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Evolution and Taxonomy of the Polyploid True Blueberries (Vaccinium sect. Cyanococcus) Endemic to the Southern Appalachian Mountains

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Abstract:	Abstract —The Southern Appalachian region of North America harbors exceptionally high levels of endemic woody plant diversity, including several polyploids of Vaccinium sect. Cyanococcus, the true blueberries. Contrasting hypotheses for the evolutionary origins of some of these polyploids have been proposed but undermined by taxonomic uncertainty. We integrated genomic data, flow cytometry analysis, and morphological investigation to infer the origin and evolutionary history of the endemic Southern Appalachian polyploid blueberries recognized here and further circumscribed as V. constablei (6x), V. hirsutum (4x), and V. simulatum (4x). Phylogenomic analyses suggest independent origins for these three species, most likely a result of ancient autopolyploidy. Vaccinium simulatum is sister to the extant diploid V. pallidum, a likely progenitor, whereas V. hirsutum appears to be derived from a diploid V. myrtilloides-like ancestor. The origin of V. constablei remains cryptic but this species is likely an early-branching lineage without clear morphological connections to extant species within the northern clade of V. sect. Cyanococcus. With this knowledge, combined with intensive field investigation and herbarium study, we provide a taxonomic revision of the endemic polyploid Southern Appalachian members of the section. The revision includes descriptions, ecological information, county-level distribution maps, and representative specimens cited, along with a key to all members of the section that occur in the Southern Appalachian region. We designate lectotypes for V. carolinianum, V. constablei, and V. hirsutum.
Response to Reviewers:	We responded to several typographical errors pointed out by Reviewer #3 Line 313. Fix italic on simulatum Line 777. idea -> ideal Lines 977-978. Fix typeface Line 1175. Leblond -> LeBlond

	Our figures are now compliant with Syst Bot format and we have addressed Dryad and GenBank concerns.

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Dear Editors of Syst Bot:

We are pleased to submit our final, revised manuscript entitled, “Evolution and Taxonomy of the Polyploid True Blueberries (*Vaccinium* sect. *Cyanococcus*) Endemic to the Southern Appalachian Mountains” for further consideration in *Systematic Botany*.

We have addressed the minor comments made by reviewer #3 and added Appendix 2 that contains accession data and NCBI numbers – we have temporary submission ID from NCBI: SUB16039368 for several remaining numbers that we plan to add in proof, along with a Dryad number.

Thank you for your patience and efforts on behalf of the ASPT.

Sincerely yours,

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Evolution and Taxonomy of the Polyploid True Blueberries (*Vaccinium* sect. *Cyanococcus*) Endemic to the Southern Appalachian Mountains

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Abstract**—**The Southern Appalachian region of North America harbors exceptionally high levels of endemic woody plant diversity, including several polyploids of *Vaccinium* sect. *Cyanococcus*, the true blueberries. Contrasting hypotheses for the evolutionary origins of some of these polyploids have been proposed but undermined by taxonomic uncertainty. We integrated genomic data, flow cytometry analysis, and morphological investigation to infer the origin and evolutionary history of the endemic Southern Appalachian polyploid blueberries recognized here and further circumscribed as *V. constablei* (6*x*), *V. hirsutum* (4*x*), and *V. simulatum* (4*x*). Phylogenomic analyses suggest independent origins for these three species, most likely a result of ancient autopolyploidy. *Vaccinium simulatum* is sister to the extant diploid *V. pallidum*, a likely progenitor, whereas *V. hirsutum* appears to be derived from a diploid *V. myrtilloides*-like ancestor. The origin of *V. constablei* remains cryptic but this species is likely an early-branching lineage without clear morphological connections to extant species within the northern clade of *V.* sect. *Cyanococcus*. With this knowledge, combined with intensive field investigation and herbarium study, we provide a taxonomic revision of the endemic polyploid Southern Appalachian members of the section. The revision includes descriptions, ecological information, county-level distribution maps, and representative specimens cited, along with a key to all members of the section that occur in the Southern Appalachian region. We designate lectotypes for *V. carolinianum*, *V. constablei*, and *V. hirsutum*.

Keywords—allopolyploidy, autopolyploidy, Ericaceae, flow cytometry, phylogenomics.

The Southern Appalachian region of North America—encompassing the southern terminus of the Appalachian Mountains and surrounding foothills—has long been recognized for its biodiversity, with a high priority for conservation (Soltis et al. 2006; Jenkins et al. 2015). The region is generally considered floristically homogeneous within the eastern temperate forest biome because of its high elevation (up to 2,037 m) and high level of endemism. It largely corresponds to the southeastern unglaciated region of the United States defined by the Blue Ridge Ecoregion 66 but also includes elements to the west below 39°N (Ridge and Valley, Southwestern and Central Appalachian Ecoregions 67–69; US EPA 2013). An extensive history of geologic uplift, erosion, and climatic oscillation in this region has resulted in a mosaic of microclimates and ecological niches. This has fostered the diversification of myriad unique and endemic plant species across a wide range of habitats, from various wetland and forest communities to high elevation balds (Braun 1955; Schafale 2024). The region's floristic diversity has been further enriched by the movement of seed plant lineages migrating to and establishing within the Southern Appalachian region during the increasingly seasonal climates of the Miocene, and more recently during recolonization events from southern refuges during glacial-interglacial cycles (Delcourt and Delcourt 1987; Manos and Meireles 2015).

The true blueberries comprising *Vaccinium* L. sect. *Cyanococcus* A.Gray constitute a clade of species endemic to North America (Becker et al. 2024; Fritsch et al. 2024a), with a substantial portion of its variation occurring in the Southern Appalachian region. The clade comprises a mixture of diploids, tetraploids, and hexaploids, with a base chromosome number of $x = 12$. As described in a recent review (Fritsch et al. 2024a) and summarized here, the species taxonomy of the clade has largely remained unresolved. In the first comprehensive taxonomic treatment of the section, Camp (1945) recognized 24 species in the section. In the section's only other global treatment, Vander Kloet (1983, 1988, 2009) reduced the number of species to nine, mainly by lumping all of what he considered to be Camp's "highbush" blueberry species into a broad concept of *V. corymbosum* L. comprising diploids, tetraploids, and hexaploids. Subsequent regionally-based taxonomic and floristic treatments have inconsistently adopted parts of Camp's and Vander Kloet's work (e.g., Ward 1974; Uttal 1987; Weakley and Southeastern Flora Team, 2023).

Through phylogenetic analysis based on genomic data combined with morphology and flow cytometry to determine ploidy, recent work has begun to reassess the taxonomy of *Vaccinium* sect. *Cyanococcus*. Target-enrichment genomic data have confirmed species status for the seven diploid taxa of the section based on monophyly and estimated a phylogeny in which early-diverging northern clade comprising *V. boreale* I.V.Hall & Aalders and *V. myrtilloides* Michx. is sister to a clade of (((*V. fuscatum* Aiton/*V. caesariense* Mack.)(*V. tenellum* Aiton + *V. darrowii* Camp))(*V. elliottii* Chapm. + *V. pallidum* Aiton) [Crowl et al. 2022; *V. caesariense* = *V. fuscatum* in Fritsch et al. (2025)]. The diploid *V. elliottii* has been shown to be distinct in morphology and geographic range from *V. corymbosum* sensu Vander Kloet (Crowl et al. 2022; Franck and Salman 2024; Fritsch et al. 2024a), and Crowl et al. (2022) found evidence for a single hybrid edge involving *V. elliottii* Chapm., *V. pallidum*, and *V. fuscatum*, suggesting historical gene flow or perhaps homoploid hybrid speciation. Further, two of Camp's hexaploids, *V. ashei* J.M.Reade and *V. virgatum* Aiton, have been resurrected from synonymy in *V. corymbosum* sensu Vander Kloet and recognized as distinct species (Weakley et al. 2024; Fritsch et al. 2024b). These species are each sister to separate subclades containing diploids and tetraploids.

