VACCINIUM VIRGATUM (ERICACEAE): A SPECIES TO BE RECOGNIZED

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ABSTRACT

Since its original publication in 1789, *Vaccinium virgatum* has been treated by most authors as an accepted species in *V.* sect. *Cyanococcus*. In the latest comprehensive taxonomic treatment of the section, however, it is treated as a synonym of the broadly circumscribed species *V. corymbosum*. Here we use a combination of morphology, ploidy assessment with flow cytometry, and previously published phylogenomic analysis based on high-throughput DNA sequencing to support the taxonomic status of *V. virgatum* as a species to be recognized. As circumscribed here, *V. virgatum* occurs in the southeastern U.S. Coastal Plain from Arkansas, Texas, and southeastern Oklahoma to northeastern Florida and southeastern North Carolina. An updated taxonomic treatment of the species, including an expanded description, distribution map by county, and a representative list of specimens examined by county is included. We provide a means of distinguishing *V. virgatum* from *V. ashei*, a similar species recently also segregated from *V. corymbosum*, and from presumed rabbiteye blueberry escapes from cultivation, which can occur both within and outside the native range of *V. virgatum*. We designate a neotype for *V. virgatum* and lectotypes for *V. virgatum* vars. *angustifolium*, *parvifolium*, and *speciosum*.

RESUMEN

Desde su publicación original en 1789, *Vaccinium virgatum* ha sido tratada por la mayoría de los autores como una especie aceptada en *V.* sect. *Cyanococcus*. Sin embargo, en el último tratamiento taxonómico exhaustivo de la sección, se trata como sinónimo de la especie ampliamente circunscrita *V. corymbosum*. Aquí utilizamos una combinación de morfología, evaluación de la ploidía con citometría de flujo y un análisis filogenómico previamente publicado basado en secuenciación de ADN de alto rendimiento para apoyar el estatus taxonómico de *V. virgatum* como especie a reconocer. Tal como se circunscribe aquí, *V. virgatum* se da en la llanura costera del sureste de EE.UU., desde Arkansas, Texas y el sureste de Oklahoma hasta el noreste de Florida y el sureste de Carolina. Se incluye un tratamiento taxonómico actualizado de la especie, con una descripción ampliada, un mapa de distribución por condados y una lista representativa de especímenes examinados por condados. Proporcionamos un medio para distinguir *V. virgatum* de *V. ashei,* una especie similar recientemente segregada también de *V. corymbosum,* y de los presuntos escapes de cultivo de arándano rabbitye, que pueden darse tanto dentro como fuera del área de distribución nativa de *V. virgatum*. Designamos un neotipo para *V. virgatum* y lectotipos para *V. virgatum* vars. *angustifolium*, *parvifolium* y *speciosum*.

Key Words: blueberries, U.S. Coastal Plain, Southeastern United States, *Vaccinium* sect. *Cyanococcus*

INTRODUCTION

Vaccinium virgatum Aiton (*V.* sect. *Cyanococcus* A. Gray) was published as a species new to science in William Aiton's *Hortus Kewensis* (Aiton 1789). It is well established as placed within *V.* sect. *Cyanococcus* by the combination of eruptive periderm, raised stem stomata, dimorphic vegetative vs. floral buds, an articulation between the pedicel and hypanthium, an absence of anther spurs, and a pseudo-10-locular ovary (Vander Kloet 1983; Fritsch et al. 2024). Individuals with the morphology of this species group within the rest of *V.* sect. *Cyanococcus* in a phylogenetic analysis based on high-throughput DNA sequence data (Weakley et al. 2024).

In the first comprehensive treatment of *Vaccinium* sect. *Cyanococcus*, Camp (1945) treated *Vaccinium virgatum* as a species occurring from "?South Carolina, Georgia, Alabama, and northern Florida, west to

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Texas and Arkansas." Camp considered it to be a tetraploid ($2n = 4x = 48$), presumably on the sole chromosome count attributed to this species based on a sample from Summerton, South Carolina "Halfhigh (3′), glandular, black fruit" (Darrow et al. 1944). Camp (1945) considered *V. amoenum* Aiton, published on the same page as *V. virgatum* in *Hortus Kewensis* (Aiton 1789), to be a hexaploid ($2n = 6x = 72$). This was also apparently based on a single chromosome count of an individual from Ogeechee River Valley, Georgia "Highbush, suckering freely on dry land" (Darrow et al. 1944). Camp (1945) considered *V. amoenum* to range from "South Carolina to northern Florida, west to Texas and Arkansas," thus strongly overlapping in distribution with *V. virgatum*. Camp considered both species to have consistently and regularly spaced minute stipitate glands on the abaxial surface of the leaf blades, and Camp used this character as the fundamental basis with which to distinguish them from most other species in the section. Camp used metric characters to distinguish *V. virgatum* from *V. amoenum*, i.e., plants 0.5–1 m tall (versus 1.5–2.5 m tall), leaves 3–4.5 cm long (versus 4–5 cm long), and corolla 6–9 mm long (versus 9–12 mm long). Camp used the same metric characters to distinguish these two species from another species in the section with consistent and regularly spaced minute stipitate glands on the abaxial surface of the leaf blades, the diploid ($2n = 2x = 24$) *V. tenellum* Aiton (plants 0.15–0.4 m tall, leaves 2–3.5 cm long, corolla 4–6 cm long). Camp hypothesized that these three species form an autopolyploid series.

In the only other comprehensive taxonomic treatment of the section, Vander Kloet (1983, 1988) rejected many of the species concepts of Camp. In particular, Vander Kloet synonymized many of Camp's "highbush blueberry" species of the section (i.e., all species purportedly > 1 m tall) into a highly variable concept of *Vaccinium corymbosum* L. This species was considered to have arisen through multiple evolutionary origins via hybridization and introgression with the various diploids of the section, comprising diploids, tetraploids, and hexaploids. Vander Kloet placed 12 of Camp's species in synonymy under *V. corymbosum*, including both *V. amoenum* and *V. virgatum*, with *V. tenellum* remaining as distinct. Vander Kloet's treatment of *V.* sect. *Cyanococcus* has remained the standard for the section up to the present time, mainly because it forms the basis of the treatment in the widely used *Flora of North America* (Vander Kloet 2009).

Relevant regional floristic and horticultural works published at about the same time or later than the treatment of Vander Kloet have, on the whole, tended to treat *Vaccinium virgatum* as distinct from *V. corymbosum*. In a treatment of *Vaccinium* for Florida, Ward (1974) recognized both *V. amoenum* and *V. virgatum* as species (although excluding *V. virgatum* from Florida), differentiating the two by the larger habit, leaves, and flowers of *V. amoenum*, as in Camp (1945), but also by inflorescences that are limited to no more than two or three successive axils per branchlet (versus small paniculate clusters in the axils of many successive leaves per branchlet) that are more widely separated from each other. In a treatment of *Vaccinium* for Virginia, Uttal (1987a) recognized *V. virgatum* (but considered it not to occur in Virginia), placing *V. amoenum* and *V. ashei* J.M.Reade, another hexaploid from the southeastern U.S. Coastal Plain, in synonymy. Weakley and Southeastern Flora Team (2023) followed the treatment of Uttal. In the horticultural literature, the name *V. ashei* is usually used for rabbiteye blueberry cultivars because this was the species from which these cultivars originated, although the genomes of more recently developed cultivars contain some proportion of other species of the section. The status of the name *V. virgatum* as used in horticulture is either placed in synonymy under *V. ashei* (e.g., Lyrene et al. 2003; Song & Hancock 2011) or unresolved (Luby et al. 1991).

Recent studies based on a combination of data from morphology, phylogenomics, and flow cytometry have begun to reassess the treatment of Vander Kloet. From these data, several species have been resurrected from Vander Kloet's concept of *Vaccinium corymbosum*, i.e., *V. ashei*, *V. altomontanum* Ashe (possibly = *V. constablei* A. Gray, the nomenclature of which to be resolved, Manos et al. in prep.), *V. elliottii* Chapm., and *V. simulatum* Small (Crowl et al. 2022; Fritsch et al. 2024; Weakley et al. 2024; Franck & Salman 2024; Manos et al. in prep.). Here, we assess the taxonomic status of *Vaccinium virgatum* based on morphology, flow cytometry, and previously published phylogenomic data (Weakley et al. 2024). We conclude that, like the other species of "highbush blueberry" recently resurrected as species, *V. virgatum* is taxonomically distinct from *V. corymbosum* and the other species of the section. Thus, we treat it as an accepted species, i.e., one to be recognized. We include an updated morphological description of the species, full synonymy, a county-level distribution map, and a

representative list of specimens cited. We also neotypify *V. virgatum* and provide lectotypes for *V. virgatum* vars. *angustifolium* P. Watson, *parvifolium* A. Gray, and *speciosum* E.J. Palmer.

MATERIALS AND METHODS

Specimens from the following herbaria were examined in-hand: BRIT, DUKE, GA, IBE, MO, NLU, NY, SMU, and VDB. The data from these specimens were supplemented with our own field observations throughout the southeastern U.S. Coastal Plain. Specimens from the following herbaria were examined online via the SERNEC data portal (https://sernecportal.org/portal): A, BM, CLEMS, EKY, FLAS, FMUH, G-DC, GH, LSU, MISS, MISSA, MMNS, NCSC, NCU, NO, RSA, STAR, UARK, UNCC, and USCH. Citations for these specimens are followed by an asterisk to indicate that they were examined through images only.

The species distribution map was resolved to the county level, with one specimen cited per county (Appendix 1). Most of the specimens as the basis of the map were examined in hand. To generate the portion of the map based on digital images, we searched for records with an identification of *Vaccinium virgatum*. Therefore, some counties in which *V. virgatum* occur might not be represented on our map because the specimen(s) of *V. virgatum* in that county are currently misidentified. For some online images of specimens identified in the portal as *V. virgatum*, it was difficult to discern the characters needed for accurate species identification; these specimens were not used for the map.

The morphological description of *Vaccinium virgatum* herein is based on our fieldwork and herbarium research. The format of the description generally follows that of Weakley et al. (2024). The specimens examined by us formed the dried-specimen basis of the description. These consist of the specimens cited in Appendix 1 as well as many hundreds more from the herbaria cited above. *Vaccinium virgatum* was compared to other species in *V.* sect. *Cyanococcus*, especially those possessing stipitate glands on the abaxial surface of the leaves.

Flow cytometry analysis.—The methods for flow cytometry generally followed those in Crowl et al. (2022) and Weakley et al. (2024) except that individuals were analyzed for flow cytometry at either North Carolina State University, Mountain Horticultural Crops Research & Extension Center, Mills River, NC or Plant Cytometry Services, Didam, Netherlands. We sampled numerous individuals of *Vaccinium* sect. *Cyanococcus* from natural populations for flow cytometry analysis (P.S. Manos et al. unpubl. data), including nine conforming to our concept of *V. virgatum*. The latter were sampled from natural areas in Georgia, Louisiana, South Carolina, and Texas (Appendix 2).

