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Molecular and Taxonomic Reevaluation of the *Digitaria filiformis* Complex (Poaceae), Including a Globally Extinct, Single-Site Endemic from New Hampshire, USA, and a New Species from Mexico

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Abstract—We examine the *Digitaria filiformis* complex to determine the proper taxonomic rank and conservation status of each member. The taxonomy of the *D. filiformis* complex is debated and includes two widespread taxa, *D. filiformis* var. *filiformis* and *D. filiformis* var. *villosa*; a rare taxon of southern Florida and the West Indies, *D. filiformis* var. *dolichophylla*; and a possibly extinct taxon that supposedly is a single-site endemic in New Hampshire, USA, *D. filiformis* var. *laeviglumis.* We conducted molecular analyses and morphologic comparisons of the four members of the *D. filiformis* complex, together with specimens from Venezuela (morphology only) and Mexico purportedly identified as *D. filiformis* var. *laeviglumis*. Based on results of phylogenetic analyses of plastid and nuclear ITS sequences and morphologic comparisons, we elevated taxonomic ranks, recognizing four species in the *D. filiformis* complex, and circumscribe the Mexican species ***D. glabrifloris*** (sp. nov.). *Digitaria dolichophylla* is much rarer than previously recognized, moving from Secure Globally to Imperiled with extinction (G2). After research and field investigations, we changed the global rank of *D. laeviglumis* from Globally Historical (GH) to Globally Extinct (GX), as there is virtually no likelihood of rediscovery.

Keywords—Biogeography, Latin America, overcollection, phylogenetics, plastid and ribosomal DNA analyses, taxonomic rank.

Among the plant species most vulnerable to extinction are single-site endemics that naturally occur in a small geographic area, often in regions characterized by high biodiversity (Işik 2011; Pyšek et al. 2017; Humphreys et al. 2019; Knapp et al. 2021; Holz et al. 2022). In the United States and Canada these single-site endemics account for 64% of known plant extinctions (Knapp et al. 2021; Pouteau et al. 2021). Documenting the extinction of single-site endemics can be particularly challenging because of taxonomic uncertainty; often taxonomic rank cannot be determined because investigators have access to few and/or only historical specimens for morphological and genetic comparison (Knapp et al. 2021). Such is the case for the grass *Digitaria filiformis* (L.) Koeler var. *laeviglumis* (Fernald) Wipff, a purported single-site endemic from New Hampshire, USA (Fernald 1920; Wipff 2003; Haines 2011; NatureServe 2023; New Hampshire Natural Heritage Bureau 2023).

Digitaria filiformis var. *laeviglumis* is placed in the *D. filiformis* complex, with members distributed across the eastern United States, the West Indies, Mexico, and Central and South America (Wipff 2003; Haines 2011; Sánchez-Ken 2012; Vega and Rúgolo 2012; Institute for Regional Conservation 2020; NatureServe 2023). Members of the complex are annual or short-lived perennial grasses with synflorescences comprised of 1–7 raceme-like primary branches. Spikelets are appressed to the triquetrous branches. Lower lemmas and upper glumes are glabrous or with clavate hairs, and upper lemmas are dark brown to black when mature. Commonly known as the slender crabgrasses, the taxonomy of the *D. filiformis* complex has been debated (Fernald 1920; Henrard 1950; Wipff 1996), with Wipff (2003) most recently recognizing four morphologically distinct varieties of *D. filiformis* in the *Flora of North America* including *D. filiformis* var. *dolichophylla* (Henrard) Wipff, *D. filiformis* var. *filiformis*, *D. filiformis* var. *laeviglumis*, and *D. filiformis* var. *villosa* (Walter) Fernald. *Digitaria filiformis* var. *laeviglumis* is distinguished from the other three varieties by having glabrous, rather than pubescent, lower lemmas (Fernald 1920; Wipff 2003). Additional characteristics that distinguish *D. filiformis* var. *laeviglumis* from *D. filiformis* var. *filiformis* include a truncate, erose-dentate ligule and translucent upper glume (vs. *D. filiformis* var. *filiformis* with a prolonged, fimbriate-ciliate ligule and opaque upper glume). Notably, Knapp et al. (2021), applying their index of taxonomic uncertainty, described *D. filiformis* var. *laeviglumis* as "a taxon placed in synonymy by some authors, but the majority recognize it as distinct," raising the question of its correct taxonomic status, as well as the taxonomic status of the three other varieties of *D. filiformis.*

The type and supposedly sole known locality of *D. filiformis* var. *laeviglumis* is Rock Rimmon in Manchester, New Hampshire (Fig. 1; 42°59′57″N, 71°29′09″W), a small hill supporting a temperate ridge–cliff–talus system (Sperduto 2011) with a long history of recreational use (Eaton 2011). The ledgy prominence rises 30 m above the adjacent urban landscape and has a geology consisting mainly of Massabesic gneiss with pegmatite intrusions (Lyons et al. 1997). Last collected in 1931 by Fernald and Griscom (Table 1), 12 rare plant surveys conducted by the New Hampshire Natural Heritage Bureau between 1992 and 2021 have been unsuccessful in relocating *D. filiformis* var. *laeviglumis* at Rock Rimmon (New Hampshire

FIG. 1. A. Small portion of the human-trampled summit of Rock Rimmon with a view to the southeast of urban Manchester, New Hampshire, USA. B. View of Rock Rimmon from just beyond the southeast base of the prominence. Photographs taken by W. F. Nichols.

TABLE 1. Specimen collection records of *Digitaria laeviglumis* from Rock Rimmon (Manchester, New Hampshire, USA) identified by searching the following herbaria portals: Consortium of California Herbaria 2 (2021), Consortium of Midwest Herbaria (2021), Consortium of Northeastern Herbaria (2021), Consortium of Pacific Northwest Herbaria (2021), Global Biodiversity Information Facility (2021), Global Plants Database (2021), Integrated Digitized Biocollections (2021), National Autonomous University of Mexico (2021), Southeast Regional Network of Expertise and Collections (2021), Southwest Environmental Information Network (2021), Tropicos (2021), and Vascular Plants of Canada (2020). Herbarium acronyms follow Index Herbariorum (Thiers 2020). One collection, WVA 11741, was found incidentally by one of the authors at a university currently not a participant in digital consortia portals.

Date	Collector	Herbarium & No.
1901–9-11	Batchelder, F. W.	GH 00023526 (Holotype)
1901–9-11	Batchelder, F. W.	NEBC 00106486 (Isotype)
1901–9-11	Batchelder, F. W.	NEBC 00106487 (Isotype)
1901–9-11	Batchelder, F. W.	US 1299779 (Isotype)
1902–9-8	Batchelder, F. W.	NHA 565615
1902–9-8	Batchelder, F. W.	NHA 600737
1905–9-27	Batchelder, F. W.	VT 109768
1931–8-23	Weatherby, C. A. & L. Griscom	CONN 00040066
1931–8-27	Fernald, M. L. & L. Griscom	BRU 00013069
1931–8-27	Fernald, M. L. & L. Griscom	BSN 04646
1931–8-27	Fernald, M. L. & L. Griscom	CAN 159985
1931–8-27	Fernald, M. L. & L. Griscom	COLO 01457050
1931–8-27	Fernald, M. L. & L. Griscom	CONN 00040210
1931–8-27	Fernald, M. L. & L. Griscom	DAO 000465660
1931–8-27	Fernald, M. L. & L. Griscom	DAO 000471493
1931–8-27	Fernald, M. L. & L. Griscom	GH 00354529
1931–8-27	Fernald, M. L. & L. Griscom	GH 00354530
1931–8-27	Fernald, M. L. & L. Griscom	GH 00354531
1931–8-27	Fernald, M. L. & L. Griscom	GH 00354532
1931–8-27	Fernald, M. L. & L. Griscom	GRCH 00003628
1931–8-27	Fernald, M. L. & L. Griscom	ISC-V-0011202
1931–8-27	Fernald, M. L. & L. Griscom	K 001056182
1931–8-27	Fernald, M. L. & L. Griscom	K 001056183
1931–8-27	Fernald, M. L. & L. Griscom	MACN 77263
1931–8-27	Fernald, M. L. & L. Griscom	MASS 359140
1931–8-27	Fernald, M. L. & L. Griscom	MASS 359141
1931–8-27	Fernald, M. L. & L. Griscom	MO 1636219
1931–8-27	Fernald, M. L. & L. Griscom	MUHW 030130
1931–8-27	Fernald, M. L. & L. Griscom	NEBC 00354529
1931–8-27	Fernald, M. L. & L. Griscom	NEBC 00354532
1931–8-27	Fernald, M. L. & L. Griscom	NHA 565614
1931–8-27	Fernald, M. L. & L. Griscom	LSU 0028299
1931–8-27	Fernald, M. L. & L. Griscom	PAC 0070108
1931–8-27	Fernald, M. L. & L. Griscom	PH 00011529
1931–8-27	Fernald, M. L. & L. Griscom	SEINet 19574
1931–8-27	Fernald, M. L. & L. Griscom	TENN-V-0018631
1931–8-27	Fernald, M. L. & L. Griscom	WVA 11741
1931–8-27	Fernald, M. L. & L. Griscom	YU 252859

Natural Heritage Bureau 2023). Since 1931, it is likely that several less well documented searches were also made for the crabgrass at Rock Rimmon and other nearby open, rocky habitat. For example, between 1951 to 1977, Albion Hodgdon and Frederic Steele searched the site at least 12 times (Consortium of Northeastern Herbaria 2021; New Hampshire Natural Heritage Bureau 2023). It is very likely that these accomplished New England botanists were aware of the endemic crabgrass and repeatedly surveyed Rock Rimmon, knowing the importance of rediscovering the taxon.

Vega and Rúgolo (2005) described the discovery of *D. filiformis* var. *laeviglumis* in Venezuela based on the presence of glabrous spikelets. Sánchez-Ken (2019) later reported the variety from Mexico, noting minor differences between the type collection from Rock Rimmon and collections from Latin America in plant height, raceme-like branch number and lengths, spikelets, and leaf blades. A comparison of fruit characteristics described in Sánchez-Ken (2019) to those in the type description (Fernald 1920) also revealed important discrepancies in glume and lemma characteristics (Table 2), diagnostic characters in *Digitaria*. Given these morphological differences and their vastly disjunct distributions with disparate climates, we hypothesize that specimens from Mexico and Venezuela belong to distinct genetic lineages, likely representing one or more undescribed taxa closely allied with *D. filiformis*. Alternatively, but less likely, the plants in Latin America and New Hampshire belong to the same taxonomic entity, expressing broad phenotypic plasticity across a vastly disjunct distributional range.