In the Southern Appalachian region, *Vaccinium* sect. *Cyanococcus* comprises a component of species whose taxonomy is largely now resolved (the diploids *V. fuscatum*, *V. myrtilloides*, and *V. pallidum*, and the tetraploids *V. angustifolium* Aiton and *V. hirsutum* Buckley; Weakley and Southeastern Flora Team 2023) but also contains a residual polyploid complex. Of the diploids, *V. pallidum* is widespread in the eastern United States, whereas *V. myrtilloides* is found throughout much of northern North America, with a southern extension in the Appalachians. *Vaccinium fuscatum*, thought to only rarely occur in the Southern Appalachian region, has had an unstable taxonomic history but is being resolved through active taxonomic revision (Fritsch et al. 2025). Of the tetraploids, the Southern Appalachian endemic *V. hirsutum* has been consistently recognized across all taxonomic treatments since its original publication because of its unique possession of stipitate-glandular trichomes on the bracts, pedicels, hypanthium, corolla, and fruit. Like *V. myrtilloides*, *V. angustifolium* also occurs in the Southern Appalachians as a narrow southward extension into Virginia, West Virginia, and (one collection) North Carolina from its widespread distribution in the northeastern United States and Canada (Uttal 1986, 1987, P. W. Fritsch pers. obs.).

Conversely, the number and taxonomic limits of the other polyploids in the region have varied widely. As part of the first comprehensive monograph of the section, W. H. Camp (1945) recognized the tetraploid *Vaccinium simulatum* Small and the hexaploid *V. constablei* A.Gray as endemic and also recognized *V. altomontanum* Ashe as a tetraploid distributed mainly in the region but perhaps extending to southern Ohio, Arkansas, and Missouri. In the only global revision of the section, Vander Kloet (1988, 2009) rejected Camp's treatment of these taxa, relegating *V. constablei* and *V. simulatum* to synonymy under a broadly conceptualized *V. corymbosum* L. with diploid, tetraploid, and hexaploid lines and placing *V. altomontanum* under

V. pallidum with diploid and tetraploid lines. In key regional treatments that include the Southern Appalachian region, Radford et al. (1968) recognized *V. corymbosum* as occurring in the Appalachians and elsewhere and placed *V. simulatum* under *V. constablei*. Uttal (1987) recognized *V. corymbosum* and *V. simulatum* as distinct, retaining *V. constablei* in the synonymy of *V. corymbosum*. Weakley and Southeastern Flora Team (2023) accepted Uttal's treatment with the caveat that "the appropriate taxonomic treatment of these plants is unclear and not reliably identifiable based on morphology." The uncertain taxonomic status for these taxa has persisted to the present.

The seemingly closely related and taxonomically challenging species in *Vaccinium* sect. *Cyanococcus* prompts the question of whether multiple modes of polyploidization (autopolyploidy and/or allopolyploidy) account for the origins of its tetraploids and hexaploids, but this question has remained unaddressed. Based on morphology, crossing studies, and ploidy assessed with the few chromosome counts known at the time, Camp (1945) considered a broad range of speciation mechanisms and variously complex pathways in the evolution of the "highbush" polyploids of the section (plants > 1 m tall; for review, see Fritsch et al. 2024a). Vander Kloet (1980, 1983), however, took a very different view of the origins of these taxa, considering them to form the "compilospecies" *V. corymbosum*. Vander Kloet conceptualized this species as actively evolving, having been derived multiple times from various diploid "lowbush" ancestors.

Specific to the Southern Appalachian polyploids, Camp considered *Vaccinium simulatum* to be an autotetraploid of *V. pallidum*, and *V. constablei* to be an allohexaploid of tetraploid *V. simulatum* and *V. altomontanum*, the latter in Camp's opinion to be an autotetraploid of diploid *V. vacillans* Kalm ex Torr. If *V. vacillans* can be considered synonymous with *V. pallidum*, as have all authors since Camp's treatment, then this hypothesis is essentially one of an autopolyploid series of 2*x V. pallidum*, 4*x V. simulatum*/*V. altomontanum*, and 6*x V. constablei*. A potential problem with this hypothesis is that the type of *V. altomontanum* has been missing from before the time of Camp, and so Camp's concept of this species is unclear. Camp left the origin of *V. hirsutum* ambiguous. In contrast, as part of his "compilospecies" concept, Vander Kloet (1980, 1983) considered Camp's concept of *V. simulatum* to comprise part of the *V. corymbosum* complex. *Vaccinium constablei*, placed in the synonymy of the "lowbush" species *V. pallidum*, would (presumably) be considered an autopolyploid derivative of *V. pallidum*. Like Camp, Vander Kloet left the origin of *V. hirsutum* unresolved.

Here, we aim to shed light on the taxonomy, mode of origin, and evolutionary history for the polyploids of *Vaccinium* sect. *Cyanococcus* endemic to the Southern Appalachian region. We incorporate samples representing the range of morphotypes and ploidal levels into the diploid blueberry phylogeny based on high-throughput DNA sequence data of Crowl et al. (2022) to assess whether the polyploids are derived from modern diploids, and whether it is possible to distinguish between autopolyploid and allopolyploid origins. As to the polyploid species under study, we predict high similarity between autopolyploid and diploid progenitors in both morphology, nuclear genomes, and gene trees (e.g., Eriksson et al. 2017; Carnicero et al. 2023). Discriminating allopolyploidy from autopolyploidy will be more challenging, but we can reasonably predict that allopolyploids will exhibit combinations of intermediate morphology, nuclear genome admixture and/or sets of divergent gene trees derived from diploid parental species (e.g., Crowl et al. 2017). In either scenario, the age of the polyploids and extinction of diploid ancestors will contribute some level of uncertainty (Leal et al. 2024; Twyford et al. 2025). Based on these results and interpretations, and those from intensive field and herbarium study, we provide a taxonomic revision of the endemic polyploid representatives of the section that occur in the Southern Appalachian region.

Materials and Methods

Flow Cytometry**—**As part of a large sampling strategy for scoring ploidal level of individuals from natural populations across the entire *Vaccinium* sect. *Cyanococcus* clade (474 individuals in total; P. S. Manos et al. unpubl. data), we sampled 54 individuals conforming to the morphology of the three endemic species of the section from the Southern Appalachian region; 27 for *V. constablei*, two for *V. hirsutum*, and 25 for *V. simulatum* (Appendix 1). For *V. constablei* and *V. simulatum*, the samples extended throughout much of the ranges of the species, whereas the samples for *V. hirsutum* were localized because of the relative rarity of this species. 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 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 is concurrent with an equivalent increase in ploidy.

DNA Sequence Data**—**We used a subset of samples that were employed for flow cytometry for the other analyses in this study so that a ploidal level estimate was associated with each sample (see Appendix 2). For these analyses, we included five samples of *Vaccinium* *constablei*, two of *V. hirsutum* and four of *V. simulatum,* in addition to diploid *Cyanococcus* and outgroup (Crowl et al. 2022). We extracted DNA by following a modified CTAB protocol for all samples (Doyle and Doyle 1987) and quantified DNA concentrations with a Qubit 2.0 (Invitrogen, Carlsbad, California, USA). Samples ranging from 115 to 3000 ng of DNA were sent to Arbor Biosciences (Ann Arbor, Michigan, USA) for library preparation, target enrichment with the Angiosperms353 v1 target capture kit (Johnson et al. 2019), and DNA sequencing on a NovaSeq S4 sequencer (Illumina, San Diego, California, USA) with 2×150 bp chemistry. Raw reads were filtered and processed with the Trim Galore wrapper script (version 0.6.5). We used Cutadapt (version 2.6; Martin 2011) and FastQC (version 0.11.9; Andrews 2010) to trim adapters and low-quality reads based on a Phred quality score cutoff of 20 and then used HybPiper (version 1.3.1; Johnson et al. 2016) with default settings to assemble supercontig consensus loci (containing intronic and exonic regions). We included available Ericales sequences in the target reference file to improve the recovery of targeted loci (McLay et al. 2021). All loci flagged as containing potential paralogs were removed from the data set.

Allele Phasing**—**To create an allele dataset, we used the recently developed allele-phasing pipeline, PATÉ (Tiley et al. 2024a; 2024b), which can accommodate polyploids. We used consensus loci (supercontig sequences assembled with HybPiper) as reference sequences, and mapped Illumina reads back to these loci with the BWA-MEM algorithm from BWA (Li and Durbin 2009). We carried out variant calling using the ploidal level determined by flow cytometry for each individual and HaplotypeCaller (GATK; McKenna et al. 2010). To reduce potentially erroneous calls, we filtered the data using the following parameters with the VariantFiltration program in GATK: QD < 2.0; FS > 60.0; MQ < 40.0; ReadPosRankSum < 8.0.