Phylogenetic analysis.—To assess the phylogenetic placement of *Vaccinium virgatum* within *V.* sect. *Cyanococcus*, we used the previously generated molecular phylogenomic methods and analysis of the *V. ashei* section of Weakley et al. (2024), as briefly summarized here. The DNA sequence dataset was based on the Angiosperms353 v1 target capture kit (Johnson et al. 2019), individual genes were aligned with MAFFT v7.245 (Katoh & Standley 2013), and phylogenetic analysis was performed with IQ-TREE (v1.6.9; Nguyen et al. 2015). A partitioned maximum-likelihood analysis was performed with gene partitions inferred from PartitionFinder (Lanfear et al. 2014), and 1000 ultrafast bootstrap replicates were used to assess topological support. The final DNA alignment file is available from the Dryad Digital Repository: doi:10.5061/dryad.18931zd5w.

RESULTS AND DISCUSSION

All nine samples of *Vaccinium virgatum* sampled for the analysis of flow cytometry are hexaploids. Other ploidal levels recovered for sampled *V.* sect. *Cyanococcus* taxa are indicated in Fig. 1. Prior phylogenomic analysis of *V.* sect. *Cyanococcus* yielded a monophyletic group formed by the samples of *V. virgatum*. This clade was distinct from the samples of *V. altomontanum* and *V. ashei*, the only other hexaploid species known in the section (Weakley et al. 2024; Fig. 1). Manos et al. (in prep.) provide strong evidence that *V. altomontanum* is a species distinct from both *V. ashei* and *V. virgatum*. Thus, the data from flow cytometry and phylogenomic analysis warrant both the removal of *V. virgatum* out of the synonymy of *V. corymbosum* sensu Vander Kloet (1983,

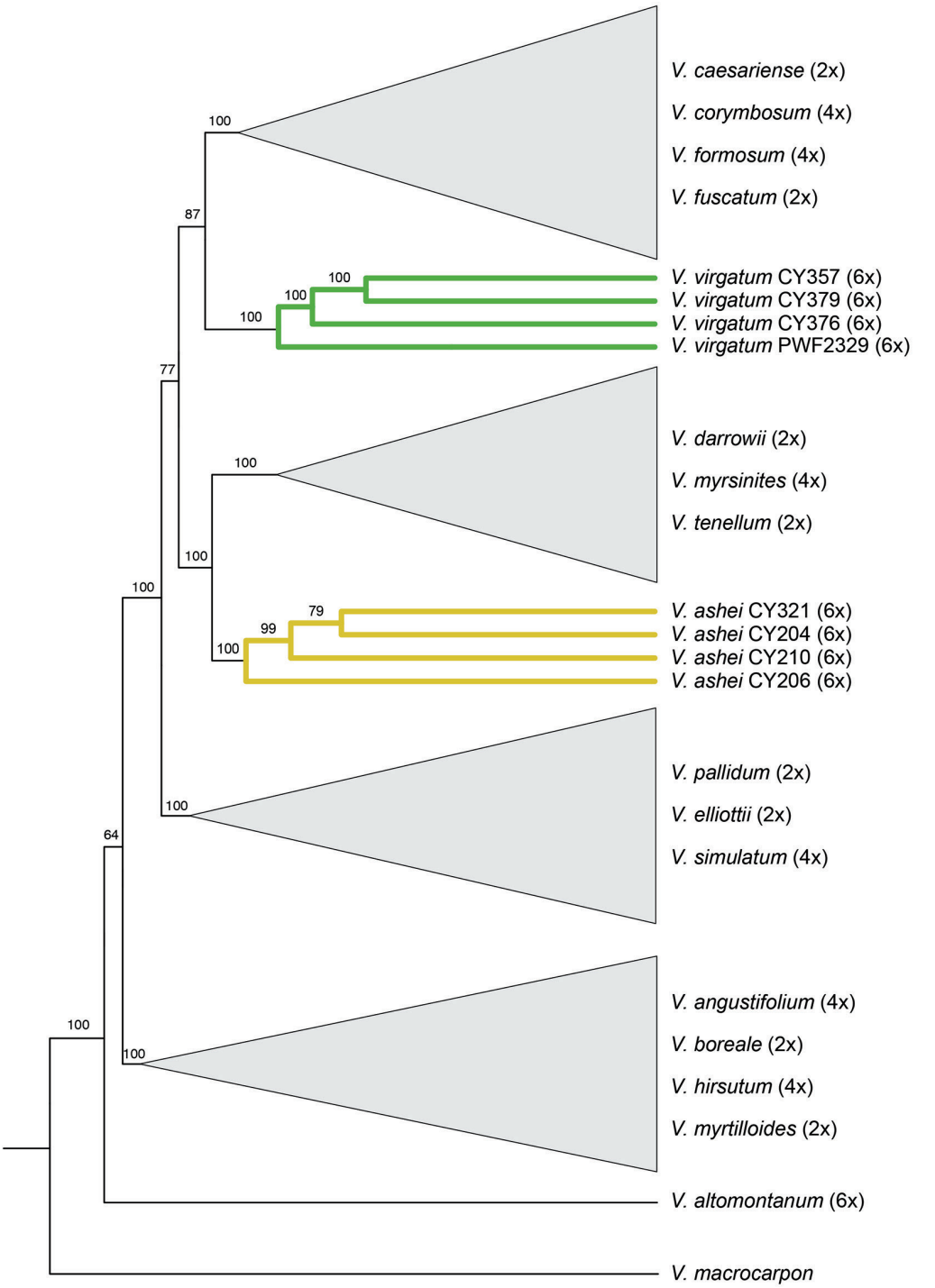

Fig. 1. Summary tree from a maximum-likelihood analysis of *Vaccinium* sect. *Cyanococcus* with multiple samples of *V. virgatum* (clade in green) and *V. ashei* (clade in yellow) to assess the taxonomic distinctness of these species. Numbers above branches indicate bootstrap support values. Clades containing taxa which are not the focus of this study have been collapsed. Ploidy is indicated next to each sample/taxon. Reproduced from Weakley et al. (2024).

1988, 2009) and its recognition as a distinct species. In the Taxonomic Treatment section below, we provide further evidence supporting its recognition as a species with morphological data.

Despite the shared presence of consistent and regularly distributed stipitate-glandular trichomes on the abaxial surface of the leaf blades in both *Vaccinium ashei* and *V. virgatum*, they do not group together (Weakley et al. 2024). The least-inclusive clade that includes both of these species also includes *V. darrowii* Camp, *V. myrsinites* Lam., *V. tenellum*, and the "residual highbush" clade of *V. caesariense* Mack., *V. corymbosum* L., *V. formosum* Andrews, and *V. fuscatum* Aiton. Both *V. myrsinites* and *V. tenellum* have consistent and regularly distributed stipitate-glandular trichomes on the abaxial surface of the leaf blades. *Vaccinium darrowii* and the "residual highbush" clade are considered not to possess such glands, although the "residual highbush" clade has them sporadically, e.g., in samplings and sucker branchlets, and *V. darrowii* may also occasionally produce them (P.W. Fritsch, pers. obs.). Thus, the presence of glands in these species could be synapomorphic for this least-inclusive clade, with losses in *V. darrowii* and the "residual highbush" clade. Both *V. myrsinites* and *V. tenellum* have clavate- to ellipsoid-headed stipitate abaxial glands, unlike the globose- or at most obovoid-headed stipitate abaxial glands of *V. ashei* and *V. virgatum*. This gland morphology could be a synapomorphy for their least-inclusive clade, with a loss of the glands in *V. darrowii*.

The lack of detection of tetraploid *Vaccinium virgatum* in our samples across Camp's (1945) stated geographic range of this species suggests that Camp's concept of this taxon at the tetraploid level is erroneous. If a naturally occurring tetraploid version of *V. virgatum* was in fact documented by Darrow et al. (1944) from South Carolina, it has not been rediscovered since, in which case it could be rare or extinct in South Carolina and vicinity. Because we have found no vouchers from the study of Darrow, we cannot assess the morphology of the original sample or how it might differ from hexaploid *V. virgatum*. Camp's metric character differences appear to be unreliable, with morphology varying continuously and without correlated gaps in character states throughout the geographic distribution of *V. virgatum* in our sense of the species (but see below).

As shown in the key of Weakley et al. (2024), *Vaccinium virgatum* can be distinguished from the other species in the section that possess consistent and regularly produced stipitate-glandular trichomes on the abaxial leaf surface by the following combination of characters: plants 0.3–2.5 m tall; leaf blades chartaceous, abaxial surface *in situ* green to pale green, with stipitate glands on the abaxial leaf surface usually moderately dense and bearing obovoid to globose heads, and with eglandular trichomes 0.44–1.02 mm long; hypanthium without glaucescence; and fruits 4–11 mm in diameter. See also Weakley et al. (2024) for characters distinguishing *V. virgatum* from *V. ashei*. Other characters that can aid in distinguishing *V. virgatum* from the other species of the section include a deciduous or rarely semi-evergreen habit, current-year branchlets consistently puberulent, vegetative bud scales short (1.1–2.4 mm long), leaf blade surface abaxially (as well as adaxially) more or less shiny *in situ*, eglandular trichomes present on the abaxial surface of the leaf blade at least on the midvein, leaf blade margins consistently (stipitate-glandular-) serrulate, inflorescences often borne at many contiguous nodes along elongate or virgate shoots, hypanthium without stipitate glands, corollas 5.5–11 mm long, styles exserted from the corolla, and fruits non-glaucescent.

As noted for *Vaccinium ashei* by Weakley et al. (2024), it is likely that cultigens of rabbiteye blueberry have escaped into natural habitats. These appear similar to *V. ashei* or *V. virgatum* but occur well outside the presumed native range of *V. ashei* (U.S. East Gulf Coastal Plain extending eastward to Charlton Co , Georgia and Duval County, Florida) and occasionally outside the native range of *V. virgatum* (see below). The putative escapes have stipitate-glandular trichomes on the abaxial surface of the leaf blades, as in *V. virgatum* and *V. ashei*, but unlike these species usually lack eglandular trichomes there. Such plants can also be distinguished from those of native *V. virgatum* by their bluish green and glaucous leaf blade surfaces (versus green to pale green and shiny). Moreover, they will not have the inflorescences borne at many contiguous nodes along elongate or virgate shoots, as is occasionally seen in *V. virgatum*, and the fruits will be larger and often with glaucescence.

