Fig. 4 Maximum likelihood phylogenetic tree continued. The *Dichanthelium ashei* clade was sister to the *D. dichotomum* clade. Within the *D. dichotomum* clade, intraspecific taxa did not form clades but were interdigitated within the complex. *Dichanthelium acuminatum* ssp. *spretum*, *D. boreale*, and *D. hirstii* were nested within the *D. dichotomum* clade.

supported, and relationships should be treated with caution. Both the *D. malacophyllum* clade and the *D. ravenelii* clade were well supported (for *D. malacophyllum*: BS = 98; for *D. ravenelii*: BS = 100) and nested within *D. acuminatum*. Two accessions of *D. ovale* were successive sisters to *D. malacophyllum*. Other accessions of *D. ovale* formed two separate clades, both of which were nested within *D. acuminatum*, and multiple accessions of *D. depauperatum* formed two separate clades, with *D. linearifolium* and *D. perlongum* recovered as close relatives. *Dichanthelium wilcoxianum* was recovered as a clade (BS = 81) sister to accessions of *D. depauperatum* and *D. linearifolium* (fig. 7). *Dichanthelium acuminatum* formed several clades, however, and no infraspecific taxa were monophyletic. *Dichanthelium acuminatum* ssp. *acuminatum* was resolved with one accession of *D. acuminatum* ssp. *fasciculatum* (Torr.) Freckmann & Lelong and *D. acuminatum* ssp. *implicatum* (Scribn.) Freckmann & Lelong nested within. Most accessions of *D. acuminatum* ssp. *fasciculatum* formed a clade with one accession of *D. acuminatum* ssp. *implicatum* nested within. Another clade was formed by accessions of *D. acuminatum* ssp. *acuminatum* with *D. viscidellum* nested within it, as well as multiple accessions of *D. acuminatum* ssp. *fasciculatum*. *Dichanthelium acuminatum* ssp. *lindheimeri* (Nash) Freckmann & Lelong formed a clade, although this was unsupported statistically.

The two putative hybrids analyzed, *D. portoricense* × *D. laxiflorum* (*Majure 5242*) and *D. scabriusculum* × *D. lucidum* (*Majure 5325*), showed clear nucleotide polymorphisms in ITS that were indicative of hybrid origin (fig. 8). These two putative hybrids showed clear recombinant ITS genotypes between their suspected parents based upon observation of electropherograms.

Discussion

Biogeographic Patterns

A South American grade of taxa was successive sister to the rest of the *Dichanthelium* clade (*D. aequivaginatum* (Swallen) Zuloaga, *D. pycnoclados* (Tutin) Davidse, *D. sabulorum*, *D. sciurotis* (Trin.) Davidse, *D. surrectum* (Chase ex Zuloaga & Morrone) Zuloaga), which was composed of the hyperdiverse and mostly North American clade. Previous analyses have shown a similar pattern with the South American taxon *D. cumbucana* (Renvoize) Zuloaga (not sampled in our phylogeny) that was sister to the North American taxa (Morrone et al. 2012; Zuloaga et al. 2014) based on a reduced *ndhF* dataset. Our biogeographic analyses suggested that South America was the most likely ancestral area for *Dichanthelium*, before spreading to North America and radiating much more extensively (figs. S6, S7).

Two dispersals out of continental North America seem clear from our topology. The Central and South American taxon *D. viscidellum* was nested within *D. acuminatum*, suggesting a dispersal south from that clade. Likewise, the Hawaiian clade, a small radiation of four species, was nested deeply within the North American clade, and our biogeographic analyses suggested a clear dispersal into the islands from mainland North

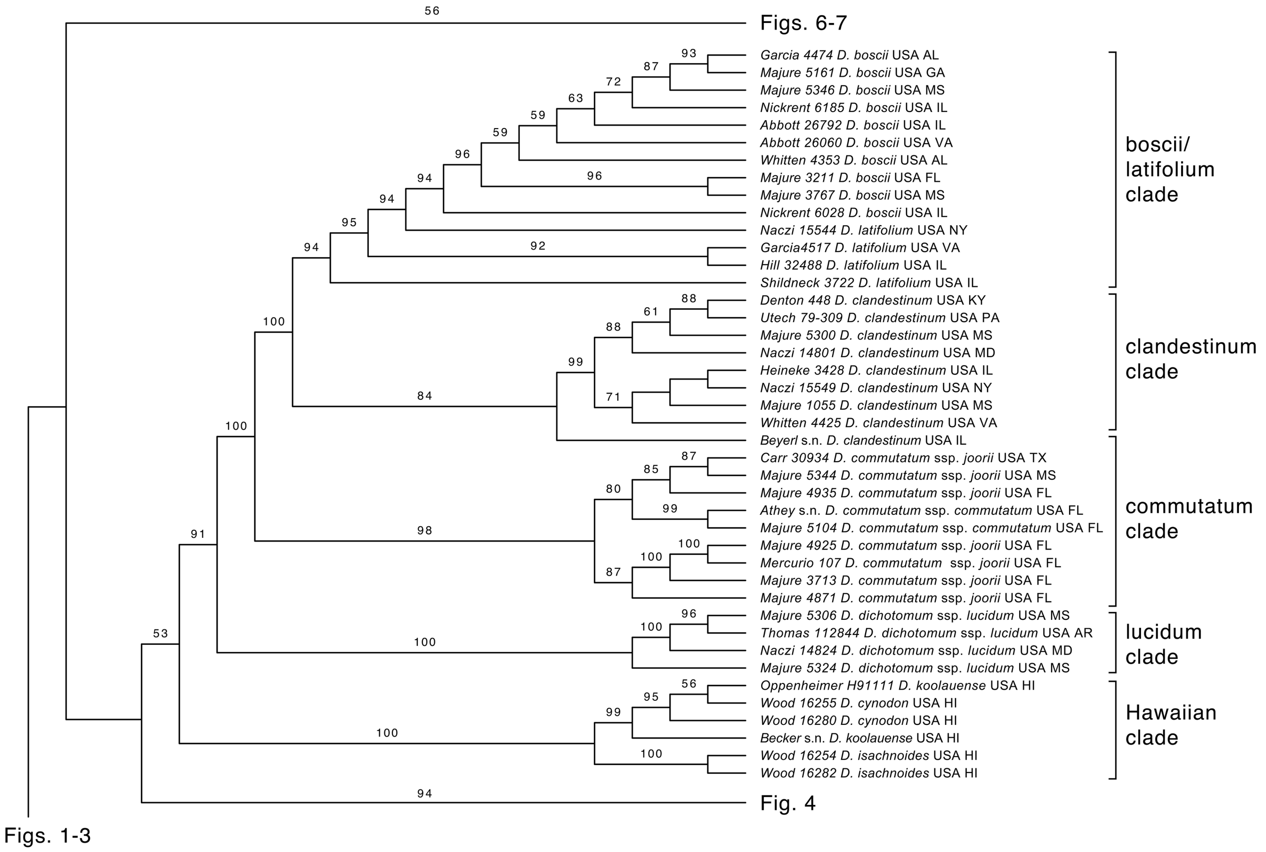

Fig. 5 Maximum likelihood phylogenetic tree continued. The Hawaiian clade was sister to the *Dichanthelium lucidum*, *D. commutatum*, *D. clandestinum*, and *D. boscii/D. latifolium* clades. *Dichanthelium latifolium* formed a grade with *D. boscii* nested within it.

America (figs. S6, S7). Dispersals out of North America are a common pattern in Hawaiian taxa (Price and Wagner 2018). Given that several subclades are represented by populations outside of mainland North America (*D. aciculare*, *D. acuminatum*, *D. commutatum*, *D. dichotomum*, *D. erectifolium*, *D. laxiflorum*, *D. scoparium*, *D. strigosum*, and *D. wrightianum*), it may be likely that dispersals south into the Caribbean, Central America, and northern South America have commonly occurred. A more thoroughly resolved phylogeny with broadscale sampling within species will be necessary to further test these intriguing biogeographic patterns.

Taxonomic Implications of Phylogenetic Relationships

Although *Dichanthelium* is often considered to be a taxonomically frustrating and complicated genus, our phylogenetic results suggest that previous species circumscription and assessments of potential relationships based on species groupings (e.g., Hitchcock 1935, 1950; Zuloaga et al. 1993; Freckmann and Lelong 2003; LeBlond 2020) were quite accurate. Thus, morphological data within the genus reflect, in most instances, our phylogenetic hypothesis (e.g., *D. aciculare* complex and, in part, *D. dichotomum* complex).

However, the current circumscription of some species of *Dichanthelium* across different treatments is apparently inaccurate given their phylogenetic relationships shown here. In our taxonomic treatment below, we highlight taxa that should be regarded as species rather than synonyms or infraspecific taxa based on our analyses. For example, Zuloaga and Morrone (2003) placed *D. dichotomum* ssp. *lucidum* and *D. tenue* in synonymy with *D. dichotomum* s.l. However, those three taxa were resolved in separate clades in our analysis. Likewise, *D. erectifolium* was placed by those authors in synonymy with the phenetically similar *D. sphaerocarpon*—two species that do not form a clade and that occur in very different habitats (wet, acidic sandy soils vs. dry sandy soils or clay/rocky soils). *Dichanthelium chamaelonche* was placed in synonymy with *D. ensifolium* by Zuloaga and Morrone (2003), although our analyses place *D. chamaelonche* as being more closely related to *D. portoricense* than to *D. ensifolium*. Our results support the close relationship of the phenetically similar *D. polyanthes* and *D. sphaerocarpon*; the former is often considered an infraspecific taxon of the latter (Zuloaga and Morrone 2003). The two taxa form clear sister clades in our phylogeny and mostly occupy different ecological niches (see below).

The *D. acuminatum* complex appears to be the most polyphyletic in our analyses and likewise the most taxonomically confused. Freckmann and Lelong (2003) circumscribed *D. acuminatum* ssp. *leucothrix*, *D. acuminatum* ssp. *longiligulatum*, and *D. acuminatum* ssp. *spretum* as infraspecific taxa within

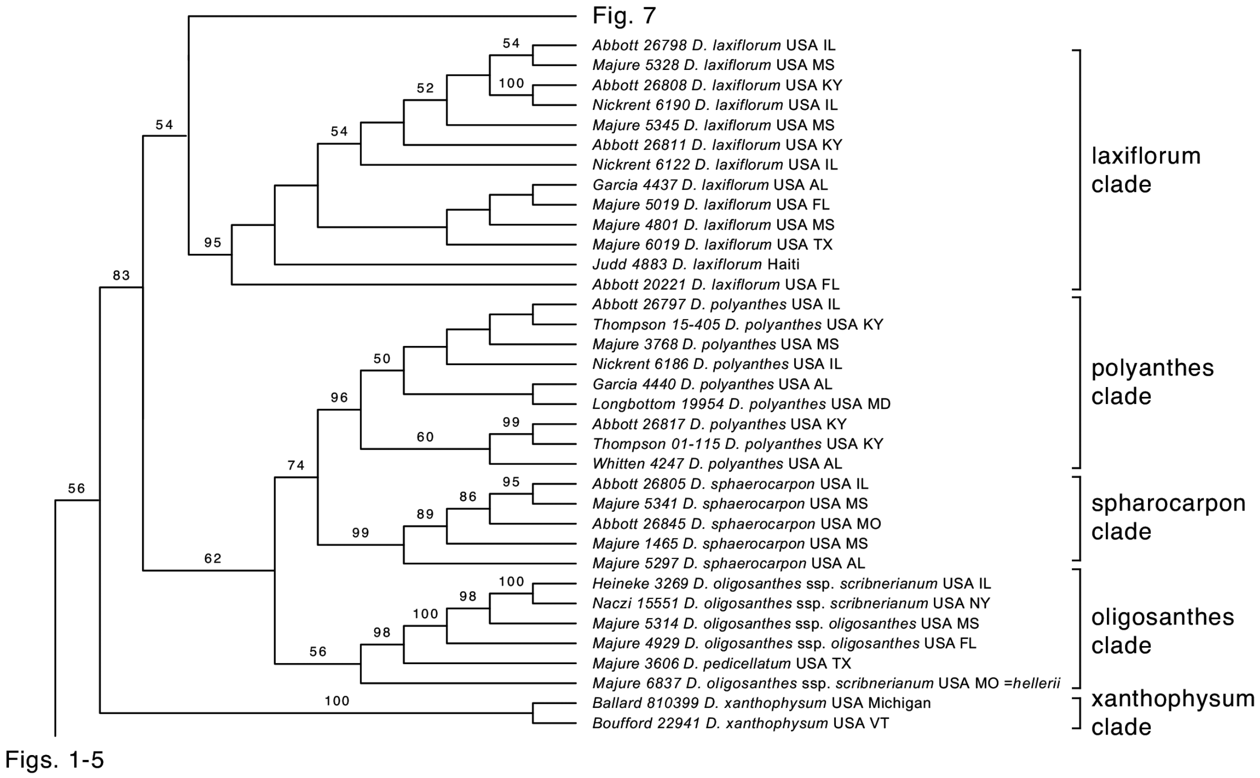

Fig. 6 Maximum likelihood phylogenetic tree continued. The tetraploid *Dichanthelium xanthophysum* clade was recovered as an isolated lineage, and the *D. oligosanthes* clade was poorly supported as sister to the *D. polyanthes* + *D. sphaerocarpon* clade. The widespread *D. laxiflorum* formed a well-supported clade.

D. acuminatum. Zuloaga and Morrone (2003) further placed *D. acuminatum* ssp. *leucothrix*, *D. acuminatum* ssp. *spretum*, and *D. wrightianum* within their concept of *D. acuminatum* s.l. (as *D. acuminatum* var. *densiflorum* and *D. acuminatum* var. *longiligulatum*). Likewise, Thomas (2015) included *D. acuminatum* ssp. *leucothrix*, *D. acuminatum* ssp. *longiligulatum*, *D. acuminatum* ssp. *spretum*, and *D. wrightianum* in the *D. acuminatum* group. In our results, *D. acuminatum* ssp. *longiligulatum* was nested within multiple accessions of *D. acuminatum* ssp. *leucothrix*, and *D. wrightianum* formed a clade within a broader *D. acuminatum* ssp. *leucothrix*/*longiligulatum* + *D. ensifolium* + *D. nudicaule* + *D. tenue* clade. On the other hand, *D. acuminatum* ssp. *spretum* was deeply nested within *D. dichotomum*. Freckmann and Lelong (2003) mentioned the large size of *D. spretum* and its overlap with *D. dichotomum*. However, the long-ciliate ligules of that taxon led them to place it with *D. acuminatum*, a seemingly anomalous placement based on our phylogenetic results or perhaps a morphological signal of hybridization in its history and in need of further attention.

However, none of these infraspecific taxa were resolved as close relatives of *D. acuminatum*. The long-ciliate ligule has been considered a unifying morphological trait for the *D. acuminatum* species complex; however, it is apparently homoplasious or perhaps could have been acquired through hybridization.