Here we reevaluate the appropriate taxonomic rank and global conservation status of all members included in the *Digitaria filiformis* complex using a combination of molecular phylogenetic analyses, morphological comparisons, review of historical specimens, and targeted field surveys. For simplicity, we refer to the investigated taxa by their specific combinations, *Digitaria dolichophylla* Henrard, *Digitaria filiformis* (L.) Koeler, *Digitaria laeviglumis* Fernald, and *Digitaria villosa* Michx., henceforth.

MATERIALS AND METHODS

Taxon Sampling—We investigated the taxonomic status of all members of the *D. filiformis* complex by conducting molecular analyses of the four recognized varieties of the complex, as well as a specimen identified as *D. laeviglumis* from Mexico and another species, *D. sanguinalis* (L.) Scop. (Appendix 1). We broadly sampled the two widespread members of the complex, *D. filiformis* (n = 3; from LA, SC, and WV) and *D. villosa* (n = 3; from GA and NC) but were limited by material available at WVA (Appendix 1; Fig. 2). Despite our best efforts, we were unable to acquire a loan or receive a tissue sample for DNA extraction of the purported specimens of *D. laeviglumis* from Venezuela (Darwinian Institute of Botany, SI).

DNA Extraction, Library Preparation, and Sequencing—Leaf tissue was sampled from approximately 1 cm^2 of herbarium or silica dried tissue for each specimen (Appendix 1). A modified CTAB DNA extraction protocol was used, scaled to 0.1 × volume (Doyle and Doyle 1987). DNA extractions were run on a 1% agarose gel to check the degree of degradation. Extractions were then quantified using the Qubit Broad Range dsDNA assay (Thermo Fisher, Waltham, Massachusetts, USA) and diluted to 20 ng/μl in nanopure water for library preparation. Dual-indexed sequencing libraries were prepared with the SparQ DNA Frag & Library Kit (Quantabio, Beverly, Massachusetts, USA) following the manufacturer's protocol but with a 20 μl starting reaction volume. Libraries

TABLE 2. Cursory comparison of *Digitaria laeviglumis* glume and lemma characteristics between the New Hampshire type specimen description (Fernald 1920) and the taxon description from Mexico (Sánchez-Ken 2019).

Characteristic	New Hampshire Type Specimen Described in Fernald (1920)	Taxon Described in Sánchez-Ken (2019)
Upper glume length compared to spikelet	> 3/4	≤ 3/4
Midvein of upper glume	Prominent entire length	Lower portion usually not very prominent
Lower glume	Obsolete	Absent
Lower lemma venation pattern	± Equidistant	Inequidistant
Lower lemma vein number	5 or 7	7

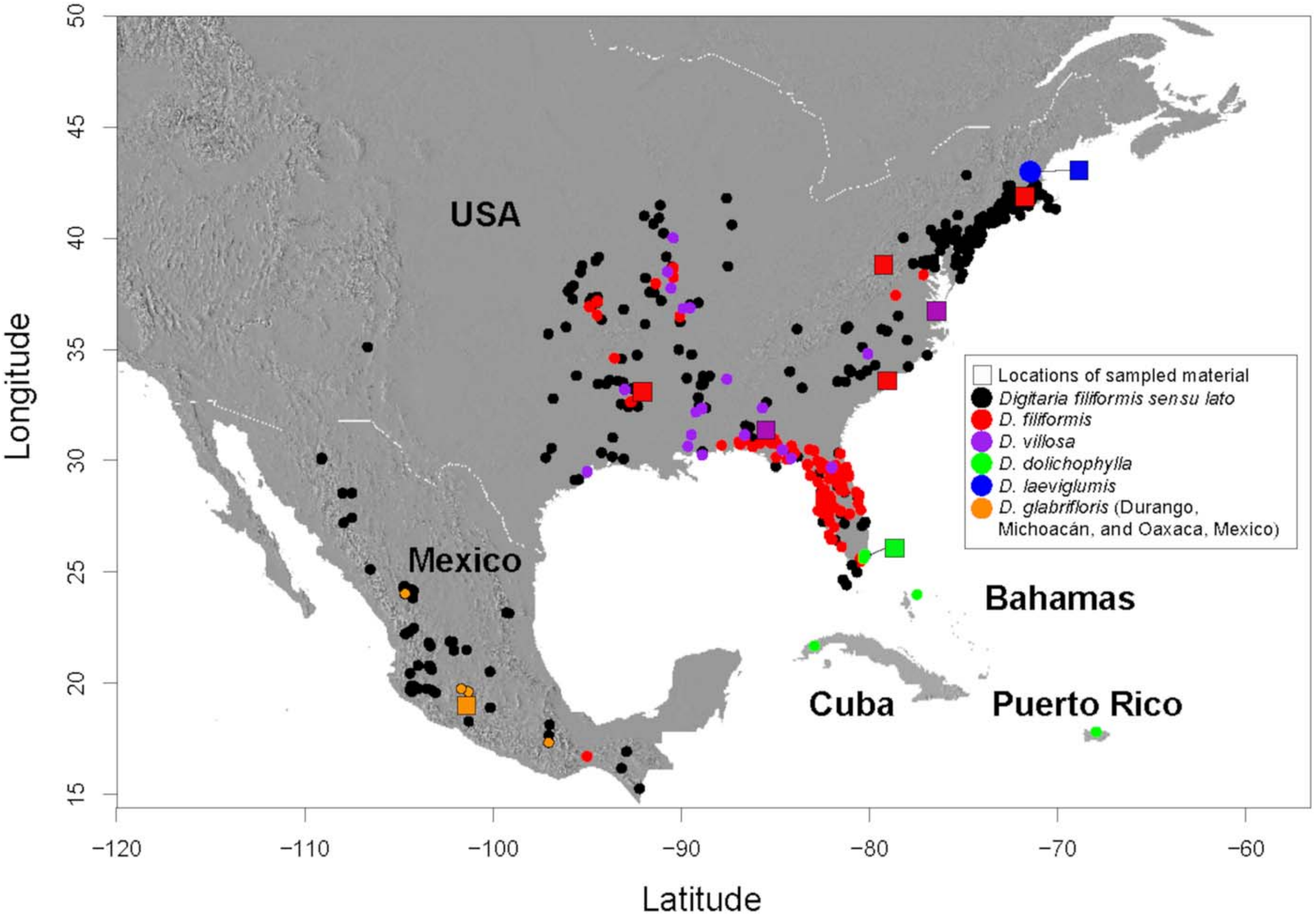


FIG. 2. Species distributions and locations of the molecular samples in the *Digitaria filiformis* complex together with *D. glabrifloris*, the new species mistaken for *D. laeviglumis* in two earlier publications (Vega and Rúgolo 2005; Sánchez-Ken 2019).

were quantified with the Qubit High Sensitivity dsDNA assay. Resulting libraries with low concentration (i.e. < 5 ng/μl) were amplified with the Kapa Library Amplification Kit (Roche, Basel, Switzerland) and re-quantified. Final libraries were pooled at equimolar ratios and the fragment size distribution was visualized on an Agilent Bioanalyzer (Agilent, Santa Clara, California, USA) and further quantified via quantitative PCR at the West Virginia University Genomics Core Facility. Pools of *Digitaria* libraries were sequenced on an Illumina NextSeq2000 (v.3 chemistry, 2 × 100 bp reads; Illumina, San Diego, California, USA) at the West Virginia University-Marshall University Shared Sequencing Facility with samples from another project.

Sequence Assembly—Plastid, mitochondrial, and ribosomal DNA (rDNA) reads were assembled using a custom genome assembly pipeline that conservatively trims reads, filters the resulting BAM alignments, and calls variants (Sinn et al. 2021; https://github.com/btsinn/ISSRseq/wiki). In addition to the newly sequenced accessions (Appendix 1), read sets were downloaded from the National Center for Biotechnology Information (NCBI) Sequence Read Archive for 15 *Digitaria* species and one accession of *Panicum virgatum* Muhl. as an outgroup taxon. We took this approach for two reasons. First was the difficulty in early attempts to assemble complete plastid and especially mitochondrial genomes with sequence data derived from herbarium tissues. Second was the lack of publicly available reference sequences (i.e. complete plastid and mitochondrial genomes) for *Digitaria* in NCBI GenBank. Briefly, all reads were trimmed, and adapters were removed via a sliding window with FASTP (Chen et al. 2018) using the following parameter values: "-w 16 –trim_poly_g –trim_poly_x -l 75 –cut_right." *Digitaria sanguinalis* was used as a reference plastid genome (NCBI GenBank accession OK637269, with one copy of the inverted repeat removed). To generate a rDNA reference sequence, we assembled a nearly complete rDNA sequence from trimmed reads of *D. sanguinalis* (WVA accession *Sieren-1016*, North Carolina, USA, 1972) using GetOrganelle v1.7.6.1 (Jin et al. 2020) using 50 iterations and SPAdes (v. 3.15.4) kmer values of 21, 31, 45, 65, and 85 (Prjibelski et al. 2020). The resulting reference rDNA sequence was 7547 bp in length. To generate a mitochondrial reference genome, we downloaded long read sequences (Pacific Biosciences) from *Digitaria exilis* Stapf NCBI accession SRX8771997 and conducted BLAST searches (maximum e-value 0.1, "hit vs. no hit") in Geneious v. 10 (http://www.geneious.com) against a custom database composed of the mitochondrial genomes of *Oryza sativa* L. and *Zea mays* L. (NCBI GenBank accessions JF281153 and OP832500, respectively). We then assembled the reads with positive BLAST hits de novo with FLYE (Kolmogorov et al. 2019), followed by ten rounds of error-correction with the original PacBio reads. This assembly resulted in five contigs corresponding to three plastid contigs and two mitochondrial contigs, as identified via the 'live annotation' feature in Geneious, using the same annotated *Oryza* and *Zea* accessions as above, with an 85% similarity threshold. The two mitochondrial contigs were 109,590 bp and 217,247 bp in length, respectively. Geneious was then used to detect repeat regions greater than 50 bp in the two mitochondrial contigs. One copy of each repeat was removed to avoid mapping redundancy downstream.

Trimmed read pairs were then mapped to the plastome, mitochondrial genome, and rDNA references with BBMAP v. 38.51 (https://jgi.doe.gov/data-and-tools/software-tools/bbtools/). The resulting bam alignment files were sorted with SAMTOOLS v. 1.7–13 (Li et al. 2009) and duplicate reads were removed with PICARD v. 2.22.8 (Broad Institute; http://broadinstitute.github.io/picard). Single nucleotide polymorphisms were called with GATK4 (Van der Auwera and O'Connor 2020), gVCF files were created with GATK HaplotypeCaller (Poplin et al. 2017), and the combined raw variant call (vcf) files were hard-trimmed with GATK SelectVariants following GATK best practices (Van der Auwera et al. 2013) specifying a haploid model. The resulting vcf files were converted to NEXUS format with vcf2phylip v. 2.7 (Ortiz 2019) and concatenated into a single alignment in Geneious. Voucher information and NCBI Sequence Read Archive BioSample accession numbers are provided in Appendix 1.

