EVOLUTION AND TAXONOMIC REVISION OF THE "RESIDUAL HIGHBUSH" BLUEBERRIES OF *VACCINIUM* SECT. *CYANOCOCCUS* (ERICACEAE)

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ABSTRACT

The taxonomy of naturally occurring *Vaccinium corymbosum* has varied widely. The original monograph of *V.* sect. *Cyanococcus* treated the species narrowly as a tetraploid of the northeastern U.S. and adjacent Canada, whereas the most recent treatment of the section synonymized many species under a single polymorphic species ranging across eastern North America. Data from morphology, phylogenomics, and flow cytometry to assess ploidy have recently been used to resurrect several of the original species from the synonymy of *V. corymbosum*. This has left remaining a "residual highbush" blueberry group of uncertain species number and delimitation. We assessed the taxonomy of this group in the context of its origin and evolution with the same types of data and analyses used to segregate the prior species. Phylogenomic analysis yielded a monophyletic residual highbush group corroborated by several morphological characters. Neither the diploids nor the tetraploids in the clade formed monophyletic groups, but principal component and genetic structure analyses provided evidence of mostly distinct groups aligned with ploidy. The two ploidal levels have largely nonoverlapping geographic ranges, with the diploids in the southeastern U.S. and tetraploids in the northeastern U.S. and adjacent Canada, overlapping along the Atlantic Coastal Plain and East Gulf Coastal Plain. The nonmonophyly of the tetraploids, together with the prior finding of high frequencies of unreduced gametes in the residual highbush clade, suggest multiple autopolyploid origins. The lack of tetraploids throughout the entire western range of the diploids suggests that polyploid formation is localized or rare and that the two ploidal levels have largely followed separate evolutionary trajectories. We found higher genetic diversity in the tetraploid than in the diploid, suggesting that if gene flow is occurring between ploidal levels, it is not recent. Based on a synthesis of the data, we recognize two species, the diploid *V. fuscatum* and the tetraploid *V. corymbosum*, differentiated morphologically, at least in part, by characters that may be associated with the polyploid gigas effect. We provide a taxonomic revision, including a key, full synonymy, a discussion of character variation, nomenclatural and ecological notes, geographic distribution maps, and lists of representative specimens examined. We place four names variably recognized in recent floristic and horticultural literature in synonymy, i.e., the diploids *V. atrococcum* and *V. caesariense* under *V. fuscatum*, and the tetraploids *V. formosum* and *V. marianum* under *V. corymbosum*. We provide lectotypes for *Cyanococcus holophyllus*, *V. atlanticum*, *V. caesariense*, *V. corymbosum*, *V. corymbosum* var. *atrocarpum*, *V. corymbosum* var. *glabrum*, *V. formosum*, *V. fuscatum*, *V. marianum*, *V. vicinum*, and *V. virgatum* var. *parvifolium*. *Vaccinium cuthbertii* is placed under the synonymy of *V. fuscatum* but warrants further investigation as to its possible taxonomic distinctness.

RESUMEN

La taxonomía de *Vaccinium corymbosum* en estado natural ha variado mucho. La monografía original de *V.* sect. *Cyanococcus* trataba la especie de forma restringida como un tetraploide del noreste de EE.UU. y Canadá adyacente, mientras que el tratamiento más reciente de la sección sinonimiza muchas especies bajo una única especie polimórfica que se extiende por el este de Norteamérica. Los datos de morfología, filogenómica y citometría de flujo para evaluar la ploidía se han utilizado recientemente para resucitar varias de las especies originales de la sinonimia de *V. corymbosum*. Esto ha dejado un grupo de arándanos «residual highbush» de número de especies y delimitación inciertos. Evaluamos la taxonomía de este grupo en el contexto de su origen y evolución con los mismos tipos de datos y análisis utilizados para segregar las especies anteriores. El análisis filogenómico arrojó un grupo residual monofilético de arándanos altos corroborado por varios caracteres morfológicos. Ni los diploides ni los tetraploides del clado formaban grupos monofiléticos, pero los análisis de componentes principales y de estructura genética proporcionaron pruebas de la existencia de grupos mayoritariamente distintos alineados con la ploidía. Los dos niveles ploidales tienen rangos geográficos que no se solapan, con los diploides en el sureste de EE.UU. y los tetraploides en el noreste de EE.UU. y Canadá adyacente, solapándose sólo a lo largo de la Llanura Costera Atlántica y la Llanura Costera del Este del Golfo.

J. Bot. Res. Inst. Texas 19(4): 419–476. 2025
https://doi.org/10.17348/jbrit.v19.i4.1439
Published online: 16 December 2025

La no monofilia de los tetraploides, junto con el hallazgo previo de altas frecuencias de gametos no reducidos en el clado highbush residual, sugieren múltiples orígenes autopoliploides. La ausencia de tetraploides en todo el área de distribución occidental de los diploides sugiere que la formación de poliploides es localizada o rara y que los dos niveles de ploidía siguen en gran medida trayectorias evolutivas separadas. Encontramos una mayor diversidad genética en el tetraploide que en el diploide, lo que sugiere que si se está produciendo flujo genético entre niveles ploidales, no es reciente. Basándonos en una síntesis de los datos, reconocemos dos especies, la diploide *V. fuscatum* y la tetraploide *V. corymbosum*, diferenciadas al menos en parte morfológicamente por caracteres que pueden estar asociados al efecto gigas poliploide. Proporcionamos una revisión taxonómica, incluyendo una clave, sinonimia completa, una discusión de la variación de caracteres, notas nomenclaturales y ecológicas, mapas de distribución geográfica y listas de especímenes representativos examinados. Colocamos en sinonimia cuatro nombres reconocidos de forma variable en la literatura florística y hortícola reciente, es decir, los diploides *V. atrococcum* y *V. caesariense* bajo *V. fuscatum*, y los tetraploides *V. formosum* y *V. marianum* bajo *V. corymbosum*. Proporcionamos lectotipos para *Cyanococcus holophyllus*, *V. atlanticum*, *V. caesariense*, *V. corymbosum*, *V. corymbosum* var. *atrocarpum*, *V. corymbosum* var. *glabrum*, *V. formosum*, *V. fuscatum*, *V. marianum* y *V. vicinum*. *Vaccinium cuthbertii* se incluye bajo el sinónimo de *V. fuscatum*, pero merece una investigación más profunda en cuanto a su posible distinción taxonómica.

Key Words: blueberry, eastern United States, Ericaceae, polyploidy, *Vaccinium* sect. *Cyanococcus*

INTRODUCTION

Vaccinium corymbosum L , "highbush blueberry," is a member of *V.* sect. *Cyanococcus* A. Gray, a monophyletic group of outcrossing insect-pollinated species mainly endemic to eastern North America, with one species extending west to British Columbia (Becker et al. 2024; Fritsch et al. 2024a). As in other species of the section, *V. corymbosum* constitutes an essential component of wet acidophilic plant communities and serves a key source of food for wildlife. It also forms an important component of the blueberry crop industry, having been the source of the first selections of plants from the wild brought into cultivation and whose genome has since been widely used in breeding programs for cultivar improvement (Luby et al. 1991; Song et al. 2011; Mengist et al. 2022).

Despite these key roles in ecology and commerce, the taxonomy of *Vaccinium corymbosum* has remained unstable (Fritsch et al. 2024a). In the first global treatment of the section, Camp (1945) recognized what is now considered to be a narrow concept of the species. In this circumscription, *V. corymbosum* was strictly a tetraploid ($2n = 4x = 48$) with plants deciduous, 1–4 m tall; leaf blades 4–8 × 2–3 cm with abaxial surface green to whitish green, glabrous or pubescent, non-stipitate-glandular, and with margins entire or serrate; corolla white often flushed pink, urceolate or occasionally slightly campanulate or slightly globose, 6–10 mm long; and fruits 5–10 mm in diameter and usually with or occasionally without glaucescence. Under Camp's concept, the species ranged from Michigan east to Nova Scotia south to the boundary of the last glacial maximum, occurring in low wet acidic habitats of many types. Camp hypothesized that the species evolved through repeated hybridization and introgression with most of the other tetraploids recognized in his treatment followed by segmental allopolyploidization and proposed that the overall morphology of *V. corymbosum* will generally trend toward one or more of these species in areas where it occurs with them.

In the only other global treatment of the section, Vander Kloet (1980, 1988) treated the species broadly by placing 12 of Camp's species of *Vaccinium* sect. *Cyanococcus* in the synonymy of a highly variable *V. corymbosum* complex that encompassed diploids, tetraploids, and hexaploids. Vander Kloet more definitively divided the section into "highbush" and "lowbush" blueberries than did Camp, with the cutoff at 1 m in height, and considered *V. corymbosum* to be the only "highbush" blueberry in the section. Vander Kloet described this "highbush" blueberry concept as a "compilospecies," i.e., a species that acquires the heredities of closely related sympatric species through genetically aggressive hybridization and introgression (Harlan & deWet 1963). Vander Kloet proposed that *V. corymbosum* originated from hybridization from the other diploid ("lowbush") blueberries of the section through repeated crossing, introgression, and polyploidization where they contact each other. As part of the most recent global treatment of *V.* sect. *Cyanococcus*, Vander Kloet's work must be considered the most authoritative taxonomic reference for the group, as borne out by its use in, e.g., *Flora of North America* (Vander Kloet 2009).

Subsequent studies questioned the sweeping extent of species synonymy in Vander Kloet's treatments. Such work began with regional floristic treatments of the section based primarily on morphology (Ward 1974;

Uttal 1986b, 1987a; Weakley & Southeastern Flora Team 2023) and culminated in a review of the taxonomy and evolution of the section by Fritsch et al. (2024a). Further, we and other members of our research team conducted a phylogenomic analysis of the diploid species of the section (Crowl et al. 2022). In both the concatenated maximum-likelihood (ML) and ASTRAL species-tree analyses of Crowl et al. (2022), the "highbush" diploids *Vaccinium caesariense* Mack. and *V. fuscatum* Aiton sensu Camp formed a clade with strong support overall that was sister to a clade of the "lowbush" species *V. darrowii* and *V. tenellum*. The "highbush" species *V. elliottii* Chapm. grouped outside these clades, thus rejecting at least in part the wide concept of *V. corymbosum*, within which *V. elliottii* was treated as a "highbush" synonym by Vander Kloet. Fritsch et al. (2024a) and Franck & Salman (2024) also provided morphological characters that may be used to distinguish *V. elliottii* from the rest of *V. corymbosum* sensu Vander Kloet. More recently, our research team has used a combination of morphology, estimation of ploidy with flow cytometry, and phylogenomic data based on the Angiosperms353 probe set to resurrect several other species from *V. corymbosum* sensu Vander Kloet, i.e., *V. ashei* J.M. Reade (Weakley et al. 2024), *V. virgatum* Aiton (Fritsch et al. 2024b), and *V. constablei* A. Gray and *V. simulatum* Small (Manos et al., in press).

After the removal of these species from synonymy, the remainder of *Vaccinium corymbosum* sensu Vander Kloet has been termed the "residual highbush" blueberry group (Fritsch et al. 2024a). In Camp's (1945) taxonomy, this group comprises *V. atrococcum* A. Heller (= *V. fuscatum* Aiton; Vander Kloet 1977, 1980, 1988) and *V. caesariense* Mack. at the diploid level, and *V. arkansanum* Ashe, *V. corymbosum*, *V. formosum* Andrews (= *V. australe* Small; Uttal 1986a), and *V. marianum* P. Watson at the tetraploid level. Luby et al. (1991) and later Fritsch et al. (2024a) hypothesized that diploid *V. atrococcum* and *V. caesariense* are two ends of a continuous spectrum of leaf pubescence (densely pubescent versus glabrous, respectively) and perhaps of other characters such as fruit glaucescence, where intermediates reflect morphological variation within a single diploid species. Similarly, these sets of authors hypothesized that tetraploid *V. arkansanum* and *V. formosum* comprise a single species with the same patterns of morphological variation as in the diploids, with the supposed intermediate tetraploid *V. marianum* sensu Camp as a synonym. Fritsch et al. (2024a) noted that these hypotheses would be consistent with several sources of data, including 1) anecdotal crossing (Vander Kloet 1980) and field studies (Ballington et al. 1980, 1982), 2) the overall genetic similarity in diploid *V. atrococcum* and *V. caesariense* observed in an allozyme study (Bruederle & Vorsa 1994), and 3) the documentation of diploids and tetraploids growing together in a natural population of *V. corymbosum* sensu Vander Kloet (Poster et al. 2017). However, the in-depth level of study necessary to resolve the taxonomy of the residual highbush group has not yet been conducted.

Here we assess the various hypotheses proposed for the origin, evolution, and species circumscription of the residual highbush blueberries with data from morphology, flow cytometry, phylogenomics, and genetic clustering analyses. Based on the results, including the recovery of monophyly for this group, we present a taxonomic revision of the residual highbush clade. We recognize two species, a diploid and a tetraploid, providing descriptions, comprehensive synonymy, lists of representative specimens examined, and a distribution map for each.

MATERIALS AND METHODS

Flow cytometry analysis.—We sampled numerous individuals of *Vaccinium* sect. *Cyanococcus* from natural populations for flow cytometry analysis (P.S. Manos et al. unpubl. data), including 238 individuals conforming to the morphology of the residual highbush clade. The samples extended throughout most of the range of the group (Fig. 1; Appendix 1). The methods and analysis for flow cytometry were conducted as in Crowl et al. (2022) and Weakley et al. (2024) except that samples were sent to either the North Carolina State University Mountain Horticultural Crops Research & Extension Center, Mills River, NC or Plant Cytometry Services, Didam, Netherlands. The validity of this method for estimating ploidal levels in *Vaccinium* has been previously demonstrated by Hummer et al. (2015), Redpath et al. (2022), and Costich et al. (1993), the latter showing that an observed increase in nuclear DNA content parallels an equivalent increase in ploidy.

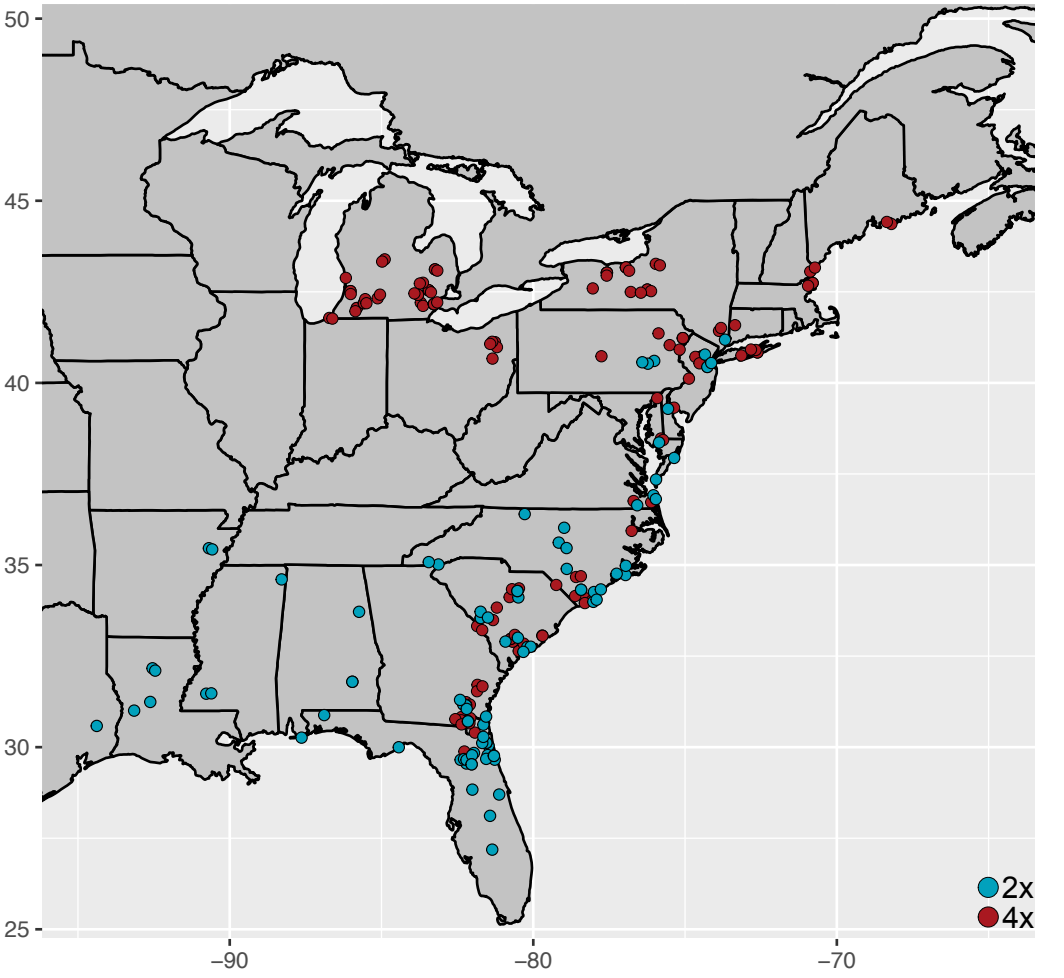

Fig. 1. Geographic locations of samples used for flow cytometry analysis, by ploidy. Blue dots = diploids, red dots = tetraploids. The locations of overlapping dots have sometimes been jittered for visibility.

DNA sequence-based phylogenetic analysis.—We used a subset of samples employed in the flow cytometry analysis for the other analyses in this study, such that for each sample used, an estimate of ploidy was also available, with the exception of *P.W. Fritsch 2267*, for which we assumed diploidy based on morphology and geographic location. For these analyses, we employed 31 samples of the residual highbush group, 15 diploids and 16 tetraploids (Appendix 1). DNA extraction, quantification, sequencing, sequence filtering and processing, as well as allele phasing were conducted as in Manos et al. (in press). The final DNA alignment file is available from the Mendeley Data repository at https://data.mendeley.com/datasets/nc2rfn9b49/1 (doi:10.17632/nc2rfn9b49.1).

To assess the monophyly of the residual highbush group and its placement within the *Vaccinium* sect. *Cyanococcus* clade, we conducted a diploid-only set of phylogenetic analyses with our newly generated data added to the diploid dataset for *V.* sect. *Cyanococcus* of Crowl et al. (2022), with *V. macrocarpon* Aiton of *V.* sect. *Oxycoccus* (Hill) W.J.D. Koch as the outgroup. We then added the tetraploids to the analysis. Individual gene alignments were constructed with MAFFT v7.245 (Katoh & Standley 2013). We concatenated the alignments

and partitioned genes with PartitionFinder (Lanfear et al. 2014) and performed a partitioned ML analysis with IQ-TREE (v1.6.9; Nguyen et al. 2015) using 1000 ultrafast bootstrap (BS) replicates to assess topological support.

Principal component and clustering analyses.—To measure the extent of clustering, admixture, and gene flow among species of the section in the context of hypotheses for the origin and evolution of the residual highbush group, we performed principal component and clustering analyses with our DNA data. For these analyses, we used the PATÉ polyploid phasing pipeline (Tiley et al. 2024) to create an allele dataset. To genotype individual samples, the supercontig assemblies from HybPiper were used as reference sequences. Low-quality variants were filtered with the Genome Analysis Toolkit v4.2.0 (McKenna et al. 2010; DePristo et al. 2011) and phased haplotype sequences were constructed with HPOP-G (Xie et al. 2016). Variant calling was conducted at the ploidal level determined by flow cytometry. We used the fasta2structure.py script (https://github.com/gtiley/fasta-conversion) to convert the allele alignments into a principal component analysis (PCA) matrix and an integer-formatted file (STRUCTURE input). We filtered the alignment to only include SNPs present in 50% of samples. To avoid sampling linked loci, we then pruned the dataset to include a single SNP per gene region.

We performed PCA analysis with the R package *adegenet* (Jombart & Ahmed 2011) and clustering analysis with STRUCTURE v.2.3.4 (Pritchard et al. 2000). For these analyses, we included all diploids plus our residual highbush samples as well as our samples from the phylogenomic analysis of the tetraploids *Vaccinium angustifolium* Aiton and *V. simulatum*, hypothesized by Camp (1945) to be involved in the ancestry of *V. corymbosum* in Camp's concept of this species. In the STRUCTURE analysis, we determined the "best" *K* value using the method of Evanno et al. (2005).We conducted 20 independent runs on each *K* value from 6 to 11 in the first analysis, and from 2 to 7 in the second, based on our *a priori* minimum number of taxa (clusters) sampled in each dataset.

Taxonomic revision.—We examined specimens from the following herbaria in-hand: BRIT, CHRB, GA, GMUF, MO, NLU, NY, ODU, SMU, UMO, VDB, WILLI, and WVA (acronyms as in Thiers 2024, updated continuously). We supplemented the data from these specimens with our own field collections (1003 numbers, with sets at BRIT and DUKE) and observations, including photographs of most collections. Specimens from the following herbaria were examined as digital images online via the SERNEC (https://sernecportal.org/portal) and Canadensys (https://www.canadensys.net) data portals: ACAD, APSC, ASC, AVCH, BALT, BAYLU, BM, BRU, CGCC, CHAS, CHRB, CHRV, CLEMS, CM, CMC, DOV, DSC, DUKE, ECUH, EKY, ETSU, F, FLAS, FTG, FUGR, GAS, GH, GSW, ICHAUWAY, ILL, LFCC, LINN, LL, LSU, LYN, MARY, MCA, MICH, MISS, MISSA, MMNS, MOAR, MOR, MT, MUHW, MWCF, NBYC, NCSC, NCU, NCZP, NEBC, NY, OKL, OS, OUHC, PAC, PH, PIHG, PLAT, QFA, RSA, TENN, TEX, UCHT, UNCC, URV, USAM, USCH, USCS, USF, USMS, UTC, UV, VCU, VSC, VT, WCUH, WEWO, WIS, WS, and WVW. Type specimens were examined either in-hand or as digital images available online at JSTOR Global Plants (https://plants.jstor.org). The specimens at ACAD were downloaded from their local campus server. Specimen citations followed by "[image!]" in taxon entries or "[i]" in the Appendices indicate that the specimens were examined as digital images only.

The species distribution maps were resolved to the level of subdivision within a state (U.S.) or province (Canada), with one specimen cited per subdivision of presumed naturally occurring populations. The subdivisions were counties except for parishes in Louisiana, regional county municipalities in Quebec, and some independent cities in Virginia. The specimens used as the basis for the maps were also those cited as representative specimens examined (Appendices 2 and 3). To generate the portion of the maps based on digital images (43% of subdivisions), we searched for all records of *Vaccinium* in a subdivision, sorted the records by species name, and examined images of specimens identified in the database to any of the species names that have been used for the residual highbush group. Therefore, some subdivisions in which the species occur might not be documented here because the specimen(s) of a species in that subdivision are currently identified as something other than one of the residual highbush taxon names. For some online images, it was difficult to discern the characters for which accurate identification to one of the species in our treatment are required; these specimens were not used for constructing the maps. An MS Excel file of the label data of the specimens used

for the maps and lists of representative specimens examined is available from the Mendeley Data repository at https://data.mendeley.com/datasets/nc2rfn9b49/1 (doi:10.17632/nc2rfn9b49.1).

The morphological descriptions were based on our fieldwork and herbarium research. The format of the descriptions generally followed that used for *Vaccinium ashei* in Weakley et al. (2024). The specimens examined by us formed the dried-specimen basis of the descriptions. These consisted of 1) the specimens cited in Appendices 2 and 3, 2) our herbarium specimen vouchers of the treated species collected specifically for this study (ca. 571 diploid collections and ca. 455 tetraploid collections, with ploidy estimated from morphology and, when available, flow cytometry), and 3) many hundreds more from the herbaria cited above, either through visits to EKY, GMUH, MO, MICH, NY, ODU, and WILLI by the first author at various stages in assessing the species taxonomy of *V.* sect. *Cyanococcus*, or through loans from GA, MO, NY, UMO, and WVA to BRIT, where specimens could be studied in more detail. The species were compared to each other as well as the other species of *V.* sect. *Cyanococcus* overlapping in the range of the residual highbush group, with differentiating characters identified.

RESULTS

Flow cytometry.—Of the 238 samples assessed for ploidy with flow cytometry, 93 were found to be diploid and 145 tetraploid (Fig. 1; Appendix 1). The geographic distributions of these ploidal levels were found to be distinct across a substantial portion of the overall geographic range of the residual highbush group. Our diploid samples ranged from extreme southern Maine south along the Coastal Plain and Piedmont to south-central Florida, then west throughout much of the southeastern U.S., including the southern Appalachians, to eastern Texas. The tetraploids ranged from Wisconsin east to southern Canada and New England, south along the Coastal Plain to northern Florida and Alabama, extending to Virginia and West Virginia in the Appalachians.

Phylogenomic data.—The concatenated ML analysis yielded a monophyletic residual highbush group (BS = 100; Fig. 2) that was placed as sister to *Vaccinium virgatum*. The other "highbush" species of the section recognized by Camp (1945) and synonymized under *V. corymbosum* by Vander Kloet (1980, 1988) grouped outside the residual highbush clade. Within the residual highbush clade, neither the diploids nor the tetraploids formed single clades. A clade of two tetraploids (*CY-132* and *CY-197*; BS = 100) grouped within an otherwise diploid clade ("main clade;" BS = 100). A clade (BS = 100) of one diploid (CY-350) and one tetraploid (CY-360) grouped (BS = 100) as sister to the main clade. The rest of the tetraploids were placed in three clades (BS = 100, 91, and 87) each of which grouped successively outside the main clade (BS = 100 and 100, respectively). Little geographic partitioning could be discerned from the analysis. For example, the tetraploids CY-132 and CY-197 from Essex Co., Massachusetts and Kershaw Co., South Carolina, respectively, formed a clade (BS = 100), and the diploids PWF2358, PWF2359, and PWF2267, from Arkansas and Texas, grouped with CY-372 from Ware Co., Georgia.

Camp's (1945) species segregates in each ploidal level of the residual highbush clade, as best as we could identify them as such, did not form groups, but were instead scattered throughout the clade. The characters used for distinguishing these segregates, i.e., the presence or absence, and arrangement, of stem pubescence, leaf pubescence, leaf glaucescence, and fruit glaucescence, and a serrate or entire leaf blade margin, did not correlate with any subclades in the residual highbush clade. Variable morphological characters in this clade were found only to correlate with ploidal level: corolla size, larger in tetraploids, and stem stomatal bump prominence and density, more raised and less dense in tetraploids (see Discussion). The diploid sample CY-350, with consistent and regularly spaced stipitate-glandular trichomes on the leaf blades abaxially but with characters otherwise consistent with residual highbush, grouped within the residual highbush clade. The sample is denoted henceforth as "*Vaccinium cuthbertii*" (Small) Uphof because its morphology is consistent with the type of this name and the only name applicable to specimens with this morphology.

Principal component and clustering analyses.—The first two components of the PCA exhibited six clusters corresponding to 1) *Vaccinium darrowii* + *V. tenellum,* 2) *V. elliottii,* 3) *V. pallidum* Aiton, 4) *V. simulatum,* 5) *V.*

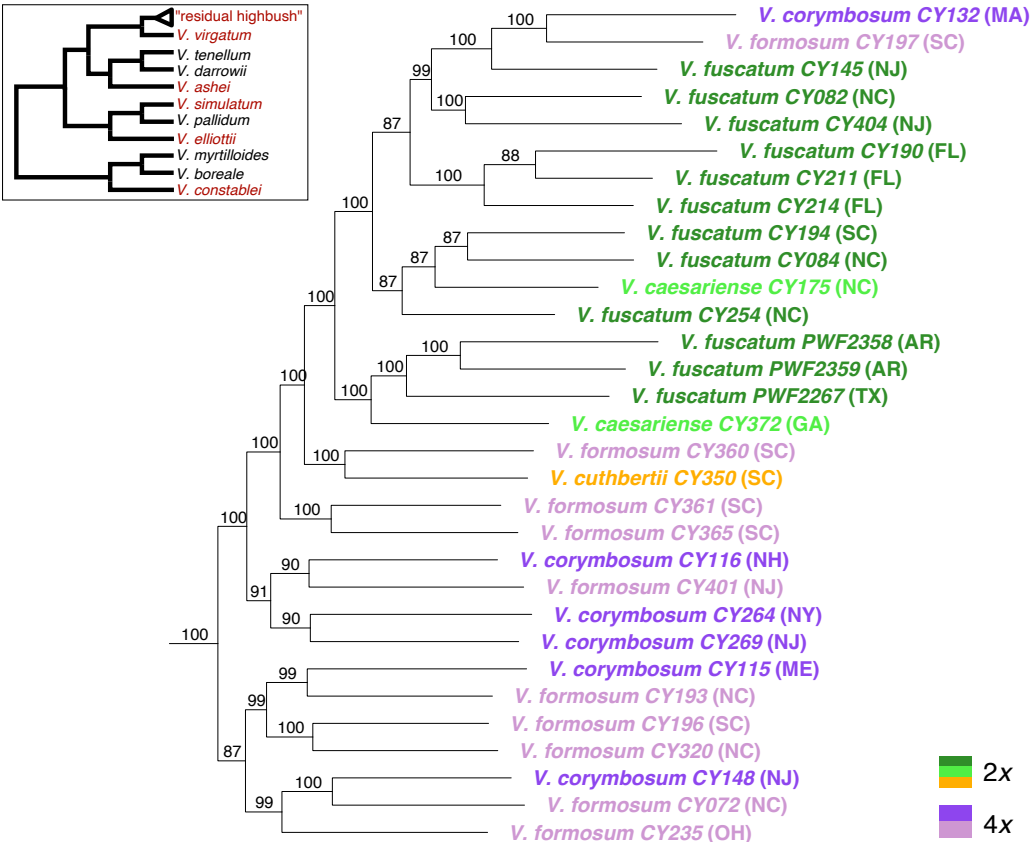

Fig. 2. Summary tree from a maximum-likelihood phylogenetic analysis of *Vaccinium* sect. *Cyanococcus* based on the concatenated Angiosperms353 probe set with multiple samples of the residual highbush clade added to the diploid-only dataset of Crowl et al. (2022). Species names approximate the taxonomic concepts of Camp (1945), each indicated with a different color; green and yellow colors are diploids, and purple colors are tetraploids. Numbers above branches indicate bootstrap support values. The two-letter abbreviation of the U.S. state in which the sample was collected is indicated next to each sample label. The inset shows the wider sectional phylogeny with the highbush species of Camp (1945), as combined together into *V. corymbosum* by Vander Kloet (1980, 1988), depicted in red.

angustifolium + *V. boreale* I.V. Hall & Aalders + *V. myrtilloides* Michx., and 6) the residual highbush clade (Fig. 3). Within the residual highbush cluster, diploids and tetraploids each formed subgroups, with *V. cuthbertii* placed closest to the tetraploid group and the tetraploids CY-132 and CY-197 placed closest to the diploid group. In the phylogenomic analysis, these tetraploids were the same samples that grouped in the otherwise diploid clade.

In the clustering analysis, the best *K* value was determined to be $K = 8$; we also assessed the *K* values of 6, 7, and 9 for comparison (Fig. 4). The diploid residual highbush samples were nearly all distinct in genetic structure from the tetraploid residual highbush samples at all *K* values; the exception was *Vaccinium cuthbertii*, which shared a genetic profile with the tetraploids. Except for *V. cuthbertii*, little if any substructure was detected within each of the residual highbush ploidal levels: no distinction was apparent within or between *V. caesariense* and *V. fuscatum*, or within or between *V. corymbosum* and *V. formosum*. Both diploid and tetraploid residual highbush samples were each largely distinct in genetic structure from the other species included in the analysis at all *K* levels assessed except for *V. fuscatum* with possible admixture with *V. elliottii*, and *V. darrowii* and/or *V. tenellum*, as seen at $K = 8$. As inferred from the greater number of genotypes represented by

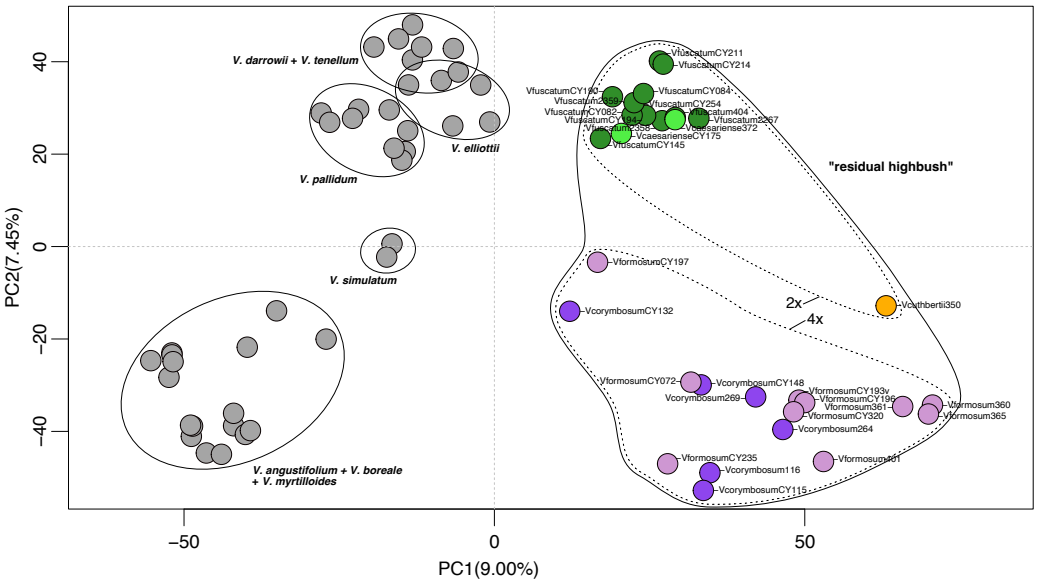

Fig. 3. Two-dimensional principal component analysis plot (PC1 and PC2) with ingroup samples of residual highbush *Vaccinium* sect. *Cyanococcus* colored as in Fig. 2 and outgroup taxa in gray. The samples are the same as those in the phylogenomic analysis except for the addition of samples of the tetraploids *V. angustifolium* and *V. simulatum*. Circles around points (solid and dotted lines) are drawn manually around groups based on a combination of morphospecies and ploidal level.

colors in Fig. 4, genetic diversity was substantially higher in the tetraploid group than in the diploid group, especially at $K = 9$.

DISCUSSION

Evolution of the residual highbush clade.—Our phylogenomic results provide strong evidence for the monophyly of residual highbush blueberries, regardless of ploidy. The results are consistent with previous findings that yielded a single clade of residual highbush diploids (Crowl et al. 2022). Monophyly is corroborated by morphology: the samples in this clade all share the combination of plants with clumped stems, not clonal, tall stature [(0.5–)0.9–5.0 m], eruptive periderm common on (aerial) branchlets of the third- or fourth-year and older (helpful with herbarium material to distinguish from low clonal species, where eruptive periderm is mainly found only on subterranean stems with roots visible), large vegetative buds (1.9–4.5 mm long), the presence of sessile glands near the leaf blade base on most leaves per specimen, revolute leaf blade margins, and exserted styles. The large vegetative buds in particular were found to usually distinguish this clade from the other species in the section. In cases where these buds are smaller than normal, we found that the combination of the other characters could be used to distinguish individuals of this clade from those of the rest of the section.

The genetic clustering analysis and PCA yielded a pattern of strong genetic distinction between the residual highbush clade and the other diploids in *Vaccinium* sect. *Cyanococcus*. No evidence for admixture was detected between the tetraploids of the residual highbush clade and the diploids of the section, with the possible exception of residual highbush *V. cuthbertii*, whose genetic profile resembled that of the tetraploids. Camp's (1945) concept of a highly complex allotetraploid residual highbush species combining the genomes of many diploids and/or tetraploids is not supported by our data. Camp proposed an origin of *V. corymbosum* involving many of his tetraploid species of the section, i.e. (our taxonomy in parentheses; see Taxonomic Treatment section), *V. simulatum*, *V. brittonii* (= *V. angustifolium*), *V. lamarckii* (= *V. angustifolium*), *V. australe* (= *V.*

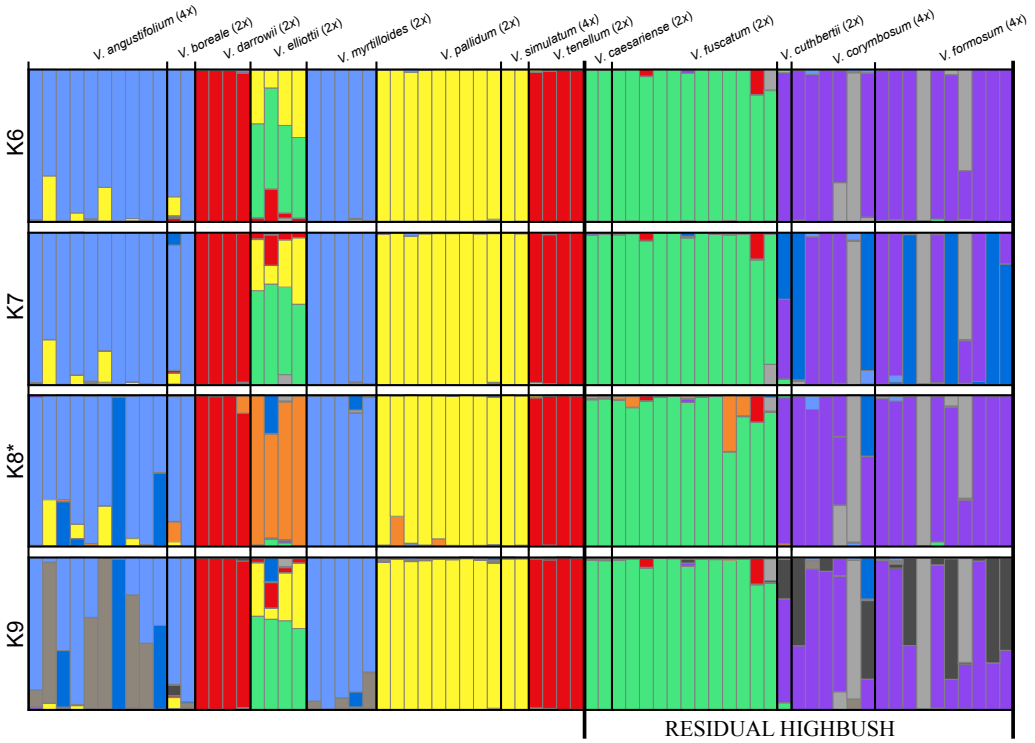

Fig. 4. Results of genetic clustering analysis with STRUCTURE of *Vaccinium* sect. *Cyanococcus* diploids, residual highbush blueberry tetraploids, and the tetraploids *V. angustifolium* and *V. simulatum*, with *K* ranging from 6 to 9. The samples are the same as those in the principal component analyses. The asterisk indicates the best *K* value.

formosum to other authors; = *V. corymbosum* to us), *V. marianum* (= *V. corymbosum*), and *V. arkansanum* (but probably diploid). Because we have synonymized *V. australe* (= *V. formosum*) and *V. marianum* under *V. corymbosum*, and because the synonymy of *V. brittonii* and *V. lamarckii* under *V. angustifolium* has been well justified in later studies (Aalders & Hall 1963; Vander Kloet 1978), this hypothesis reduces to involvement of *V. simulatum* and *V. angustifolium*. There is no evidence from our study to support Camp's hypothesis: our samples of *V. simulatum* and *V. angustifolium* consistently group in other clades within the section, without apparent admixture with residual highbush species. Similarly, Vander Kloet's (1980, 1988) compilospecies concept of *V. corymbosum* is not supported because genetic profiles and the PCA cluster of tetraploid *V. corymbosum* in our sampling are distinct overall from those of the diploids, which would otherwise be expected to show admixture and overlap.

The presence of both diploids and tetraploids occurring uniquely in the same clade supports an autopolyploid origin of the tetraploid residual highbush blueberries from diploid residual highbush progenitors. Neither the diploid nor tetraploid components of the residual highbush clade were recovered as monophyletic. Further, no morphological characters were found that support the monophyly of either ploidal level other than those associated with polyploidy itself, with the possible exception of the relative phenology of leafy shoots versus flowers (see "Taxonomic implications" section below). The phylogenetic nesting of the diploids within the tetraploids implies either that we have not sampled diploid individuals that would have grouped more basally to the tetraploid samples were they included, or that ancient diploid genotypes of residual highbush blueberry ancestral to the clade no longer exist. Alternatively, this pattern could be an artifact of the concatenated ML analysis, which does not account for multiple subgenomes present in polyploids.

Our data are consistent with the hypothesis of Lyrene et al. (2003) and Soltis et al. (2007) that tetraploid *Vaccinium corymbosum* was derived through autopolyploidy, although this hypothesis may have been formulated solely on the basis of autopolyploidy in the genetic or cytological, versus taxonomic, sense of polysomic inheritance patterns. Also unclear in these studies is the taxonomic concept of (tetraploid) *V. corymbosum* employed, e.g., whether it included *V. simulatum*. Whether all tetraploids of *Vaccinium* arose through autopolyploidy, as asserted by Lyrene et al. (2003), must await further studies but is being tested further in *V.* sect. *Cyanococcus* (Manos et al , in press).

Our results are less clear as to whether the tetraploids of the residual highbush clade arose from diploid progenitors through a single event or multiple events. Multiple origins are supported by the nonmonophyly of the tetraploids and the presence of several clades of mixed ploidy. Under simple parsimony reconstruction (not shown), tetraploidy would be inferred to have evolved at least three times from diploidy (assuming that diploidy is assigned to the stem node). The high frequency of unreduced pollen in natural populations of diploid species of *Vaccinium* sect. *Cyanococcus*, including in the residual highbush clade, has been well documented (Ortiz et al. 1992). As inferred through crossing experiments, unreduced ovules may occur as well (Lyrene et al. 2003). The strong triploid block in the section, which negates the viability of most hybrids between parents of differing ploidy (Lyrene et al. 2003), could be overcome in natural populations by the production of unreduced gametes in diploids (Ortiz et al. 1992; Poster 2017; Fritsch et al. 2024a). The union of two such gametes could result in the direct production of tetraploids and thus multiple tetraploid origins if the unions occurred multiple times and if they resulted in viable progeny.

However, results from prior studies as well as several aspects of our results suggest that the establishment of tetraploid plants from unreduced diploid gametes is rare, and therefore we might expect few origins or even a single origin of tetraploid residual highbush. In a study of unreduced pollen production in the diploid component of *Vaccinium* sect. *Cyanococcus*, diploid residual highbush populations (identified as "*V. corymbosum*" in the study) yielded the lowest percentage of unreduced pollen producers, at 7.4% (Ortiz et al. 1992), although this percentage would still allow some opportunity for crosses involving unreduced diploid gametes. Moreover, Poster et al. (2017) found that tetraploids flower on average one week later than diploids in a mixed population in the Great Swamp, New Jersey. This would be expected to reduce the opportunity for crosses between ploidal levels versus complete overlap in flowering times, although the observed partial overlap in flowering times would still allow for the possibility of crossing. Five aspects of our results bear on this issue, as follows:

1) The entire western half of the diploid residual highbush range is distinct from that of the tetraploid; range overlap is restricted to the Atlantic Coastal Plain and East Gulf Coastal Plain (Figs. 1, 8, 12). If viable tetraploids were commonly being produced via unreduced gametes in diploid parents, then one would expect tetraploids to be found at least sporadically throughout the range of the diploid. However, no such tetraploids have been detected, either with our flow cytometry data or morphology, although it remains possible that our flow and herbarium specimen sampling has missed them.
2) As noted by Poster et al. (2017), if gene flow is occurring between the diploid and tetraploid levels in the residual highbush blueberries, it is more likely through the fusion of unreduced diploid gametes with reduced tetraploid gametes. This would result in gene flow from the diploid level into the tetraploid level. If such unidirectional gene flow is present in the residual highbush clade, then it would likely be occurring only in sympatry. However, except for *Vaccinium cuthbertii*, the pattern of genetic structuring in our analyses does not support gene flow between ploidal levels, and in any case, sympatry should not be taken as evidence for *in-situ* derivation of tetraploids.
3) If local multiple origins of the tetraploids were occurring, then we would expect the diploids not involved in interploidal gene flow to be paraphyletic with respect to the diploids and tetraploids involved in the gene flow. Our phylogenomic analysis, however, did not recover this relationship. For example, the diploids from Texas, Louisiana, and Arkansas, where tetraploids are absent, group in

various places on the tree, intermingled with diploids from other areas as well as tetraploids. Nonetheless, it is possible that our data are not tracking population-level events.

4) In our PCA results, again except for *V. cuthbertii*, the samples of the residual highbush clade clustered by ploidy.
5) Finally, our genetic clustering analysis yielded higher genetic diversity within the tetraploid versus diploid component of the residual highbush clade, consistent with the results from studies of diploids and their autotetraploid derivatives in other groups of plants (e.g., Soltis & Soltis 1989; Brown & Young 2000; Luttikhuizen et al. 2007). This has been explained in part through the inherently larger effective population size of the autotetraploids because each tetraploid individual harbors twice the number of gene copies and four alleles within loci instead of two (Luttikhuizen et al. 2007). For this pattern to emerge would require sufficient time for new mutations to become prevalent in the tetraploid. Therefore, our results suggest that at least some of the genetic component of the tetraploids in the residual highbush clade is not of recent origin and that diploids and tetraploids have been separated genetically for some time.

Taken as a whole, and in the context of the prior evidence for a strong triploid block in the section, our data provide strong evidence for a diploid-tetraploid progenitor-derivative species pair in the residual highbush clade, with the tetraploid plants behaving like a population system distinct from the diploid, i.e., operating as a reproductively isolated species. The evolution of widespread tetraploid is a noteworthy example of autopolyploid speciation, one of the fastest speciation mechanisms known in nature (Soltis et al. 2007; Levin 2019). The tendency for tetraploid "highbush" blueberries to occur farther north than diploids had already been generally noted by both Camp (1945) and Vander Kloet (1980). Although their taxon concepts differ substantially from ours (see Taxonomic Treatment section), we found the same general trend within the residual highbush clade (cf. Figs. 8 and 12). The geographic distribution of ploidal levels in the residual highbush group found here is consistent with the global trend of increasing ploidal level with latitude (Rice et al. 2019). We postulate a biogeographical scenario in which one or several populations of tetraploid residual highbush cytotypes emerged locally among diploid populations along the Atlantic Coastal Plain soon after the Last Glacial Maximum (LGM), with only the polyploids spreading northward and westward into the newly available habitats upon glacial retreat. This would be consistent with the association found between the formation of autopolyploid linages and environmental change, particularly from the Pleistocene onward (Parisod et al. 2010).

Further progress on the origin and evolution within the residual highbush clade will require more detailed study at the population level, both locally and regionally. Of particular interest would be 1) the further assessment of the distribution of ploidy both geographically and especially phylogenetically, 2) more detailed assessment of possible gene flow into the residual highbush clade from other species, and within the clade from the diploid level into the tetraploid level; 2) an attempt to detect trends in habitat differences between the two ploidal levels, and 3) the study of morphological characters across the ploidal levels associated with heritable traits. During field work, we often observed the two ploidal levels growing together on the Atlantic Coastal Plain without apparent habitat differentiation, but in other localities we found populations of either diploids or tetraploids. In population-level studies, the ploidal level of each individual should be determined, ideally through flow cytometry, or if this is not possible in all cases, then at least through morphological characters documented below that are thought to be associated with ploidy. Sampling throughout the geographic distribution of the clade, including areas in which one of the ploidal levels is absent, would ensure that polymorphisms in the area of sympatry reflect gene flow rather than group-wide polymorphism. Also helpful would be to sample other diploids in *Vaccinium* sect. *Cyanococcus* in the area of sympatry to test for admixture with higher sample sizes than employed here.