We additionally removed variants present in < 5% and > 95% of reads (AF < 0.05 || AF > 0.95) and variants with a depth of < 10 reads (DP < 10).

Phylogenetic analysis**—**To assess the phylogenetic placement of the endemic Southern Appalachian polyploids within *Vaccinium* sect. *Cyanococcus*, we used the previously generated molecular data (for diploid *V.* sect. *Cyanococcus* taxa) and phylogenomic methods and analysis of Crowl et al. (2022), as summarized here. We aligned individual genes with MAFFT v7.245 (Katoh and Standley 2013). The final DNA alignment file is available from the Dryad Digital Repository (Manos et al. 2026). We performed a partitioned concatenated maximum-likelihood (ML) analysis using the supercontigs assembled with HybPiper (consensus loci). Gene partitions were inferred with PartitionFinder (Lanfear et al. 2014) in IQ-TREE (v1.6.9; Nguyen et al. 2015) and 1000 ultrafast bootstrap replicates were run to assess topological support. We conducted a species tree analysis in ASTRAL-III (version 5.5.6; Zhang et al. 2018) using the best individual gene trees from the ML analysis. Clade support was assessed with local posterior probabilities. To assess the phylogenetic placement of polyploid taxa, we created three individual datasets in which each polyploid species was added to the diploid dataset and the above analyses were run. Additionally, we additionally created a total-evidence dataset in which all three polyploid taxa were included with diploids.

Principal Component and Structure 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 Southern Appalachian species, we performed principal component and clustering analyses. We used the fasta2structure.pl script (https://github.com/gtiley/fasta-conversion) to convert the allele alignments generated with PATÉ into a principal component analysis (PCA) matrix and an integer-formatted file. We filtered the alignment to include only

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 and Ahmed 2011), and clustering analysis using genotype calls with STRUCTURE v.2.3.4 (Pritchard et al. 2000). In STRUCTURE, we carried out 20 independent runs on *a priori* clusters (K) from 4 to 7. To determine the 'best' K value, we calculated ΔK using the method of Evanno et al. (2005).

***Taxonomic Revision*—**We examined specimens from the following herbaria in-hand: BRIT, DUKE, EKY, GA, GMUF, MO, NLU, NY, ODU, SMU, VDB, WILLI, and WVA (acronyms as in Thiers 2024, updated continuously). We supplemented the data from these specimens with our own field observations in the geographic ranges of the species. Specimens from the following herbaria were examined online via the SERNEC data portal (https://sernecportal.org/portal): APSC, CLEMS, DUKE, ETSU, F, GEO, GH, GSMNP, HTTU, IND, K, MTSU, NBYC, NCSC, NCU, NY, OS, PH, TENN, UCHT, UNCC, US, USF, and WIS. Type specimens were examined either in-hand or as digital images available online at JSTOR Global Plants (https://plants.jstor.org). Specimen citations followed by "[image!]" in taxon entries or "[i]" in the Representative Specimens Examined section indicate that the specimens were examined as digital images only.

The species distribution maps were resolved to the county level, with one specimen cited per county of presumed naturally occurring populations. The specimens used as the basis for the map are also cited in the Representative Specimens Examined section for each species. Most of the specimens used for the basis of the maps were examined in hand. To generate the portion of the map based on digital images, we searched for records with identifications of the three species. Therefore, some counties in which they occur might not be documented here because the specimen(s) of a species in that county are currently identified as something other than one of the names that have been applied to the Southern Appalachian taxa. For some online images of specimens identified in the portal as the species, it was difficult to discern the characters needed for accurate species identification; these specimens were not used for the map. Specimen data used for maps and lists of representative specimens examined are listed in the Taxonomic Treatment.

The morphological descriptions are based on our fieldwork and herbarium research. The format of the descriptions generally follows that of *Vaccinium ashei* in Weakley et al. (2024). The specimens examined by us formed the dried-specimen basis of the descriptions. These consist of the specimens cited in the Representative Specimens Examined sections, our herbarium specimen vouchers of the treated species collected specifically for this project (79 *V. constablei*, one *V. hirsutum*, and 51 *V. simulatum*, duplicates deposited at BRIT and DUKE), and several hundred more from the herbaria cited above. The species were compared to each other as well as the other species of *V*. sect. *Cyanococcus* overlapping in the range, with differentiating characters identified. In the key to species in the Taxonomic Treatment, we use some of these characters to distinguish among all species of the section that occur in the Southern Appalachian region

Lectotypes were designated in accordance with Article 9 of the *International Code of Nomenclature for Algae, Fungi, and Plants* (*ICNAFP*; Turland et al. 2025).

RESULTS

***Flow Cytometry*—**Average 2C values from 1.08 to 1.65 pg were considered diploids, those from 2.44 to 3.02 pg tetraploids, and those ranging from 3.80 to 4.36 pg hexaploids. All estimates matched expectations based on results from Redpath et al. (2022) and were consistent within the species as circumscribed in the taxonomic section, with *Vaccinium hirsutum* and *V. simulatum* inferred as tetraploids, and *V. constablei* as hexaploid. Our two accessions of *V. hirsutum* were determined to be tetraploid, confirming the single chromosome count made from this distinctive taxon (Longley 1927).

***Molecular Data*—**The final dataset consisting of diploid and polyploid taxa included 58 samples representing eight diploid *Vaccinium* sect. *Cyanococcus* species from across North America and three polyploids endemic to the Southern Appalachian region. After the removal of columns containing < 50% missing data, the concatenated aligned individual supercontigs comprised a DNA sequence dataset of 873,609 bases in length. Introducing the polyploid taxa one-at-a-time into the diploid-only alignment resulted in the following datasets. The *V. constablei* + diploid concatenated alignment was 875,481 bases in length, the *V. hirsutum* + diploid concatenated alignment was 874,944 bases in length, and the *V. simulatum* + diploid concatenated alignment was 873,626 bases in length.

***Concatenated Maximum-Likelihood Analysis*—**Concatenated ML analyses of the supercontig loci resulted in overall well-supported topologies (Fig. 1A–C; Supp. Fig. 1A). *Vaccinium constablei* was strongly supported as non-monophyletic, forming a grade with respect to the northern clade of diploid taxa (*V. boreale* + *V. myrtilloides*). *Vaccinium hirsutum* was inferred as monophyletic, with maximum BS support, and sister to the northern clade. *Vaccinium* *simulatum* was maximally supported as monophyletic and sister to the widespread species *V. pallidum*.

Species Tree Analysis**—**ASTRAL analyses resulted in phylogenetic placement of the polyploid taxa consistent with the ML analyses (Supp. Fig. 2). *Vaccinium constablei* was again inferred as paraphyletic, although the branching order of sampled populations differed in the species tree. Whereas its placement in the northern clade was strongly supported (PP = 0.97), relationships within *V. constablei* were low (PP = 0.37–0.49).

Principal Component Analysis and Genetic Structure**—**The best *K* value for the STRUCTURE analyses was determined to be *K* = 7 in each dataset. Given the low number of individuals sampled and exploratory nature of these analyses, we present multiple *K* values as a way to visualize how taxa cluster at these different values. PCA and structure analyses showed overall consistent patterns with the phylogenetic results (Figs. 1, 2). *Vaccinium constablei* showed affinity for the northern clade across PCA axes, although it appears to be somewhat distinct from all sampled taxa. The STRUCTURE analysis (Fig. 2) verified this finding, with *V. constablei* indistinguishable from the northern species *V. boreale* and *V. myrtilloides* at *K* = 4 but becoming distinct by *K* = 5, although with some potential introgression from these northern populations. By *K* = 7, substructure was evident within *V. constablei*. *Vaccinium hirsutum* was found near the northern taxa in PCA space. This taxon was indistinguishable from the northern species at *K* = 4 and *K* = 5 but became a distinct cluster with larger *K* values. *Vaccinium simulatum* showed close affinity with *V. pallidum* in the PCA analysis. STRUCTURE plots grouped *V. simulatum*, *V. pallidum*, and *V. elliottii* in the same cluster at *K* = 4. The inclusion of *V. elliottii* in this group is likely the result of this taxon being a homoploid hybrid species in which *V. pallidum* is one parent. At *K* = 5, *V. simulatum* and *V. pallidum* remained indistinguishable, and at $K = 7$, *V. simulatum* formed a distinct cluster. Combined diploid and polyploid PCA and STRUCTURE plots were consistent with the results of examining the polyploid taxa individually (Supp. Fig. 1B, C).