Dichanthelium acuminatum, in a more restricted sense, formed several subclades, although infraspecific taxa previously recognized were not always each other's closest relatives and, in general, were scattered throughout different parts of the tree, along with some members of the *D. ovale* group. A notable exception was *D. acuminatum* ssp. *lindheimeri*; although not well supported, it was monophyletic.

The *D. ovale* group was recovered in three phylogenetic positions, with one clade formed by five accessions of *D. ovale* s.l., another clade formed by one accession of *D. ovale* ssp. *villosissimum* and one of *D. ovale* ssp. *pseudopubescens*, and then two accessions formed a grade of successive sisters to the *D. malacophyllum* clade. The infraspecific taxa *D. ovale* ssp. *ovale* and *D. ovale* ssp. *villosissimum* were interdigitated where they were recovered in the phylogeny.

The *D. commutatum* species complex was resolved in several places in our phylogeny and likely represents several highly variable species rather than one. *Dichanthelium commutatum* ssp. *commutatum* and *D. commutatum* ssp. *joorii* were resolved in a clade that was sister to the *D. clandestinum* + *D. boscii*/*D. latifolium* clade. The taxon *D. commutatum* ssp. *equilaterale*, which is common in parts of Florida in sandy soils of mesic to xeric hammocks, was resolved as a clade sister to the *D. chamaelonche* + *D. portoricense* clade. Thus, although cryptic, that taxon should be recognized at the species level as *D. equilaterale*. Likewise, a clade formed by *D. commutatum* ssp. *ashei* and *D. commutatum* s.l. (*Panicum mutabile* form) was recovered outside of *D. commutatum* s.s. and was sister to the *D. dichotomum* clade. Thus, these two taxa should likely also be recognized at the species level as *D. ashei* and *D. mutabile*, respectively. Both

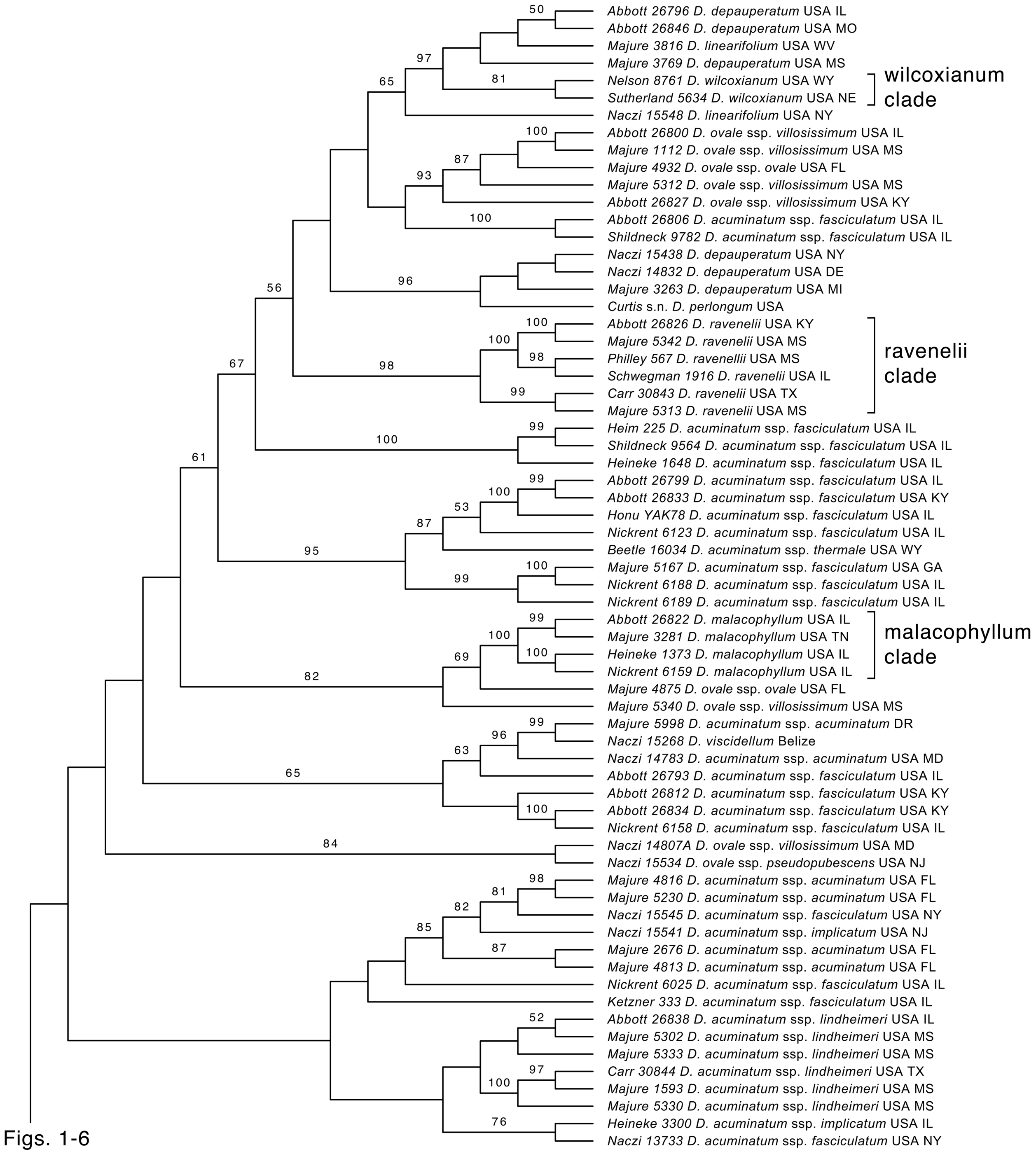

Fig. 7 Maximum likelihood phylogenetic tree continued. The *Dichanthelium acuminatum* complex was resolved in several clades with other subclades nested within; however, there was little resolution along the backbone in this part of the tree. The *D. malacophyllum*, *D. ravenelii*, and *D. wilcoxianum* groups formed well-supported clades within the poorly supported *D. acuminatum* complex.

taxa have abaxially glaucous light green leaves, which helps to separate them from *D. commutatum* ssp. *commutatum*, *D. commutatum* ssp. *joorii*, and *D. equilaterale*. Wipff (2020) recently recognized both *D. equilaterale* and *D. mutabile* for the Flora of Texas, although with no explanation as to their circumscription outside of *D. commutatum*.

Within the *D. dichotomum* complex, several patterns emerge. *Dichanthelium dichotomum* ssp. *microcarpon* mostly forms a

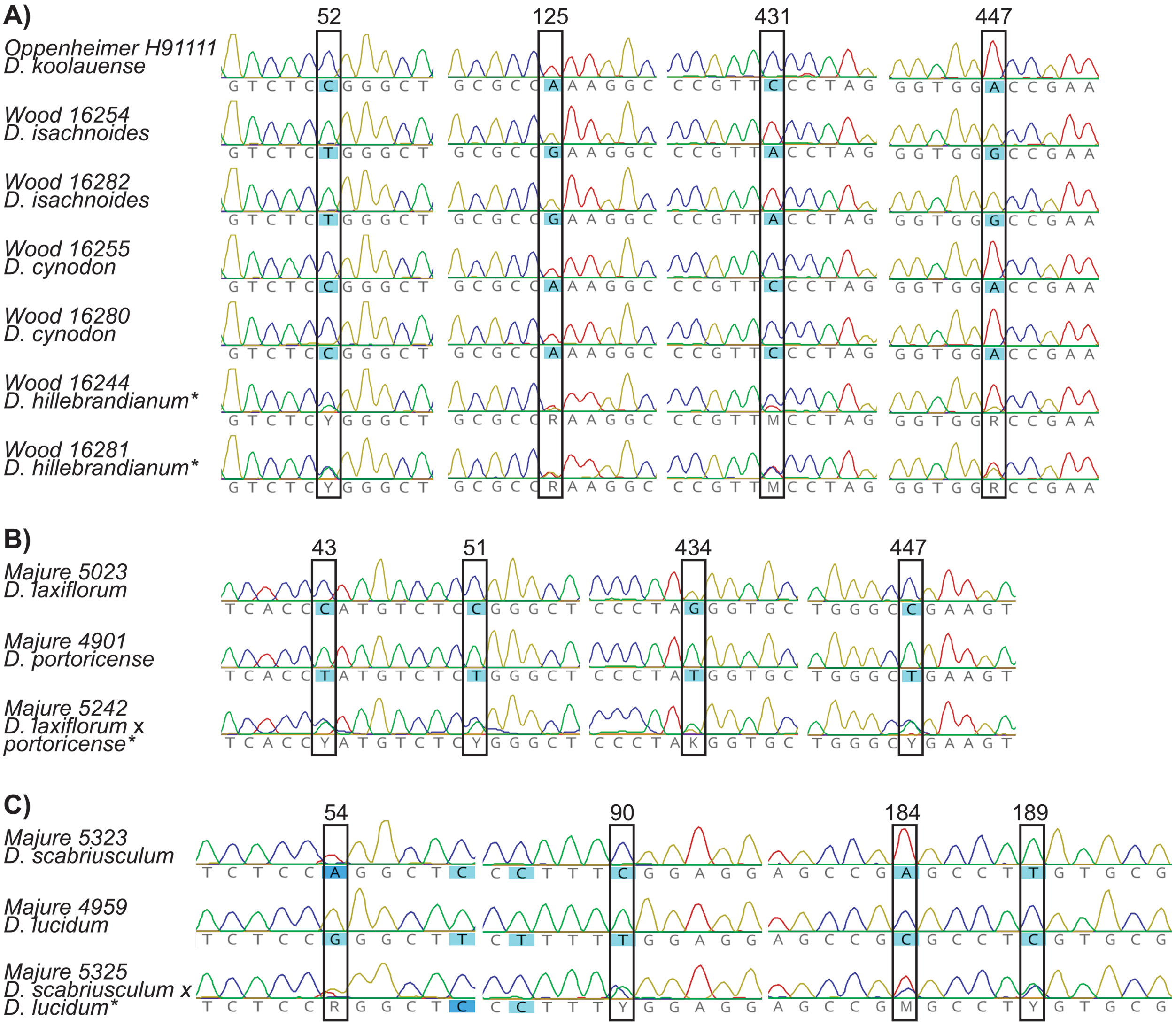

Fig. 8 Electropherogram representations of putative hybrids (denoted with asterisks) using internal transcribed spacer in *Dichanthelium*, showing the well-established Hawaiian species *D. hillebrandianum* (*A*) and two putative F_1 hybrids (*Majure 5242, Majure 5323; B, C*). Putative hybrids were polymorphic, showing recombinant genotypes matching their putative parents. Given our data, we could not distinguish between *D. koolauense* and *D. cynodon* for the parentage of *D. hillebrandianum*.

clade. However, *D. dichotomum* ssp. *mattamuskeetense*, *D. dichotomum* ssp. *nitidum*, *D. dichotomum* ssp. *yadkinense*, and *D. dichotomum* s.s. do not form clades, and likewise, *D. boreale* and *D. spretum* are nested within the *D. dichotomum* clade. Only one accession of *D. dichotomum* ssp. *roanokense* was included, and thus, its monophyly cannot be evaluated, but it is resolved as sister to the morphologically very similar *D. hirstii*, which was only recently revived (LeBlond et al. 2017). The *D. aciculare* complex mostly consisted of intermixed infraspecific taxa in our topology. For example, some accessions of *D. aciculare* ssp. *aciculare* were resolved in a clade with *D. aciculare* ssp. *neuranthum* and the Florida-endemic *D. pinetorum* (LeBlond 2016). *Dichanthelium pinetorum* was included within the concept of *D. aciculare* ssp. *neuranthum* by Freckmann and Lelong (2003). In fact, the two accessions of *D. pinetorum* sequenced here (*Harriman 13566*, *Workman* s.n.) were most closely related to *D. aciculare* ssp. *neuranthum* (*Majure 3060*) or otherwise nested within *D. aciculare* s.l. The morphologically similar *D. consanguineum* was nested within the *D. aciculare* clade and perhaps either belongs within that taxon or could be derived, in part, from hybridization with *D. aciculare* (see further below).

Further Taxonomic Considerations regarding Taxon Nonmonophyly

Based on the substantial fieldwork by the authors, the data given here, and the abundant referrals in the literature (Freckmann and Lelong 2003), it is evident that hybridization in *Dichanthelium* occurs regularly, although polyploidy does not seem to be very common (Gould and Clark 1978; Dubcovsky and Zuloaga 1991). Given the nonmonophyly of several species of *Dichanthelium* (such as *D. depauperatum*, *D. dichotomum*, and *D. leucothrix*), it is perhaps possible, and maybe even likely, that certain recognized taxa within *Dichanthelium* have been derived from hybridization. Weakley et al. (2011) considered that *D. curtifolium* was perhaps the result of hybridization based on its combination of morphological characters. Recurrent hybridization between the same putative parental taxa is known to commonly occur in plants (reviewed in Soltis and Soltis 2009); thus, a taxon regarded as a species could be derived from multiple hybridization events. Successful hybrids, irrespective of the number of times derived, may develop substantial distributions and sizable populations, becoming well established and worthy of taxonomic recognition (e.g., Majure 2022).

Likewise, as is in the case of the diploid *D. latifolium*, the tetraploid *D. boscii* has apparently arisen from within the former species, at least in part, thus making *D. latifolium* paraphyletic. Speciation models, especially those involving polyploidy and peripheral isolate speciation (Frey 1993), could lead to this type of phylogenetic pattern of paraphyletic species. Polyploidy, which may lead to reproductive isolation (Stebbins 1950) and sympatric speciation (Soltis and Soltis 2009), is likely responsible for the pattern we see in *D. latifolium* and *D. boscii*, and both taxa should probably be recognized at the species level. It is unclear, however, whether *D. boscii* is the product of autopolyploidy or allopolyploidy. This will need to be carefully examined with appropriate separate datasets from the chloroplast and nuclear genomes.

Given these caveats, until we have more detailed information about nonmonophyletic taxa and the processes driving nonmonophyly (such as hybridization, incomplete lineage sorting, or merely poorly circumscribed species), we must use caution when applying taxon names or relegating them to synonymy. This is especially the case in a group, such as *Dichanthelium*, where taxa are often cryptically separable and thus spontaneous hybrid taxa may easily be misidentified as merely intraspecific morphological heterogeneity or, on the contrary, considered novel species.