Camp (1945) considered the species with consistent and regularly produced stipitate glands on the abaxial leaf blade of *Vaccinium* sect. *Cyanococcus* to comprise an autoploid lineage, with *V. tenellum* as the

diploid, *V. virgatum* as the tetraploid, *V. amoenum* as the hexaploid, and with *V. myrsinites* Lam. as an allotetraploid hybrid species between *V. darrowii* and *V. tenellum*. From our data and observations, we find little evidence for the autoploid line hypothesis of Camp. Firstly, *V. tenellum* and *V. virgatum* are each part of distinct clades. Secondly, *V. tenellum* has a different type of stipitate leaf gland, with heads that are clavate to ellipsoid versus globose to obovoid in *V. virgatum* (Fritsch et al. 2024). Thus, although these different gland types could be homologous and thus could have evolved from globose-headed to clavate-headed along the autoploid lineage, they could also be homoplasious, with the different gland type having evolved independently. Thirdly, we did not detect a ploidy difference between plants that might be considered *V. amoenum* versus *V. virgatum*. Camp (1945) provided no indication that he had seen the nomenclatural types of either of these taxa. His assumption that the type of *V. virgatum* was a tetraploid seems arbitrary and, to us, the type of *V. amoenum* is consistent with the common hexaploid treated here. The distinction based on inflorescence number and placement between the two species indicated by Ward (1974) is also not supported. We suspect that the perceived differences were based on variation of this character in the species and inconsistent presence on herbarium specimens.

Although the basis for considering *Vaccinium virgatum* to be a tetraploid is tenuous at best, we may have found evidence for a diploid-tetraploid-hexaploid line corresponding to the morphology of *V. virgatum* that could help to elucidate its evolutionary origins. The collection of *P.W. Fritsch 2561* [north end of the Okefenokee Swamp, Ware County, Georgia, 3 Apr 2024 (BRIT, DUKE)] has the same type of globose-headed stipitate glands on the abaxial leaf surface as found in *V. virgatum* but the leaves are smaller; results from flow cytometry indicate that it is a tetraploid. This might corroborate the report in Darrow et al. (1944) of a stipitate-glandular tetraploid from Summerton, South Carolina, although Darrow et al. did not indicate whether the samples were collected from wild-collected or greenhouse plants. Further, our sample *A.A. Crowl CY-218* (BRIT; Moses Creek Conservation Area, St. Augustine County, Florida, 7 April 2019), also with globose-headed stipitate glands on the abaxial leaf surface but with a stature < 1 m tall and with leaves more the size of *V. tenellum*, was found with flow cytometry to be diploid. However, the specimen appears not to be *V. tenellum* because the stipitate glands are globose-headed rather than ellipsoid to clavate, and *V. tenellum* is considered not to occur in Florida (Ward 1974). Whether these plants represent the diploid and tetraploid progenitors of hexaploid *V. virgatum* must await corroborating evidence based on more data. From our preliminary data, a search for putative diploids and tetraploid progenitors of *V. virgatum* might likely be most productive in the far southeastern Atlantic Coastal Plain of east-central South Carolina, eastern Georgia, and northeastern Florida.

Vander Kloet (1983, 1988) considered *Vaccinium virgatum* to be a part of a complex "highbush blueberry" group (*V. corymbosum* s.l.) comprising diploids, tetraploids, and hexaploids with continual introgression from "lowbush" diploid species in areas of geographic overlap. At least in the case of *V. virgatum*, results from our phylogenomic analysis, field observations, and herbarium studies do not support this view. The samples of *V. virgatum* form a monophyletic group, and individuals are readily identifiable in the field and the herbarium. Our view had already been suggested by other authors, e.g., Ward (1974), Uttal (1987a), Luby et al. (1991), and Weakley & Southeastern Flora Team (2023) based on morphological observations. Strong evidence has also been compiled for the taxonomic distinctness of *V. altomontanum*, *V. elliottii*, and *V. simulatum* from *V. corymbosum* (Fritsch et al. 2024; Franck & Salman 2024; Manos et al. in prep.). Both Camp (1945) and Vander Kloet (1983, 1988) considered natural hybridization to be rampant in the section, but other authors have thought it much less frequent than these authors asserted (Ward 1974; Uttal 1987; Weakley & Southeastern Flora Team 2023). Evidence for any naturally occurring hybridization has so far been anecdotal rather than shown with hard (i.e., molecular) evidence and this aspect of the group needs a specific focus.

TAXONOMIC TREATMENT OF *VACCINIUM VIRGATUM*

Vaccinium virgatum Aiton, Hort. Kew. [W. Aiton] 2:12. 1789. (**Figs. 2–5**). *Vaccinium corymbosum* var. *virgatum* (Aiton) G.Don, Gen. Hist. 3:854. 1834. *Cyanococcus virgatus* (Aiton) Small, Man. S.E. Fl. [Small], 1014. 1933. Type: not designated. "Nat. of North America. Mr. William Young. Introd. 1770." [protologue]. ("probably Georgia" [Camp 1945]). **Neotype, designated here:** U.S.A. Georgia. Charlton County: Okefenokee National Wildlife Refuge, Stephen C Foster State Park, along boardwalk, 30.82819°, –82.36532°, 27 Mar 2021, *A.A. Crowl CY-374* (BRIT BRIT792851!).

Vaccinium amoenum Aiton, Hort. Kew. [W. Aiton] 2:12. 1789. *Vaccinium corymbosum* var. *amoenum* (Aiton) A. Gray, Manual [Gray], ed. 2, 250. 1856. *Cyanococcus amoenus* (Aiton) Small, Man. S.E. Fl. [Small], 1014. 1933. Type: "Mr. John Cree. Introd. 1765." [protologue], Hort. Kew – 74, Introduced by John Cree [specimen] (holotype: BM BM001125627*).

Vaccinium virgatum var. *angustifolium* P. Watson, Dendrol. Brit. 1, tab. 34. 1825. Type: NORTH AMERICA: Messrs Whitley and Co's., Fulham [protologue] (holotype: HUL, destroyed; **lectotype, designated here:** G-DC (G00322793*).

Vaccinium virgatum var. *speciosum* E.J. Palmer, J. Arnold Arbor. 7:133. 1926. Type: U.S.A. Arkansas. Garland Co.: rocky open banks along Gulpha Creek, near High Point, 25 Apr 1924, *E.J. Palmer 24548* (**lectotype, designated here:** MO 6500883!; isolectotype: A 00015937*).

Vaccinium amoenum and *V. virgatum* were published on the same page in Aiton (1789). Rehder (1940), the first to synonymize *V. amoenum* and *V. virgatum* as far as we know, used the name *V. virgatum* for the species. Thus, in accordance with *International Code of Nomenclature for Algae, Fungi, and Plants* (Turland et al. 2018) Art. 11.5, if *V. virgatum* and *V. amoenum* are synonymized, as in our treatment, then *V. virgatum* is the accepted name. This is also reflected in the comment of Uttal (1987b: p. 294).

No original material of *Vaccinium virgatum* has been determined or located. Nearly all types of the first edition of *Hortus Kewensis* (Aiton 1789) are at BM (Stafleu 1976). Despite an extensive search, no original material on which *V. virgatum* could be based has been found at BM (J. Yesilyurt, Senior Curator in Charge, pers. comm.). We assume that the original material of *V. virgatum*, if it ever existed, is now lost. As such, we have selected the specimen *A.A. Crowl CY-374* (BRIT BRIT792851) as neotype. We chose this specimen because it is from the probable type location (Georgia), has excellently preserved flowers, and matches both the original description of *V. virgatum* as well as the one provided below (Fig. 2).

Type material of *Vaccinium virgatum* var. *angustifolium* was presumably at HUL, but this herbarium was destroyed in June 1943 (Stafleu & Cowan 1988). Dunal (1839) indicated that he saw a specimen of this taxon in the De Candolle herbarium. The image of the G-DC specimen on JSTOR Global Plants (https://plants.jstor.org) has two labels: "*Vaccinium* affine" with "Kew" below this, and "*angustifolium*" added in different ink and handwriting; and "*Vaccinium virgatum angustifolium* Wats. Dend. brit. 34." The characters of the specimen on the sheet are consistent with those mentioned in the original illustration, which confirms that the G-DC sheet is likely part of the type material. The description in the protologue mentions leaves abaxially "glab. strewed with brown, minute, pedicelled glands," and these are visible on the JSTOR Global Plants image of the type. The illustration on the plate shows flowers without styles exserted from the corolla, unlike the flowers of *V. virgatum* and exclusive to those of *V. elliottii* in *V.* sect. *Cyanococcus*. However, this is likely a mere omission in the illustration because stigmas are apparent as just outside the throat in several corollas on the G-DC sheet, thus confirming an identification of *V. virgatum*. We designate this specimen as the lectotype of *V. virgatum* var. *angustifolium*; it is the only other element of the type material known to us.

Two gatherings were cited in the protologue of *Vaccinium virgatum* var. *speciosum*, one in flower (*E.J. Palmer 24548*), the other in fruit (*E.J. Palmer 27127*; "37127" in protologue, presumed here to be a typographical error because the date of the collection in the protologue is the same as that on the specimen label). For each of these collections, we know of four specimens: 25 April 1924, *E.J. Palmer 24548*, MO 650883! and A 00015937*, and 10 May 2025, *E.J. Palmer 27127*, MO 6500884! and A 00015936*, respectively. These are all syntypes. We selected *E.J. Palmer 24548* as the lectotype because we consider flowers of *V. virgatum* to be a more informative taxonomic character than fruits in *V.* sect. *Cyanococcus*. No herbaria housing the specimens cited were indicated in the protologue; we selected the MO specimen as the lectotype because P.W.F. has seen the physical specimen.

Fig. 2. Neotype of *Vaccinium virgatum*, A.A. Crowl CY-374 (BRIT BRIT792851).