Taxonomic implications of the results.—We combined the results from flow cytometry, phylogenomics, and allele-based PCA and clustering analyses with our examination of morphology to synthesize a taxonomic revision of the residual highbush clade. We relied on the combination of stem stomatal bump prominence and

density and, when available, corolla size as proxies for ploidal level in the many herbarium specimens examined, including online digitized images, for which ploidal level was otherwise not ascertainable. Corolla size has been shown to differ significantly between diploids and tetraploids in a population of residual highbush in the Great Swamp, New Jersey (Poster et al. 2017), with some overlap. We observed the same general pattern in the flowering vouchers of our flow estimates. In our field work, we also noted a general trend of brighter white and less translucent corollas in the tetraploid flowers, paler white to greenish white and more translucent in the diploids, although, like corolla size, these characters overlap to some degree. The difference likely results from thicker corollas in tetraploids. In the Great Swamp population, tetraploids were found to exhibit a peak flowering time about one week later than diploids (Poster et al. 2017). Others have noted this difference anecdotally (see discussion of William Oakes on page 435).

Esparza Garcia et al. (in prep.) found a strong correlation between ploidy and leaf stomatal size and density in *Vaccinium* sect. *Cyanococcus*, where size increases and density decreases with increasing ploidy. The stems in this section also have stomata, generally raised above the surface such that each stomate is associated with a protuberance or "bump" (Odell et al. 1989) resulting in a verrucose appearance. Fritsch et al. (2024a) investigated whether the same pattern of stomatal variation in the leaves among ploidal levels could also be observed on stems and found the pattern in at least some of the species, including those of the residual highbush group. Although we have not rigorously tested the pattern for the stems as in Esparza Garcia et al. (in prep.) did for leaves, we found the stem pattern to be generally consistent among the vouchers used for our flow estimates in the residual highbush clade—the stomatal bumps are less prominent and denser in diploids relative to the tetraploids (cf. Figs. 5C and 6A versus 9B and 10A). There are some clear exceptions, e.g., tetraploids of the Okefenokee Swamp area with closely spaced stomatal bumps (e.g., *A.A. Crowl CY-375*, *CY-380*, and *CY-383*). These plants are also unusual for tetraploids in having nearly smooth stems with the stomata not notably raised.

Using these characters as proxies for ploidy, we discovered two other characters that may help to distinguish ploidal levels in the members of the residual highbush clade. Fruit size is generally larger in the tetraploids than in the diploids (8–15 mm diameter versus 4–12 mm). This difference had already been reflected in some of the species descriptions of Camp (1945), although not specifically denoted. We also found a consistent difference in leaf phenology at anthesis, with leaf flush tending to occur after the full opening of flowers in diploids and prior to the full opening of flowers in the tetraploids (cf. Figs. 7, 11). This difference was first brought to the attention of one of us (P.W.F.) by Z. Bradford (pers. comm.) while this author was conducting field work at Twin Hickory Recreation Area, Henrico Co., Virginia. It may be related to an overall difference in flowering time between diploid and tetraploid residual highbush, where the tetraploid was found to flower on average ca. one week later (Poster et al. 2017). We found that this character facilitated the identification of diploids and tetraploids of residual highbush herbarium specimens, even as digital images, when they were collected at the proper stage of leaf flush. The more prominent stem stomata and the larger leaf stomata, flowers, and fruits of the tetraploids relative to the diploids may be considered as associated with the polyploid gigas effect (Sattler et al. 2016), as may the later flowering period (Levin 1983) and possibly the paler white corollas if this character results from greater thickness. The difference in floral versus leaf flush between the two ploidal levels may be associated with later flowering time but this needs careful assessment. The pattern may be weaker in the southern part of the range of the diploid, e.g., Florida, where leaf flush appears to progress earlier relative to anthesis (P.W.F., pers. obs.).

The characters used previously to distinguish species segregates within a ploidal level in the residual highbush clade, i.e , stem and leaf pubescence, leaf margin, and leaf and fruit glaucescence, showed no correlated gaps in any two character states; i.e , no association with ploidy was evident. This supports the hypothesis of Luby et al. (1991) and Fritsch et al. (2024a) in which these characters were proposed as polymorphisms within both diploid and tetraploid lines and not useful for species delimitation. It also finds support with anecdotal evidence by Vander Kloet (1980: p. 1190), who grew F1 progeny from two adjacent wild-growing plants from Robeson Co., North Carolina with dense stem and leaf pubescence and shiny black berries. We consider it likely that Vander Kloet's plants were individuals of diploid residual highbush because in North

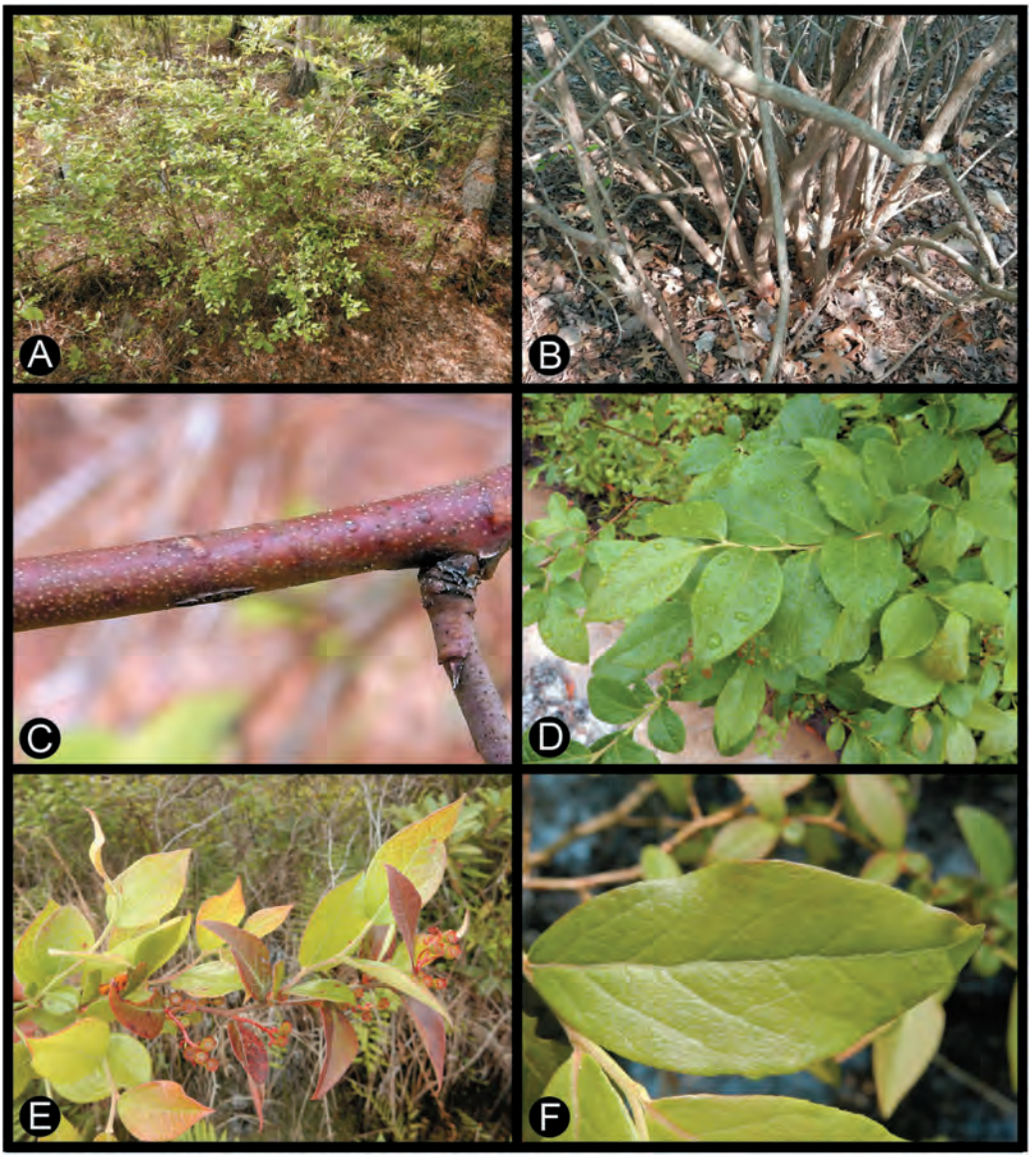

Fig. 5a. *Vaccinium corymbosum*. **A.** Habit. **B.** Basal portion of plant showing clumped stems. **C.** Second-year branchlet. **D.** Leafy branchlet. **E.** Branchlet of semi-evergreen plant. **F.** Leaf, adaxial view. Photos: A, *P.W. Fritsch 2553*; B, *P.W. Fritsch 2516*; C, *P.W. Fritsch 2447*; D, *P.W. Fritsch 2556*; E, *P.W. Fritsch 2550*; F, *P.W. Fritsch 2483*.

Carolina they most commonly exhibit this morphology, in contrast to the generally less pubescent stems and leaves and glaucous fruit in residual highbush tetraploids. The progeny exhibited a mix of glabrous or pubescent stems and/or leaves, and dull or shiny fruit with or without glaucescence, thus demonstrating that these characters do not breed true, at least at the ploidal level sampled.

Other characters could be associated with ploidy in the residual highbush clade but have yet to be studied in detail. We could not detect differences between the ploidal levels for plant height, vegetative bud size and color, leaf size, second-year branchlet width (although difficult to consistently measure), and fruit glaucescence. Fruit

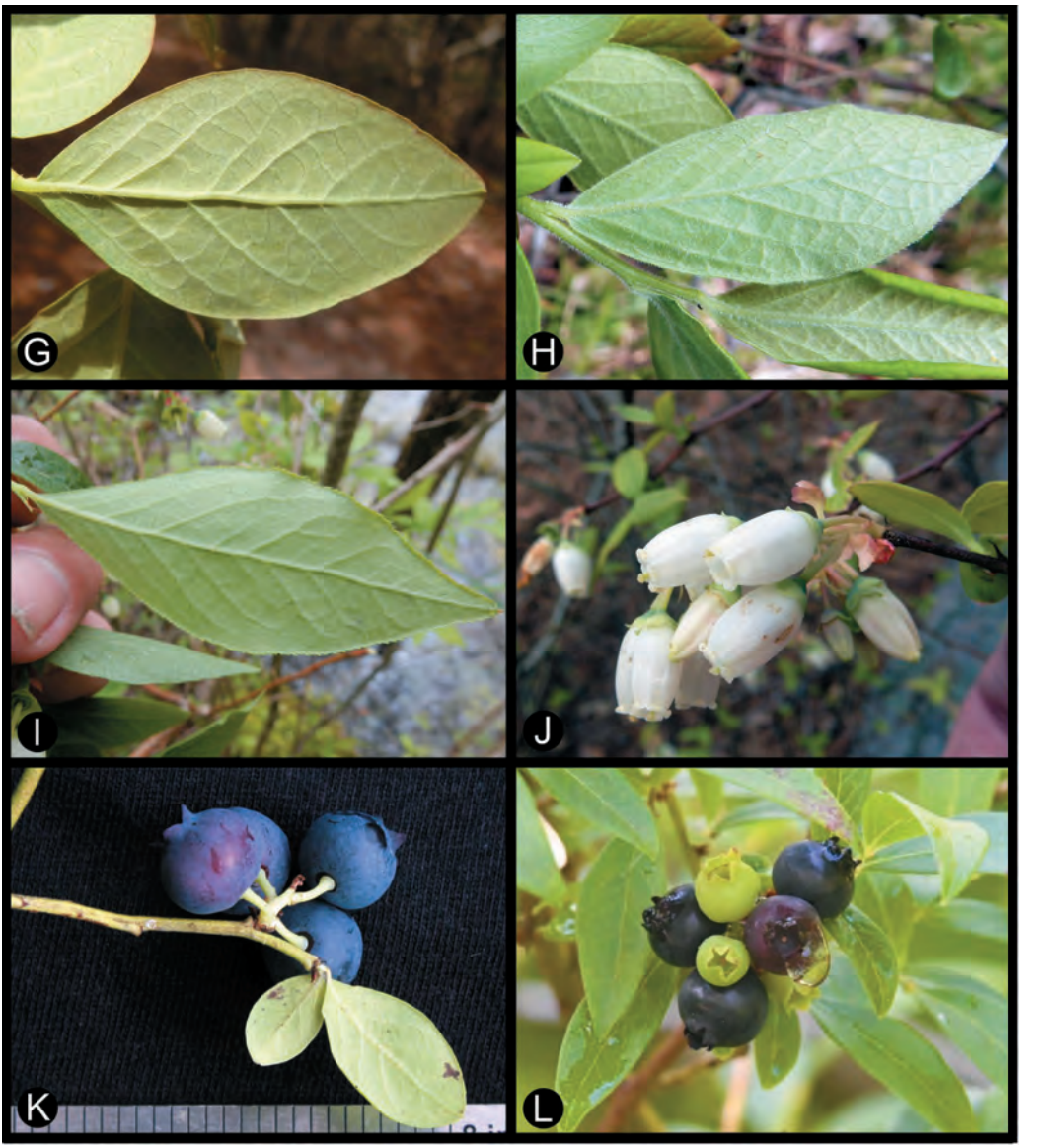

Fig. 5b. *Vaccinium corymbosum*. **G–I.** Variation in leaf margin and surface pubescence, abaxial view. **G.** Sparsely pubescent (midvein only), entire-margined. **H.** Pubescent, entire-margined. **I.** Glabrous, serrate-margined. **J.** Inflorescence. K, L. Variation in fruit glaucescence. **K.** Typical glaucous fruit. **L.** Non-glaucous fruit. Photos: G, *P.W. Fritsch 2453*; H, *P.W. Fritsch 2490*; I, *P.W. Fritsch 2495*; J, *P.W. Fritsch 2447*; K, *R. Carmickle RC121*; L, inaturalist.org/observations/227378772.

does appear to be more commonly glaucescent in the tetraploids, but the absence of fruit glaucescence was also observed in many tetraploid individuals, as already documented by Camp through notes on herbarium specimens from Stark Co., Ohio (see Taxonomic Treatment section). As far as we are aware, pollen size has not been assessed for a correlation between ploidal levels in natural populations in the residual highbush clade. This character could well show a correlation, as has been shown between diploids and artificially induced tetraploids of *Vaccinium darrowii* and *V. elliottii* (Dweikat & Lyrene 1991; Chavez & Lyrene 2009).

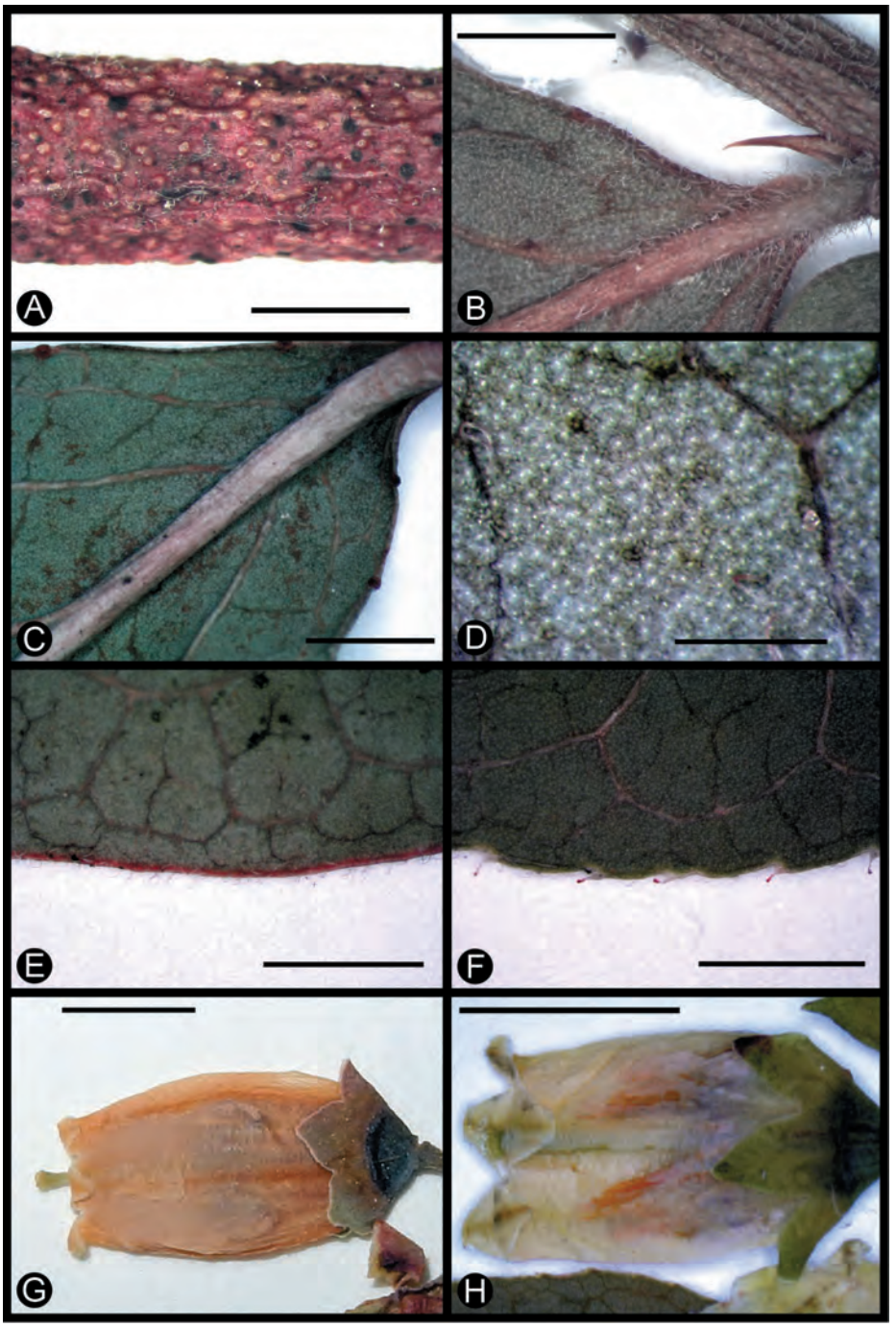

Fig. 6. *Vaccinium corymbosum*. **A.** Stem. **B.** Vegetative bud and leaf base. **C.** Example of glabrous abaxial leaf surface. Note also conspicuous sessile marginal leaf glands. **D.** Abaxial surface of leaf blade. E, F. Variation in leaf margin. **E.** Entire-margined. **F.** Serrate-margined. G, H. Flower. **G.** Typical large form. **H.** Smaller form. Scale bars, A–C, E, F = 2 mm; D = 500 µm; G, H = 4 mm. A, *A.A. Crowl CY-232* (BRIT BRIT698782); B, *P.W. Fritsch 2251* (BRIT BRIT1058603); C, *A.A. Crowl CY-319* (BRIT BRIT698834); D, E, *R. Carmickle RC126* (BRIT BRIT927793); F, *R. Carmickle RC118* (BRIT BRIT927451); G, *A.A. Crowl CY-361* (BRIT BRIT792840); H, *P.W. Fritsch 2484* (BRIT BRIT914484).

Fig. 7. Exemplar herbarium specimen of *Vaccinium corymbosum* in flower showing stage of leaf expansion, *P.W. Fritsch 2449* (BRIT BRIT914492). Compare Fig. 11 collected in the same area on the same day in Henrico County, Virginia, 30 March 2023.

We could not substantiate the utility of some of the morphological characters not already mentioned above and used in the key of Uttal (1987a) for the identification of residual highbush blueberries in Virginia [*Vaccinium caesariense*, *V. corymbosum*, *V. formosum*, *V. fuscatum*, and *V.* × *marianum* (*V. formosum* × *V. fuscatum*)]. These characters are: leaves dark green (versus medium to pale green or glaucous to dark green), darkening on drying (versus not darkening on drying); leaves red-veined on undersurface (versus not); branchlet and leaf trichomes dingy (versus whitish or dark to white); branchlets brownish green to black (versus green or glaucous to brown); bud scales brownish green to black (versus peach to red); and leaves widest at or above middle (versus below middle).

The nature of the variation in some of the same characters observed for residual highbush blueberries at both ploidal levels is similar to that seen within *Vaccinium angustifolium*, which has been more carefully documented for similar variation with crossing studies. The shiny green versus dull whitish green leaves and absence or presence of glaucescence on the fruit, used by Camp (1945) to segregate *V. brittonii* Porter ex E.P. Bicknell and *V. lamarckii* Camp from *V. angustifolium*, do not breed true (Aalders & Hall 1963; Vander Kloet 1978). The variants with dull whitish green leaves and/or fruits without glaucescence are typically found as sporadic clones growing among the more common clones with shiny green leaves and glaucous fruits (Vander Kloet 1980; P.W.F., pers. obs.).

As found by Poster (2017) with flow cytometry data in a smaller sample size at one location, we found diploids and tetraploids growing together at localities of the Atlantic Coastal Plain and East Gulf Coastal Plain, often side-by-side [e g., South Carolina, Kershaw Co., Goodale State Park, *Vaccinium fuscatum*, *P.W. Fritsch 2580* (BRIT BRIT1058632), and *V. corymbosum*, *P.W. Fritsch 2581* (BRIT BRIT1058633)]. At these sites, the differences in stem stomatal bump prominence and density, leaf versus floral phenology, and corolla size and color are evident, although if used separately sometimes not diagnostic for identification because of overlapping character states. The differences in morphology mentioned above to distinguish the ploidal levels have been noted, explicitly or implicitly, by others. Perhaps the earliest expression of these differences was noted on a specimen collected from Ipswich Woods in Essex Co., Massachusetts by William Oakes, GH 00519414 (without number or date but collected sometime prior to 31 July 1848, the year of his death, and type material of *V. corymbosum* var. *atrocarpum* A. Gray (see Taxonomic Treatment section): "grows generally intermingled with *V. corymbosum* in Essex and Plymouth Co…Fruit always much smaller, black, destitute of the glaucous bloom, always ripe a week or more earlier than *V. corymbosum*, and also flowers earlier—I am in doubt whether it is more than a variety—but I have seen no intermediate fruit. *V. corymbosum* sometimes has the bloom washed off but is still easily dinstin. [distinguishable]." Although Oakes did not specifically mention the difference in relative floral versus leaf phenology, it is clear that he detected phenological differences between these plants. This has been corroborated by Poster et al. (2017), who documented a difference in flowering time of ca. one week, the same interval as observed by Oakes. Other collectors have more indirectly noted the differences between the ploidal levels growing at the same locality by collecting them at the same location on the same day, and identifying one as, e.g., *V. corymbosum* (corresponding to the tetraploid, whether or not that was understood) and the other as, e.g , *V. atrococcum* (corresponding to the diploid). Sometimes a difference in fruit glaucescence was noted, with *V. corymbosum* applied to the glaucescent plants and *V. fuscatum* or one of its synonyms such as *V. atrococcum* applied to the plants without glaucescence. We were not able to assess fruiting time differences.

Based on the sum of data presented above, we revise the taxonomy of residual highbush blueberries. We found the combination of stem stomatal bump prominence and density, corolla size, leaf flush versus flowering phenology, and fruit size to delimit these species. The maps of geographic distribution produced as a result of taxon identifications based on these characters showed largely distinct geographic distributions, with overlap only in the Atlantic Coastal Plain and East Gulf Coastal Plain, thus corroborating their overall treatment as two species despite the lack of flow cytometry data to assess ploidal level for most herbarium specimens. We have opted to name these species with conventional species names as recommended for autopolyploids meeting the criteria of various species concepts (Judd et al. 2006; Soltis et al. 2007; Eriksson et al. 2017), versus other proposed naming schemes such as the use of "agg." or "2*x*" and "4*x*" (see Judd et al.

2007; Kadereit et al. 2012). We were prevented from using the prefixes "diplo-" or "tetra-" (see Judd et al. 2007; Soltis et al. 2007) because both ploidal levels already have species names. We acknowledge that our data are not robust for assessing the occurrence or frequency of gene flow from the diploid to tetraploid levels, the presence of which might compromise our treatment, depending in part on the species concept employed. In the absence of such data, our treatment provides a working hypothesis of two species in the clade that is testable with more detailed population-level data.

The two species are the diploid *Vaccinium fuscatum* and the tetraploid *V. corymbosum*. A formal taxonomic revision, including a key to the species, full synonymy, descriptions, distribution maps, and lists of representative specimens examined, is provided below. We place four names variably recognized in recent floristic and horticultural literature in synonymy, i.e., the diploids *V. atrococcum* and *V. caesariense* under *V. fuscatum*, and the tetraploids *V. formosum* and *V. marianum* under *V. corymbosum*. The name *V. cuthbertii* is placed under the synonym of *V. fuscatum* but warrants further investigation as to its possible taxonomic distinctness.

TAXONOMIC TREATMENT OF "RESIDUAL HIGHBUSH" BLUEBERRIES OF *VACCINIUM* SECT. *CYANOCOCCUS*

KEY TO THE SPECIES

1. Stems with stomatal bumps generally evident and widely spaced (ca. 12 to 21/mm^2); flowering usually when leaves have attained ca. 1/20 to full size; corolla (4.0–)5.2–11.7 × (3.2–)3.5–8.0 mm; fruit 8–15 mm in diameter _____ **V. corymbosum**
1. Stems with stomatal bumps generally faint and closely spaced (ca. 18 to 38/mm^2); flowering as leaves emerge or occasionally just prior and continuing until leaves have attained ca. ≤ 1/20 to 1/4 full size or rarely larger; corolla 3.5–9.0(–10.0) × 1.9–5.3(–6.7) mm; fruit 4–12 mm in diameter _____ **V. fuscatum**

Vaccinium corymbosum L., Sp. Pl. 1:350. 1753. (**Figs. 5–8**). *Cyanococcus corymbosus* (L.) Rydb., Brittonia 1:94. 1931. TYPE: U.S.A. Habitat in America septentrionali, *P. Kalm s.n.* (**LECTOTYPE, designated here:** LINN LINN-HL-497-6 [image!], flowering branchlet on sheet).

Vaccinium formosum Andrews, Bot. Repos. 2, t. 97. 1800. TYPE: U.S.A. "This species...was first introduced (according to the Kew Catalogue,) in 1770, by Mr. William Young, from N. America" [protologue] (**LECTOTYPE, designated here:** Bot. Repos. 2, t. 97. 1800).

Vaccinium marianum P. Watson, Dendrol. Brit. 2, t. 124. 1823–1825. TYPE: not indicated; specimen at HUL, if such existed, presumably destroyed (**LECTOTYPE, designated here:** *A. Menzies s.n.*, LINN LINN-HS678-1-1 [image!], specimen labeled "1" on sheet).

Vaccinium corymbosum var. *glabrum* A. Gray, Manual [Gray] ed. 2, 250. 1856. *Vaccinium corymbosum* f. *glabrum* (A. Gray) Camp, Amer. Midl. Naturalist 23:177. 1940. TYPE: U.S.A. MASSACHUSETTS. Essex Co.: Herb. A. Gray, Hort. Cantab. Anno 1854, near crab apple trees, *A. Gray s.n.* (**LECTOTYPE, designated here:** GH 00015920 [image!]).

Vaccinium australe Small, Fl. S.E. U.S. [Small], 895, 1336. 1903. TYPE: U.S.A. GEORGIA. Liberty Co.: Altamaha River Swamp, 18–21 Jun 1895, *J.K. Small s.n.* (LECTOTYPE, designated by Uttal 1986a NY 00010575!; ISOLECTOTYPES: F 180430 [image!], F 180436 [image!], NY 00010576!).

Vaccinium atlanticum E.P. Bicknell, Bull. Torrey Bot. Club 41:422. 1914. TYPE: U.S.A. MASSACHUSETTS. Nantucket Co.: Nantucket Island, Millbrook Swamp, 31 May 1909, *E.P. Bicknell s.n.* (**LECTOTYPE, designated here:** NY 00010573!; ISOLECTOTYPE: NY 00010572!).

Vaccinium vicinum E.P. Bicknell, Bull. Torrey Bot. Club 41:425. 1914. TYPE: U.S.A. MASSACHUSETTS. Nantucket Co.: Nantucket Island, near Maxcy's [Maxey] Pond, 30 May 1909, *E.P. Bicknell s.n.* (**LECTOTYPE, designated here:** NY 00010615!; ISOLECTOTYPE: NY00010616!).

Vaccinium corymbosum f. *viride* F. Seym., Fl. New England ed. 2, 434. 1982. TYPE: U.S.A. NEW HAMPSHIRE. Merrimack Co.: Hooksett, 8 May 1921, *C.F. Batchelder* (HOLOTYPE: NEBC 00052972 [image!]).

Vaccinium corymbosum f. *laeve* F. Seym., Fl. New England ed. 2, 434. 1982. TYPE: U.S.A. NEW HAMPSHIRE. Coos Co.: shore of Forest Lake, Whitefield, 3 Aug 1932, *A.S. Pease 23031* (HOLOTYPE: NEBC 00052971 [image!]).

***Nomenclature.*—**Uttal (1986c) claimed that, of the two branchlets on the LINN 497.6 specimen of the type of *Vaccinium corymbosum*, Vander Kloet (1980) chose the spring branch in anthesis and just leafing out. However, Vander Kloet did not provide any indication that he was using only one of the two branchlets for (inadvertent) lectotypification. Vander Kloet's description includes the flowers of the flowering branchlet with young leaves, and the margins of the leaves on most likely the sterile branchlet, as determined by the more advanced stage of leaf flush than that of the flowering branchlet; the sterile branchlet was clearly collected at a different time of year and thus constitutes a separate gathering. Thus, the selection of a lectotype from among the two gatherings on the sheet at LINN is warranted. We chose the flowering branchlet on the sheet as lectotype because flowering material is more reliable for identification in *V.* sect. *Cyanococcus* than

sterile material. This branch is thought to have been collected in Gloucester County, New Jersey (Uttal 1986c). The leaf margins are entire, as stated by Vander Kloet (1980), and the flowers and stem stomata conform to the size of a tetraploid.

Because no type specimens of Andrews are known to exist (Stafleu & Cowan 1976), we have lectotypified *Vaccinium formosum* on the original illustration in the protologue. Uttal (1986a) convincingly asserted that this illustration shows characters justifying its treatment here as a synonym of *V. corymbosum*. Of the characters used by Uttal, the combination of large leaves with entire margins and especially the relatively large corollas (10–11 mm long, according to Uttal 1986a, although a scale is not included in the illustration) may be considered reliable enough for identification. The plants introduced into Kew Gardens in 1770 by William Young, Jr. as *V. formosum* probably originated from South Carolina (Britten 1894; Uttal 1987a).

In a letter to James Edward Smith, Peter William Watson refers to five numbered specimens, the first of which is *Vaccinium marianum*. The numbered specimens are on a single herbarium sheet that accompanied the letter; both the specimens and the letter, both of which are available as images at JSTOR Global Plants under *V. marianum*. Smith's specimens are at LINN (Stafleu & Cowan 1985). In the letter, Watson indicates that the specimen labeled "1" was collected by Archibald Menzies and matches Watsons's specimens that were used for the illustration. The specimen may therefore be considered original material and we have lectotypified *V. marianum* on this specimen. The specimen comprises a single branchlet with several leaves and an infructescence. The written note on the sheet "1. marianum Wats" clearly matches the handwriting of the letter. Moreover, the specimen is consistent with the description of the plant in the protologue, particularly by the glabrous leaves abaxially with entire margins.

Six probable syntypes of *Vaccinium corymbosum* var. *glabrum* A. Gray are known to us: 1) Massachusetts. Essex Co.: Ipswich, *Oakes s.n.*, with Asa Gray's annotation "Herb. A. Gray, *Vaccinium corymbosum* β. *glabrum*," GH 00519416 [image!], excluding top-left element on sheet (which is pubescent); 2) Herb. A. Gray, Hort. Cantab. [cultivated at the Harvard Botanic Garden] Anno 1854, near Gardener's house, GH 00015917 [image!]; 3) Herb. A. Gray, Fresh Pond (rest illegible and cut off in image), GH 00015918 [image!]; 4) Herb. A. Gray, Hort. Cantab. 1853, near crab apple, GH 00015919 [image!]; 5) Herb. A. Gray, Hort. Cantab. Anno 1854, near crab apple trees, GH 00015920 [image!]; and 6) Hort. Cantab. 1854, with "*V. corymbosum* var. *glabrum*" in Asa Gray's handwriting, NY 02544959!. We selected the GH 00015920 specimen as lectotype because Gray is presumed to have collected this specimen and it has excellently preserved flowering material. The word "TYPE" is indicated in Camp's handwriting on this specimen, and "Lectotype" in someone else's handwriting. This name, however, has not been lectotypified until now as far as we are aware. It is unclear whether any of the other specimens can be considered isolectotypes.

In the protologue of *Vaccinium atlanticum* E.P. Bicknell, the type material was cited as comprising two collections deposited in NY, and thus are syntypes: Milbrook Swamp, 31 May 1909, *E.P. Bicknell s.n.* (NY 00010573! and NY 00010573!; both flowering) and Pocomo, 11 July 1912, *E.P. Bicknell s.n.* (NY 00010574!; fruiting). We lectotypified on the NY 00010573 sheet because 1) we consider flowering material to be more taxonomically informative in *V.* sect. *Cyanococcus* than fruiting material, 2) it has the most flowering material, and 3) the label is in Bicknell's handwriting, unlike that of the other flowering specimen (although it does have Bicknell's field label).

In the protologue of *Vaccinium australe*, Small (1903) cited only herbarium material from Columbia University; this material is now at NY. Two specimens of *J.K. Small s.n.* bear the Columbia College stamp: NY 00010575 and NY 00010576, with "NY negative 11890" and "NY negative 11891" on the sheets, respectively. By indicating that the 11890 specimen is the holotype, Uttal (1986a) inadvertently lectotypified *V. australe* on this specimen.

In the protologue of *Vaccinium vicinum* E.P. Bicknell, the type material was cited as comprising two collections deposited in NY and thus are syntypes: near Maxcy's [Maxey] Pond, 30 May 1909, *E.P. Bicknell s.n.* (NY 00010615!, NY 00010616!; both flowering) and Trot's Swamp, 3 July 1912, *E.P. Bicknell s.n.* (NY 00010617!,

NY 00010618!; both in young fruit). We lectotypified on the NY 00010615 sheet because it includes the original field notes of the collector. It is also in flower, and we consider flowering material more taxonomically informative than fruiting material in the residual highbush clade.

Description.—Shrubs, deciduous or rarely semi-evergreen, clumped (not clonal), (0.5–)0.9–4.3 m tall (when fertile—may be shorter when sterile). Branchlets *in situ* green often flushed reddish until ca. third year, older branchlets gray to brown; eruptive periderm common on third- or fourth-year and older branchlets. Current-year branchlets without or rarely (on saplings or sterile branchlets) with stipitate-glandular trichomes, with or without white eglandular trichomes ± in 2 lines to throughout, straight to curved, up to 0.12–0.62 mm long; second-year branchlets with stomatal bumps generally evident and widely spaced (ca. 12 to 21/mm^2), with white eglandular trichomes or glabrous, trichomes in ± narrow to broad lines or throughout, usually not broken; outer vegetative bud scales 2.0–4.5 mm long, glabrous or puberulent. **Leaves** with petiole 0.9–4.5 mm long, sulcate and/or margins narrowly winged to base, abaxially with white eglandular trichomes or glabrous, adaxially with white eglandular trichomes or glabrous; leaf blade narrowly to broadly elliptic or slightly ovate, rarely broadly lanceolate or slightly oblanceolate, 3.4–10.6 × (1.1–)1.4–5.3 cm, chartaceous or occasionally (when semi-persistent) thick-chartaceous, abaxial surface *in situ* dull, pale green, *in sicco* dull pale green to often pale brown or tan-brown or pinkish brown, glabrous or with white, curved, undulate, or (especially on major veins) straight eglandular trichomes up to (0.31–)0.40–0.92 mm long distributed on major veins and often least sparsely on surface (often denser on major veins), without or rarely with sparse stipitate-glandular trichomes on major veins (stipitate-glandular trichomes up to 0.22–0.44 mm long, only on leaves of sterile branchlets or saplings, stipes flattened, often notably flanged proximally, gland-heads translucent to orangish, reddish, or black, globose to ovoid), adaxial surface *in situ* green, *in sicco* green to brown, glabrous or at least sparsely with white eglandular trichomes on surface (most easily seen in young leaves), occasionally only on major veins, glabrate, without stipitate glandular trichomes or rarely with stipitate-glandular trichomes on midvein and near margin or rarely also sparsely on surface, base cuneate to subrounded or rarely rounded, margins entire, subentire, or sparsely to densely serrulate with each tooth tipped by a stipitate gland (then occasionally adaxial surface near margin also with such glands), ciliate-pubescent with white eglandular trichomes or glabrous, narrowly revolute or occasionally planar, tapering into petiole, apex acute-obtuse to acute, occasionally slightly acuminate, sessile marginal glands usually present on most leaves, occasionally present only as slightly stalked glands of otherwise similar morphology, 0.10–0.32 mm wide (width parallel to margin), marginal teeth (not including stipitate gland) when present oriented at a wide angle or perpendicular to leaf axis with generally curved or occasionally straight outer edges and shallow narrow to deep sinuses or sinuses absent. **Inflorescences** axillary or pseudoterminal racemes, borne at one node or several or rarely many contiguous nodes along main stems, or one to several nodes along branchlets, 1- to 11-flowered, rachis 1–33 mm long, bracts white or green often strongly flushed pink or red, obovate to subrotund, cucullate, glabrous or occasionally with white eglandular trichomes, margins eciliate, pedicels glabrous or rarely puberulent with white eglandular trichomes, bracteoles white or green often flushed pink or red, narrowly elliptic, oblanceolate, or linear, glabrous or rarely puberulent, margins eciliate; flowering usually when leaves have attained ca. 1/20 to full size. **Flowers:** hypanthium 0.5–2.0 × 1.5–3.6 mm, glabrous, without or more often with glaucescence; calyx connate portion 0.4–1.1 mm long, lobes deltoid to ± hemispherical, 0.4–2.8 × 1.6–2.5 mm, without or occasionally with glaucescence, margin eciliate or rarely ciliate with white eglandular trichomes, apex acute to rounded; corolla white, creamy white, slightly greenish white, slightly yellowish white, occasionally slightly flushed pink or red, urceolate, cylindrical-urceolate, or cylindrical, not constricted or slightly constricted near apex or slightly and gradually narrowing distally, (4.0–)5.2–11.7 × (3.2–)3.5–8.0 mm, glabrous on both sides except rarely with several short white eglandular trichomes on inner lobes; stamens 4.5–8.8 mm long; filaments 1.8–4.9 mm, glabrous on surface, with white eglandular trichomes marginally, trichomes to 0.28–0.60 mm long; anthers 3.5–5.2 mm long, thecae 1.2–2.0 mm long, tubules 2.0–3.8 mm long; style exerted or rarely slightly inserted, 5.5–10.6 mm long, glabrous. **Fruits** at maturity

blue, black, dark purple, dark purplish blue, dark bluish black, bluish purple, or (possibly immature) reddish purple, with glaucescence or occasionally without, subglobose, 8–15 mm diameter.

Phenology.—Flowering mid-February to early June; fruiting late May to late October.

Distribution and habitat.—Wisconsin east to southern Canada and New England, south along the Coastal Plain to northern Florida and Alabama, extending to Virginia and West Virginia in the Appalachians (Fig. 8); sea level to ca. 671 m elevation; usually lowland situations, rarely drier upland habitats; pine savannas, pine barrens, mixed pine/hardwood forests, broadleaf forests, deciduous forests, wet flatwoods, edges of swamps, wooded seeps, meadows, thickets, swales, borders of wetlands and drainages of many types, hummocks in water, bogs, pocosins, forest edges, rock outgroups.

Chromosome number.—$2n = 4x = 48$ (tetraploid).

Proposed common name.—Camp (1945) and Weakley & Southeastern Flora Team (2023) indicated a series of common names for various segregates of *Vaccinium corymbosum*. Vander Kloet applied both "Highbush Blueberry" and "Rabbiteye Blueberry" to his "compilospecies" but Rabbiteye Blueberry is best reserved for *V. ashei*. The names "Northern Highbush Blueberry" and "Southern Highbush Blueberry" have been applied to the northern and southern components of our concept of *V. corymbosum*, respectively. We propose the common name of "Large-flowered Highbush Blueberry" to distinguish it from its diploid counterpart (see under *V. fuscatum*). We advocate that common names in this section that include "highbush" should be restricted to *V. corymbosum* and *V. fuscatum* to help distinguish them from other blueberry species that attain roughly the same stature as these two species (e g , *V. simulatum*) but are not in their clade.

Representative specimens examined.—See Appendix 2.

Notes.—W.H. Camp conducted an apparently unpublished study on variation of residual highbush blueberry populations in Lymans Bog, Beach City, Stark County, Ohio in the year 1934. Camp tagged, monitored, and collected populations from this area over the course of a field season, making observations on morphological variation recorded on the field labels of the vouchers [deposited at NY; e.g., Tagged plant #21, 4 Jul 1934, *W.H. Camp 576* (NY 02545403)]. Only tetraploids have been documented in this region. It is clear from our examination of the specimens in Camp's study that within the population there is variation in stem and leaf pubescence, leaf margin, and fruit surface. The stems may be glabrous or pubescent and if pubescent then the trichomes are usually arranged in more or less two lines but may also be continuously pubescent around the circumference of the stem. The abaxial surface of the leaf blades may be glabrous or sparsely to densely pubescent (± hirsute). The leaf blade margins may vary from entire or subentire to sparsely to densely serrulate and the fruit is usually glaucous but may occasionally be without glaucescence (described by Camp as black). During field work, one of the authors (P.W.F.) observed the same variation in these characters within and among populations in Michigan [e.g , West Lake Nature Preserve, Kalamazoo Co., *P.W. Fritsch 2502* (BRIT BRIT914515), *2503* (BRIT BRIT914487), *2504* (BRIT BRIT914514), and *2505* (BRIT BRIT 94513)], as did our project technician within populations in various regions of New York and Pennsylvania (e.g., *R. Carmickle RC152* (BRIT BRIT927786), *RC129* (BRIT BRIT927796), *RC144* (BRIT BRIT927779), *RC145* (BRIT BRIT927780), *RC146* (BRIT BRIT927781), *RC139* (BRIT BRIT899943), *RC148* (BRIT BRIT927783), and *RC148* (BRIT BRIT927783). From our examination of herbarium material, these characters have been found to vary in the species (e.g., Figs. 5G–I, K, L, 6B, C, E, F). We also observed that the hypanthium may vary from its most common form of dark green and shiny to dull green or glaucous. It seems likely that these characters hold during fruit development, although this needs more rigorous assessment.

In the northern half of the range, especially in bog habitats, we commonly observed plants of *Vaccinium corymbosum* with numerous (> 15) clumped stems of (presumed) single plants [e.g., Michigan, Lapeer Co., *P.W. Fritsch 2490* (BRIT BRIT914415); Fig. 5B], whereas farther south this number is typically lower, just one to several. In the southern half of the range of *V. corymbosum* along the Atlantic Coastal Plain and East Gulf Coastal Plain, the stems and leaves are less often densely pubescent and more often glabrous and the leaf blades are usually entire-margined. However, exceptions exist throughout the southern portion of the range,

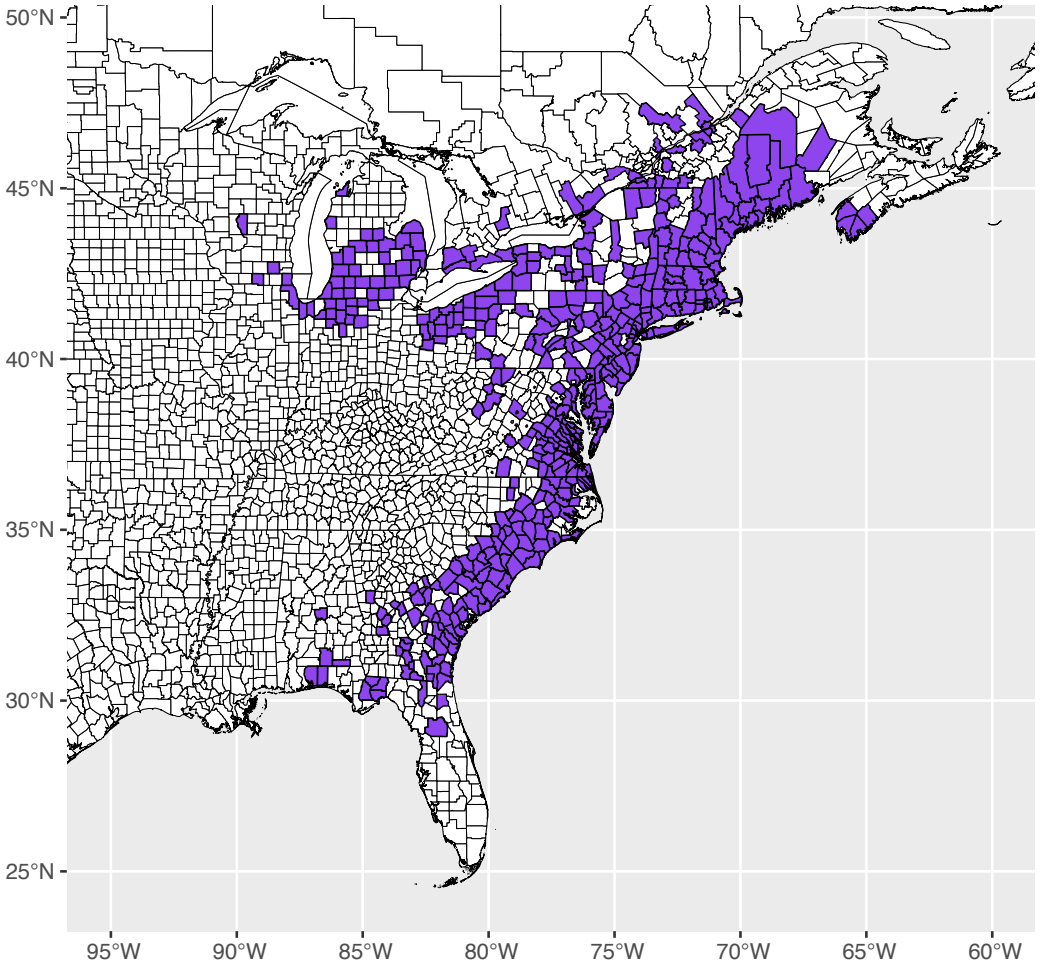

Fig. 8. Geographic distribution of *Vaccinium corymbosum* with resolution to the first level of political subdivision within states (U.S.) or provinces (Canada).

e.g., densely pubescent leaves in the Okefenokee Swamp area, Charlton Co., Georgia [*A.A. Crowl CY-375* (BRIT BRIT792852), *P.W. Fritsch 2549* (BRIT BRIT1058601)], and serrulate margins [e.g., *A.A. Crowl CY-380* (BRIT BRIT792857) *CY-461* (BRIT BRIT914404), *P.W. Fritsch 2453* (BRIT BRIT914488)]. Camp (1945) considered *V. marianum* a tetraploid hybrid between his *V. atrococcum* (diploid) and *V. caesariense* (diploid). Uttal (1987a) treated it as a general hybrid intermediate between the extremes of variation of stem/leaf pubescence, corolla size, and fruit glaucescence, whether at the diploid or tetraploid level. From our examination of the type material, *V. marianum* appears to be most consistent with Camp's concept of *V. australe* (= *V. formosum*) by its glabrous leaves with entire margins and glaucous fruit. Camp apparently did not see the LINN type material, referring only to the plate and original description, because he considered the fruit of *V. marianum* to be dark whereas the fruit on the Menzies collection appears to be glaucescent.