Phylogenetic Analyses—Phylogenetic analyses of the resulting concatenated single nucleotide polymorphic (SNP) matrix were conducted using maximum likelihood with IQ-TREE2 (Minh et al. 2020) and RAxML-NG (Kozlov et al. 2019). The best-fit model was calculated with ModelFinder in IQ-TREE 2 (Kalyaanamoorthy et al. 2017). IQ-TREE 2 analysis was conducted under the best-fit model (TVMe), allowing free rate heterogeneity among sites, and choosing 1000 ultrafast bootstrap pseudoreplicates. RAxML-NG analysis was conducted under a GTR+GAMMA model, with 25 rate categories, and using 1000 standard bootstrap pseudoreplicates. Trees and support values were visualized and edited with FigTree v. 1.4.4 (https://github.com/rambaut/figtree/releases) and Adobe Illustrator (Adobe Inc. 2019).

Morphological Examination—A stereoscopic microscope was used to examine specimens from Mexico collected in 2021 that were published as *D. filiformis* var. *laeviglumis* (Sánchez-Ken 2019) to compare against *D. laeviglumis* specimens (including the type specimen) collected in 1901 and 1931 from Rock Rimmon, Manchester, New Hampshire. Characters and structures examined included habit, life span, leaves, stems, synflorescence, and spikelets. We also examined a high-resolution digital image of the Venezuelan specimen published as *D. filiformis* var. *laeviglumis* (Vega and Rúgolo 2005; Fig. 3).

Assessing Historical Collection Records and Occurrence Data—To investigate the collection history of *Digitaria laeviglumis* and identify all its known and purported geographic localities, we searched for the names "*Digitaria laeviglumis*," "*Digitaria filiformis* var. *laeviglumis*," "*Digitaria filiformis*," and "*Syntherisma filiformis*" in the following internet databases that aggregate collection information from herbarium specimens and/or direct observations: Consortium of California Herbaria 2 (2021), Consortium of Midwest Herbaria (2021), Consortium of Northeastern Herbaria (2021), Consortium of Pacific Northwest Herbaria (2021), Global Biodiversity Information Facility (2021), Global Plants Database (2021), Integrated Digitized Biocollections (2021), National Autonomous University of Mexico (2021), Southeast Regional Network of Expertise and Collections (2021), Southwest Environmental Information Network (2021), Tropicos (2021), and Vascular Plants of Canada (2020). Additionally, we queried the New Hampshire Natural Heritage Bureau database (2023), which contains information from more than 5000 rare plant surveys across the state, to determine if *D. laeviglumis* had been identified at or in the vicinity of Rock Rimmon in Manchester, New Hampshire since its most recent collection in 1931. Between mid-August and early October in 2020 and 2021, we conducted seven targeted field surveys for *D. laeviglumis* at and in the vicinity of Rock Rimmon. Aware of publications describing occurrences of *D. laeviglumis* in Latin America (Vega and Rúgolo 2005; Sánchez-Ken 2019), we also conducted a literature review and searched online collection records to determine if *D. laeviglumis* has been documented outside of New Hampshire.

Assessment of Conservation Status—A NatureServe Global Conservation Rank Assessment was conducted following Faber-Langendoen et al. (2012) for all taxa in the *Digitaria filiformis* complex. Data on the overall geographic range, extent of occurrence, and area of occupancy was obtained by searching for specimens at online portals including: Consortium of California Herbaria 2 (2021), Consortium of Midwest Herbaria (2021), Consortium of Northeastern Herbaria (2021), Consortium of Pacific Northwest Herbaria (2021), Global Biodiversity Information Facility (2021), Global Plants Database (2021), Integrated Digitized Biocollections (2021), National Autonomous University of Mexico (2021), Southeast Regional Network of Expertise and Collections (2021), Southwest Environmental Information Network (2021), Tropicos (2021), and Vascular Plants of Canada (2020). These data were entered into the NatureServe Rank Calculator (NatureServe 2020) to determine the global imperilment for each species.

Results

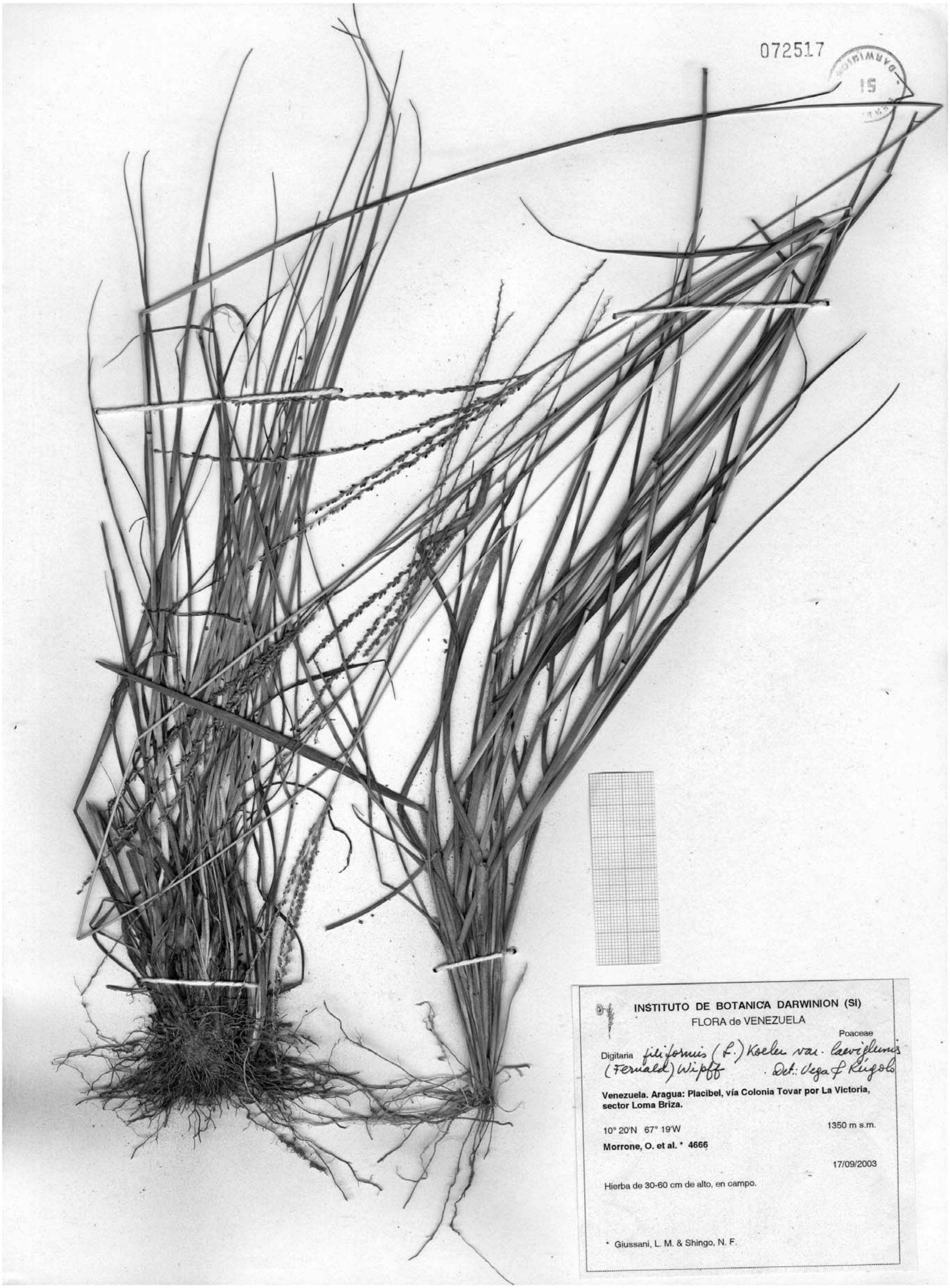
Phylogenetic Analyses—Analyses of the concatenated data matrix (14,598 aligned sites, with 36.4% missing data) resulted in the identification of 12,265 variable sites, of which 4905 were parsimony-informative. Sequence data are available via the NCBI Sequence Read Archive under BioProject number PRJNA956885. Alignments are available via Zenodo (https://doi.org/10.5281/zenodo.8422149) and on the Dryad Digital Repository (Nichols et al. 2024).

Phylogenetic analyses using maximum likelihood inference with IQ-TREE 2 and RaxML-NG recovered identical tree topologies with similar maximum likelihood bootstrap support values (MLBS), consisting of two strongly supported major ingroup clades (Fig. 4). The first major clade had complete MLBS support (100%/100% for IQ-TREE2/RAxML hereafter) for all relationships among 16 *Digitaria* species. The major second clade included a clade of three *Digitaria* species [*D. argillacea* (Hitchc. & Chase) Fernald, *D. aristulata* (Steud.) Stapf, and *D. monodactyla* Stapf], collectively sister to all other accessions of the *D. filiformis* complex. Within this *D. filiformis* complex clade, *D. glabrifloris* (sp. nov.) was sister of a clade comprising one accession of *D. abyssinica* (Hochst. ex A.Rich.) Stapf plus all members of the *D. filiformis* complex with MLBS = 100%/100%. Two accessions of *D. dolichophylla* from Florida, USA, were sister of the remaining members of the complex (MLBS = 100%/100%). Within this clade were all accessions of *D. filiformis*, *D. villosa*, and *D. laeviglumis*. The three accessions of *D. laeviglumis* formed a clade (MLBS = 100%/100%) that is sister of one accession of *D. filiformis* from South Carolina, USA (MLBS = 75/86). However, two accessions of *D. villosa* (from Georgia and North Carolina, USA, MLBS = 99%/97%) were united as sister of a *D. filiformis* accession from Louisiana, USA (MLBS = 99/97), collectively sister of a *D. filiformis* accession from West Virginia, USA (MLBS = 85/97). A third accession of *D. villosa* was sister of the clade comprising the three accessions of *D. laeviglumis* and one accession of *D. filiformis*, albeit with low support (MLBS = 53%/30%).

Morphological Examination—Morphological examination of *D. laeviglumis* specimens collected in 1901 and 1931 from Rock Rimmon, Manchester, New Hampshire together with specimens from Mexico published as *D. filiformis* var. *laeviglumis* confirmed the taxon from Mexico is not *D. laeviglumis* but rather a previously undescribed species (see Taxonomic Treatment section for circumscription of *Digitaria glabrifloris* Wipff, Sánchez-Ken, & W.F.Nichols).