Discussion

Taxonomy—Through the combination of flow cytometry data, phylogenomic data, and intensive field and herbarium study, we have resolved the taxonomy of the Southern Appalachian species of *Vaccinium* sect. *Cyanococcus*. We recognize seven species as occurring in this region: three diploids, *V. fuscatum*, *V. myrtilloides*, and *V. pallidum*; three tetraploids, *V. angustifolium*, *V. hirsutum*, and *V. simulatum*; and one hexaploid, *V. constablei*. Of these, *V. hirsutum*, *V. simulatum* and *V. constablei* are endemic to the region and thus the primary focus of the current work. The taxonomy of *V. angustifolium*, *V. hirsutu*m, and *V. myrtilloides* has been relatively stable since the work of Vander Kloet, who resolved *V. angustifolium* as a tetraploid and placed *V. brittonii* and *V. lamarckii* (recognized by Camp as distinct from *V. angustifolium*) in synonymy. The recognition of *V. hirsutum* as a species has been uncontroversial ever since its initial publication because of distinctive morphology, particularly the stipitate-glandular trichomes on the hypanthium and fruit. The "lowbush" species *V. myrtilloides* has been recognized as distinct from other species by both Camp (1945) and Vander Kloet (1980, 1983, 2009).

The taxonomy of the other plants of the true blueberry species in the Southern Appalachian region has been highly unstable. From current and ongoing work, our project team has been able to segregate the diploid species *Vaccinium fuscatum* from the remainder of Vander Kloet's "highbush blueberry" (*V. corymbosum*) of eastern North America (Fritsch et al. 2025). This species occurs only rarely in the Southern Appalachian region (e.g., North Carolina, Jackson Co., *P.S. Manos CY-254* [BRIT BRIT698799]). *Vaccinium simulatum*, when considered as a distinct species, has been conflated with *V. constablei*, and *V. pallidum* has been conflated with both *V. altomontanum* and *V. constablei*. Further, the ploidy levels of these taxa have not been firmly established until now. In the current study, we show that the problems in the prior attempts at taxonomic resolution of these taxa mainly resulted from the use of morphological characters that are taxonomically trivial and/or polymorphic within and among these species. We found more reliable characters, most of which newly define the remaining species in the Southern Appalachian region.

The application of the name *Vaccinium altomontanum* has remained ambiguous in prior treatments. Here, we relegate it to the status of an unresolved name (see Taxonomic Treatment) because its type is missing and the description is ambiguous as to application. If or when the type is discovered, we predict that it will be found to be a synonym of *V. constablei*, *V. pallidum*, or *V. simulatu*m; it is highly unlikely to be a distinct species of the section.

In the Taxonomic Treatment below, we focus on the three endemic southern Appalachian polyploids studied and taxonomically recognized here—*Vaccinium constablei*, *V. hirsutum*, and *V. simulatum*. For these species, we provide a key (together with the other species occurring in the Southern Appalachian region), along with synonymy, descriptions, range maps, photographs of diagnostic characters and in-situ plants, and a list of representative specimens cited (Figs. 3–11). We found that each of the species differs in their patterns of genomic variation. Below we discuss the most likely pathways to species origination in this curious regional pool of polyploids.

Evolution and diagnostic traits—*VACCINIUM SIMULATUM*—We confirmed that *Vaccinium simulatum* is tetraploid, monophyletic, and consistently placed as sister to a monophyletic *V. pallidum* across phylogenetic analyses. Population-level analysis based on STRUCTURE ($K = 4$, $K = 5$; Fig. 2) revealed that these two species are not easily separated, strongly suggesting high genomic similarity resulting from a uniquely shared evolutionary history. In the 3D representation from the PCA, the two taxa were only slightly separated on PCA1 (Fig. 1C). Because there is no evidence for admixture with other taxa, and with stable placement across all phylogenetic analyses, our data support Camp's (1945) hypothesis that tetraploid *V. simulatum* is derived from a *V. pallidum*-like diploid ancestor via autoploidy and do not support the idea of Vander Kloet (1980, 1983) for synonymy within his concept of *V. corymbosum*.

This evolutionary pathway of *Vaccinium simulatum* is also supported by several shared characters with *V. pallidum*. One apparent synapomorphy is the tendency of many of the leaf blades within individuals of these species to lack sessile marginal glands (Fig. 9B). In the other species of the section, these glands are commonly present on most or all leaf blades of an individual (e.g., Figs. 3B, 6B). Other possible synapomorphies are: (1) the shared clonal and rhizomatous habit (Fig. 10B), although *V. simulatum* often does not show clonality but instead has clumped, non-rhizomatous stems; (2) smooth or only slightly verrucose stems (versus prominently verrucose; Fig. 9A); and (3) similar flowering phenology, where flowering occurs more or less as leaves emerge and continues until the leaves have attained one-half to full size. The general difference in the size of the plants, leaves, and corollas, with these characters larger in *V. simulatum* than in *V. pallidum*, can be ascribed to their difference in ploidal level and associated gigas effect (Sattler et al. 2016); this extends to the larger size of the leaf stomata and their lower density in *V. simulatum* relative to *V. pallidum* (E. Esparza-Garcia et al. in mss.). *Vaccinium* sect. *Cyanococcus* is the only section in tribe Vaccinieae to produce raised stomata (bumps) on the stems, and this latter difference between the two species is also apparent, with the bumps of *V. pallidum* usually more closely spaced and smaller than those of *V. simulatum* (see Fritsch et al. 2024a).

There are, however, several characters not obviously associated with ploidy that differ between the two species: (1) *Vaccinium simulatum* is often clumped versus rhizomatous in *V. pallidum*; (2) the serrations of the leaf blade margins have generally outcurved outer edges and deep and broad sinuses in *V. simulatum* (Fig. 9D), whereas in *V. pallidum* the serrations are more like those of *V. constablei* in having generally straight outer edges and shallow narrow sinuses; (cf. Fig. 3D) the leaf blade margin is planar in *V. simulatum* (Fig. 9D), versus often revolute in *V. pallidum*; and (4) the leaf blade apex is short-acuminate to acuminate in *V. simulatum* (Fig. 10D, E) versus obtuse to acute or at most slightly acuminate in *V. pallidum*. The geographic ranges of the two species also differ, with *V. simulatum* nearly endemic to the Southern Appalachian region and *V. pallidum* widespread throughout the eastern U.S., although they seem to share similar ecology where their ranges overlap in shallow soils along ridges and outcrops at generally lower elevations (i.e., at the highest elevations in the range of *V. pallidum* and the lowest of *V. simulatum*).

VACCINIUM HIRSUTUM—We confirmed the ploidy (4*x*) and resolved the phylogenetic placement of *Vaccinium hirsutum* in a clade with the diploid northern taxa *V. boreale* and *V. myrtilloides* (Fig. 1A). STRUCTURE plots ($K = 4$, $K = 5$) suggest that *V. boreale*, *V. hirsutu*m, and *V. myrtilloides* are indistinguishable population systems, and that only at $K = 6$ and $K = 7$

does *V. hirsutum* become distinct from other taxa in the northern clade (Fig. 2B). Only in PC3 do we see some level of separation of *V. hirsutum* from a subset of samples of *V. boreale* and *V. myrtilloides* (Fig. 1B). Powell and Kron (2002) suggested an intersectional hybrid origin for *V. hirsutum* based on a single ITS sequence that was placed outside of *Cyanococcus* samples, but this seems unlikely based on our data as well as recent broad-based phylogenomic analyses across Vaccinieae (Becker et al. 2024).