It is clear that our current classifications, which are based on a combination of morphological cohesiveness within a species or species complex, have led to some arbitrary species delimitations. As an example, Freckmann and Lelong (2003) and LeBlond (2020) suggest that *D. commutatum* is composed of numerous morphotypes that they recognize as subspecies (*D. commutatum* ssp. *ashei*, *D. commutatum* ssp. *equilaterale*, *D. commutatum* ssp. *joorii*, etc.), but several infraspecific taxa within this complex are shown here to be distinct phylogenetically (e.g., *D. ashei*, *D. equilaterale*, *D. mutabile*). On the contrary, other species complexes have been circumscribed as separate species, although their diagnosability is still rather cryptic and is at least on par with, or even less diagnosable than, the *D. commutatum* complex mentioned above (e.g., *D. dichotomum* var. *dichotomum*, *D. dichotomum* var. *nitidum*, *D. microcarpon*, *D. roanokense*, *D. yadkinense*; LeBlond 2020). However, we phylogenetically resolve these taxa as all part of the same clade and, in most cases, as interdigitated and unresolved within those species complex clades, thus rendering them less easily justified to be considered species. Perhaps the simplest solution in this case would be to recognize these clades as species and phylogenetically nested taxa as infraspecific taxa. The best overall solution in these cases will be to more fully understand species complexes phylogenetically and with increasing biological information, such as chromosome number and information on biological origin (e.g., reticulation vs. cladogenetic processes). These types of studies will be crucial to reduce the arbitrary delimitation of species across *Dichanthelium* based simply on perceived morphological discontinuities or personal preference in classification.

The patterns seen in *Dichanthelium*, especially within species complexes, should be expected given that both chasmogamous and cleistogamous flowers are produced annually (Bell and Quinn 1985; Freckmann and Lelong 2003), so at least the North American members of the genus are predominantly facultatively autogamous (Spellenberg 1975). Thus, the production of taxa that could be defined as autogamous microspecies (Grant 1971) are likely to be more frequent in such a group. Patterns including morphologically cohesive species complexes forming clades of autogamous taxa, resulting in high levels of homozygosity (Allard 1975), are seen in *Dichanthelium*. This is likely coupled with cryptically differentiated taxa that are perhaps derived from outcrossing, including that which leads to occasional hybridization (Spellenberg 1975). Hammer et al. (2012) found this pattern in populations of *D. acuminatum* ssp. *lindheimeri*, which were mostly homozygous but showed a low-level frequency of hybridization, apparently occurring through less frequent outcrossing events. Autogamous microspecies are thought to be derived mostly from hybridization (Grant 1971), and if (in the case of *Dichanthelium*) those autogamous taxa were derived from hybridization within one species complex, then we might expect the phylogenetic pattern seen here (with many such infraspecific taxa nested within species but not necessarily forming clades). Further biological data will help to clarify the nature of the origin of these infraspecific taxa within species complex clades.

These types of systems, predominantly selfing with occasional outcrossing, were thought by Stebbins (1957) to be advantageous for annual taxa in disturbed environments. Indeed, there is a wealth of evidence to support the idea that cleistogamy may be induced through increasing environmental heterogeneity or harsh conditions (Bell and Quinn 1985; Culley and Klooster 2007; Winn and Moriuchi 2009; Ansaldi et al. 2018), regardless of plant duration (i.e., annual vs. perennial). Campbell (1982, 1983) found that for perennial autogamous taxa within *Andropogon*, cleistogamous infraspecific taxa occupy distinctive ecological niches, even though they grow within meters of one another, while mostly maintaining reproductive isolation through selfing. Campbell (1982) argued that the cleistogamous taxa within *Andropogon* were likely much more common today as a result of human occupation of landscapes promoting the dispersal of those taxa, which commonly occupy disturbed habitats. Many species of *Dichanthelium* in the eastern United States occur in ecosystems that were historically maintained through frequent burning, such as in the longleaf pine communities of the coastal plain (Abrahamson and Hartnett 1990), and likewise may be commonly disturbed during extreme weather events, such as hurricanes, especially in the southeastern United States. It is likely that anthropogenic disturbance must also be a factor in modifying contemporary populations of *Dichanthelium* species. Perhaps cleistogamy would then become advantageous under such environmental pressures. Campbell et al. (1983) reviewed cleistogamy in grasses and associated selective pressures driving this syndrome, with one of those being disturbance in fire-dominated ecosystems. Pine flatwoods and associated fire-dominated ecosystems in the southeastern United States house the greatest diversity of *Dichanthelium* and thus could have played a role in driving the evolution of cleistogamy in the genus.

The production of cleistogamy is common across angiosperms, having evolved at least 40 times, and especially prevalent in Poaceae (Culley and Klooster 2007). Many taxa also show mixed mating patterns similar to those demonstrated by *Dichanthelium*, producing both chasmogamous and cleistogamous flowers (i.e., dimorphic cleistogamy of Culley and Klooster 2007). These may be produced either simultaneously (Ansaldi et al. 2018) or as those in *Dichanthelium*, with chasmogamous flowers produced earlier in the season and cleistogamous flowers produced later in the year (see Bell and Quinn 1985; Culley and Klooster 2007; Winn and Moriuchi 2009). Cheplick (2023) found that seasonality and habitat play a major role in the frequency of cleistogene production in a perennial grass, *Danthonia compressa* Austin. It is currently unknown how habitat might affect the production of cleistogmaous flowers in *Dichanthelium*, but work by Bell and Quinn (1985) suggests that it is also likely a factor. It is also unknown how frequently chasmogamous flowers may increase selfing through geitonogamy, which could further promote cleistogamy (see Culley and Klooster 2007).

Is Speciation Tied to Niche Specialization in Dichanthelium*?*

There are clear instances where closely related species occur in distinct ecological niches. For example, *D. polyanthes*, which is sister to *D. sphaerocarpon*, is generally found in wet to mesic soils near rivers, streams, or other water bodies, while *D. sphaerocarpon* is most commonly found on drier sites, including upland forests, dry roadsides, and pine sand hills. *Dichanthelium clandestinum*, which is sister to the *D. boscii*/*D. latifolium* complex, is found in moist soils along watercourses, while the latter two species are more common in rich mesic forests. Certain infraspecific taxa within *Dichanthelium* also occur in clearly different habitats. *Dichanthelium aciculare* ssp. *neuranthum* is found in wet, acidic soils of pinelands, while other members of *D. aciculare*, especially *D. aciculare* ssp. *angustifolium* and *D. aciculare* ssp. *fusiforme*, are commonly found in drier soils.

Selfing is thought to reduce adaptability to different environmental conditions within a species (Stebbins 1957; Allard 1975), which could explain habitat specificity across species and infraspecific taxa in *Dichanthelium*. However, species complexes taken as a whole may actually benefit from niche specificity (or reduced niche breadth) of these autogamous taxa and would increase the overall habitat niche breadth of the entire species. Campbell (1983) also noted habitat specificity in cleistogamous taxa within *Andropogon*. Perhaps autogamy in combination with niche specificity may provide a speciation mechanism in *Dichanthelium*.

Sympatry and syntopy among numerous species of *Dichanthelium* are quite common. Although hybridization is known to occur in the genus, species boundaries may likely be enforced given the presence of autogamy in at least the North American species, which would promote reproductive isolation and inbreeding (Levin 1971; Wendt et al. 2002; Martin and Willis 2007; Wright et al. 2013). Autogamy has been considered a speciation mechanism by numerous authors (Levin et al. 1971; Widmer et al. 2009; Wright et al. 2013) and could have been a driver for diversification of *Dichanthelium* in the most species-rich part of their distribution (Hitchcock 1950; Freckmann and Lelong 2003), the coastal plain of the eastern United States.

Hybridization in Dichanthelium

Hybridization has been reported frequently in *Dichanthelium*. Freckmann and Lelong (2003) list many potential hybrids in their treatment of the species for North America. Although Weakley et al. (2011) and LeBlond (2016, 2020) mention that there are very few studies that substantiate claims of hybridization, there are several studies that do provide evidence for hybridization in *Dichanthelium* (Church 1929; Lelong 1965; Spellenberg 1970; Hammer et al. 2012), and we provide data here that further support the existence of hybrids. L. C. Majure has collected many potential hybrids, which often appear to be F_1 generation hybrids and are commonly found alongside their putative parents (see *Majure 4535*, *D. aciculare* × *D. portoricense*, FLAS; *Majure 5242*, *D. laxiflorum* × *D. portoricense*, FLAS; *Majure 5325*, *D. lucidum* × *D. scabriusculum*, FLAS; *Majure 7767*, *D. portoricense* × *D. strigosum*, FLAS; *Majure 8226*, *D. portoricense* × *D. tenue*, FLAS; *Majure 8286*, *D. laxiflorum* × *D. sphaerocarpon*, FLAS; *Majure 8322*, *D. laxiflorum* × *D. acuminatum*, FLAS; *Majure 10484*, *D. commutatum* × *D. laxiflorum*, FLAS); this is based on morphological data and, in some cases (such as those given here, e.g., *Majure 5242*, *Majure 5325*), DNA sequence data (fig. 8).

Using ITS genotypes, we showed here that two putative hybrids based on morphology, as well as the Hawaiian taxon *D. hillebrandianum*, were most likely of hybrid origin. While the two putative hybrid accessions appeared to be spontaneous or F_1 generation hybrids when collected, *D. hillebrandianum* is considered a species of hybrid origin (Clark and Gould 1978). Hammer et al. (2012), using GBSSI, restriction fragment length polymorphisms, and morphological data, provided evidence for hybridization between *D. acuminatum* ssp. *lindheimeri* and another taxon. Church (1929) provided cytological data and pollen viability estimates suggesting that hybridization was likely common in the group of *Dichanthelium* being considered. For example, *D. acuminatum* ssp. *lindheimeri* was shown to produce essentially no viable pollen, suggesting hybridization as a potential mechanism behind the origin of the taxon.

Given the possibility of frequent hybridization across *Dichanthelium*, there also exists the likelihood that some currently or previously recognized taxa are actually early-generation hybrid derivatives and may or may not be evolutionarily significant. One such example is *Panicum calliphyllum* Ashe, which is a sterile triploid hybrid apparently derived from hybridization between *D. boreale* and either *D. acuminatum* or, perhaps more likely, the tetraploid *D. xanthophysum* (Freckmann and Lelong 2003). Spontaneous hybrids within *Dichanthelium* that have been named (Spellenberg 1970) should be reevaluated as to their origin and whether they truly deserve species recognition.

It is not certain what role hybridization might have played in the evolution of what appear to be well-established species (Stebbins 1959) and whether those hybrids were derived from one or multiple hybridization events (i.e., recurrent hybridization; reviewed in Soltis and Soltis 2009). Above, we showed that *D. hillebrandianum* is clearly one of these taxa. Another such potential hybrid is *D. curtifolium*, a species with a wide distribution that is obviously well established and presumably stable across its range. Correll and Johnston (1970) and Weakley et al. (2011), based on morphological comparisons, suggested that *D. curtifolium* could be of hybrid origin, possibly involving the *D. acuminatum* complex; indeed, our phylogenetic data suggest the same, with *D. curtifolium* potentially originating from *D. ensifolium* s.s. and *D. acuminatum* ssp. *leucothrix*, based on its phylogenetic placement within that broader clade containing both of those taxa.

Another such potential hybrid is *D. wilcoxianum*, which Lelong (1965) proposed may have been of hybrid origin based on population structure and morphological characters. *Dichanthelium filiramum*, recognized by LeBlond (2016), has also been noted as a potential hybrid by that author, perhaps between the *D. acuminatum* and *D. aciculare* species complexes. It is resolved here within *D. aciculare* (*Naczi 14785*).

It is unclear how the tetraploids *D. boscii*, *D. clandestinum*, *D. sabulorum*, *D. viscidellum*, and *D. xanthophysum* or the octoploid *D. davidsei* originated. Polyploidy is commonly associated with hybridization (Stebbins 1950); thus, it is possible that these taxa were derived from ancient hybridization events, maybe even perhaps from now-extinct parents. These scenarios need further investigation, and the frequency and evolutionary consequences of hybridization need to be verified with empirical studies across *Dichanthelium*. Given the mixed mating system in *Dichanthelium*, perhaps hybridization may be more restricted to specific times of the year, such as the spring, when chasmogamous flowers are mostly produced and thus higher rates of outcrossing should occur.

Future Work

Future work in *Dichanthelium* should build on the current phylogenetic understanding of species relationships shown here, as well as the excellent and careful systematic work that has been carried out in this genus (e.g., Hitchcock 1935, 1950; Lelong 1965; Gould and Clark 1978; Dubcovsky and Zuloaga 1991; Morrone and Zuloaga 1991; Zuloaga et al. 1993; Freckmann and Lelong 2003; Thomas 2015; LeBlond 2020). In our current dataset, although we sampled nearly all recognized taxa according to Freckmann and Lelong (2003), not all morphotypes across the eastern United States were included (see LeBlond 2020). It is possible that there are what are currently considered to be morphotypes of certain taxa that could actually represent true species, and future work should incorporate those entities not yet sampled (e.g., *D. sphagnicola*, which is currently considered synonymous with *D. lucidum* by some authors; Freckmann and Lelong 2003; but see LeBlond 2001).

Given the potential for hybridization and the likelihood of homoploid hybrid speciation in *Dichanthelium*, developing datasets (e.g., morphological, phylogenetic, chromosomal) that would uncover such reticulation is paramount to developing a greater understanding of speciation and diversification in this clade. Broad-scale chloroplast and nuclear phylogenetic datasets would greatly aid our ability to test for putative reticulation in *Dichanthelium* and its potential effects on diversification, especially in eastern North America.

A broader geographic sampling will be necessary to fully understand morphological evolution and the biogeographic history of this clade. This is especially important for understanding relationships among South American taxa and how they relate to North American taxa. It seems clear from our current topology that South American taxa form a grade and so are successive sisters to the North America clade, suggesting a South American origin. These hypotheses, however, remain to be robustly tested with greater taxon sampling and phylogenetic resolution.

Finally, genome-scale data, such as the recently published genome for *D. oligosanthes* (Studer et al. 2016), will be important for teasing apart poorly resolved parts of the tree. This is especially true in the *D. acuminatum*, *D. depauperatum*, and *D. ovale* species complexes. Likewise, although forming clades, relationships among taxa within the *D. aciculare* and *D. dichotomum* clades are not resolved, so it is crucial that these complexes be much more greatly explored with larger datasets to further resolve relationships and produce a finer-level understanding of phylogeographic relationships within these complexes. Determining the origin of infraspecific taxa within species complexes, whether that be through hybridization for autogamous microspecies (Grant 1971) or some other means, will aid in developing a deeper understanding of the evolution of species in this genus.

Taxon Recognition in *Dichanthelium*

The taxonomy of *Dichanthelium*, even in the light of phylogenetic relationships, is not straightforward, and there are multiple avenues that could be taken to devise a stable classification for the genus. We consider the following possibilities: (1) all morphologically diagnosable taxa could be separated as species (e.g., LeBlond 2016), regardless of whether their phylogenetic placement shows them to be nonmonophyletic and deeply nested within other species; (2) clades, which in this case are most often referable to species complexes, could be recognized at the species level, and infraspecific taxa could be recognized within those species to illuminate the morphological diversity within each species; or (3) species complexes that form clades, along with morphologically cryptic but phylogenetically unrelated taxa, could be recognized as species, and well-established taxa of potential hybrid origin that are morphologically diagnosable could be recognized at the species level, regardless of whether they make species nonmonophyletic. Nonmonophyletic species would be expected in cases of hybridization or peripheral isolate speciation (Frey 1993; Judd et al. 2015; Majure et al. 2023).