An examination of the digital specimen from Venezuela (Fig. 3) published as *D. filiformis* var. *laeviglumis* (Vega and Rúgolo 2005) confirmed that it was misidentified and is likely an undescribed taxon. Compared to the type specimen of *D. laeviglumis* collected at Rock Rimmon, the Venezuelan crabgrass is perennial, densely cespitose with thick fibrous roots, more robust in habit, spikelets 3.8–4.2 mm long and 1.7–1.8 mm wide, and with an inequidistant venation pattern on lower lemmas. In contrast, *D. laeviglumis* is an annual or short-lived perennial, loosely cespitose with thin fibrous roots, less robust in habit, spikelets 1.7–1.9 mm long and 0.7–0.8 mm wide, and with a ± equidistant venation pattern on lower lemmas.

Assessment of Historical Collection Records and Occurrence Data—Our survey of historical specimen records in consortium databases (Table 1), revealed that *D. laeviglumis* was first collected at Rock Rimmon, Manchester, New Hampshire by Frederick Batchelder in 1901 (Fig. 5) under the name *Syntherisma filiformis* (L.) Nash (= *D. filiformis* (L.) Koeler). Fernald (1920) described these collections as a new species, *D. laeviglumis* Fernald, which was later named by Wipff (1996) as *D. filiformis* (L.) Koeler var. *laeviglumis* (Fernald) Wipff. In total, we identified 38 herbarium sheets with collections of *D. laeviglumis* from Rock Rimmon, all made between 1901 and 1931 (Table 1). Of these, specimens on 31 sheets were



INSTITUTO DE BOTANICA DARWINION (SI)
FLORA de VENEZUELA
Poaceae

Digitaria filiformis (L.) Koeler var. laeviglumis (Fernald) Wipff . Det.: Vega & Rúgolo

Venezuela. Aragua: Placibel, vía Colonia Tovar por La Victoria, sector Loma Briza.

10° 20'N 67° 19'W 1350 m s.m.

Morrone, O. et al. * 4666

17/09/2003

Hierba de 30-60 cm de alto, en campo.

* Giussani, L. M. & Shingo, N. F.

FIG. 3. Specimen from Venezuela published as *Digitaria laeviglumis* (Vega and Rúgolo 2005). Herbarium specimen image provided by Universidad Central de Venezuela (VEN).

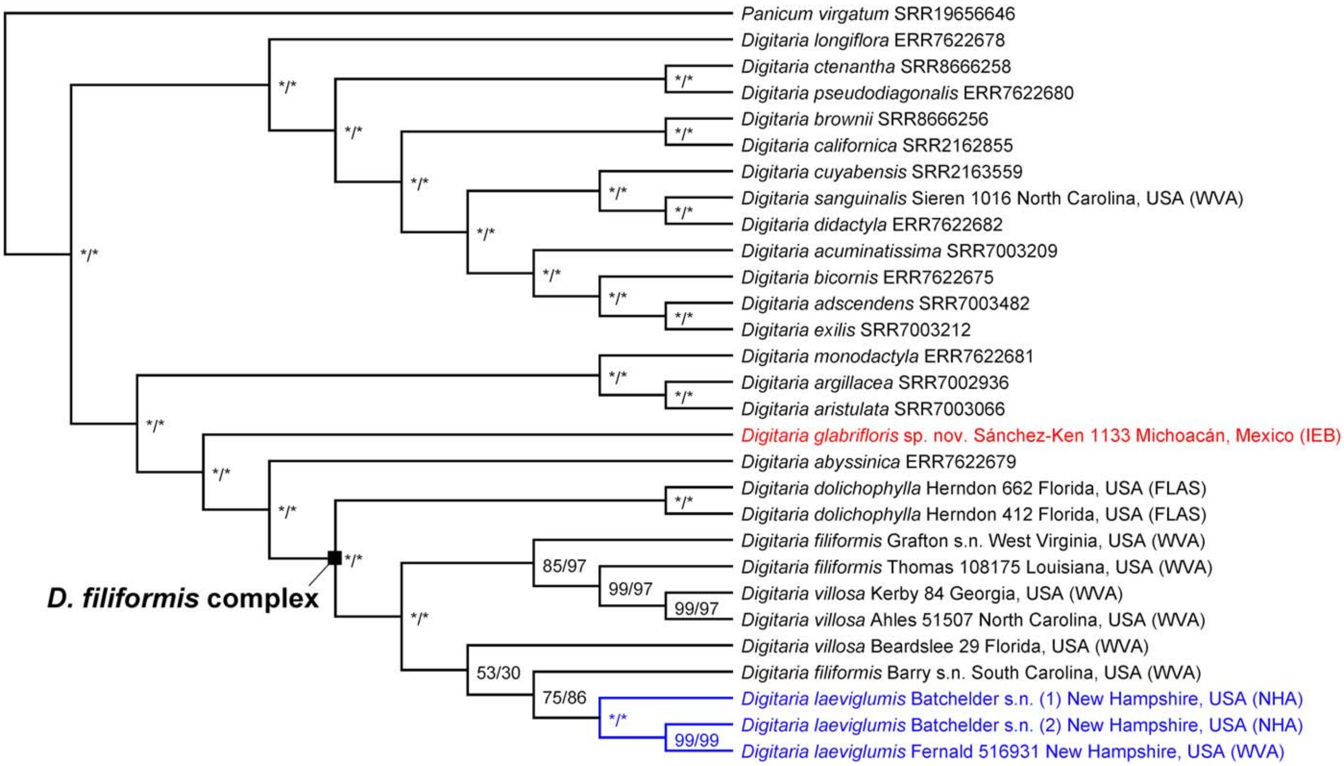


FIG. 4. Maximum likelihood tree based on 12,265 single nucleotide polymorphisms in IQ-TREE2, highlighting the relationships within the *Digitaria filiformis* complex and other members of *Digitaria* available in public databases [4905 parsimony-informative SNPs, best-fit model under the Bayesian information criterion (BIC) = TVNe, BIC score = 187,159.27, log-likelihood = -93,296.77]. Numbers adjacent to branches indicate IQ-TREE2 maximum likelihood bootstrap support values (MLBS, left) and bootstrap support from RAxML-NG (right); '*/*' indicates MLBS = 100%/100% for both analyses. Red text shows the specimen from México (*D. glabrifloris* sp. nov.). Accessions of *D. laeviglumis* are shown in blue text.

collected between August 23 and August 27, 1931, each with an average of three individual plants with roots and fruit.

Our query of the New Hampshire Natural Heritage Bureau database (2023) revealed records for botanical surveys at Rock Rimmon on at least 26 different occasions since *Digitaria laeviglumis* was last collected in 1931 [number of surveys in a particular year in parentheses: 1951(2), 1955(3), 1956(2), 1958(1), 1959(1), 1969(2), 1977(1), 1992(1), 2005(1), 2009(1), 2010(1), 2012(3), 2020(4), and 2021(3)]. Among these surveys, at least 12 between 1992 and 2021 were dedicated but unsuccessful searches for *D. laeviglumis* (New Hampshire Natural Heritage Bureau 1993; Nichols and Hoy 2014; Nichols pers. obs.). During a 2012 survey, 11 botanists from the New Hampshire Task Force (part of the Native Plant Trust's New England Plant Conservation Program) searched the 5.5 ha site for 44 person-hours. Most of the survey time was spent in open and semi-open habitats (1 ha) suitable for the crabgrass, with much less time in more shaded woodland areas (4.5 ha). Of the hundreds of crabgrass patches that were checked during the 2020 and 2021 surveys all were of the non-native crabgrasses *D. ischaemum* or *D. sanguinalis* (Nichols pers. obs.).

Sánchez-Ken (2019) and Vega and Rúgolo (2005) reported five locations of *D. laeviglumis* in Mexico and Venezuela. In addition, two other specimens were later found at the National Herbarium of Mexico (MEXU) and Herbarium of the Bajio Regional Center (IEB) collected from Mexico (Sánchez-Ken pers. obs.).

Assessment of Conservation Status—The results of the Conservation Status Assessments for each member in the *Digitaria filiformis* complex are available on NatureServe Explorer (https://explorer.natureserve.org/). *Digitaria filiformis* and *D. villosa* are ranked as G5 (Secure Globally). *Digitaria dolichophylla* calculates as G2 (Imperiled Globally) based on its narrow geographic range (Bahamas, Cuba, Florida, and Puerto Rico) combined with the threats and trends to the species given the development pressure in these areas. The rank of *D. laeviglumis* has been changed from GH (Possibly Extinct) to GX (Extinct).

For taxa not part of the *Digitaria filiformis* complex, *Digitaria bakeri* is endemic to Florida (Weakley and Southeastern Flora Team 2024) and has not yet been assessed by NatureServe (GNR; Unranked); it is very likely globally rare. Both *D. abyssinica* and *D. glabrifloris* (the latter we circumscribe below) have native ranges outside the United States and Canada (conservation statuses not assessed by NatureServe). However, *D. abyssinica* we informally estimate to be G4 or G5 (Apparently Secure or Secure Globally). The rank of GU (Unrankable) would apply for *D. glabrifloris*, as not enough information is currently known about the range and frequency of the species to determine the necessary factor scores to calculate a numerical rank.

TAXONOMIC TREATMENT

DIGITARIA FILIFORMIS (L.) Koeler complex (Wipff 2003).

Plants annual or short-lived perennial; cespitose, not rhizomatous. **Culms** 9–150 cm long, erect or decumbent, branching, sometimes rooting at the lower nodes; cauline nodes 1–6. **Leaves** with keeled sheaths; sheaths usually with papillose-based hairs basally, rarely glabrous; ligules 0.5–1.5 mm long,