At the southern edge of the species range in southern Georgia and northern Florida, the leaves may be semi-persistent [e.g., *A.A. Crowl CY-383* (BRIT BRIT792859), *P.W. Fritsch 2551* (BRIT BRIT1058603); Fig. 5E]. Unlike in *Vaccinium fuscatum*, there appears to be no corresponding difference in the size of the leaves relative to those of the typical deciduous plants (see under *V. fuscatum*, next page). Also unlike in *V. fuscatum*, the

leaves of *V. corymbosum* only rarely bear stipitate-glandular trichomes on the abaxial side of the leaf blades of adult plants; we only observed this in the southern half of the range [(*A.A. Crowl CY-380* (BRIT BRIT792857)]. The leaf blades appear to be slightly smaller on average in the northern half of the range and there is a tendency toward thinner and more delicate leaves.

For discussion of sapling morphology, see Notes under *Vaccinium fuscatum*.

Vaccinium fuscatum Aiton, Hort. Kew. [W. Aiton] 2:11. 1789. (**Figs. 9–12**). *Vaccinium corymbosum* var. *fuscatum* (Aiton) Hook. in Bot. Mag. [Curtis] 62: t. 3433. 1835. *Cyanococcus fuscatus* (Aiton) Small, Man. S.E. Fl. [Small] 1013. 1933. Type: U.S.A. North America, Mr. William Young, Introd. 1770, probably from South Carolina [protologue] (Britten 1894; Uttal 1987a), *Hort Kew–74* [specimen] (**lectotype, designated here:** BM BM015730026 [image!], middle branch on sheet).

Vaccinium corymbosum var. *atrocarpum* A. Gray, Manual [Gray], ed. 2, 250. 1856. *Vaccinium corymbosum* var. *atrococcum* A. Gray, Manual [Gray], ed. 2, 250. 1857, nomen. illeg. *Vaccinium atrococcum* A. Heller, Bull. Torrey Bot. Club 21(1):24. 1894. *Cyanococcus atrococcus* (A. Heller) Small, Man. S.E. Fl. [Small], 1014. 1933. Type: U.S.A. Massachusetts. Essex Co.: Ipswich Woods, [*W.*] *Oakes s.n.* (**lectotype, designated here:** GH 00519414 [image!], the two flowering branchlets on sheet).

Vaccinium corymbosum f. *leucococcum* W. Deane, Rhodora 3:265. 1901. *Vaccinium atrococcum* f. *leucococcum* (W. Deane) W. Deane, Rhodora 24:156, 228. 1922, as *V. atrococcum* f. "*leucoccum*," emended in Rhodora 24:228. 1922. Type: U.S.A. Massachusetts. Essex Co.: Andover, near the Reservoir, 27 Jul 1901, *A.S. Pease 1034* (holotype: NEBC 00055525 [image!]).

Vaccinium caesariense Mack., Torreya 10:230. 1910. *Vaccinium corymbosum* f. *caesariense* (Mack.) Camp, Amer. Midl. Naturalist 23:177. 1940. Type: U.S.A. New Jersey. Ocean Co.: Tom's River, 30 May 1907, *K.K. Mackenzie 2583* (**lectotype, designated here:** GH 00218110 [image!]; isolectotypes: GH 00015892 [image!], NCU NCU00000642, flowering branchlet on sheet [image!], PH 00028660, flowering branchlet on sheet [image!], US 00116894, flowering branchlet on sheet [image!]).

Vaccinium atrococcum var. *longianum* Ashe, Rhodora 33:196. 1931. Type: U.S.A. Pennsylvania. Chester Co.: serpentine barrens, Paoli, 26 Jun 1912, *F.W. Pennell & B. Long 7592* (holotype: NCU n.v.; isotype: PH PH00395229 [image!]).

Vaccinium fuscatum var. *pullum* Ashe, Rhodora 33:196. 1931. Type: U.S.A. Florida. Marion Co.: N of Sellers Lake, 14 May 1929, *W.W. Ashe s.n.* (holotype: NCU NCU00000644 [image!]).

Cyanococcus holophyllus Small, Man. S.E. Fl. [Small], 1015, 1507. 1933. *Vaccinium holophyllum* (Small) Uphof, Mitt. Deutsch. Dendrol. Ges. 48:19. 1936. Type: U.S.A. Florida. Highlands Co.: ancient sand-dunes about Lake Jackson, 15 Apr 1923, *J.K. Small, J.B. DeWinkeler, & C.A. Mosier 10861* (**lectotype, designated here:** NY 00009956!; isolectotype: GH 00015925 [image!]).

Cyanococcus cuthbertii Small, Man. S.E. Fl. [Small], 1015, 1507. 1933. *Vaccinium cuthbertii* (Small) Uphof, Mitt. Deutsch. Dendrol. Ges. 48:18. 1936. Type: U.S.A. Georgia. Richmond Co.: Augusta, swamp along Rice's Creek, 6 Jun 1900, *A. Cuthbert 259* (lectotype, designated by Uttal 1987b (NY 0009955!, element "B" indicated by L.J. Uttal on sheet).

Nomenclature.—When Uttal (1987a) lectotypified *Vaccinium fuscatum* with the sheet at BM, he apparently did not realize that there are actually two gatherings on the sheet, one of which is "*Hort Kew–74*," the other of which is "*Hort. Loddiges 1778*." This information is found on the upper-left corner on the back of the sheet, with "*Hort. Loddiges 1778*" written below "*Hort Kew–74*.".There are three branchlets on the sheet. The middle branchlet is labeled "1" on the bottom strap that helps to secure the branchlet to the sheet. According to Jovita Yesilyurt, Senior Curator in Charge of the General Herbarium III and IV at BM, this "1" indicates that it is the *Hort Kew–74* specimen and not the *Hort. Loddiges 1778* specimen. The other two branchlets have no number and thus presumably comprise the *Hort. Loddiges 1778* material, although the branchlet on the right seems to better match the middle branchlet because it is in the same stage of flowering whereas the branchlet on the left has fully expanded leaves and is sterile. In any case, this is enough information to lectotypify specifically on the middle branchlet of the sheet.

Uttal considered the type material of *Vaccinium fuscatum* to match the northern deciduous phase, versus the small-leaved semi-evergreen phase of Florida and southern Georgia. Camp applied *V. fuscatum* to the latter plants (considering them tetraploid but without evidence) but we agree with Uttal (1987a) that the type matches the deciduous northern phase of the species. These phases are considered conspecific in our treatment.

As partly reviewed by Uttal (1987a), A. Gray published *Vaccinium corymbosum* var. *atrocarpum* A. Gray in his *Manual of Botany* (1856) but changed the name to *V. atrococcum* in the revised edition (Gray 1857) without explanation or indication of a printer error. Further, Gray annotated the presumed type material that we know of as *V. corymbosum* var. *atrocarpum*. Therefore, *V. corymbosum* var. *atrococcum* A. Gray should be

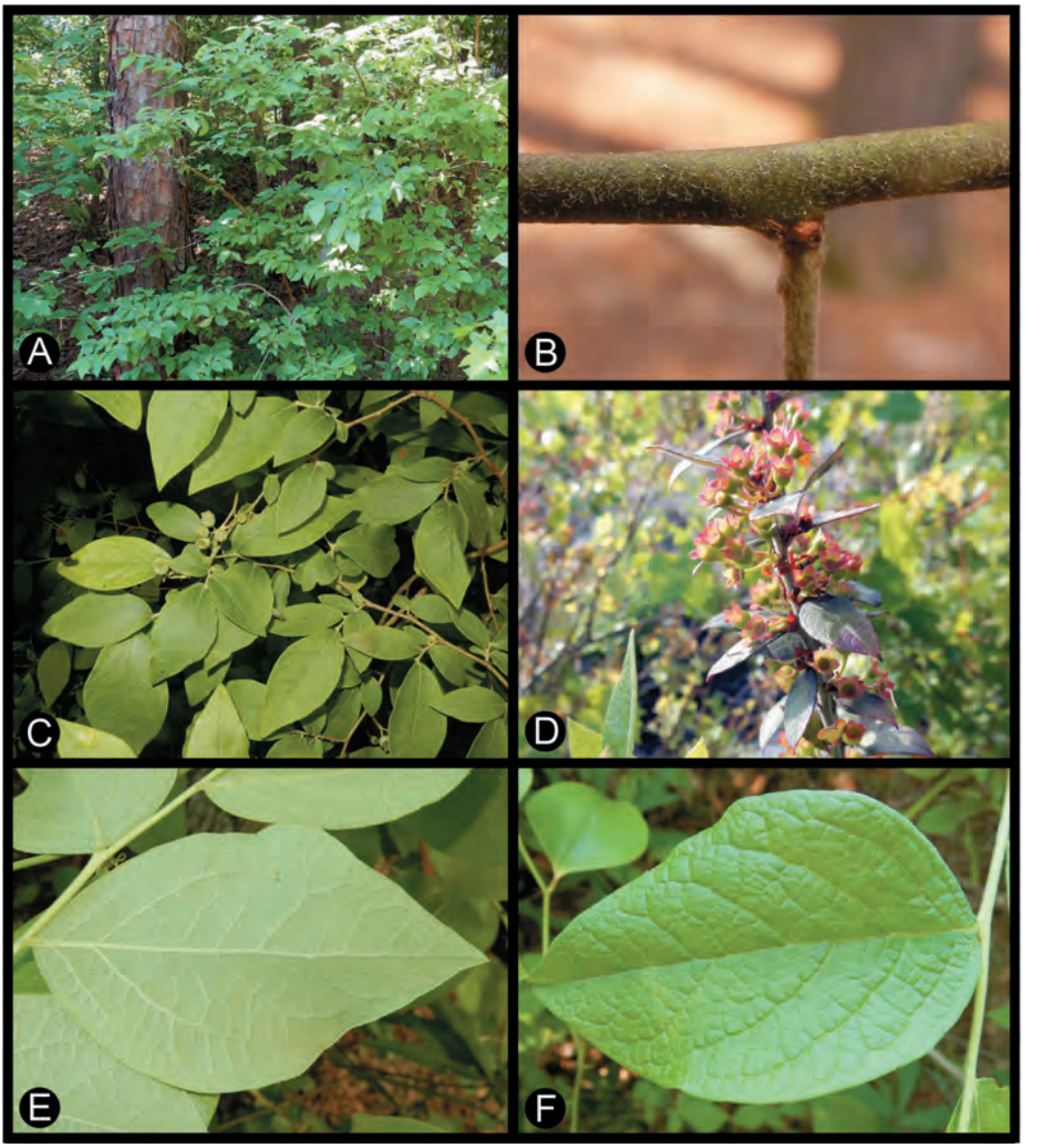

Fig. 9. *Vaccinium fuscatum*. A. Habit. B. Second-year branchlet. C. Leafy branchlet. D. Branchlet of semi-evergreen plant with smaller leaves than is typical. E. Leaf, abaxial view. F. Leaf, adaxial view. Photos: A, *P.W. Fritsch 2266*; B, *P.W. Fritsch 2446*; C, *P.W. Fritsch 2250*; D, *P.W. Fritsch 2522*; E, F, *P.W. Fritsch 2265*.

considered an illegitimate name (versus an orthographic error) and Heller's *V. atrococcum* is a replacement name at the species rank.

We found four specimens with A. Gray's annotation of *Vaccinium corymbosum* var. *atrocarpum*: [Massachusetts,] Northern States, Fresh Pond, 29 May 1854 (GH 00387910 [image!], two fruiting branchlets); [Massachusetts,] Hort. Cantab. [cultivated at the Harvard Botanic Garden, 1843–4] (NY 00010585!, one flowering branchlet and one fruiting branchlet); [Massachusetts,] Hort. Cantab. [cultivated at the Harvard Botanic Garden] Anno 1854 (NY 00010584!, three branchlets, one in flower, one in fruit, and one sterile [post-fruiting?]); and Massachusetts, Essex Co.: Ipswich Woods, [*W.*] *Oakes s.n.* (GH 00519414 [image!], two flowering

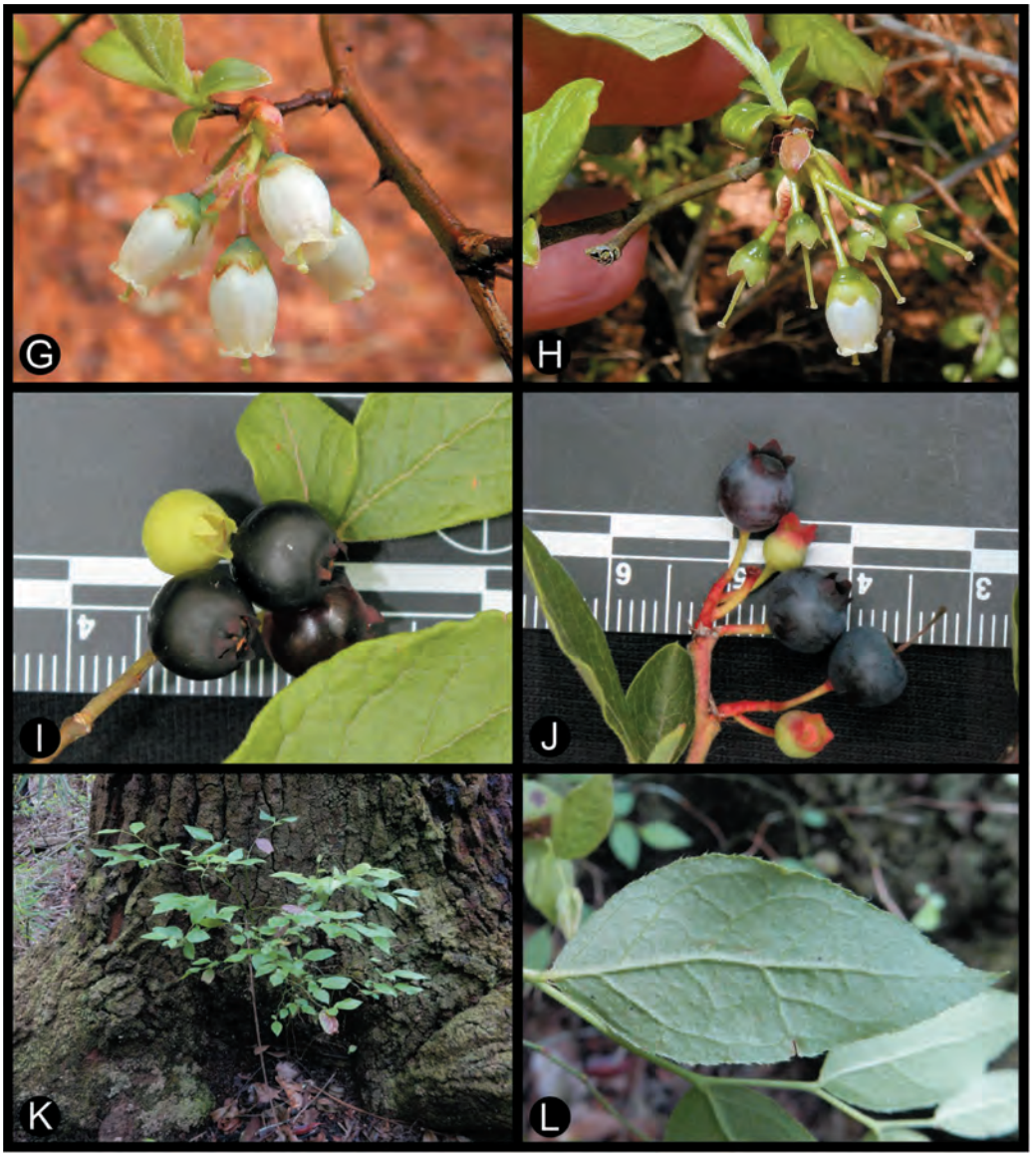

Fig. 9. *Vaccinium fuscatum*. **G.** Inflorescence. **H.** Inflorescence with non-glaucous and shiny hypanthia; compare in (G). **I, J.** Infructescences showing variation in fruit glaucescence. **I.** Typical non-glaucous fruit. **J.** Glaucous fruit. **K.** Sapling. **L.** Abaxial surface of sapling leaf. Note serrate margins. Photos: G, *P.W. Fritsch 2463*; H, *P.W. Fritsch 2468*; I, *R. Carmickle RC135*; J, *R. Carmickle RC131*; K, L, *P.W. Fritsch 2547*.

branchlets and two fruiting branchlets; the annotation is presumably *V. atrocarpum* but "carpum" is covered by another label in a different handwriting by "coccum" with "SYN. FL. N. AMER."). We lectotypified on the two flowering branchlets of the Oakes specimen because GH was Gray's herbarium, and flowering material is generally more informative taxonomically than fruiting material in the residual highbush clade.

Two collection numbers were cited in the protologue of *Vaccinium caesariense*, both collected from the same bush: *K.K. Mackenzie 2583*, collected on 30 May 1907 in flower, and *K.K. MacKenzie 2780*, collected on 28 July 1907 in fruit. The label indicates both dates regardless of whether flowering branchlets, fruiting

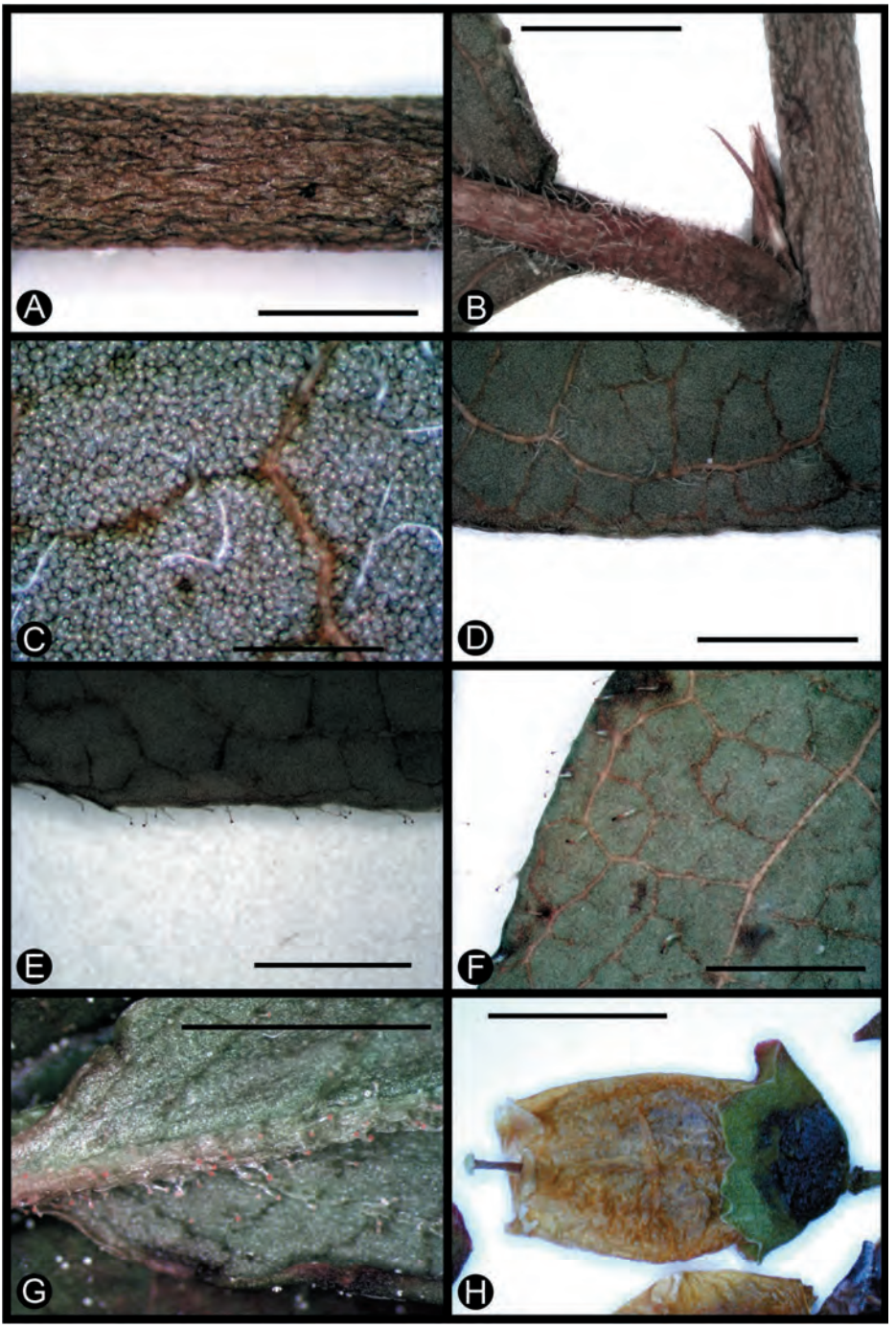

Fig. 10. *Vaccinium fuscatum*. **A.** Stem. **B.** Vegetative bud and leaf base. **C.** Abaxial surface of leaf blade. D, E. Variation in leaf margin. **D.** Entire-margined. **E.** Serrate-margined. **F.** Example of sparse stipitate-glandular trichomes on leaf abaxial surface near margin. **G.** Numerous stipitate-glandular trichomes on abaxial surface of leaf surface of *V. cuthbertii* variant. **H.** Flower. Scale bars, A, B, D–G = 2 mm; C = 500 µm; H = 4 mm. A, *A.A. Crowl CY-317* (BRIT BRIT698832); B–D, *P.W. Fritsch 2313* (BRIT BRIT698995); E, *P.W. Fritsch 2265* (BRIT BRIT792799); F, *P.W. Fritsch 2273* (BRIT BRIT792807); G, *P.W. Fritsch 2578* (BRIT BRIT1058630); H, *A.A. Crowl CY-488* (BRIT BRIT945230.

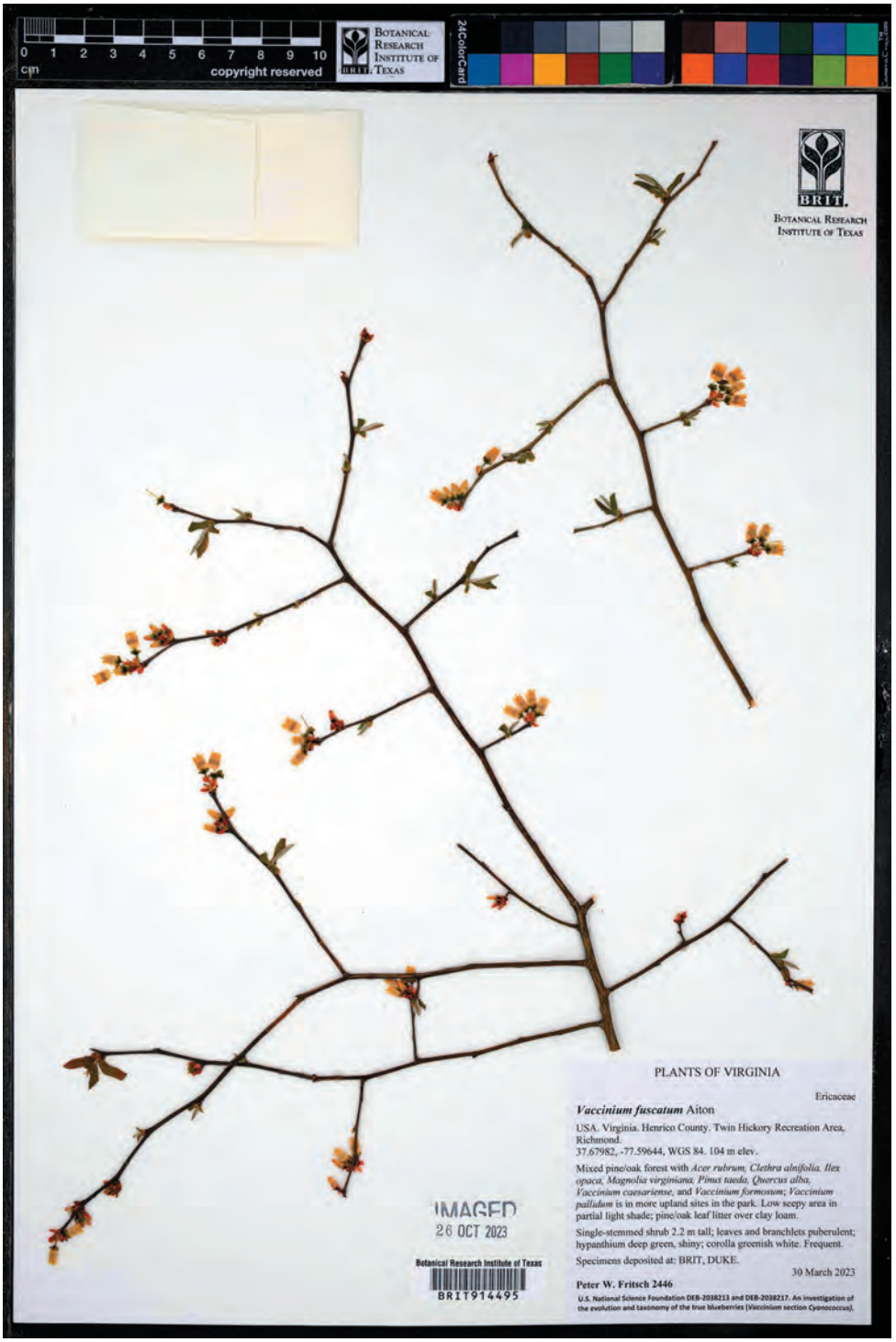

Fig. 11. Herbarium specimen of *Vaccinium fuscatum* in flower showing stage of leaf expansion. Compare Fig. 7 collected in the same area on the same day in Henrico County, Virginia, 30 March 2023, *P.W. Fritsch 2446* (BRIT BRIT914495).

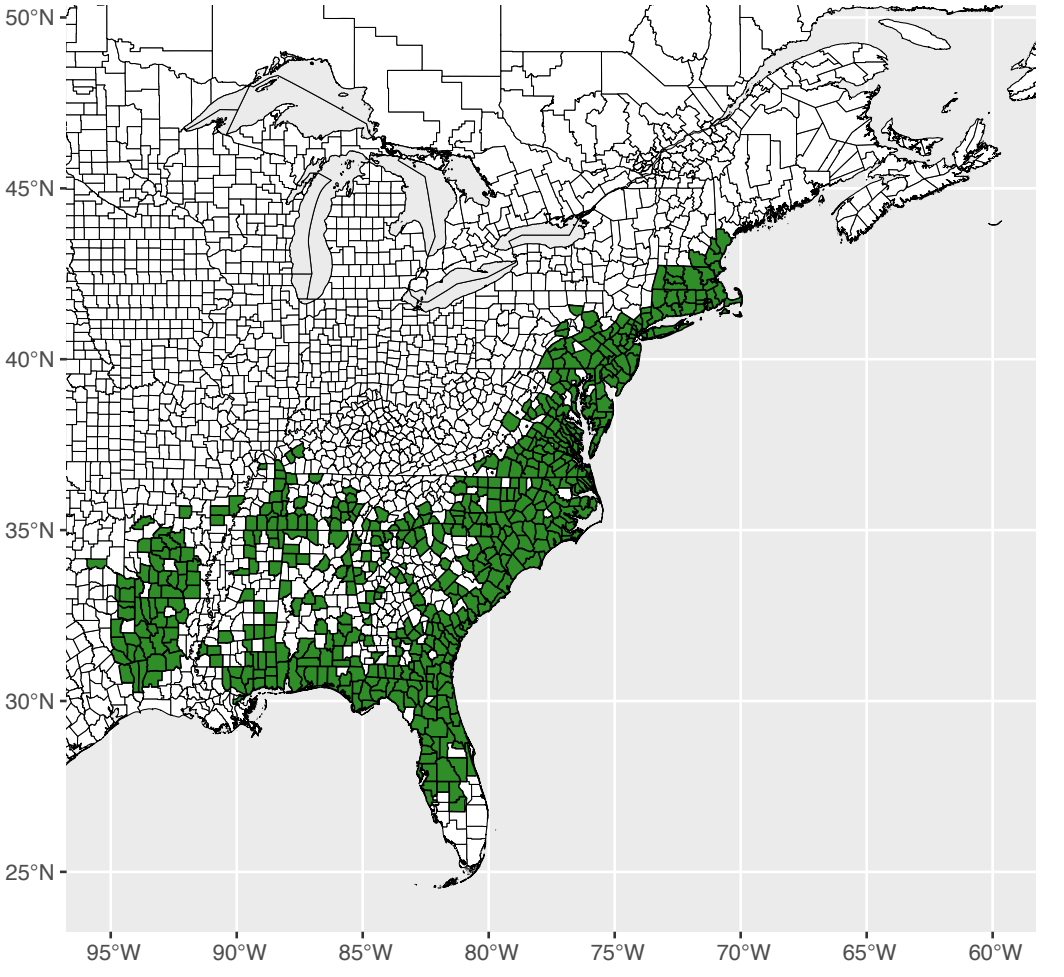

Fig. 12. Geographic distribution of *Vaccinium fuscatum* with resolution to the first level of political subdivision within a state.

branchlets, or both comprise the material on each sheet. We found the following sheets of these collections as images on JSTOR Global Plants: GH 00015892 [image!] (fl), GH 00015908 [image!] (fr; both of these are on the same sheet); GH 00218109 [image!] (fr); GH 00218110 [image!] (fl); NCU NCU00000642 [image!] (fl, fr); PH 00028660 [image!] (fl, fr); and US 00116894 [image!] (fl, fr). We lectotypified on the GH 00218110 sheet because 1) GH is specifically mentioned in the protologue (along with NY, although we did not find any of the original material at NY), and 2) of the GH sheets, it has the best flowering material; we consider flowering material more taxonomically informative overall than fruiting material in the residual highbush clade.

Two collections were cited in the protologue of *Cyanococcus holophyllus* Small as type material from NY. We have found specimens of this material at NY and on JSTOR Global Plants: Florida, Highlands Co.: sandhills east of Sebring, 30 April 1924, *J.K. Small, J.B. DeWinkeler, & C.A. Mosier 11347* (NY 00009957!); and ancient sand-dunes about Lake Jackson, 15 April 1923, *J.K. Small, J.B. DeWinkeler, & C.A. Mosier 10861* (GH 00015925 [image!], NY 00009956!). We selected the 10861 NY collection as lectotype because NY was cited in the protologue and, of the two collections, this one is in flower. We consider flowering material more taxonomically informative overall than fruiting material in the residual highbush clade.

***Description.*—Shrubs,** deciduous or occasionally semi-evergreen, clumped (not clonal), (0.6–)1.0–5.0 m tall (when fertile—may be shorter when sterile). Branchlets *in situ* green often flushed reddish until ca. third year, older branchlets gray to brown; eruptive periderm common on third-year and older branchlets. Current-year branchlets without or rarely with sparse stipitate glandular trichomes, with or without white eglandular trichomes ± in 2 lines to throughout, trichomes straight to curved, up to 0.14–0.40 mm long; second-year branchlets with stomatal bumps generally faint and closely spaced (ca. 18 to 38/mm^2), with white eglandular trichomes or glabrous, trichomes in ± narrow to broad lines or more often throughout, not broken; outer vegetative bud scales 1.9–4.0 mm long, glabrous or more often puberulent. **Leaves** with petiole 0.5–3.0 mm long, sulcate and/or margins narrowly winged to base, abaxially with white eglandular trichomes or less often glabrous, adaxially with white eglandular trichomes or occasionally glabrous; leaf blade narrowly to broadly elliptic or slightly ovate, rarely slightly oblanceolate, (2.0–)3.7–9.3 × (1.0–)1.6–5.4 cm, chartaceous or occasionally (when semi-persistent) thick-chartaceous, abaxial surface *in situ* dull, pale green, *in sicco* dull pale green to often pale brown or tan-brown or pinkish brown, occasionally glabrous or more often with white usually curved or undulate eglandular trichomes (occasionally straight, usually on major veins) up to (0.26–)0.38–1.04 mm long distributed on major veins and usually at least sparsely on surface (often denser on major veins), without or occasionally with sparse stipitate-glandular trichomes on major veins (stipitate-glandular trichomes up to 0.28–0.44 mm long, usually only on leaves of sterile branchlets or saplings, rarely densely scattered throughout (*V. cuthbertii* variant), stipes flattened, often notably flanged proximally, gland-heads translucent to orangish, reddish, or black, globose to ovoid), adaxial surface *in situ* green, *in sicco* green to brown, usually at least sparsely with white eglandular trichomes on surface (most easily seen in young leaves), occasionally only on major veins or glabrous, glabrate, without stipitate glandular trichomes or rarely with stipitate-glandular trichomes on midvein and near margin or rarely also sparsely on surface, base cuneate to rounded, margins entire or occasionally sparsely to densely serrulate with each tooth tipped by a stipitate gland (then usually one or both surfaces also with such glands), ciliate-pubescent with white eglandular trichomes or occasionally glabrous, narrowly revolute or rarely planar, tapering into petiole, apex acute-obtuse to acute, occasionally slightly acuminate, rarely acuminate, sessile marginal glands usually present on most leaves, 0.08–0.26 mm wide (width parallel to margin), marginal teeth (not including stipitate gland) when present oriented at a wide angle or perpendicular to leaf axis with generally straight outer edges (i.e., teeth dentate) and shallow narrow sinuses or sinuses absent. **Inflorescences** axillary or pseudoterminal racemes, borne at one node or several to many contiguous nodes along main stems, or one to several nodes along branchlets, 1- to 9-flowered, rachis 1–18 mm long, bracts white or green often strongly flushed pink or red, obovate to subrotund, cucullate, glabrous or occasionally with white eglandular trichomes, margins eciliate, pedicels glabrous or rarely with white eglandular trichomes, bracteoles white or green often flushed pink or red, narrowly elliptic, oblanceolate, or linear, glabrous, margins eciliate; flowering as leaves emerge or occasionally just prior and continuing until leaves have attained ca. ≤ 1/20 to 1/4 full size or rarely larger. **Flowers:** hypanthium 0.6–1.5 × 1.2–2.7 mm, glabrous, with or more often without glaucescence; calyx connate portion 0.2–0.9 mm long, lobes deltoid to ± hemispherical, 0.3–1.8 × 1.0–2.0 mm, without or less often with glaucescence, margin eciliate or rarely ciliate with white eglandular trichomes, apex acute to rounded; corolla white, creamy white, dull white, yellowish white, pink, greenish white, or white flushed pink and/or green, urceolate, cylindrical-urceolate, or cylindrical, not constricted or slightly constricted near apex or slightly and gradually narrowing distally, 3.5–9.0(–10.0) × 1.9–5.3(–6.7) mm, glabrous on both sides except occasionally with several short white eglandular trichomes on inner lobes; stamens 4.0–7.5(–8.2) mm long; filaments 1.3–3.6 mm, glabrous on surface, with white eglandular trichomes marginally, trichomes to 0.18–0.48 mm long; anthers 2.9–5.1 mm long, thecae 1.0–2.0 mm long, tubules 1.5–3.1 mm long; style exerted, 5–10 mm long, glabrous. **Fruits** at maturity black, blue, dark purplish blue, dark purple, or (possibly immature) dark reddish purple, with glaucescence or more often without, subglobose, 4–12 mm diameter.

***Phenology.*—**Flowering late January to early June; fruiting early May to late August.

Distribution and habitat.—Extreme southern Maine south along the Coastal Plain and Piedmont to south-central Florida, then west throughout much of the southeastern U.S., including the southern Appalachians, to eastern Texas (Fig. 12); sea level to ca. 500 m (to 741) m elevation; usually lowland situations, less commonly drier upland habitats; rarely highland wet areas [e.g., North Carolina, Jackson Co., *P.S. Manos CY-254* (BRIT BRIT698799)]; pine savannas, mixed pine/hardwood forests, broadleaf forests, deciduous forests, wooded seeps, swales, wet flatwoods, baygall forests, borders of wetlands and drainages of many types, forest edges, rock outcrops. The geographic distribution based on herbarium material exhibits a paucity of records in the core of the range in the southeastern U.S., i.e., Mississippi, Alabama, and Georgia (Fig. 12). The extent to which this gap represents true absence remains unclear, but we suspect that it at least partly may be accounted for by the under-collection of vascular plants in some areas of these states (see Barger et al. 2012; Kees 2022).

Proposed common name.—The common names "Black Highbush Blueberry" and "Hairy Highbush Blueberry" have been applied to part of our concept of this species (e.g., Weakley & Southeastern Flora Team 2023), but neither of these names encompasses the range of morphological variation observed. For example, the morphology corresponding to *V. caesariense*, with glabrous leaves and glaucescent fruits, is not represented by either common name. Therefore, we suggest the common name of "Small-flowered Highbush Blueberry" for this species to distinguish it from its tetraploid counterpart *V. corymbosum*.

Chromosome number.—$2n = 2x = 24$ (diploid).

Representative specimens examined.—See Appendix 3.

Notes.—Although our genetic clustering results showed more homogeneity in diploid residual highbush than in the tetraploid component, *Vaccinium fuscatum* appears to be somewhat more variable in morphology than *V. corymbosum*. In *V. fuscatum*, stems and especially leaves are most commonly densely pubescent, but glabrous and sparsely pubescent variants exist sporadically throughout much of the range of the species, occurring within populations of pubescent-leaved individuals [e.g., Alabama, Pike Co., *P.W. Fritsch 2436* (BRIT BRIT698887), cf. the pubescent-leaved *P.W. Fritsch 2435* (BRIT BRIT698886)]. Most commonly the stems have pubescence continuously throughout the circumference of the stem, but stems with pubescence arranged in two lines or even with a glabrous surface are common. Plants with the combination of glabrous stems and glabrous leaf blades on the abaxial surface are known only from Alabama eastward and northward along the Coastal Plain and perhaps the Piedmont; we have not observed them in collections from Texas, Arkansas, Louisiana, Mississippi, Tennessee, or Kentucky. Such glabrous plants at the diploid level correspond more or less to plants recognized by some authors as *V. caesariense*. The abaxial surface of the leaf blades is most commonly densely pubescent with wavy trichomes, but glabrous and intermediate variants are common and the trichomes on at least the major veins may be straight.

As in *Vaccinium corymbosum*, *V. fuscatum* may have semi-persistent leaves in the far southeastern parts of its range (Georgia and Florida) [e.g., Florida, Osceola Co., *P.W. Fritsch 2528* (BRIT BRIT1058580; Fig. 9D)]. This variant is far more prevalent in *V. fuscatum* than in *V. corymbosum*, perhaps because the range of *V. fuscatum* extends substantially farther south in Florida (cf. Figs. 8 and 12). Unlike the leaves of *V. corymbosum*, those of semi-persistent variants of *V. fuscatum* are often smaller, either on parts of the plants or throughout [e.g., Florida, Highlands Co., *P.W. Fritsch 2522* (BRIT BRIT1058574), Osceola Co., *J.K. Small et al. 10760* (NY 02545053)]. These plants may also have stipitate-glandular trichomes on the abaxial surface of the leaf blade and/or serrulate margins [e.g., Florida, Saint Johns Co., *W.H. Camp 5089* (NY 02551735)].

Uttal (1987a) considered these smaller- and persistent-leaved plants to be a variant of *Vaccinium fuscatum*, as opposed to hybrids with *V. darrowii*, a common "lowbush" evergreen diploid in Georgia and Florida. Camp (1945) restricted *V. fuscatum* to the smaller- and persistent-leaved plants, speculating that they are allotetraploid hybrids between *V. darrowii* and his concept of *V. atrococcum* and reserving *V. atrococcum* for the typical larger-leaved and fully deciduous diploid plants. However, Camp seems to have misapplied the name *V. fuscatum* to these plants because, as noted by Uttal (1987a), its type matches the normal-leaved variant (Camp's *V. atrococcum* and our wide sense of *V. fuscatum*). Vander Kloet (1977) found that the smaller- and persistent-leaved plants

are diploid, consistent with our findings. Uttal (1987a) proposed that if these plants were to be separated taxonomically from *V. fuscatum* in the wide sense at the species level, then a new name would be needed, considering that the small leaves of *V. holophyllum* (Small) Uphof (which might otherwise be used) suggested a hybrid with *V. darrowii*. However, to us, the type of *V. holophyllum* matches the variant well and its leaves are not glaucous (see below). The variant has also been recognized at the varietal level as *V. fuscatum* var. *pullum* Ashe. The size of the leaves in the semi-evergreen variant of *V. fuscatum* seems to be uncorrelated with habitat.

Plants of *Vaccinium fuscatum* usually have leaf blades without stipitate-glandular trichomes on the abaxial surface, but plants with such glands are occasional and much more common than in *V. corymbosum* [e.g., Texas, Tyler Co., *P.W. Fritsch 2273* (BRIT BRIT792807); Florida, Saint Johns Co., *A.A. Crowl CY-219* (BRIT BRIT698770); Fig. 10F]. Often the glands only appear on some leaves of a branchlet. Some specimens with these glands may also have them on the stem in places (e.g , *A.A. Crowl CY-219*; most specimens of the *V. cuthbertii* variant). As noted in Fritsch et al. (2024b), the stipitate glands in *V. fuscatum* tend to have relatively longer and flatter stipes than those of *V. virgatum*, a species that often attains a height similar to that of *V. fuscatum*. *Vaccinium elliottii*, another species that may attain a height typical of *V. fuscatum*, may also have leaf blades with stipitate-glandular trichomes on the abaxial surface (Franck & Salman 2024; Fritsch et al. 2024a). However, the glands in this species are usually few in number and are restricted to the basal part of the midvein or occasionally also the basal portions of the secondary veins, whereas in *V. fuscatum* they are more abundant (but still usually not as abundant as in *V. virgatum* except in the *V. cuthbertii* variant) and more commonly scattered on all the major (midvein and secondary) veins. Plants of *V. fuscatum* with these stipitate glands may be found throughout the range of the species, even in the semi-persistent variants. When present, the glands are most commonly found on the leaves of sterile sucker shoots. Because such leaves often persist into the next season, branchlets may be found in which the persistent leaves have the stipitate-glandular trichomes, but the new leaves do not. The stipitate glands often occur on leaves that are also serrulate and in such cases they also may occur on the adaxial surface of the leaf blades near the margins, or even across the adaxial surface.

From the vicinity of the northern edge of the Okefenokee Swamp in Georgia to south and west-central South Carolina, a variant of *Vaccinium fuscatum* with more or less consistent and dense stipitate glands on the abaxial surface of the leaf blades may be found (Fig. 10G; Appendix 4). This is the variant referred to above as "*V. cuthbertii*." In lectotypifying *V. cuthbertii*, Uttal (1987b) considered it to be a synonym of *V. virgatum*, mainly by the presence of stipitate-glandular trichomes and serrulate leaf margins. However, this variant is distinct from *V. virgatum* by its generally larger vegetative buds and absence of non-stipitate-glandular trichomes on the abaxial surface of the leaf blade. Camp (1945, annotation labels) considered it to be a hybrid between his *V. elliottii* and *V. tenellum* and between his *V. caesariense* and *V. tenellum*, but this it unlikely because the stipitate-glandular trichomes have globose- to obovoid-headed glands, unlike the elongate- to clavate-headed glands of *V. tenellum*, and the stipitate-glandular trichomes of *V. elliottii* are infrequent and, when present, usually have longer stipes. The glands of this variant tend to be caducous, sometimes only appearing on the young leaves of new shoots, although they are often persistent as in *V. virgatum*. Moreover, the stipes tend to be longer than in *V. virgatum*, although sometimes they are roughly the same length and they tend to cluster more densely on the major veins, especially the basal half of the midvein. The glands are also usually present on the petioles and young stems and the plants are deciduous without any persistent leaves. The length of the simple non-glandular trichomes on the stems are much shorter than those in *V. virgatum* and often shorter than in more typical *V. fuscatum*, usually being no longer than 0.1 mm. The variant seems to not occur north of Aiken and Charleston counties, South Carolina.

Our flow cytometry data recovered diploidy for all samples of the *Vaccinium cuthbertii* variant tested (*P.W. Fritsch 2567*, *2573*, *2574*, *2575*, *2576*, *2578*, *2623*, and *2625*, and *A.A. Crowl CY-350*, *CY-366*, and *CY-469*; Appendix 1). The sample used for molecular analysis (*A.A. Crowl CY-350*) grouped strongly within the residual highbush clade (Fig. 2), thus providing key evidence as to the exclusion of the variant from *V. elliottii* and *V. virgatum*. Anomalously, our genetic clustering analysis showed a genotype of this sample that was nearly

identical to those of our individuals sampled of *V. corymbosum* (Fig. 4); further, this sample grouped the closest of all diploids sampled to the tetraploid samples in the PCA (Fig. 3). We speculate that *V. cuthbertii* represents an independent diploid residual highbush line leading to a progenitor or progenitors of the tetraploid residual highbush. It shares a profile with two other tetraploid samples, CY-360 and CY-361, both from Colleton Co., South Carolina adjacent to Charleston Co , where CY-350 was collected; however, it also shares a similar profile with CY-193 and CY-401, from New Jersey and North Carolina, respectively. At one locality in Ware Co., Georgia, we observed *V. cuthbertii* growing together with the non-glandular glabrous- and pubescent-leaved (only simple trichomes present abaxially) variants of *V. fuscatum* [e.g., *P.W. Fritsch 2625*, *2618*, and *2621* (BRIT, DUKE) respectively]. In another locality in Charleston Co., South Carolina [*A.A. Crowl CY-353* (BRIT)], we observed a plant with characters intermediate between *V. cuthbertii* and the more typical *V. fuscatum*. This plant has the glands of *V. cuthbertii* abaxially without simple trichomes and serrulate leaf margins on old leaves, but in some of the new leaves the margins are entire and the old leaves are semi-persistent. This intermediacy suggests that the two variants may crossbreed and thus may not be distinct. On this basis we have opted to place *V. cuthbertii* in the synonymy of *V. fuscatum* with the caveat that this decision should be assessed with a more in-depth population-level study.

We initially considered two of our collections with low stature [< 1 m tall; Florida, Duvall Co., *P.W. Fritsch 2547* (BRIT BRIT1058599), Mississippi, Franklin Co., *P.W. Fritsch 2379* (BRIT BRIT698899; Fig. 9K, L)] to be sterile specimens of *Vaccinium virgatum* because of the presence of stipitate-glandular trichomes on the abaxial surface of the leaf blades and serrulate leaf blade margins. However, flow cytometry analysis yielded diploidy for them and they were collected in places where reproductive adults of *V. fuscatum* were present but no reproductive adults of *V. virgatum*. From this we conclude that these collections are saplings of *V. fuscatum*. They have smaller and more delicate leaves than are typical in adult plants (Fig. 9K, L). We identified two herbarium specimens with the same morphology of our sapling specimens [Mississippi, Pearl River Co., McNeill, Coastal Experiment Station, without plant descriptive data, 8 May 1930, *W.W. Ashe E6768* (GA GA201410) and ibid., *W.W. Ashe E6769* (GA GA201408)] as likely saplings of *V. fuscatum* as well. We observed the same morphology on an herbarium specimen that is clearly a sapling because of the presence of roots and with the size and density of stem stomatal bumps consistent with a tetraploid, indicating an identification of *V. corymbosum* (*F. Hyland s.n.*, NY 02543391). Leaf blades with stipitate-glandular trichomes abaxially and serrulate margins may well be the common morphology of both *V. corymbosum* and *V. fuscatum* saplings. If so, then care must be taken in the field to ensure that these plants are not mistaken for sterile plants of *V. virgatum* or a different species of low stature with such stipitate glands in adults, such as *V. tenellum*.