Without any evidence to suggest a more complex origin, we consider *Vaccinium hirsutum* to be another example of an older autopolyploid, perhaps derived from an ancestor of diploid *V. myrtilloides*. These two species uniquely share long outer scales of the vegetative buds (up to 4.0 mm long; Fig. 6B), and this appears to be a synapomorphy uniting these two species. The species also share low-stature habit (generally up to 0.6 m tall), membranaceous leaves with consistently entire leaf blade margin, and consistently hirsute indumentum on the branchlets and leaves (Figs. 7A–C). They differ most obviously in the presence, unique in the section, of stipitate-glandular trichomes on the pedicels, hypanthium, calyx, corolla, and fruit in *V. hirsutum* (Figs. 6E, F; 7E, F). *Vaccinium hirsutum* is also the only species in the section with leaf-like bracts (Fig. 6E). The stems of *V. myrtilloides* are prominently verrucose whereas those of *V. hirsutum* are only faintly so (Fig. 6A). The corollas of the two species differ in size and shape, with those of *V. hirsutum* 6.5–11.1 mm long and narrowed toward the apex (Fig. 6F) and those of *V. myrtilloides* 3–5 mm long and not narrowed toward the apex. Finally, the fruit is without glaucescence in *V. hirsutum* (Fig. 7F) and usually with glaucescence, rarely without, in *V. myrtilloides* (Vander Kloet 1988; Voss 1996).

Vaccinium constablei—*Vaccinium constablei* is phylogenetically distinct as well, but seemingly more divergent than *V. hirsutum* from the core of the northern clade. Both in

STRUCTURE analysis ($K = 5$) and in PC space, *V. constablei* begins to separate from the northern clade and also shows some differentiation among accessions (Figs. 1A, 2A). All analyses suggest no admixture with taxa outside of the northern clade, and thus the data do not support Camp's original hypothesis for an allopolyploid origin derived from a putative autotetraploid of diploid *V. vacillans* (confusingly referred to by Camp as *V. altomontanum*) and *V. simulatum* (see Camp 1945: p. 271) as well as our re-statement of his idea as an autopolyploid series of 2*x* *V. pallidum*, 4*x* *V. simulatum*/*V. altomontanum*, and 6*x* *V. constablei*. This lack of support is corroborated by differences in morphology in *V. constablei* versus both *V. pallidum* and *V. simulatum*, i.e., the prominently verrucose stems (Fig. 3A; versus smooth to merely faintly verrucose) and the consistent presence of sessile glands on the leaf margin (Fig. 3B; versus frequent absence). The genetic and morphological profiles of *V. constablei* suggest yet another example of an old autopolyploid derived from an extinct progenitor within the northern clade, as appears to be the case for the more coastal polyploids *V. ashei* and *V. virgatum* (Fritsch et al. 2024b; Weakley et al. 2024).

Based on the three test cases studied here, we observe no evidence for allopolyploidy in the evolution of these taxa. Among the diploid taxa we sampled, *Vaccinium elliottii* is a putative homoploid hybrid species (Fig. 2; Supp. Fig. 1C) and provides an example of what we would expect to observe for an allopolyploid species origin. Instead, the results suggest autopolyploid origins for each taxon, likely through the production and fusion of unreduced gametes (Ortiz et al. 1992). In contrast to our preliminary results in other diploid-tetraploid cases where we have observed patterns consistent with more recent and possibly repeated origins of 4*x* cytotypes (e.g., *Vaccinium fuscatum* (2*x*) and *V. corymbosum* (4*x*; Fritsch et al. 2025); *V. boreale*, 2*x* and *V. angustifolium*, 4*x* (P. W. Fritsch et al. in mss.), the Southern Appalachian tetraploids are each distinct and cohesive genomically, suggesting single origins, and placed as monophyletic lineages with more distant relationships to potential diploid progenitors. We can also rule out the allopolyploid derivation of hexaploid *V. constablei* involving contributions of the more northerly tetraploid, *V. angustifolium,* given that we sampled its likely diploid progenitor, *V. boreale*. In sum, *V. constablei* has distant affinities with diploid and tetraploid taxa in the northern clade, but with more genotypic heterogeneity, possibly related to its discontinuous distribution.

Taxonomic Treatment of the Polyploid Species of *Vaccinium* sect. *Cyanococcus* Endemic or near-endemic to the Southern Appalachian Region

Key to the Species of *Vaccinium* sect. *Cyanococcus* Occurring in the Southern Appalachian Region

In addition to the three endemic polyploids, the key includes the diploids *Vaccinium fuscatum*, *V. myrtilloides*, and *V. pallidum*, and the tetraploid *V. angustifolium*. These are the only other species of *V.* sect. *Cyanococcus* that occur in the Southern Appalachian region, none of which are endemic. In the Southern Appalachian region, *V. fuscatum* occurs in Alabama, Georgia, North Carolina, and Tennessee; *V. myrtilloides* in Virginia and West Virginia; *V. pallidum* in all states of the region; and *V. angustifolium* in North Carolina, Virginia, and West Virginia. See Table 1 for the main differences among the three Southern Appalachian polyploid taxa.

1. Plants 0.2–1.3(–1.8) m tall; above-ground stems without eruptive periderm.

2. Inflorescence bracts planar, leaf-like; pedicels, hypanthium, calyx, corolla, and fruit bearing long-stipitate-glandular trichomes.. *V. hirsutum*

2. Inflorescence bracts cucullate; pedicels, hypanthium, calyx, corolla, and fruit not bearing stipitate-glandular trichomes.

3. Outer vegetative bud scales 1.9–4.0 mm long; leaves membranaceous; abaxial surface of leaf blade densely hirsute.....................................*V. myrtilloides*

3. Outer vegetative bud scales 0.9–2.5 mm long; leaves chartaceous; abaxial surface of leaf blade glabrous or usually not densely pubescent, any hirsute portion restricted to major veins.

4. Stems smooth or faintly verrucose; abaxial surface of leaf blades dull, pale green to whitish green; sessile glands of leaf blade margin often absent on some leaves; corolla usually slightly narrowed toward apex (slightly curved in outline).........................*V. pallidum*

4. Stems prominently verrucose; abaxial surface of leaf blades usually shiny and green, occasionally dull and pale green to whitish green; sessile glands of leaf blade margin present on all leaves, or occasionally replaced by stipitate glands on some leaves; corolla usually not narrowed toward apex (straight in outline)... *V. angustifolium*

1. Plants (0.3–)1.0–5.0 m tall; above-ground stems three years old or older with eruptive periderm.

5. Leaves thin-chartaceous; leaf blade margins planar distally beyond base at least on some leaves or rarely slightly revolute, sessile glands often absent, marginal teeth (not including stipitate gland) when present with generally outcurved outer edges and deep and broad sinuses..*V. simulatum*

5. Leaves chartaceous or thick-chartaceous; leaf blade margins revolute or rarely planar, sessile glands usually present on most leaves, marginal teeth (not including stipitate gland) when present with generally straight outer edges and shallow or narrow sinuses.

 6. Plants not clonal (stems clumped); stems faintly verrucose, bumps closely spaced; outer vegetative bud scales 1.9–4.0 mm long, glabrous or more often puberulent; abaxial surface of leaf blade in situ dull pale green.. *V. fuscatum*

 6. Plants clonal; stems prominently verrucose, bumps widely spaced; outer vegetative bud scales 1.5–2.5 mm long, glabrous; abaxial surface of leaf blade in situ dull whitish green to grayish whitish green or subglaucous...*V. constablei*

1. VACCINIUM CONSTABLEI A.Gray, Amer. J. Sci. Arts 42: 42. 1842 [as "*constablæi*"]. TYPE: USA. North Carolina or Tennessee: "In summo jugo 'Roan Mountain' dicto, (Tennessee et Carolina Septentrionali,) ad alt. 6000 pedes" [protologue], In monte "Roan" dicto, Carolina Septentrionalis, July 1841, *A. Gray and J. Carey s.n.* (lectotype, here

designated: GH 00015915, the three flowering branchlets at the bottom of the sheet [image!]; isolectotypes: GH 00015916 [left-hand collection on sheet] [image!], K K000780843 [image!], NY 00010582!, NY 00010583!, NY 02543220! [right-hand element on sheet], US 00116898 [image!]).