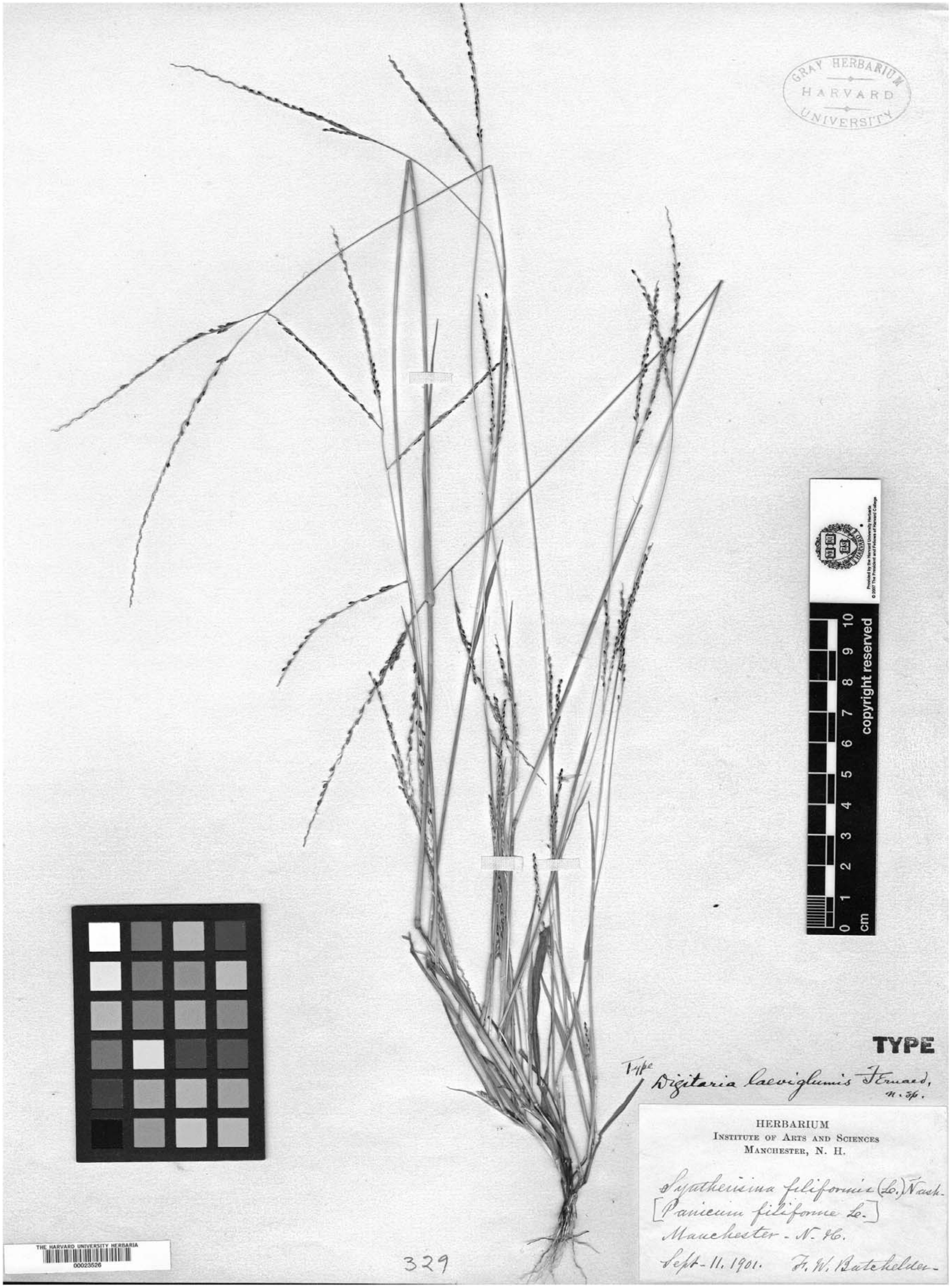


FIG. 5. *Digitaria laeviglumis* Fernald holotype collected in 1901 by Frederick Batchelder at Rock Rimmon, Manchester, New Hampshire, USA. Herbarium specimen image provided by Gray Herbarium (GH), accessed through the Consortium of Northeastern Herbaria (2021) portal.

entire (eciliate to fimbriate-ciliate) to erose-dentate; leaf blades 1.5–25 cm long, 1–6 mm wide, flat, folded, or involute, glabrous or pilose. **Synflorescence** with 1–7 raceme-like primary branches, these digitate or the rachises to 1 cm; longest primary branches 20–25 cm, axes triquetrous, not winged or scarcely winged, with spikelets in unequally pedicellate groups of 2–5 on the basal 1/2. **Spikelets** (1.3–)1.5–2.8 mm long, elliptic to lanceolate; lower (first) glumes absent or to 0.1 mm; upper (second) glumes 1–2 mm long, from 2/3 to almost as long as the spikelets, glabrous or sparsely to densely pubescent with clavate hairs (use 20 × magnification); glume apices rounded; lower (first) lemmas 0.1 mm shorter than or equaling the spikelets, glabrous or with clavate hairs, 5 or 7 ± equidistant veined, outer 3 veins on each side of lemma somewhat nearer each other than midvein is to inner lateral veins; upper (second) lemmas 1.3–2.5 mm long, apiculate, dark brown to black at maturity; anthers 0.3–0.6 mm. **2*n*** = 36, 54, or unknown.

Distribution: Members of the *Digitaria filiformis* complex occur throughout the eastern United States, and the West Indies, Mexico, and Central and South America.

Taxa: *D. dolichophylla*, *D. filiformis*, *D. laeviglumis*, and *D. villosa*.

Common Name: Slender crabgrasses.

KEY TO SPECIES IN THE *DIGITARIA FILIFORMIS* COMPLEX (ADAPTED FROM WIPFF 2003)

1\. Lower lemmas glabrous; endemic to New Hampshire, USA .... *Digitaria laeviglumis*
1\. Lower lemmas pubescent with glandular-tipped hairs 2
  2\. Basal leaf sheaths glabrous; cauline blades about 1 mm wide, folded or involute .... *Digitaria dolichophylla*
  2\. Basal leaf sheaths glabrous to pilose with papillose-based hairs; cauline blades 2–6 mm wide, flat 3
    3\. Spikelets (1.3–)1.5–2.0(–2.2) mm long; panicle branches 3–10(–13) cm long; plants 10–80(–100) cm tall; upper sheaths glabrous; lower sheaths glabrous to sparsely pilose .... *Digitaria filiformis*
    3\. Spikelets 2–2.8 mm long; panicle branches (10–)15–25 cm long; plants 75–150 cm tall; upper sheaths glabrous or pilose; lower sheaths densely pilose .... *Digitaria villosa*

DIGITARIA LAEVIGLUMIS Fernald.

Adapted from Wipff (2003) and Fernald (1920).

Synonyms—Digitaria filiformis (L.) Koeler var. *laeviglumis* (Fernald) Wipff.

Plants annual or short-lived perennial; cespitose. **Culms** 9–42 cm tall, erect or ascending, thin, slender, glabrous, firm, lustrous; not branching at lower nodes; cauline nodes 3–4. **Leaves** remote; basal leaf sheaths with papillose-based hairs or glabrous; ligules ca. 1 mm long, glabrous, scarious, hyaline, truncate, erose-dentate; leaf blades 1.5–9 cm long, 1–3 mm wide, flat, straight, glabrous, apex acute. **Synflorescence** to 29 cm long, long-exserted, with 2–3 primary branches; primary branches 2–9 cm long, 1–2 mm wide, strongly ascending, loosely flowered, mid-branches with 2–3 groups of spikelets per node, along an axis ca. 1 cm long; rachis flexuous, angulate-filiform, triangular, angles wingless, scabrous. **Spikelets** 1.7–1.9 mm long, 0.7–0.8 mm wide, ellipsoid, strictly glabrous; lower glumes obsolete; upper glumes 3/4 as long as to slightly shorter than the spikelet, translucent, hyaline, elliptic-oblong, apex rounded, prominently 3-veined, glabrous; lower lemmas as wide as the upper lemma, with 5 or 7 ± equidistant veins, glabrous (very rarely [seen once on one spikelet] with a few micro-capitellate hairs visible only under high magnification), apex rounded; upper lemmas elliptic, acuminate, black, longitudinally puncticulate-striate, apex acute, generally smooth, usually similar in color to the rest of the upper lemma; caryopses ellipsoid, pale.

Habitat: Dry peaty hollows in gneiss bedrock.

Distribution: Single-site endemic, Manchester, New Hampshire.

Conservation Status: Presumed Globally Extinct (GX).

Etymology: The specific epithet *laeviglumis* refers to the smooth lower lemmas found in this species.

Common Name: Smooth crabgrass.

DIGITARIA DOLICHOPHYLLA Henrard.

Adapted from Henrard (1934).

Synonyms—Digitaria filiformis (L.) Koeler var. *dolichophylla* (Henrard) Wipff.

Plants short-lived perennial; dense tufts. **Culms** 50–115 cm tall, erect, firm, slender, glabrous, lustrous; branching at the lower nodes; cauline nodes 3–6. **Leaves** overlap below, upper leaves remote; sheaths glabrous, the lower sheaths with reduced leaf blades; ligules ca. 1 mm long, glabrous, hyaline, truncate, entire; leaf blades to 25 cm long, about 1 mm wide, folded or involute, flexuous, slightly pubescent above, with some hairs at the base, apex setaceous. **Synflorescence** 10–20 cm long, long exserted, with 1–4 primary branches; primary branches (5–)10–20 cm long, 1–2 mm wide, ascending or the longer ones curved, loosely flowered, mid-branches with groups of 3–5 spikelets per node, along an axis ca. 1 cm long; rachis flexuous, subangular, triangular, scarcely winged. **Spikelets** 1.5–1.6 mm long, ca. 0.6 mm wide, pubescent; lower glumes absent; upper glumes about 2/3 as long as the spikelet, distinctly narrower, elliptic subacute, 3-veined, with long clavate hairs between the veins and especially towards the margins; lower lemmas as wide as the upper lemma, with 5 ± equidistant veins and acute-acuminate apex, pilose, with long clavate hairs between the lateral veins and towards the margins, but glabrous near the midvein; upper lemmas linear-lanceolate, apex distinctly apiculate, puncticulate-striate, protruding, dark brown.

Habitat: Moist pine barrens and open ground.

Distribution: Southern Florida and the northern Caribbean Islands.

Conservation Status: Imperiled Globally (G2) based on its narrow geographic range combined with the threats and trends to the species given the development pressure in these areas.

Etymology: Specific epithet *dolichophylla* refers to long-leaved.

Common Name: Caribbean crabgrass.

DIGITARIA FILIFORMIS (L.) Koeler.

Adapted from Wipff (2003).

Synonyms—Panicum filiforme L.; *Syntherisma filiformis* (L.) Nash.; *Paspalum furcatum* var. *filiforme* (L.) Döll.

Plants annual; cespitose. **Culms** 10–80(–100) cm tall, erect, thin, glabrous, slender, lustrous; branching at the lower nodes; cauline nodes 3–6. **Leaves** remote; lower sheaths glabrous to sparsely pilose with papillose-based hairs, upper sheaths glabrous; ligules prolonged, glabrous, membranous, hyaline, fimbriate-ciliate; leaf blades (2–)10–25 cm long, 2–6 mm wide, flat, straight, lower blades sparsely to densely hirsute, upper blades glabrous or pubescent, apex acute. **Synflorescence** (2–)4–14 cm long, long exserted, with 1–6 primary branches; primary branches 3–10(–13) cm long, 1–1.5 mm wide, slender; flowers loosely to slightly crowded along axes 5–7 cm long; rachis straight to curved, angular, angles wingless, with secondary branches in groups of 2–5 spikelets alongside the branches. **Spikelets** (1.3–)1.5–2.0(–2.2) mm long, ca. 0.7 mm wide, elliptic, pubescent; lower glumes to 0.1 mm long or absent; upper glumes about 3/4 as long as the spikelet, distinctly narrower, narrowly elliptic, acute, 3-veined, opaque, pilose, with clavate hairs, margins pubescent; lower lemmas as wide as the upper lemma, with 7 ± equidistant veins, pilose with clavate hairs, margins pubescent, apex rounded; upper lemmas elliptic, apex apiculate, longitudinally punctulate-striate, dark brown.