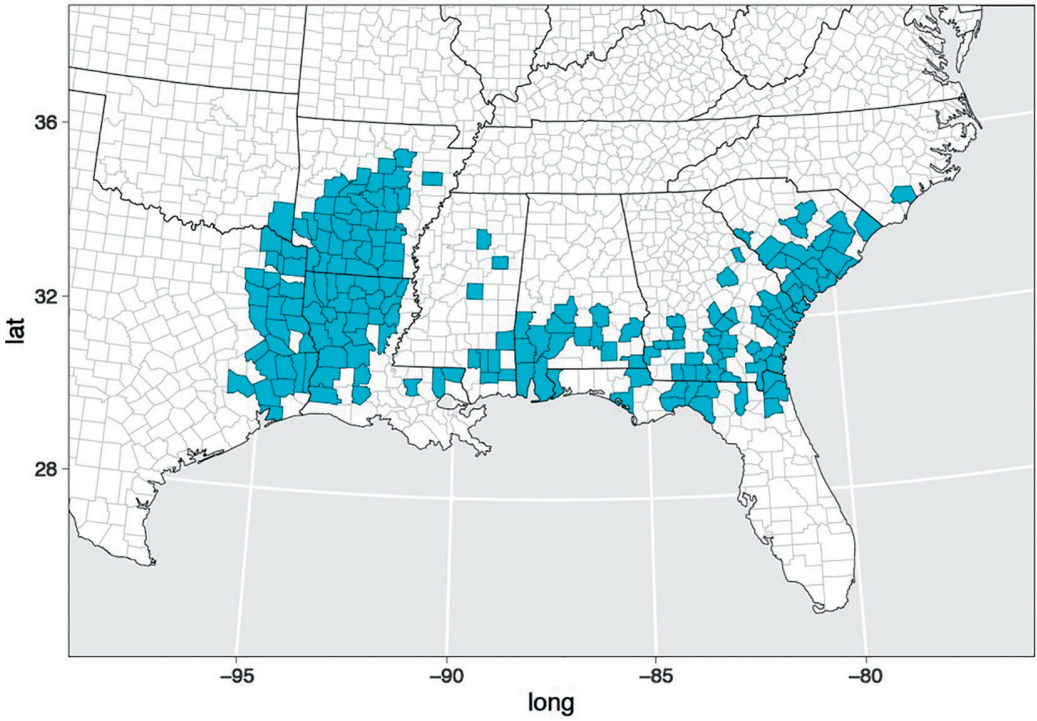

Fig. 3. Geographic distribution of *Vaccinium virgatum* with resolution to the level of county.

Description.—Shrubs, deciduous or occasionally semi-evergreen, clumped and multi-stemmed or clonal, often somewhat sprawling, 0.3–2.5 m tall. Branchlets *in situ* green until ca. third or fourth year, older branchlets gray to brown, with raised stem stomata; eruptive periderm common on third-year and older branchlets. Current-year branchlets without or rarely with sparse stipitate-glandular trichomes, with white eglandular trichomes ± in 2 to several lines or occasionally throughout, generally curved, up to 0.24–0.72 mm long; second-year branchlets glabrous or with white eglandular trichomes ± in narrow to broad lines or throughout, usually not broken; outer vegetative bud scales 1.1–2.4 mm long, glabrous or occasionally with white eglandular trichomes. Leaves with petiole 0.3–2.0(–3.0) mm long, sulcate and/or margins narrowly winged to base, abaxially and adaxially with white eglandular trichomes; leaf blade narrowly to broadly oblanceolate, less often elliptic to broadly so or obovate, often slightly rhombic, 2.8–7.2 × 0.9–3.4 cm, chartaceous, abaxial surface *in situ* green to pale green, shiny, *in sicco* often pale to tan-brown, with white erect straight to ± curved eglandular trichomes (largest trichomes on each individual 0.44–1.02 mm long, borne from base of midvein to apex or nearly so, often also on secondary veins and occasionally on surface, variously becoming less prevalent with age), with ± evenly scattered moderately dense stipitate-glandular trichomes on veins and surface (largest on each individual 0.12–0.40 mm long, stipes usually not notably flattened, not notably flanged proximally, gland-heads creamy white, orangish, reddish, or black, globose to obovoid), adaxial surface *in situ* green, *in sicco* green to brown, with ascending to erect ± curved white eglandular trichomes along midvein, without stipitate-glandular trichomes, base narrowly to broadly cuneate, margins serrulate with each tooth tipped by a stipitate gland, with sparse to dense white eglandular trichomes at least proximally, narrowly revolute or occasionally planar, tapering into petiole, apex (obtuse to) acute to slightly acuminate, sessile marginal glands present, 0.05–0.14 mm wide (width parallel to margin) or occasionally absent and then margin stipitate-glandular to base, marginal teeth (not including stipitate gland) oriented

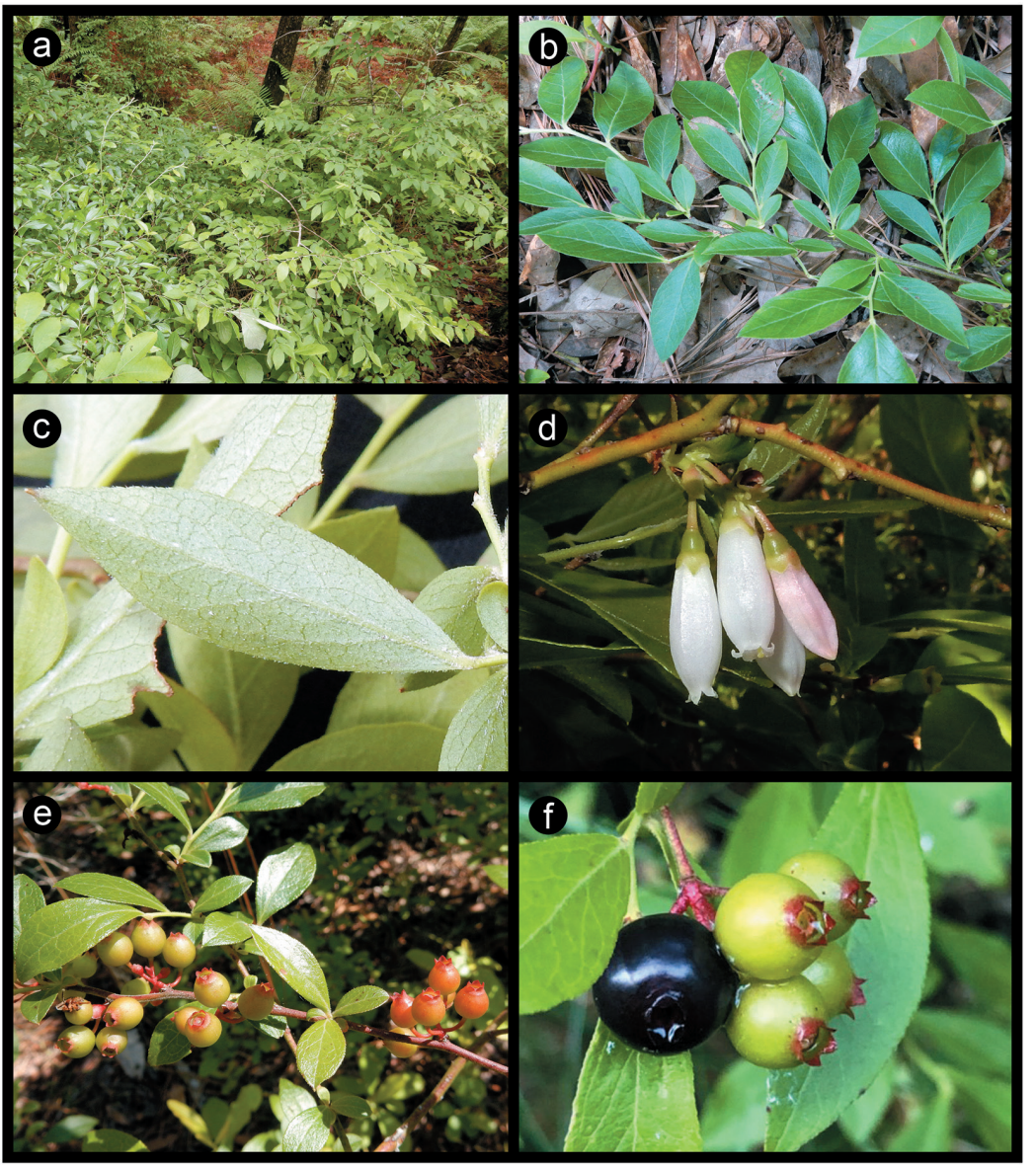

Fig. 4. *Vaccinium virgatum*. **a.** typical sprawling habit; b. branchlets and adaxial surfaces of leaves; c. abaxial surface of leaf with typical eglandular trichomes, and stipitate-glandular trichomes visible as stubs; d. inflorescence; e. immature fruit; f. immature fruit and one mature (shiny, black) fruit. [Photos, a–e, by PWF, f by odobenine at https://www.inaturalist.org/observations/166707456; a, P.W. Fritsch 2352; b, P.W. Fritsch 2329; c, P.W. Fritsch 2344; d, P.W. Fritsch 2571; e, P.W. Fritsch 2370.