Here, we use the third approach, where phylogenetically disparate but morphologically similar taxa (e.g., *D. commutatum* s.s. vs. *D. equilaterale*), species complexes forming clades with infraspecific taxa included within them (e.g., *D. dichotomum* s.l.), and putative hybrid taxa that are well established (e.g., *D. curtifolium*, *D. hillebrandianum*) are recognized at the species level. However, given the lack of resolution in some clades and the lack of basic biological data regarding species origin (e.g., hybrid origin, chromosome number), we cannot be fully confident in species circumscription at this point. So we have also chosen to use a combination of traditional taxonomies (cf. Freckmann and Lelong 2003), such as in most of the members of the *D. acuminatum* complex (which is still unresolved), and an updated taxonomy based on our current phylogenetic hypotheses, such as in the recognition of *D. leucothrix* (=*D. acuminatum* ssp. *leucothrix*). In most cases, we continue to recognize morphologically disparate taxa, although they may be nested within other taxa (e.g., *D. consanguineum*, which is nested within *D. aciculare*), given that morphological distinctiveness could perhaps suggest hybrid origin for some of these widespread and well-established species.

The use of infraspecific taxa, although perhaps not truly satisfactory, does appear warranted in some situations for species complexes, especially where phylogeny does not resolve relationships and morphological characters are greatly overlapping, such as in the *D. aciculare* and *D. acuminatum* complexes. We elect to use the infraspecific rank of subspecies, given the inconsistent way varieties and subspecies have been implemented in the botanical community (see Ellison et al. 2014). Traditionally, some authors used the rank of subspecies for infraspecific taxa with cohesive and allopatric geographic distributions along with phenetic disparities, while varieties have been used to delimit morphotypes within a species without geographically or genetically isolated populations (see Stebbins 1950). Weakley et al. (2017) argue for using varieties in the botanical sciences, regardless of the scenario. We promote the use of subspecies here to further standardize its use for morphologically, and oftentimes ecologically, distinctive taxa. We also hope that this will lead to more taxonomic stability in *Dichanthelium*, as the rank of subspecies has already been used widely by Freckmann and Lelong (2003); thus, fewer nomenclatural changes would be needed. The morphological and often ecological distinctiveness of these taxa deserves recognition, given their potential for speciation.

Campbell (1983) used infraspecific taxon circumscriptions to recognize facultatively cleistogamous taxa within the *Andropogon virginicus* complex, although there appears to be relatively little hybridization within that group of species. More recent treatments have tended to recognize most of those taxa, however cryptic, at the species level (Weakley 2020). The same fine-scale splitting approach could be taken with *Dichanthelium*, although we consider that more comprehensive biological information (such as chromosome number, hybrid origin, and sterility) and phylogenetic resolution are necessary before making those species complex–dependent determinations. It could be that low levels of outcrossing within these species complexes more greatly obscure species boundaries morphologically, which would also be reflected as taxon nonmonophyly in resulting phylogenetic topologies, a common feature exhibited in our current dataset for infraspecific taxa within species complexes.

Taxonomic Treatment

Below, we provide a taxonomic treatment based, in part, on our phylogenetic results. Given that several species complexes still require much systematic work and that it is unclear based on our phylogenetic topology whether certain taxa should be regarded as species or infraspecific taxa, we have used caution when recognizing those taxa and have mostly maintained those as they have been treated previously at either the specific rank or the infraspecific rank (e.g., *D. depauperatum*, *D. acuminatum* ssp. *fasciculatum*), which is in line with previous treatments (e.g., Freckmann and Lelong 2003; LeBlond 2020). We provide justification where we have deviated from infraspecific ranks and do not have clear phylogenetic resolution. In general, we do not treat taxa or morphotypes that we did not sample in our phylogeny (e.g., *D. acuminatum* ssp. *columbianum*, *D. malacon*, *D. patentifolium*). This is not meant to be a comprehensive treatment for North American taxa but mostly to provide clarification of species boundaries, where warranted, based on our taxon sampling and to provide a starting point based on phylogenetic relationships for further investigations into the taxonomic complexity of this genus. Altogether, we recognize 48 species (72 taxa) for North America (including Central America) and Hawaii.

***Dichanthelium aciculare* (Desv. ex Poir.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1116. 1979.** *Panicum aciculare* Desv. ex Poir. Encycl. Suppl. 4: 274. 1816.

Panicum arenicoloides Ashe J. Elisha Mitchell Sci. Soc. 16: 89. 1900. *Panicum aciculare* var. *arenicoloides* (Ashe) Beetle Phytologia 48: 192. 1981. *Dichanthelium arenicoloides* (Ashe) LeBlond J. Bot. Res. Inst. Texas 11: 314. 2017.

Dichanthelium aciculare* ssp. *aciculare

***Dichanthelium aciculare* ssp. *angustifolium* (Elliott) Freckmann & Lelong Sida 20: 167. 2002.** *Panicum angustifolium* Elliott Sketch Bot. S. Carolina 1: 129. 1816. *Panicum nitidum* var. *angustifolium* (Elliott) A.Gray N. Amer. Gram. 2: 112. 1835. *Chasea angustifolia* (Elliott) Nieuwl. Amer. Mid. Naturalist 2: 64. 1911. *Dichanthelium angustifolium* (Elliott) Gould Brittonia 26: 59. 1974.

***Dichanthelium aciculare* ssp. *fusiforme* (Hitchc.) Freckmann & Lelong Sida 20: 167. 2002.** *Panicum fusiforme* Hitchc. Contr. U.S. Natl. Herb. 12: 222. 1909. *Dichanthelium fusiforme* (Hitchc.) Harvill Castanea 42: 177. 1977.

Panicum neuranthum var. *ramosum* Griseb. Cat. Pl. Cub. 232. 1866. *Dichanthelium aciculare* var. *ramosum* (Griseb.) Davidse Novon 2: 104. 1992.

***Dichanthelium aciculare* ssp. *neuranthum* (Griseb.) Freckmann & Lelong Sida 20: 167. 2002.** *Panicum neuranthum* Griseb. Cat. Pl. Cub. [Grisebach] 232. 1866. *Panicum aciculare* var. *neuranthum* (Griseb.) Wipff Sida 20: 1044. 2003. *Dichanthelium neuranthum* (Griseb.) LeBlond J. Bot. Res. Inst. Texas 5: 448. 2011.

***Dichanthelium aciculare* ssp. *pinetorum* (Swallen) Majure comb. et stat. nov.** *Panicum pinetorum* Swallen Proc. Biol. Soc. Washington 55: 93. 1942. *Dichanthelium pinetorum* (Swallen) LeBlond J. Bot. Res. Inst. Texas 10: 40. 2016.

***Dichanthelium acuminatum* (Sw.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1121. 1979.** *Panicum acuminatum* Sw. Prodr. [O.P.Swatrz] 23. 1788. *Panicum dichotomum* var. *acuminatum* (Sw.) Griseb. Fl. Brit. W. I. 553. 1864.

Dichanthelium acuminatum* ssp. *acuminatum

***Dichanthelium acuminatum* ssp. *fasciculatum* (Torr.) Freckmann & Lelong Sida 20: 167. 2002.** *Panicum dichotomum* var. *fasciculatum* Torr. Fl. N. Middle United States 145. 1824. *Panicum lanuginosum* var. *fasciculatum* (Torr.) Fernald Rhodora 36: 77. 1934. *Dichanthelium acuminatum* var. *fasciculatum* (Torr.) Lelong Brittonia 36: 269. 1984.

Panicum lanuginosum Elliott Sketch Bot. S. Carolina 1: 123. 1816. *Dichanthelium lanuginosum* (Elliott) Gould Brittonia 26: 60. 1974.

***Dichanthelium acuminatum* ssp. *implicatum* (Scribn.) Freckmann & Lelong Sida 20: 167. 2002.** *Panicum implicatum* Scribn. Bull. Div. Agrostol. U.S.D.A. 11: 43. 1898. *Panicum unciphyllum* var. *implicatum* (Scribn.) Scribn. & Merr. Rhodora 3: 123. 1901. *Panicum lindheimeri* var. *implicatum* (Scribn.) Fernald Rhodora 23: 228. 1922. *Panicum lanuginosum* var. *implicatum* (Scribn.) Fernald Rhodora 36: 77. 1934. *Dichanthelium acuminatum* var. *implicatum* (Scribn.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1126. 1979.

***Dichanthelium acuminatum* ssp. *lindheimeri* (Nash) Freckmann & Lelong Sida 20: 168. 2002.** *Panicum lindheimeri* Nash

Bull. Torrey Bot. Club 24: 196. 1897. *Panicum lanuginosum* var. *lindheimeri* (Nash) Freckmann Phytologia 39: 270. 1978. *Dichanthelium acuminatum* var. *lindheimeri* (Nash) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1127. 1979.

***Dichanthelium acuminatum* ssp. *thermale* (Bol.) Freckmann & Lelong Sida 20: 168. 2002.** *Panicum thermale* Bol. Proc. Calif. Acad. Sci. 2: 181. 1862.

***Dichanthelium ashei* (T.G.Pearson ex Ashe) Mohlenbr. Phytoneuron 2015–12: 8. 2015.** *Panicum ashei* T.G.Pearson ex Ashe J. Elisha Mitchell Sci. Soc. 15: 35. 1898. *Panicum commutatum* var. *ashei* (T.G.Pearson ex Ashe) Fernald Rhodora 36: 83. 1934. *Dichanthelium commutatum* var. *ashei* (T.G. Pearson ex Ashe) Mohlenbr. Erigenia 6: 26. 1985. *Dichanthelium commutatum* ssp. *ashei* (T.G.Pearson ex Ashe) Freckmann & Lelong Sida 20: 169. 2002.

***Dichanthelium boreale* (Nash) Freckmann Phytologia 39: 269. 1978.** *Panicum boreale* Nash Bull. Torrey Bot. Club 22: 421. 1895.

Note. Although *D. boreale* is nested deeply within *D. dichotomum*, we suggest that more work needs to be carried out to make a determination about its species status, especially given its distinctive morphological features (Freckmann and Lelong 2003).

***Dichanthelium boscii* (Poir.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1101. 1979.** *Panicum boscii* Poir. in Lam. Encycl. [J.Lamarck et al.] Suppl. 4. 278. 1816.

***Dichanthelium chamaelonche* (Trin.) Freckmann & Lelong Sida 20: 168. 2002.** *Panicum chamaelonche* Trin. Gram Panic. [Trinius] 242. 1826.

Dichanthelium chamaelonche* ssp. *chamaelonche

***Dichanthelium chamaelonche* ssp. *breve* (Hitchc. & Chase) Freckmann & Lelong Sida 20: 168. 2002.** *Panicum breve* Hitchc. & Chase Contr. U.S. Natl. Herb. 15: 271. 1910, *Dichanthelium dichotomum* var. *breve* (Hitchc. & Chase) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1120. 1979. *Dichanthelium chamaelonche* var. *breve* (Hitchc. & Chase) Lelong Brittonia 36: 267. 1984. *Dichanthelium ensifolium* var. *breve* (Hitchc. & Chase) B.F.Hansen & Wunderlin Ann. Missouri Bot. Gard. 75: 1646. 1989. *Dichanthelium breve* (Hitchc. & Chase) LeBlond J. Bot. Res. Inst. Texas 12: 58. 2018.

***Dichanthelium clandestinum* (L.) Gould Brittonia 26: 59. 1974.** *Panicum clandestinum* L. Sp. Pl. 1: 58. 1753. *Millium clandestinum* (L.) Moench Methodus (Moench) 204. 1794. *Panicum latifolium* var. *clandestinum* (L.) Pursh Fl. Amer. Sept. (Pursh) 1: 68. 1813. *Chasea clandestina* (L.) Nieuwl. Amer. Midl. Naturalist 2: 64. 1911.

***Dichanthelium commutatum* (Schult.) Gould Brittonia 26: 59. 1974.** *Panicum commutatum* Schult. Mant. 2 (Schultes) 242. 1824.

Dichanthelium commutatum* ssp. *commutatum

***Dichanthelium commutatum* ssp. *joorii* (Vasey) Freckmann & Lelong Sida 20: 169. 2002.** *Panicum joorii* Vasey Bull. Div. Bot. U.S.D.A. 8: 31. 1889.

Note. *Dichanthelium commutatum* ssp. *commutatum* and *D. commutatum* ssp. *joorii* often grow in close proximity to one another and are not always easily separable, with growth habit, leaf morphology, and glume apex shape not always being consistent for one taxon or the other. Relationships between the two taxa are also not completely resolved in our phylogeny. We recognize that this is a species complex with many morphotypes (some of which are unsampled here) still needing systematic work.

***Dichanthelium consanguineum* (Kunth) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1115. 1979.** *Panicum consanguineum* Kunth Revis. Gramin. 1: 36. 1829. *Panicum commutatum* var. *consanguineum* Beal Grasses N. Amer. 2: 141. 1896. *Panicum acuminatum* var. *consanguineum* (Kunth) Wipff & S.D.Jones Phytologia 77: 458. 1995.

Note. *Dichanthelium consanguineum* is morphologically and ecologically distinctive from putative close relatives, such as *D. aciculare* (see Freckmann and Lelong 2003; LeBlond 2020), and nested within the *D. aciculare* clade in our phylogenetic analyses, but relationships are not totally resolved. Thus, we continue to recognize it at the species level here. *Dichanthelium consanguineum* is clearly not conspecific with *D. ovale*, as circumscribed in Zuloaga and Morrone (2003).

***Dichanthelium curtifolium* (Nash) LeBlond J. Bot. Res. Inst. Texas 5: 450. 2011.** *Panicum curtifolium* Nash Bull. Torrey Bot. Club 26: 569. 1899. *Panicum ensifolium* var. *curtifolium* (Nash) Lelong Brittonia 36: 266. 1984. *Dichanthelium ensifolium* ssp. *curtifolium* (Nash) Freckmann & Lelong Sida 20: 170. 2002.

Note. *Dichanthelium curtifolium* is resolved in two places in our phylogeny, which may suggest a hybrid origin (as proposed, in part, by Weakley et al. 2011) perhaps between *D. ensifolium* s.s. and *D. leucothrix*. However, this is unresolved, and more work will be necessary to make this determination. This species is clearly distinguishable from *D. ensifolium* s.s. and exists over a wide distribution; thus, we maintain it separately here.

***Dichanthelium cynodon* (Reichardt) C.A.Clark & Gould Brittonia 30: 58. 1978.** *Panicum cynodon* Reichardt Sitzungsber. Akad. Wien IXXVI. 724. 1878.

***Dichanthelium depauperatum* (Muhl.) Gould Brittonia 26: 59. 1974.** *Panicum depauperatum* Muhl. Descr. Gram. (Muhlenberg) 112. 1817.

Note. *Dichanthelium depauperatum* is unresolved along with putative close relatives in our phylogeny, which necessitates future work to clarify relationships in this part of the tree.