Habitat: Sandy fields and open, disturbed ground.

Distribution: Eastern United States, Mexico.

Conservation Status: Secure Globally (G5).

Etymology: The specific epithet *filiformis* refers to thread-like.

Common Name: Slender crabgrass.

DIGITARIA VILLOSA (Walt.) Pers.

Adapted from Wipff (2003).

Synonyms—Digitaria filiformis (L.) Koeler var. *villosa* (Walter) Fernald; *Digitaria pilosa* Michx.; *Syntherisma villosa* Walter.

Plants short-lived perennial; in large tufts. **Culms** 75–150 cm tall, erect or ascending, glabrous, firm, lustrous; branching basally, rarely branched above base; cauline nodes 3–6. **Leaves** mostly basal; basal sheaths densely papillose-pilose, upper sheaths glabrous or pilose; ligules to 1.5 mm long, glabrous, membranous, hyaline, truncate, entire; leaf blades 10–25 cm long, 3–6 mm wide, flat, ascending to flexuous, glabrous to pilose, apex acute. **Synflorescence** 11–25 cm long, long exserted, with 2–7 primary branches; primary branches (10–)15–25 cm long, 1–2 mm wide, straight to ascending, loosely flowered, mid-branches with groups of 2–5 spikelets per node, along an axis longer than 1 cm; rachis flexuous, angulate, triangular, angles wingless, scabrous. **Spikelets** 2.0–2.8 mm long, ca. 0.7 mm wide, ellipsoid, pubescent; lower glumes absent or obscure; upper glumes almost as long as the spikelet, translucent, hyaline, elliptic, apex acute, 5-veined, pubescent with clavate hairs; lower lemmas as wide as the upper lemma, with 7 ± equidistant veins, short-pilose, with clavate hairs, apex acute; upper lemmas elliptic, acuminate, dark brown, longitudinally puncticulate-striate, apex acute and similar in color to the rest of the upper lemma.

Habitat: Sandy soil.

Distribution: Eastern United States.

Conservation Status: Secure globally (G5).

Etymology: The specific epithet *villosa* refers to shaggy, with long soft hairs.

Common Name: Shaggy crabgrass.

KEY TO *DIGITARIA* SPECIES WITH GLABROUS SPIKELETS IN MEXICO (ADAPTED FROM SÁNCHEZ-KEN 2012)

The following key separates the three species of *Digitaria* with glabrous spikelets in Mexico. The key includes the new species *D. glabrifloris* (circumscribed below), originally published as *D. filiformis* var. *laeviglumis* (Sánchez-Ken 2019). *Digitaria bakeri* was not included in molecular analyses because our focus was on members in the *D. filiformis* complex and those specimens from Mexico purportedly identified as *D. filiformis* var. *laeviglumis* (=*D. laeviglumis*). The inclusion of *D. abyssinica* in our molecular analyses (Fig. 4) was incidental.

1. Spikelets paired along the primary branch; upper lemmas light brown to purplish .... *Digitaria abyssinica*
1. Spikelets in groups of three or more at least in the middle of the primary branch; upper lemmas dark brown to black 2
    2. Plants annual; spikelets (1.7–)1.8–2.0(–2.1) mm long .... *Digitaria glabrifloris*
    2. Plants perennial; spikelets 2.3–2.4 mm long .... *Digitaria bakeri*

Digitaria glabrifloris Wipff, Sánchez-Ken, & W.F. Nichols, sp. nov. TYPE: MEXICO. Michoacán: Mpio Tzintzunztan Ihuatzio, cerros pasando las pirámides de Ihuatzio, pastizal, suelo volánico, 19°34′47″N, 101°37′02″W, 2103 m, 6 Sep 2021, *J.G. Sánchez-Ken 1133* (holotype: IEB; isotypes BRIT, MEXU, US).

Digitaria glabrifloris is similar to the now extinct *D. laeviglumis*, and was mistaken for the latter in two earlier publications (Vega and Rúgolo 2005; Sánchez-Ken 2019). *Digitaria glabrifloris* differs in having plants 7–60 cm tall (vs. 9–42 cm); racemose panicle branches (2–)4–7 (vs. 2–3); spikelets (1.7–)1.8–2.0(–2.1) mm long (vs. 1.7–1.9 mm) and 0.7–0.9 mm wide (vs. 0.7–0.8 mm); upper glumes $\leq$ 0.75 times the length of the spikelet (vs. $>$ 0.75 times to just shorter than the spikelet); lower lemma as wide to often slightly narrower than the upper lemma (vs. as wide as the upper lemma), with 7 inequidistant veins (vs. 5 or 7 ± equidistant veins; Fig. 6); apex of the upper lemma umbonate and minutely papillate, lighter in color than the rest of the lemma (vs. apex acute, generally smooth, usually similar in color to the rest of the upper lemma); mid-branch of panicle branches with 3–5 spikelets per node (vs. 2–3).

Plants annual; cespitose. **Culms** 7–60 cm tall, erect or slightly decumbent, thin, slender, glabrous delicate, lustrous; branching at the base; cauline nodes 3–4. **Leaves** basal and remote; lower sheaths purplish and usually hirtellous, rarely glabrous; upper sheaths only distally shortly pilose, becoming glabrous; ligules 0.5–1.5 mm long, glabrous, membranous, hyaline, apex erose; leaf blades (3–)4–7 cm long, 2–5 mm wide, flat, straight, glabrous on both surfaces, base sometimes with a few long hairs on the sides. **Synflorescence** (2–)5–10 cm long, long-exserted, with (2–)4–7 primary branches; primary branches 4–9 cm long, to 1.5 mm wide, strongly ascending, loosely flowered, mid-branches with groups of 3–5 spikelets per node, axis longer than 1 cm, bases hirtellous; rachis flexuous, angulate-filiform, triangular, angles wingless, scabrous. **Spikelets** (1.7–)1.8–2.0(–2.1) mm long, 0.7–0.9 mm wide, elliptic, glabrous; lower glumes absent; upper glumes 2/3–3/4 as long as the spikelets, elliptic, apex rounded, 3-veined, glabrous, rarely very few clavate hairs on margins on upper half; lower lemmas as wide to often slightly narrower

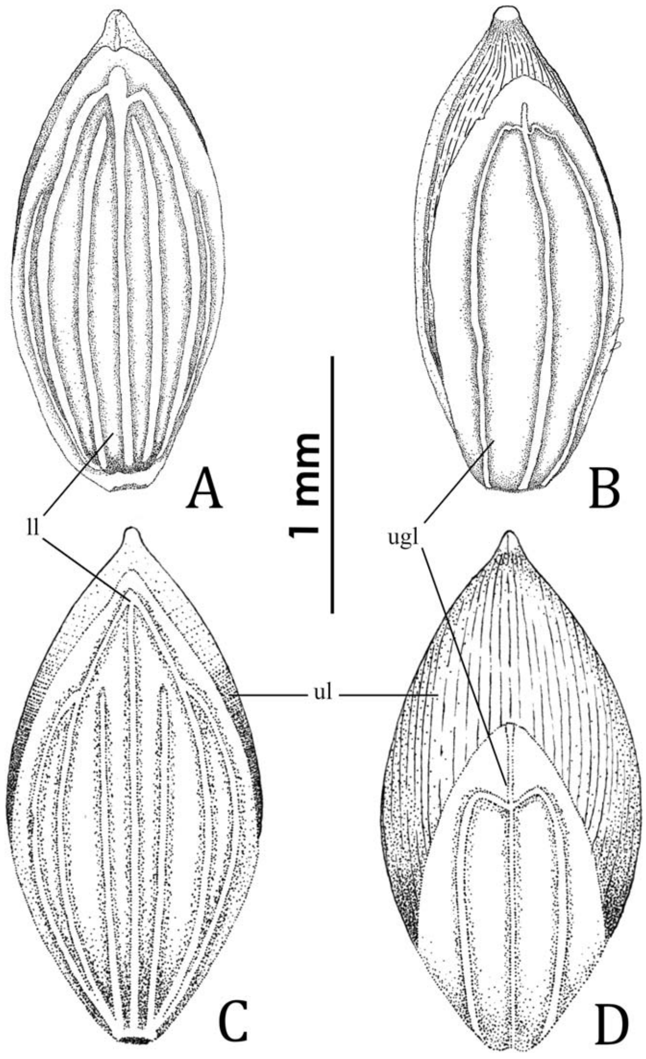


FIG. 6. Lower lemma and upper glume venation patterns of *Digitaria laeviglumis* Fernald (A–B) and *Digitaria glabrifloris* Wipff, Sánchez-Ken, & W.F. Nichols, sp. nov. (C–D). ugl: upper glume. ll: lower lemma. ul: upper lemma. Note: *D. laeviglumis* lower lemma (A) with 5 or 7 ± equidistant veins and upper glume (B) $>$ 0.75 times the length of the spikelet; *D. glabrifloris* lower lemma (C) with 7 inequidistant veins and upper glume (D) $\leq$ 0.75 times the length of the spikelet. Drawings A–B by J. G. Sánchez-Ken; C–D by Moisés Emanuel Bernal Hernández.

than the upper lemmas, with 7 inequidistant veins, glabrous, apex rounded to acute; sterile paleas ca. 0.2 mm long, papillose; upper lemmas elliptic-lanceolate, acuminate, dark brown, puncticulate-striate, apex umbonate, minutely papillate, lighter in color; caryopses elliptic, about 1/2 as long as the upper lemma, pale; embryos about 1/3 as long as the caryopsis, hilum punctiform. Figure 7.

Habitat: Gravel and sandy soils among other grasses in disturbed pine-oak or oak forest between 80–2013 m elevation.

Distribution: Currently known from five locations in three states in Mexico.

Conservation Status: The distribution and frequency is poorly understood and is data deficient. NatureServe methodology would assign a global conservation status rank of unrankable (GU).

Etymology: The specific epithet *glabrifloris* refers to glabrous spikelets found in this species.

Common Name: Glabrous crabgrass.

Additional Specimens Examined—**Mexico.** —DURANGO: municipality Canatlán, Agua Blanca, 11 km al N de Benjamín Aranda, 2025 m, 24°29′06″N, 104°29′06″W, 25.IX.1983, *Y. Herrera 303* (IEB, mixed with *Digitaria filiformis*). —MICHOACÁN: municipality Erongarícuaro, Pedregal de Arocutín, 2104 m, 19°33′13″N, 101°42′10″W, 15.IX.2022, *J. G. Sánchez-Ken et al. 1198* (IEB); municipality Tzintzuntzan, cerros pasando las pirámides de Ihuatzio, 2103 m, 19°34′47″N, 101°37′02″W, 04.X.2018, *J. G. Sánchez-Ken et al. 935, 1184* (IEB, MEXU); municipality Pátzcuaro, Cerro Blanco, ladera norte 2299 m, 19°31′49″N, 101°36′01″W, 17.X.2021, *J. G. Sánchez-Ken 1196* (IEB). —OAXACA: district Tlacolula, municipality San Pedro Totolapa, about 66 mi NW of Tehuantepec, 1430 m, 19°32′23″N, 95°56′45″W, 29.VIII.1953, *J. R. Reeder and C. G. Reeder 2171* (MEXU).