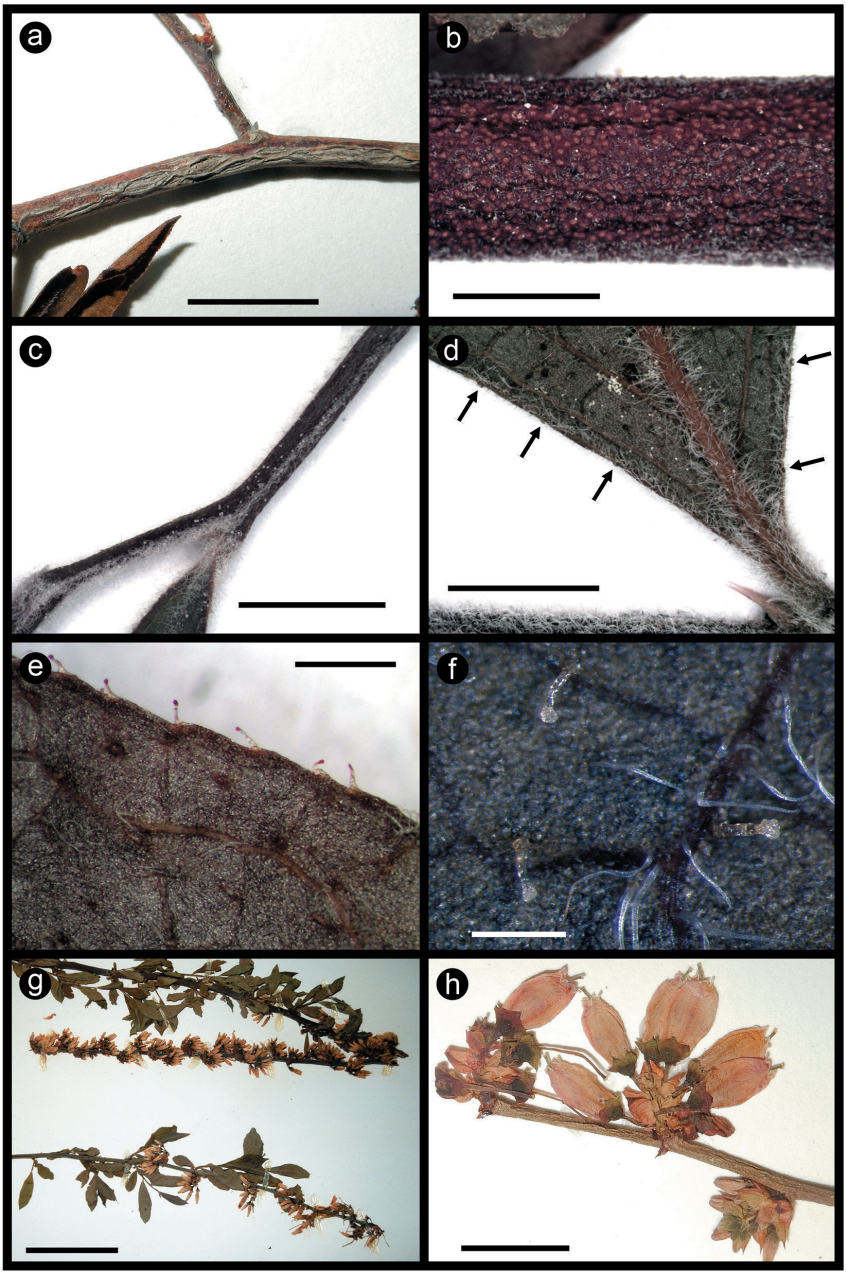

Fig. 5. *Vaccinium virgatum*. **a.** third-year branchlet showing eruptive periderm characteristic of the species of *V.* sect. *Cyanococcus*; **b.** second-year sucker branchlet showing stem stomatal bumps characteristic of the species of *V.* sect. *Cyanococcus*; **c.** first-year branchlet showing pubescence of eglandular trichomes in a line; **d.** vegetative bud, and base of abaxial side of leaf blade showing straight to curved eglandular trichomes, and marginal sessile glands (arrows); **e.** margin of leaf blade (abaxial view) showing stipitate-glandular-tipped teeth; **f.** abaxial side of leaf blade showing tertiary veins, eglandular trichomes, and stipitate-glandular trichomes; **g.** two examples (on the same herbarium sheet) of "virgate" branchlets bearing many inflorescences (ca. 22 on upper branchlet, 8 on lower branchlet) at adjacent nodes; **h.** inflorescences showing strongly exserted styles. (f, modified from Fritsch et al. 2024, used by permission; scale bars, a, h = 10 mm, b–d = 3 mm, e = 1 mm, f = 300 µm, g = 5 cm). a, P.W. Fritsch 2204 (BRIT BRIT792828); b, g, S.B. Jones, Jr. 2716 (GA GA202336); c, P.E. Hyatt 11409 (GA GA201388); d, f, P.W. Fritsch 2263 (BRIT BRIT792797); e, P.W. Fritsch 2239 (BRIT BRIT698943); h, A.A. Crowl CY-354 (BRIT BRIT792833).

toward leaf apex with straight to outcurved outer edges and shallow and narrow to deep and broad sinuses. Inflorescences axillary or pseudoterminal racemes, borne at one node or several contiguous nodes along non-elongate or non-virgate distal portions of branches and often additionally at many contiguous nodes along elongate or virgate shoots, 1- to 10-flowered, rachis 1–12 mm long, bracts white or green, often strongly flushed pink, obovate to subrotund, cucullate, glabrous, margins eciliate or ciliate with eglandular trichomes, pedicels glabrous or puberulent, bracteoles white often flushed pink, narrowly elliptic to linear, glabrous, margins eciliate or rarely ciliate with eglandular trichomes; flowering before leaves emerge and continuing until leaves have attained ca. 1/2–3/4 full size. Flowers: hypanthium 0.6–1.6 × 1.1–2.5 mm, glabrous, without glaucescence; calyx limb 0.1–1.4 mm long; calyx lobes deltoid to ± hemispherical, 0.4–1.5 × 0.7–2.0 mm, without glaucescence, margin eciliate or ciliate with eglandular trichomes, apex acuminate to rounded; corolla white, creamy white, white with pink or red tinge, pale pink, or pink, ± cylindrical, broadest at or above middle to 3/4 the total length, slightly constricted subapically, 5.5–11 × 2.5–7.0 mm, glabrous on both sides except often with sparse to moderate white eglandular trichomes on inner lobes; stamens 5.6–8.3 mm long; filaments 2.0–4.0 mm long, glabrous on surface, with white eglandular trichomes marginally, trichomes to 0.60 mm long; anthers 3.2–4.8 mm long, thecae 1.2–1.7 mm long, tubules 2.0–3.6 mm long; style slightly to more often strongly exserted from corolla throat, 8–11 mm long, glabrous. Fruits lustrous green when immature often turning red, then shiny black or purplish black at maturity, without glaucescence, subglobose, 4–12 mm in diameter.

Phenology.—Flowering from late February to early May; fruiting from mid-June to late September. The label of *P. Amerson & G. Watson 186* (SMU; Texas, Hardin County) states that the species flowers about a month after *Vaccinium elliottii*.

Distribution and habitat.—The geographic range of *Vaccinium virgatum* extends from far eastern Texas north to eastern Oklahoma, east through Arkansas, Louisiana, Mississippi, Alabama, Georgia, northern Florida, South Carolina, and extreme southeastern North Carolina (Fig. 3). Specimen labels yield the following habitat descriptors, which generally range from wet to dry forests of many types: river bottoms, baygalls, bayous, forested floodplains, mixed pine/broadleaved bottomland forests, edges of boggy areas, low rises in flooded areas, hammocks, mesic hardwoods, pine flatwoods, broadleaved forests, pine plantations, forest edges, thickets, pine savannas, dry woods, dry bluffs, dry pine forests, among rocks, and limestone outcrops. We observed a rough trend in the field where, if *V. elliottii*, *V. fuscatum*, and *V. virgatum* are found growing near each other, *V. fuscatum* is most commonly found in the wettest habitats and *V. virgatum* the driest, with *V. elliottii* intermediate between these two.

Chromosome number.—$2n = 6x = 72$ (hexaploid).

Notes.—Camp (1945) noted correctly that the stipitate glands on the abaxial surface of the leaf blade are typically lacking in the juvenile leaves, i.e., the smaller leaves toward the base of the current-year innovations (shoots). Thus, when attempting to identify species of the section with this character, care must be taken to examine the mature leaves. This can be a challenge when leaves are first expanding and the mature leaves are hidden by the juvenile leaves. The corolla is usually narrower in width relative to length than in other species of *Vaccinium* sect. *Cyanococcus*, such as *V. fuscatum* and *V. pallidum*, and is closest in shape to that of *V. tenellum*. The style is often more strongly exserted from the corolla than that of other species and, outside of any pink or red flushing, the corolla is usually a creamy white, in contrast to species of the section with a greenish to yellowish white corolla, such as *V. fuscatum*, *V. pallidum*, and *V. simulatum*.

Some species of *Vaccinium* sect. *Cyanococcus* other than those indicated in the key of Weakley et al. (2024; *V. ashei*, *V. myrsinites*, *V. tenellum*, and *V. virgatum*) also have stipitate glands on the abaxial surface of the leaf blade, i.e., *V. elliottii* (Fritsch et al. 2024; Franck & Salman 2024), *V. corymbosum* s.s , and *V. fuscatum* (P.W. Fritsch, pers. obs.)]. The glands in these species, however, typically occur only sporadically in individual plants and/or are fewer in number per leaf, unlike in *V. virgatum*. An exception is found in the densely glandular leaves of some plants of *V. fuscatum* occurring from east-central South Carolina to southeastern Georgia, but these plants can be distinguished from those of *V. virgatum* by their larger vegetative buds and diploid

condition (P.W. Fritsch et al., in prep.). The stipes of the glands in these species are also often longer and flattened in appearance in cross section at the base, versus shorter and round in cross section at the base in *V. virgatum*. In *V. corymbosum* and *V. fuscatum*, they often appear on the leaves of saplings and sucker shoots.

***Additional specimens examined.*—**See Appendix 1.

DUBIOUS NAMES

Vaccinium virgatum var. *latifolium* Dunal, Prodr. [A.P. de Candolle] 7:572. 1839. TYPE: not designated. Dunal refers to "Bot. rep. t. 181," as well as plate 33 in the first volume of *Dendrologia Britannica* (Watson 1825), the description and illustration in which both are consistent with *V. virgatum*. However, Dunal also indicates that he had seen a specimen in the De Candolle herbarium. A specimen on JSTOR Global Plants, G-DC (G00323251*), has a label with "*Vaccinium virgatum* α *latifolium* Bot. Reg. 181" and so this likely represents type material; it has another label "*Vaccinium acuminatum*, *virgatum*?, Halesworth, 18 mai 1819." The sheet, however, with three separate branchlets, may comprise a specimen of more than one gathering because branchlets and leaves on one of the branchlets appear to be glabrous or nearly so, and branchlets and leaves of the other two branchlets are pubescent. Although the resolution of the image is too low to be certain, we believe that the material on the sheet is *V. corymbosum* s.s. (i.e., not including *V. virgatum* in our sense) based on the large vegetative buds and entire leaf margins. Another specimen in JSTOR Global Plants that provides evidence of type material is a putative isotype at MPU (MPU012425*), with label information (some writing illegible) "*Vaccinium virgatum* α *latifolium*, [year] 1838, HERB. DUNAL." However, this specimen, comprising a single branchlet, appears not to be *V. virgatum* because the leaves have entire margins and the flowers are short-cylindrical. It appears not to belong to the same gathering as the G-DC specimen above; it may be *V. fuscatum*.

Vaccinium virgatum var. *ozarkense* Ashe, Torreya 25:10. 1925. TYPE: U.S.A. ARKANSAS. Montgomery Co.: head of Polk Creek, 2 May 1924, *W.W. Ashe s.n.* Type material has been found neither physically nor in various specimen data portals such as JSTOR Global Plants and SERNEC.

Note.—The description mentions small flowers 5–6 mm long and makes no mention of stipitate-glandular trichomes on the abaxial leaf blades. The leaf margins are entire, unlike in *V. virgatum* and like in some individuals of *V. pallidum*. The plants described are likely *V. pallidum* because this species is common in the Ozarks whereas *V. virgatum* is mostly absent from these mountains.

EXCLUDED NAME

Vaccinium virgatum var. *parvifolium* A. Gray, Syn. Fl. N. Amer. 2(1):22. 1878. TYPE: U.S.A. LOUISIANA (fl.): *S. Hale s.n.* (**lectotype, designated here:** GH 00015935*, right-hand element on sheet). No type was indicated in the protologue.