The fruit of *Vaccinium fuscatum* most often lacks glaucescence, but fruits with various degrees of glaucescence occur, especially those with the stems and leaves tending toward less pubescence (Fig. 9I, J). The leaf blades of such variants are usually entire but occasionally are serrulate. As in *V. corymbosum*, we have observed hypanthia to also vary, in this case from more commonly dark green and shiny to less commonly dull green or glaucous. We are uncertain if this extends into the fruiting stage in all cases.

NATURAL HYBRIDIZATION BETWEEN THE RESIDUAL HIGHBUSH CLADE AND OTHER SPECIES OF *VACCINIUM* SECT. *CYANOCOCCUS*

Camp (1945) asserted that natural hybridization is rampant in the section. From our field work we have observed what appear to be hybrids, especially among certain diploids species, but in a much lower frequency than Camp's wording would suggest. The strong triploid block in the section likely prevents most hybridization events among ploidal levels from occurring. Therefore, triploid F1 hybrids between diploids and *V. corymbosum*, and between polyploids and *V. fuscatum*, may be expected to be rare or nonexistent in the wild. However, as noted above, unidirectional gene flow between *V. fuscatum* (diploid) and *V. corymbosum* (tetraploid) is possible and population-level studies should be conducted to assess its existence or prevalence. In the context of the discussion below it must be stressed that molecular data have not yet been used to test the hybrid nature of individuals with intermediate morphology to confirm their hybrid status.

As discussed above, our data do not support Camp's (1945) hypothesis of a complex origin for (tetraploid) *Vaccinium corymbosum* involving many of his tetraploid species of the section. As documented here and elsewhere (Manos et al., in press), the geographic range of *V. simulatum*, a species of the southern Appalachians, is distinct from that of *V. corymbosum*; thus, the likelihood of hybridization between these two species is low. Hybrids between *V. corymbosum* and *V. angustifolium* have been reported and seem probable where their ranges overlap. In the far northeastern U.S. and far eastern Canada, some individuals of *V. corymbosum* resemble plants of *V. angustifolium* in their shiny leaf blades abaxially and sometimes apparently accompanied by reduced stature [e.g., Maine, Hancock Co., *P.S. Manos CY-310* (BRIT BRIT698674)]. Camp (1945) considered such plants hybrids between the two species where they grow together, applying the name *V. atlanticum* E.P. Bicknell to these plants. We find that such hybrids are difficult to recognize with certainty, at least in herbarium specimens. Apparently consistent with this uncertainty, Bicknell (1914), as part of a floristic treatment of the plants of Nantucket Island, considered *V. atlanticum* to be a distinct species (an assessment with which we disagree), but of relevance here observed other plants on the island that he recognized as (unnamed) hybrids between *V. angustifolium* and *V. corymbosum*. Thus, it is clear that, unlike Camp (1945), he did not consider *V. atlanticum* a hybrid between these two species.

Vaccinium fuscatum seems to hybridize more commonly than *V. corymbosum*. Based on morphological intermediacy, F1 hybrids between *V. fuscatum* appear to occur sporadically with two other diploids of the section, *V. darrowii* and *V. elliottii*. In these cases, both parents were often found in the vicinity of the putative hybrids, although sometimes only one of the parents was observed. Examples of *V. fuscatum* × *V. elliottii* are (all deposited at BRIT and DUKE) Florida, Gilchrist Co., *P.W. Fritsch 2583*; Louisiana, Jackson Par., *P.W. Fritsch 2323*; Louisiana, Vernon Par., *P.W. Fritsch 2297*; and Mississippi, Jones Co., *P.W. Fritsch 2399*. Hybrids of *V. fuscatum* with *V. darrowii* appear to be more common than those with *V. elliottii* and were observed by us to be common in Florida, consistent with the observations of Lyrene (2017). Intermediacy in morphological characters of the hybrids is variable, such that hybrids may have some combination of the characters typical of *V. darrowii,* e.g., low stature, persistent leaves with glaucous surfaces and serrulate margins, and glaucous fruit. However, the leaves are usually of intermediate size between the two parents, with the leaves of *V. darrowii* being much smaller than those of *V. fuscatum*. The hybrids tend to have stipitate-glandular trichomes on the leaves more often and more densely on the leaves than the parents, at least on leaves from vegetative sucker branchlets, but also on those of short branchlets, and the heads of the glands can be subglobose to clavate. This might be case of a novel character state in the hybrids, but this needs more study. Two localities with a high prevalence of putative hybrids between *V. fuscatum* and *V. darrowii* are Florida, Seminole Co., Geneva Wilderness Area, *P.W. Fritsch 2604*, *2606*, *2607*, *2608*, and *2609* (BRIT, DUKE), and Florida, Sumter Co., Lake Okahumpka Park, *P.W. Fritsch 2532*, *2536*, *2599*, *2600*, and *2601* (BRIT, DUKE). Some historical herbarium specimens also have morphologies that preclude their placement in either parent and are likely hybrids (intermediate stature, slightly glaucous leaves of intermediate size), e.g., Florida, Jackson Co., *S. McDaniel 4023* (BRIT BRIT311717), Florida, Franklin Co., *R. Kral 57889* (BRIT BRIT311926), and Florida, Wakulla Co., *S. McDaniel 3989a* (BRIT BRIT312180).

In our field and herbarium studies, we did not detect putative hybrids between *Vaccinium fuscatum* and other diploids of the section: *V. pallidum*, *V. tenellum*, *V. boreale*, or *V. myrtilloides,* although our genetic clustering analysis suggests some admixture between *V. fuscatum* and *V. tenellum* (Fig. 4). *Vaccinium pallidum* generally occurs in more upland habitats than the low wet habitats of *V. fuscatum* and thus does not commonly occur together with it, although it may be found in adjacent uplands. The geographic ranges and habitats of the latter *V. boreale* and *V. myrtilloides* either do not overlap with *V. fuscatum* (*V. boreale*) or only slightly overlap (*V. myrtilloides*) and thus these species would not be expected to commonly produce natural hybrids with *V. fuscatum*.

One observation not directly related to this study but worthy of note here is the apparently strong admixture in *Vaccinium elliottii* involving the genomes of *V. fuscatum* and *V. pallidum* (Fig. 4). Prior gene network analysis suggested a hybrid origin of *V. pallidum* with the stem lineages of *V. elliottii* and the northern clade of

species (Crowl et al. 2022), providing evidence supporting a diploid hybrid origin of *V. pallidum*. Our clustering analysis conversely might be interpreted to support a diploid hybrid origin of *V. elliottii* from *V. fuscatum* and *V. pallidum*. These apparently conflicting results will clearly require additional sampling and analysis.

DUBIOUS NAME

Vaccinium arkansanum Ashe, Rhodora 33:195. 1931. Syntypes: U.S.A. Arkansas. Garland Co.: 6 mi N of Hot Springs, on the Little Rock road, 15 Apr 1928 and 27 Jun 1929, *W.W. Ashe s.n.* (missing).

***Note.*—**The protologue does not provide specific insight as to the ploidal level of the type material of *Vaccinium arkansanum* Ashe, and the type material is missing. Camp did not see the type material but nonetheless accepted it as a tetraploid species—to Camp, it represented the pubescent partner of his *V. australe* (= *V. formosum*), thus paralleling the variation seen at the diploid level with *V. caesariense* as the glabrous species and *V. atrococcum* (= *V. fuscatum*) as the pubescent species. Camp predicted that pubescent plants would eventually be found at the tetraploid level that otherwise correspond to the morphology of *V. atrococcum* and used *V. arkansanum* to represent these (at the time) hypothetical plants. Although we have found such plants in the wild, they occur only in areas far distant from the type locality (Arkansas), where only diploids are known. As such, we predict that, if found, the type would have morphology consistent with *V. fuscatum* and thus be placed as a synonym under that species. Because the nomenclature and taxonomic status of this name are uncertain, we refrain from designating a neotype.

EXCLUDED NAMES

Vaccinium grandiflorum P. Watson, Dendrol. Brit., t. 125 A. 1823–1825. Type: not indicated; specimen at HUL, if such existed, presumably destroyed. Probable type material: LINN (LINN-HS678-1-2 [image!], specimen labeled "2"; a single leaf).

***Note.*—**Vander Kloet (1988) placed V*accinium grandiflorum* P. Watson in the synonymy of *V. corymbosum*. In a letter to James Edward Smith, Peter William Watson referred to five numbered specimens, the second of which was *Vaccinium grandiflorum*. The numbered specimens are on a single herbarium sheet that accompanied the delivery of the letter (both of which are available as images at JSTOR Global Plants under *V. grandiflorum*). Smith's specimens are at LINN (Stafleu & Cowan 1985). Handwriting on the sheet matches that of the letter; the specimen may therefore be considered original material. The specimen on the sheet comprises a single leaf and from the image does not provide characters or character resolution sufficient for identification. However, the illustration shows inflorescences with leafy bracts and the description states that the style is included within the corolla; further, the anther "lobes" are described as "each with a long horn!" On this basis, the specimen is inconsistent with a placement in *V.* sect. *Cyanococcus*, the species of which lack projections (i.e., spurs) on the anthers. Thus, regardless of the precise identification of *V. grandiflorum*, it should be excluded from the section.

Vaccinium virgatum var. *parvifolium* A. Gray, Syn. Fl. N. Amer. 2(1):22. 1878. Type: U.S.A. Louisiana: *S. Hale s.n.* (**lectotype, designated here:** GH 00015935 [image!], right-hand element on sheet).

***Note.*—**A type for *Vaccinium virgatum* var. *parvifolium* A. Gray was not indicated in the protologue; the only specimen cited was Louisiana: *S. Hale s.n.* In notes on the sheet containing the lectotype, Camp considered the sheet to comprise two separate gatherings, Louisiana, *S. Hale s.n.*, the right-hand element on the sheet, in flower (according to Camp's handwriting on the sheet: "by viewing against a strong light, it may be seen that the original label under the right hand specimen reads: "Louisiana. Hale."), and Arkansas: [Ouachita County:] Camden, 19 May 1850, *A. Fendler s.n.*, the left-hand element on the sheet, in fruit. Camp considered both elements to comprise type material, presumably based on the annotation in Gray's handwriting "*V. virgatum* var. *parvifolium*, SYN. FL. N. AMER," a view with which we agree. Gray (1878) considered this an "ambiguous form," citing *V. elliottii* Chapm. in synonymy and stating a geographic range of "South Carolina to Arkansas and Louisiana." Gray did not list *V. elliottii* elsewhere in this treatment and so he appears to have thought it to be the same as Chapman's *V. elliottii* but lowered its status to variety. From examination of the image of the syntypes on JSTOR Global Plants, we conclude, as did Camp in specimen annotations, that both elements on the sheet are *V. elliottii*. We lectotypify on the *S. Hale s.n.* specimen, which matches the specimen citation in the protologue.

APPENDIX 1

Specimen vouchers of samples of the residual highbush blueberry group (*Vaccinium corymbosum* and *V. fuscatum*) used for analyses in this study. All vouchers listed were used for ploidal assessment except for *P.W. Fritsch 2267*, for which a ploidal estimate was unavailable, but which is assumed to be diploid (see text). Vouchers used for phylogenomic data are indicated by the collector and collection number in boldface. All vouchers are deposited at BRIT, often with a duplicate set at DUKE.

Vaccinium corymbosum—**U.S.A. DELAWARE. Kent Co.:** just outside W edge of Bombay Hook National Wildlife Refuge along Hay Point Landing Road (Hwy 9), 39.282069°, –75.517314°, 25 Apr 2022, *A.A. Crowl CY-487* (BRIT914522). **FLORIDA. Clay Co.:** Camp Crystal Lake, NE shore of small lobe of Crystal Lake, between the shore and Cross Seminole Trail, 29.83195°, –82.04488°, 41 m elev., 27 Mar 2025, *P.W. Fritsch 2597*. **Nassau Co.:** Cary State Forest, edge of swamp along boardwalk, 30.39923°, –81.92392°, 28 Mar 2021, *A.A. Crowl CY-386*

(BRIT792862). **GEORGIA. Charlton Co.:** Okefenokee National Wildlife Refuge, Stephen C Foster State Park, along boardwalk, 30.82826°, –82.36276°, 27 Mar 2021, *A.A. Crowl CY-375* (BRIT792852); E side of Okefenokee National Wildlife Refuge, edge of pond along Okefenokee Pkwy/Wildlife Drive, 30.72909°, –82.13743°, 27 Mar 2021, *A.A. Crowl CY-380* (BRIT792857); E side of Okefenokee National Wildlife Refuge, Chesser Island boardwalk, 30.71290°, –82.16666°, 28 Mar 2021, *A.A. Crowl CY-383* (BRIT792859); ibid., *A.A. Crowl CY-384* (BRIT792860); Chesser Island Boardwalk Trail, along E side of boardwalk, Okefenokee National Wildlife Refuge, ca. 0.5 mi W of parking area, 30.71236°, –82.17000°, 37 m elev., 2 Apr 2024, *P.W. Fritsch 2549* (BRIT1058601); ibid., *P.W. Fritsch 2550* (BRIT1058602); Okefenokee National Wildlife Refuge, E edge of pond along W side of Wildlife Drive, ca. 0.55 mi due S of Boat House Road, 30.72931°, –82.13726°, 41 m elev., 2 Apr 2024, *P.W. Fritsch 2551* (BRIT1058603); Okefenokee National Wildlife Refuge, just outside the NW edge of Stephen C Foster State Park, along S side of boardwalk, 30.82801°, –82.36361°, 38 m elev., 2 Apr 2024, *P.W. Fritsch 2553* (BRIT1058605); Okefenokee National Wildlife Refuge, Chesser Island Boardwalk Trail, along SE side of boardwalk, ca. 13 m NE of the tower at the end of the boardwalk, 30.71075°, –82.1716°, 38 m elev., 2 Mar 2025, *P.W. Fritsch 2612*. **Long Co.:** Griffin Ridge Wildlife Management Area, main (east) entrance off of US Hwy. 301, ca. 0.33 mi NW of US 301, ca. 8 m E of dirt road, 31.69344°, –81.79254°, 19 m elev., 5 Mar 2025, *P.W. Fritsch 2626*; ibid., *P.W. Fritsch 2628*; ibid., 31.69513°, –81.7941°, 16 m elev., 5 Mar 2025, *P.W. Fritsch 2629*. **Ware Co.:** S of Laura Walker Road, dirt road on edge of golf course, 31.12933°, –82.22888°, 26 Mar 2021, *A.A. Crowl CY-373* (BRIT792850); Sam's Road, S side, ca. 100 m W of Laura Walker Road (Hwy. 177), ca. 0.9 mi due S of US 82, 31.15540°, –82.21993°, 42 m elev., 3 Apr 2024, *P.W. Fritsch 2559* (BRIT1058611); along N side Apple Drive, ca. 125 m E of Hwy. 177 (Laura Walker Road), 31.15548°, –82.21734°, 41 m elev., 3 Mar 2025, *P.W. Fritsch 2620*. **MAINE. Hancock Co.:** Mount Desert Island, Acadia National Park, Sieur de Monts Road, 44.362019°, –68.204757°, 13 Jul 2018, *A.A. Crowl CY-115* (BRIT698667); Mount Desert Island, Acadia National Park, N end of Eagle Lake, 44.378384°, –68.248140°, 12 Jul 2018, *P.S. Manos CY-130* (BRIT698674). **MARYLAND. Cecil Co.:** Elk Neck State Forest, Pete Bond Scenic Overlook Trail, 39.581268°, –75.916234°, 25 Apr 2022, *A.A. Crowl CY-489* (BRIT914524). **Wicomico Co.:** Chesapeake Forest lands, along Old Bradley Road 0.25 km NE of intersection with US Hwy., 50 38.473246°, –75.794390°, 24 Apr 2022, *A.A. Crowl CY-484* (BRIT914519). **Wicomico Co.:** Chesapeake Forest lands, along Old Bradley Road, 1.5 km NE of intersection with US Hwy. 50, Blackwater National Wildlife Refuge, 38.483518°, –75.789790°, 24 Apr 2022, *A.A. Crowl CY-486* (BRIT914521). **MASSACHUSETTS. Essex Co.:** Plum Island, Hellcat Trail, dune loop, 42.742735°, –70.795838°, 7 Jul 2018, *A.A. Crowl CY-101* (BRIT698656); ibid., 16 Jul 2018, *P.S. Manos CY-131* (BRIT698675); ibid., *P.S. Manos CY-132* (BRIT698676). **MICHIGAN. Allegan Co.:** Allegan State Game Area, SW shore of Crooked Lake, ca. 100 m SE of terminus of dirt access road to Crooked Lake, ca. 0.4 km N of 113th Avenue, ca. 0.6 km W of 48th Street, 42.51944°, –86.02083°, 211 m elev., 22 May 2023, *P.W. Fritsch 2513* (BRIT914428); ibid., *P.W. Fritsch 2514* (BRIT914429); ibid., 42.51817°, –86.02127°, 228 m elev., 22 May 2023, *P.W. Fritsch 2515* (BRIT914430). **Berrien Co.:** ca. 64 m SE of the S-most part of the parking area for the New Buffalo Eastbound Weigh Station on Interstate 94, 41.78312°, –86.71835°, 208 m elev., 22 May 2023, *P.W. Fritsch 2509* (BRIT914471); ibid., *P.W. Fritsch 2510* (BRIT914426). **Calhoun Co.:** Ott Biological Preserve, ca. 0.3 km E of parking area for the preserve off Jameson Avenue, 42.32232°, –85.12717°, 263 m elev., 23 May 2023, *P.W. Fritsch 2520* (BRIT914435); ibid., *P.W. Fritsch 2521* (BRIT914436). **Cass Co.:** ca. 30 m N of NW shore of Pine Lake, ca. 56 m W of W-most house along North Court, 42.05540°, –85.81365°, 273 m elev., 22 May 2023, *P.W. Fritsch 2506* (BRIT914474); ibid., *P.W. Fritsch 2507* (BRIT914473); ibid., *P.W. Fritsch 2508* (BRIT914472). **Kalamazoo Co.:** West Lake Nature Preserve, along boardwalk E of the boardwalk circle, 42.18847°, –85.58170°, 261 m elev., 21 May 2023, *P.W. Fritsch 2502* (BRIT914515); ibid., *P.W. Fritsch 2503* (BRIT914487); ibid., *P.W. Fritsch 2504* (BRIT914514); ibid., *P.W. Fritsch 2505* (BRIT914513). **Lapeer Co.:** Kresge Environmental Center, trail along ridge traversing NE from the dormitory building, ca. 0.4 km from dormitory, 43.11727°, –83.23835°, 271 m elev., 19 May 2023, *P.W. Fritsch 2490* (BRIT914415); ibid., *P.W. Fritsch 2491* (BRIT914416); ibid., *P.W. Fritsch 2492* (BRIT914417). **Montcalm Co.:** Alma College Ecological Station at Davis Lake, Vestaburg Bog, 0.21 km S of Deaner Road, on trail heading S from the station building, 43.39169°, –84.89458°, 277 m elev., 23 May 2023, *P.W. Fritsch 2517* (BRIT914432); ibid., *P.W. Fritsch 2518* (BRIT914433). **Oakland Co.:** ca. 0.7 km E of Hwy. M-5, ca. 90 m S of the parking lot for shops and restaurants parallel and S of W Maple Road, ca. 20 m W of transmission lines, 42.54191°, –83.44347°, 287 m elev., 20 May 2023, *P.W. Fritsch 2496* (BRIT914420); ibid., *P.W. Fritsch 2497* (BRIT914421); ibid., *P.W. Fritsch 2498* (BRIT914422); ibid., *P.W. Fritsch 2499* (BRIT914423); Rose Oaks County Park, ca. 190 m W of Buckhorn Lake Road, ca. 50 m S of S edge of small lake between Esler Lake and Cogger Lake, N end of spit of upland surrounded by marsh, 42.74853°, –83.63371°, 296 m elev., 20 May 2023, *P.W. Fritsch 2500* (BRIT914424); ibid., *P.W. Fritsch 2501* (BRIT914516). **Ottawa Co.:** Port Sheldon Natural Area, ca. 0.28 km S of Port Sheldon Street, ca. 0.4 km E of 16th Avenue, on trail that starts ca. 0.4 km E of 16th Avenue on S side of Port Sheldon Street., 42.88230°, –86.17447°, 194 m elev., 23 May 2023, *P.W. Fritsch 2516* (BRIT914431). **Washtenaw Co.:** Thomas Woods/Marsh, ca. 56 m N of E Textile Road between Platt Road and Thomas Road, across the road from the parking lot for Old Hickory Trail at Pittsfield Preserve, 42.20125°, –83.70599°, 254 m elev., 18 May 2023, *P.W. Fritsch 2482* (BRIT914486); ibid., *P.W. Fritsch 2483* (BRIT914485); Mud Lake Bog, ca. 0.35 km S of Barker Road aligned with the terminus of S Hamburg Road, 42.41786°, –83.79578°, 271 m elev., 19 May 2023, *P.W. Fritsch 2493* (BRIT914480); ibid., *P.W. Fritsch 2494* (BRIT914418); ibid., *P.W. Fritsch 2495* (BRIT914419). **Wayne Co.:** ca. 0.5 km S of Sibley Road and 0.5 km W of Telegraph Rd, ca. 130 m W of transmission lines, NE end of a buttonbush pond, 42.16228°, –83.27315°, 187 m elev., 18 May 2023, *P.W. Fritsch 2484* (BRIT914484); ibid., *P.W. Fritsch 2485* (BRIT914483); ibid., *P.W. Fritsch 2486* (BRIT914518); ibid., *P.W. Fritsch 2487* (BRIT914481); ibid., *P.W. Fritsch 2488* (BRIT914482); ibid., *P.W. Fritsch 2489* (BRIT914517). **NEW HAMPSHIRE. Rockingham Co.:** Great Bay National Wildlife Reserve 43.089755°, –70.854681°, 7 Jul 2018, *P.S. Manos CY-116* (BRIT698668); ibid., *P.S. Manos CY-118* (BRIT698669). **NEW JERSEY. Middlesex Co.:** Cheesequake State Park, parking lot edge near New Landing *P.S. Manos CY-144* (BRIT698629). **Middlesex Co.:** Cheesequake State Park, trail to Hooks Creek Lake, Yellow Trail, 40.437405°, –74.266786°, *P.S. Manos CY-146* (BRIT698631). **Morris Co.:** Great Swamp National Wildlife Refuge, along boardwalk, 40.711694°, –74.490815°, *P.S. Manos CY-147* (BRIT698632); ibid., *P.S. Manos CY-148*; ibid., *P.S. Manos CY-149* (BRIT698633); ibid., *P.S. Manos CY-150* (BRIT698634); ibid., *P.S. Manos CY-152* (BRIT698635); ibid., *P.S. Manos CY-155* (BRIT698636); ibid., *P.S. Manos CY-157* (BRIT698637); ibid., *P.S. Manos CY-159* (BRIT698638); ibid., *P.S. Manos CY-160*

(BRIT698639); ibid., *P.S. Manos CY-166* (BRIT698640). **Union Co.:** Westfield, Brightwood Park, 17 Jul 2019, *P.S. Manos CY-269* (BRIT698813); ibid., *P.S. Manos CY-271* (BRIT698815); Watchung Reservation, along shore of Surprise Lake, 17 Jul 2019, *P.S. Manos CY-273* (BRIT698817); Westfield, Brightwood Park, 40.661091°, –74.371559°, 1 May 2021, *P.S. Manos CY-401* (BRIT792874). **NEW YORK. Cortland Co.:** Lime Hollow Nature Center, SW of Munsons Corners, NY, from jct. of McLean Road, Lime Hollow Road, and Gracie Road drive S along Gracie Road ca. 0.6 mi to parking area on left (parking for Phillips Memorial Trail). Follow trail E over hills and down to floating docks on margin of Chicago Bog, 42.562381°, –76.243305°, 275 m elev., 15 Jul 2023, *R. Carmickle RC126* (BRIT927793); ibid., 42.562296°, –76.243425°, 363 m elev., 15 Jul 2023, *R. Carmickle RC127* (BRIT927794); ibid., 42.562439°, –76.243529°, *R. Carmickle RC128* (BRIT927795). **Duchess Co.:** Fahnestock State Park, "AT&T Meadow," from jct. Dennytown Road and Indian Brook Road (SW of State Park HQ) drive WSW along Indian Brook Road to a metal gate and drystack stone wall past woods on right, walk around gate and uphill along right edge of pasture/along old 2 track road for ca. 325 m, 41.427638°, –73.881366°, 247 m elev., 11 Jul 2023, *R. Carmickle RC105* (BRIT927464); ibid., 41.427452°, –73.881310°, 247 m elev., 11 Jul 2023, *R. Carmickle RC106* (BRIT927463). **Monroe Co.:** Mendon Ponds Park, Devil's Bathtub Trail, from Devil's Bathtub parking area hike down steps to base on slope/pond margin, 43.024488°, –77.573405°, 121 m elev., 14 Jul 2023, *R. Carmickle RC118* (BRIT927451); ibid., 43.024386°, –77.573333°, *R. Carmickle RC119* (BRIT927450); ibid., 43.024316°, –77.573417°, *R. Carmickle RC120* (BRIT927449); ibid., 43.024603°, –77.573182°, *R. Carmickle RC121* (BRIT927448); ibid., 43.024604°, –77.573155°, *R. Carmickle RC122* (BRIT927789). **Oswego Co.:** N of Oneida Lake, 3.6 km NE of Constantia (NE of Syracuse), E end of Kibbie Lake, 43.267941°, –75.963632°, 15 June 2020, *A.J. Shaw CY-334a* (BRIT698846); ibid., *A.J. Shaw CY-334b* (BRIT698847). **Schuyler Co.:** Finger Lakes National Forest, 5.2 km N of NY-227 on Potomac Road, at the entrance to the Potomac Group Campground, 42.496200°, –76.788220°, 15 June 2020, *A.J. Shaw CY-333* (BRIT698845). **Suffolk Co.:** Quogue Wildlife Preserve, 40.835269°, –72.615219°, 16 Jul 2019, *P.S. Manos CY-263* (BRIT698807); ibid., *P.S. Manos CY-264* (BRIT698808); Cranberry Bog Nature Preserve, 40.903456°, –72.672193°, 16 Jul 2019, *P.S. Manos CY-267* (BRIT698811); ibid., *P.S. Manos CY-268* (BRIT698812); Connetquot River State Park, from park offices follow blue trail (dirt road) across bridge and around S end of Main Pond, stay left at fork, 40.752225°, –73.146155°, 42 m elev., 21 Jul 2023, *R. Carmickle RC154* (BRIT927788). **Tompkins Co.:** Sapsucker Woods Sanctuary, from Cornell Lab of Ornithology Visitor Center drive S along Sapsucker Woods Road for ca. 0.3 mi to trailhead parking, follow Wilson Trail (W side of road) for ca. 0.3 mi, 40 m off S side of trail, from just past the end of a boardwalk, 42.476435°, –76.455306°, 236 m elev., 15 Jul 2023, *R. Carmickle RC125* (BRIT927792). **Wayne Co.:** Huckleberry Swamp Trail (Olga Fleischer Ornithological Foundation), Boardwalk/Loop Trail, from trailhead parking area walk along trail to boardwalk, 43.171068°, –76.949497°, 47 m elev., 14 Jul 2023, *R. Carmickle RC115* (BRIT927454); ibid., 43.170811°, –76.949598°, *R. Carmickle RC116* (BRIT927453); ibid., 43.169325°, –76.948754°, *R. Carmickle RC117* (BRIT927452). **Wyoming Co.:** Letchworth State Park, Trout Pond Area, from Trout Pond Trail parking area walk around gate near N end of parking area (E side of road), follow trail to boggy pond, NE for ca. 30 m, then E for ca. 85 m, then N for ca. 95 m, then W for ca. 45 m, 42.593389°, –78.039323°, 303 m elev., 15 Jul 2023, *R. Carmickle RC123* (BRIT927790). **NORTH CAROLINA. Bertie Co.:** 10.9 mi SE of Windsor on NC-308, S side of road, 35.937740°, –76.759040°, 17 Apr 2018, *B. Aguero CY-072* (BRIT698697). **Bladen Co.:** Bladen Lakes State Forest, 1 mi S of Jones Lake along dirt access road, 34.671603°, –78.591540°, 7 Sep 2019, *A.A. Crowl CY-319* (BRIT698834); ibid., *A.A. Crowl CY-320* (BRIT698835). **Brunswick Co.:** Green Swamp Preserve, 34.093228°, –78.297307°, 22 Apr 2022, *A.A. Crowl CY-472* (BRIT914469); Green Swamp Game Land, 33.988851°, –78.021751°, 22 Apr 2022, *A.A. Crowl CY-473* (BRIT914470); ibid., *A.A. Crowl CY-474* (BRIT914449). **Columbus Co.:** 4 mi E of Lake Waccama, N side of Hwy., 214 34.321827°, –78.424172°, 7 Sep 2019, *A.A. Crowl CY-316* (BRIT698831). **Robeson Co.:** Butler Road, Fairmont, 0.25 mi from NC/SC border, 34.452648°, –79.243546°, 30 Mar 2019, *A.A. Crowl CY-193* (BRIT698746). **OHIO. Portage Co.:** Triangle Lake Bog State Nature Preserve, 41.118853°, –81.262031°, 5 Jun 2019, *A.A. Crowl CY-232* (BRIT698782); ibid., *A.A. Crowl CY-233* (BRIT698783); Tom S. Cooperrider-Kent Bog State Nature Preserve, 41.128489°, –81.352784°, 5 Jun 2019, *A.A. Crowl CY-235* (BRIT698784); ibid., *A.A. Crowl CY-236* (BRIT698785). **Stark Co.:** Fry Family Park, edge of pond, 40.666564°, –81.343449°, 3 Jun 2019, *A.A. Crowl CY-229* (BRIT698779). **PENNSYLVANIA. Bucks Co.:** Silver Lake Nature Center, Delhaas Woods, from Nature Center parking lot cross Bath Road to Delhaas Woods trailhead follow yellow trail ca. 0.5 mi, 40.116285°, –74.8723°, 22 m elev., 20 Jul 2023, *R. Carmickle RC152* (BRIT927786). **Centre Co.:** Bear Meadows, from Bear Meadows Trailhead parking area follow trail SW along bog/stream margins for ca. 50 m, 40.731606°, –77.754112°, 562 m elev., 16 Jul 2023, *R. Carmickle RC129* (BRIT927796). **Clinton Co.:** Bushkill Road, from parking area just SE of jct. SR402 and Old Bushkill Road/2003 (S of Porters and Pickerel Lakes), follow ATV trail SSE, 41.229202°, –75.0725°, 410 m elev., 18 Jul 2023, *R. Carmickle RC144* (BRIT927779); ibid., 41.229404°, –75.072731°, *R. Carmickle RC145* (BRIT927780); ibid., 41.229394°, –75.072868°, *R. Carmickle RC146* (BRIT927781). **Luzerne Co.:** Memorial Shrine Cemetery (1831 W 8th St, Wyoming, PA 18644), from entrance drive to top of hill and park near large evergreen and bible statue, walk along seepy margin of woods at top of hill, 41.359198°, –75.874442°, 409 m elev., 18 Jul 2023, *R. Carmickle RC139* (BRIT899943). **Monroe Co.:** The Nature Conservancy Long Pond Barrens, from parking area off SR115 (SE of Pocono Raceway) hike NE along two track road, 41.036986°, –75.505645°, 540 m elev., 19 Jul 2023, *R. Carmickle RC148* (BRIT927783). **Northampton Co.:** Minsi Lake Corridor Greenway, from NW corner of parking area follow Minsi Lake Nature Trail NNW for ca. 30 m, 40.914082°, –75.178744°, 180 m elev., 19 Jul 2023, *R. Carmickle RC151* (BRIT927785). **SOUTH CAROLINA. Aiken Co.:** Aiken State Park, along SW side of Picnic Circle, ca. 0.5 mi due W of Hwy. 53 (State Park Road), 33.55831°, –81.49156°, 84 m elev., 6 Apr 2024, *P.W. Fritsch 2577* (BRIT1058629). **Barnwell Co.:** Audubon's Silver Bluff Sanctuary, 33.323021°, –81.848959°, 20 Apr 2022, *A.A. Crowl CY-459* (BRIT914406); ibid., *A.A. Crowl CY-461* (BRIT914404). **Berkeley Co.:** Francis Marion National Forest, along firebreak road, 33.064620°, –79.703473°, 22 Apr 2022, *A.A. Crowl CY-470* (BRIT914468); Francis Marion National Forest, near Halfway Creek campsite, 33.055521°, –79.695464°, 22 Apr 2022, *A.A. Crowl CY-471* (BRIT914529). **Charleston Co.:** ACE Basin Wildlife Refuge, E of State Road S-10-346, firebreak (Oak Ridge Road), 32.68572°, –80.39049°, 25 Mar 2021, *A.A. Crowl CY-355* (BRIT BRIT792834); Ernest F. Hollings ACE Basin National Wildlife Refuge, along S side of Oak Ridge Road Upper (Nature Trail), 0.12 mi E of State Road S-10-346 (Jehosee Island Road), 32.68568°, –80.39001°, 22 m elev., 5 Apr 2024, *P.W. Fritsch 2566* (BRIT1058618); ibid., 32.68579°,

–80.39008°, 22 m elev., 5 Apr 2024, *P.W. Fritsch 2568* (BRIT1058620). **Colleton Co.:** Walterboro Wildlife Sanctuary, 32.89402°, –80.68305°, 25 Mar 2021, *A.A. Crowl CY-360* (BRIT792839); 4.76 mi SE of Ruffin, E edge of Big Hill Road, N of the Ruffin Road (SSR44) intersection, 32.97062°, –80.74465°, 25 Mar 2021, *A.A. Crowl CY-361* (BRIT792840); ibid., *A.A. Crowl CY-365* (BRIT792844); ca. 4 m E of Big Hill Road, along a furrow paralleling the road, ca. 100 NNW of State Road S-15-44 (Ruffin Road), 32.97061°, –80.74465°, 29 m elev., 5 Apr 2024, *P.W. Fritsch 2572* (BRIT1058624). **Kershaw Co.:** McRay Road (SR-28-131), 0.5 mi S of Goodale State Park, 34.285900°, –80.523900°, 30 Mar 2019, *A.A. Crowl CY-196* (BRIT698749); along Hwy. 12 (Fort Jackson Road), on N side of road, across from gravel pullout, 34.119877°, –80.780377°, 30 Mar 2019, *A.A. Crowl CY-197* (BRIT698750); Goodale State Park, 34.286302°, –80.523279°, 21 Apr 2022, *A.A. Crowl CY-468* (BRIT914532); Goodale State Park, along E side of Nature Trail, ca. 137 m ENE of trail head, 34.28635°, –80.52306°, 65 m elev., 6 Apr 2024, *P.W. Fritsch 2581* (BRIT1058633). **Lexington Co.:** Peachtree Rock Preserve, along trail to the rock, 33.830945°, –81.199795°, 30 Mar 2019, *A.A. Crowl CY-199* (BRIT698752). **VIRGINIA. Suffolk Co.:** ca. 8 km S of Suffolk along Hosier Road, 36.644729°, –76.578184°, 23 Apr 2022, *A.A. Crowl CY-478* (BRIT914453). **Virginia Beach Co.:** First Landing State Park, 36.913331°, –76.044473°, 24 Apr 2022, *A.A. Crowl CY-480* (BRIT914455).

Vaccinium fuscatum—**U.S.A. ALABAMA. Baldwin Co.:** ca. 4 m S of boardwalk, ca. 35 m W of Rosemary Dunes Trail, ca. 0.20 mi NNE of parking area, ca. 0.25 mi S of AL-182, Gulf State Park, 30.26134°, –87.63327°, 3 m elev., 5 May 2022, *P.W. Fritsch 2443* (BRIT698895). **Calhoun Co.:** E side of road to Moorman Lookout at Fort McClellan, ca. 16 m from Bains Gap Road at Bain Gap, Mountain Longleaf National Wildlife Refuge, 33.71535°, –85.73866°, 437 m elev., 30 Apr 2022, *P.W. Fritsch 2423* (BRIT698874). **Pike Co.:** ca. 110 m S of Pell Avenue at Troy University Arboretum, ca. 390 m E of entrance road to the arboretum, Troy, 31.79485°, –85.95865°, 145 m elev., 2 May 2022, *P.W. Fritsch 2435* (BRIT698886); ca. 92 m S of Pell Avenue at Troy University Arboretum, ca. 218 m E of entrance road to the arboretum, Troy, 31.79520°, –85.96057°, 146 m elev., 2 May 2022, *P.W. Fritsch 2436* (BRIT698887). **ARKANSAS. Poinsett Co.:** ca. 90 m N of Mink Road along S bank of creek, ca. 0.5 mi W of AR-163, Crowley's Ridge, 35.46157°, –90.68546°, 95 m elev., 22 May 2021, *P.W. Fritsch 2358* (BRIT698963); ibid., 35.46164°, –90.68549°, *P.W. Fritsch 2359* (BRIT698964). **DELAWARE. Kent Co.:** just outside W edge of Bombay Hook National Wildlife Refuge along Hay Point Landing Road (Hwy. 9), 39.282069°, –75.517314°, 25 Apr 2022, *A.A. Crowl CY-488* (BRIT914523). **FLORIDA. Alachua Co.:** along Gainesville-Hawthorn Trail, 29.591233°, –82.188450°, 7 Oct 2018, *A.A. Crowl CY-190* (BRIT698743); Gainesville, Morningside Nature Center, 29.65693°, –82.27785°, 29 Mar 2021, *A.A. Crowl CY-388* (BRIT792863); Newnans Lake Conservation Area (Gumroot Swamp), 29.68521°, –82.22550°, 29 Mar 2021, *A.A. Crowl CY-390* (BRIT792864); ibid., *A.A. Crowl CY-391* (BRIT792865). **Clay Co.:** Mike Roess Gold Head Branch State Park, in head ravine of Gold Head Branch, 29.84001°, –81.95404°, 49 m elev., 28 Feb 2025, *P.W. Fritsch 2594*; Camp Crystal Lake, NE shore of small lobe of Crystal Lake, between the shore and Cross Seminole Trail, 29.83199°, –82.04504°, 40 m elev., 28 Feb 2025, *P.W. Fritsch 2596*. **Duval Co.:** Racetrack Road near intersection with FL-9B, 30.105055°, –81.513254°, 4 Apr 2019, *A.A. Crowl CY-211* (BRIT698761); Julington Durbin Nature Preserve, at edge of swamp just after first bridge, 30.120074°, –81.546396°, 4 Apr 2019, *A.A. Crowl CY-213* (BRIT698764); ibid., 30.119862°, –81.546420°, 1 Sep 2019, *A.A. Crowl CY-310* (BRIT698825); ibid., 30.120074°, –81.546396°, 1 Sep 2019, *A.A. Crowl CY-311* (BRIT698826); Julington-Durbin Creek Preserve, ca. 30 m N of northern spur trail off N part of Yellow Blaze Loop Trail, ca. 1.4 mi W of parking area, 30.12896°, –81.56807°, 1 m elev., 1 Apr 2024, *P.W. Fritsch 2546* (BRIT1058598); ibid., *P.W. Fritsch 2547* (BRIT1058599). **Flagler Co.:** Pellicer Creek Conservation Area, white blaze trail, 29.65612°, –81.26956°, 0 m elev., 27 Feb 2025, *P.W. Fritsch 2589*. **Highlands Co.:** Archbold Biological Station, ca. 0.2 mi N of the main parking area, ca. 7 m W of railroad tracks, 27.18666°, –81.35216°, 44 m elev., 27 Mar 2024, *P.W. Fritsch 2522* (BRIT1058574). **Nassau Co.:** Yulee, Mentorial Road near jct. with Rte. 200, 30.617185°, –81.645520°, 4 Apr 2019, *A.A. Crowl CY-214* (BRIT698765). **Osceola Co.:** Disney Wilderness Preserve, W stretch of the yellow trail, ca. 0.5 mi due S of the jct. with the red trail and ca. 1 mi SSE of the main buildings, 28.11447°, –81.42412°, 22 m elev., 29 Mar 2024, *P.W. Fritsch 2528* (BRIT1058580). **Putnam Co.:** Paul Lyrene's property near Star Lake, around edge of sinkhole pond, 29.52970°, –82.03003°, 29 Mar 2021, *A.A. Crowl CY-392* (BRIT792866); Paul Lyrene's property near Star Lake, on edge of lake near dock, 29.52872°, –82.03129°, 29 Mar 2021, *A.A. Crowl CY-395* (BRIT792869). **Saint Johns Co.:** St. Augustine, Moses Creek Conservation Area, N of Hwy. 302, West Trail, 29.765004°, –81.298614°, 7 Apr 2019, *A.A. Crowl CY-219* (BRIT698770); Deep Creek Conservation Area, Deep Creek North section, N side of trail, ca. 0.53 mi W of trailhead on County Road 13 S, 29.78280°, –81.50074°, 2 m elev., 1 Apr 2024, *P.W. Fritsch 2543* (BRIT1058595); ibid., 29.78161°, –81.50274°, 1 m elev., 1 Apr 2024, *P.W. Fritsch 2544* (BRIT1058596); Moses Creek Conservation Area, W side Golf Course Trail (trailhead at N side Hwy. 206), 29.75972°, –81.29582°, 8 m elev., 27 Feb 2025, *P.W. Fritsch 2591*. **Santa Rosa Co.:** Blackwater River State Forest, E side of Hwy. 191 (Munson Hwy.), ca. 0.63 mi S of intersection of Hwy. 191 and Westwood Drive, at culvert, 30.88043°, –86.88763°, 46 m elev., 7 Mar 2025, *P.W. Fritsch 2637*. **Seminole Co.:** Little Big Econ State Forest, NE edge, S side of short trail bordering wetland, ca. 0.5 mi W of Snow Hill Road, 28.69966°, –81.12307°, 12 m elev., 31 Mar 2024, *P.W. Fritsch 2537* (BRIT1058589) . **Sumter Co.:** Lake Okahumpka Park, ca. 37 m S of track that encircles the wetland area, ca. 209 m WSW of main entrance at E County Road 44, 28.83405°, –82.00651°, 23 m elev., 1 Mar 2025, *P.W. Fritsch 2602*. **Wakulla Co.:** St. Mark's National Wildlife Refuge, Rte. 372 (Surf Road), 5 mi SE of Hwy. 319, 29.998149°, –84.430501°, 2 Apr 2019, *A.A. Crowl CY-209* (BRIT698760). **GEORGIA. Camden Co.:** Crooked River State Park, along Bay Boardwalk Trail, 30.838577°, –81.554257°, 4 Apr 2019, *A.A. Crowl CY-216* (BRIT698767). **Charlton Co.:** Okefenokee National Wildlife Refuge, ca. 5 m NE of edge of Chesser Island Road, ca. 5 mi W of Okefenokee Parkway, 30.709340°, –82.151160°, 38 m elev., 2 Mar 2025, *P.W. Fritsch 2613*; ibid., *P.W. Fritsch 2614*. **Ware Co.:** N of Laura S Walker Lake, W of Hwy-117 on Sam's Road (dirt road), edge of pine plantation 31.15534°, –82.21981°, 26 Mar 2021, *A.A. Crowl CY-372* (BRIT792849). **Ware Co.:** N of Laura S Walker Lake, W of Hwy. 117 on Sam's Road (dirt road), 31.155403°, –82.219780°, 19 Apr 2022, *A.A. Crowl CY-456* (BRIT914409); S side of Apple Drive, along sand track ca. 12 m E of edge of Hwy. 177 (Laura Walker Road), 31.155290°, –82.218510°, 43 m elev., 3 Mar 2025, *P.W. Fritsch 2618*; along N side Apple Drive, ca. 28 m E of Hwy. 177 (Laura Walker Road, 31.155500°, –82.218330°, 41 m elev., 3 Mar 2025, *P.W. Fritsch 2621*; Sam's Road, N side, ca. 100 m W of Laura Walker Road (Hwy. 177), ca. 0.9 mi due S of U.S. 82, 31.15555°, –82.21991°, 41 m elev., 3 Mar 2025, *P.W. Fritsch 2623*; along S side Apple Drive, ca. 9 m E of Hwy. 177 (Laura Walker Road), 31.155420°, –82.218540°, 41 m elev., 3 Mar 2025, *P.W. Fritsch 2625*. **LOUISIANA. Jackson**