DIGITARIA BAKERI (Nash) Fernald.

Adapted from Wipff (2003).

Synonyms—*Syntherisma bakeri* Nash; *Digitaria gracillima* (Scribn.) Fernald.

Plants perennial, densely tufted. **Culms** 40–100 cm tall, erect, thick, glabrous, firm, lustrous, unbranched; cauline nodes 4–5. **Leaves** basal and remote; sheaths densely hirsute with papillose-hairs; ligules 0.8–2.2 mm long, glabrous, hyaline, truncate, entire, eciliate; leaf blades 10–24(–40) cm long, 2–4.5 mm wide, flat to involute, straight to flexuous, glabrous but hirsute with papillose-based hairs toward the base, apex setaceous. **Synflorescence** 5–22 cm long, long-exserted with 2–3 primary branches; primary branches 4–22 cm long, 1–5 mm wide, slender, loosely flowered, along a 4–7 cm axis, mid-branches with secondary branches and groups of 2–5 spikelets per node alongside the branch; rachis slightly flexuous to straight, angular, triangular, angles wingless. **Spikelets** 2.3–2.4 mm long, ca. 0.8 mm wide, elliptic, sparsely pubescent; lower glumes absent; upper glumes slightly longer than 1/2 the length of spikelet, distinctly narrower, ovate-elliptic, apex rounded, 3-veined, sparsely pilose, with scattered short clavate hairs; lower lemmas about as long as the spikelets, with 7 ± equidistant veins, sparsely pilose, with scattered clavate hairs, apex rounded; upper lemmas ovate-elliptic, dark brown to black, longitudinally puncticulate-striate, apex acute, usually similar in color to the rest of the upper lemma.

Habitat: Longleaf pine sandhills and dry, sandy pastures.

Distribution: Endemic to Florida Coastal Plain. Purported to be conspecific with a crabgrass native from Panama to Mexico (Flora of North America Editorial Committee 2003; Hall 2019; Weakley and Southeastern Flora Team 2024).

Conservation Status: Global rank not yet assessed (GNR), though very likely globally rare.

Etymology: The specific epithet *bakeri* refers to name of original collector, C. H. Baker.

Common Name: Baker's crabgrass.

DIGITARIA ABYSSINICA (Hochst. ex A. Rich.) Stapf.

Adapted from Wipff (2003).

Synonyms—*Panicum abyssinicum* Hochst. ex A.Rich.; *Syntherisma abyssinica* (Hochst. ex A.Rich.) Newbould.

Plants perennial; rhizomatous, stoloniferous, mat-forming. **Culms** 5–80 cm long, decumbent, slender, glabrous, firm, lustrous, occasionally rooting at the lower nodes, branching below and above; cauline nodes 4–9. **Leaves** remote; midculm sheaths glabrous or papillose-hirsute above; ligules 0.8–2.1 mm long, glabrous, membranous, hyaline, obtuse to truncate; leaf blades 4–15 cm long, 3–10 mm wide, lanceolate, flat, divergent, glabrous or sparsely papillose-pilose. **Synflorescence** 4.5–10 cm long, long exserted, with 2–25 primary branches; axis 1–9.5 cm; primary branches 1.5–10 cm long, ca.

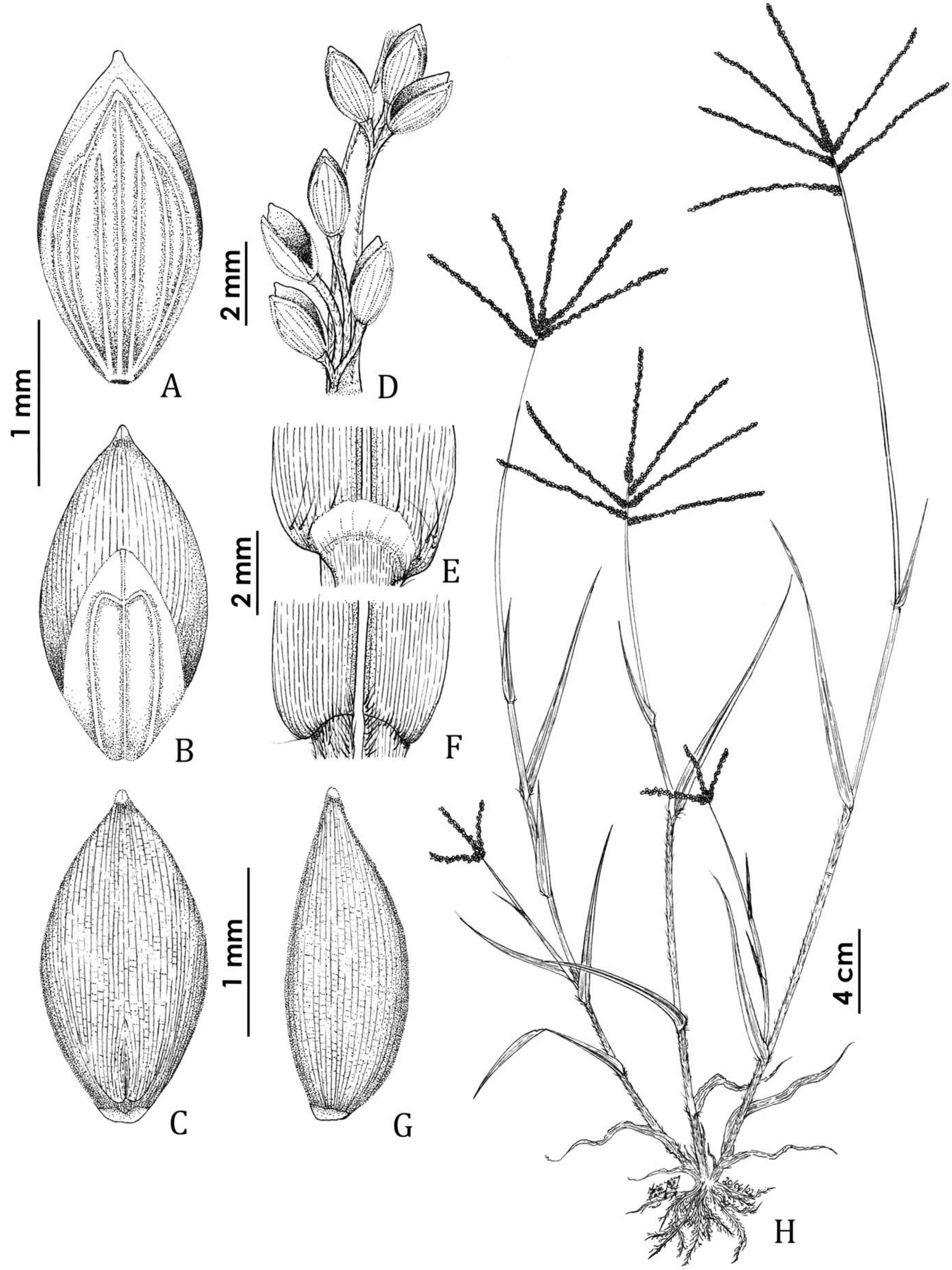


FIG. 7. *Digitaria glabrifloris* Wipff, Sánchez-Ken, & W.F. Nichols, sp. nov. A. Lower lemma. B. Upper glume. C. Upper (fertile) lemma, dorsal view. D. Synflorescence branch close-up. E. Ligule. F. Collar region. G. Upper lemma, lateral view. H. Habit. Drawing by Moisés Emanuel Bernal Hernández.

1–2 mm wide, midbranches with secondary branches and paired spikelets, occasionally the lower one abortive at the extremes or with more spikelets per node at the base; rachis flexuous, angulate, triangular, angles wingless, scabrous. **Spikelets** 1.5–2.5 mm long, 0.8–0.95 mm wide, ovate-elliptic to broadly elliptic, glabrous, usually plump and purple-tinged; lower glumes 0.3–0.8 mm long, occasionally absent, ovate-deltoid, 1-veined; upper glumes 4/5 as long as the spikelet, firm, scarious, ovate-elliptic, apex acute to rounded, with 3–5(–7) prominent veins; lower lemmas as wide as the upper lemma, with 7 ± equidistant and prominent veins, glabrous, occasionally obscurely puberulent on the margins, apex acute; upper lemma ovate-lanceolate, light brown to purplish, puncticulate-striate, apex acute, generally smooth, similar in color to the rest of the upper lemma; caryopses oblong-elliptic, brownish.

Habitat: Disturbed mesic soil, often a crop weed.

Distribution: Native to tropical and Southern Africa to Sri Lanka, Vietnam, Peninsula Malaysia, and New Guinea; introduced in Hawaii (USDA 2023) and from Mexico to Central and northern South America (Plants of the World Online 2023). *Digitaria abyssinica* is not known to be established in the continental United States although it has occasionally been cultivated in the southern U.S.

Conservation Status: Although NatureServe does not publish assessments for species whose native ranges occur outside the United States or Canada, the rank of G4 or G5 (Apparently Secure or Secure Globally) conceivably would apply due to its broad distributional range and affinity for disturbed habitats.

Etymology: The specific epithet *abyssinica* refers to of or from Ethiopia.

Common Name: East African couchgrass.

Discussion

Reevaluating the Taxonomy of the Digitaria filiformis Complex—Reassessing the taxonomic status of *D. laeviglumis*, as well as other varieties in the *D. filiformis* complex (Wipff 2003) is an important prerequisite for determining whether *D. laeviglumis* is Globally Extinct (Knapp et al. 2021). Phylogenetic analyses of the combined plastid, mitochondrial, and rDNA datasets reveal that specimens of *D. laeviglumis* from Rock Rimmon, Manchester, New Hampshire represent a lineage distinct from the crabgrass previously identified as *D. laeviglumis* from México (Fig. 4; Sánchez-Ken 2019). The New Hampshire specimens of *D. laeviglumis* appear most closely allied with *D. filiformis* and *D. villosa*, whereas the included Mexican specimen (now *D. glabrifloris* sp. nov.) is strongly supported as being outside the *D. filiformis* complex. *Digitaria dolichophylla* (Florida, USA and the Caribbean Islands) represents a distinct clade in our analyses, but we did not find evidence for distinct clades of the more widespread taxa *D. filiformis* and *D. villosa*. Nevertheless, we do not believe our phylogenetic results warrant the recircumscription of *D. filiformis* and *D. villosa* at this time, as their placement relative to one another is somewhat weakly supported in our analyses (Fig. 4). Low support may be the result of low levels of differentiation in the organellar and ribosomal markers used in this study, reflecting the recent divergence of these two widespread taxa. Other data sources, most notably morphological data, suggest that they are distinct taxonomic entities. Future studies of this complex should include additional, field-based collections of *D. filiformis* (sensu stricto) and *D. villosa* from across their geographic ranges to generate additional herbarium vouchers and expand genetic sampling. Further, the application of genome-wide SNP data, in addition to increased sample sizes, would provide a powerful test of our species delimitations.