Note.—W.H. Camp considered the sheet containing the lectotype to comprise two separate gatherings, the other gathering being Arkansas: [Ouachita County:] Camden, 19 May 1850 (fr.), *A. Fendler s.n.* (GH 00015935*, left-hand element on sheet). Camp considered both elements to comprise type material, presumably by the annotation in Gray's handwriting "*V. virgatum* var. *parvifolium*, SYN. FL. N. AMER," an assessment with which we agree. Gray considered this an "ambiguous form," citing *V. elliottii* Chapm. in synonymy and indicating a geographic range of "South Carolina to Arkansas and Louisiana." Gray did not list *V. elliottii* elsewhere in this treatment, and so he apparently considered 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 also conclude, as did Camp (as annotation), that this is *V. elliottii*.

APPENDIX 1

Representative specimens of presumed naturally occurring populations of *Vaccinium virgatum* examined for this study, one specimen per county or parish.

U.S.A. ALABAMA. **Baldwin Co.:** Holly Creek Road, ca. 1.4 mi W jct. with AL 59, S of Chrysler, 10 May 2000, *R. Kral 89677* (VDB). **Barbour Co.:** Ala. 10 W of Clio, 20 May 1968, *R. Kral 30853* (SMU). **Bullock Co.:** Hwy. 82 Hwy. 110, 0.7 mi W jct. RR tracks, 2 Aug 1982, *R.L. Jones 3908* (EKY*). **Butler Co.:** Oakey Streak, ca. 1.5 mi W of Butler County 59, T7N R15E S16, Red Hills area, 28 Jun 1985, *A.R. Diamond 969* (GA). **Choctaw Co.:** 2 mi N of Silas, 20 Apr 1964, *S. McDaniel 4221* (GA). **Clarke Co.:** Little Stave Creek, 1 Jul 1966, *S. Taylor 66-176-1* (GA). **Coffee Co.:** by AL 87, 3 mi N of Jack, 5 Jun 1995, *R. Kral 84866* (VDB). **Crenshaw Co.:** 4.8 mi S of Luverne, 1 Apr 1953, *J.W. Hardin 15047* (GA). **Dallas Co.:** ca. 1 mi WNW Cahaba, 31 Mar 1972, *R. Kral 45335* (VDB). **Houston Co.:** by U.S.-84, just W Saffold, 25 Jul 1969, *R. Kral 35760* (VDB). **Mobile Co.:** 4.7 mi S of Mt. Vernon, 20 Apr 1958, *L.H. Shinners 27057* (SMU). **Monroe Co.:** 1 mi NE of Goodway, 31 May 1972, *R. Kral 46985* (BRIT). **Montgomery Co.:** U.S.-231, 16 mi SE jct. Montgomery Loop bypass, 24 May 1975, *R. Kral 55836* (VDB). **Washington Co.:** St. Stephen, 8 Jun 1973, *R. Kral 50439* (GA). **Wilcox Co.:** by Ala. 5, 0.5 mi S Kimbrough, 28 Jun 1974, *R. Kral 53594* (VDB). **ARKANSAS. Ashley Co.:** P.O. Hamburg, 16 Apr 1939, *D. Demaree 18909* (SMU). **Bradley Co.:** P.O. Warren, 17 Apr 1941, *D. Demaree 22901* (SMU). **Calhoun Co.:** P.O. Tinsman, 17 May 1941, *D. Demaree 22118* (SMU). **Clark Co.:** Little Missouri River, P.O. Gurdon, 20 Jul 1971, *D. Demaree 63965* (GA). **Cleburne Co.:** ca. 4.5 mi SW of Pangburn, T9N R8W S30, along banks of Big Creek, 29 Jul 1972, *D. Babb 869* (STAR*). **Cleveland Co.:** ca. 50 m SE of U.S.-79, ca. 80 m E of Bell Road, ca. 2.7 mi W of Kingsland, 19 May 2021, *P.W. Fritsch 2347* (BRIT, DUKE). **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-89 and County Road 85, ca. 64 m SE of Scott Branch (creek), 18 May 2021, *P.W. Fritsch 2342* (BRIT, DUKE). **Conway Co.:** Petit Jean Mountain, P.O. Morrilton, 1 Jul 1955, *D. Demaree 37156* (SMU). **Cross Co.:** Hickery Ridge, 1 Aug 1927, *D. Demaree 3864* (SMU). **Dallas Co.:** P.O. Carthage, 17 Jun 1975, *D. Demaree 69731* (GA). **Drew Co.:** P.O. Monticello, 12 May 1937, *D. Demaree 14955A* (SMU). **Faulkner Co.:** P.O. Palarm, 14 Jun 1940, *D. Demaree 21238* (SMU). **Garland Co.:** Jack Mountain, P.O. Lake Hamilton, 12 Apr 1971, *D. Demaree 63371* (GA). **Grant Co.:** along N side of AR-35, ca. 0.16 mi E of intersection of AR-35 and County Road 572, ca. 4 mi NW of Sheridan, 19 May 2021, *P.W. Fritsch 2348* (BRIT). **Hempstead Co.:** beside U.S.-371 (formerly Ark. 24) W of McKaskill, Sec. 36, 26 May 1999, *R.D. Thomas 160360* (NLU). **Hot Spring Co.:** Ark. 222 at the Grant County Line E of Lono and Ark. 9, Sec. 12, 12 May 1996, *R.D. Thomas 149088* (GA). **Howard Co.:** near Briar Creek, 12 mi N of Nashville on Ark. 369 near Briar Plant of Weyerhaeuser Company, 25 May 1974, *D. Lawson et al. 1693* (NLU). **Independence Co.:** P.O. Pleasant Plains, 2 Aug 1948, *D. Demaree 27182* (SMU). **Jefferson Co.:** bluffs of Arkansas River, P.O. Redfield, 17 Aug 1937, *D. Demaree 15836* (SMU). **Lafayette Co.:** road bank of paved road 0.5 mi S of McKamie and Ark. 53 S of Stamps, 20 May 1998, *R.D. Thomas 156534* (NLU). **Lincoln Co.:** P.O. Star City, 27 Mar 1938, *D. Demaree 16746* (SMU). **Lonoke Co.:** W of Ark. 367 at White Oak Creek near jct. with U.S.-67 and U.S.-167 SW of Cabot, 30 Jun 2001, *R.D. Thomas 170492* (BRIT). **Miller Co.:** ca. 135 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 2336* (BRIT, DUKE). **Montgomery Co.:** Little Mo. River, Greasey Cove, P.O. Hopper, 17 Oct 1932, *D. Demaree 9833* (SMU). **Nevada Co.:** ca. 47 m NE of AR-335 just W of Clear Creek, ca. 0.2 mi NW of intersection of AR-355 and County Road 104, 18 May 2021, *P.W. Fritsch 2339* (BRIT, DUKE). **Ouachita Co.:** P.O. Camden, 11 Apr 1937, *D. Demaree 14425* (SMU). **Perry Co.:** Ouachita Mountain Seep, ca. 18 m SE of U.S. Forest Service Road 210 (County Road 362), ca. 0.45 mi SW of intersection of U.S. Forest Service Road 210 and U.S. 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 2352* (BRIT, DUKE). **Pike Co.:** P.O. Daisy, 14 May 1955, *D. Demaree 36779* (SMU). **Prairie Co.:** P.O. Hazen, Rice region, 25 Jul 1937, *D. Demaree 15467* (SMU). **Pulaski Co.:** Camp Robinson, N of Little Rock, 4 Apr 1939, *M. Merrill 1541* (GA). **Saline Co.:** ca. 46 m E of unnamed U.S. Forest Service road, ca. 0.8 (road) mi SE of intersection of this road and County Road 5 (U.S. Forest Service Road 132; Winona Scenic Drive), ca. 3 mi (direct) NE of intersection of County Road 5 and AR-7, Alum Creek Experimental Forest in Ouachita National Forest, 20 May 2021, *P.W. Fritsch 2350* (BRIT, DUKE). **Sevier Co.:** ca. 5 m W of AR-41, ca. 2.3 mi (direct) S of De Queen, 25 May 2021, P.W. Fritsch 2370 (BRIT, DUKE). **Union Co.:** ca. 13 m E of Ward Road near houses, ca. 0.15 mi SW of Peace Street, Calion, 18 May 2021, P.W. Fritsch 2344 (BRIT, DUKE). **White Co.:** P.O. Rose Bud, 8 Apr 1972, *D. Demaree 64447* (SMU). **Yell Co.:** from Yell/Montgomery Co. line on SH 27, head N 0.3 mi and turn right onto Iron Forks Road, drive 3.6 mi to where the Iron Forks River crosses the road, T1N R23W S10 NW1/4, 9 Jun 2004, *R. McElderry 152* (UARK*). **FLORIDA. Bay Co.:** bridge beyond Youngstown, 16 Mar 1937, *Exploration Party 1937 s.n.* (FLAS*). **Clay Co.:** along Florida State Hwy. 215, 0.5–1.5 mi S of its intersection with 21, 20 Mar 1965, *I.L. Wiggins 19507* (FLAS*). **Columbia Co.:** Lake City, 18 Jun 1893, *P.H. Rolfs 221* (FLAS*). **Duval Co.:** 0.5 mi W of Alt. 1 on Beach Blvd., 26 Feb 1971, *G.H. Morton 4650* (SMU). **Escambia Co.:** vicinity of Bratt, 7 Mar 7065, *H.E. Ahles 7065* (MISSA*). **Gadsden Co.:** Aspalaga Bluff, 26 Apr 1924, *J.K. Small et al. 11288* (NY*). **Jackson Co.:** 10 mi E of Marianna, 15 Mar 1937, *Exploration Party 1937 s.n.* (FLAS*). **Jefferson Co.:** NW of Ward Creek bridge, T2N R4E SE 1/4 S15, 19 Mar 1982, *L.C. Anderson 5739* (BRIT). **Leon Co.:** 8 mi N of Tallahassee, 16 Mar 1955, *R.K. Godfrey 52999* (VDB). **Liberty Co.:** White-cedar swamp near Telogia, 27 Apr 1924, *J.K. Small et al. 11297* (NY*). **Madison Co.:** 1 mi N Pinella, 17 Mar 1958, *R. Kral 6289* (VDB). **Nassau Co.:** Fernandina, Apr 1893, *A. Ruth s.n.* (BRIT). **Taylor Co.:** Salem, 17 Mar 1976, *R. Kral 57335* (VDB). **Wakulla Co.:** McBride's Slough, *s.d., R.K. Godfrey 65781* (MO). **Walton Co.:** 6 mi SW of DeFuniak Springs, 30 Mar 1951, *E.L. Tyson 539* (FLAS*). **GEORGIA. Atkinson Co.:** by GA 135, just N of Willacoochee River, ca. 2 mi S Willacoochee, 14 Jul 1994, *R. Kral 83752* (VDB). **Ben Hill Co.:** ca. 12 mi S of Abbeville and 10 mi N of Fitzgerald, 25 Apr 1953, *R.L. Wilbur 3069* (GA). **Berrien Co.:** intersection of GA-645 with GA-168, 1.5 mi W of the Lanier-Berrien County Line, 19 Jul 1966, *W.R. Faircloth 3631* (GA). **Brantley Co.:** 5 mi N of Nahunta, E side of Hwy. U.S.-301 on old paved road next to highway, 26 Mar 2021, *A.A. Crowl CY-371* (BRIT). **Brooks Co.:** Grooverville, 10.3 mi WSW of Quitman, 13 Jul 1966, *W.R. Faircloth 3466* (GA). **Bryan Co.:** between Midway and Savannah, 1.3 mi S of the Ogeechee River, 18 Apr 1932, *H.M. McKay s.n.* (GA). **Bulloch Co.:** ca. 7 mi SW of Statesboro on Rte. 25, 16 May 1953, *R.L. Wilbur 3284* (GA). **Burke Co.:** 0.75 mi E U.S. at Greens Cut, 22 Jun 1962, *G.J. Galletta Clone B* (NCSC*). **Calhoun Co.:** along Keel Creek, 5 mi S of Leary, 28 Jul 1947, *R.F. Thorne 5684a* (GA). **Camden Co.:** Little Cumberland Island, just E of LH Trail, N of Cross Trail 2, 20 May 1997, *J.M. Sharpe 512* (GA). **Charlton Co.:** Okefenokee National Wildlife Refuge, Stephen C Foster State Park, 27 Mar 2021, *A.A. Crowl CY-374* (BRIT). **Chatham Co.:** ca. 0.8 mi N15°E of Morgan Bridge in W corner of county, 16 Jun 1958, *W.H. Duncan 21092* (GA). **Coffee Co.:** along Rocky Creek above Rocky Creek Swamp, 15 May 1966, *D. Blake s.n.* (GA). **Colquitt Co.:** 0.25 mi N of Indian Creek, 1.8 mi N of Berlin, 6 Jul 1966, *W.R. Faircloth 3274* (GA). **Dodge Co.:** ca. 6 mi NW of Eastman, 22 May 1953, *R.L. Wilbur*