Par.: along W side of Walker Road (LA-147), ca. 1.3 mi NE of intersection of LA-147 and LA-34, 32.16473°, –92.54328°, 64 m elev., 15 May 2021, *P.W. Fritsch 2321* (BRIT792786); ibid., 32.16650°, –92.54425°, 63 m elev., 15 May 2021, *P.W. Fritsch 2324* (BRIT792789). **Rapides Par.:** Wild Azalea Seep, along Wild Azalea Trail (trailhead is at Evangeline Primitive Camp on W side of Messina Road), ca. 3 m from creek, Calcasieu Ranger District, Kisatchie National Forest, 31.24121°, –92.61673°, 31 m elev., 13 May 2021, *P.W. Fritsch 2313* (BRIT698995). **Vernon Par.:** ca. 15 m S of US Forest Service road 421 along a tributary of Drakes Creek, ca. 1.6 mi (direct) from LA-10 (Pitkin Hwy.), Kisatchie National Forest, 31.00324°, –93.14857°, 64 m elev., 10 May 2021, *P.W. Fritsch 2296* (BRIT698977). **MARYLAND. Wicomico Co.:** Chesapeake Forest lands, Tom Tyler Nature Trail, 38.485309°, –75.783394°, 24 Apr 2022, *A.A. Crowl CY-485* (BRIT914520). **MISSISSIPPI. Franklin Co.:** 0.10 mi E of the end of an unnamed Forest Service road, ca. 0.5 mi W of Scott-Murray Road, Homochitto National Forest, 31.46732°, –90.77223°, 105 m elev., 20 Apr 2022, *P.W. Fritsch 2378* (BRIT698898); ibid., *P.W. Fritsch 2379* (BRIT698899). **Tishomingo Co.:** ca. 94 m SE of Crows Neck Road (County Road 115), ca. 2.2 mi SW of the W end of County Road 961, Crows Neck Recreation and Environmental Center, 34.60503°, –88.28923°, 160 m elev., 27 Apr 2022, *P.W. Fritsch 2410* (BRIT698930). **NEW JERSEY. Middlesex Co.:** Cheesequake State Park, trail to Hooks Creek Lake, Yellow Trail, 40.437405°, –74.266786°, *P.S. Manos CY-145* (BRIT698630). **Union Co.:** Watchung Reservation, along shore of Surprise Lake, 17 July 2019, *P.S. Manos CY-272* (BRIT698816); ibid., 40.686923°, –74.376800°, 2 May 2021, *P.S. Manos CY-403* (BRIT792876); ibid., *P.S. Manos CY-404* (BRIT792877). **NEW YORK. Westchester Co.:** Westmoreland Sanctuary, near pond on new land tract, ca. 500 m due N of N edge of Bochtel Lake, 41.186013°, –73.68263°, 186 m elev., 10 Jul 2023, *R. Carmickle RC101* (BRIT927468). **NORTH CAROLINA. Brunswick Co.:** Green Swamp Game Land, 33.988851°, –78.021751°, 22 Apr 2022, *A.A. Crowl CY-475* (BRIT914450). **Carteret Co.:** Patsy Pond, on the Blue and Orange trails, 34.726000°, –76.961100°, 5 Jun 2020, *P.S. Manos CY-324* (BRIT698839); ibid., *P.S. Manos CY-325* (BRIT698840). **Chatham Co.:** White Pines Nature Preserve, 35.615339°, –79.160332°, 13 Jun 2020, *P S. Manos CY-328* (BRIT698843). **Columbus Co.:** 4 mi E of Lake Waccama, N side of Hwy. 214, 34.321827°, –78.424172°, 7 Sep 2019, *A.A. Crowl CY-317* (BRIT698832); ibid., *A.A. Crowl CY-318* (BRIT698833). **Craven Co.:** Neuse River Recreation Area, 34.978663°, –76.951272°, 23 Apr 2022, *A.A. Crowl CY-476* (BRIT914451). **Cumberland Co.:** Hope Mill, Chicken Foot Road, 3 mi E of I-95, 34.893577°, –78.896810°, 30 Mar 2019, *A.A. Crowl CY-192* (BRIT698745). **Durham Co.:** Duke Forest off of Gate 10 entrance, 36.022586°, –78.982696°, 12 Jun 2018, *P S. Manos CY-082* (BRIT698705); ibid., *P S. Manos CY-083* (BRIT698706), *P S. Manos CY-084.* **Harnett Co.:** Raven Rock State Park, Raven Rock Loop Trail, 35.466053°, –78.904169°, 15 Aug 2018, *P S. Manos CY-175* (BRIT698731). **Jackson Co.:** W edge of Dulaney Bog, Bull Pen Road, near Highlands, 35.015477°, –83.124350°, 3 Jun 2019, *P.S. Manos CY-254* (BRIT698799). **Macon Co.:** North fork of Coweeta Creek, off Coweeta Gap Road W of Otto, Jack Johnson Property, 35.080173°, –83.442463°, 27 Jun 2023, *P S. Manos CY-510* (BRIT1082248). **New Hanover Co.:** Halyburton City Park, 34.176225°, –77.906227°, 7 Sep 2019, *A.A. Crowl CY-312* (BRIT698827); ibid., *A.A. Crowl CY-313* (BRIT698828); Carolina Beach State Park, edge of swamp near boardwalk along Flytrap Trail, 34.047912°, –77.913984°, 7 Sep 2019, *A.A. Crowl CY-315* (BRIT698830). **Stokes Co.:** Moore's Knob, lower elevation, in a seep, 36.399186°, –80.282819°, 8 Aug 2017, *P.S. Manos CY-070* (BRIT698695). **Surrey Co.:** Pilot Mtn., Grindstone Trail, 36.347191°, –80.473510°, 23 May 2018, *P.S. Manos CY-075* (BRIT698700). **PENNSYLVANIA. Berks Co.:** Hawk Mountain Sanctuary, from Visitor Center follow staff roads SE to State Lands gate, walk around gate and along two track road for ca. 0.5 mi then uphill (northward) into woods, walk ca. 40 m NE from road, 40.624269°, –75.976537°, 388 m elev., 17 Jul 2023, *R. Carmickle RC135* (BRIT899946). **Schuylkill Co.:** Weiser State Forest, Appalachian Trail, N of Schubert, PA, from jct. of 419 and 183 drive N along 183 ca. 1.2 mi to Appalachian Trail parking area (W side of road), hike W along trail ca. 90 m then keep right at fork, continue for ca. 80 m to a clearing, 40.526920°, –76.225441°, 418 m elev., 17 Jul 2023, *R. Carmickle RC131* (BRIT927798); ibid., 40.527033°, –76.225432°, *R. Carmickle RC134* (BRIT899940). **SOUTH CAROLINA. Aiken Co.:** Hitchcock Woods, ca. 120 m WSW of entrance at the end of Fermata Place SW, 33.54464°, –81.73127°, 144 m elev., 6 Apr 2024, *P.W. Fritsch 2574* (BRIT1058626); ibid., *P.W. Fritsch 2575* (BRIT1058627); ibid., *P.W. Fritsch 2576* (BRIT1058628); Aiken State Park, along Jungle Nature Trail, ca. 90 m due W of Picnic Circle, ca. 0.57 mi due W of Hwy. 53 (State Park Road), 33.55798°, –81.49220°, 85 m elev., 6 Apr 2024, *P.W. Fritsch 2578* (BRIT1058630). **Charleston Co.:** Dungannon Heritage Preserve, 32.74899°, –80.19677°, 25 Mar 2021, *A.A. Crowl CY-350* (BRIT792829); ibid., 32.748985°, –80.196768°, 21 Apr 2022, *A.A. Crowl CY-469* (BRIT914467). Ernest F. Hollings ACE Basin National Wildlife Refuge, along S side of Oak Ridge Road Upper (Nature Trail), 0.13 mi E of State Road S-10-346 (Jehosee Island Road), 32.68567°, –80.38975°, 22 m elev., 5 Apr 2024, *P.W. Fritsch 2567* (BRIT1058619). **Colleton Co.:** 4.76 mi SE of Ruffin, E edge of Big Hill Road, N of the Ruffin Road (SSR44) intersection, 32.97062°, –80.74465°, 25 Mar 2021, *A.A. Crowl CY-366* (BRIT792845); ca. 4 m E of Big Hill Road, along a furrow paralleling the road, ca. 100 NNW of State Road S-15-44 (Ruffin Road), 32.97061°, –80.74465°, 29 m elev., 5 Apr 2024, *P.W. Fritsch 2573* (BRIT1058625). **Kershaw Co.:** Dr. Humphries Road just before jct. with Rte. 34, 34.234087°, –80.531890°, 30 Mar 2019, *A.A. Crowl CY-194* (BRIT698747); Goodale State Park, 34.286302°, –80.523279°, 21 Apr 2022, *A.A. Crowl CY-467* (BRIT914526); Goodale State Park, along E side of Nature Trail, ca. 137 m ENE of trail head, 34.28635°, –80.52306°, 65 m elev., 6 Apr 2024, *P.W. Fritsch 2580* (BRIT1058632). **TEXAS. Nacogdoches Co.:** ca. 18 m N of Farm to Market Road 1087 (Camp Tonkawa Road), ca. 4 mi E of TX-259, 6 May 2021, *P.W. Fritsch 2267* (BRIT792801). **Tyler Co.:** ca. 44 m S of County Road 4777 (Red Oak Lane), ca. 55 m N of shore of Hyatt Lake, Watson Rare Native Plant Preserve, 30.58262°, –94.38035°, 36 m elev., 7 May 2021, *P.W. Fritsch 2272* (BRIT792806). **VIRGINIA. Accomack Co.:** Island Nature Trail, SE of Hallie Whealton Smith Drive, 37.940343°, –75.359498°, 24 Apr 2022, *A.A. Crowl CY-483* (BRIT914458). **Northampton Co.:** Savage Neck Road, 0.6 km W of US Hwy. 13, 37.346386°, –75.955810°, 24 Apr 2022, *A.A. Crowl CY-482* (BRIT914457). **Suffolk Co.:** ca. 8 km S of Suffolk along Hosier Road, 36.641104°, –76.576309°, 23 Apr 2022, *A.A. Crowl CY-477* (BRIT914452). **Virginia Beach Co.:** First Landing State Park, 36.915122°, –76.041750°, 24 Apr 2022, *A.A. Crowl CY-479* (BRIT914454); ibid., 36.913331°, –76.044473°, *A.A. Crowl CY-481* (BRIT914456).

APPENDIX 2

Representative specimens of *Vaccinium corymbosum* examined for this study, one specimen per county (regional county municipalities in Quebec; some independent cities in Virginia).

CANADA. NEW BRUNSWICK. York Co.: Hinckley Point vicinity Spednik Lake, 16 Aug 1983, *H.R. Hinds 6473* (MT MT00272869 [i]). **NOVA SCOTIA. Digby Co.:** Hectanooga, 7 Jul 1920, *C.H. Bissell et al. 22210* (NCSC NCSC00086195 [i]). **Queens Co.:** Broad River, 20 Aug 2001, *C S. Blaney & C.D. Spicer 4103* (ACAD 024771 [i]). **Shelburne Co.:** Barrington, 20 Aug 1925, *H.H. Rusby s.n.* (NY 02543293 [i]). **Yarmouth Co.:** Jassy Lake, 29 Jul 1929, *R.C. Bean et al.* 22219 (ACAD 67619 [i]). **ONTARIO. Elgin Co.:** 5 mi SW of Aylmer, 25 Jul 1952, *L.E. James 1777* (ILL ILL00174910 [i]). **Frontenac Co.:** Hebert Bog, 18 Aug 1969, *S.P. Vander Kloet s.n.* (GA GA201357). **Leeds and Grenville Co.:** Blue Mt., Charleston Lake, 12 Aug 1968, *S.P. Vander Kloet s.n.* (GA GA201405). **Middlesex Co.:** 3 mi W of London, 29 Jun 1952, *L.E. James 1773* (ILL ILL00174909 [i]). **Niagara Co.:** Point Abino, 8 May 1921, *F.W. Johnson s.n.* (NY 2545349). **Norfolk Co.:** Turkey Pt., 20 May 1933, *T.M.C. Taylor 6048* (MUHW MUHW018888 [i]). **Oxford Co.:** Ingersoll, 1 Jun 1891, *M.A. Chrysler s.n.* CHRV CHRB0010847 [i]). **Russell Co.:** Cumberland Twp., Mer Bleue, 4 Jun 1939, *E.W. Hart 1457* (WIS v0350284WIS [i]). **Toronto Co.:** Edmonton [now Snelgrove], 3 Jun 1892, *J. White 6683* (RSA RSA0184910 [i]). **QUEBEC. Beauharnois-Salaberry R.C.M.:** Le long du Saint-Laurent, entre Melocheville et Coteau-du-Lac, Saint-Louis-de-Gonzague, 1940, *F. Marie-Victorin et al. 4315a* (NY 02544957 [i]). **Brome-Missisquoi R.C.M.:** Farnham, 2 Jun 1933, *F. Marie-Victorin et al. B-9* (UMO 132687). D'Autray **R.C.M.:** Lanorie, comté Berthier, 24 Jun 1943, *F. Marie-Victorin et al. 56983* (NY 02543280 [i]). **Le Haut-Richelieu R.C.M.:** Henryville, comté d'Iberville, Ferme Jean Savoy, Rte. 133, 15 May 1979, *M. Bélanger 279* (NLU NLU0141864). **Le Haut-Saint-Laurent R.C.M.:** Saint-Chrysostome, comté de Chateauguay, 25 Jun 1944, *E. Rouleau 1009* (WIS v0350288WIS [i]). **L'Érable R.C.M.:** Saint-Ferdinand, comté de Megantic, 15 Jul 1944, *F. Marie-Victorin et al. 521* (WIS v0385892WIS [i]). **Les Jardins-de-Napierville R.C.M.:** Napierville, comté de Napierville, 22 Aug 1959 *F. Rolland-Germain 7726* (ASC ASC00055492 [i]). **Les Maskoutains R.C.M.:** Sainte-Madeline, comté de Saint-Hyacinthe, 2 Jun 1931, *FF. Marie-Victorin & Rolland-Germain 46714* (MUHW MUHW018887 [i]). **Lévis R.C.M.:** Tourbière La Grande Plée bleue, à l'extemite du grand canal de drainage, 2 Aug 2001, *R. Gaulthier 2001-128* (QFA 620906 [i]). **L'Islet R.C.M.:** Ilet Canuel, Rimouski, 9 Sep 1941, *De Champlain, ptre 1115* (MT MT00069809 [i]). **Longueuil R.C.M.:** St.-Hubert, 21 Jul 1931, *A. Dubois s.n.* (NY 02545212 [i]). **Lotbiniere R.C.M.:** Dosquet, environ 5 km au sud-est du village, 11 Aug 1996, *R. Gaulthier 96-210* (QFA 433392 [i]). **Mékinac R.C.M.:** Lac-Croche, 2 Aug 1972, *H. Contant s.n.* (MT MT00045141 [i]). **Memphrémagog R.C.M.:** Comté Standstead, Lac Lovering, baie du coté nord-ouest, 13 Jul 1965, *Fr. L. Levesque et al. 650713-2683* (MT MT00109375 [i]). **Nicolet-Yamaska R.C.M.:** St-Thomas-de-Pierreville, terre de Adolphe Rousseau, 2 Jun 1873, *T.-M.-O. Maurault s.n.* (QFA 621464 [i]). **Quebéc R.C.M.:** Sainte-Foy, bords de tourbière superficielle, 27 Sep 1969, *V. Lavoie s.n.* (QFA 603018 [i]). **Vaudreuil-Soulang**es **R.C.M.:** Ile Lynch, Aug 1941, *B. Boivin 4400* (NY 02544958 [i]).

U.S.A. ALABAMA. Autauga Co.: by I-65, ca. 13.5 mi NW Montgomery, 12 Apr 1975, *R. Kral 54948* (VDB BRIT118524). **Covington Co.:** 13 mi S Opp, 1 Jun 1970, *R. Kral 39450* (VDB BRIT110777). **Geneva Co.:** 16/6 5 mi E jct. AL 87, 25 May 2001, *R. Kral 91142* (VDB BRIT110719). **CONNECTICUT. Fairfield Co.:** Newtown, The Boulevard, S of I-84, 8 May 2002, *S.D. Glenn 6516* (GA GA201345). **Hartford Co.:** West Street, across from Dinosaur State Park, Rocky Hill, 12 May 1992, *S.R. Hill 23057* (MO MO-3586237). **Litchfield Co.:** Rte. 63, East Morris Road, Watertown, 11 May 1941, *W. Lucian 42* (NY 2545065). **Middlesex Co.:** Middletown, 18 May 1889, *J.H. Barnhart 275* (NY 02545160 [i]). **New Haven Co.:** Sachem's Head, Guilford, 28 Jul 1935, *H.W. Rickett 903* (UMO 23537). **New London Co.:** Millstone, ca. 0.5 mi NE of Bay Point, Jul 1973, *B.J. Cox & W. Buchanan 4813* (UMO 132017). **Tolland Co.:** N side of Walder's Reservoir at intersection of Rtes. 15 and 31, 1 May 1968, *O. Bissett 255* (NLU NLU0141223). **Windham Co.:** East Killingly, Jul 1899, collector not indicated, *s.n.* (NY 2543366). **DELAWARE. Kent Co.:** just outside W edge of Bombay Hook National Wildlife Refuge along Hay Point Landing Road (Hwy 9), 25 April 2022, *A.A. Crowl CY-487* (BRIT BRIT914522). **New Castle Co.:** 2.3 mi SW of Blackbird, Blackbird State Forest, Tybout Tract, W side of Blackbird Forest Road, 9 May 2009, *R.F.C. Naczi 12358* (NY 2544904). **Sussex Co.:** Sowbridge Branch, W of Cedar Creek Road, ca. 1 km SW of Waples Pond and 1 mi E of Reynolds Pond, along N bank, 24 April 2022, *B. Aguero CY-496* (BRIT BRIT914499). **FLORIDA. Clay Co.:** Camp Crystal Lake, NE shore of small lobe of Crystal Lake, between the shore and Cross Seminole Trail, 28 Feb 2025, *P.W. Fritsch 2597* (BRIT). **Columbia Co.:** U.S. 441, 0.8 mi S of Ga.-Fla. state line, 19 Jun 1967, *J.R. Bozeman 10046* (NCU NCU00352902 [i]). **Gadsden Co.:** 5.7 mi S of Wetumpka, 29 Mar 1967, *S. McDaniel 8701* (SMU BRIT446544). **Leon Co.:** Apalachicola National Forest, Dog Lake Road, ca. 2 mi W of Spring Hill Road, 2 Apr 1976, *S. McDaniel 8717* (GA GA201297). **Liberty Co.:** Telogia Creek, 21 Mar 1976, *A. Gholson, Jr. 5737* (FLAS FLAS258720). **Marion Co.:** Silver River State Park, S side Trailside, 18 Feb 1990, *M.B. Buckner 36* (GA GA265308). **Nassau Co.:** Cary State Forest, 28 Mar 2021, *A.A. Crowl CY-385* (BRIT BRIT792861). **Okaloosa Co.:** 3 mi S Crestview along Fla. 85, 2 Apr 1966, *R. Kral 26132* (GA GA201333). **Santa Rosa Co.:** just W of Pace, S of Rte. 197, vicinity of power line clearing ca. 100 yds. W of Hwy. 90, 18 Jun 1981, *G. Wilhelm 9114* (USF 173061 [i]). **Wakulla Co.:** beside trail along E side of Bradwell Bay Wilderness Area, 0.5 mi S of Forest Hwy. 13 and 0.25 mi W of Sopchoppy River, Apalachicola National Forest, 24 Mar 1984, *M.A. Garland 225* (GA GA201300). **GEORGIA. Appling Co.:** Big Pond near Baxley, 3 Jun 1929, *G.A. Schulze 384* (GA GA058557). **Ben Hill Co.:** top of Red Bluff, Okmulgee River, County Road 41 near Coffee Co. line, 23 Apr 1988, *H. Brasell 229* (VSC VSC0022604 [i]). **Berrien Co.:** SSE of Nashville, 2 Mar 1953, *W.H. Duncan 14824* (GA GA058467). **Bibb Co.:** Ocmulgee National Monument, 1.78 mi E of downtown Macon, 15 Sep 2004, *L.L. Gaddy s.n.* (GA GA083668). **Brantley Co.:** 28 mi W of Darien near Wild Cat Spring, 6 May 1929, *G.A. Schulze 368* (GA GA058351). **Bryan Co.:** Fort Stewart Military Reservation, Training Area C2, Fort Stewart Road 69, just S of Tire House Range, 16 Mar 1992, *T.M. Zebryk 0039* (GA GA058549). **Bulloch Co.:** near Stilson, 29 May 1930, *G.A. Schulze 620* (GA GA058473). **Camden Co.:** St. Marys, Mar 1857, *R.H. Ward s.n.* (ILL ILL00174889 [i]). **Candler Co.:** 0.4 mi W of Upper Lott's Creek Primitive Baptist Church, 6 May 1982, *N. Craft Coile 2682* (GA GA058477). **Charlton Co.:** Okefenokee National Wildlife Refuge; Stephen C Foster State Park, 27 Mar 2021, *A.A. Crowl CY-375* (BRIT BRIT792852). **Chatham Co.:** along Quacco Road ca. 1.8 mi from Darien Hwy. and 10 mi from Savannah City Hall, 17 Jun 1958, *W.H. Duncan 21126* (GA GA058353). **Echols Co.:** alongside U.S. 129, 5.4 mi S of Mayday,

8 Apr 1965, *W.R. Faircloth 1667* (GA GA058543). **Effingham Co.:** Springfield, SR 21, 7 mi N of Springfield, ca. 2 mi W of SR 21 off Springfield Egypt Road, 4 May 2011, *D. Floyd 48* (GA GA086107). **Emanuel Co.:** roadside along Interstate Hwy 16 East, 2.2 mi W of Candler County line, W of Aline and Adrian, 10 Apr 1996, *D.D. Taylor 18151* (NLU NLU0141380). **Evans Co.:** N side of Canoochee River, off Ga. Hwy. 169, 12 Oct 1968, *J. Peabody s.n.* (GAS GAS018420 [i]). **Glascock Co.:** 5.1 mi W of Gibson, 4 May 1953, *W.H. Duncan 15810* (GA GA058482). **Hancock Co.:** ca. 4 mi SE of Sparta, 25 Mar 1954, *W.H. Duncan 17510* (GA GA058466). **Irwin Co.:** Paulk's Landing, Alapaha River, 1 mi N Alapaha River bridge, Landing Road on E side of Hwy. at Hammock Lake, 5 Jun 2009, *B. Sanderson 292* (VSC VSC0002909 [i]). **Jefferson Co.:** 1 mi S of Louisville N side of Ogeeche River, 20 Apr 1941, *W.H. Duncan 3187* (GA GA058484). **Lanier Co.:** ca. 1 mi NW of U.S. 221 check station, 11 Apr 1994, *C. Wilson 93* (VSC VSC0005053 [i]). **Laurens Co.:** ca. 15 mi S of Dublin, 6 Apr 1941, *W.H. Duncan 3122* (GA GA058362). **Liberty Co.:** ca. 2 mi N of Midway, 18 Mar 1939, *W.H. Duncan 1262* (GA GA058468). **Long Co.:** 4 mi E of Glennville, 28 Apr 1940, *W.H. Duncan 2220* (GA GA058475). **Lowndes Co.:** 8 mi E of Valdosta Courthouse on U.S. 84, 1.5 mi S of CCC Road, 10 Mar 1985, *R. Carter 3907* (GA GA058481). **Macon Co.:** 3 mi E of Macon, 1 Apr 1922, *E.T. Wherry s.n.* (DUKE DUKE10100880 [i]). **McDuffie Co.:** Fall Line Sand-hills, vicinity of Thomson, 6 Sep 1907, *H.H. Bartlett 894* (RSA RSA0184704 [i]). **McIntosh Co.:** 1.25 N of Ft. Barrington-Cox Road, along Altamaha River, 7 Oct 1962, *J.R. Bozeman 2174* (GAS GAS018416 [i]). **Meriwether Co.:** Pine Mt. along Cooler Branch, 2.5 mi SSE of Warm Springs and 3.3 mi WNW of Manchester, 8 Jun 1972, *S.B. Jones 21993* (GA GA058333). **Montgomery Co.:** SW of Charlotteville on county road, 8 Jul 1966, *J.R. Bozeman 5731* (NCU NCU00351033 [i]). **Richmond Co.:** ca. 1.5 mi SW of Fort Gordon exit along Hwy. US 1, 12 Apr 1986, *R. Carter 4763* (GA GA274172). **Screven Co.:** Sylvania, Dennis B. Dixon Bay Tract of Tuckahow WMA [Dixon Bay Wildlife Management Area (2021)], N border = intersection of Sweetheart Road and Duck Pond Road, 26 May 2000, *E. Van de Genachte s.n.* (GA GA278432). **Sumter Co.:** just W of Harry Priddy Road and S of NW arm of Youngs Millpond, ca. 4.3 (air) mi N, and slightly W, of Plains, 18 Mar 1997, *R.A. Norris 6788* (GA GA058552). **Tattnall Co.:** 2.8 mi 16° SE of Glennville, 19 Mar 1966, *M.G. Padgett 174* (GA GA058474). **Taylor Co.:** 7.1 mi S of Butler by Hwy. GA 137, vic. Hwy. GA 137 bridge over Whitewater Creek, along W side of hwy., 23 Apr 1989, *R. Carter 7806* (NCU NCU00445067 [i]). **Tift Co.:** ca. 6 mi N of Tifton at Gum Lake, 8 Jun 1931, *H.M. McKay s.n.* (UMO 151964). **Twiggs Co.:** 6 mi SW of Marion, 1 Apr 1930, *G.A. Schulze 566* (GA GA201343). **Ware Co.:** S of Laura Walker Road; dirt road on edge of golf course, 26 Mar 2021, *A.A. Crowl CY-373* (BRIT BRIT792850). **Washington Co.:** Ogeechee River along GA 88, NE sect. of co., 5 Aug 1966, *J.R. Bozeman 7130* (NCU NCU00351852 [i]). **Wayne Co.:** edge of Jessup, 27 Mar 1973, *F.G. Meyer & P.M. Mazzeo 13278* (GA GA058479). **ILLINOIS. Cook Co.:** Markham Prairie, 30 Jul 1972, *K. Bartel s.n.* (MOR 0035244MOR [i]). **Lake Co.:** 3 mi E of Antioch, 16 Jul 1944, *G.D. Fuller 9234* (ILL ILL00174869 [i]). **Winnebago Co.:** 3 mi W of South Beloit, 38 Jul 1949, *E.W. Fell & G.B. Fell 49-263* (ILL ILL00174872 [i]). **INDIANA. Allen Co.:** Spring Lake, just S of Lake Everett, 13 mi NW of Ft. Wayne, 26 Jul 1916, *C.C. Deam 20831* (IND IND-0096933 [i]). **DeKalb Co.:** ca. 1 mi S of Garrett, 17 May 1908, *C.C. Deam 3003* (NY 2545413). **Elkhart Co.:** SE corner of Sec. 24, ca. 4 mi NE of Middlebury, 18 Jul 1932, *C.C. Deam 52329A* (IND IND-0096936 [i]). **Fulton Co.:** Frank Zimmerman farm ca. 0.5 mi NW of Disko, 24 Jun 1938, *C.C. Deam 58990* (IND IND-0096937 [i]). **Kosciusko Co.:** McClary estate, Leesburg, 20 Jul 1935, *M. McGee s.n.* (NY 2545567). **LaGrange Co.:** 0.75 mi SE of Mongo, 8 May 1921, *C.C. Deam 33792* (NY 2545412). **Lake Co.:** Millens, 11 May 1878, *E.J. Hill s.n.* (NY 2545566). **LaPorte Co.:** 0.5 mi N of Mill Creek, 25 Aug 1920, *C.C. Deam 32382* (IND IND-0096955). **Marshall Co.:** Jake Follmen estate, 3–4 mi SW of Bremen, 17 Jul 1935, *W.H. Welch 2099* (NY 2545568). **Noble Co.:** S of Alcinda, 25 Jul 1931, *C.C. Deam 50708* (IND IND-0096960 [i]). **Porter Co.:** Old dune slope, vicinity of Goose Lake, 31 Aug 1955, *T.G. Yuncker & W.H. Welch 16337* (NY 2545569). **St. Joseph Co.:** ca. 5 mi W of South Bend, 10 May 1916, *C.C. Deam 19527* (IND IND-0096966 [i]). **Starke Co.:** just S of Koontz Lake, 24 May 1923, *C.C. Deam 38509* (IND IND-0096971 [i]). **Steuben Co.:** 12 mi N of Salem, 29 Jun 1916, *C.C. Deam 20602* (IND IND-0096975 [i]). **Wabash Co.:** T30N, R6E, S36, SE 1/4, 10 Jul 1955, *P.A. Orpurt s.n.* (IND IND-0096976 [i]). **Whitley Co.:** SW side of Goose Lake, 5 Jul 1920, *C.C. Deam 31233* (IND IND-0096978 [i]). **MAINE. Androscoggin Co.:** near Round Pond, 7 Jul 1915, *Turner s.n.* (NEBC 00519206 [i]). **Aroostook Co.:** Crystal, Crystal Bog, 27 Jul 1938, *F. Hyland 1015* (NY 2545061). **Cumberland Co.:** Brunswick, Jun 1892, *K. Furbish s.n.* (NEBC 00519211 [i]). **Franklin Co.:** Sandy River Valley, Farrington, 13 Aug 1894, *M.L. Fernald s.n.* (NEBC 00519130 [i]). **Hancock Co.:** Mount Desert Island, Acadia National park, Sieur de Monts Road, 13 Jul 2018, *A.A. Crowl CY-115* (BRIT BRIT698667). **Kennebec Co.:** Manchester, Jun 1874, *F.L. Scribner s.n.* (NEBC 00519194 [i]). **Knox Co.:** back of Baptist Church, Tenants Harbor, 22 Aug 1938, *R.C. Friesner 12800* (WVA 117749). **Lincoln Co.:** Lake Damariscotta, Nobleboro, Glidden's Island, 6 Jun 1931, *D. Potter & W.B. Brierly 1146* (GH 00519187 [i]). **Oxford Co.:** Stow, 14 Aug 1975, *C S. Campbell et al. 3131* (NEBC 00519148 [i]). **Penobscot Co.:** Pleasant Lake, Stetson, 10 Jul 1941, *F. Hyland s.n.* (NY 2543391). **Piscataquis Co.:** Milo, 20 Sep 1900, *M.L. Fernald s.n.* (NEBC 00519127 [i]). **Sagadahoc Co.:** S of the town of Phippsburg, 2.4 km (1.5 mi) E of Maine Rte. 216 on Maine Rte. 209, 9 Jun 1985, *E.W. Wood & D.E. Boufford 4806* (NY 02545285 [i]). **Somerset Co.:** Moscow, 7 Jul 1925, *A.H. Norton s.n.* (WIS v0350294WIS [i]). **Waldo Co.:** Northport, 23 Jul 1940, *R.C. Bean s.n.* (NEBC 00519174 [i]). **Washington Co.:** valley of Saint Croix River, Baileyville to Princeton, 22 Jul 1909, *K.M. Wiegand 315* (NY 02545657 [i]). **York Co.:** along hedges by roadside, Ocean Park, 26 May 1931, *C.E. Moldenke 1593* (NY 2545063). **MARYLAND. Anne Arundel Co.:** Leatherleaf Land, Eagle Hill, 28 Jun 1981, *S.R. Hill 10446* (GA GA201376). **Baltimore Co.:** along Windlass Run on S side of the Bird River, 10 Jun 1987, *J. Sweringen s.n.* (BALT BALT0003815 [i]). **Calvert Co.:** Cove Point Marsh, Cove Point, Chesapeake Bay, 11 May 1996, *B.W. Steury 960511.49* (PH PH00395684 [i]). **Caroline Co.:** 1.5 mi S, W of Denton, along the drainage of the Choptank River on the grounds of Camp Mardela, 30 May 1971, *A. Dolgos 332* (BRIT BRIT446596). **Cecil Co.:** Elk Neck State Forest, Pete Bond Scenic Overlook Trail, 25 Apr 2022, *A.A. Crowl CY-489* (BRIT BRIT914524). **Charles Co.:** roadside, SW Charles Co., 17 Oct 1968, *Brown & Yarwood s.n.* (MARY MARY1039964 [i]). **Dorchester Co.:** Rhodesdale, Chesapeake Forest Land, along logging road of of Lecompte Road, 24 Apr 2013, *W.D. Longbottom 18976* (NY 2200641). **Garrett Co.:** Finzel Swamp, 16 Aug 1965, *D. Wilson s.n.* (WVA 117733). **Harford Co.:** Oakington area, 6 May 1951, *G.R. Fessenden 5172* (MARY MARY1039976 [i]). **Kent Co.:** 3 mi E, 1 mi S of Chestertown, 27 Apr 1974, *A. Dolgos 42913* (BRIT BRIT446545). **Montgomery Co.:** N end Rock Creek Park, 14 Aug 1910, *H.H. Bartlett 2241* (GA GA201396). **Prince George's Co.:** E of RR tracks behind Hollywood, E end of Lackawanna St., College Park, 3 May 1970, *S. Kulczyk s.n.* (MARY MARY1039990 [i]). **Queen Anne's Co.:** roadside,

5.75 mi ESE of Centerville, 29 Apr 1939, *E.C. Earle 1976* (PH PH00395688 [i]). **Somerset Co.:** 7 mi W of Princess Anne, 17 Apr 1938, *J.M. Fogg 14600* (NY 02542727 [i]). **Talbot Co.:** 4.5 mi WNW Easton, 25 Apr 1937, *E.C. Earle 1349* (PH PH00395689 [i]). **Wicomico Co.:** Chesapeake Forest lands, along Old Bradley Road 0.25 km NE of intersection with US Hwy. 50, 24 Apr 2022, *A.A. Crowl CY-484* (BRIT BRIT914519). **Worcester Co.:** Pokomoke State Forest, N of Forest Tract Public Recreation Area parking lot and Governor Smith Lane, 23 Apr 2022, *B. Aguero CY-492* (BRIT BRIT914500). **MASSACHUSETTS. Barnstable Co.:** 0.5 mi E of Woods Hole, 23 Jun 1934, *F. Drouet 1521* (UMO 27115). **Berkshire Co.:** West Stockbridge, 31 May 1919, *A.W. Evans et al. s.n.* (NEBC 00519828 [i]). **Bristol Co.:** Horseneck Beach area ca. 10 mi SW of New Bedford, 11 May 1976, *W.H. Duncan 29792* (GA GA201364). **Dukes Co.:** Kings Hwy., 0.5 mi N of Meeting House Road, Chilmark, Martha's Vinyard Island, 13 Jul 1975, *M.A. Breiding s.n.* (WVA 147002). **Essex Co.:** Plum Island, Hellcat Trail, dune loop, 7 Jul 2018, *A.A. Crowl CY-101* (BRIT BRIT698656). **Franklin Co.:** Greenfield, *J.B. Patten s.n.* (NEBC 00519771 [i]). **Hampden Co.:** Fairview bog, S of Hadley Falls, 10 May 1930, *W.E. Manning s.n.* (VDB BRIT311229). **Hampshire Co.:** railroad crossing on South Maple St., Hadley, 16 Jul 1972, *H.E. Ahles 75714* (UMO 109412). **Middlesex Co.:** Natick, moor of mud pond, 27 May 1911, *K.M. Wiegand 2078* (NY 2542698). **Nantucket Co.:** Nantucket, 15 May 1906, *N.F. Flynn s.n.* (VT UVMVT088884 [i]). **Norfolk Co.:** Tupelo Point Campus, 25 May 1909, *K.M. Wiegand s.n.* (NY 2543338). **Plymouth Co.:** near Hingham Bridge, Hingham, 4 May and 13 Jul 1902, *F.F. Forbes 2789* (NEBC 00519563 [i]). **Suffolk Co.:** along Blue Hills Ave., near Boston, 17 Jun 1922, *E.J. Palmer 20196* (UMO 71091). **Worcester Co.:** Old Turnpike, 4 Jun 1909, *G.E. Douglass s.n.* (NY 2543343). **MICHIGAN. Allegan Co.:** Allegan State Game Area, SW shore of Crooked Lake, ca. 100 m SE of terminus of dirt access road to Crooked Lake, ca. 0.4 km N of 113th Avenue, ca. 0.6 km W of 48th Street, 22 May 2023, *P.W. Fritsch 2513* (BRIT BRIT914428). **Michigan Barry Co.:** Otis Lake, 22 Aug 1981, *W.J. Byce s.n.* (BRIT BRIT446575). **Berrien Co.:** ca. 64 m SE of the S-most part of the parking area for the New Buffalo Eastbound Weigh Station on Interstate 94, 22 May 2023, *P.W. Fritsch 2509* (BRIT BRIT914471). **Calhoun Co.:** Ott Biological Preserve, ca. 0.3 km E of parking area for the preserve off Jameson Avenue, 23 May 2023, *P.W. Fritsch 2520* (BRIT BRIT914435). **Cass Co.:** Ca. 30 m N of NW shore of Pine Lake, ca. 56 m W of W-most house along North Court, 22 May 2023, *P.W. Fritsch 2506* (BRIT BRIT914473). **Gratiot Co.:** about Alma, 10 May 1896, *C.A. Davis s.n.* (MICH 1268871 [i]). **Hillsdale Co.:** E side of Bankers road, ca. 80 m from road, near a house, 10 May 1987, *P.W. Fritsch 341* (MICH 1268869). **Huron Co.:** the Wilderness Arboretum, ca. 14 miles NW of Bad Axe, 28 Jun 1952, *E.G. Voss 1215* (MICH 1268852 [i]). **Isabella Co.:** Mt. Pleasant, Union Township, 27 Oct 1978, *L. Ward s.n.* (CMC CMC00014743 [i]). **Jackson Co.:** Waterloo Recreation Area, 3.5 mi W of Waterloo, wood road E of Moeckel Road, just N of jct. with Hoffman Road, 21 Aug 1985, *L.J. Uttal 13989* (FLAS 160562 [i]). **Kalamazoo Co.:** West Lake Nature Preserve, along boardwalk E of the boardwalk circle, 21 May 2023, *P.W. Fritsch 2502* (BRIT BRIT914515). **Kent Co.:** Grattan Twp., ca. 3 mi E of Cannonsburg on 6 Mile Road and 0.5 mi N on gravel road/driveway, Saul Lake Bog Preserve, 28 Jul 2015, *D. Leisman et al. EC-15-893* (MICH 1552615 [i]). **Lapeer Co.:** Kresge Environmental Center, trail along ridge traversing NE from the dormitory building, ca. 0.4 km from dormitory, 19 May 2023, *P.W. Fritsch 2490* (BRIT BRIT914415). **Leelanau Co.:** 50 m from Johnson Road, 0.4 mi W of M-22 intersection, Soper Natural Area, 1 mi SW of Northport on Johnson Road, 14 Jul 2016, *L.N. May* 148 (MICH 1517212 [i]). **Lenawee Co.:** NW of Demings L., E of Benner Hwy., Dover Twp., 24 May 1997, *R.W. Smith 3096* (MICH 1268847 [i]). **Livingston Co.:** ca. 7 mi N of Hartland, 30 May 1978, *E.G. Voss* 14972 (MICH 1268838 [i]). **Macomb Co.:** Washington, 4 Aug 1927, *O.A. Farwell* 8050 (MICH 1268828 [i]). **Mason Co.:** SW end of Hopkins Lake, ca. 5 mi SE of Ludington, 5 Jul 1963, *E.G. Voss 11195* (MICH 1268839 [i]). **Midland Co.:** 3 mi SW of Midland, 24 Jul 1932, *R.R. Dreisbach 7765* (MICH 1268853 [i]). **Montcalm Co.:** Alma College Ecological Station at Davis Lake, Vestaburg Bog, 0.21 km S of Deaner Road, on trail heading S from the station building, 23 May 2023, *P.W. Fritsch 2517* (BRIT BRIT914432). **Oakland Co.:** Ca. 0.7 km E of Hwy. M-5, ca. 90 m S of the parking lot for shops and restaurants parallel and S of W Maple Road, ca. 20 m W of transmission lines, 20 May 2023, *P.W. Fritsch 2496* (BRIT BRIT914420). **Ottawa Co.:** Port Sheldon Natural Area, ca. 0.28 km S of Port Sheldon Street, ca. 0.4 km E of 16th Avenue, on trail that starts ca. 0.4 km E of 16th Avenue on S side of Port Sheldon Street, 23 May 2023, *P.W. Fritsch 2516* (BRIT BRIT914431). **Saginaw Co.:** S of Roetheke Park, Thomas Twp., 29 Jun 1986, *R.W. Smith 1686* (MICH 1268877 [i]). **Sanilac Co.:** Big swamp near Palms, 5 Sep 1917, *C.K. Dodge 517* (MICH 1268881 [i]). **Shiawassee Co.:** Bath, 27 Apr 2023, *J. Young 12* (OUHC OUHC000173 [i]). **St. Clair Co.:** near Port Huron, 10 Jun 1892, 30 Jun 1892, *C.K. Dodge s.n.* (MICH 1268845 [i]). **St. Joseph Co.:** Constantine Twp., ca. 4.5 mi NW of Constantine, 2 May 1964, *E.G. Voss 11403* (MICH 1268840 [i]). **Tuscola Co.:** Cat Lake Road, 4 May 1985, *J.V. Freudenstein 1515* (MICH 1268872 [i]). **Van Buren Co.:** 0.2 mi W of U.S. 31, 13 Jun 1985, *J.V. Freudenstein 1604* (MICH 1268875 [i]). **Washtenaw Co.:** Thomas Woods/Marsh, ca. 56 m N of E Textile Road between Platt Road and Thomas Road, across the road from the parking lot for Old Hickory Trail at Pittsfield Preserve, 18 May 2023 *P.W. Fritsch 2482* (BRIT BRIT914486). **Wayne Co.:** ca. 0.5 km S of Sibley Road and 0.5 km W of Telegraph Road, ca. 130 m W of transmission lines, NE end of a buttonbush pond, 18 May 2023, *P.W. Fritsch 2484* (BRIT BRIT914484). **NEW HAMPSHIRE. Belknap Co.:** Gilford, 21 May 1937, *A S. Pease 26550* (NEBC 00519308 [i]). **Carroll Co.:** town of Ossipee, Heath Pond Bog, ca. 3.2 km NE of the village of Center Ossipee, along NH-Rte. 25, Apr-Oct 1991, *L.L. Fahey HPB-196 GA* (GA201387). **Cheshire Co.:** Marlboro, 13 Jul 1919, *H.H. Rusby s.n.* (NY 2542606). **Coos Co.:** roadside, Whitefield, 7 Jul 1896, *W. Deane s.n.* (NEBC 00519260 [i]). **Grafton Co.:** Lebanon, 2 Jun 1888, *J.Y. Jewett s.n.* (RSA RSA0184901 [i]). **Hillsborough Co.:** New Ipswich, 5 Jul 1937, *H.W. Youngken s.n.* (BRIT BRIT528939). **Merrimack Co.:** Dunbarton, Twist Hill Road, ca. 0.7 mi N of Goffstown town line, 9 May 2001, *M. Nazaire 67* (RSA RSA0259390 [i]). **Rockingham Co.:** Great Bay National Wildlife Reserve, 7 Jul 2018, *P S. Manos CY-116* (BRIT BRIT698668). **Strafford Co.:** Farmington, above Place, 21 Jul 1947, *A.R. Hodgdon & G. Stuart 5409* (NEBC 00519283 [i]). **Sullivan Co.:** East Lempster, Lemster, 22 Aug 1963, *F.C. Seymour 20972* (SMU BRIT446354). **NEW JERSEY. Atlantic Co.:** Weymouth to DaCosta, 12 May 1924, *W. Pennel 12050* (NY 2545179). **Bergen Co.:** Carlstadt, 11 Jul 1870, *W.H. Leggett s.n.* (NY 2543350). **Burlington Co.:** Southampton Twp., Bear Swamp, ca. 3.5 mi SE of Medford, along Hawkins Road at power lines, 13 May 2003, *K. Barringer 9447* (VDB BRIT311238). **Camden Co.:** Pensauken, 2 May 1909, *W. Stone 11256* (PH PH00395504 [i]). **Cape May Co.:** W of Cape May Court House, 11 May 1924, *W. Pennel 12047* (NY 2545177). **Cumberland Co.:** Foster Run, ca. 2 mi SSE Deerfield, 25 Apr 1925, *B. Long 31949* (PH PH00395557 [i]). **Essex Co.:** Millburn, 26 Jul 1903, *K.K. MacKenzie 284* (NY 02545701 [i]). **Gloucester Co.:** along Four Mile Branch, NNE of Radix, 7 May 1939,

B. Long 53475 (PH PH00395454 [i]). **Hudson Co.:** New Durham, 24 Aug 1894, *T.H. Kearney, Jr. s.n.* (OS 175832 [i]). **Hunterdon Co.:** Kingwood, 1886, *Schuh s.n.* (PH PH00395319 [i]). **Mercer Co.:** 1.5 mi ESE of Robbinsville, 5 May 1935, *B. Long 45708* (PH PH00395323 [i]). **Middlesex Co.:** Cheesequake State Park, parking lot edge near New Landing, *s.d.*, *P.S. Manos CY-144* (BRIT BRIT698629). **Monmouth Co.:** Poplar Creek, NE of Poplar Road and Deal Road, 13 Jul 1994, *S. Clemants & S. Glenn 6090* (GA GA201384). **Morris Co.:** Great Swamp National Wildlife Refuge, along boardwalk from Observation Center, 23 Apr 2022, *P.S. Manos CY-491* (BRIT BRIT914505). **Ocean Co.:** at Burlington Co. line, 1.4 mi W of Rte. 539 on road to Naval Firing range, 5 mi N of exit 58 of Garden State Parkway, 16 May 1981, *S.R. Hill 10022* (NY 2545326). **Passaic Co.:** West Milford Twp., Green Turtle Pond WMA, 0.5 mi SE of Awoosting, along the N shore of the pond, 11 May 2004, *K. Barringer 11874* (PH PH00395313 [i]). **Salem Co.:** along Maurice Road, ca. 1 mi N of Brotmanville, 14 May 1939, *B. Long 53525* GA GA201359. **Sussex Co.:** Byram, Allamuchy State Park, along the Sussex Branch Trail, along Jefferson Lake shore, 25 Sep 2001, *K. Barringer 7401* (GA GA201347). **Union Co.:** Westfield, Brightwood Park, 17 Jul 2019, *P.S. Manos CY-269* (BRIT BRIT698813). **Warren Co.:** roadside below Milbrook, Jun 1916, *E.B. Bartram s.n.* (PH PH00395315 [i]). **NEW YORK. Albany Co.:** W side of rod, 1 mi SE of Meadowdale, 18 Jul 1908, *S.H. Burnham s.n.* (NY 4169383). **Bronx Co.:** Van Cortlandt Park, along John Muir Trail W of 242 St. entrance, 3 May 2003, *G. Moore 5721* (VDB BRIT311234). **Cattaraugus Co.:** Chamberlain's Bog, Steamburg, July 1932, *R.B. Gordon s.n.* (OS 175836 [i]). **Chautauqua Co.:** Mr. Francis farm, 8 Sep 1919, *H.W. Mossman s.n.* (CM 293771 [i]). **Chenango Co.:** near Meads Pond, 25 May 1887, *H.L. Stewart s.n.* (RSA RSA0185000 [i]). **Clinton Co.:** Flat Rock-Comp. 17, West Chazy, Chazy, 31 May 1988, *L.J. MacArthur s.n.* (PLAT PLAT0001104 [i]). **Columbia Co.:** 1 mi SW of Clermont, 15 Jul 1935, *R. McVaugh 3259* (GA GA201380). **Cortland Co.:** Lime Hollow Nature Center, SW of Munsons Corners, Phillips Memorial Trail, 15 Jul 2023, *R. Carmickle RC126* (BRIT BRIT927793). **Dutchess Co.:** Fahnestock State Park, AT&T Meadow, from jct. Dennytown Road and Indian Brook Road until metal gate and drystack stone wall past woods on right, 11 Jul 2023, *R. Carmickle RC105* (BRIT BRIT927464). **Erie Co.:** along N end of sewer treatment plant access road W of Meadow Dr. on Alden Village-Town line, 30 Jun 1983, *D.D. Taylor 4098* (NLU NLU0141037). **Franklin Co.:** Roakdale Bog, 21 Aug 1962, *R. Handle s.n.* (PLAT PLAT0001103 [i]). **Genesee Co.:** Bergen Swamp, 3 Jun 1935, *M.W. Allen s.n.* (NY 02545329 [i]). **Greene Co.:** near Cairo, 18 July 1893, *G.V. Nash s.n.* (NY 2545168). **Herkimer Co.:** Graefenberg Swamp, 28 May 1881, *J.V. Haberer s.n.* (OS 175826 [i]). **Jefferson Co.:** 0.5 mi W of Redwood on Hwy. 26, 21 Jul 1971, *S.P. Vander Kloet s.n.* (GA GA201406). **Monroe Co.:** Mendon Ponds Park, Devil's Bathtub Trail, 14 Jul 2023, *R. Carmickle RC118* BRIT (BRIT927451). **Nassau Co.:** Hempstead, Long Island, *W.C. Ferguson s.n.* (NY 2545175). **New York Co.:** Inwood near S. Creek, Manhattan Island, 31 May 1893, *E.P. Bicknell 6928* (NY 2545418). **Niagara Co.:** Grand Island, 11 May 1899, *M. Maxcey s.n.* (RSA RSA0185351 [i]). **Onondaga Co.:** upper end of Tully Lake, Tully, 4 Aug 1916, *G.T. Hastings s.n.* (NY 02545288 [i]). **Orange Co.:** along Old West Pt. Road, 17 May 1937, *H.M. Raup 8066* (NY 2545251). **Oswego Co.:** N of Oneida Lake, 3.6 km NE of Constantia (NE of Syracuse), E end of Kibbie Lake, 15 Jun 2020, *A.J. Shaw CY-334a* (BRIT BRIT698846). **Putnam Co.:** ca. 7 km (by air) W of New York/Connecticut state border and ca. 10 km (by air) N of Putnam/Westchester county border, Ice Pond Conservation Area, E of Ice Pond Road, N or Rte. 31, N of Rte. 312 and W of Ice Pond, 13 May 2008, *D. Atha & D. Adamsons 6175* (NY 1087526). **Queens Co.:** N of Jamaica, Long Island, 15 Jul 1905, *E.P. Bicknell 6864* (NY 2545419). **Rensselaer Co.:** Poestenkill Twp., Davitt Lake, Rotary Boy Scout Camp, 29 Jun 1985, *B. Gerbino s.n.* (CGCC 1044 [i]). **Richmond Co.:** Court House, 7 Jul 1889, *N.L. Britton s.n.* (NY 2543269). **Rockland Co.:** Sneeden Landing, 10 May 1909, *N. Taylor 112* (NY 25433820. **Schoharie Co.:** Gilboa Village, 22 Sep 1990, *A. Payson 34* (CGCC 1045 [i]). **Schuyler Co.:** Finger Lakes National Forest, 5.2 km N of NY-227 on Potomac Road, at the entrance to the Potomac Group Campground, 15 Jun 2020, *A.J. Shaw CY-333* (BRIT BRIT698845). **Seneca Co.:** Pout Pond, 3 Jun 1934, *M.W. Allen s.n.* (NY 02545080 [i]). **Suffolk Co.:** Quogue Wildlife Preserve, 16 Jul 2019, *P.S. Manos CY-263* (BRIT BRIT698807). **Sullivan Co.:** Wolf Lake Road, 6 mi SE of Rock Hill, below dam, 4 mi SW of Emerald Green, near South Shore Drive, 3 Jul 1999, *W. Hess et al. 8660* (NY 2545163). **Tioga Co.:** Oakley Corners Swamp, ca. 5 mi SE of Newark Valley, 3 Jul 1937, *S.J. Smith 707* (GA GA201362). **Tompkins Co.:** Sapsucker Woods Sanctuary, Cornell Lab of Ornithology Visitor Center, 15 Jul 2023, *R. Carmickle RC124* (BRIT BRIT927791). **Ulster Co.:** Hunter Pond, 1.5 mi S of Debruce, Rockland, 14 Jul 1940, *W.H. Camp 3043* (NY 2545016). **Warren Co.:** 2.5 mi N by W of Luzerne, 15 Aug 1958, *J.M. Fogg, Jr. 22020* (PH PH00395660 [i]). **Washington Co.:** W of Stone Schoolhouse, N of Tripoli, southern W. Fort Ann, 24 Jul 1918, *S.H. Burnham s.n.* (MO MO-3888345). **Wayne Co.:** Huckleberry Swamp Trail (Olga Fleischer Ornithological Foundation), Boardwalk /Loop Trail, 14 Jul 2023, *R. Carmickle RC115* (BRIT BRIT927454). **Westchester Co.:** Zofnass Family Preserve, Southern Loop, 31 Jul 2013, *J. Jiang & R.F.C. Naczi 40* (NY 1421041). **Wyoming Co.:** Letchworth State Park, Trout Pond Area, from Trout Pond Trail parking area, follow trail to boggy pond from N ed of parking area (E side of road), 15 Jul 2023, *R. Carmickle RC123* (BRIT BRIT927790). **Yates Co.:** Penn Yan, *H.P. Sartwell s.n.* (NY 025455287 [i]). **NORTH CAROLINA. Beaufort Co.:** 5 mi S of Washington, 5 Apr 1939, *R.K. Godfrey & R.N. White 7062* (DUKE DUKE10100398 [i]). **Bertie Co.:** 10.9 mi SE of Windsor on NC-308, S side of road, 17 Apr 2018, *B. Aguero CY-072* (BRIT BRIT698697). **Bladen Co.:** Lakes State Forest, 1 mi S of Jones Lake along dirt access road, 7 Sep 2019, *R. Carmickle CY-319* (BRIT BRIT698834). **Brunswick Co.:** Green Swamp Preserve, 22 Apr 2022, *A.A. Crowl CY-472* (BRIT BRIT914469). **Camden Co.:** along W side of Western Bay canal, ca. 0.5 mi S of Corapeake ditch, 24 Jul 1975, *D. Nickrent 662* (ODU ODU00021039 [i]). **Carteret Co.:** 5.8 air km ENE of Stella, near intersection of Carteret, Craven and Jones Counties, Croatan National Forest, 6 May 2011, *D. Atha 10106* (NY 01400406 [i]). **Chowan Co.:** 4 mi W of Small's Crossroads, 24 Jun 1958, *H.E. Ahles 44218* (NCU NCU00297552 [i]). **Columbus Co.:** 4 mi E of Lake Waccama, N side of Hwy. 214, 7 Sep 2019, *A.A. Crowl CY-316* (BRIT BRIT698831). **Cumberland Co.:** without specific locality, 25 Mar 1929, *W.W. Ashe E6745* (GA GA201298). **Currituck Co.:** 0.3 mi W of Aydlett, 8 May 1958, *H.E. Ahles 40133* (NCU NCU00315149 [i]). **Duplin Co.:** roadside 2.4 mi N of Warsaw on U.S. Hwy. 117, 4 Apr 1970, *J. Hackney 33* (FUGR FUGR0011427 [i]). **Edgecombe Co.:** 0.3 mi NE of Gethsemane, 23 Apr 1958, *A.E. Radford 32052* (NCU NCU00315152 [i]). **Gates Co.:** just S of Allison Road at jct. with Atlantic Road, Weyerhauser tract, 26 Mar 1975, *H.J. Ecklund 120* (NLU NLU0141030). **Greene Co.:** 2 mi S of Marlboro, 27 Apr 1958, *A.E. Radford 32636* (NCU NCU003303300 [i]). **Halifax Co.:** 2 mi SE of Halifax on N.C. Rte. 561, 19 Jun 1956, *H.E. Ahles 14873* (NCU NCU00315169 [i]). **Harnett Co.:** Spout Springs, 22 Apr 1970, *R. Wyatt 104* (GA GA201255). **Hertford Co.:** Chowan River, 25 Jun 1972, *A. Herford s.n.* (NCSC NCSC00085419