***Dichanthelium dichotomum* (L.) Gould Brittonia 26: 59. 1974.** *Panicum dichotomum* L. Sp. Pl. 1: 58. 1753. *Chasea dichotoma* (L.) Nieuwl. Amer. Midl. Naturalist 2: 64. 1911.

Dichanthelium dichotomum* ssp. *dichotomum

***Dichanthelium dichotomum* ssp. *mattamuskeetense* (Ashe) Freckmann & Lelong Sida 20: 169. 2002.** *Panicum mattamuskeetense* Ashe J. Elisha Mitchell Sci. Soc. 15: 45. 1898. *Panicum dichotomum* var. *mattamuskeetense* (Ashe) Lelong Brittonia 36: 265. 1984. *Dichanthelium mattamuskeetense* (Ashe) Mohlenbr. Erigenia 6: 26. 1985.

***Dichanthelium dichotomum* ssp. *microcarpon* (Muhl. ex Elliott) Freckmann & Lelong Sida 20: 169. 2002.** *Panicum microcarpon* Muhl. ex Elliott Sketch Bot. S. Carolina [Elliott] 1: 127. 1816. *Dichanthelium microcarpon* (Muhl. ex Elliott) Mohlenbr. Erigenia 6: 26. 1985.

Panicum nitidum var. *ramulosum* Torr. Fl. N. Middle United States 1: 146. 1824. *Dichanthelium dichotomum* var. *ramulosum* (Torr.) LeBlond Sida 19: 830. 2001.

***Dichanthelium dichotomum* ssp. *nitidum* (Lam.) Freckmann & Lelong Sida 20: 169. 2002.** *Panicum nitidum* Lam.

Tabl. Encycl. 1: 172. 1791. *Dichanthelium dichotomum* var. *nitidum* (Lam.) LeBlond Sida 19: 829. 2001.

Note. L. C. Majure (personal observation) has observed *D. dichotomum* ssp. *nitidum* and *D. dichotomum* ssp. *roanokense* growing together along roadsides in Alachua (see *Majure 3057*, *Majure 3061*), Levy (see *Majure 7664*, *Majure 7665*), and Citrus (see *Majure 10029*, *Majure 10030*) Counties in Florida. It is curious that these taxa are separated by minor differences in node pubescence and leaf orientation but are otherwise nearly identical. They also have essentially the same distribution, from the eastern United Sates to the West Indies (Freckmann and Lelong 2003; L. C. Majure, personal observation), and occupy similar habitats.

***Dichanthelium dichotomum* ssp. *roanokense* (Ashe) Freckmann & Lelong Sida 20: 170. 2002.** *Panicum roanokense* Ashe J. Elisha Mitchell Sci. Soc. 15: 44. 1898. *Panicum dichotomum* var. *roanokense* (Ashe) Lelong Brittonia 36: 265. 1984. *Dichanthelium dichotomum* var. *roanokense* (Ashe) LeBlond Sida 19: 831. 2001.

***Dichanthelium dichotomum* ssp. *yadkinense* (Ashe) Freckmann & Lelong Sida 20: 170. 2002.** *Panicum yadkinense* Ashe J. Elisha Mitchell Sci. Soc. 16: 85. 1900. *Panicum dichotomum* var. *yadkinense* (Ashe) Lelong Brittonia 36: 266. 1984. *Dichanthelium yadkinense* (Ashe) Mohlenbr. Erigenia 6: 27. 1985.

***Dichanthelium ensifolium* (Baldwin ex Elliott) Gould Brittonia 26: 59. 1974.** *Panicum ensifolium* Baldwin ex Elliott Sketch Bot. S. Carolina [Elliott] 1: 126–127. 1816.

***Dichanthelium equilaterale* (Scribn.) Wipff Phytologia 102: 173. 2020.** *Panicum equilaterale* Scribn. Bull. Div. Agrostol. U.S.D.A. 11: 42. 1898. *Panicum commutatum* var. *equilaterale* (Scribn.) Wipff Sida 20: 1044. 2003. *Dichanthelium commutatum* ssp. *equilaterale* (Scribn.) Freckmann & Lelong Sida 20: 169. 2002.

Note. Dichanthelium equilaterale is not resolved within *D. commutatum* in our phylogeny; thus, we consider it, although cryptic, distinctive from *D. commutatum*. It is perhaps of hybrid origin between a member of the *D. portoricense* + *D. chamaelonche* clade (most likely *D. lancearium* based on morphological comparisons and sympatry) and *D. commutatum* s.s. This species is a common component of mesic to xeric hammocks in north Florida (L. C. Majure, personal observation) and commonly cooccurs with *D. commutatum* s.s. and *D. lancearium* s.l. (syn. = *D. portoricense*, see below).

***Dichanthelium erectifolium* (Nash) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1105. 1979.** *Panicum erectifolium* Nash Bull. Torrey Bot. Club 23: 148. 1896.

Panicum sphaerocarpon var. *floridanum* Vasey Bull. Div. Bot. U.S.D.A. 8: 33. 1889.

***Dichanthelium helleri* (Nash) Mohlenbr. Phytoneuron 2015–67: 2. 2015.**

Panicum helleri Nash Bull. Torrey Bot. Club 26: 572. 1899. *Panicum oligosanthes* var. *helleri* (Nash) Fernald Rhodora 36: 80. 1934. *Dichanthelium oligosanthes* var. *helleri* (Nash) Mohlenbr. Erigenia 6: 26. 1985.

Note. Dichanthelium helleri, although normally considered closely related to, or synonymous with, *D. oligosanthes* ssp. *scribnerianum* based on the phenetic similarity of the two, is not resolved with *D. oligosanthes* ssp. *scribnerianum* in our phylogeny. Thus, based on its morphological distinctiveness (including greatly elongated vernal culms) and sister relationships to the broader *D. oligosanthes* clade, we recognize this taxon at the species level here.

***Dichanthelium hillebrandianum* (Hitchc.) C.A.Clark & Gould Brittonia 30: 57. 1978.** *Panicum hillebrandianum* Hitchc. Mem. Bishop Mus. Honolulu VIII. 197. 1922.

***Dichanthelium hirstii* (Swallen) Kartesz Synth. N. Amer. Fl. Nomencl. Innov. 5. 1999.** *Panicum hirstii* Swallen Rhodora 63: 236. 1961.

Note. Although *D. hirstii* is nested within *D. dichotomum* and exhibits features of the species, we reserve making any formal changes here until further systematic work can be carried out. It is interesting to note that in our phylogeny, *D. hirstii* is sister to *D. dichotomum* ssp. *roanokense*, the same taxon that *D. hirstii* has been compared to and perhaps is synonymous with (Hitchcock and Chase 1910; Freckmann and Lelong 2003). *Dichanthelium hirstii* also bears a striking resemblance to *D. dichotomum* ssp. *nitidum*, sharing the pubescent nodes (at least the lower nodes) of that taxon. *Dichanthelium hirstii* perhaps is most morphologically similar to *D. sphagnicola* (a taxon not sampled in our phylogeny), which also exhibits ascending leaves and contracted panicles and could merely be an extreme form of that taxon, although spikelet shape and size differ. *Dichanthelium hirstii* has been compared to *D. aciculare* ssp. *neuranthum* because of its contracted panicles (McAvoy et al. 2015) and the *D. aciculare* group in general (LeBlond et al. 2017; Weakley et al. 2017), but it is clearly not closely related to that species complex in our phylogeny and morphologically appears more similar to the *D. dichotomum* complex.

***Dichanthelium isachnoides* (Munro ex Hillebrand) C.A.Clark & Gould Brittonia 30: 57. 1978.** *Panicum isachnoides* Munro J. Bot. 7: 178. 1869.

***Dichanthelium koolauense* (H.St.John & Hosaka) C.A.Clark & Gould Brittonia 30: 58. 1978.** *Panicum koolauense* H.St.John & Hosaka Occas. Pap. Bernice Pauahi Bishop Mus. 11: 3. 1935.

***Dichanthelium latifolium* (L.) Harvill Castanea 42: 177. 1977.** *Panicum latifolium* L. Sp. Pl. 1: 58. 1753.

***Dichanthelium lancearium* (Trin.) Greuter & R.Rankin Espermat. Cuba Invent. Prelim. XIII. 2016.** *Panicum lancearium* Trin. Clav. Agrostogr. 234. 1822.

Dichanthelium lancearium* ssp. *lancearium

Panicum nashianum Scribn. Bull. Div. Agrostol. U.S.D.A. 7: 79. 1897. *Panicum portoricense* var. *nashianum* (Scribn.) Lelong Brittonia 36: 267. 1984.

Panicum nashianum var. *patulum* Scribn. & Merr. Circ. Div. Agrostol. U.S.D.A. 27: 9. 1900. *Panicum patulum* (Scribn. & Merr.) Hitchc. Rhodora 8: 209. 1906. *Panicum lancearium* var. *patulum* (Scribn. & Merr.) Fernald Rhodora 36: 80. 1934. *Dichanthelium sabulorum* var. *patulum* (Scribn. & Merr.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1113. 1979. *Panicum sabulorum* var. *patulum* (Scribn. & Merr.) C.F.Reed Phytologia 67: 452. 1989. *Dichanthelium portoricense* ssp. *patulum* (Hitchc.) Freckmann & Lelong Sida 20: 170. 2002. *Dichanthelium patulum* (Scribn. & Merr.) Wipff Phytologia 102: 174. 2020.

Note. Although all other authors addressing the name *Panicum lancearium* have considered it synonymous with other taxa (Hansen and Wunderlin 1988; LeBlond 2020), Greuter and Rankin Rodríguez (2016) recognized that the name *Panicum* *lancearium* is older and thus has priority over *D. portoricense*. LeBlond (2020) placed *P. lancearium* in synonymy with *D. portoricense* var. *patulum*, while Hansen and Wunderlin (1988) merely considered it under a broad circumscription of *D. portoricense*, which also included members of the *D. acuminatum* complex in their treatment. Based on the type of *P. lancearium*, we consider it to most closely match the material of *P. nashianum* (glabrous spikelets and larger-sized plants; see also Hitchcock 1906). Although material of *P. nashianum* is said to have glabrous or puberulent spikelets (Hitchcock 1935), thus also placing it within the morphospace of *D. portoricense* ssp. *patulum*. The material of *D. portoricense* ssp. *patulum* and the taxon *D. webberianum* (as *D. portoricense* ssp. *patulum*; see *Abbott 22490*, *Majure 3098*, *Majure 5229*) were both nested within *D. portoricense* ssp. *portoricense* in our phylogeny, but given the large size of *D. webberianum* and its contrasting large, ascending leaves, we believe that it likely does merit taxonomic recognition under *D. lancearium* (see below). *Dichanthelium portoricense* ssp. *portoricense* (= *D. lancearium* var. *portoricense*) can be recognized by its small puberulent spikelets and generally smaller-sized plants (Hitchcock 1935).

***Dichanthelium lancearium* ssp. *portoricense* (Desv. ex Ham.) Majure comb. et stat. nov.** *Panicum portoricense* Desv. ex Ham. Prodr. Pl. Ind. Occid. [Hamilton] 11. 1825. *Dichanthelium portoricense* (Desv. ex Ham.) B.F.Hansen & Wunderlin Ann. Missouri Bot. Gard. 75: 1649. 1989.

Note. *Dichanthelium lancearium* ssp. *portoricense* and *D. lancearium* ssp. *lancearium* often grow in close proximity to one another, especially in Florida. However, *D. lancearium* ssp. *portoricense* tends to occur in more open and drier sites, while *D. lancearium* ssp. *lancearium* tends to occur in shadier and more mesic conditions. But this is not universal, and both are found in mesic to wet and xeric conditions in sandy soils (L. C. Majure, personal observation).

***Dichanthelium lancearium* ssp. *webberianum* (Nash) Majure comb. et stat. nov.** *Panicum webberianum* Nash Bull. Torrey Bot. Club 23: 149. 1896. *Dichanthelium webberianum* (Nash) LeBlond J. Bot. Res. Inst. Texas 5: 450. 2011.

***Dichanthelium laxiflorum* (Lam.) Gould Brittonia 26: 60. 1974.** *Panicum laxiflorum* Lam. in Lamarck Encycl. 4: 748. 1798. *Panicum dichotomum* var. *laxiflorum* (Lam.) Beal Grasses N. Amer. 2: 139. 1896.

Panicum xalapense Kunth Nov. Gen. Sp. 1: 103. 1816. *Dichanthelium xalapense* (Kunth) Wipff Phytologia 102: 174. 2020.

Panicum xalapense var. *strictirameum* Hitchc. & Chase Contr. U.S. Natl. Herb. 15: 161. 1910. *Panicum laxiflorum* var. *strictirameum* (Hitchc. & Chase) Fernald Rhodora 36: 75. 1934. *Dichanthelium xalapense* var. *strictirameum* (Hitchc. & Chase) Wipff Phytologia 102: 174. 2020.

Note. *Dichanthelium laxiflorum* is the oldest name available for the species and thus has priority over *D. xalapense*. *Panicum laxiflorum* var. *strictirameum* (*D. xalapense* var. *strictirameum* Wipff) is an uncommon morphological entity within *D. laxiflorum* and develops ascending, appressed inflorescence branches but otherwise is indistinguishable from *D. laxiflorum* (see *Majure 2313*, MMNS; *Majure 8253*, FLAS); thus, we consider this taxon within the circumscription of *D. laxiflorum*.

***Dichanthelium leibergii* (Vasey) Freckmann Phytologia 39: 271. 1978.** *Panicum scoparium* var. *leibergii* Vasey Bull. Div. Bot. U.S.D.A. 8: 32. 1889. *Panicum leibergii* (Vasey) Scribn. Bull. Div. Agrostol. U.S.D.A 8: 6. 1897.

***Dichanthelium leucothrix* (Nash) Freckmann Phytologia 48: 101. 1981.** *Panicum leucothrix* Nash Bull. Torrey Bot. Club 24: 41. 1897. *Dichanthelium acuminatum* ssp. *leucothrix* (Nash) Lelong Brittonia 36: 271. 1984. *Panicum spretum* var. *leucothrix* (Nash) D.B.Ward Phytologia 94: 472. 2012. *Dichanthelium acuminatum* ssp. *leucothrix* (Nash) Freckman & Lelong Sida 20: 167. 2002.

Dichanthelium leucothrix* (Nash) Freckmann ssp. *leucothrix

***Dichanthelium leucothrix* (Nash) Freckmann ssp. *longiligulatum* (Nash) Majure comb. et. stat. nov.** *Panicum longiligulatum* Nash Bull. Torrey Bot. Club 26: 574. 1899. *Dichanthelium acuminatum* var. *longiligulatum* (Nash) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1127. 1979. *Dichanthelium longiligulatum* (Nash) Freckmann Phytologia 48: 102. 1981. *Panicum acuminatum* var. *longiligulatum* (Nash) Lelong Brittonia 36: 270. 1984. *Dichanthelium acuminatum* ssp. *longiligulatum* (Nash) Freckmann & Lelong Sida 20: 168. 2002. *Panicum spretum* var. *longiligulatum* (Nash) D.B.Ward Phytologia 94: 472. 2012.