3305 (GA). **Dougherty Co.:** Albany, Jul 1923, *J.W. Gillespie E1509* (GA). **Early Co.:** near Big Cypress Pond and the Baker Co. line, 24 Apr 1947, *R.F. Thorne 3283* (RSA*). **Echols Co.:** along the last side of Little River, 7 mi SE of Lake Park, 15 Jul 1965, *W.R. Faircloth 2252* (GA). **Effingham Co.:** S of Rincon, 12 Apr 1958, *F.R. Dulany s.n.* (GA). **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* (GA). **Glynn Co.:** St. Simons Island, N side of S Harrington Road, 25 Mar 1993, *C. Nordman s.n.* (GA). **Grady Co.:** S side U.S.-84 ca. 0.5 mi W of Wolf Creek bridge, 23 Mar 2003, *R. Kral 93705* (VDB). **Irwin Co.:** Paulk's Landing, Alapaha River, 1 mi N Alapaha River bridge, Landing Road, on E side of hwy. at Hammock Lake, 23 May 2009, *B. Sanderson 221* (GA). **Lanier Co.:** 1.4 mi NE of the junction of GA-168 and U.S.-221, 18 Jul 1966, *W.R. Faircloth 3554* (GA). **Lee Co.:** Americus, 5 May 1931, *G.M. Dudley s.n.* (GA). **Liberty Co.:** St. Catherines Island, N end, King New Ground Road, 12 Jun 1984, *S.B. Jones 24155* (GA). **Long Co.:** Griffin Ridge Wildlife Management Area, ca. 20 m N of trail (dirt road), ca. 0.25 mi from parking area, ca. 0.30 mi due N of U.S.-301, 4 Apr 2024, *P.W. Fritsch 2562* (BRIT, DUKE). **Lowndes Co.:** SE shore of Ocean Pond S of Lake Park, 16 Jul 1965, *W.R. Faircloth 2326* (GA). **McDuffie Co.:** area of Fall Line Sand-hills, vicinity of Thomson, 16-17 Sep 190, *H.H. Bartlett 1475* (GA). **McIntosh Co.:** Fort Barrington, 11 Mar 1992, *C. Nordman s.n.* (GA). **Pierce Co.:** Satilla River at U.S.-84, 4 May 1958, *E. Cypert 32* (GA). **Sumter Co.:** just SW of Muckalee Creek (near its confluence with Wolf Creek), ca. 1.7 mi WNW of Americus, 26 May 1991, *R.A. Norris 6301* (GA). **Tattnall Co.:** along NW side of Beards Creek, 27 Jul 1941, *W.H. Duncan 3773* (GA). **Telfair Co.:** ca. 10 mi S of McRae on Rte. 441, 22 May 1953, *R.L. Wilbur 3344* (GA). **Thomas Co.:** 5 mi E Thomasville, 18 Mar 1939, *D. Eyles 3928* (GA). **Washington Co.:** 1 1/3 mi NW of Tennile, 11 May 1952, *W.H. Duncan 13514* (GA). **Wheeler Co.:** Little Ocmulgee State Park, N end of park, 9 Aug 2001, *T. Govus 1250* (GA). **LOUISIANA. Acadia Par.:** vicinity of Bayou Plaquemine, near Crowley, 30 Mar 1959, *J. Ewan 19710* (NLU). **Beauregard Par.:** ca. 9 mi W of DeRidder, 19 Jun 1968, *J.W. Thieret 29498* (SMU). **Bienville Par.:** 11 mi SE of Minden, 26 Jul 1950, *L.H. Shinners 12608* (SMU). **Bossier Par.:** Black Cypress Recreational Area, 22 Apr 1983, *F.M. Givens 2974* (BRIT). **Caddo Par.:** ca. 18 m S of Kendrick Road, ca. 0.3 mi W of LA-1, 16 May 2021, *P.W. Fritsch 2334* (BRIT, DUKE). **Calcasieu Par.:** ca. 3 mi N of Nibletts Bluff, 21 Mar 1964, *J.W. Thieret 16966* (GA). **Caldwell Par.:** ca. 5 mi N Columbia above Ouachita River, 29 Mar 1964, *R. Kral 19514* (SMU). **Catahoula Par.:** 2.5 mi S Rosenfeld, 29 Mar 1964, *R. Kral 19537* (SMU). **Claiborne Par.:** ca. 17 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 2332* (BRIT, DUKE). **De Soto Par.:** ca. 7.7 mi SE of Mansfield, ca. 2 mi W of Hwy. 175, near Chatman Bayou, 30 Apr 1979, *G. Ajilvsgi 6021* (BRIT). **East Baton Rouge Par.:** on grounds of Emory Smith at 11855 Highland Road, Baton Rouge, 27 Sep 1968, *R. Kirkpatrick 187* (LSU*). **Evangeline Par.:** cemetery just off U.S.-167, 1 mi S of Clearwater and 1.5 mi S of Rapides Parish, T1S R1E S8, 10 Apr 1979, *K. Cormier 1457* (NLU). **Franklin Par.:** S of La. 132, 7.3 mi W of La. 857 at gravel road and old school house, T16N R8E S12, 6 May 1981, *R.D. Thomas 76186* (BRIT). **Grant Par.:** Kisatchie National Forest, Catahoula District, Shell Oil Seep site T8N R1W S11, 2 Apr 2003, *P.E. Hyatt 11409* (GA). **Jackson Par.:** ca. 3.25 mi SE of Clay, section 10, 24 Jun 1968, *J.W. Thieret 29592* (SMU). **LaSalle Par.:** Greeley Pasture, Urania, 2 May 1930, *L.J. Pessin 1710 L-147* (BRIT). **Lincoln Par.:** 6 mi W of Ruston off La. 507, 20 Mar 1973, *P. Lohman 16* (GA). **Morehouse Par.:** along high line right-of-way at International Paper Company Land Fill NE of Bastrop, T21E, R6E, S16, 19 May 1989, *R.D. Thomas 109934* (GA). **Natchitoches Par.:** ca. 150 m W of Mount Olive Baptist Church, ca. 370 m (direct) N of LA-6 (Natchitoches Highway), ca. 2.5 mi E of Hagewood, 9 May 2021, *P.W. Fritsch 2287* (BRIT, DUKE). **Ouachita Par.:** 8.7 mi NE of Eros, 18 Apr 1960, *L.H. Shinners 28241* (GA). **Rapides Par.:** near Zimmerman RR sta., Red River Valley, 24 Apr 1948, *J. Ewan 17604* (GA). **Red River Par.:** ca. 1.5 mi W of Armistead and Hwy. 1, 4 May 1977, *G. Ajilvsgi 4481* (BRIT). **Richland Par.:** N of I-20 at rest area W of Delhi and E of Dunn, T17N R9E S21, 3 Jun 1984, *R.D. Thomas 89189* (NLU). **Sabine Par.:** ca. 4 mi SW of Hornbeck, 7 Jun 1966, *J.W. Thieret 23101* (GA). **St. Tammany Par.:** Primate Research Center, Covington, 13 Jun 1943, *M.K. Rylander 391* (NO*). **Tangipahoa Par.:** Southeastern Louisiana University campus, at GSA car wash along N Oak St., 27 Mar 1997, *G.N. Montz 8587* (LSU*). **Union Par.:** along E side of Canaan Church Road (Parish Road 3355), ca. 0.21 mi N of Parish Road 3353, ca. 0.1 mi (direct) E of LA-558 (Iron Mountain Road), 16 May 2021, *P.W. Fritsch 2329* (BRIT, DUKE). **Vernon Par.:** ca. 17 m SE of Walter James Road (U.S. Forest Service Road 400), ca. 116 m NE of LA-10 (Pitkin Highway), Kisatchie National Forest, 10 May 2021, *P.W. Fritsch 2292* (BRIT, DUKE). **Washington Par.:** across street from 602 North Bankston Drive, Bogalusa, 15 Apr 1972, *B S. Morris s.n.* (SMU). **Webster Par.:** bluff above Indian Creek, section 11, 5 mi ENE of Serepta, 24 Mar 1967, *J.W. Thieret 25472* (SMU). **West Carroll Par.:** 1 mi N of Poverty Point State Comm. Area, T19N R10E S10, 6 Apr 1978, *R. Gough 871* (BRIT). **Winn Par.:** along W side of unpaved road in disuse, ca. 0.2 mi N of Sand Dump Road, Compartments 48 and 49, Winn District, Kisatchie National Forest, 14 May 2021, *P.W. Fritsch 2317* (BRIT, DUKE). **MISSISSIPPI. Calhoun Co.:** 0.5 mi W of Chickasaw-Calhoun county line, N side of State Hwy. 8, 8 Jul 1966, *T.M. Pullen 66803* (MISS*). **Forrest Co.:** Ragland Hills, 1 Jul 1970, *K.E. Rogers 3635-B* (VDB). **George Co.:** 1 mi W of Lucedale, Hwy. 98, 21 Jun 1966, *S.B. Jones 7010* (GA). **Lamar Co.:** 4 mi W of Hattiesburg, 12 Apr 1965, *S.B. Jones 2716* (GA). **Leake Co.:** on bluff of Pearl River, 7.5 mi via road from Good Hope at Low Head Dam, Ross Barnett Reservoir, 16 Jul 1970, *S.B. Jones 19288* (MISS*). **Oktibbeha Co.:** 10 mi S of Starkville, 8 Apr 1961, *S. McDaniel 2373* (MO). **Perry Co.:** N of Range 40 in headwaters of Garraway Creek, CSTS Training area 21, T2N R11W S6, 2 May 2006, *S.W. Leonard 12263* (NCU*). **Stone Co.:** ca. 12 mi SE of Wigins, near Old Creek and Indian Camp Branch, S16, 30 Jul 1981, *S. McDaniel 25262* (MMNS*). **Wayne Co.:** Piney Woods Rec Area SE of Waynesboro, 4 Jul 1967, *S.B. Jones 14032* (SMU). **NORTH CAROLINA. Pender Co.:** N of Wilmington, 12 Apr 1942, *H.H. Iltis 1295* (SMU). **OKLAHOMA. McCurtain Co.:** Clear Creek on NE side of U.S. Hwy. 70, bridge just E of the McCurtain-Choctaw County line, 14 Jun 1983, *C. Taylor 31866* (BRIT). **SOUTH CAROLINA. Aiken Co.:** W edge of Hitchcock Woods along Dibble Road E off S.C. 478 By-pass, SW of Aiken, 16 Apr 1978, *T.L. Mellichamp & J.F. Matthews s.n.* (UNCC*). **Bamberg Co.:** secondary road off Hwy. 78 ca. 8 mi N of jct. with SC 61, 6 Apr 1980, *D.R. Carter C-102* (CLEMS*). **Barnwell Co.:** Audubon's Silver Bluff Sanctuary, 20 Apr 2022, *A.A. Crowl CY-458* (BRIT). **Beaufort Co.:** Port Royal Bridge (Savanna side), 18 May 1965, *R. Kral 24134* (VDB). **Berkeley Co.:** 10 mi N of Charleston, 16 Apr 1930, *G.A. Schultze 639* (GA). **Charleston Co.:** S edge of Roxbury Park, N side of Little Britton Road, 25 Mar 2021, *A.A. Crowl CY-351* (BRIT). **Clarendon Co.:** 2.5 mi E of Manning, 2 Apr 1930, *G.A. Schultze 585* (GA). **Colleton Co.:** Jacksonboro, Edisto Nature Trail, NEW side of U.S.-1, trail E of the parking area, 25 Mar 2021, *A.A. Crowl CY-357* (BRIT). **Dorchester Co.:** near The Forks behind brick church where SC61 and U.S.-17A split, ca. 7 mi SW of Summerville, 25 May 2001, *R.L. Wilbur 73604* (GA). **Florence Co.:** Bluff Boat Landing Sant. Coop. 3 mi N Kingsburg, 18 Apr 1882, *L.F. Swails 82/183* (USCH*). **Hampton Co.:** along county road 852, 2 mi S of jct. with S.C. 333, SSE of Scotia, 4 Apr 1984, *C.A. Aulbach-Smith 3028* (NLU). **Horry Co.:** E of Little Pee Dee River along Hwy. 37E, ca. 10 mi W of Conway, 21 Apr 1965, *H.H. Iltis 23105* (NCU*). **Jasper Co.:** 2 mi E of Tillman, 9 Apr 1930, *G.A. Schultze 614* (GA). **Kershaw Co.:** unnumbered dirt roadway, E of S-775, 2.3 mi N of jct. with S-101, N of Elgin, 25 Jun 1984, *R. Ross & D. Chastain 15* (USCH*). **Lee Co.:** Lynches River Road and 0.66 air mi SW of jct. of Sec Hwys. 187 and 13, 2.8 air mi SW of downtown Ashland, 27 Jun 2014, *J.B. Nelson 33172* (USCH*). **McCormick Co.:** Steven's Creek, off