[i]). **Hoke Co.:** Carolina Horse Park.com, 26 May 2001, *J.T. Donaldson 4787* (ETSU ETSU031576 [i]). **Johnston Co.:** 5 mi E of Smithfield, 1 Apr 1949, *H.L. Blomquist* 14404 (DUKE DUKE10100406 [i]). **Lee Co.:** 0.9 mi S of jct. U.S. 1 and 15-501, on U.S. 1, 18 Jun 1968, *G.J. Galletta PI346548 (8-4-2)* (CLEMS CLEMS0045094 [i]). **Lenoir Co.:** private dirt roads of Hunting Club ca. 200 yds. N of the Jones Co. line on NC 258 ca. 2 mi S of Jonestown or 14 mi S of the 258 intersection from Kinston on Rte. 70, 14 May 1992, *R.L. Wilbur 60527* (DUKE DUKE10100319 [i]). **Martin Co.:** Williamston Dump along U.S. 64, just E of the U.S. 17 intersection, 24 Jun 1969, *S.W. Leonard et al. s.n.* (UNCC 9091 [i]). **Moore Co.:** Weymouth Woods-SNP, Southern Pines, 24 Mar 1973, *J.H. Carter III 408* (WEWO WEWO0001726 [i]). **Nash Co.:** W of Hwy. 301, Sharpsburg, 2 Apr 1956, *M.M. Eason 3* (NCU NCU00315202 [i]). **New Hanover Co.:** UNC-Wilmington campus, 3 Apr 1979, *D.J. Sieren 1805* (NLU NLU0141010). **Northampton Co.:** 2.8 mi NNW of Rich Square on NC 305, 7 Jul 1958, *H.E. Ahles 45744* (NCU NCU00315210 [i]). **Onslow Co.:** old railway right-of-way ca. 2 mi N of the intersection of U.S. 17 and State Road 1103 and just S of Verona, 16 May 1991, *R.L. Wilbur 58831* (DUKE DUKE10100331 [i]). **Orange Co.:** Blackwood Division, Duke Forest, Compartment 17, in plot 16, 11 May 1986, *M.W. Palmer 679* (DUKE DUKE10100332 [i]). **Pasquotank Co.:** 1.2 mi N of Nixonton, 10 May 1958, *H.E. Ahles 40070* (NCU NCU00315216 [i]). **Pender Co.:** just SW Holly Shelter Refuge, 11 May 1960, *R. Kral 10137* (VDB BRIT311452). **Person Co.:** 3.9 mi N of Mt. Tirzah, 22 Apr 1958, *C.R. Bell 11218* (NCU NCU0031527 [i]). **Pitt Co.:** off Hwy. 903, 1 mi N of Stokes, 23 Apr 1956, *F. Dawson 6* (NCU NCU00330345 [i]). **Richmond Co.:** County Road 1602 on the S edge of Hoffman, 19 May 1994, *R.L. Wilbur 62178* (DUKE DUKE10100335 [i]). **Robeson Co.:** Butler Road, Fairmont, 30 Mar 2019, *A.A. Crowl CY-193* (BRIT BRIT698746). **Sampson Co.:** Roseboro, 10 Apr 1938, *R.K. Godfrey 3379* (DUKE DUKE10100411 [i]). **Scotland Co.:** ca. 8.5 mi N of Laurinburg on U.S. 15-501, 18 Jun 1968, *G.J. Galletta PI346551* (8-5-2) (GA GA201296). **Wake Co.:** Umstead State Park at the Ebenezer Church Road entrance to the Crabtree Creek Stone Bridge, northern outskirts of Greater Raleigh just W of Rte. 70, 8 Jul 1988, *R.L. Wilbur 48828* (DUKE DUKE10100417 [i]). **Washington Co.:** bay ca. 150–200 yds. W of Lake Phelps, 27 Jul 1967, *G.J. Galletta PI346590 (7-42-2)* (NCU NCU00297555 [i]). **Wayne Co.:** pocosin (without specific locality), 31 Mar 1935, *J.F. Reed & M.S. Reed s.n.* (DUKE DUKE10100419 [i]). **OHIO. Ashland Co.:** Lake Twp., 17 Jun 1933, *F. Bartley & L.L. Pontius s.n.* (OS 28896 [i]). **Ashtabula Co.:** Wiswell Road, 0.5 mi S U.S. Rte. 322, Windsor Twp., 21 Jul 1973, *L.W. Tandy 1629* (VDB BRIT311251). **Columbiana Co.:** Butler Twp., Watercress Marsh, W of road, 22 May 1960, *F. Buchanan 437* (OS 117159 [i]). **Cuyahoga Co.:** near Bradley Road, Olmstead Twp., 22 Apr 1973, *G.T. Jones 73_4_22_221* (OS 370351 [i]). **Geauga Co.:** roadside, Rte. 306, 0.5 mi S of Bainbridge, 20 May 1958, *E.M. Herrick s.n.* (OS 60719 [i]). **Holmes Co.:** N side of Rte. 179 at Rte. 3, near Ashland county line, 23 Sep 1959, *E.M. Herrick s.n.* (OS 62952 [i]). **Huron Co.:** Richmond Twp., Centerton Quad., 1.40 mi N of Crawford-Huron County Road and 1.63 mi W of State Hwy. 103, Sec. 1, 13 Jul 2008, *T.L. Walters 12029* (OS 429926 [i]). **Knox Co.:** back of Baptist Church, Tenants Harbor, 22 Aug 1938, *R.C. Friesner 12800* (WVA 117749). **Lorain Co.:** Camden Lake, Camden, 2 Aug 1887, *F.E. Leonard 87-129* (CHRB CHRB0010844 [i]). **Medina Co.:** Hinckley Twp., County Road 44, at east branch of Rocky River, 24 Jul 1959, *E.M. Herrick s.n.* (OS 62958 [i]). **Portage Co.:** Triangle Lake Bog State Nature Preserve, 5 Jun 2019, *A.A. Crowl CY-232* (BRIT BRIT698782). **Richland Co.:** near Ganges, 7 Aug 1940, *J.C. Myers s.n.* (WVA 117732). **Stark Co.:** Fry Family Park, edge of pond, 3 Jun 2019, *A.A. Crowl CY-229* (BRIT BRIT698779). **Summit Co.:** Copley, 29 Mar 1897, *A.D. Selby s.n.* (OS 94867 [i]). **Trumbull Co.:** Braceville Twp., N side Rte. 5, 0.2 mi E of Portage County line, 28 Aug 1959, *E.M. Herrick s.n.* (OS 63996 [i]). **Wayne Co.:** Fox Lake, 27 Jul 1899, *A.D. Selby & J.W.T. Duvel 897* (OS 94869 [i]). **Williams Co.:** S side of Mud Lake Bog, ca. 1.25 mi SW of Cooney, 18 Sep 1967, *R.L. Stuckey 6073* (OS 87250 [i]). **PENNSYLVANIA. Berks Co.:** 2.5 mi NW of Bethel, 18 Jul 1948, *D. Berkheimer 9953* (PH PH00392296 [i]). **Blair Co.:** Canoe Creek, State Game Lands #166, from Duncansville follow U.S. 22 E then slight left onto Huntingdon Pike, then another slight left onto Beaver Dam Road, follow to SGL 166 entrance, 11 Jun 2013, *S. Schuette 1277* (CM 531184 [i]). **Bradford Co.:** 1.75 mi E of Ulster, 23 Jun 1955, *E.T. Wherry s.n.* (PH PH00392088 [i]). **Bucks Co.:** Silver Lake Nature Center, Delhaas Woods, 20 Jul 2023, *R. Carmickle RC152* (BRIT BRIT927786). **Butler Co.:** 1.5 mi W of West Liberty, 28 Jun 1941, *O.E. Jennings s.n.* (CM 076708 [i]). **Carbon Co.:** 1 mi NW of East Mauch Chunk, 31 May 1914, *H.W. Pretz 6540* (PH PH00392062 [i]). **Centre Co.:** Bear Meadows, from Bear Meadows Trailhead parking area follow trail SW along bog/stream margins for 50 m, 16 Jul 2023, *R. Carmickle RC129* (BRIT BRIT927796). **Chester Co.:** Valley Forge, 11 May 1902, *W. Stone 2727* (PH PH00395226 [i]). **Clinton Co.:** Bushkill Road, from parking area just SE of jct. SR402 and Old Bushkill Road/2003, follow ATV trail SSE, 18 Jul 2023, *R. Carmickle RC144* (BRIT BRIT927779). **Columbia Co.:** 2 mi NNW of Bendertown, 8 Aug 1958, *E.T. Wherry s.n.* (PH PH00395254 [i]). **Crawford Co.:** Mud Lake, W of Hartstown, 18 May 1932, *E.H. Graham 437* (GA GA201363). **Dauphin Co.:** 4.25 mi SSW of Lykens, 10 Jul 1952, *D. Berkheimer 14049* (PH PH00395256 [i]). **Delaware Co.:** Buckingham Mountain, Jul 1896, *N. Williams s.n.* (PH PH00395736 [i]). **Elk Co.:** Jones Township, Rasselas, near church, 26 May 2003, *J.A. Isaac 16055* (CM 503559 [i]). **Erie Co.:** Presque Isle, 29 Jul 1940, *N. Ammons et al. s.n.* (WVA 117736). **Fayette Co.:** Ohiopyle, 1932, *W.R. Van Dersal s.n.* (CM 076736 [i]). **Franklin Co.:** 0.5 mi E of Chambersburg, 9 May 1886, *T. Seal s.n.* (PH PH00395220 [i]). **Huntingdon Co.:** Stone Valley, 4 May 1919, *L.O. Overholts & M.F. Overholts s.n.* (PAC PAC0057122 [i]). **Juniata Co.:** along Juniata River just SE of Mexico, 14 Jun 1940, *P.R. Wagner 8653* (PH PH00395197 [i]). **Lackawanna Co.:** along Rte. 11, 0.5 mi NW of Dalton, 15 Jun 1946, *S.L. Glowenke 6151* (PH PH00392020 [i]). **Lawrence Co.:** 2 mi SE of Leesburg, 22 Sep 1954, *L.K. Henry s.n.* (CM 076706 [i]). **Lebanon Co.:** 2 mi NE of Mount Gretna, 12 May 1937, *F.S. Fender 3116* (MOAR MOAR0004577 [i]). **Lehigh Co.:** ca. 1-1/8 mi W by SW of Wescoesville crossroads, 8 May 1921, *H.W. Pretz 10695* (VDB BRIT311255). **Luzerne Co.:** Memorial Shrine Cemetery, 18 Jul 2023, *R. Carmickle RC139* (BRIT BRIT899943). **Lycoming Co.:** a few mi SE of Williamsport, 16 Jul 1908, *O.E. Jennings s.n.* (CM 076721 [i]). **Mercer Co.:** 0.5 mi E of jct. U.S. 19 and PA 208 (Leesburg) on PA 208, State Game Lands 284, 23 May 1985, *S. Thompson 2364* (NLU NLU0141150). **Monroe Co.:** The Nature Conservancy Long Pond Barrens, along two track road SW of easement, 19 Jul 2023, *R. Carmickle RC148* (BRIT BRIT927783). **Montgomery Co.:** Willow Grove, 25 May 1899, *A. MacElwee 323* (PH PH00395744 [i]). **Northampton Co.:** Minsi Lake Corridor Greenway, from NW corner of parking area follow Minsi Lake Nature Trail NNW for ca. 30 m, 19 Jul 2023, *R. Carmickle RC151* (BRIT BRIT927785). **Northumberland Co.:** Montandon-Milton backroad, 22 May 1946, *W.E. Manning s.n.* (PH PH00395255 [i]). **Perry Co.:** near New Bloomfield, 16 Jul 1920, *E.M. Gress s.n.* (CM 076833 [i]). **Philadelphia Co.:** along Knights Road, ca. 1.5 mi S of Byberry, 15 Aug 1951, *B. Long 73013* (PH PH00395200 [i]). **Pike Co.:** Rte. 42, by Peck's Pond, 9 Jun 1975, *G.B. Rossbach 9218* (WVA 117698). **Sullivan Co.:**

Lopez to Bella Sylva, Crane Swamp, 19 Jun 1909, *W. Stone 11493* (PH PH00395190 [i]). **Susquehanna Co.:** Ararat Church, 1 Aug 1957, *W.L. Dix 1893* (PH PH00392017 [i]). **Tioga Co.:** Reynolds Spring Natural Area, ca. 3 mi (6.2 km) S of Leetonia, 3 Aug 1994, *C.S. Keener 94048* (PAC PAC0057153 [i]). **Venango Co.:** along State Game Lands Rte. 428, 2–3 mi S of Diamond, 14 May 1959, *L.K. Henry s.n.* (CM 076688 [i]). **Warren Co.:** Sulphur Springs bog, 3 mi NE of Columbus, 14 May 1949, *L.K. Henry s.n.* (CM 076775 [i]). **Washington Co.:** along northern floodplain of Monongahela River, 2000 ft. SW of Vesta No. 6 village, Centerville Borough, 9 May 2005, *L. Speedy LSB299* (CM 512291 [i]). **Wayne Co.:** Newfoundland, 5 Aug 1954, *R. Robacker FS 854-3* (NY 2543365). **York Co.:** Highmount, 14 Jul 1919, *E.M. Gress s.n.* (CM 076795 [i]). **RHODE ISLAND. Bristol Co.:** vicinity of Nayatt, Barrington, 30 May 1911, *E.J. Winslow s.n.* (NEBC 00519859 [i]). **Kent Co.:** Warwick, 13 Apr 1834, *J.W. Congdon s.n.* (CHAS 4662 [i]). **Newport Co.:** Little Compton, Simmons Mill Pond Wildlife Management Area, 50 m SW of John Dyer Road trailhead, 26 May 2017, *T.J S. Whitfield 1498* (NEBC 01582508 [i]). **Providence Co.:** around lake near Slaterville, 17 Jul 1937, *E.J. Palmer 43353* (UMO 71099). **Washington Co.:** town of Westerly, Woody Hill Management Area, S of Bradford and N of Haversham along dirt extension of Fern Dr. W of Woody Hill Extension (dirt road), S of Woody Hill Road, between Hwys. 91 and 216, NE of Nunns Corners, 24 Jun 2009, *A.C. Sanders 37094* (MO MO-3888350). **SOUTH CAROLINA. Aiken Co.:** Aiken State Park, 20 Apr 2022, *A.A. Crowl CY-463* (BRIT BRIT914411). **Barnwell Co.:** Audubon's Silver Bluff Sanctuary, 20 Apr 2022, *A.A. Crowl CY-459* (BRIT BRIT914406). **Berkeley Co.:** Francis Marion National Forest, along firebreak road, 22 Apr 2022, *A.A. Crowl CY-470* (BRIT BRIT914468). **Calhoun Co.:** W of creek where Hwy. 176 crosses, Sandy Run Creek, 6 Jun 1993, *G. Newberry 11807* (USCS USCS0009127 [i]). **Charleston Co.:** ACE Basin Wildlife Refuge, E of State Road S-10-346, firebreak (Oak Ridge Road), 25 Mar 2021, *A.A. Crowl CY-355* (BRIT BRIT792834). **Chesterfield Co.:** 1.5 mi S of jct. of U.S. 52 on U.S. 1, 5 Apr 1968, *S.W. Leonard 1223* (GA GA201310). **Clarendon Co.:** 10 mi E of Manning, 2 Apr 1930, *G.A. Schulze 584* (GA GA201299). **Colleton Co.:** Walterboro Wildlife Sanctuary, 25 Mar 2021, *A.A. Crowl CY-360* (BRIT BRIT792839). **Darlington Co.:** along Kilgore's Branch back of Hartsville Print and Dye Works, 15 Apr 1940, *B.E. Smith 1044* (NCU NCU00331628 [i]). **Dillon Co.:** 3.9 mi NE of Bingham on County Rte. 28, 18 Apr 1957, *H.E. Ahles 23247* (NCU NCU00331635 [i]). **Dorchester Co.:** Summerville, 30 Mar 1924, *H.J. Davis & A.M. Ottley 1722* (NY 2543341). **Florence Co.:** 1 mi S of Lake City, 2 Apr 1930, *G.A. Schulze 571* (GA GA201301). **Georgetown Co.:** 20 mi SE of Andrews, 2 Apr 1930, *G.A. Schulze 581* (GA GA201341). **Hampton Co.:** along Co. Rte. 39, 3.5 mi W of jct. with U.S. 321 in the town of Estill, 2 Mar 2017, *C.N. Horn* 22405 (CLEMS CLEMS0070032 [i]). **Horry Co.:** 8 mi N of Myrtle Beach, 20 Apr 1951, *M.G. Henry 6208* (PH PH00397022 [i]). **Jasper Co.:** 3 mi E of Tillman, 2 Apr 1930, *G.A. Schulze 611* (GA GA201549). **Kershaw Co.:** McRay Road (SR-28-131), 0.5 mi S of Goodale State Park, 30 Mar 2019, *A.A. Crowl CY-196* (BRIT BRIT698749). **Lee Co.:** Swimming-Pen Swamp, Rte. 401, SW of Rte. 154 & 12 mi NE of Sumter, 6 Apr 1961, *G.B. Rossbach & C.E. Murphy 2492* (WVW WVW019123 [i]). **Lexington Co.:** Peachtree Rock Preserve, along trail to the rock, 30 Mar 2019, *A.A. Crowl CY-199* (BRIT BRIT698752). **Marion Co.:** 3 mi N of Mullins, 1 Apr 1930, *G.A. Schulze 564* (GA GA201302). **Marlboro Co.:** S.C. 381, ca. 5 mi S of McColl, 18 Jun 1968, *G.J. Galletta PI346557 (8-6-6)* (VDB BRIT311727). **Orangeburg Co.:** 1 mi N of Bowman, Hwy. 178, 20 May 1972, *C.L. Rodgers 0460* (FUGR FUGR0011420 [i]). **Richland Co.:** along the southern border of Goodwill Plantation, adjacent to U.S. 378, 1.7 mi W of Wateree River, 12 Jun 2003, *Y.A. McLeod III 240* (USCH USCH0027360 [i]). **Sumter Co.:** Poinsett Air Force Weapons Range, a. 0.7 mi E of SC 261, this area a portion of Manchester State Forest, 21 May 1993, *J.B. Nelson 14113* (USCH USCH0027218 [i]). **Williamsburg Co.:** 5 mi E of Kingstree, 2 Apr 1930, *G.A. Schulze 573* (GA GA201311). **VERMONT. Addison Co.:** Region Scanlon Swamp, Leicester and Brandon, 5 Jun 1926, 27 Aug 1926, *D.L. Dutton s.n.* (VDB BRIT311714). **Bennington Co.:** Pownal, June, *W.A. Nason s.n.* (ILL ILL00174920 [i]). **Chittenden Co.:** Colchester, 17 May 1903, *C.G. Pringle s.n.* (NLU NLU0141266). **Essex Co.:** E of Concord, 6 Jun 1964, *A.E. Roland & E.C. Smith s.n.* (ACAD 59973 [i]). **Franklin Co.:** Swanton, 18 May 1943, *R.H. MacCauley s.n.* (VT UVMVT088656 [i]). **Lamoille Co.:** Morrisville, Molly bog, 14 Jun 1976, *P. Chairavalle 76-152* (NLU NLU0141265). **Rutland Co.:** Middletown Springs, *D.S. Carpenter s.n.* (ILL ILL00174921 [i]). **Windham Co.:** Townshend, 4 Jul 1912, *L.A. Wheeler 108301* (VDB BRIT311262). **Windsor Co.:** Windsor, 1876, *G.H. Leland s.n.* (NEBC 00519390 [i]). **VIRGINIA. Accomack Co.:** 0.2 mi N of Painter and W of US Hwy. 13, 5 May 1975, *T.F. Wieboldt 201*0 (WILLI 32112). **Alexandria City:** City of Alexandria, Winkler Botanical Preserve, ca. 0.35 km ENE of the NE terminus of Roanoke Avenue, 12 Aug 2017, *R.H. Simmons 4299* (AVCH AVCH-0001847 [i]). **Amelia Co.:** 0.25 mi NW of St. Rte. 612, 4 km N of Mannboro, 9 Jun 1993, *T.F. Wieboldt 8595* (VSC VSC0060489 [i]). **Amherst Co.:** Arlington Run, ca. 0.15 km NW of the intersection of S. Abingdon Street and S 5th Street, 20 May 2017, *R.H. Simmons 4259* (GMUF GMUF-0042741 [i]). **Brunswick Co.:** 0.3 mi N of jct. Co. 630 and US 1 on Co. 630, 21 Apr 1968, *F.C. James 13203* (WILLI 34321). **Buckingham Co.:** Fort A.P. Hill Military Reservation, headwaters of Cattlet Creek, 0.5 mi NE of Lonesome Gulch Pond, 3.2 mi N of Bowling Green, 28 Apr 1992, *G.P. Fleming 6342* (WILLI 58242). **Caroline Co.:** 12 mi S of Fredericksburg on US Hwy. 2, 9 Jun 1948, *H.H. Iltis 3905* (WILLI 83114). **Charles City Co.:** Tomahund Plantation (Hofmeyer Estate) ca. 0.5 mi W of Chickahominy, 23 May 1971, *D.M. Eggers Ware 3585* (WILLI 9443 [i]). **Chesapeake City:** intersection of Hwy. 168 and 624, 28 Jul 1965, *F.C. James 778* (WILLI 34337). **Chesterfield Co.:** 0.25 mi NE of Bevils Bridge on the Appomattox River floodplain, 11 Oct 2005, *D.A. DeBerry 790* (WILLI 78497). **Dinwiddie Co.:** 1 mi E of Burgess, 3 May 1966, *A.M. Harvill 13756* (NCU NCU00044281 [i]). **Essex Co.:** along the Occupacia River, off of Rte. 661 E of jct. with Rt 637, 22 Sep 1974, *T. Bradley 7189* (WILLI 28407). **Fluvanna Co.:** powerline/gas line ROW just W of Rte. 605, 0.5 mi N of Stage Junction, 12 Jul 2021, *G.P. Fleming 18605* (GMUF GMUF-0047737). **Gloucester Co.:** 0.7 mi NW of jct. Co. 614 and U.S. 17 on Co. 614, 5 Jul 1966, *F.C. James 4881* (WILLI 34361). **Goochland Co.:** powerline clearing along S side of US 250, 0.2 mi SE of jct. with Rte. 629, 1.1 mi NE of Hadensville, 22 May 1993, *G.P. Fleming 7980* (WILLI 61967). **Greensville Co.:** 0.8 mi SW of jct. of Co. 616 and U.S. 301 on U.S. 301, 23 Jun 1966, *F.C. James 4310* (WILLI 34305). **Hampton City:** Sandy Bottom Lake within Sandy Bottom Nature Park off of Big Bethel Road, 24 Apr 2014, *P.B. Baldwin 8302* (WILLI 80176). **Hanover Co.:** 1.4 mi N of jct. Co. 623 and U.S. 1 on Co. 623, 26 Apr 1968, *F.C. James 13533* (WILLI 34308). **Henrico Co.:** Twin Hickory Recreation Area, 30 Mar 2023, *P.W. Fritsch 2247* (BRIT BRIT914494). **Isle of Wight Co.:** along the Blackwater River at Joyners Bridge Landing (S side of VA-601), 22 Apr 2022, *B. Aguero CY-495* (BRIT BRIT914498). **James City Co.:** N of Rte. 5 entrance, S of Walnut Hills Church, The College Woods, the College of William and Mary, 18 Apr 1968, *A.C. Barans 60* (WILLI 1769). **King and Queen Co.:** near road, E on 609, 0.3 mi from Clancie, 30 Jun 1982, *A. Vascott 354* (WILLI

45787). **King George Co.:** Caledon marsh, Caledon State Park, 12 Apr 1983, *D.M. Eggers Ware 8005* (VDB BRIT311447). **King William Co.:** roadside, 1 mi W of Rte. 604 n. on Va. 30. W of Mongohick, 11 Apr 1981, *T. Bradley 16804* (NLU NLU0141260). **Lancaster Co.:** ca. 1 km NNW from trail head and parking lot on W side of Regina Road (State Route 604), Cabin Swamp Trail, Hickory Hollow Natural Area Preserve, 5 Apr 2023, *P.W. Fritsch 2478* (BRIT BRIT914478). **Louisa Co.:** property of Will and Margaret Shaw, 3.3 mi NNW of Zion Crossroads, tributary of Wheeler Creek, 0.8 mi N of jct. Rtes. 615 and 617, 19 May 2021, *G.P. Fleming 18397* (GMUF GMUF-0047867). **Lunenburg Co.:** 1.1 mi S of jct. Co. 646 and 637 on 637 (S of Kenbridge), 19 Sep 1965, *F.C. James 3059* (WILLI 34331). **Mathews Co.:** roadside, 0.2 mi E of Grimstead and Rte. 634 on Rte. 633, 15 Apr 1989, *T. Bradley 22549* (GA GA201361). **Middlesex Co.:** 1.0 mi W of Rte. 17 from Dragon Run bridge along jeep road, 23 Apr 1977, *E.L. Train 42* (NLU NLU0140706). **New Kent Co.:** 5 mi NE of Barhamsville, 5 Aug 1949, *B. Mikula 3301* (BRIT BRIT446370). **Newport News City:** ca. 6 mi NE of Newport News, Rte. 17, Warwick County, 2 Apr 1939, *J.T. Baldwin, Jr. 98* (WILLI 49792). **Norfolk City:** by Dismal Swamp Canal, 9 Apr 1939, *J.T. Baldwin, Jr. L30* (WILLI 49790). **Northampton Co.:** roadside, off Rte. 618 just S of jct. of jct. with Rte. 625, S of Johnsontown, 20 May 1986, *T. Bradley 21450* (GMUF GMUF-0030486). **Northumberland Co.:** at jct. Co. 605 and Co. 606 on Co. 605, 19 Jul 1966, *F.C. James 5838* (WILLI 34323). **Nottoway Co.:** jct. State 49 and US 460 on 460 at Crewe, Va., 11 Jun 1967, *F.C. James 6719* (WILLI 34341). **Petersburg City:** W arm of loop of Loop Road, near S end of meadow S of Cooper Field, Lee Park, 2 May 2000, *D.M. Eggers Ware 11798* (WILLI 80878). **Pittsylvania Co.:** roadside on Co. Road 916, 0.7 mi from intersection with Co. Road 604, 22 Jun 1968, *W.F. Ruska s.n.* (NCU NCU00044276 [i]). **Portsmouth City:** Frederick College, 2 mi off of Rte. 17, 17 Apr 1971, *J.H. Person 35* (ODU ODU00021043 [i]). **Powhatan Co.:** Powhatan State Park, just SW of the Big Woods Trail and 1.0 mi N of park entrance, 2.2 mi WNW of Maidens, 29 Jun 2020, *G.P. Fleming 17872* (GMUF GMUF0048017). **Prince George Co.:** ca. 1 mi S of Petersburg, 7 Jul 1961, *R. Kral 13223* (VDB BRIT311728). **Prince William Co.:** Occoquan Bay National Wildlife Refuge (old Harry Diamond Laboratories - U.S. Military Reservation), just E of Woodbridge, 30 May 1998, *M.T. Strong 1611* (GMUF GMUF-0030475). **Richmond City:** Libbie Road, 21 Apr 1941, *A. Frank s.n.* (URV URV008378 [i]). **Richmond Co.:** Farnham Creek and Rte. 608, SE of Ivandale, *T. Bradley 22387* (GMUF GMUF-0030487). **Rockingham Co.:** large sink-hole pond at W foot of the Blue Ridge, 1.0 mi N of jct. of Rtes. 663 and 708, 2.2 mi ENE of Grottoes, 3 Jun 1991, *G.P. Fleming 5558* (WILLI 57314). **Southampton Co.:** 0.3 mi NE of Ivor city limits on US 460, 13 Aug 1965, *F.C. James 2300* (WILLI 34333). **Spotsylvania Co.:** Alexander Berger Memorial Sanctuary, Rappahannock River 5 mi below Fredericksburg, 16 May 1965, *F.R. Fosberg 46127* (RSA RSA0184926 [i]). **Stafford Co.:** roadside, ca. 0.3 mi E of Rte. 603 on Rte. 601, E of Wildcat Corner, 30 Apr 1995, *T. Bradley 26551* (GMUF GMUF-0030473). **Suffolk City:** ca. 8 km S of Suffolk along Hosier Road, 23 Apr 2022, *A.A. Crowl CY-478* (BRIT BRIT914453). **Surry Co.:** head of E arm of second ravine W of canal intake, Surry Vepco Nuclear Power Station, 6 Jun 1973, *D.M. Eggers Ware 4864* (NLU NLU0141263). **Sussex Co.:** city limits Walsefield, 2 mi NW of Sussex and Southampton Co. line on US 460, 22 Jun 1966, *F.C. James 4160* (WILLI 34329). **Virginia Beach City:** First Landing State Park, 24 Apr 2022, *A.A. Crowl CY-480* (BRIT BRIT914455). **Westmoreland Co.:** ca. 2 mi N of Erica, 27 Jun 1950, *B. Mikula 5913* (BRIT BRIT792166). **Williamsburg City:** N of Rte. 5 entrance, S of Walnut Hills Church, The College Woods, The College of William and Mary, 18 Apr 1968, *A.C. Barnes 60* (WILLI 1769 [i]). **York Co.:** Grafton Ponds Natural Area Preserve, 1 Apr 2023, *P.W. Fritsch 2461* (BRIT BRIT914437). **WEST VIRGINIA. Barbour Co.:** County Rte. 56, E of Junior, 6 Aug 2000, *W.N. Grafton s.n.* (WVA 099452). **Preston Co.:** near Cranesville, 19 Jul 1940, *A.J. Sharp s.n.* (TENN TENN-V-0170187 [i]). **Randolph Co.:** Proudfoot Road 250/9, 6 Aug 2000, *W.N. Grafton s.n.* (WVA 099453). **Webster Co.:** along Jerry's Run 3 mi S of Cleveland, 9 Jun 1942, *R. Anderson s.n.* (NCU NCU00352915 [i]). **WISCONSIN. Adams Co.:** T17N, R5E, approx. sec. 28, 31 May 1974, *M. Bigger s.n.* (WIS v0137241WIS [i]). **Walworth Co.:** Whitewater, 7 Jun 1892, *A.E. Fuller 63* (WIS v0135578WIS [i]).

APPENDIX 3

Representative specimens of *Vaccinium fuscatum* examined for this study, one specimen per county (parishes in Louisiana; some independent cities in Virginia).

U.S.A. ALABAMA. Baldwin Co.: ca. 4 m S of boardwalk, ca. 35 m W of Rosemary Dunes Trail, ca. 0.20 mi NNE of parking area, ca. 0.25 mi S of AL-182, Gulf State Park, 5 May 2022, *P.W. Fritsch 2443* (BRIT BRIT698895). **Barbour Co.:** public access area to W.F. George Reservoir ca. 7 mi S Eufaula, 20 May 1968, *R. Kral 30923* (SMU BRIT446346). **Bibb Co.:** Oakmulgee District of the Talladega National Forest, Forest Service Road 718 just E of FS Road 418-C, 28 May 2003, *A.R. Diamond 13957* (VDB BRIT110773). **Blount Co.:** without specific locality, 22 Apr 1962, *Avery s.n.* (VDB BRIT109943). **Bullock Co.:** Wehle Land Conservation Center, 4.30 mi SE of Midway, 19 Apr 2012, *B. Dykes 538* (VDB BRIT521737). **Calhoun Co.:** E side of road to Moorman Lookout at Fort McClellan, ca. 16 m from Bains Gap Road at Bain Gap, Mountain Longleaf National Wildlife Refuge, 30 Apr 2022, *P.W. Fritsch 2423* (BRIT BRIT698874). **Cherokee Co.:** Little River ca. 1.6 mi above canyon, 20 Jun 1984, *S. McDaniel 27747* (VDB BRIT109775). **Chilton Co.:** 28.8 mi NW Prattville, 30 May 1970, *R. Kral 39387* (VDB BRIT109752). **Cleburne Co.:** Ivory Mountain off FSR-512 in the Shoal Creek Ranger District in the Talladega National Forest, 29 May 2005, *D.D. Spaulding 12272* (VDB BRIT532841). **Coffee Co.:** above Buck Mill Creek 3.2 mi S jct. U.S. 84 and Ala 87, 11 Jun 1971, *R. Kral 43245* (VDB BRIT118521). **Conecuh Co.:** Brownville-Flat Rock road (dirt)., 10 Jun 2006, *A.R. Diamond 16508* (VDB BRIT110772). **Covington Co.:** near Possum Pocket, 18 mi SSW of Andalusia, 31 Mar 1953, *J.W. Hardin 15021* (GA GA201557). **Crenshaw Co.:** Hwy. 106 just W of Alken Road (dirt), 31 May 2008, *A.R. Diamond 19360* (VDB BRIT532512). **DeKalb Co.:** DeSoto State Park & Little River Canyon atop Lookout Mountain above Fort Payne, roadside at the jct. of Ala. Rte. 35 with the Scenic Drive (County Road 81) around Little River Canyon, 20 Apr 1958, *H.L. Sherman 068* (SMU BRIT446421). **Escambia Co.:** by U.S. 31, just N of Pollard, 9 May 1984, *R. Kral 71387B* (VDB BRIT446606). **Franklin Co.:** 1.2 mi N Hackleburg above Bear Creek, 7 May 1966, *R. Kral 26458* (VDB BRIT111009). **Geneva Co.:** 6.5 mi S of Samson, 26 Apr 1967, *S. McDaniel 8788* (GA GA201547). **Hale Co.:** edge of Payne Lake at campground, Talladega National Forest, 1653, *M. Nee & R. Peet 1653* (WIS v0385937WIS [i]). **Houston Co.:** S side Dothan on Ala 52, 24 Mar 1969, *R. Kral 33957* (SMU BRIT419146). **Jackson Co.:** without specific locality, 16 Jul

1940, *H.W. Youngken s.n.* (BRIT BRIT528950). **Lauderdale Co.:** by U.S. 43 ca. 0.5 mi W Green Hill, 4 Jun 1968, *R. Kral 31045* (SMU BRIT446357). **Limestone Co.:** by US 31 turnoff to Athens and I-65, 25 Mar 2000, *R. Kral 89204* (VDB BRIT110812). **Lowndes Co.:** Manack, 25 Jul 1967, *R.C. Clark 16648* (NCU NCU00344621 [i]). **Macon Co.:** by U.S. 80, 7 mi W Marvyn, 1 May 1972, *R. Kral 46103* (VDB BRIT109757). **Marion Co.:** 9 mi E of Hamilton along North Fork Creek, 14 Apr 1988, *S. McDaniel 29740* (VDB BRIT110758). **Mobile Co.:** Mobile, 18 Apr 1839, *Gates et al. s.n.* (MICH 1509374 [i]). **Monroe Co.:** 2.5 mi W Repton along Escambia Creek, 9 Jun 1965, *R. Kral 24450* (VDB BRIT109758). **Pickens Co.:** 4.2 mi E of Gordo, 5 Apr 1968, *S. McDaniel 10435* (VDB BRIT109759). **Pike Co.:** ca. 110 m S of Pell Avenue at Troy University Arboretum, ca. 390 m E of entrance road to the arboretum, Troy, 2 May 2022, *P.W. Fritsch 2435* (BRIT BRIT698886). **Randolph Co.:** ca. 0.6 mi S of the Cleburne-Randolph Co. line on U.S. Hwy. 431, 2 Apr 1986, *C.F. Nixon 2101* (VDB BRIT109761). **Washington Co.:** ca. 1 mi N Tibbie, 8 Jun 1973, *R. Kral 50432* (GA GA201265). **Winston Co.:** beside Ala 74, 1 mi E of Ala 5, E of Natural Bridge, 16 Apr 1968, *R.D. Thomas 7100* (NLU NLU0456467). **ARKANSAS. Ashley Co.:** P.O. Fountain Hill, 11 May 1941, *D. Demaree 22086A* (SMU BRIT446411). **Bradley Co.:** P.O. Banks, 5 May 1940, *D. Demaree 20998* (SMU BRIT446410). **Calhoun Co.:** P.O. Hampton, 3 May 1941, *D. Demaree 22051* (SMU BRIT446409). **Clark Co.:** P.O. Arkadelphia, 4 May 1941, *D. Demaree 22080* (SMU BRIT446408). **Cleburne Co.:** Big Creek Natural Area, Main tract, Multi-Agency Wetlands Planning Team plot, 29 Apr 2004, *T. Witsell 04-0182* (LSU LSU00213833 [i]). **Cleveland Co.:** ca. 50 m SE of US 79, ca. 80 m E of Bell Road, ca. 2.7 mi W of Kingsland, 19 May 2021, *P.W. Fritsch 2345* (BRIT BRIT698949). **Columbia Co.:** ca. 13 m SW of County Road 8, ca. 50 m NW of intersection of County Road 8 and AR-98, ca. 0.2 mi NW of intersection of AR-98 and County Road 85, ca. 64 m SE of Scott Branch (creek), 18 May 2021, *P.W. Fritsch 2341* (BRIT BRIT698945). **Cross Co.:** Mississippi Valley Loess Plains, Bluff Hills Ecoregion, Wittsburg Natural Area, SW portion of natural area, along N fork of Rice Branch, ca. 0.5 air mi WNW of Cross Co. Road 739 crossing of Rice Branch, just S of Wittsburg, 3 May 2012, *B. Baker 12-0074* (APSC APSC0052442 [i]). **Drew Co.:** P.O. Monticello, 22 Apr 1938, *D. Demaree 17162* (SMU BRIT446407). **Garland Co.:** P.O. Hot Springs National park, 27 Mar 1942, *D. Demaree 22728* (SMU BRIT446424). **Grant Co.:** roadbank of Ark. 35, 4 mi NW of Sheridan, 19 May 1994, *R.D. Thomas 135445* (NLU NLU0140402). **Hempstead Co.:** Tokio, 22 Oct 1932, *D. Demaree 9940* (SMU BRIT446394). **Hot Spring Co.:** Malvern, 6 Sep 1934, *D. Demaree 11042* (SMU BRIT446395). **Jefferson Co.:** between two branches of Eastwood Bayou on Pine Bluff Arsenal, 24 May 1975, *R.D. Thomas 44078* (NLU NLU0141834). **Lincoln Co.:** Cane Creek State Park, 5.3 mi E of U.S. 425 via Ark. 293 at Star City, 13 Apr 1992, *R.D. Thomas 127827* (NLU NLU0140399). **Logan Co.:** Ozark National Forest, W end of Magazine Mt., 4 mi of St. Hwy. 309 & 16 mi SE of Paris, 14 Apr 1987, *W. Hess 6299* (NLU NLU0140733). **Miller Co.:** ca. 150 m W of County Road 237 (Blackman Ferry Road), ca. 0.2 mi N of County Road 72, Miller County Sandhills Natural Area, 18 May 2021, *P.W. Fritsch 2335* (BRIT BRIT698939). **Montgomery Co.:** Ouachita National Forest, P.O. Slatington, 17 Oct 1932, *D. Demaree 9788* (SMU BRIT446597). **Nevada Co.:** ca. 47 m NW of AR-355 just W of Clear Creek, ca. 0.2 mi W of intersection of 355 and County Road 104, 18 May 2021, *P.W. Fritsch 2338* (BRIT BRIT698942). **Ouachita Co.:** P.O. Stephens, 2 Apr 1938, *D. Demaree 16852* (SMU BRIT446403). **Perry Co.:** Ouachita Mountain Seep, ca. 18 m SE of US Forest Service Road 210 (County Road 362), ca. 0.45 mi SW of intersection of USFS Road 210 and US Forest Service Road 249 (County Road 325), ca. 0.3 mi (direct) W of South Fourche LaFave River, South Fourche Botanical Area of Ouachita National Forest, 20 May 2021, *P.W. Fritsch 2351* (BRIT BRIT698956). **Poinsett Co.:** ca. 90 m N of Mink Road along S bank of creek, ca. 0.5 mi W of AR-163, Crowley's Ridge, 22 May 2021, *P.W. Fritsch 2358* (BRIT BRIT698963). **Pulaski Co.:** Pinnacle, 1 Jun 1923, *E.J. Palmer 22297* (UMO 71093). **Saline Co.:** N of East End, just W of Chicot Road, 16 Jun 1973, *G.E. Tucker 11230* (SMU BRIT446413). **Union Co.:** Pugh's Dry Creek property off an oilfield road E of Telephone Road and S of Philadelphia Road SW of New London, 19 Jun 1999, *R.D. Thomas 161271* (NLU NLU0140393). **CONNECTICUT. Fairfield Co.:** Fairfield, 17 May 1896, *E.H. Eames s.n.* (VT UVMVT126634 [i]). **Hartford Co.:** N. Granby, along East St. across from Heminway Pond, 8 May 1989, *W. Fertig 865* (WS WS026607 [i]). **Litchfield Co.:** Barkhamsted, 15 Jul 1912, *A.E. Blewitt 1576* (NEBC 00519954 [i]). **Middlesex Co.:** East Hampton, 5 Jul 1942, *B.T. Chamberlain s.n.* (NY 02545149 [i]). **New Haven Co.:** Wallingford Road, Rte. 68, Reeds Gap, town of Wallingford, 2 May 1981, *P.F. Zika 2897* (VT UVMVT088908 [i]). **New London Co.:** Latimer Point, Latimer Point Road, Stonington, S of Rte. 1, 13 May 1992, *S.R. Hill 23097* (BRIT BRIT446363). **Tolland Co.:** Andover, 22 Jul 1907, *C.A. Weatherby 2241* (NEBC 00519909 [i]). **Windham Co.:** roadside of Rte. 101 ca. 0.1 mi E of Rte. 52, 6 May 1924, *A. Dolgos 453* (BRIT BRIT446375). **DELAWARE. Kent Co.:** just outside W edge of Bombay Hook National Wildlife Refuge along Hay Point Landing Road (Hwy. 9), 25 Apr 2022, *A.A. Crowl CY-488* (BRIT BRIT914523). **New Castle Co.:** Ogletown Swamp along Red Mill Road at end of Paradise Road, 0.25 mi W of Rte. 273 at Rte. 4, 14 Apr 1990, *C.F. Reed 135077* (MO MO-3586185). **Sussex Co.:** 2.2 mi ENE of Lewes, Cape Henlopen State Park, Pineland Nature Trail, 25 Apr 2011, *R.F.C. Naczi 13485* (NY 02545138). **DISTRICT OF COLUMBIA.** Woodridge, 10 May 1904, *A. Chase 2149* (ILL ILL00174885 [i]). **FLORIDA. Alachua Co.:** along Gainesville-Hawthorn trail, 7 Oct 2018, *A.A. Crowl CY-190* (BRIT BRIT698743). **Baker Co.:** S of Taylor, 17 Feb 1929, 31 May 1929, *W.W. Ashe s.n.* (GA GA201544). **Bay Co.:** roadside ca. 5 mi NE of Youngstown, 3 Apr 1969, *John Taylor & Connie Taylor 5241* (BRIT BRIT446385). **Bradford Co.:** N side of Fla. 100, 3 mi E of intersection with Fla. 235, 5 Jul 1977, *L. Conde s.n.* (FLAS FLAS129761 [i]). **Brevard Co.:** Mims, E of the NE corner of the retention pond located between Dairy Road and the South Lake Conservation Area, 24 Feb 2007, *D S. des Hons et al. 2/2* (USF 260928 [i]). **Calhoun Co.:** 8 mi NW of Clarkesville, 20 Aug 1957, *E.S. Ford 5320* (FLAS FLAS81735 [i]). **Citrus Co.:** Hollins zone 72 NE, 21 Feb 2001, *J. Scanlon 170* (FLAS FLAS205201 [i]). **Clay Co.:** along Rte. 16 ca. 0.6 mi E of jct. with Rte. 21, ca. 4 mi W of Penney Farms, 11 Mar 1980, *W.S. Judd 2575* (VDB BRIT311470). **Columbia Co.:** near fire tower, 18 Feb 1929, 31 May 1929, *W.W. Ashe s.n.* (GA GA201541). **DeSoto Co.:** N of Wood's Road off U.S. 17, SW of Nocatee, *J.A. Reynolds 1969* (NLU NLU0141804). **Duval Co.:** Racetrack Road near intersection with FL-9B, 4 Apr 2019, *A.A. Crowl CY-211* (BRIT BRIT698761). **Escambia Co.:** Bayou San Marcus Creek, ca. 1 mi W of limits Pensacola along U.S. 90, 3 Apr 1966, *R. Kral 26178* (BRIT BRIT446379). **Flagler Co.:** Pellicer Creek Conservation Area, white blaze trail, 27 Feb 2025, *P.W. Fritsch 2588* (BRIT). **Franklin Co.:** Tate's Hell Swamp, plot 36, 2) plot 83, 27 Jul 1995, *D. Lindholm s.n.* (GA GA201244). **Gadsden Co.:** W side S/R 65, 4.1 mi S from jct. with S/R 65B, N side Ocklawaha Creek, 20 Jun 1982, *A. Gholson Jr. 9856* (FLAS FLAS168305 [i]). **Gilchrist Co.:** 9 mi W of Newberry and 5.8 mi W of Gilchrist line, 9 Mar 1965, *I.L. Wiggins 19383* (USF 76441 [i]). **Glades Co.:** Fisheating Creek Campground, near Palmdale, 3 Mar 1979, *J. Popenoe 1604* (NCU NCU00352901 [i]).