Shrubs, deciduous, clonal by rhizomes, 0.3–2.1 m tall. Branchlets (second and third year) in situ red to reddish brown, older branchlets, and stems, often gray to brown; eruptive periderm common on third-year and older branchlets and stems. Current-year branchlets without stipitate-glandular trichomes, with white eglandular (occasionally sparse) trichomes ± in 2 to several lines, trichomes generally curved, up to 0.10–0.38 mm long; second-year branchlets prominently verrucose with widely spaced bumps, with white eglandular trichomes or glabrous, trichomes ± in lines, not broken; outer vegetative bud scales 1.5–2.5 mm long, glabrous. **Leaves** with petiole 0.8–3.0 mm long, sulcate and/or margins narrowly winged to base, abaxially glabrous or pubescent, adaxially pubescent; leaf blade elliptic, slightly ovate-lanceolate, or slightly obovate-oblanceolate, 3.0–6.7 × 1.4–3.0 cm, chartaceous, abaxial surface in situ dull, whitish green to grayish whitish green or subglaucous, in sicco often whitish brown or subglaucous, usually glabrous or occasionally with white eglandular trichomes proximally along midvein (and then occasionally secondary veins; trichomes straight to curved, up to 0.34–0.44 mm long), without stipitate-glandular trichomes, adaxial surface in situ green to pale green, in sicco often brown, with eglandular trichomes on midvein proximally and often secondary veins, otherwise these lacking, without stipitate-glandular trichomes, base cuneate to subrounded, margins serrulate with each tooth tipped by a stipitate gland to subentire or entire, at least sparsely ciliate-pubescent at least on some leaves, occasionally only so at very base, rarely glabrous or glabrate throughout, narrowly revolute throughout on at least some leaves or rarely planar, tapering into petiole, apex acute to acuminate, sessile marginal glands usually present on most leaves, 0.11–0.24(–0.30) mm wide (width parallel to margin), marginal teeth (not including stipitate gland) when present with generally straight outer edges and shallow narrow sinuses. **Inflorescences** axillary or pseudoterminal racemes, borne at ends of branchlets singly or in clusters of 2 and also occasionally in a penultimate leaf axil, 1- to 12-flowered, 2- to 12-flowered, rachis 1–12 mm long, bracts white often flushed pink, broadly elliptic, obovate, oblanceolate, or subrotund, cucullate, glabrous, not stipitate-glandular, margins eciliate or ciliate, pedicels glabrous or puberulent, bracteoles white often flushed pink, narrowly elliptic to linear, glabrous, margins eciliate or ciliate; flowering just as leaves emerge or just after and continuing until leaves have attained full size or nearly so. **Flowers**: hypanthium 0.7–2.4 × 2.0–3.8 mm, glabrous, with glaucescence; calyx connate portion 0.2–1.0 mm long, lobes 1.2–2.3 × 1.5–2.5 mm, deltoid to ± oblong-hemispherical, glabrous, with glaucescence, margin eciliate or slightly ciliate, apex acute to subrounded; corolla whitish green, creamy green, white flushed pink, pale orange, or creamy yellow flushed pink, broadly cylindrical to short-campanulate, 5.2–8.0 × 4.4–7.0 mm, glabrous both sides except rarely with up to a few short eglandular trichomes on inner lobes; stamens 4.7–6.5 mm long; filaments 2.6–3.9 mm long, glabrous on surface, white-hirtellous marginally, trichomes to 0.34–0.56 mm long; anthers 2.3–3.5 mm long, cells 1.0–1.5 mm long, tubules 1.2–2.1 mm long; style exserted, 6–7 mm long, glabrous. **Fruits** at maturity blue, with glaucescence, subglobose, 4–10 mm diam. Figs. 3–5.

Chromosome Number—*Vaccinium constablei* is a hexaploid ($2n = 6x = 72$).

Phenology—The species flowers from latest April to mid-June, and fruits from latest July to mid-August.

Distribution and Habitat**—***Vaccinium constablei* is endemic to the Southern Appalachian region, in the Blue Ridge, Valley and Ridge, and Central Appalachian Ecoregions. It ranges from eastern and southern West Virginia and western Virginia south to western North Carolina, eastern Tennessee, and extreme-northeastern Georgia, occurring at elevations ranging from (295 to)1053 to 1846 m, between 34.5°N and 38.5°N (Fig. 6). Habitats include patches between bare rock, rock outcrops, grassy balds, heath balds, wind-swept scrub, recovering burned-over areas, stunted forests, pine forests, and mixed forests. It has the highest average elevational range of the species of *V.* sect. *Cyanococcus* and is often sympatric with *V. simulatum* (see below).

Proposed Common Name**—**Because the circumscription and the application of scientific names for this species has been uncertain until now, it has not been clear which common names have been applied to what actually is this species. Therefore, it seems best to use Camp's proposed common name, "Constable's Blueberry" derived directly from the epithet for this species "...in honor of James Constable, who (with John Carey) was Gray's associate on the trip to Roan Mountain, in 1841. In his discussion Gray states that the species was first noticed by Mr. Constable." (Camp 1945: p. 241).

Notes**—**The stature of the fruiting specimens from Giles Co., Virginia [Mann's Bog, 28 Jul 1966, *A. Crooks 375* (VDB); along John's Creek Trail, Salt Pond Mt., 17 Aug 1966, *A. Crooks 483* (VDB; 3 sheets)] are indicated on the labels as 1.8 and 1.3 m tall, respectively. These are thus at the extreme upper end of the species' height but are consistent with *V. constablei* in essentially all other respects. Another specimen from Giles Co., *G.J. Galletta and C.R. Bell PI346669 (18453)* (BRIT; see below) is indicated as (0.3–)0.5 m tall, more typical in height.

No specimens were cited in the protologue of *Vaccinium constablei*, nor was there an accompanying illustration. By 1842 Asa Gray was based at GH; there are two sheets of the presumed type material of *V. constablei* at GH, together consisting of branchlets in flower, those just post-anthesis without corollas, and those with young fruits. Fruiting occurs distinctly later than flowering in the species of *Vaccinium* sect. *Cyanococcus*, and so it is likely that these represent three different gatherings (different times of collection, whether or not at the same locality on Roan Mountain). Therefore, the designation of a lectotype is warranted. We have designated the flowering material (i.e., with corollas present) on sheet GH 00015915 (the three branchlets toward the bottom of the sheet) as the lectotype of *V. constablei* because the protologue only mentions flowers and not fruit, and GH 00015915 contains better material in that it has three flowering branchlets whereas 00015916 has only one. Camp noted on the sheet (in his handwriting) that there is variation among branchlets on the sheet in leaf characters (glabrous versus pubescent, margins serrulate or entire) and stem pubescence (glabrous versus pubescent in lines). We consider this to represent variation within *V. constablei* among individuals. To the extent that this is relevant for lectotypification, there is no evidence to suggest that the flowering individuals on the sheet are from separate gatherings. The isolectotype NY 02543220 ("Roan Mt Dr. Gray," originally from the Princeton University Herbarium and deposited at NY in 1945) is the right-hand element (branchlet) on the sheet only; the left-hand element (branchlet) is *V. myrtilloides*.

***Representative Specimens Examined*—USA.**—GEORGIA: Rabun Co., top of Rabun Bald Mt., 1 Jun 1968, *S. B. Jones 15488* (VDB BRIT311459).

NORTH CAROLINA. Alleghany Co., near Sparta, 1 Aug 1937, *P. O. Schallert 12316* (SMU BRIT427864). Ashe Co., Bluff Mt., Perkins Rock, 29 May 1965, *G. E. Tucker 2283* (SMU

BRIT427737). Avery Co., 1.1 mi. S of Carver [Carver's] Gap, 6000 ft. [ca. 5100 ft.], 14 Jul 1982, *R. Carter 3204* (VDB BRIT312594). Buncombe Co., near the summit of Craggy Mt., 6000 ft., 8 Jun and 12 Aug 1897, *Biltmore Herbarium 4751a* [(SMU BRIT446592). Burke Co., Wisemans [Wiseman's] Overlook, E of Old NC 105 (Forest Service Rd. 1238) on W side of Linville Gorge, 3400 ft., 9 May 2018, *C. N. Horn 23602* (NBYC NBYC020509 [i]). Caldwell Co., Grandmothers Mountain, 9 Jun 1935, *O. Veerhoff 342* (NCSC NCSC00085275). Haywood Co., Blue Ridge Parkway, near mile post 440, "Blueberry Bald," 35.433436°, −83.039195°, 13 Jun 2017, *P. S. Manos CY-053* (BRIT BRIT698684). Jackson Co., along dirt road to top of Yellow Mountain, near Jackson-Macon county line E of Gneiss and W of Norton, 2 Jun 1985, *D. D. Taylor 8854* (BRIT NLU0141163). Macon Co., Fodderstack and Little Fodderstack Mts., 23 Jun 1974, *E.W. Wood 1244* (BRIT BRIT311462). Mitchell Co., Round Bald Mt., NC 261, Pisgah National Forest at Roan Mt., 8 Jun 1977, *R. Dale Thomas 52951* (BRIT NLU0140585). Stokes Co., Moore's Knob, near top, 36.399186°, −80.282819°, 8 Aug 2017, *P. S. Manos CY-071* (BRIT BRIT698696). Swain Co., N.C. Road leading to Mile High Mtn. (Heintooga Ridge Spur Rd.) at Laurel Gap, 0.3 mi. off Blue Ridge Pkwy, 18 Aug 1967, *G. J. Galletta and D. T. Lambeth PI346603* (7-63-3b) (GA GA201283). Transylvania Co., NC Blue Ridge Parkway, 2.6 mi. S of loc 7-54, 15 Aug 1967, *G. J. Galletta and D. T. Lambeth PI346459 (7-55-9)* (VDB BRIT311375). Watauga Co., Grandfather Mt. below Grandfather Profile and E of Profile Trail, 3 Jun 1989, *T.F. Wieboldt 6905* (WILLI 55428).