Note. *Dichanthelium leucothrix* ssp. *longiligulatum* is phylogenetically nested within *D. leucothrix* and is essentially a vegetatively glabrous (other than the long ligules) and more robust form of that species, with which it commonly grows syntopically in the southeastern United States and Belize (R. F. C. Naczi, personal observation).

***Dichanthelium linearifolium* (Scribn.) Gould Brittonia 26: 60. 1974.** *Panicum linearifolium* Scribn. In Britton & A.Br. Ill. Fl. N. U.S. 3: 500. 1898.

***Dichanthelium lucidum* (Ashe) LeBlond Sida 19: 831. 2001.** *Panicum lucidum* Ashe J. Elisha Mitchell Sci. Soc. 15: 47. 1898. *Dichanthelium dichotomum* ssp. *lucidum* Freckmann & Lelong Sida 20: 169. 2002.

***Dichanthelium malacophyllum* (Nash) Gould Brittonia 26: 60. 1974.** *Panicum malacophyllum* Nash Bull. Torrey Bot. Club 24: 198. 1897.

***Dichanthelium mutabile* (Scribn. & J.G.Sm.) Wipff Phytologia 102: 174. 2020.** *Panicum mutabile* Scribn. & J.G.Sm. Fl. S.E.U.S. [Small] 103, 1327. 1903.

***Dichanthelium nodatum* (Hitchc. & Chase) Gould Brittonia 26: 60. 1974.** *Panicum nodatum* Hitchc. & Chase Contr. U.S. Natl. Herb. 15: 293. 1910.

***Dichanthelium nudicaule* (Vasey) Wunderlin & B.F.Hansen Novon 11: 367. 2001.** *Panicum nudicaule* Vasey Dept. Agric. Bot. Div. Bull. 8: 31. 1889.

***Dichanthelium oligosanthes* (Schult.) Gould Brittonia 26: 60. 1974.** *Panicum oligosanthes* Schult. Mant. 2: (Schultes) 256. 1824.

Dichanthelium oligosanthes* ssp. *oligosanthes

***Dichanthelium oligosanthes* ssp. *scribnerianum* (Nash) Freckmann & Lelong Sida 20: 170. 2002.** *Panicum scribnerianum* Nash Bull. Torrey Bot. Club 22: 421. 1895. *Dichanthelium oligosanthes* var. *scribnerianum* (Nash) Gould Brittonia 26: 60. 1974.

***Dichanthelium ovale* (Elliott) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1114. 1979.** *Panicum ovale* Elliott Sketch Bot. S. Carolina [Elliott] 1: 123. 1816.

Dichanthelium ovale* ssp. *ovale

***Dichanthelium ovale* ssp. *pseudopubescens* (Nash) Freckmann & Lelong Sida 20: 170. 2002.** *Panicum pseudopubescens* Nash Bull. Torrey Bot. Club 26: 577. 1899.

***Dichanthelium ovale* ssp. *villosissimum* (Nash) Freckmann & Lelong Sida 20: 170. 2002.** *Panicum villosissimum* Nash Bull. Torrey Bot. Club 23: 149. 1896. *Dichanthelium lanuginosum* var. *villosissimum* (Nash) Gould Brittonia 26: 60. 1974. *Dichanthelium villosissimum* (Nash) Freckmann Phytologia 39: 270. 1978.

Note. The *D. ovale* species complex is in great need of systematic work, alongside the *D. acuminatum* complex, with which it is, in part, phylogenetically nested. Given that *D. ovale* ssp. *ovale*, *D. ovale* ssp. *pseudopubescens*, and *D. ovale* ssp. *villosissimum* are interdigitated in our phylogeny and recovered in multiple places so that it is poorly (or not at all) supported, we refrain from considering any major taxonomic changes or species recognition for infraspecific taxa, as currently circumscribed, until further work illuminates relationships in this complex.

***Dichanthelium pedicellatum* (Vasey) Gould Brittonia 26: 60. 1974.** *Panicum pedicellatum* Vasey Bull. Div. Bot. U.S.D.A. 8: 28. 1889. nom. illeg., non *P. pedicellatum* Saporta.

***Dichanthelium perlongum* (Nash) Freckmann Phytologia 39: 269. 1978.** *Panicum perlongum* Nash Bull. Torrey Bot. Club 26: 575. 1899. *Panicum depauperatum* var. *perlongum* (Nash) B.Boivin Naturaliste Canad. 94: 526. 1967.

***Dichanthelium polyanthes* (Schult.) Mohlenbr. Erigenia 6: 26. 1985.** *Panicum polyanthes* Schult. Mant. 2 (Schultes) 257. 1824. *Dichanthelium sphaerocarpon* var. *polyanthes* (Schult.) Gould Brittonia 26: 60. 1974.

***Dichanthelium ravenelii* (Scribn. & Merr.) Gould Brittonia 26: 60. 1974.** *Panicum ravenelii* Scribn. & Merr.Bull. Div. Agrostol. U.S.D.A. 24: 36. 1901.

***Dichanthelium sabulorum* (Lam.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1112. 1979.** *Panicum sabulorum* Lam. Encycl. [J.Lamarck et al.] 4: 744. 1798.

Dichanthelium sabulorum* ssp. *sabulorum

***Dichanthelium sabulorum* ssp. *polycladum* (Ekman) Majure comb. et stat. nov.**

Panicum polycladum Ekman Ark. Bot. 11: 24. 1912. *Panicum sabulorum* var. *polycladum* (Ekman) R.A.Palacios in Burkart Fl. Illustr. Entre Rios 2: 316. 1969. *Dichanthelium sabulorum* var. *polycladum* (Ekman) Zuloaga Amer. J. Bot. 90: 817. 2003.

Note. Although *D. sabulorum* ssp. *polycladum* tends to be more glabrous than *D. sabulorum* ssp. *sabulorum*, we have noticed gradation from one morphotype to the other, and these two taxa are likewise interdigitated in our phylogenetic topology. Thus, maintaining these as infraspecific taxa within *D. sabulorum* appears warranted. In Uruguay, these two taxa tend to occur in slightly different habitats, with *D. sabulorum* ssp. *polycladum* in more mesic conditions and *D. sabulorum* ssp. *sabulorum* in more xeric conditions (L. C. Majure, personal observation).

***Dichanthelium scabriusculum* (Elliott) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1110. 1979.** *Panicum scabriusculum* Elliott Sketch Bot. S. Carolina [Elliott] 1: 121 (–122). 1816.

***Dichanthelium scoparium* (Lam.) Gould Brittonia 26: 60. 1974.** *Panicum scoparium* Lam. Encycl. [J.Lamarck et al.] 4: 744. 1798.

***Dichanthelium sphaerocarpon* (Elliott) Gould Brittonia 26: 60. 1974.** *Panicum sphaerocarpon* Elliott Sketch Bot. S. Carolina [Elliott] 1: 125. 1816.

***Dichanthelium sphagnicola* (Nash) LeBlond Sida 19: 834. 2001.** *Panicum sphagnicola* Nash Bull. Torr. Bot. Club 22: 422. 1895.

Note. We were not able to sample *D. sphagnicola* for our phylogenetic analysis. Freckmann and Lelong (2003) considered *D. sphagnicola* to be synonymous with *D. lucidum* based on their expanded concept of *D. dichotomum*. *Dichanthelium sphagnicola* is occasional in parts of Florida, forming dense colonies in wet forests dominated by *Taxodium ascendens* Brongn., and can be distinguished from *D. lucidum*, given its moderately pubescent spikelets; ascending, nearly appressed panicle branches; larger, thicker, olive green leaves; and more robust plants, in general (L. C. Majure, personal observation). This taxon appears to be most closely related to *D. dichotomum* ssp. *roanokense* and *D. hirstii*, especially based on its ascending leaves and contracted panicles. We tentatively recognize it here.

***Dichanthelium spretum* (Schult.) Freckmann Phytologia 48: 102. 1981.** *Panicum spretum* Schult. Mant. 2 (Schultes) 248. 1824. *Dichanthelium lanuginosum* var. *spretum* (Schult.) Harvill Castanea 42: 177. 1977. *Dichanthelium acuminatum* ssp. *spretum* (Schult.) Freckmann & Lelong Sida 20: 168. 2002.

Note. Although deeply nested within *D. dichotomum*, *D. spretum* is morphologically disparate from *D. dichotomum*, given its long ligules, which are more like those of the *D. acuminatum* group, which led Freckmann and Lelong (2003) to place it there. However, based on its size, authors have mentioned its similarity to *D. dichotomum* (Freckmann and Lelong 2003), and Hitchcock (1935) treated the species as being directly in between the two species complexes. Thomas (2015) likewise mentions that this species does not seem to fit well in the *D. acuminatum* complex, which is further supported by our phylogeny. We tentatively recognize this species here until more resolution can be provided to determine the origin of this taxon, which with its heterogeneous suite of morphological characters overlapping both *D. acuminatum* and *D. dichotomum*, as well as its disjunct distribution (see Thomas 2015), may suggest a hybrid taxon with multiple origins.

***Dichanthelium strigosum* (Muhl. ex Elliott) Freckmann Brittonia 33: 457. 1981.** *Panicum strigosum* Muhl. ex Elliott Skeetch Bot. S. Carolina [Elliott] 1: 126. 1816.

Dichanthelium strigosum* ssp. *strigosum

***Dichanthelium strigosum* ssp. *glabrescens* (Griseb.) Freckmann & LelongSida 20: 171. 2002.** *Panicum dichotomum* var. *glabrescens* Griseb. Fl. Brit. W.I. [Grisebach] 553. 1864. *Dichanthelium strigosum* var. *glabrescens* (Griseb.) Freckmann Brittonia 33: 457. 1981.

***Dichanthelium strigosum* ssp. *leucoblepharis* (Trin.) Freckmann & Lelong Sida 20: 171. 2002.** *Dichanthelium strigosum* var. *leucoblepharis* (Trin.) Freckmann Brittonia 33: 457. 1981. *Panicum leucoblepharis* Trin. Clav. Agrostogr. Antiq. 234. 1822.

***Dichanthelium tenue* (Muhl.) Freckmann & Lelong Sida 20: 171. 2002.** *Panicum tenue* Muhl. Descr. Gram. (Muhlenberg) 118. 1817. *Dichanthelium dichotomum* var. *tenue* (Muhl.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1119. 1979. *Panicum dichotomum* var. *tenue* (Muhl.) C.F.Reed Phytologia 67: 453. 1989.

***Dichanthelium viscidellum* (Scribn.) Gould Brittonia 32: 357. 1980.** *Panicum viscidellum* Scribn. Circ. Div. Bot. U.S.D.A. 19: 2. 1900.

Note. We continue to recognize *D. viscidellum* at the species level until more resolution is provided in the *D. acuminatum* species complex within which it is nested. This species is a tetraploid and is divergent morphologically from *D. acuminatum*, both vegetatively and with regard to the inflorescence architecture, spikelet shape, and pubescence.

Dichanthelium wilcoxianum **(Vasey) Freckmann Phytologia 39: 269. 1978.** *Panicum wilcoxianum* Vasey Bull. Div. Bot. U.S.D.A. 8: 32. 1889. *Milium wilcoxianum* (Vasey) Lunell Amer. Midl. Naturalist 4: 213. 1915. *Dichanthelium oligosanthes* var. *wilcoxianum* (Vsey) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1107. 1979.

Note. Although considered by Lelong (1965) to potentially represent a hybrid, we saw no evidence for a hybrid origin in our dataset.

Dichanthelium wrightianum **(Scribn.) Freckmann Phytologia 48: 101. 1981.** *Panicum wrightianum* Scribn. Bull. Div. Agrostol. U.S.D.A. 11: 44. 1898. *Dichanthelium acuminatum* var. *wrightianum* (Scribn.) Gould & C.A.Clark Ann. Missouri Bot. Gard. 65: 1126. 1979. *Panicum acuminatum* var. *wrightianum* (Scribn.) C.F.Reed Phytologia 80: 284. 1996.

Note. Although recovered within the same clade as *D. leucothrix*, *D. wrightianum* forms a well-supported clade apart from the former species and shows consistent morphological differences (vegetative and inflorescence structure) that can be used to distinguish the two taxa. Thus, we disagree with Zuloaga and Morrone (2003) in placing this taxon in synonymy with *D. acuminatum* var. *longiligulatum* (=*D. leucothrix* ssp. *longiligulatum*, here) or *D. leucothrix*, as in Hansen and Wunderlin (1988).

Dichanthelium xanthophysum **(A.Gray) Freckmann Phytologia 39: 271. 1978.** *Panicum xanthophysum* A.Gray N. Amer. Gram. 1, no. 28. 1834.

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Appendix

Samples used in this study are shown below. Data fields, respectively, include taxon, voucher (institution of deposition), country of origin, state of origin (where available), data source (Sanger, Illumina, or GenBank), GBSSI GenBank accession, ITS GenBank accession, and *rpl32-trnL* GenBank accession. Missing information is denoted by a hyphen. Herbarium acronyms follow Thiers (2023).

Outgroups

Adenochloa adenophora: *Banda 3504* (NY), -, -, Sanger, OP106659, OP079984, OP094353; *Coleataenia anceps*: *Majure 5317* (FLAS), USA, MS, Sanger, OP106775, OP080110, OP094470; *Echinochloa* sp.: -, -, -, GenBank, AB668987, AM404346, KR822685; *P. dichotomiflorum*: *Majure 4157* (FLAS), USA, FL, Sanger, OP106722, OP080056, OP094416; *P. miliaceum*: -, -, -, GenBank, GU199266, MF029722, CM009689; *P. trichoides*: *Guedes 7005* (NY), Brazil, Bahia, Sanger, -, OP080009, -; *Setaria italica*: -, -, -, GenBank, KF372879, KM051455, MK348605.