Gulf Co.: 3 mi NE of Wetapo Ranger Station, 1 Aug 1957, *E S. Ford 5055* (FLAS FLAS81472 [i]). **Hamilton Co.:** 1 mi S Jennings, 17 Mar 1958, *R. Kral 6298* (VDB BRIT312752). **Hardee Co.:** Tributary of Charley Bowlegs Creek, ca. 2 mi NW of NW corner of Highlands Hammock State Park, 12 mi E of Zolfo Springs, 5 Nov 1966, *D.B. Ward 6121* (FLAS FLAS114031 [i]). **Hernando Co.:** Weeki Wachee, Jungle Trail, 22 Feb 1971, *P. Genelle & G. Fleming 466* (GA GA201534). **Highlands Co.:** Archbold Biological Station, ca. 0.2 mi N of the main parking area, ca. 7 m W of railroad tracks, 27 Mar 2024, *P.W. Fritsch 2522* (BRIT BRIT1058574). **Hillsborough Co.:** Plant City, Walden Lake Park, 0.4 km S of parking lot, at fork of trail, 5 Mar 2016, *R.E. O'Donnan s.n.* (GA GA263588). **Jackson Co.:** Alliance, 1 Apr 1973, *A.L. Moldenke & H.N. Moldenke 26715* (LL 00507434 [i]). **Jefferson Co.:** roadside along Rte. 59, ca. 2.0 mi S of Wacissa, 24 Mar 1995, *V.E. McNeilus 95-25* (NLU NLU0141390). **Lafayette Co.:** Cypress swamp, Road 69, 15 mi S of Mayo, 20 May 1941, *West & Arnold s.n.* (FLAS FLAS42629 [i]). **Lake Co.:** Mount Dora, 28 Feb 1944, *F.W. Hunnewell 17965* (NY 02545634). **Leon Co.:** Bloxham, ca. 1 mi E of Talquin Dam, 24 Mar 1967, *S. McDaniel 8605* (VDB BRIT312751). **Levy Co.:** near Dunnellon, Goethe State Forest, along Big Cypress Boardwalk, off Cow Creek Road, 28 Apr 2010, *R.E. Weaver Jr. 5278* (PIHG PIHG011220 [i]). **Liberty Co.:** 2.5 mi N Hosford Fire Tower, 13 May 1977, *R. Kral 60030* (VDB BRIT312750). **Madison Co.:** 6 mi W of Greenville on Hwy. 90, 14 Jun 1961, *G.W. Ramsey & R S. Mitchell 24* (SMU BRIT446425). **Manatee Co.:** in bayhead, Bradentown, 19 Apr 1917, *A. Cuthbert s.n.* (FLAS FLAS19022 [i]). **Marion Co.:** along road to Sparr, ca. 3 mi S of Citra, 3 Mar 1968, *W.G. D'Arcy 2360* (VDB BRIT310895). **Nassau Co.:** Yulee, Mentorial Road near jct. with Rte. 20, 4 Apr 2019, *A.A. Crowl CY-214* (BRIT BRIT698765). **Okaloosa Co.:** 3 mi. E of Munson, 23 Feb 1967, *S. McDaniel 8488* (VDB BRIT311692). **Osceola Co.:** Disney Wilderness Preserve, western stretch of the yellow trail, ca. 0.5 mi due S of the junction with the red trail and ca. 1 mi SSE of the main buildings, 29 Mar 2024, *P.W. Fritsch 2528* (BRIT BRIT1058580). **Pasco Co.:** along Hwy. 41, 24 Mar 1958, *G.R. Cooley 5694* (USF 80821 [i]). **Pinellas Co.:** Brooker Creek Swamp, 18 Mar 1976, *J.E. Poppleton 2162* (USF 140444 [i]). **Polk Co.:** 4.5 mi E of Haines City, via Fla 580, sec. 19, 22 May 1964, *H.S. Conard s.n.* (NY 02545502). **Putnam Co.:** Paul Lyrene's property near Star Lake, around edge of sinkhole pond, 29 Mar 2021, *A.A. Crowl CY-392* (BRIT BRIT792866). **Santa Rosa Co.:** S of Bear Creek and W of Range B-75, ca. 1.8 mi E of intersection of RR 700 and RR 211 and ca. 0.10 mi N of RR 700, 8 Apr 1998, *B. Herring 1368* (NLU NLU0141218). **Sarasota Co.:** ca. 5 mi E of Sarasota along S side of Fla 78, at Fordville, 8 Feb 1980, *B. Hansen & R. Sauleda 6864* (UMO 159415). **Seminole Co.:** Little Big Econ State Forest, NE edge, S side of short trail bordering wetland, ca. 0.5 mi W of Snow Hill Road, 31 Mar 2024, *P.W. Fritsch 2537* (BRIT BRIT1058589). **St. Johns Co.:** St. Augustine, Moses Creek Conservation Area, N of Hwy. 302, West Trail, 7 Apr 2019, *A.A. Crowl CY-219* (BRIT BRIT698770). **Sumter Co.:** Lake Okahumpka Park, ca. 46 m S of track that encircles the wetland area, ca. 212 m WSW of main entrance at E County Road 44, 30 Mar 2024, *P.W. Fritsch 2533* (BRIT BRIT1058585). **Suwannee Co.:** ca. 5 map km NE of Live Oak, Suwannee River Water Management District property (access off County Road 136A on Dusty Road), Woods Ferry Conservation Area, Woods Ferry Tract, ca. 0.8 km S of Suwannee River, 20 Apr 1997, *J.R. Abbott 10123* (FLAS FLAS207770 [i]). **Taylor Co.:** ca. 1 mi N Shady Grove, 9 Apr 1977, *R. Kral 59588* (VDB BRIT312748). **Volusia Co.:** along NE edge of the DeLand Airport, 27 Mar 1953, *E.C. Prichard 562* (GA GA201551). **Wakulla Co.:** St. Mark's National Wildlife Refuge, Rte. 372 (Surf Road), 5 mi SE of Hwy. 319, 2 Apr 2019, *A.A. Crowl CY-209* (BRIT BRIT698760). **Walton Co.:** along Road 218, 3 mi E of jct. with Road 212, 2.5 mi W of Portland, 6 Mar 1967, *C. Chapman 0305* (FLAS FLAS106599 [i]). **Washington Co.:** 7.8 mi E jct. Fla 20 and 77, 24 Mar 1975, *S. McDaniel 19753* (FLAS FLAS192345 [i]). **GEORGIA. Appling Co.:** Big Pond, near Baxley, 3 Jun 1929, *G.A. Schulze 383* (GA GA058558). **Atkinson Co.:** near Pearson, 15 Feb 1964, *D. Norris 32528* (TENN TENN-V-0170202 [i]). **Bacon Co.:** bayhead, E side of Hurricane Creek, off Ga. 32, 20 Mar 1966, *J.R. Bozeman 3393* (GAS GAS018443 [i]). **Baker Co.:** Collin's Pond, Pond-4, ca. 0.75 mi NW of Ichauway Church (USGS Bethany Quad.), 7 May 1992, *L.K. Kirkman 2118* (ICHAUWAY 0001247 [i]). **Bartow Co.:** ca. 4.5 mi SE of Adairsville on Cassville Mountain, 20 Jun 1964, *P. F-C. Greear 64256* (GA GA058508). **Ben Hill Co.:** top of Red Bluff, Okmulgee River, County Road 41 near Coffee Co. line, 23 Apr 1988, *H. Rasell 229* (GA GA058478). **Brantley Co.:** Waycross State Forest, North Shore of "Big Creek," 0.5 mi below Laura S Walker State Park dam, 10 mi ESE of Waycross, Station 12–A, 29 Jul 1961, *M.L. Kuns 335* (WIS v0385922WIS [i]). **Brooks Co.:** 1 mi N of Quitman, 5 May 1940, *R. Renfroe 11* (GA GA058563). **Bryan Co.:** Fort Stewart Military Reservation, Training Area F18, off road T43, "Stella Pond", 10 Mar 1992, *M.O. Moore 1364* (VDB BRIT311472). **Bulloch Co.:** ca. 2 mi S of Ga. Southern College on Ga. Hwy. 67, 11 Apr 1966, *R.L. Park s.n.* (NCU NCU00351011 [i]). **Camden Co.:** Crooked River State Park, along Bay Boardwalk Trail, 4 Apr 2019, *A.A. Crowl CY-216* (BRIT BRIT698767). **Candler Co.:** 0.25 mi W of Upper Lotts Creek, 26 Apr 1973, *Robison 6-7* (GAS GAS018409 [i]). **Carroll Co.:** along stream 6 mi S of Carrolton, 23 Apr 1950, *W.H. Duncan 10798* (VDB BRIT311477). **Charlton Co.:** Okefenokee Swamp, boardwalk at Suwanee Canal area, 10 Jul 1979, *S.B. Jones 23306* (SMU BRIT446402). **Chatham Co.:** 14.2 mi W 4.5°N of Savannah City Hall and 3.1 mi SW of Bloomingdale, 9 Jun 1958, *W.H. Duncan 20855* (SMU BRIT446400). **Chattahoochee Co.:** Lakeland Sandhills UEA, Fort Benning Military Installation, central portion of installation in training compartment D-14 and J-7, 19 May 2005, *T.E. Govus 1350* (GA GA059103). **Chattooga Co.:** Gorge of East Fork Little River, Camp Juliette Low, 22 Aug 1984, *S.B. Jones 24452* (NY 02545069). **Clarke Co.:** near head of lake, Hulm Farm, Winterville, 2 Apr 1931, *J.M. Reade 4653* (GA GA058507). **Clinch Co.:** 3 mi N of Ga. 94 on Ga. 177, 24 May 1967, *G.J. Galletta PI346519 (7-18-1)* (NCU NCU00351020 [i]). **Cobb Co.:** along banks of Soap Creek W of Marietta, 18 Jun 1953, *W.H. Duncan 16527* (GA GA058529). **Coffee Co.:** Broxton Rocks Nature Preserve, ca. 400 m W of Rocky Creek Road, burn unit 8, vicinity of "Falling Down Rock", 18 Mar 2014, *R. Carter 21560* (VSC VSC0067194 [i]). **Colquitt Co.:** 2.5 mi E Hartsfield, 20 May 1965, *R. Kral 24229* (VDB BRIT311711). **Crisp Co.:** N side of Cork Ferry Road, ca. 0.6 mi W of jct. Coney Road, ca. 8 (air) mi SW of Cordele, 7 Aug 1989, *R.A. Norris 5810* (GSW 00005182 [i]). **Dawson Co.:** Dawson Forest Wildlife Management Area, Amicalola Tract, W side of Amicalola River, 1.1 mi S of State Hwy. 53 Amicalola bridge, 5 Apr 2003, *L. Kruse 03-04* (GA GA058376). **Decatur Co.:** Willacooche Creek drainage, 3.6 mi drive E of Faceville along road to Attapulgus, 9 Jun 1982, *L.C. Anderson 5962* (GA GA058526). **DeKalb Co.:** Stone Mountain Park, NW side of Stonewall Jackson Drive, between Missouri Picnic Area and Old Catfish Hole fishing pond, 9 May 1995, *M.O. Moore 2099* (GA GA058335). **Dodge Co.:** 6.6 mi W of Milan, alongside Hwy. U.S. 280, 1 May 1981, *W.R. Faircloth 8607* (GA GA058505). **Echols Co.:** roadside along Rte. 94, ca. 1.0 mi W of Statenville, 9 Apr 1997, *V.E. McNeilus 97-76* (VDB BRIT311480). **Effingham Co.:** S of Ricon, 20 Apr 1958, *F.R. Dulany s.n.* (GA GA058545). **Emanuel Co.:** Ga. 46, 0.6 mi W of Emanuel-Candler

Co. line, 15 Jun 1966, *J.R. Bozeman 4274* (NCU NCU00334525 [i]). **Evans Co.:** Fort Stewart Military Reservation, Training Area F12, along Fort Stewart Road T15, W of Fort Stewart Road 15, 11 Mar 1992, *M.O. Moore 1385* (GAS GAS022454 [i]). **Fannin Co.:** Blue Ridge, Jul 1900, *A. Ruth s.n.* (NCU NCU00051924 [i]). **Forsyth Co.:** Suwanee Mountain, 25 Jun 1941, *W.H. Duncan 3610* (SMU BRIT446412). **Gilmer Co.:** Coosawattee River, below Dell Mt. Public Access area in place to be flooded by Carters Reservoir, 21 Jul 1973, *R. Kral 50876* (VDB BRIT311698). **Glynn Co.:** roadside, St. Simon's Island, near Brunswick, 11 Apr 1947, *A. Cronquist 4261* (SMU BRIT446420). **Grady Co.:** by Pine Park Road, ca. 4 mi E of GA 93, SE of Cairo, 17 Mar 2001, *R. Kral 90637* (VDB BRIT311519). **Greene Co.:** Oconee National Forest, at jct. of Rte. 15 and Oconee River, 26 Mar 1980, *W S. Judd 2582* (WILLI 38984). **Habersham Co.:** Rabun-Habersham Counties, Tallulah River Gorge, base of gorge, E of U.S. Rtes. 23-441, S of Clayton, 3 Jul 1975, *D.E. Boufford & E.W. Wood 1843* (GA GA058518). **Hancock Co.:** 2 mi SE of Sparta, 25 Mar 1954, *W.H. Duncan 17498* (GA GA058504). **Haralson Co.:** E of Bremen, off U.S. Hwy. 78, on county road 70, 26 Apr 1986, *N. Craft Coile 4610* (GA GA058668). **Harris Co.:** Pine Mtn. just E of Charlie 1, 16 Mar 2000, *Sweeney 778* (GA GA058329). **Johnson Co.:** Harrison property, 22 Mar 1994, *J.O. Harrison 41* (GA GA058487). **Lanier Co.:** 0.2 mi S of Stockton on U.S. 129, roadside, 23 May 1967, *G.J. Galletta PI346487 (7-15-3)* (NCU NCU00344629 [i]). **Liberty Co.:** Fort Stewart Military Reservation, Training Area B3, red-cockaded woodpecker colony 106, S of hand grenade range, S of Small Arms Hotel firing range, 8 May 1992, *T.M. Zebryk 0229* (GA GA059061). **Long Co.:** Wildcat Spring in Altamaha swamp, 11 Apr 1930, *G.A. Schulze 634* (GA GA058472). **Lowndes Co.:** 8 mi E of Valdosta courthouse on U.S. 84, 0.7 mi S on CCC Road, 10 Mar 1985, *R. Carter 3913* (VDB BRIT312743). **McIntosh Co.:** 1 mi N of Plantation Buildings, 3 Apr 1954, *W.H. Duncan 17667* (GA GA058547). **Meriwether Co.:** Pine Mt. along Cooler Branch, 2.5 mi SSE of Warm Springs and 3.3 mi WNW of Manchester, 8 Jun 1972, *S.B. Jones 21995* (VDB BRIT312742). **Morgan Co.:** edge of dirt road near Walton County line, 18 May 1980, *J.W. Hill 1356* (GA GA058757). **Pike Co.:** 4 mi S of Zebulon, 12 May 1946, *W.H. Duncan 6218* (GA GA058765). **Quitman Co.:** Cool Branch State Park, riverside boat dock and natural park S of Georgetown, 8 Apr 1978, *J.P. Folsom 7289* (VDB BRIT312854). **Rabun Co.:** across Ga. Hwy. 441 from Rabun Gap post office, 16 Apr 1991, *A. Deal s.n.* (GA GA058319). **Randolph Co.:** Cuthbert, 9 May 1918, *T.G. Harbison 4225?* (NCU NCU00334537 [i]). **Richmond Co.:** Augusta, Mar 1881, *A. Cuthbert s.n.* (CHRB CHRB0010825 [i]). **Spalding Co.:** Experiment, 17 Apr 1926, *J.G. Woodroof s.n.* (GA GA058713). **Tattnall Co.:** by roadside, 2.7 mi 45° NE of Glennville, 19 Mar 1966, *M. Padgett 176* (GA GA058537). **Telfair Co.:** ca. 3 mi NW of Lumber City on Rte. 23, 9 May 1953, *R.L. Wilbur 3150* (GA GA058536). **Thomas Co.:** ca. 2 mi N of bypass U.S. 319/84, E side of U.S. 319, 26 Apr 2002, *R. Kral 932462* (VDB BRIT311488). **Tift Co.:** ca. 6 mi N of Tifton at Gum Lake, 3 Jun 1931, *H.M. McKay s.n.* (GA GA058532). **Toombs Co.:** 3 mi E of RR depot in Lyons, 21 Apr 1962, *G.L. Plummer & T.M. Pullen Jr. s.n.* (GA GA058530). **Turner Co.:** power line r-o-w on the NW side of GA 112, 2.3 mi E of crossing of Deep Creek and 2.8 mi E of jct. with GA 107, 18 Mar 2001, *J.W. Horn 3927* (DUKE DUKE10100881 [i]). **Union Co.:** N of Neal's Gap ca. 2 mi, 1 Jul 1931, *H.M. McKay s.n.* (GA GA058352). **Walker Co.:** Brushy Pond, 4.2 mi S 59°E of Lafayette, 20 May 1951, *W.H. Duncan 12496* (VDB BRIT311699). **Walton Co.:** along stream ca. 5 mi SW of Dry Shoals, 25 Mar 1953, *R.L. Wilbur 2933* (GA GA058758). **Ware Co.:** N of Laura S Walker Lake, W of Hwy. 117 on Sam's Road (dirt road), 26 Mar 2021, *A.A. Crowl CY-372* (BRIT BRIT792849). **Washington Co.:** without specific locality, 12 Apr 1942, *W.H. Duncan 4745* (VDB BRIT311490). **Wayne Co.:** SW of Jesup, 10 Apr 1942, *W.H. Duncan 4671* (GA GA058755). **Wheeler Co.:** 2 mi W Alamo, 21 Apr 1962, *G.L. Plummer & T.M. Pullen Jr. s.n.* (GA GA058761). **Wilcox Co.:** Ga. Hwy. 112, 1.1 mi N of Alapaha River, SW of Rochelle, 7 Jul 1966, *J.R. Bozeman 5592* (NCU NCU00351041 [i]). **KENTUCKY. Caldwell Co.:** Dawson Springs, 29 May 1920, *E.J. Palmer 17675* (UMO 71095). **Calloway Co.:** Hwy. 641 S from Murray to Laycock Road, then E to Williams Road, 18 Apr 1990, *L.E. McKinney 4075* (BRIT BRIT446382). **Carlisle Co.:** Sandy Branch, 7.0 km SW Bardwell, 3.7 km SE Laketon, 24 Apr 1975, *L.M. Wilson 164* (GA GA201366). **Hopkins Co.:** above Tradewater River floodplain, Hwy. 109 at S boundary of county, 5 Jun 1995, *T.J. Weckman 1591* (EKY 31234100408531 [i]). **Marshall Co.:** Mathia Road off Ky. 94E, 0.6 mi from Calloway Co. line, 10 Apr 1973, *R. Athey 2209* (BRIT BRIT446377). **LOUISIANA. Beauregard Par.:** beside La. 27 S of Oretta, 27 Jun 1971, *R.D. Thomas 42047* (NLU NLU0140016 [i]). **Bienville Par.:** 0.1 mi from Saline on Mill Creek Reservoir Road, ca. 60 m off road, 8 May 1980, *W.C. Holmes 3851* (NLU NLU0414703). **Bossier Par.:** roadbank beside La. 3, 4.5 mi S of Plain Dealing at a branch of Collinsburg Creek, 14 Oct 1975, *R.D. Thomas 47720* (BRIT BRIT446389). **Caddo Par.:** 2 mi S of La. 168 and W of Rodessa and Black Bayou, 7 May 1982, *R.D. Thomas 80937* (BRIT BRIT446393). **Claiborne Par.:** ca. 36 m E of LA-520, ca. 0.35 mi N of Colquitt (intersection of LA-520 and LA-2), 16 May 2021, *P.W. Fritsch 2331* (BRIT BRIT698935). **De Soto Par.:** E of La. 174, 1.4 mi S of La. 539, S of Hunter, 8 Oct 1980, *R.D. Thomas 73639* (NLU NLU0139993 [i]). **Grant Par.:** beside North Tower Road, Kisatchie National Forest, SW of Georgetown, 22 Jun 1970, *R.D. Thomas 19558* (VDB BRIT234046). **Jackson Par.:** along W side of Walker Road (LA-147), ca. 1.3 mi NE of intersection of LA-147 and LA-34, 15 May 2021, *P.W. Fritsch 2321* (BRIT BRIT792786). **Natchitoches Par.:** Natchitoches, 8 May 1915, *E.J. Palmer 7568* (MO MO-3586176). **Orleans Par.:** New Orleans, 27 May 1976, *G.D. Wallace 1532* (NLU NLU0332993). **Ouachita Par.:** beside paved road at Mills Pond and La. 144 SW of Calhoun, 21 Sep 1994, *R.D. Thomas 142337* (NLU NLU0139647). **Rapides Par.:** just W of Evangeline primitive camp site W of USFS Road 273, N of La. 488 and S of La. 28, 29 Sep 1974, *R.D. Thomas 41629* (NLU NLU0140062). **Red River Par.:** ca. 1 mi W of Martin on LA Hwy. 155, 1 Apr 1981, *W.C. Holmes 4025* (TEX 00507694 [i]). **Sabine Par.:** 1 mi S of Many, E of La. 171, 31 Aug 1980, *N. Carroll 1979* (NLU NLU0140060). **St. Tammany Par.:** from La. 434 turn E onto Horse Shoe Island Road and travel 2.1 mi to a gate, 9 Apr 1989, *L.E. Urbatsch 5389* (BRIT BRIT446388). **Tangipahoa Par.:** across from Hammond Airport, S of Hwy. 190, ca. 3 mi E of Hammond, 18 Dec 1986, *N.M. Gilmore & L.M. Smith 2733* (NLU NLU0140050 [i]). **Union Par.:** beside Union Parish Road 3325 N of La. 15 and Spearsville near Little Hope Cemetery, 5 May 1993, *R.D. Thomas 133588* (NLU NLU0140496). **Vernon Par.:** ca. 15 m S of US Forest Service road 421 along a tributary of Drakes Creek, ca. 1.6 mi (direct) from LA-10 (Pitkin Highway), Kisatchie National Forest, 10 May 2021, *P.W. Fritsch 2296* (BRIT BRIT698977). **Washington Par.:** ca. 2 mi E of Franklinton by roadside park, 13 May 1972, *K. Rogers 8075* (VDB BRIT234048). **Webster Par.:** Kisatchie National Forest, Caney District, Compt. 24, NE corner of Stand 13, NW of CN24L , N of Caney Lake, 8 Jun 1998, *R.D. Thomas 156894* (NLU NLU0140027). **Winn Par.:** Kisatchie National Forest, Winn District, Compt. 4, Stand 4, along creek N of W004E, W of USFS 554, N of La. 126, W of Mill, 5 Aug 1997, *R.D. Thomas 154880* (NLU NLU0139652). **MAINE. York Co.:** York Harbor, roadside, 1 Jun 1902, *F.T. Hubbard s.n.* (SMU BRIT446350). **MARYLAND. Anne Arundel**

Co.: Pasadena, Jacobsville Park, along Magothy Beach Road between Woods Road and MD Rte. 100, 22 Apr 2008, *W.D. Longbottom 10975* (NY 02545639). **Baltimore Co.:** Gunpowder Falls State Park, Hereford Area, Gunpowder Falls Trail, along river, 25 Apr 2022, *A.A. Crowl CY-490* (BRIT BRIT914525). **Calvert Co.:** woods along Duvall Road at Creek Road N of Solomons, 11 Sep 1980, *C.F. Reed 148183* (MO MO-3586228). **Caroline Co.:** N of Federalburgon Faulkner Creek, 18 Jun 1941, *J.B S. Norton & R.G. Brown s.n.* (MARY MARY1039891 [i]). **Carroll Co.:** Liberty Reservoir, 3 mi W on Rte. 91 from Finksburg, S on Rte. 32 1 mi, W on Bollinger Hill Road 1 mi to fire road, 22 Apr 1986, *M.M. Yaffe 010* (MARY MARY1010457 [i]). **Cecil Co.:** E slope of Grays Hill, 2 mi E of Elkton, 15 May 1940, *R.R. Tatnall 4487* (PH PH00392112 [i]). **Charles Co.:** ca. in Block 8N7E, 12 Apr 1974, *L. Morrow & K. Miles 45* (MARY MARY1036502 [i]). **Dorchester Co.:** Vienna Hebron, 16 Jun 1908, *P.M. Novik 8176* (MARY MARY1039977 [i]). **Frederick Co.:** Catoctin Mountain Park, 14 Jul 1973, *C.J. Hickey II 442* (BALT BALT0003824 [i]). **Howard Co.:** Old Court and Old Frederic roads, Woodstock, 15 Apr 1956, *F.J. Forgione s.n.* (MARY MARY1039931 [i]). **Kent Co.:** 1.9 mi E of Hartly, along E side of Judith Road (Road 17), 0.3 mi N of its jct. with Rte. 44, 23 Apr 2011, *R.F.C. Naczi 13470* (NY 02545135). **Montgomery Co.:** near Rockville, 7 Apr 1929, *E.H. Walker 188* (MARY MARY1039906 [i]). **Prince George's Co.:** along Soil Conservation Road at Beltsville Agricultural Farm, 13 Apr 1977, *K.E. Peterson 13* (BRIT BRIT446356). **Queen Anne's Co.:** Entry Run, DE 176, ca. 0.5 mi N of intersection with DE 178, 1000 ft. from roadway, 19 Jul 1985, *R. Driskill et al. CEP85-618 CEP85-618* (DOV DOV0019247 [i]). **Somerset Co.:** 7 mi W of Princess Anne, 17 Apr 1938, *J.M. Fogg 14598* (PH PH00392137 [i]). **Talbot Co.:** 2 mi SW of Eastern, 16 Apr 1938, *M.T. Travis 420* (GA GA201397). **Wicomico Co.:** Chesapeake Forest lands, Tom Tyler Nature Trail, 24 Apr 2022, *A.A. Crowl CY-485* (BRIT BRIT914520). **Worcester Co.:** just WNW of North Beach parking lots near intersection with Bayside camp road, 28 Apr 1984, *S.R. Hill 13567* (BRIT BRIT446365). **MASSACHUSETTS. Barnstable Co.:** Pond Road, North Truro, 1 Aug 1973, *H.E. Ahles 78040* (VT UVMVT088882 [i]). **Berkshire Co.:** near East Otis, 29 May 1932, *E.J. Palmer 40062* (UMO 142507). **Bristol Co.:** Dighton, 16 May 1956, *F.C. Seymour 16496* (SMU BRIT446340). **Dukes Co.:** near Look's Brook, Chilmark, 8 Jun 1917, *F.C. Seymour 1760* (NEBC 00519681 [i]). **Essex Co.:** Newbury, 21 Jul 1942, *E.J. Palmer 46285* (UMO 71142). **Franklin Co.:** Deerfield, 1 Jun 1967, *R.G. Poland s.n.* (NY 02542668 [i]). **Hampden Co.:** Spectacle Pond on U.S. Rte. 20, North Wilbraham, 15 May 1980, *H.E. Ahles 87836* (GA GA201381). **Hampshire Co.:** roadside, North Amherst, 20 May 1950, *R.J. Tisdell s.n.* (TEX 00507545 [i]). **Middlesex Co.:** Bedford, 27 May 1906, *H.H. Bartlett 447* (RSA RSA0184786 [i]). **Nantucket Co.:** Tom Nevers Pd., 10 Jun 1960, *F.C. MacKeever 423* (NY 02546193). **Norfolk Co.:** riverbank, Wellesley, 12 May 1894, *J.B. Patten s.n.* (BRIT BRIT528949). **Plymouth Co.:** vicinity of 3-cornered Pond and Round Pond, Miles Standish State Forest, Plymouth, 21 Jun 1975, *H.E. Ahles 80029* (WVA 117741). **Suffolk Co.:** West Roxbury, by White Birches below Cow Island, 22 Jul 1912, *F.F. Forbes s.n.* (SMU BRIT446548). **Worcester Co.:** Ashby to Fitchburg, 30 May 1914, *J.H. Emerton & C.H. Knowlton s.n.* (NEBC 00519707 [i]). **MISSISSIPPI. Alcorn Co.:** Beaver Creek, Pontotoc Ridge, W of Wenasoga, 6 Jun 1957, *G.R. Cooley & J.D. Ray Jr. 5151* (MISSA MISSA011207 [i]). **Amite Co.:** ca. 175 m W of Tower Road, ca. 200 m W of Stephenson Lookout Tower, ca. 1.3 mi NW of State Hwy 33, Homochitto National Forest, 21 Apr 2022, *P.W. Fritsch 2383* (BRIT BRIT698903). **Attala Co.:** ca. 6.0 mi E of Kosciusko, stream crossing, roadside, 2 Jul 1984, *T.E. Smith 592* (MMNS MMNS004108 [i]). **Benton Co.:** Wolf River; ca. 1.5 mi NE of Spring Hill, 6 Jun 1957, *G.R. Cooley & J.D. Ray Jr. 5135* (USF 17851 [i]). **Calhoun Co.:** ca. 13 mi NW of Bruce on high ridge, 22 Sep 1990, *R.A. Stewart 3747* (MISS MISS0054770 [i]). **Clarke Co.:** Clarkco State Park, 14 Jun 1969, *S.B. Jones 16477* (MISS MISS0054769 [i]). **Copiah Co.:** 5.7 mi W of Georgetown, 13 Jul 1967, *S.B. Jones 14449* (MISS MISS0054630 [i]). **Covington Co.:** 5 mi S of Hot Coffee, Hwy. 37 and 84, 29 May 1967, *S.B. Jones 12554* (MISS MISS0054757 [i]). **Forrest Co.:** U.S. Hwy. 13, ca. 10 mi W of Hwy. 49, 20 Jun 1971, *K.E. Rogers 6548* (SMU BRIT446401). **Franklin Co.:** 0.10 mi E of the end of an unnamed Forest Service road, ca. 0.5 mi W of Scott-Murray Road, Homochitto National Forest, 20 Apr 2022, *P.W. Fritsch 2378* (BRIT BRIT698898). **George Co.:** 0.5 mi S of intersection Hwy. 49S and Hwy. 98E S of Hattiesburg, ca. 100 yds. W of Hwy. 49S, 12 May 1982, *K.L. Gordon 2773* (MISS MISS0054762 [i]). **Greene Co.:** Leaf, 15 May 1946, *P. Goodrum s.n.* (BRIT BRIT400496). **Grenada Co.:** ca. 0.75 mi E of Tie Plant, Loess Bluffs/North Central Plateau, 21 Jun 1987, *M.W. Morris 2895* (DSC DSC102886 [i]). **Hancock Co.:** gas line right-of-way and roadbank of Miss. 602 just E of Miss. 604 SE of I-10, N of Pearlington, 11 Oct 1996, *R.D. Thomas 152747* (NLU NLU0140388). **Harrison Co.:** S side Northwood Street, ca. 116 m W of Oakland Avenue and Pass Christian High School, Pass Christian, 22 Apr 2022, *P.W. Fritsch 2389* (BRIT BRIT698909). **Jackson Co.:** T5N, R15W, S14, 25 Oct 1969, *K.E. Rogers 2469* (MISS MISS0054761 [i]). **Jasper Co.:** Mrs. Lena Cook's farm S of Bay Springs, via. Miss. 15, 9 Sep 1978, *P. Pias 3850* (NLU NLU0140956). **Lafayette Co.:** Minnows Inc., 12.5 mi NE of Oxford, 10 Apr 1964, *T.M. Pullen 6472* (GA GA201399). **Lamar Co.:** 4 mi W of Hattiesburg, near Hwy. 98 and Interstate, 5 Apr 1965, *S.B. Jones 2685* (NCU NCU00351047 [i]). **Lauderdale Co.:** S side of York Road, ca. 1.25 mi W of Rutherford Road, ca. 3 mi W of state line, 26 Apr 2022, *P.W. Fritsch 2404* (BRIT BRIT698924). **Marshall Co.:** ca. 280 m NE of the end of Chewalla Dam Road, ca. 350 m N of Chewalla Dam, ca. 0.5 mi S of the S border of Chewalla Lake Recreation Area, ca. 0.92 mi E of Higdon Road, 27 Apr 2022, *P.W. Fritsch 2407* (BRIT BRIT698927). **Monroe Co.:** E of Rte. 8 and U.S. 78, 10 mi E of Amory, 12 Jun 1956, *J.D. Ray Jr. 6971* (VDB BRIT234035). **Neshoba Co.:** 5.3 mi S of Noxapater, 30 Mar 1969, *S. McDaniel & G. Anding 11526* (MISS MISS0054748 [i]). **Pearl River Co.:** along Hurricane Creek, Gum Pond, 6 mi SE of Lumberton, 19 Apr 1957, *J.D. Ray Jr. 8098* (USF 17852 [i]). **Perry Co.:** Camp Shelby Training Site, Training Area 34, LCTA plot 12, Hwy. 29, 2.4 mi S of Hwy. 98 at New Augusta, 1.15 mi E on FS Road 312, 0.7 mi S on bermed road, E of this road, 27 Oct 1993, *B. Pessoney & S. Whisler 188* (USMS USMS000009705 [i]). **Prentiss Co.:** ca. 1.5 mi N of Booneville, E and W of Hwy. 45, 8 Apr 1979, *K.E. Rogers 46473* (MMNS MMNS006433 [i]). **Smith Co.:** N end of Shongelo Lake, ca. 0.16 mi N of the dam, ca. 0.11 mi E of MS-35, State Roadside Park, 25 Apr 2022, *P.W. Fritsch 2400* (BRIT BRIT698920). **Stone Co.:** 3.1 mi S of intersection U.S. Hwy. 49 and Miss. Hwy. 26, E of Hwy. 49 ca. 50 ft., 22 Oct 1972, *K.E. Rogers 8838* (MISSA MISSA011163 [i]). **Tishomingo Co.:** ca. 94 m SE of Crows Neck Road (County Road 115)., ca. 2.2 mi SW of the W end of County Road 961, Crows Neck Recreation and Environmental Center, 27 Apr 2022, *P.W. Fritsch 2410* (BRIT BRIT698930). **Wayne Co.:** ca. 5.1 mi SE of Buckatunna, 11 May 1981, *K.L. Gordon 2497* (MMNS MMNS003784 [i]). **NEW HAMPSHIRE. Hillsborough Co.:** Fox Forest, Jul 1936, *A.A. Beetle 501* (RSA RSA0184903 [i]). **Rockingham Co.:** Derry, 10 May 1913, *C.F. Batchelder s.n.* (NEBC 00519320 [i]). **Strafford Co.:** Lee Hill Bog, Lee, 21 Oct 1959, *W.D. Countryman et al. 45* (UV UVMVT088867 [i]). **NEW JERSEY. Atlantic Co.:** Mays Landing, 10 May 1924, *W. Pennell 12025* (NY 02542836). **Bergen Co.:** Noonachie,

near Losen Slofe Br. of Hackesack River, 16 Jun 1970, *W. Sipple s.n.* (PH PH00395676 [i]). **Burlington Co.:** Bass River Twp., Bass River State Forest, along Allen Road, Oswego Lake Quadrangle, 20 Jul 2001, *G. Moore & G. Zimmermann 5041* (VDB BRIT312849). **Camden Co.:** along railroad, 0.25 mi WNW of Pine Valley, 3 May 1935, *J.M. Fogg Jr. 8161* (PH 00073598 [i]). **Cape May Co.:** behind sand-dunes, S of Peermont, 5 May 1935, *F S. Fender 290* (PH 00073835 [i]). **Cumberland Co.:** Hankens Pond on Petticoat Br. of Maurice River, Millville, 18 Jul 1926, *J.W. Adams 392* (PH 00073761 [i]). **Essex Co.:** North Caldwell, E of Mountain Ave., N of electric ROW, 9 May 1995, *S. Glenn 837* (CHRB CHRB0010726 [i]). **Gloucester Co.:** along streamlet tributary to South Branch Timber Creek, Blackwood, 27 Apr 1919, *B. Long 20322* (PH 00060973 [i]). **Hunterdon Co.:** 1.5 mi S of Milltown, 27 Apr 1941, *B. Long 56323* (GA GA201383). **Mercer Co.:** 1.5 mi ESE of Robbinsville, 5 May 1935, *B. Long 45708* (PH 00073794 [i]). **Middlesex Co.:** Cheesequake State Park, trail to Hooks Creek Lake, Yellow Trail, *P.S. Manos CY-145* (BRIT BRIT698630). **Monmouth Co.:** Farmingdale, 4 Jul 1910, *N. Taylor 2151* (NY 02543345). **Morris Co.:** Great Swamp National Wildlife Refuge, behind parking area on Headquarters Access Road, 0.8 km NE of intersection of Whitebridge Road and Pleasant Plains Road, 7 May 2014, *L.S. Poster s.n.* (CHRB CHRB0112299). **Ocean Co.:** along Pinewald-Keswick Road, 0.5 mi W of jct. with Dover Road, ca. 2.5 mi SW of Toms River, 11 May 1975, *G.H. Morton et al. 5600* (BRIT BRIT446362). **Passaic Co.:** Bearfort Mt. S of West Milford, 1964, *R. Villamil s.n.* (CHRB CHRB0010640 [i]). **Salem Co.:** 1.5 mi NNE of Eldridges Hill, 9 May 1934, *J.M. Fogg Jr. 6465* (PH 00060984 [i]). **Somerset Co.:** Second Mountain, Watchung, 12 May 1934, *H.N. Moldenke 7974* (NY 02542683). **Sussex Co.:** Sparta Twp., Mahlon Dickerson Reservation, NW Section, N of Milton Road, 2 Jul 2002, *K. Barringer 8253* (VDB BRIT311241). **Union Co.:** Watchung Reservation, along shore of Surprise Lake, 17 Jul 2019, *P S. Manos CY-272* (BRIT BRIT698816). **Warren Co.:** 0.75 mi SE of Cold Spring School, 10 Jul 1959, *H.W. Pretz 59139* (MCA MCA0035041 [i]). **NEW YORK. Bronx Co.:** D's woods, Riverdale, 24 Jul 1892, *E.P. Bicknell s.n.* (NY 02543356). **Nassau Co.:** Plattsdale, 17 Jul 1925, *W.C. Ferguson 4154* (NY 02545421). **Putnam Co.:** ca. 7 km (by air) W of New York/Connecticut state border and ca. 10 km (by air) N of Putnam/Westchester county border, Ice Pond Conservation Area, E of Ice Pond road, N of Rte. 312 and W of Ice Pond, 10 May 2008, *D. Atha & D. Adamsons 6156* (MO MO-3844228). **Queens Co.:** Flushing, 8 Jul 1902, *A.J. Grout 5* (NY 02544996 [i]). **Rockland Co.:** West Nyack, May 1900, *C S. Williamson s.n.* (PH PH00392125 [i]). **Suffolk Co.:** Ronkonkoma, 12 May 1925, *W.C. Ferguson 3667* (NY 02543352). **Westchester Co.:** Westmoreland Sanctuary (260 Chestnut Ridge Road, Mt Kisco, NY 10549) near pond on new land tract (not yet on trail map), ca. 500 m due N of N edge of Bochtel Lake, 10 Jul 2023, *R. Carmickle RC101* (BRIT BRIT927468). **NORTH CAROLINA. Alamance Co.:** Cane Creek Mountains Natural Area, below fire tower, 5 Mar 2023, *C.A. McCormick s.n.* (NCU NCU00446536 [i]). **Alleghany Co.:** Blue Ridge Parkway, Mile 240.3 L, Doughton Park, bog, 10 Jul 1977, *T. Govus 186* (WCUH WCUH0028173 [i]). **Anson Co.:** 3 mi E of Polkton, Conrad Lane, 25 Feb 2023, *B. Dill 2023-008* (NCU NCU00446028 [i]). **Beaufort Co.:** U.S. Rte. 17, 6 mi S of Chocowinity, 15 Apr 1940, *M. Caughey 822* (ECUH ECUH0003002 [i]). **Bladen Co.:** without specific locality, 3 May 1929, *W.W. Ashe E6744* (GA GA201291). **Brunswick Co.:** Green Swamp Game Land, 22 Apr 2022, *A.A. Crowl CY-475* (BRIT BRIT914450). **Buncombe Co.:** Biltmore, 25 Apr and 29 May 1896, *W.W. Eggleston 1061* (NCU NCU00014038 [i]). **Cabarrus Co.:** Rocky River at NC Road 73, 29 Apr 1966, *T. Daggy 3422* (UNCC 28610 [i]). **Camden Co.:** Dismal Swamp, U.S. 17, just beyond Virginia Border, 31 Mar 1963, *N.H. Holmgren 614* (UTC UTC00254841 [i]). **Carteret Co.:** Patsy Pond, on the Blue and Orange trails, 5 Jun 2020, *A.A. Crowl CY-324* (BRIT BRIT698839). **Catawba Co.:** Beach 1.8 mi N of Long Island at bridge, 18 Apr 1960, *J.A. McNeely 1251* (NCU NCU00330386 [i]). **Chatham Co.:** White Pines Nature Preserve, 13 Jun 2020, *P.S. Manos CY-328* (BRIT BRIT698843). **Chowan Co.:** 10 mi N of Edenton, 10 May 1941, *W.V. Brown s.n.* (TEX 00506677 [i]). **Clay Co.:** Whittmire farm on Little Brasstown Creek ca. 5.2 km (3.2 mi) W of Brasstown on S.R. 1564, 25 Jun 1986, *D. Pittillo 9227* (WCUH WCUH0011523 [i]). **Cleveland Co.:** 4.3 mi N of Polkville on N.C. 10, 19 Apr 1956, *C.R. Bell 1992* (NCU NCU00330393 [i]). **Columbus Co.:** 4 mi E of Lake Waccama, N side of Hwy. 214, 7 Sep 2019, *A.A. Crowl CY-317* (BRIT BRIT698832). **Craven Co.:** Neuse River Recreation Area, 23 Apr 2022, *A.A. Crowl CY-476* (BRIT BRIT914451). **Cumberland Co.:** Hope Mill, Chicken Foot Road, 3 mi E of I-95, 30 Mar 2019, *A.A. Crowl CY-192* (BRIT BRIT698745). **Currituck Co.:** ca. 300 ft. of Highway 158, Poplar Branch, 15 Apr 1965, *E. Murrell 41* (WCUH WCUH0011521 [i]). **Dare Co.:** Kill Devil Hills, 11 Jun 1949, *W.B. Fox & R.K. Godfrey 2320* (GA GA201289). **Davie Co.:** 1.5 mi E Farmington, 27 Aug 1951, *W.T. Batson Jr. 1113* (DUKE DUKE10102287 [i]). **Duplin Co.:** ca. 2 mi N of Pin Hook on NC 50, 25 Apr 1995, *R.L. Wilbur 63796* (DUKE DUKE10100491 [i]). **Durham Co.:** Duke Forest off of Gate 10 entrance, 31 Mar 2016, *P.S. Manos CY-005* (BRIT BRIT698708). **Edgecombe Co.:** 0.3 mi NE of Gethsemane, 23 Apr 1958, *A.E. Radford 32053* (NCU NCU00330413 [i]). **Forsyth Co.:** near Biol. Bld., Wake Forest, W.S., roadside, 9 Apr 1975, *S. Tswana 74* (APSC APSC0098710 [i]). **Franklin Co.:** 0.6 mi N of NC Rte. 56 on State Road 1467 ca. 10 mi E of Louisburg, 14 May 1988, *R.L. Wilbur 46493* (DUKE DUKE10100493 [i]). **Gaston Co.:** Crowder Mountain S of Gastonia, 4 Apr 1972, *T. Daggy 6562* (NLU NLU0141009). **Gates Co.:** beside Rte. 1200, 0.9 mi S of Rte. 1203, 17 Mar 1975, *H.J. Ecklund 112* (NLU NLU0141032). **Granville Co.:** 3–4 mi N of Culbreth on the county road leading to U.S. 158, intersecting it just E of Berea, 6 Jun 1982, *C.M. Taylor 1526* (DUKE DUKE10100498 [i]). **Guilford Co.:** between U.S. 421 and NC 62, near jct. NW of Julian, 8 Aug 1958, *C.R. Bell s.n.* (NCU NCU00315159 [i]). **Halifax Co.:** County Road 1226 ca. 1 mi W of County Road 1222 near the Nash County Line, 12 Jun 1997, *R.L. Wilbur 67354* (DUKE DUKE10100499 [i]). **Harnett Co.:** Raven Rock State Park, Raven Rock Loop Trail, 15 Aug 2018, *P S. Manos CY-175* (BRIT BRIT698731). **Henderson Co.:** Flat Rock, 10 Apr 1887, *E.R. Memminger s.n.* (NCU NCU00330429 [i]). **Hertford Co.:** roadside, 4 mi N of Barretts Crossroads and 0.4 mi NE, 19 Apr 1958, *H.E. Ahles 38490* (NCU NCU00330430 [i]). **Hoke Co.:** near bridge over U.S. 501 over Drowning Creek, 6 Apr 1940, *Radford & Stewart 9* (NCU NCU00315186 [i]). **Hyde Co.:** roadside just N of the drawbridge over the Intercoastal waterway on NC94 ca. 4.5 mi N of Fairfield, 6 Jun 1996, *R.L. Wilbur 65853* (DUKE DUKE10100422 [i]). **Iredell Co.:** William Knox farm on Co. Road 1137, 1 mi E of N.C. Road 115, 20 Apr 1971, *T. Daggy 6112* (NBYC NBYC020040 [i]). **Jackson Co.:** W edge of Dulaney Bog, Bull Pen Road, near Highlands, 3 Jun 2019, *P.S. Manos CY-254* (BRIT BRIT698799). **Johnston Co.:** 2 mi E of Bagley, 11 Mar 1956, *H.E. Ahles 10056* (NCU NCU00330438 [i]). **Jones Co.:** ca. 3 mi SE Maysville, 31 May 1980, *R. Kral 65248* (VDB BRIT311705). **Lee Co.:** ca. 2 mi NW jct. Deep and Haw Rivers, 25 Mar 1955, *L S. Beard 296* (NCU NCU00330446 [i]). **Lenoir Co.:** ca. 6 mi S of Kinston on State Road 1910, 16 May 1991, *R.L. Wilbur 58914* (DUKE DUKE10102288 [i]). **Lincoln Co.:** without specific locality, 24 Apr 1978, *B. Sherbecoe 15610* (UNCC 28615 [i]). **Macon Co.:** North fork of Coweeta Creek, off Coweeta Gap Road W of Otto, Jack Johnson Property, 27 Jun 2023,