TENNESSEE: Carter Co., Roan Mountain Park, Appalachian Trail from Windy Gap parking lot up to the top of the bald, 31 May 2010, *M. B. Martin 12* (ETSU ETSU034680). Greene Co., Rocky Fork, Bald inholding, 4600 ft., 30 Jul 2009, *F. Levy and T. McDowell*

RF1529 (ETSU ETSU007250 [i]). Unicoi Co., Appalachian Trail Rd. at Pleasant Garden, Unicoi Quad, 4800 ft., 3 Jul 1986, *J. Whitaker 56-86* (BRIT BRIT110850).

VIRGINIA: Augusta Co., Bald Mt. along fire road to Green Pond, 25 Jun 1966, *R. S. Freer and G. W. Ramsey 3988* (NLU NLU0141258). Giles Co., campground along Appalachian Trail toward Stoney Creek Lookout, 0.3 mi. NE of Giles Co., Rd. 613, 4.6 mi. from Mountain Lake Biological Station, 26 Jul 1966, *G. J. Galletta and C. R. Bell PI346669 (18453)* (BRIT NLU0446083).

WEST VIRGINIA: Fayette Co., Meadow River at Deegans, US Rte. 19, 15 Jun 1986, *W. N. Grafton s.n.* (WVA 077466). Monroe Co., SR 8, Moncove Lake Road, Moncove State Park, Roxalia, 2510 ft., 29 Jul 2019, *K. Campbell KC08013* (WVA 179778). Nicholas Co., mouth of Meadow River and 1 mi. downstream, 10 May 1986, *W. N. Grafton s.n.* (WVA 077617). Pendleton Co., top of North Fork Mt., 4000 ft., 10 May 1952, *J. F. Clovis s.n.* (WVA 53697). Webster Co., Camp Caesar, near Cowan, near lake, 17 Jun 1994, *W. N. Grafton s.n.* (WVA 077472).

2. VACCINIUM HIRSUTUM Buckley, Amer. J. Sci. Arts 45: 175. 1843. *Cyanococcus hirsutus* (Buckley) Small, Man. S.E. Fl. [Small]: 1016. 1933. TYPE: USA. NORTH CAROLINA: Cherokee Co, mountains, without date, *S. B. Buckley s.n.* (lectotype, here designated: MO 2543485 [image!]; probable isolectotypes: GH 00015923 [image!], GH 01154998 [image!], MO 2543486 [image!], NY 00010593!, NY 00010594!, NY 00010595!, PH 00028663 [image!], P (n. v.), WIS v0257088WIS [image!]).

Shrubs, deciduous, clonal by rhizomes, 0.4–0.6 m tall. Stems and branchlets in situ green to near base of plant; eruptive periderm absent or sparse. Current-year branchlets without stipitate glandular trichomes, hispid with white eglandular trichomes throughout, trichomes straight, up to 0.66–0.96 mm long; second-year branchlets faintly verrucose with moderately spaced bumps, largely obscured by pubescence, white-hirsute with trichomes throughout, trichomes not broken; outer vegetative bud scales 2.3–4.0 mm long, puberulent. **Leaves** with petiole 0.5–2.4 mm long, sulcate and/or margins narrowly winged to base, pubescent both sides; leaf blade elliptic, slightly ovate, slightly lanceolate, or slightly oblanceolate, 2.2–6.2 × 1.2–2.5 cm, membranaceous, abaxial surface in situ lustrous to shiny, green to pale green, in sicco occasionally brown, with white mainly straight (especially on major veins) trichomes up to 0.64–0.84 mm long, without stipitate-glandular trichomes or rarely with a few scattered on midvein, adaxial surface in situ green, in sicco occasionally brown, with eglandular trichomes, without stipitate-glandular trichomes, base cuneate to subrounded, margins entire, ciliate-pubescent, narrowly revolute on at least some leaves, tapering into petiole, apex obtuse to acuminate, sessile marginal glands present on most leaves, 0.06–0.24 mm wide (width parallel to margin). **Inflorescences** axillary or pseudoterminal racemes, borne near ends of branchlets singly or in clusters of 2, 1- to 12-flowered, rachis 4–35 mm long, bracts usually green and leaf-like, occasionally scarious and smaller, oblanceolate to oblong-oblanceolate, planar, glabrous or pubescent, margins usually ciliate and occasionally stipitate-glandular, pedicels white-pubescent and stipitate-glandular, bracteoles green or scarious, lanceolate or oblanceolate to linear-lanceolate, glabrous or white-pubescent, margins ciliate and often stipitate-glandular; flowering after the leaves have attained full size. **Flowers**: hypanthium 0.8–2.4 × 1.8–3.0 mm, with dense long-stipitate-glandular trichomes and occasionally white eglandular trichomes; calyx connate portion 0.2–1.1 mm long, lobes deltoid, 1.0–2.4 × 0.9–2.0 mm, margin eciliate or ciliate and often stipitate-glandular, apex acute to occasionally obtuse; corolla white or pink, urceolate-cylindrical, often slightly dilated distally, apex usually slightly constricted, 6.5–11.1 × 3.1–6.1 mm, with at least sparse stipitate-glandular trichomes and white eglandular trichomes outside, with white eglandular trichomes inside distally; stamens 5.2–8.9 mm long; filaments 2.7–4.8 mm long, white-hirsute on surface and more densely so marginally, trichomes to 0.60–1.2 mm long; anthers 2.7–5.1 mm long, cells 1.0–1.6 mm long, tubules 1.3–4.2 mm long; style exserted, 6–11 mm long, hirsute. **Fruits** at maturity black, without glaucescence, subglobose, 6–25 mm diam. Figs. 6–8.

Chromosome Number—*Vaccinium hirsutum* is a tetraploid ($2n = 4x = 48$).

Phenology—The species flowers from mid-May to late June, and fruits from mid-July to latest August.

Distribution and Habitat—*Vaccinium hirsutum* is endemic to the Southern Appalachians, specifically the Blue Ridge, Valley and Ridge, and Southwestern Appalachian Ecoregions. It ranges from western North Carolina and eastern Tennessee to northern Georgia, occurring at elevations ranging from 430 to 1500 m, between 34°N and 36.5°N (Fig. 8). Habitats include rocky ridgetops, acidic woods, dry or mesic woods, most rocky slopes, low wet areas, along creeks and bogs.

Proposed Common Name—Weakley and Southeastern Flora Team (2023) recorded the common names of "Woollyberry" and "Hairy Blueberry" for *Vaccinium hirsutum*. Although "Woollyberry" is appropriate for this species because of the presence of long-stipitate-glandular trichomes on the mature fruit, "Hairy Blueberry" does not seem as apropos because other species in the section, e.g., *V. fuscatum*, are also hairy. In any case, we propose the common name used by Camp (1945) of “Hairy-fruited Blueberry” because it is the only species of the section that has trichomes on the fruit.

Notes**—**Vander Kloet (1989) indicated the type of *Vaccinium hirsutum* as “HT.: U.S.A. North Carolina, Cherokee Co, Buckley s.n. (P!).” This might be considered an “inadvertent lectotypification” except for the fact that in the methods section in which this typification was presented Vander Kloet clearly distinguished “...holotype (HT.), lectotype (LT.) or neotype (NT.)...” However, no specimens were cited in the protologue of *Vaccinium hirsutum*, nor was there any accompanying illustration. Therefore, designation of a lectotype is still warranted and needed for *V. hirsutum*.