Despite not being able to include Venezuelan specimens purportedly identified as *D. laeviglumis* (Vega and Rúgolo 2005) in our phylogenetic analyses, we were able to include it in a morphological comparison (using a digital herbarium image) with specimens from the type locale of Rock Rimmon, Manchester, New Hampshire and specimens from Mexico. Based on morphologic examination we were able to conclude that the specimens from Mexico and Venezuela are distinct from *D. laeviglumis* in New Hampshire, as well as from each other. Phylogenetic analysis corroborates the specimen from Mexico as a distinct species, named here *D. glabrifloris* sp. nov., and placed closely outside the *D. filiformis* and *D. abyssinica* clade. The position of the latter is intriguing in our analysis (Fig. 4) because *D. abyssinica*, based on nuclear ITS and five plastid loci (Touafchia et al. 2023), appears embedded in the Binate group, that have solitary or paired spikelets (e.g. *D. ciliaris* and *D. sanguinalis*).

A synthesis of the phylogenetic and morphological results—most strikingly, the distinct placement of *Digitaria glabrifloris* relative to members of the *D. filiformis* complex—indicate that these taxa need revision. The *D. filiformis* complex is well supported as a monophyletic group, but the relationships within remain unclear. However, *D. laeviglumis* appears as a coherent and well supported clade that is distantly related to the Mexican *D. glabrifloris*, the new species that, because of its similar morphology, was incorrectly identified as the former species (Sánchez-Ken 2019). The presence of *D. abyssinica* and the absence of many of the other species of *D.* section *Clavipilae* (previously called *D.* section *Filiformes*) does not allow us to fully establish the membership of the *D. filiformis* complex nor phylogenetic relationships with the other species of the section. Our results support the hypothesis that *D. glabrifloris* is a distinct species from *D. laeviglumis*, based on molecular data and morphological analysis. Overall, the whole topology of the phylogenetic tree agrees with those found in other recent studies (Vega et al. 2009; Touafchia et al. 2023). It is clear that more taxonomic and phylogenetic work is needed to fully resolve and provide support for phylogenetic relationships among the species of the genus *Digitaria.* Based on our analyses, we choose to recognize the four varieties of *D. filiformis* described by Wipff (2003) at the specific level; *D. laeviglumis* Fernald, *D. filiformis* (L.) Koeler, *D. villosa* Michx., and *D. dolichophylla* Henrard. Furthermore, we describe the plants from Mexico as a new species, *D. glabrifloris* Wipff, Sánchez-Ken, & W.F. Nichols.

Conservation Status of Digitaria laeviglumis—Given the results of our phylogenetic and morphological analyses, we assert that *D. laeviglumis* is indeed a single-site endemic species that was known only from Rock Rimmon in Manchester, New Hampshire. Our extensive searches of historical collection records, documentation of previous rare plant surveys, and our recent searches of Rock Rimmon and nearby open rocky habitat specifically for *D. laeviglumis,* failed to yield any evidence of the existence of the species since its last documented collection in 1931 by Fernald and Griscom (Table 1). Regrettably, we must conclude that *D. laeviglumis* is Globally Extinct. Additionally, *D. laeviglumis* is the first documented plant extinction for the state of New Hampshire, at least the fifth plant extinction to have occurred in New England, and the second documented extinct Poaceae taxon in the United States and Canada (Knapp et al. 2021).

Rock Rimmon is a botanical hotspot supporting one Vulnerable (moderate risk of extirpation) and three Critically Imperiled (very high risk of extirpation) natural communities within New Hampshire (New Hampshire Natural Heritage Bureau 2023). Seven state endangered or threatened (E/T; Critically Imperiled/Imperiled) and four state watch (W; Vulnerable) plant taxa have been recorded at the site in the last 123 yrs (Nichols and Hoy 2014). Three of the seven E/T taxa are believed to have been extirpated from the site (in the case of the single site endemic *Digitaria laeviglumis*, extirpated and Globally Extinct) due to the impact of a long recreational history (Eaton 2011; New Hampshire Natural Heritage Bureau 2023); two of the remaining four taxa are historical (not seen at Rock Rimmon in over 25 yr). Rock climbers utilize the site's small cliff and ledges (Mountain Project Inc. 2012). Charring on the tree trunks of *Pinus rigida* Mill and campfire rings are frequent on the summit (Nichols pers. obs.). Trampling, climbing, littering, and frequent recreational fires have led to decreased plant cover on open portions of the prominence, and caused substantial soil erosion (New Hampshire Natural Heritage Bureau 1993; Nichols and Hoy 2014; Nichols pers. obs.).

Notably, heavy recreational use is likely not the only factor contributing to the extinction of *D. laeviglumis.* Thirty-one (31) collections of *D. laeviglumis* were made by Fernald and Griscom during a span of four days (Table 1), when last documented in 1931. Overcollection could have been an unintended contributing factor in the taxon's extinction, perhaps making the population more susceptible to stochastic events or other extrinsic threats, as well as from increased vulnerability from genetic drift (Norton et al. 1994; Minteer et al. 2014). Unfortunately, this isn't the only example where overcollecting likely contributed to the extinction of a species. *Govenia floridana* P.M.Br. was a single-site endemic orchid discovered in 1957 in the Everglades. Last documented in 1964, the orchid is believed to have been pushed to extinction due to over-collection and poaching (Gann et al. 2002; NatureServe 2023). Similarly, a single-site endemic in Massachusetts, *Juncus pervetus* Fernald, went extinct in large part to over-collection (Brooks and Clemants 2000; Knapp and Naczi 2016; Knapp et al. 2021). Searches of consortium databases reveal 56 herbarium sheets of *J. pervetus*, the vast majority of which contain large sections of rhizomes.

The global extinction of *D. laeviglumis* is a reminder of the unique susceptibility of single-site endemics to anthropomorphic threats (Knapp et al. 2021; Pouteau et al. 2021) and offers a cautionary tale of the potential impact of overcollection by both amateur and professional botanists. It also offers an opportunity to reprioritize the conservation of sites that harbor disproportional numbers of endemic, endangered, or threatened species, often representative of insular, uncommon, or imperiled natural communities (Kelso et al. 2001; Cartwright 2019). Such is the case with Rock Rimmon in Manchester, New Hampshire, a small prominence (5.5 ha) supporting a temperate ridge–cliff–talus system with eleven documented rare or uncommon plant taxa located in or adjacent to four rare natural communities: pitch pine rocky ridge, Appalachian oak–pine rocky ridge, pitch pine–Appalachian oak–heath forest, and Appalachian wooded talus communities (Sperduto and Nichols 2004; Sperduto 2011; Nichols and Hoy 2014). Because the site is an anthropogenically impaired biodiversity hotspot, increased conservation efforts at Rock Rimmon will be particularly important for preserving plant species that simply have "nowhere else to go."

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Author Contributions

WFN conceived and coordinated the project, conducted ten surveys for *Digitaria laeviglumis* at Rock Rimmon, investigated the crabgrass' search history and collection history, aided with the type description of *D. glabrifloris* and the overall taxonomic treatment, and otherwise wrote and organized the majority of the first draft (except those portions related to DNA analyses). CFB conducted the DNA analyses and wrote the portion of the methods, results, and discussion sections related to those analyses. JKW conducted the morphological examination of *D. laeviglumis* specimens from New Hampshire and purported specimens from Mexico and Venezuela and was the primary author of the taxonomic treatment for *D. glabrifloris* from Mexico. JGSK collected *Digitaria* specimens in Mexico for the morphological examination and DNA analyses, reviewed the digital image of the *Digitaria* specimen from Venezuela, assisted with the keys and species descriptions, provided taxonomic perspicacity, as well as project planning. WMK provided research assistance, examined the global conservation status of *D. dolichophylla*, and contributed to manuscript review and editing. EMS provided research assistance and contributed to overall manuscript review and editing, with particular attention to molecular analyses. LK and CC assisted with the DNA analyses of the *D. filiformis* complex. All authors contributed to the review of the phylogenetic and morphological analyses and the final version of the manuscript.

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Appendix 1. *Digitaria* taxa included for analysis of plastid, mitochondrial, and nuclear ribosomal data. Each entry is listed as: species and authority, collector and collection number, collection location, year collected, herbarium (code) where voucher was deposited, and NCBI Sequence Read Archive BioSample accession number. Herbarium codes are as follows: IEB (Bajío Herbarium, Instituto de Ecología); NHA (Albion R. Hodgdon Herbarium, University of New Hampshire); WVA (West Virginia University Herbarium); FLAS (University of Florida Herbarium). *Indicates specimen collected in silica within two months prior to molecular analysis. All other samples were obtained from herbarium specimens collected 15-121 years prior to molecular analysis.

**Digitaria glabrifloris* Wipff, Sánchez-Ken, & W.F.Nichols, sp. nov., *Sánchez-Ken 1133*, Michoacán, 2021, IEB, SAMN34231872; *D. laeviglumis* Fernald, *Batchelder s.n.*, New Hampshire (1), 1902, NHA, SAMN34231866; *D. laeviglumis* Fernald, *Batchelder s.n.*, New Hampshire (2), 1902, NHA, SAMN34231867; *D. laeviglumis* Fernald, *Fernald 516931*, New Hampshire, 1931, WVA, SAMN34231868; *D. filiformis* (L.) Koeler, *Thomas 108175*, Louisiana, 1988, WVA, SAMN34231865; *D. filiformis* (L.) Koeler, *Grafton s.n.*, West Virginia, 2008, WVA, SAMN34231864; *D. filiformis* (L.) Koeler, *Barry s.n.*, South Carolina, 1967, WVA, SAMN41798566; *D. sanguinalis* (L.) Scop., *Sieren 1016*, North Carolina, 1972, WVA, SAMN34231874; *D. villosa* (Walt.) Pers., *Ahles 51507*, North Carolina, 1958, WVA, SAMN34231869; *D. villosa* (Walt.) Pers., *Beardslee 29*, Florida, 1930, WVA, SAMN41798567; *D. villosa* (Walt.) Pers., *Kerby 84*, Georgia, 1976, WVA, SAMN41792560; *D. dolichophylla* Henrard, *Herdon 412*, Florida, 1980, FLAS, SAMN34231862; *D. dolichophylla* Henrard, *Herdon 662*, Florida, 1982, FLAS, SAMN34231861.