P.S. Manos CY-510 (BRIT BRIT1082248). **Martin Co.:** near Parmele, 10 Jun 1940, *R.F. Martin 1958* (DUKE DUKE10100512 [i]). **Mecklenburg Co.:** Latta Place at end of Co. Road 2125 (Sample Road), on Mountain Island Lake, 3 Apr 1975, *T. Daggy 7669* (UNCC 28616 [i]). **Montgomery Co.:** Uwharrie National Forest, 2 mi E of Stanly-Montgomery Co. line, on St. 24 & 27., 12 Jul 2001, *W. Hess et al. 9587* (NLU NLU0141005). **Moore Co.:** Weymouth Woods State Park, 13 Jul 1965, *H.E. Ahles 59543* (SMU BRIT446427). **Nash Co.:** W of Hwy. 301, Sharpsburg, 2 Apr 1956, *M.M. Eason 4* (ECUH ECUH0003005 [i]). **New Hanover Co.:** Carolina Beach State Park, 20 Apr 2017, *P.S. Manos CY-038* (BRIT BRIT698725). **Northampton Co.:** County Road 1126 ca. 4 mi SW of Jackson at intersection with County Road 1127, 23 May 1991, *Z.E. Murrell 5914* (DUKE DUKE10100521 [i]). **Onslow Co.:** U.S. 17, 9.2 mi S of Jacksonville, 24 May 1941, *Radford & Stewart 1232* (GA GA201533). **Orange Co.:** Mason Farm, along dirt road which forks with left road to lake, right road to higher land, 27 Apr 1966, *J.E. Freeman 51* (GA GA201539). **Pamlico Co.:** Lumbering site on State Road 1126 and 0.8 mi SE of the Craven County line and ca. 6 mi NE of Bridgeton, 2 Jun 1992, *R.L. Wilbur 06854* (DUKE DUKE10100537 [i]). **Pasquotank Co.:** dirt road along U.S. 158 ca. 11 mi NW of Elizabeth City and just S of Morgans Corner, 25 May 1994, *R.L. Wilbur 62315* (DUKE DUKE10100540 [i]). **Pender Co.:** N part of Big Savannah, 2 mi NW of Burgaw, 24 Mar 1954, *G.B. Rossbach s.n.* (WVA WVA-V-0010494). **Perquimans Co.:** River Bank, Apr 1932, *M. Glasson s.n.* (DUKE DUKE10100541 [i]). **Person Co.:** 3.9 mi N of Mt. Tirzah, 22 Apr 1958, *C.R. Bell 11218* (NCU NCU00315228 [i]). **Pitt Co.:** E.C.C. Campus, 9 Mar 1956, *R.F. Williams 4* (ECUH ECUH0003006 [i]). **Polk Co.:** beyond the trestle, Tryon, 20 Apr 1923, *D.C. Peattie 1867* (NCU NCU00330474 [i]). **Randolph Co.:** along service road spur connecting Cypress Swamp animal holding facility with main North America service road, L6E6EE, 18 Mar 1997, *P. Diamond 152* (NCZP 00000238 [i]). **Richmond Co.:** by U.S. 1, 5 mi N Rockingham, 29 May 1977, *R. Kral 60254* (VDB BRIT311725). **Robeson Co.:** 5.5 mi SE of Red Springs along Raft Swamp, 5 Apr 1958, *R.F. Britt 1617* (NCU NCU00330476 [i]). **Rockingham Co.:** 2 mi E of Thompsonville on N.C. 87, 13 Apr 1956, *A.E. Radford 9701* (VDB BRIT312122). **Rowan Co.:** Gold Hill District, Union Mine, Jul 1971, *J. Antonovics s.n.* (DUKE DUKE10100554 [i]). **Sampson Co.:** 5 mi E of Clinton, 31 Mar 1938, *H.L. Blomquist 10222* (NY 02545562). **Scotland Co.:** vicinity of Lake Kinney Cameron in the State Game Lands of the Village of Hoffman on State Road, 16 Apr 2000, *R.L. Wilbur 72744* (DUKE DUKE10100555 [i]). **Stanly Co.:** Rock Hole Creek between Co. Road 1122 and Rocky River, 29 Apr 1987, *T. Daggy 15611* (UNCC 28618 [i]). **Stokes Co.:** Moore's Knob, lower elevation, 8 Aug 2017, *P.S. Manos CY-070* (BRIT BRIT698695). **Surry Co.:** Pilot Mountain, Grindstone Trail, low elevation, 23 May 2018, *P.S. Manos CY-075* (BRIT BRIT698700). **Transylvania Co.:** roadside between Brevard and Rosman, 27 Apr 1937, *H.R. Totten s.n.* (NCU NCU00330493 [i]). **Tyrrell Co.:** along U.S. 64 between Columbia and Alligator River, 27 May 1978, *J. Carlton s.n.* (USF 135583 [i]). **Union Co.:** 2.4 mi SE of jct. U.S. 601-74 and NC 200, then 0.6 mi E on paved road (SE of Monroe), 7 Jun 1957, *H.E. Ahles 27546* (NCU NCU00330495 [i]). **Wake Co.:** Camp Durant, along north bank of lower lake, 14 Apr 1981, *J.D. Skean Jr. 231* (GA GA201247). **Warren Co.:** between railroad and U.S. 158, 2.5 mi E of Vaughan, 17 Apr 1968, *S.W. Leonard & A.E. Radford 1326* (NCU NCU00330498 [i]). **Washington Co.:** Albermarle Sound at the northern terminus of State Road 1344 perhaps 1 mi E of Hwy. 32 bridge across the sound, 21 Jun 1994, *R.L. Wilbur 62702* (DUKE DUKE10100575 [i]). **Wayne Co.:** Goldsboro, Co. Road 1728 near Walnut Creek, 17 Mar 1973, *T. Daggy 6968* (UNCC 28624 [i]). **Wilkes Co.:** N bank of Mort Branch, ca. 1 mi NW of Ball Mill Site, Brushy Mts., 3 May 1941, *L.M. Stewart 1911* (GA GA201286). **Wilson Co.:** Wilson swamp on Lambs Cross Road 0.4 mi W of Rte. 301, 12 Apr 1970, *J.A. Churchill s.n.* (SMU BRIT446550). **OKLAHOMA. Choctaw Co.:** NE of Swink at "Swink Bog"/"Swink Bog 2," best area is E of standing water, 14 Mar 2012, *A. Buthod & B. Hoagland AB-9416* (OKL 20001550 [i]). **PENNSYLVANIA. Adams Co.:** between highway and Carbaugh Run, 5.5 mi WNW of Cashtown, 8 May 1955, *E.T. Wherry s.n.* (PH PH00395185 [i]). **Berks Co.:** Hawk Mountain Sanctuary, from Visitor Center, follow staff roads SE (not toward exit) to State Lands gate. Walk around gate and along two track road for ca. 0.5 mi then tuck uphill (northward) into woods. Walk ca. 40 m NE from road, 17 Jul 2019, *R. Carmickle RC135* (BRIT BRIT899946). **Bucks Co.:** along Lower Mt. Road, ca. 2 mi NE of Buckingham Valley, 24 Apr 1957, *W.L. Dix s.n.* (PH PH00395868 [i]). **Carbon Co.:** 2 mi ENE of Normal Square, 5 May 1951, *E.T. Wherry s.n.* (PH PH00392034 [i]). **Chester Co.:** Valley Forge, 1 May 1892, *A. MacElwee s.n.* (PH PH00395909 [i]). **Cumberland Co.:** King's Gap State Park, S of Montsera, 2 Jun 2012, *B.L. Isaac et al. 21518* (CM 527022 [i]). **Dauphin Co.:** Peters Mountain, 29 Jul 1917, *J. Bright s.n.* (CM 076715 [i]). **Delaware Co.:** on road above Gap Rock, Nockamixon Twp., 9 May 1930, *W.H. White s.n.* (CHRB CHRB0010660 [i]). **Franklin Co.:** Pond Bank, 22 Apr 1919, *O.E. Jennings 6211* (CM 076712 [i]). **Lancaster Co.:** Grade Rock Island, NW side, 21 May 1970, *J. Parks 60* (WILLI 11104). **Lehigh Co.:** ca. 0.5 mi S of Mountainville, P.O., 7 Jul 1918, *H.W. Pretz 9454* (VDB BRIT311374). **Luzerne Co.:** 6.2 km NW of Wyoming, edge of cemetery, 29 Apr 2017, *B.L. Isaac 24106* (CM 539645 [i]). **Montgomery Co.:** along Flint Road, ca. 0.5 mi SW of Eureka, 30 Jun 1946, *B. Long s.n.* (PH PH00395901 [i]). **Northampton Co.:** between C.R.R. and canal 1 mi N of Walnutport, 20 Apr 1913, *H.W. Pretz 5201* (PH PH00395812 [i]). **Perry Co.:** near New Bloomfield, 16 Jun 1920, *E.M. Gress s.n.* (CM 076714 [i]). **Philadelphia Co.:** below "the spring" 64th Ave. and 2nd. St., Oak Lane, 17 Apr 1952, *B. Long 74842* (CHRB CHRB0010661 [i]). **Schuylkill Co.:** Weiser State Forest - Appalachian Trail, N of Schubert, PA; from jct. of 419 and 183, drive N along 183 ca. 1.2 mi to Appalachian Trail parking area (W side of road). Hike W along trail ca. 90 m then keep right at fork. Continue for ca. 80 m to a clearing, 17 Jul 2023, *R. Carmickle RC131* (BRIT BRIT927798). **Snyder Co.:** 3 mi SW of Penn's Creek P.O., 3 May 1939, *D.E. Wade 939* (PH PH00395188 [i]). **Sullivan Co.:** Shady Nook, 18 Jul 1901, *S. Brown s.n.* (PH PH00392071 [i]). **Union Co.:** power line, 5 mi W of White Deer, 22 Aug 1955, *W.F. Westerfield 17650* (PAC PAC0057154 [i]). **York Co.:** without specific locality, 14 Jul 1919, *E.M. Gress s.n.* (CM 076716 [i]). **RHODE ISLAND. Bristol Co.:** Barrington, 5 May 1906, *E.S. Reynolds 0672* (BRU PBRU00007617 [i]). **Kent Co.:** near Bailey Pond, West Greenwich Road, 12 Aug 1914, *E.B. Harger s.n.* (NEBC 00519865 [i]). **Newport Co.:** Newport, 24 Aug 1901, *E.A. Mearns 566* (NEBC 00519861 [i]). **Providence Co.:** near Sneech Pond, Cumberland, 17 Jun 1947, *E.J. Palmer 48165* (VDB BRIT311713). **Washington Co.:** near Peace Deal, 18 Jul 1937, *E.J. Palmer 43393* (UMO 135569). **SOUTH CAROLINA. Aiken Co.:** Aiken, Hitchcock Woods, 20 Apr 2022, *A.A. Crowl CY-462* (BRIT BRIT914407). **Allendale Co.:** 1 mi E of Allendale, 9 Apr 1930, *G.A. Schulze 606* (GA GA201548). **Anderson Co.:** Toby's Hill Road, 26 May 1976, *C.L. Rodgers 76272* (FUGR FUGR0011410 [i]). **Bamberg Co.:** along SC 64, 3.5 mi W of jct. with U.S. 601 in town of Ehrhart, 8 Mar 2017, *C.N. Horn 2244* (CLEMS CLEMS0070057 [i]). **Barnwell Co.:** SW corner of the Savannah River Plant, Road A-17.1 near Road A-13, powerline right-of-way, 22 Mar 1989, *N. Coile 4913* (GA GA261468). **Beaufort Co.:** along Atlantic Ocean E of Hwy.

287, "Palmetto Dunes" Subdivision on Hilton Head Island, 1 Jul 1971, *M.G. Lelong 5991* (USAM USAM000005805 [i]). **Berkeley Co.:** 11 mi. NE of Wando at intersection of road to Witherbee with county line road, 22 mi. NW of Charleston, 9 Apr 1944, *W.H. Duncan 5932* (GA GA201550). **Charleston Co.:** S edge of Roxbury Park, N side of Little Britton Road across from Roxbury Mercantile Restaurant, 25 Mar 2021, *A.A. Crowl CY-353* (BRIT BRIT792832). **Cherokee Co.:** 0.25 S of 99 dam on W side of Broad River, 27 Jun 1983, *G. Newberry 2768* (USCS USCS0009160 [i]). **Chesterfield Co.:** 1.5 mi S of jct. of U.S. 52 on U.S. 1, 5 Apr 1968, *S.W. Leonard & A.E. Radford 1221* (SMU BRIT446397). **Clarendon Co.:** 1 mi E of Manning, 2 Apr 1930, *G.A. Schulze 587* (GA GA201295). **Colleton Co.:** 4.76 mi SE of Ruffin, E edge of Big Hill Road, N of the Ruffin Road (SSR44) intersection, 25 Mar 2021, *A.A. Crowl CY-366* (BRIT BRIT792845). **Darlington Co.:** Hartsville, 10 Jun 1942, *B.E. Smith s.n.* (PAC PAC0057452 [i]). **Dillon Co.:** W side of Sec Hwy. 22 and just N of Little Pee Dee River, vic. Little Pee Dee State Park, 20 Mar 1985, *J.B. Nelson 3797* (USCH USCH0027402 [i]). **Dorchester Co.:** (in town) Summerville, 11 May 1940, *H.H. Keifer KV36* (GA GA201553). **Florence Co.:** 1.8 mi WSW of Hyman, 24 May 1957, *C.R. Bell 7552* (NCU NCU00331689 [i]). **Georgetown Co.:** N of old rice field and nearby observation deck, Brookgreen Gardens, between Litchfield and Murrells Inlet, 10 Mar 2001, *J.B. Nelson 21728* (BRIT BRIT446360). **Horry Co.:** bay margin, Cotton Patch Bay, 18 May 1987, *W.T. Batson & E.F. Thompson s.n.* (USCH USCH0027215 [i]). **Jasper Co.:** along U.S. 321, 0.7 mi W of jct. with Co. Rte. 50 and 0.5 mi E of Hampton County line, 2 Mar 2017, *C.N. Horn 22415* (NBYC NBYC000621 [i]). **Kershaw Co.:** Dr. Humphries Road just before jct. with Rte. 34, 30 Mar 2019, *A.A. Crowl CY-194* (BRIT BRIT698747). **Laurens Co.:** Enoree River at Van Patton Shoals, NW edge of county, 12 Jun 1986, *G. Newberry & M.Q. Hague 6511* (USCS USCS0009161 [i]). **Lee Co.:** roadside and powerline cut along Co. Rte. 101, 2.3 mi SW of jct. with Co. Rte. 53, ca. 17 mi SE of Bishopville, 17 Jun 1995, *C.N. Horn 9559* (NBYC NBYC004436 [i]). **Marion Co.:** Brittions Neck, from the confluence of the Great Pee Dee and Little Pee Dee Rivers to Hwy. 378. From Columbia take Hwy 378 E towards the coast, after you cross Great Pee Dee River go ca. 7 mi then right onto unimproved road next to Brittons Neck lookout tower and cemetery, 26 Apr 2006, *B. Pittman 04260609* (USCH USCH0027203 [i]). **Marlboro Co.:** W side of Sec. Hwy. 30 and just S of Wolf Creek ca. 6 mi NE of SC 6, 5 Apr 1984, *J.B. Nelson 3119* (USCH USCH0027403 [i]). **Oconee Co.:** near Westminster, 14 May 1923, *W.W. Ashe s.n.* (NY 02551747). **Pickens Co.:** Ca. 1 mi E of Morgan's store on old Hwy. 11, 8 Jul 1969, *C.L. Rodgers & G. Shiftlet Jr. 69428* (FUGR FUGR0011418 [i]). **Richland Co.:** N side of Buffalo Creek, ca. 0.3 mi W of Century Division Road, 25 May 1992, *J.B. Nelson 12579* (NLU NLU0141278). **Saluda Co.:** near S.C. 23, 2 mi W of Ridge Spring, 6 Apr 1957, *A.E. Radford 20661* (NCU NCU00331704 [i]). **Spartanburg Co.:** Woodland SE of Woodruff High School, S of jct. of SC 146 and Co. Rte. 450 (Workman Road), E of downtown Woodruff, 19 May 2009, *C.N. Horn 18724* (NBYC NBYC004437 [i]). **Sumter Co.:** Poinsett Air Force Weapons Range, "Dry Pond," just over 1 mi due E of main entrance at SC 261, 21 May 1993, *J.B. Nelson 14135* (USCH USCH0027388 [i]). **Williamsburg Co.:** Indiantown Community near Hemingway, 18 Mar 1956, *C. Bartell 15877* (UNCC 28621 [i]). **York Co.:** powerline r.o.w. between Apple Road and Camp York, 8 Jun 1993, *D.E. Kennemore Jr. 645* (USCH USCH0027232 [i]). **TENNESSEE. Benton Co.:** Lakeside Drive, 31 May 1993, *H.R. DeSelm s.n.* (TENN TENN-V-0169336 [i]). **Bledsoe Co.:** ca. 2.5 mi from Rte. 111, under powerline, 20 Apr 1990, *V.E. McNeilus 90-8* (TENN TENN-V-0169194 [i]). **Bradley Co.:** Red Clay State Historical Area, 8 Apr 1989, *D. Houck 2659* (TENN UCHT033842 [i]). **Cannon Co.:** ca. 7 mi S Woodbury by Tenn 53, 20 May 1974, *R. Kral 52784* (VDB BRIT112980). **Carroll Co.:** 1.9 mi ENE of the community of Westport, on S side of powerline r.o.w. along Bateman Branch just S of Robinson Swamp, ca. 0.3 mi W of Dollar Road, 5 Jun 2009, *D. Estes 10506* (APSC APSC0051114 [i]). **Chester Co.:** S Fork of the Forked Deer River, SE side of Hwy. 100 crossing just E of Henderson, 15 Apr 1983, *V. Bates 3935* (TENN TENN-V-0169337 [i]). **Coffee Co.:** just S of Manchester along E side of railroad tracks by hwy., 8 Jun 1966, *R. Kral 26810* (SMU BRIT446416). **Decatur Co.:** near Rushing Creek, E of Scott's Hill, 13 Oct 1949, *E.H. Cooley et al. 14835* (TENN TENN-V-0169013 [i]). **DeKalb Co.:** Smithville, 100 ft. W of Hwy. 56, 2 mi N of Hwy. 70, 24 Jun 1981, *R. Thornton 25* (UCHT UCHT022554 [i]). **Fayette Co.:** Wolf River preserve, SE of La Grange and E side of Yager River, along dirt road on the N side of Wolf River, 19 Oct 2022, *M. Brock 4985* (APSC APSC0140155 [i]). **Franklin Co.:** Carter Mt. along gravel road 0.8 mi from Rowe Gap Church on Hwy. 16, Pitcher Ridge Quad., 1 Jul 1987, *R.L. Jones 5001* (TENN TENN-V-016352 [i]). **Giles Co.:** 0.25 mi N of Fall River Road on Mayfield Road, 14 Jun 1999, *D. Estes 00038* (VDB BRIT113021). **Grundy Co.:** by Tenn 56, 2 mi S Coalmont, 29 Sep 1971, *R. Kral 44544* (VDB BRIT113023). **Hardeman Co.:** Bolivar, 14 May 1920, *E.J. Palmer 17502* (VDB BRIT112995). **Hardin Co.:** S portion of Shiloh National Military Park, 21 Apr 1981, *R.L. Jones 3507* (VDB BRIT112977). **Henderson Co.:** Lexington, 20 May 1920, *E.J. Palmer 17573* (UMO 71094). **Henry Co.:** ca. 3 mi NW of Jones Mill on the farm of Robert Orr, 30 Mar 1974, *D.H. Webb s.n.* (VDB BRIT112978). **Hickman Co.:** ca. 12 mi SW of Centerville, ca. 2 mi NW of Hwy. 100, E side of Sulphur Creek Road, just S of camp proper on Church Camp property, 28 May 2003, *D. Estes 04697* (TENN TENN-V-016358 [i]). **Lawrence Co.:** U.S. 43, ca. 13 mi NNE Lawrenceburg, 27 Jun 1990, *R. Kral 77832* (VDB BRIT112996). **Lewis Co.:** Natchez Trace Parkway, ca. 3.5 mi N Meriwether Lewis Park Hq., 25 May 1970, *R. Kral 39138* (BRIT BRIT446378). **Madison Co.:** Jackson, May 1893, *S.M. Bain s.n.* (OS 175839 [i]). **McNairy Co.:** along creek N of Stanton Ville, 8 Jul 1947, *A.J. Sharp et al. 198* (TENN TENN-V-0169367 [i]). **Monroe Co.:** vicinity of the town of Coker Creek, 7.4 km N of the Polk County line on Tenn. Rte. 68, 18 May 1985, *E.W. Wood & D.E. Boufford 4798* (VDB BRIT113000). **Moore Co.:** 3.0 mi WSW Tullahoma by Tenn 55, 4 May 1971, *R. Kral 42510* (VDB BRIT113002). **Polk Co.:** Walkertown Branch, ca. 1 mi W of Ducktown, Ducktown Quad., 19 Apr 1980, *P. DE Priest 77* (NLU NLU0140996). **Putnam Co.:** by Tn 56, ca. 13 mi S of Gainesboro, 14 May 1992, *R. Kral 80446* (VDB BRIT113004). **Robertson Co.:** Cedar Hill Swamp, S of L & N Railroad, 31 May 1979, *E.W. Chester 4022* (APSC APSC0015415 [i]). **Sequatchie Co.:** White Oak Swamp Road, Smartt Mt. Quadrangle, 11 Jun 1987, *R.L. Jones 4892b* (VDB BRIT113005). **Stewart Co.:** Pine ridge W of Dover, 17 Oct 1941, *R.E. Shanks 1212* (TENN TENN-V-0169298 [i]). **Van Buren Co.:** under power lines, ca. 3 mi from Bellview Church on gravel road, Smartt Mt. Quad., 14 May 1989, *R. Jones 6071* (APSC APSC0102249 [i]). **Warren Co.:** E side of Morrison at jct. of Rte. 55 and Morrison Bypass between Rte. 55 and old railroad line, 2 Aug 1978, *P. Somers 1325* (VDB BRIT113007). **Wayne Co.:** Second Creek, ca. 2.2 mi S of Weatherford Road, 8 Jun 1994, *H.R. DeSelm s.n.* (TENN TENN-V-0169309 [i]). **White Co.:** N of Sparta, 18 Apr 1957, *A.J. Sharp 22084* (SMU BRIT446396). **TEXAS. Angelina Co.:** Angelina National Forest near Boykin Springs area, 8 Jun 1966, *S.W. Oetinger Jr. 542* (BRIT BRIT400497). **Bowie Co.:** near Texarkana, 27 Oct 1925, *E.J. Palmer 29394* (UMO 711101). **Cass Co.:** ca. 2 mi NE of McLeod on unnumbered road between Hwy. 125 and 77 at Clear Creek, 6 May 1979, *G.*

Majlisi 7309 (BRIT BRIT373018). **Harrison Co.:** W fork of Brandy Branch, N of Shreveport-Camden Road, NW of Rogers Lake, ca. 5.5 mi SE of Hallsville, 26 Apr 1977, *G. Ajilvsgi 4008* (BRIT BRIT373017). **Jasper Co.:** 13 mi N and ca. 2.5 mi E of Jasper, 4 Jun 1976, *B.L. Lipscomb 1767* (VDB BRIT234036). **Marion Co.:** Irish Bog, 6.58 mi NE of Jefferson, 25 May 2011, *W.C. Holmes et al. 15528* (BAYLU BAYLU015275 [i]). **Morris Co.:** ca. 300 m E of western edge of forest and trail head along S side of Rustling Leaves Trail at N end of Daingerfield State Park Lake, Daingerfield State Park, 6 May 2021, *P.W. Fritsch 2265* (BRIT BRIT792799). **Nacogdoches Co.:** ca. 4 m N of Farm to Market Road 1087 (Camp Tonkawa Road), ca. 4 mi E of TX-259, 6 May 2021, *P.W. Fritsch 2266* (BRIT BRIT792800). **Newton Co.:** ca. 4.5 mi SW of Newton, 19 Apr 1950, *V.L. Cory 57227* (SMU BRIT372727). **Rusk Co.:** Dogwood Creek just N of its jct. with Hwy. 322, 29 Mar 1985, *E S. Nixon 14605* (NLU NLU0140954). **Sabine Co.:** 4 mi ENE Milam, 18 Mar 1965, *R. Kral 23373* (VDB BRIT311261). **San Augustine Co.:** 15 mi SE of Zavalla near Boykin Spring Recreational Area, 20 May 1959, *F.W. Gould 8657* (SMU BRIT373023). **Shelby Co.:** 9.5 mi SW of Center, 22 May 1947, *R. McVaugh 8427* (SMU BRIT373022). **Tyler Co.:** ca. 44 m S of County Road 4777 (Red Oak Lane), ca. 55 m N of shore of Hyatt Lake, Watson Rare Native Plant Preserve, 7 May 2021, *P.W. Fritsch 2272* (BRIT BRIT792806). **VIRGINIA. Accomack Co.:** Island Nature Trail, SE of Hallie Whealton Smith Drive, 24 Apr 2022, *A.A. Crowl CY-483* (BRIT BRIT914458). **Alexandria City:** City of Alexandria, Dora Kelly Nature Park, upper E bank of the Chambliss tributary, 3 Oct 2015, *R.H. Simmons 4044* (AVCH AVCH-0001688 [i]). **Amelia Co.:** without specific locality, *J.B. Lewis 376* (NCU NCU00351051 [i]). **Appomattox Co.:** Appomattox-Buckingham State Forest, ca. 1.6 mi SE of Rose Bower, along a tributary of Fishpond Creek, 1.3 mi WNW of jct. Rtes. 626 and 640, 18 Jul 2019, *G.P. Fleming 17198* (GMUF GMUF-0042290). **Arlington Co.:** SE side of Arlington Run, ca. 0.15 km NW of the intersection of S Abingdon Street and S 5th Street, 20 May 2017, *R.H. Simmons 4259* (GMUF GMUF-0042741). **Augusta Co.:** ca. 2.5 mi SW Sherando, 29 Jul 1961, *R. Kral 11413* (SMU BRIT446353). **Brunswick Co.:** around Kennedy Bridge at Nottoway River on State 46, 21 Apr 1968, *F.C. James 13275* (WILLI 15945). **Buckingham Co.:** Lee Experimental Forest, Horsepen Creek 2.5 mi S of Headquarters, 21 Aug 1961, *E.L. Little Jr. 18741* (VDB BRIT311710). **Campbell Co.:** St. Rte. 643 ca. 5 mi N of Brookneal, 11 Apr 1977, *T.F. Wieboldt 276* (WILLI 25795). **Caroline Co.:** jct. Co. 676 and State 207, 28 Apr 1968, *F.C. James 13945* (WILLI 34311). **Charles City Co.:** near the end of Old Neck, property of the Penny family, NE of Mt. Airy, 29 Apr 1970, *D.M. Eggers Ware 2856* (WILLI 6254). **Charlotte Co.:** 1.7 mi W of Little Roanoke Creek on Va. 40 (E of Charlotte), 5 Sep 1965, *F.C. James 2672* (WILLI 34327). **Chesapeake City:** edge of Drummond near entrance to Portsmouth Ditch, 26 Mar 1973, *D.M. Eggers Ware 4565* (WILLI 15699). **Chesterfield Co.:** just E of jct. Co. 619 and U.S. 95 on Co. 619, 4 Jul 1966, *F.C. James 5110* (WILLI 37558). **Culpeper Co.:** end of Co. 619 (SE corner of Co.), 12 Sep 1965, *F.C. James 2835* (WILLI 37559). **Cumberland Co.:** 1.5 mi NE of jct. Co. 633 and State 45 on State 45 (SW of Cumberland), 6 Jul 1967, *F.C. James 7209* (WILLI 34322). **Dinwiddie Co.:** 0.3 mi W of Dinwiddie and Sussex Co. line on State 40, 18 Aug 1965, *F.C. James 2371* (WILLI 37555). **Essex Co.:** along Rte. 661 E of jct. of Rte. 637, near the Occupacia River, 6 Apr 1974, *T. Bradley 6375* (GMUF GMUF-0030499). **Fairfax Co.:** Campus of George Mason University, ca. 60 m E of Exploratory Hall, 6 Apr 2023, *P.W. Fritsch 2481* (BRIT BRIT914475). **Fauquier Co.:** head of Barton's Creek, in hollow between Bull Run Mountain and High Acre Ridge, 3.0 mi S of Hopewell Gap, 22 Apr 1989, *G.P. Fleming 3885* (WILLI 55747). **Floyd Co.:** Blue Ridge Parkway, Mile 155.7 R, 3 Sep 1977, *T. Govus 292* (WCUH WCUH0028174 [i]). **Fluvanna Co.:** edge of dirt road, 0.52 mi S of Rte. 629, 0.5 mi E of Rte. 631, 20 May 1976, *G.M. Diggs Jr. 1449-1* (NLU NLU0140988). **Franklin Co.:** Grassy Fork, NW flank of Turkeycock Mountain just below ford on St. Rte. 619, ca. 2.8 km SSE of Snow Creek, 18 Jun 1992, *T.F. Wieboldt 8135* (ODU ODU00021013 [i]). **Fredericksburg City:** 112 Braehead Drive, 2 Sep 1990, *H.J. Thompson s.n.* (MWCF MWCF-0001867 [i]). **Gloucester Co.:** 0.3 mi SE of jct. of State 216 and U.S. 17 on State 216, 5 Jul 1966, *F.C. James 4901* (WILLI 34310). **Goochland Co.:** powerline clearing along S side of U.S. 250, 0.2 mi SE of jct. with Rte. 629, 1.1 mi NE of Hadensville, 22 May 1993, *G.P. Fleming 7980* (GMUF GMUF-0030471). **Greene Co.:** along South River 1.5 mi NW of Burtonville, 23 Apr 1972, *T.F. Wieboldt 795* (WILLI 10916). **Greensville Co.:** 0.3 mi SW of jct. Co. 730 and Co. 622 on Co. 622, 23 Jun 1966, *F.C. James 4315* (WILLI 34324). **Halifax Co.:** ca. 0.5 km NW of Terry's Bridge, along floodplain of unnamed tributary of Banister River, ca. 3.2 km NNW of Five Forks, 9 Apr 1997, *J.C. Ludwig 3160* (GMUF GMUF-0030514). **Hampton City:** Langley Research and Development Park, 27 Apr 1992, *P. Baldwin 353* (WILLI 61027). **Hanover Co.:** 1.4 mi N of jct. Co. 623 and U.S. 1 on Co. 623, 26 Apr 1968, *F.C. James 13532* (WILLI 34320). **Henrico Co.:** Twin Hickory Recreation Area, Richmond, 30 Mar 2023, *P.W. Fritsch 2446* (BRIT BRIT914495). **Isle of Wight Co.:** 0.6 km N of Thomas Woods Trail (State Rte. 614) on a dirt service road, Blackwater Ecological Preserve, 8 Apr 2023, *P.W. Fritsch 2471* (BRIT BRIT914464). **James City Co.:** ca. 4 mi NW of Williamsburg, 24 Apr 1951, *B. Mikula 8324* (BRIT BRIT427879). **King and Queen Co.:** Heartquake Creek by bridge on U.S. 14, 22 Apr 1982, *A. Vascott 115* (BRIT BRIT427731). **King George Co.:** Caledon marsh, Caledon State Park near Owens, 12 Apr 1983, *D.M. Eggers Ware 8007* (VDB BRIT311715). **King William Co.:** 2.5 mi SE of jct. State 30 and Co 632 on State 30, 7 Jul 1966, *F.C. James 5434* (WILLI 34330). **Lancaster Co.:** at parking area for Hickory Hollow Natural Area Preserve, W side of Regina Road (State Rte. 604), 5 Apr 2023, *P.W. Fritsch 2480* (BRIT BRIT914476). **Louisa Co.:** along Rte. 648, 0.25 mi S of Rte. 33 jct., 28 Jun 1977, *S. Binns s.n.* (VCU VCU-0009529 [i]). **Lunenburg Co.:** Rte. 637, 1 mi S of Rte. 646, 20 May 1971, *J. Churchill s.n.* (SMU BRIT427770). **Madison Co.:** beside small tributary of the Robertson River, 1 mi S of Madison, 31 May 1971, *T.F. Wieboldt 382* (WILLI 9505). **Mathews Co.:** roadside, 2.0 mi S of North River Bridge on State Rte. 14, 8 Apr 1979, *M. van Montfrans 248* (BRIT BRIT446374). **Mecklenburg Co.:** near U.S. 58 on the farm of Mr. Henry J. and Henry W. Seaman, 7 Jul 1966, *W.D. Seaman 3164* (NCU NCU00351188 [i]). **Middlesex Co.:** E side of VA Rte. 619, 0.5 mi S of jct. with VA Rte. 33, near Locust Hill, 20 May 1981, *G. North 134* (BRIT BRIT446386). **New Kent Co.:** unmarked road not far from its jct. with Rte. 600 at Goddins Pond Dam, P.O. Barhamsville, 2 Apr 1975, *D. Soltis 726* (WILLI 18607). **Newport News City:** behind baseball diamond on Monroe Ave., Fort Eustis, 20 Mar 1973, *P.K. Appler 407* (WILLI 17054). **Northampton Co.:** Savage Neck Road, 0.6 km W of U.S. Hwy. 13, 24 Apr 2022, *A.A. Crowl CY-482* (BRIT BRIT914457). **Northumberland Co.:** 0.3 mi S of jct. Co. 679 and State 200 on State 200, 19 Jul 1966, *F.C. James 5870* (WILLI 26889). **Nottoway Co.:** Fort Pickett, N side of base in upper Tommaheton watershed, 2 May 2006, *D.A. DeBerry 886* (WILLI 79885). **Page Co.:** Sharman Hollow, junction of Darwin Lambert's property and Shenandoah National Park, 3 Jun 1978, *R.C. Simpson s.n.* (LFCC LFCC-0008155). **Petersburg City:** headwaters of Willcox Br., on S side of N&W RR tracks, a short distance N of dead end of Aleta Dr in Camelot Subdivision, S of Lee Park,

26 Sep 1998, *D.M. Eggers Ware 11585* (WILLI 80742 [i]). **Pittsylvania Co.:** ca. 3 mi E of Danville on U.S. 58 (vicinity of airport), 2 Oct 1965, *F.C. James 3249* (WILLI 34335). **Portsmouth City:** prope Portsmouth, May 1841, *F. Rugel s.n.* (VDB BRIT446601). **Powhatan Co.:** S side of Jones Creek, 0.5 mi W of Woodberry Pond, 28 Mar 1976, *C.M. Corcoran 96* (WILLI 26117). **Prince Edward Co.:** Rte. 625, 1.25 mi E of Appomattox County line, 18 Jul 1968, *G. Ramsey et al. 7866* (LYN LYN-0013630 [i]). **Prince George Co.:** 2.4 mi SE of Disputana on U.S. 460, 17 Jul 1966, *F.C. James 4027a* (NCU NCU00351195 [i]). **Prince William Co.:** ca. 0.25 mi E of Possum Point Road at pullover on Quantico Creek, ca. 1 mi SE of Rte. 1 in Dumfries, 18 May 1982, *R.L. Keyser 764* (WILLI 45026). **Richmond City:** along railroad tracks CSX/Southern between W.T. Center and Hollywood Cemetery, above Huguenot Bridge, 19 Jul 1986, *R.A.S. Wright 985* (VCU VCU-0009532 [i]). **Richmond Co.:** 2 mi NE of Tappahannock, 26 Jun 1950, *B. Mikula 5875-A* (BRIT BRIT446381). **Southampton Co.:** Assamoosick Swamp, S of Serbrell, 19 Jun 1939, *M.L. Fernald & B. Long 10377* (NY 02542678 [i]). **Spotsylvania Co.:** Alexander Berger Memorial Sanctuary, Rappahannock River 5 mi below Fredericksburg, 16 May 1965, *F.R. Fosberg 46106* (RSA RSA0184699 [i]). **Stafford Co.:** Crows Nest State Natural Area Preserve, between Accokeek and Potomac Creeks, ca. 0.1 mi E of preserve parking area and 1.4 mi NNW of Belle Plains, 6 Aug 2018, *G.P. Fleming 16682* (GMUF GMUF-0044504). **Suffolk City:** ca. 8 km S of Suffolk along Hosier Road, 23 Apr 2022, *A.A. Crowl CY-477* (BRIT BRIT914452). **Surry Co.:** near mouth of largest ravine containing tributary to Fish House Bay, N side of intake canal, VEPCO Surry Nuclear Power Station, E of Surry, 8 Mar 1974, *D.M. Eggers Ware 5187* (VDB BRIT311716). **Sussex Co.:** near Airfield Millpond, 15 Apr 1951, *B. Mikula 8281* (WILLI 16509). **Virginia Beach City:** First Landing State Park, 24 Apr 2022, *A.A. Crowl CY-479* (BRIT BRIT914454). **Westmoreland Co.:** 1 mi SW of Colonial Beach, 14 April 1951, *G. Edwin 306* (LL 00506693 [i]). **Williamsburg City:** College Woods, Strawberry Plains crossing, trailside, 13 April 2014, *C.D. Cyrus 126* (WILLI 81661). **York Co.:** Grafton Ponds Natural Area Preserve, 1 Apr 2023, *P.W. Fritsch 2462* (BRIT BRIT914444).

APPENDIX 4

Specimens examined of *Vaccinium fuscatum* with consistent stipitate-glandular trichomes on the abaxial surface of the leaf blades corresponding to *V. cuthbertii*.

U.S.A. GEORGIA. Chatham Co.: Wormsloe, 7601 Skidaway Road, Savannah, from park entrance, take dirt road SE toward Bell's Point ca. 0.5 mi, 21 Jul 2017, *R. Hattaway 6038* (GA GA264514). **Echols Co.:** 1 mi N of Mayday on U.S. 129, across from Norsworthy Farm, 11 Jul 1966, *W.R. Faircloth 3395* (GA GA059115). **Glynn Co.:** Hawkins Island, 19 Mar 1929, *G.A. Schulze 157* (GA GA059053). **Liberty Co.:** Fort Stewart Military Reservation, Training Area B3, red-cockaded woodpecker colony 106, S of hand grenade range, S of Small Arms Hotel firing range, 8 May 1992, *T.M. Zebryk 0229* (GA GA059061). **McIntosh Co.:** along the Altamaha River, about Fort Barrington, 26 Jun 895, *J.K. Small s.n.* (NY 02545581). **Richmond Co.:** 3 mi N of Augusta, 6 Apr 1930, *G.A. Schulze 593* (GA GA059112); edge of swamp of McBean Creek, ca. 1 mi NE of McBean, 26 Mar 1904, *R.M. Harper 2058* (NY 02542736). **Ware Co.:** N of Laura S Walker Lake, W of Hwy. 117 on Sam's Road (dirt road), 31.155403°, –82.219780°, 19 Apr 2022, *A.A. Crowl CY-455* (BRIT BRIT914403); Sam's Road, S side, ca. 100 m W of Laura Walker Road (Hwy. 177), ca. 0.9 mi due S of US 82, 31.15539°, –82.21976°, 42 m elev., 3 Apr 2024, *P.W. Fritsch 2557* (BRIT BRIT1058609, DUKE); Sam's Road, N side, ca. 100 m W of Laura Walker Road (Hwy. 177), ca. 0.9 mi due S of US 82, 31.15555°, –82.21991°, 41 m elev., 3 Mar 2025, *P.W. Fritsch 2623* (BRIT, DUKE); Sam's Road, S side, ca. 45 m W of Laura Walker Road (Hwy. 177), 31.15537°, –82.21923°, 42 m elev., 3 Mar 2025, *P.W. Fritsch 2624* (BRIT, DUKE); along S side Apple Drive, ca. 9 m E of Hwy. 177 (Laura Walker Road), 31.15542°, –82.21854°, 41 m elev., 3 Mar 2025, *P.W. Fritsch 2625* (BRIT, DUKE). **SOUTH CAROLINA. Aiken Co.:** Savannah River Plant, Red Hill Road, 21 Mar 1989, *N. Coile 4877* (GA GA261467); Aiken, Hitchcock Woods, 33.544869°, –81.730808°, 20 Apr 2022, *A.A. Crowl CY-462* (BRIT BRIT914407); Aiken State Park, 33.557408°, –81.490628°, 20 Apr 2022, *A.A. Crowl CY-464* (BRIT BRIT914410); Aiken Gopher Tortoise Heritage Preserve, 33.491118°, –81.438044°, 20 Apr 2022, *A.A. Crowl CY-465* (BRIT BRIT914530); Silver Bluff Audubon Center & Sanctuary, off the berm road to the cabin, 26 Mar 2011, *D.Z. Damrel 5488* (GA GA263592); Hitchcock Woods, ca. 120 m WSW of entrance at the end of Fermata Place SW, 33.54464°, –81.73127°, 144 m elev., 6 Apr 2024, *P.W. Fritsch 2574* (BRIT BRIT1058626, DUKE); ibid., *P.W. Fritsch 2575* (BRIT BRIT1058627, DUKE); ibid., *P.W. Fritsch 2576* (BRIT BRIT1058628, DUKE); Aiken State Park, along Jungle Nature Trail, ca. 90 m due W of Picnic Circle, ca. 0.57 mi due W of Hwy. 53 (State Park Road), 33.55798°, –81.49220°, 6 Apr 2024, *P.W. Fritsch 2578* (BRIT BRIT1058630, DUKE); Savannah River Plant in compartment 31 near Tyler Road along Tinker Creek, 28 Apr 2000, *A.B. Pittman 04280002* (GA GA201242); swamp at Quaker Spring near Martinez, 8 Apr 1930, *G.A. Schulze 594* (GA GA202327). **Charleston Co.:** Dungannon Heritage Preserve, 32.74899°, –80.19677°, 25 Mar 2021, *A.A. Crowl CY-350* (BRIT BRIT792829); S edge of Roxbury Park, N side of Little Britton Road across from Roxbury Mercantile Restaurant, 32.67598°, –80.34716°, 25 Mar 2021, *A.A. Crowl CY-353* (BRIT BRIT792832; but with semi-persistent leaves, new leaves entire; see text); ACE Basin Wildlife Refuge, E of State Road S-10-346; firebreak (Oak Ridge Road), 32.68572°, –80.39049°, 25 Mar 2021, *A.A. Crowl CY-356* (BRIT BRIT792835); Dungannon Heritage Preserve, 32.74899°, –80.19677°, 32.748985°, –80.196768°, 21 Apr 2022, *A.A. Crowl CY-469* (BRIT BRIT914467); by roadside, Caw Caw Swamp Road, Cottageville, SE E-8, 4 Mar 1944, *K.W. Hunt & F. Martin 2421a* (NY 02542735); ibid., *K.W. Hunt & F. Martin 2421b* (NY 0545540); by stream ¾ mi W of Rantowles, by R.R. Ravenels S. H-1, 3 Jun 1944, *K.W. Hunt 2611* (NY 02545439); Ernest F. Hollings ACE Basin National Wildlife Refuge, along S side of Oak Ridge Road Upper (Nature Trail), 0.13 mi E of State Road S-10-346 (Jehosee Island Road), 32.68567°, –80.38975°, 22 m elev., 5 Apr 2024, *P.W. Fritsch 2567* (BRIT BRIT1058619, DUKE). **Colleton Co.:** 4.76 mi SE of Ruffin, E edge of Big Hill Road, N of the Ruffin Road (SSR44) intersection, 32.97062°, –80.74465°, 25 Mar 2021, *A.A. Crowl CY-362* (BRIT BRIT792841); ibid., *A.A. Crowl CY-363* (BRIT BRIT792842); ibid., *A.A. Crowl CY-366* (BRIT BRIT792845); ca. 4 m E of Big Hill Road, along a furrow paralleling the road, ca. 100 NNW of State Road S-15-44 (Ruffin Road), 32.97061°, –80.74465°, 29 m elev., 5 Apr 2024, *P.W. Fritsch 2573* (BRIT BRIT1058625, DUKE). **Jasper Co.:** 5 mi W of Hardeeville, 30 May 1930, *G.A. Schulze 705* (GA GA202325).

ACKNOWLEDGMENTS

We thank the herbarium curators at BRIT (including NLU, SMU, and VDB), CHRB, EKY, GA, GMUF, MICH, MO, NY, ODU, UMO, WILLI, and WVA for access to physical specimens; Alain Belliveau for help with access to ACAD specimen images; Jovita Yesilyurt at BM for assistance relating to type material; Rachel Carmickle and Ashton Faulds for field work in New York and Pennsylvania for this project; Zach Bradford (Virginia Natural Heritage Program) and Anisa Khalid (University of Florida) for insights and field assistance; the staff of public and private lands and various colleagues regrettably too numerous to mention here for collecting permits, field assistance, and or sample material; and reviewers Anna Becker, James Ballington, and Jim Luteyn, for helpful comments on the manuscript. This research was supported by National Science Foundation grants DEB-2038213 and DEB-2038217.

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