Ingroups

Dichanthelium aciculare ssp. *aciculare*: *Abbott 24400* (FLAS), USA, FL, Sanger, OP106627, OP079949, OP094321; *Majure 4799* (FLAS), USA, MS, Sanger, OP106725, OP080059, OP094419; *Majure 4811* (FLAS), USA, FL, Sanger, OP106727, OP080061, OP094421; *Majure 4817* (FLAS), USA, FL, Sanger, OP106731, OP080065, OP094425; *Majure 5015* (DES), USA, FL, Sanger, OP106747, OP080081, OP094441; *Majure 5321* (DES), USA, MS, Sanger, OP106776, OP080111, OP094471; *D. aciculare* ssp. *angustifolium*: *Abbott 24431* (FLAS), USA, FL, Sanger, OP106628, OP079950, OP094322; *Majure 3750* (FLAS), USA, MS, Sanger, OP106716, OP080050, OP094410; *Majure 5311* (DES), USA, MS, Sanger, OP106770, OP080105, OP094465; *Majure 5338* (FLAS), USA, MS, Sanger, OP106782, OP080117, OP094476; *Majure 7708* (FLAS), USA, FL, Illumina, -, OP080131, OP094490; *Naczi 14785* (NY), USA, MD, Sanger, OP106802, OP080142, -; *D. aciculare* ssp. *fusiforme*: *Naczi 15257* (NY), Belize, Cayo, Sanger, OP106811, OP080151, OP094510; *Naczi 16367* (NY), Belize, Orange Walk, Sanger, OP106839, OP080178, OP094538; *D. aciculare* ssp. *neuranthum*: *Majure 3060* (FLAS), USA, FL, Sanger, OP106706, OP080040, OP094400; *D. aciculare* ssp. *neuranthum* = *pinetorum*: *Harriman 13566* (FLAS), USA, FL, Sanger, OP106680, OP080012, OP094378; *Workman* s.n. (FLAS), USA, FL, Sanger, OP106888, OP080232, OP094582; *D. acuminatum* ssp. *acuminatum*: *Majure 2676* (FLAS), USA, FL, Sanger, OP106701, OP080035, OP094395; *Majure 4813* (FLAS), USA, FL, Sanger, OP106729, OP080063, OP094423; *Majure 4816* (FLAS), USA, FL, Sanger, OP106730, OP080064, OP094424; *Majure 5230* (FLAS), USA, FL, Sanger, OP106759, OP080094, OP094454; *Majure 5998* (DES, FLAS), Dominican Republic, Independencia, Sanger, OP106789, OP080124, OP094483; *Naczi 14783* (NY), USA, MD, Sanger, OP106801, OP080141, OP094501; *D. acuminatum* ssp. *fasciculatum*: *Abbott 26793* (SIU), USA, IL, Sanger, OP106633, OP079955, OP094327; *Abbott 26799* (SIU), USA, IL, Sanger, OP106637, OP079959, OP094331; *Abbott 26806* (SIU), USA, IL, Sanger, OP106642, OP079964, OP094336; *Abbott 26812* (NY), USA, KY, Sanger, OP106646, OP079968, OP094340; *Abbott 26833* (SIU), USA, KY, Sanger, OP106652, OP079974, OP094346; *Abbott 26834* (SIU), USA, KY, Sanger, OP106653, OP079975, OP094347; *Heim 225* (SIU), USA, IL, Sanger, OP106681, OP080014, -; *Heineke 1648* (SIU), USA, IL, Sanger, OP106684, OP080017, OP094382; *Honu YAK78* (SIU), USA, IL, Sanger, OP106689, OP080022, OP094385; *Ketzner 333* (SIU), USA, IL, Sanger, OP106692, OP080025, -; *Majure 5167* (DES), USA, GA, Sanger, OP106756, OP080091, OP094451; *Naczi 13733* (NY), USA, NY, Sanger, OP106799, OP080139, OP094499; *Naczi 15545* (NY), USA, NY, Sanger, OP106833, OP080173, OP094532; *Nickrent 6025* (SIU), USA, IL, Sanger, OP106843, OP080182, OP094542; *Nickrent 6123* (SIU), USA, IL, Sanger, OP106848, OP080187, OP094547; *Nickrent 6158* (SIU), USA, IL, Sanger, OP106850, OP080189, OP094549; *Nickrent 6188* (SIU), USA, IL, Sanger, OP106855, OP080194, OP094554; *Nickrent 6189* (SIU), USA, IL, Sanger, OP106856, OP080195, OP094555; *Shildneck 9564* (SIU), USA, IL, Sanger, OP106865, OP080206, -; *Shildneck 9782* (SIU), USA, IL, Sanger, OP106866, OP080207, -; *D. acuminatum* ssp. *implicatum*: *Heineke 3300* (SIU), USA, IL, Sanger, OP106686, OP080019, -; *Naczi 15541* (NY), USA, NJ, Sanger, OP106830, OP080170, OP094529; *D. acuminatum* ssp. *leucothrix*: *Majure 5014* (DES), USA, FL, Sanger, OP106746, OP080080, OP094440; *Naczi 15258* (NY), Belize, Cayo, Sanger, OP106812, OP080152, OP094511; *Naczi 15313* (NY), Belize, Toledo, Sanger, OP106815, OP080155, OP094514; *Naczi 15317* (NY), Belize, Toledo, Sanger, OP106816, OP080156, OP094515; *Wiley 462A* (SIU), Belize, Cayo, Sanger, OP106880, OP080224, -; *D. acuminatum* ssp. *lindheimeri*: *Abbott 26838* (NY), USA, IL, Sanger, OP106655, OP079977, -; *Carr 30844* (TEX), USA, TX, Sanger, OP106666, OP079997, OP094364; *Majure 1593* (MMNS), USA, MS, Sanger, OP106698, OP080032, OP094392; *Majure 5302* (FLAS), USA, MS, Sanger, OP106765, OP080100, OP094460; *Majure 5330* (DES), USA, MS, Sanger, OP106780, OP080115, OP094474; *Majure 5333* (DES), USA, MS, Sanger, OP106781, OP080116, OP094475; *D. acuminatum* ssp. *longiligulatum*: *Naczi 15279* (NY), Belize, Toledo, Sanger, OP106814, OP080154, OP094513; *Naczi 16110* (NY), Belize, Cayo, Sanger, OP106838, -, OP094537; *D. acuminatum* ssp. *spretum*: *Naczi 14794* (NY), USA, MD, Sanger, OP106803, OP080143, OP094502; *Naczi 15536* (NY), USA, NJ, Sanger, OP106827, OP080167, OP094526; *D. acuminatum* ssp. *thermale*: *Beetle 16034* (FLAS), USA, WY, Sanger, OP106662, OP079988, OP094355; *D. aequivaginatum*: *Mori 13309* (NY), Brazil, Bahia, Illumina, -, OP080136, OP094496; *D. boreale*: *Cusick 28166* (NY), USA, OH, Sanger, OP106669, OP080000, OP094367; *Naczi 11905* (NY), USA, PA, Sanger, OP106797, OP080137, OP094497; *D. boscii*: *Abbott 26060* (UAM), USA, VA, Sanger, OP106631, OP079953, OP094325; *Abbott 26792* (SIU), USA, IL, Sanger, OP106632, OP079954, OP094326; *Garcia 4474* (FLAS), USA, AL, Sanger, OP106675, OP080006, OP094373; *Majure 3211* (FLAS), USA, FL, Sanger, OP106711, OP080045, OP094405; *Majure 3767* (FLAS), USA, MS, Sanger, OP106717, OP080051, OP094411; *Majure 5161* (FLAS), USA, GA, Sanger, OP106753, OP080088, OP094448; *Majure 5346* (FLAS), USA, MS, Sanger, OP106788, OP080123, OP094482; *Nickrent 6028* (SIU), USA, IL, Sanger, OP106845, OP080184, OP094544; *Nickrent 6185* (SIU), USA, IL, Sanger, OP106852, OP080191, OP094551; *Whitten 4353* (FLAS), USA, AL, Sanger, OP106876, OP080220, -; *D. chamaelonche* ssp. *breve*: *Huck 4036* (FLAS), USA, FL, Sanger, OP106690, OP080023, -; *D. chamaelonche* ssp. *chamaelonche*: *Abbott 22489* (FLAS), USA, FL, Sanger, OP106620, OP079942, OP094314; *Abbott 24515* (FLAS), USA, FL, Sanger, OP106629, OP079951, OP094323; *Majure 2774* (FLAS), USA, FL, Sanger, OP106702, OP080036, OP094396; *Majure 4926* (FLAS), USA, FL, Sanger, OP106738, OP080072, OP094432; *Majure 5011* (DES), USA, FL, Sanger, OP106744, OP080078, OP094438; *Naczi 15372* (NY), Belize, Belize, Sanger, OP106821, OP080161, OP094520; *D. clandestinum*: *Beyerl* s.n. (SIU), USA, IL, Sanger, OP106663, OP079989, OP094356; *Denton 448* (BEREA (EKY)), USA, KY, Sanger, OP106671, OP080002, OP094369; *Heineke 3428* (SIU), USA, IL, Sanger, OP106687, OP080020, OP094383; *Majure 1055* (MMNS, MISSA), USA, MS, Sanger, OP106695, OP080029, OP094389; *Majure 5300* (FLAS), USA, MS, Sanger, OP106763, OP080098, OP094458; *Naczi 14801* (NY), USA, MD, Sanger, OP106805, OP080145, OP094504; *Naczi 15549* (NY), USA, NY, Sanger, OP106836, OP080176, OP094535; *Utech 79-309* (SIU), USA, PA, Sanger, OP106873, OP080215, OP094569; *Whitten 4425* (FLAS), USA, VA, Sanger, OP106877, OP080221, -; *D. commutatum* ssp. *ashei*: *Abbott 26835* (SIU), USA, KY, Sanger, OP106654, OP079976, OP094348; *Naczi 15533* (NY), USA, NJ, Sanger, OP106825, OP080165, OP094524; *Whitten 4620* (FLAS), USA, AL, Sanger, OP106878, OP080222, OP094573; *D. commutatum* ssp. *commutatum*: *Athey* s.n. (SIU), USA, FL, Sanger, OP106658, OP079982, -; *Majure 5104* (DES), USA, FL, Sanger, OP106750, OP080085, OP094445; *D. commutatum* ssp. *commutatum = mutabile*: *Majure 4870* (FLAS), USA, FL, Sanger, OP106734, OP080068, OP094428; *D. commutatum* ssp. *equilaterale*: *Majure 4240* (FLAS), USA, FL, Sanger, OP106723, OP080057, OP094417; *Majure 4853* (FLAS), USA, FL, Sanger, OP106733, OP080067, OP094427; *D. commutatum* ssp. *joorii*: *Carr 30934* (NY, TEX, MO), USA, TX, Sanger, OP106667, OP079998, OP094365; *Majure 3713* (FLAS), USA, FL, Sanger, OP106715, OP080049, OP094409; *Majure 4871* (FLAS), USA, FL, Sanger, OP106735, OP080069, OP094429; *Majure 4925* (FLAS), USA, FL, Sanger, OP106737, OP080071, OP094431; *Majure 4935* (FLAS), USA, FL, Sanger, OP106743, OP080077, OP094437; *Majure 5344* (FLAS), USA, MS, Sanger, OP106786, OP080121, OP094480; *Mercurio 107* (FLAS), USA, FL, Sanger, OP106794, OP080134, OP094493; *D. consanguineum*: *Majure 8266* (FLAS), USA, MS, Illumina, -, OQ539626, OQ472797; *D. cynodon*: *Wood 16255* (FLAS, PTBG), USA, HI, Sanger, OP106884, OP080228, OP094578; *Wood 16280* (FLAS, PTBG), USA, HI, Sanger, OP106885, OP080229, OP094579; *D. depauperatum*: *Abbott 26796* (SIU), USA, IL, Sanger, OP106634, OP079956, OP094328; *Abbott 26846* (NY), USA, MO, Sanger, OP106657, OP079979, OP094350; *Majure 3263* (FLAS), USA, MI, Sanger, OP106712, OP080046, OP094406; *Majure 3769* (FLAS), USA, MS, Sanger, OP106719, OP080053, OP094413; *Naczi 14832* (NY), USA, DE, Sanger, OP106809, OP080149, OP094508; *Naczi 15438* (NY), USA, NY, Sanger, OP106823, OP080163, OP094522; *D. dichotomum* ssp. *dichotomum*: *Abbott 26801* (SIU), USA, IL, Sanger, OP106639, OP079961, OP094333; *Basinger 3333* (SIU), USA, IL, Sanger, OP106661, OP079986, -; *Majure 5162* (DES), USA, GA, Sanger, OP106754, OP080089, OP094449; *Naczi 15546* (NY), USA, NY, Sanger, OP106834, OP080174, OP094533; *Nickrent 6187* (SIU), USA, IL, Sanger, OP106854, OP080193, OP094553; *D. dichotomum* ssp. *lucidum*: *Majure 5306* (DES), USA, MS, Sanger, OP106768, OP080103, OP094463; *Majure 5324* (DES), USA, MS, Sanger, OP106778, OP080113, OP094473; *Naczi 14824* (NY), USA, MD, Sanger, OP106807, OP080147, OP094506; *Thomas 112844* (FLAS), USA, AR, Sanger, OP106869, OP080211, OP094565; *D. dichotomum* ssp. *mattamuskeetense*: *Naczi 14830* (NY), USA, MD, Sanger, OP106808, OP080148, OP094507; *D. dichotomum* ssp. *microcarpon*: *Abbott 22849* (FLAS), USA, FL, Sanger, OP106624, OP079946, OP094318; *Abbott 24399* (FLAS), USA, FL, Sanger, OP106626, OP079948, OP094320; *Abbott 26807* (NY), USA, KY, Sanger, OP106643, OP079965, OP094337; *Abbott 26819* (SIU), USA, KY, Sanger, OP106648, OP079970, OP094342; *Basinger 2598* (SIU), USA, IL, Sanger, OP106660, OP079985, -; *Garcia 4439* (FLAS), USA, AL, Sanger, OP106673, OP080004, OP094371; *Longbottom 19568* (NY), USA, MD, Sanger, OP106693, OP080027, -; *Majure 5166* (DES), USA, GA, Sanger, OP106755, OP080090, OP094450; *Majure 5301* (DES), USA, MS, Sanger, OP106764, OP080099, OP094459; *Majure 5309* (FLAS), USA, MS, Sanger, OP106769, OP080104, OP094464; *Nickrent 6030* (SIU), USA, IL, Sanger, OP106846, OP080185, OP094545; *Nickrent 6157* (SIU), USA, IL, Sanger, OP106849, OP080188, OP094548; *Whitten 4248* (FLAS), USA, AL, Sanger, OP106875, OP080219, OP094572; *D. dichotomum* ssp. *nitidum*: *Abbott 24576* (FLAS), USA, FL, Sanger, OP106630, OP079952, OP094324; *Majure 3034* (FLAS), USA, FL, Sanger, OP106703, OP080037, OP094397; *Majure 3057* (FLAS), USA, FL, Sanger, OP106705, OP080039, OP094399; *Naczi 15543* (NY), USA, NJ, Sanger, OP106831, OP080171, OP094530; *D. dichotomum* ssp. *roanokense*: *Majure 3105* (FLAS), USA, FL, Sanger, OP106709, OP080043, OP094403; *D. dichotomum* ssp. *roanokense* = *hirstii*: *Walz 2016-04* (FLAS), USA, GA, Sanger, -, OP080216, OP094570; *D. dichotomum* ssp. *yadkinense*: *Abbott 26802* (SIU), USA, IL, Sanger, OP106640, OP079962, OP094334; *Naczi 15532* (NY), USA, DE, Sanger, OP106824, OP080164, OP094523; *D. ensifolium* ssp. *curtifolium*: *Majure 2214* (FLAS), USA, MS, Sanger, OP106699, OP080033, OP094393; *Majure 3140* (FLAS), USA, MS, Sanger, OP106710, OP080044, OP094404; *Majure 5315* (DES), USA, MS, Sanger, OP106774, OP080109, OP094469; *D. ensifolium* ssp. *ensifolium*: *Davis 693* (FLAS), USA, FL, Sanger, OP106670, OP080001, OP094368; *Majure 3879* (FLAS), USA, FL, Sanger, OP106721, OP080055, OP094415; *Majure 7695* (FLAS), USA, MS, Illumina, -, OP080128, OP094487; *Naczi 14798* (NY), USA, MD, Sanger, OP106804, OP080144, OP094503; *D. erectifolium*: *Abbott 22560* (FLAS), USA, FL, Sanger, OP106622, OP079944, OP094316; *Mercurio 106* (FLAS), USA, FL, Sanger, OP106793, OP080133, OP094492; *Naczi 15339* (NY), Belize, Belize, Sanger, OP106817, OP080157, OP094516; *Naczi 15375* (NY), Belize, Belize, Sanger, OP106822, OP080162, OP094521; *Majure 7696* (FLAS), USA, MS, Illumina, -, OP080129, OP094488; *D. hillebrandianum*: *Wood 16244* (FLAS, PTBG), USA, HI, Sanger, OP106882, OP080226, OP094576; *Wood 16281* (FLAS, PTBG), USA, HI, Sanger, OP106886, OP080230, OP094580; *D. isachnoides*: *Wood 16254* (FLAS, PTBG), USA, HI, Sanger, OP106883, OP080227, OP094577; *Wood 16282* (FLAS, PTBG), USA, HI, Sanger, OP106887, OP080231, OP094581; *D. koolauense*: *Oppenheimer H91111* (FLAS), USA, HI, Sanger, OP106858, OP080197, OP094557; *Becker* s.n. (FLAS), USA, HI, Illumina, -, OP079987, OP094354; *D. latifolium*: *Garcia 4517* (FLAS), USA, VA, Sanger, OP106676, OP080007, OP094374; *Hill 32488* (USF, ILLS), USA, IL, Sanger, OP106688, OP080021, OP094384; *Naczi 15544* (NY), USA, NY, Sanger, OP106832, OP080172, OP094531; *Shildneck 3722* (SIU), USA, IL, Sanger, OP106863, OP080204, -; *D. laxiflorum*: *Abbott 20221* (FLAS), USA, FL, Sanger, OP106619, OP079941, OP094313; *Abbott 26798* (SIU), USA, IL, Sanger, OP106636, OP079958, OP094330; *Abbott 26808* (NY), USA, KY, Sanger, OP106644, OP079966, OP094338; *Abbott 26811* (SIU), USA, KY, Sanger, OP106645, OP079967, OP094339; *Garcia 4437* (FLAS), USA, AL, Sanger, OP106672, OP080003, OP094370; *Judd 4883* (FLAS), Haiti, -, Sanger, OP106691, OP080024, OP094386; *Majure 4801* (FLAS), USA, MS, Sanger, OP106726, OP080060, OP094420; *Majure 5019* (DES), USA, FL, Sanger, -, OP080084, OP094444; *Majure 5328* (DES), USA, MS, Sanger, OP106779, OP080114, -; *Majure 5345* (DES), USA, MS, Sanger, OP106787, OP080122, OP094481; *Majure 6019* (DES), USA, TX, Sanger, OP106790, OP080125, OP094484; *Nickrent 6122* (SIU), USA, IL, Sanger, OP106847, OP080186, OP094546; *Nickrent 6190* (SIU), USA, IL, Sanger, OP106857, OP080196, OP094556; *D. leibergii*: *Gunn 2459* (FLAS), USA, IA, Sanger, OP106679, OP080011, OP094377; *Heim 128* (SIU), USA, IL, Sanger, -, OP080013, OP094379; *Heim 612* (SIU), USA, IL, Sanger, OP106682, OP080015, OP094380; *Moran 753* (SIU), USA, WI, Sanger, OP106796, -, OP094495; *Shildneck 9295* (SIU), USA, IL, Sanger, OP106864, OP080205, -; *D. linearifolium*: *Majure 3816* (FLAS), USA, WV, Sanger, OP106720, OP080054, OP094414; *Naczi 15548* (NY), USA, NY, Sanger, OP106835, OP080175, OP094534; *D. malacophyllum*: *Abbott 26822* (NY), USA, IL, Sanger, OP106649, OP079971, OP094343; *Heineke 1373* (SIU), USA, IL, Sanger, OP106683, OP080016, OP094381; *Majure 3281* (FLAS), USA, TN, Sanger, OP106713, OP080047, OP094407; *Nickrent 6159* (SIU), USA, IL, Sanger, OP106851, OP080190, OP094550; *D. nudicaule*: *Wieland 7727* (MMNS), USA, MS, Sanger, OP106879, OP080223, OP094574; *Carr 6584* (FLAS), USA, FL, Illumina, -, OP079995, OP094362; *Orzell 19561* (FLAS), USA, MS, Illumina, -, OP080198, OP094558; *D. oligosanthes* ssp. *oligosanthes*: *Majure 4929* (FLAS), USA, FL, Sanger, OP106739, OP080073, OP094433; *Majure 5314* (DES), USA, MS, Sanger, OP106773, OP080108, OP094468; *D. oligosanthes* ssp. *scribnerianum*: *Heineke 3269* (SIU), USA, IL, Sanger, OP106685, OP080018, -; *Naczi 15551* (NY), USA, NY, Sanger, OP106837, OP080177, OP094536; *D. oligosanthes* ssp. *scribnerianum* = *helleri*: *Majure 6837* (FLAS), USA, MO, Illumina, -, OQ539627, OQ472798; *D. ovale* ssp. *ovale*: *Majure 4875* (FLAS), USA, FL, Sanger, OP106736, OP080070, OP094430; *Majure 4932* (FLAS), USA, FL, Sanger, OP106740, OP080074, OP094434; *D. ovale* ssp. *pseudopubescens*: *Naczi 15534* (NY), USA, NJ, Sanger, OP106826, OP080166, OP094525; *D. ovale* ssp. *villosissimum*: *Abbott 26800* (SIU), USA, IL, Sanger, OP106638, OP079960, OP094332; *Abbott 26827* (SIU), USA, KY, Sanger, OP106651, OP079973, OP094345; *Majure 1112* (MMNS, MISSA), USA, MS, Sanger, OP106696, OP080030, OP094390; *Majure 5312* (FLAS), USA, MS, Sanger, OP106771, OP080106, OP094466; *Majure 5340* (FLAS), USA, MS, Sanger, OP106783, OP080118, OP094477; *Naczi 14807A* (NY), USA, MD, Sanger, OP106806, OP080146, OP094505; *D. pedicellatum*: *Majure 3606* (FLAS), USA, TX, Sanger, OP106714, OP080048, OP094408; *D. perlongum*: *Curtis* s.n. (FLAS), USA, IL, Sanger, OP106668, OP079999, OP094366; *D. polyanthes*: *Abbott 26797* (SIU), USA, IL, Sanger, OP106635, OP079957, OP094329; *Abbott 26817* (NY), USA, KY, Sanger, OP106647, OP079969, OP094341; *Garcia 4440* (FLAS), USA, AL, Sanger, OP106674, OP080005, OP094372; *Longbottom 19954* (NY), USA, MD, Sanger, OP106694, OP080028, OP094388; *Majure 3768* (FLAS), USA, MS, Sanger, OP106718, OP080052, OP094412; *Nickrent 6186* (SIU), USA, IL, Sanger, OP106853, OP080192, OP094552; *Thompson 01-115* (BEREA (EKY)), USA, KY, Sanger, OP106870, OP080212, OP094566; *Thompson 15-404* (BEREA (EKY)), USA, KY, Sanger, OP106871, OP080213, OP094567; *Whitten 4247* (FLAS), USA, AL, Sanger, OP106874, OP080218, -; *D. portoricense* ssp. *patulum*: *Majure 4242* (FLAS), USA, FL, Sanger, OP106724, OP080058, OP094418; *Majure 4934* (FLAS), USA, FL, Sanger, OP106742, OP080076, OP094436; *Majure 5229* (DES), USA, FL, Sanger, OP106758, OP080093, OP094453; *Naczi 15368* (NY), Belize, Belize, Sanger, OP106819, OP080159, OP094518; *Naczi 15371* (NY), Belize, Belize, Sanger, OP106820, OP080160, OP094519; *Naczi 16387* (NY), Belize, Orange Walk, Sanger, OP106841, OP080180, OP094540; *D. portoricense* ssp. *patulum = webberianum*: *Abbott 22490* (FLAS), USA, FL, Sanger, OP106621, OP079943, OP094315; *Majure 3098* (FLAS), USA, FL, Sanger, OP106708, OP080042, OP094402; *D. portoricense* ssp. *portoricense*: *Abbott 22638* (FLAS), USA, FL, Sanger, OP106623, OP079945, OP094317; *Majure 4812* (FLAS), USA, FL, Sanger, OP106728, OP080062, OP094422; *Majure 5016* (DES), USA, FL, Sanger, OP106748, OP080082, OP094442; *Majure 5017* (DES), USA, FL, Sanger, OP106749, OP080083, OP094443; *D. pycnoclados*: *Laegaard 18479* (NY), Ecuador, -, Illumina, -, OP080026, OP094387; *D. ravenelii*: *Abbott 26826* (SIU), USA, KY, Sanger, OP106650, OP079972, OP094344; *Carr 30843* (TEX), USA, TX, Sanger, OP106665, OP079996, OP094363; *Majure 5313* (DES), USA, MS, Sanger, OP106772, OP080107, OP094467; *Majure 5342* (DES), USA, MS, Sanger, OP106785, OP080120, OP094479; *Philley 567* (FLAS), USA, MS, Sanger, OP106860, OP080200, OP094560; *Schwegman 1916* (SIU), USA, IL, Sanger, OP106862, OP080203, OP094563; *D. sabulorum* var. *polycladum*: *Bonifacino 6856* (FLAS, MVFA), Uruguay, -, Illumina, -, OP079990, OP094357; *Bonifacino 6872* (FLAS, MVFA), Uruguay, -, Illumina, -, OP079992, OP094359; *D. sabulorum* var. *sabulorum*: *Bonifacino 6859* (FLAS, MVFA), Uruguay, -, Illumina, -, OP079991, OP094358; *Bonifacino 6897* (FLAS, MVFA), Uruguay, -, Illumina, -, OP079993, OP094360; *Rosengurtt 11329* (NY), Uruguay, Canelones, Illumina, -, OP080202, OP094562; *Silva 24158* (NY), -, -, Illumina, -, OP080208, OP094564; *D. scabriusculum*: *Majure 5231* (FLAS), USA, FL, Sanger, OP106760, OP080095, OP094455; *Majure 5305* (DES), USA, MS, Sanger, OP106767, OP080102, OP094462; *Majure 5323* (FLAS), USA, MS, Sanger, OP106777, OP080112, OP094472; *Mercurio 116* (FLAS), USA, FL, Sanger, OP106795, OP080135, OP094494; *Naczi 15537* (NY), USA, NJ, Sanger, OP106828, OP080168, OP094527; *Proenza 426* (FLAS), USA, FL, Sanger, OP106861, OP080201, OP094561; *D. sciurotis*: *Anderson 35542* (NY), Brazil, Minas Gerais, Illumina, -, OP079980, OP094351; *D. scoparium*: *Majure 5276* (FLAS), USA, FL, Sanger, OP106761, OP080096, OP094456; *Majure 5304* (FLAS), USA, MS, Sanger, OP106766, OP080101, OP094461; *Majure 6027* (FLAS), Dominican Republic, La Vega, Sanger, OP106791, OP080126, OP094485; *Majure 6051* (FLAS), Dominican Republic, Monseñor Nouel, Sanger, OP106792, OP080127, OP094486; *Naczi 14942* (NY), USA, NJ, Sanger, OP106810, OP080150, OP094509; *Philley 557* (FLAS), USA, MS, Sanger, OP106859, OP080199, OP094559; *Slaughter 1462* (SIU), USA, LA, Sanger, OP106867, OP080209, -; *Thompson 15-405* (BEREA (EKY)), USA, KY, Sanger, OP106872, OP080214, OP094568; *Wilson 1533* (SIU), USA, IL, Sanger, OP106881, OP080225, OP094575; *D. sphaerocarpon*: *Abbott 26805* (SIU), USA, IL, Sanger, OP106641, OP079963, OP094335; *Abbott 26845* (NY), USA, MO, Sanger, OP106656, OP079978, OP094349; *Majure 1465* (MMNS), USA, MS, Sanger, OP106697, OP080031, OP094391; *Majure 5297* (FLAS), USA, AL, Sanger, OP106762, OP080097, OP094457; *Majure 5341* (DES), USA, MS, Sanger, OP106784, OP080119, OP094478; *D. strigosum* ssp. *glabrescens*: *Majure 5109* (DES), USA, FL, Sanger, OP106752, OP080087, OP094447; *Naczi 15343* (NY), Belize, Belize, Sanger, OP106818, OP080158, OP094517; *D. strigosum* ssp. *leucoblepharis*: *Majure 3067* (FLAS), USA, FL, Sanger, OP106707, OP080041, OP094401; *D. surrectum*: *Anderson 36397* (NY), Brazil, Minas Gerais, Illumina, -, OP079981, OP094352; *D. tenue*: *Abbott 22861* (FLAS), USA, FL, Sanger, OP106625, OP079947, OP094319; *Majure 3042* (FLAS), USA, FL, Sanger, OP106704, OP080038, OP094398; *Majure 4819* (FLAS), USA, FL, Sanger, OP106732, OP080066, OP094426; *Majure 5012* (DES), USA, FL, Sanger, OP106745, OP080079, OP094439; *Majure 5107* (DES), USA, FL, Sanger, OP106751, OP080086, OP094446; *Majure 5227* (DES), USA, FL, Sanger, OP106757, OP080092, OP094452; *Majure 7699* (FLAS), USA, MS, Illumina, -, OP080130, OP094489; *D. viscidellum*: *Naczi 15268* (NY), Belize, Cayo, Sanger, OP106813, OP080153, OP094512; *D. wilcoxianum*: *Nelson 8761* (FLAS), USA, WY, Sanger, OP106842, OP080181, OP094541; *Sutherland 5634* (NY), USA, NE, Sanger, OP106868, OP080210, -; *D. wrightianum*: *Gulledge 340* (FLAS), USA, FL, Sanger, OP106678, OP080010, OP094376; *Majure 2585* (MMNS, MISSA), USA, MS, Sanger, OP106700, OP080034, OP094394; *Naczi 16375* (NY), Belize, Orange Walk, Sanger, OP106840, OP080179, OP094539; *Majure 8025* (FLAS), USA, FL, Illumina, -, OP080132, OP094491; *D. xanthophysum*: *Ballard 810399* (FLAS), USA, MI, Illumina, -, OP079983, -; *Boufford 22941* (NY), USA, VT, Sanger, OP106664, OP079994, OP094361.

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