S.C. 28 at Clark's Hill, 1.5 mi NE on S. 88, 8 Apr 1976, *R.M. Hendrick 151* (CLEMS*). **Orangeburg Co.:** Santee Cooper WMA, 12 Apr 2001, *A.B. Pittman 04120118* (BRIT). **Richland Co.:** S side of SC 48 ca. 18 mi SE of Columbia, 28 Mar 2003, *J.B. Nelson 23610* (MO). **Williamsburg Co.:** Road 35 to Black River, 24 May 1984, *L. Swails 84/65* (FMUH*). **TEXAS. Angelina Co.:** Angelina National Forest, 6 mi E of Zavalla, 24 Mar 1950, *E. Whitehouse 22966* (SMU). **Bowie Co.:** 3 mi E of Maud, 5 Jun 1950, *H.R. Reed s.n.* (SMU). **Cass Co.:** along Hwy. 11 between Hughes Springs and Linden, 17 Mar 1977, *G. Ajilvsgi 6878* (BRIT). **Chambers Co.:** White Memorial Park, off Hwy. 61 N of the village of Anahuac, 15 May 2005, *L.E. Brown 30522* (BRIT). **Cherokee Co.:** ca. 15.5 mi SE of Troup, ca. 2.7 mi N of Hwy. 79, 12 Jul 1977, *G. Ajilvsgi 5112* (BRIT). **Gregg Co.:** along W bank of Sabine River at I-20 W of Longview, 10 Sep 1971, *R.D. Thomas 24977* (NLU). **Hardin Co.:** 2.5 mi W of Silsbee, 9 Apr 1947, *V.L. Cory 52789* (SMU). **Harrison Co.:** Caddo Lake State Park, Nature Trail, 30 Jun 1975, *R.J. Fleetwood 11832* (BRIT). **Jasper Co.:** ca. 10 m S of County Road 480, ca. 100 m W of Robinson Branch of Trout Creek, ca. 6 mi N of Kirbyville, 8 May 2021, *P.W. Fritsch 2282* (BRIT, DUKE). **Liberty Co.:** beside Texas 105, 1 mi W of Hardin County line, 19 May 1974, *R.D. Thomas 39696* (NLU). **Montgomery Co.:** Conroe, 13 Jul 1931, *G.L. Fisher 14400* (BRIT). **Morris Co.:** ca. 85 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 2264* (BRIT, DUKE). **Nacogdoches Co.:** ca. 66 m S of Farm to Market Road 1087 (Camp Tonkawa Road), ca. 4 mi E of TX-259, 6 May 2021, *P.W. Fritsch 2268* (BRIT, DUKE). **Newton Co.:** along W side of unmaintained dirt road, ca. 50 m N of County Road 3038 ca. 120 m W of County Road 3060, 8 May 2021, *P.W. Fritsch 2283* (BRIT, DUKE). **Panola Co.:** Hills Lake area, 29 Mar 1963, *R. Maples s.n.* (VDB). **Polk Co.:** 15.25 mi S of Livingstone, 17 Apr 1950, *V.L. Cory 57084* (SMU). **Red River Co.:** ca. 8 m S of County Road 2227, ca. 1.3 mi S of Negley, Lennox Woods Preserve, 5 May 2021, *P.W. Fritsch 2261* (BRIT, DUKE). **Rusk Co.:** Temple Industry land 2 mi N of Hwy. 1087, 21 Mar 1971, *L. Chambless 338* (NLU). **Sabine Co.:** Sabine National Forest E of Hemphill, 0.35 mi N of jct. of Forest Roads 128 and 115 on 128, 10 Apr 1981, *E.S. Nixon & J.R. Ward 10662* (BRIT). **Shelby Co.:** 1.7 mi E of Paxton, 12 Jul 1955, *L.H. Shinners 20467* (SMU). **Smith Co.:** Tyler, along Pine Bur Road in W edge of city, 12 Mar 1949, *V.L. Cory 55000* (SMU). **Titus Co.:** N of Hwy. 11, W of Cason, near Swanano Creek, 26 Jun 1974, *P.A. Amerson 1851* (SMU). **Trinity Co.:** 14 mi E of Groveton, 20 Apr 1936, *P.D. Goodrum 49* (RSA*). **Tyler Co.:** ca. 45 m S of County Road 4777 (Red Oak Lane), ca. 50 m N of shore of Hyatt Lake, Watson Rare Native Plant Preserve, 7 May 2021, *P.W. Fritsch 2270* (BRIT, DUKE). **Upshur Co.:** Big Sandy, 8 Apr 1902, *J. Reverchon 3116* (SMU). **Wood Co.:** 15 mi E of Quitman on CR 4560 off FM2088, 28 Mar 1997, *J. Baker 061* (BRIT).

APPENDIX 2

Specimen vouchers of samples used for assessing ploidy in *Vaccinium virgatum*.

U.S.A. GEORGIA. Charlton Co.: Okefenokee National Wildlife Refuge, Stephen C Foster State Park, along boardwalk, 30.82734°, –82.36270°, 27 Mar 2021, *A.A. Crowl CY-379* (BRIT). **LOUISIANA. Union Par.:** along E side of Cannan Church Road (Parish Road 3355), ca. 0.21 mi N of Parish road 3353, ca. 0.1 mi (direct) E of LA-558 (Iron Mountain Road), 32.99263°, –92.56499°, 58 m elev., 16 May 2021, *P.W. Fritsch 2329* (BRIT, DUKE). **SOUTH CAROLINA. Barnwell Co.:** Audubon's Silver Bluff Sanctuary, 33.323021°, –81.848959°, 20 Apr 2022, *A.A. Crowl CY-458* (BRIT): ibid., *A.A. Crowl CY-460* (BRIT). **Charleston Co.:** 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-352* (BRIT). **Colleton Co.:** Jacksonsboro, Edisto Nature Trail, NE side of U.S.-17, trail E of parking area, 32.76868°, –80.44902°, 25 Mar 2021, *A.A. Crowl CY-357* (BRIT); 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°, –80.744655°, 29 m elev., Apr 2024, *P.W. Fritsch 2571* (BRIT, DUKE). **TEXAS. Nacogdoches Co.:** ca. 66 m S of Farm to Market Road 1087 (Camp Tonkawa Road), ca. 4 mi E of TX-259, 31.82918°, –94.62103°, 131 m elev., 6 May 2021, *P.W. Fritsch 2268* (BRIT, DUKE); ibid., 132 m elev., *P.W. Fritsch 2269* (BRIT, DUKE).

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