Buckley’s original herbarium is now at MO, with duplicates distributed among many herbaria (Dorr 1997). Two specimens of *Vaccinium hirsutum* collected by Buckley are known to us to be housed at MO. One (MO 2543486) has “In montibus Carolinae et Georgiae, legit S.B. Buckley” printed on the label, and “1842” written on it. Buckley is known to have collected in the Southern Appalachian region in 1842 (Peterson 1989). The other specimen (MO 2543485) has “Shaw School of Botany” printed on the label and “Mts. of Cherokee Co, North Carolina, S.B. Buckley” written on it, presumably in Buckley’s handwriting. “The S. B. Buckley Herbarium” is stamped on the sheet. Buckley’s herbarium was located at the Shaw School of Botany in St. Louis and later transferred to MO, where it now resides (Dorr 1997). Although this specimen bears no date, on two of the probable duplicates of Buckley’s collection of *V. hirsutum* the year 1842 is written. Based on the evidence above, we have designated MO 2543485 as the lectotype of *V. hirsutum*. Other specimens of *V. hirsutum* collected by Buckley have labels with “In montibus Carolinae et Georgiae,” “Cherokee Mts. near Hiwassee Gap,” or “Cherokee Co. N. Car.” Because there is no indication of precise date of collection on these specimens, it is not clear as to whether they form part of the same gathering as the lectotype. However, the similar appearance of the specimens to the lectotype suggests that they are probable lectotypes and are indicated as such here. Despite an indication of collection in "Georgiae" on the labels of some of the isolectotypes, apparently there is no evidence that Buckley collected in Georgia in 1842 (Petersen 1989).

***Representative Specimens Examined*—USA.**—GEORGIA: Dawson Co., ca. 0.5 mi. above Amicolola Falls, 4 Jun 1942, *W. H. Duncan 5311* (GA GA058524, SMU BRIT424374). Fannin Co., 0.2 mi. NW of Winding Stair Gap, 3150 ft., 27 May 1953, *W. H. Duncan 16402* (SMU BRIT 424376). Gilmer Co., Appalachian Trail to SW of summit of Springer Mt., S of Forest Service Road 42, 14 Jun 2017, *C. N. Horn 22993* (CLEMS CLEMS0081065 [i]). Lumpkin Co., Vogel State Park below Neal Gap, 16 Jun 1940, *D. Eyles 7157* (GEO 13968 [i]). Murray Co., 8.5 km (5.3 mi.) E of US Rte. 411 on GA Rte. 2 (Forest Service Road 16), E of Cisco, 9 May 1979, *E. W. Wood 4110* (VDB BRIT311757). Union Co., Cooper Creek N of the Cooper Creek Recreation Area, 14 Jul 1975, *D. E. Boufford and E. W. Wood 17265* (VDB BRIT311758).

NORTH CAROLINA: Cherokee Co., near summit of mountain, Sandy Gap, Unicoi Mts., 27 May 1956, *H. E. Ahles 13147* (VDB BRIT311759). Graham Co., Little Snowbird Creek, along road 1.0 mi. below Cold Spring Gap, 13 Aug 1972, *J. L. Collins 1331* (VDB BRIT311761). Swain Co., Gregory Bald, 8 Aug 1935, *B. W. Wells s.n.* (DUKE DUKE10100577 [i]).

TENNESSEE: Bledsoe Co., along Pitts Gap Road, 29 May 2000, *M. Rhinehart 199* (TENN TENN-V-0169393 [i]). Blount Co., near Gregory's Bald, 11 Aug 1934, *T. G. Harbison s.n.* (VDB BRIT112772). McMinn Co., Cherokee National Forest, Forest Service road just E of Bowers Spring on Starr Mt., Mecca Quad, 1700 ft., 21 May 1981, *B. E. Wofford et al. 81-2*

(VDB BRIT112777). Monroe Co., near Beech Gap, Cherokee National Forest, 30 May 1940, *A. J. Sharp 703* (VDB BRIT112776). Polk Co., roadside ca. 400 yds. from Sassafras Mt. Lookout Tower, 23 Jun 1972, *L. Collins 899* (VDB BRIT112778). Rhea Co., Richland Creek Valley above Dayton, *R. E. Shanks et al. 4339* (VDB BRIT112784). Sequatchie Co., G.S. Camp, May 1931, *E. McGilliard s.n.* (UCHT UCHT022688 [i]). Sevier Co., Cades Cove, Smoky Mts., Aug 1930, *E. McGilliard s.n.* (SMU BRIT424379).

3. VACCINIUM SIMULATUM Small, Fl. S.E. U.S. [Small]: 896, 1336. 1903. *Cyanococcus simulatus* (Small) Small, Man. S.E. Fl. [Small]: 1015. 1933. TYPE: USA. Kentucky: Harlan Co., Big Black Mountain, Aug 1893, *T. H. Kearney Jr. 82* (lectotype, designated by Uttal 1986: NY 00010608!; isolectotypes: F acc. no. 255170 [image!], GH 00015931 [image!], US 00997453 [image!], US 01049753 [image!]).

Vaccinium carolinianum Ashe, Bull. Torrey Bot. Club 50: 359. 1923. TYPE: USA. North Carolina: Pink Beds, 14 Jul 1916, *W. W. Ashe 28* (lectotype, here designated: NCU NCU00096504 [image!]).

Shrubs, deciduous, 1-stemmed or clumped 2- to 5-stemmed, or often apparently clonal by rhizomes in patches 5 m diam. or more, 0.6–3.0 m tall. Branchlets in situ green until ca. third year, older branchlets and stems gray to brown; eruptive periderm common on third-year and older branchlets and stems (not often collected for herbarium material). Current-year branchlets without stipitate-glandular trichomes, with white eglandular trichomes ± in 2 to several lines or occasionally ± throughout, trichomes straight to curved, 0.16–0.40 mm long; second-year branchlets faintly verrucose with moderately spaced bumps, with white eglandular trichomes or occasionally glabrous, trichomes ± in lines or rarely ± throughout, not broken; outer vegetative bud scales 1.3–2.4 mm long, glabrous. **Leaves** with petiole 0.4–2.3 mm long, sulcate and/or margins narrowly winged to base, abaxially glabrous or pubescent, adaxially pubescent; leaf blade elliptic, slightly ovate, or slightly obovate, 3.2–8.4 × 1.4–3.9 cm, thin-chartaceous, abaxial surface in situ dull, pale green to whitish green or subglaucous, in sicco often brown, glabrous or with white eglandular trichomes proximally along midvein (and then often also along secondary veins, often glabrate, rarely pubescent between major veins but glabrate there, trichomes usually straight, especially on major veins, or less often curved, up to 0.38–0.48 mm long), without stipitate-glandular trichomes, adaxial surface in situ green to pale green, in sicco often brown, with eglandular trichomes on midvein and often secondary veins, otherwise these lacking, without stipitate-glandular trichomes or rarely several scattered near margin, base broadly cuneate to rounded, margins entire, subentire, or serrulate with each tooth tipped by a stipitate gland, the very base glabrous or ciliate-pubescent, distally beyond usually glabrous or occasionally ciliate-pubescent on at least some leaves, slightly and narrowly revolute to planar at base and planar distally beyond base or rarely slightly revolute, tapering into petiole, apex short-acuminate to acuminate, sessile marginal glands often absent, 0.08–0.16(–0.24) mm wide (width parallel to margin), marginal teeth (not including stipitate gland) when present oriented toward leaf apex with generally outcurved outer edges and deep and broad sinuses. **Inflorescences** axillary or pseudoterminal racemes, borne at ends of branchlets singly or in clusters of 2, also occasionally in the adjacent leaf axils below and often singly on short leafless shoots, 2- to 10-flowered, rachis 3–19 mm long, bracts white often flushed pink, broadly elliptic, obovate, oblanceolate, or subrotund, cucullate, glabrous, not stipitate-glandular, margins eciliate, pedicels glabrous, bracteoles white often flushed pink, narrowly elliptic to linear, glabrous, margins eciliate; flowering as leaves emerge or just after and continuing until leaves have attained ca. ½ to full size. **Flowers**: hypanthium 0.8–2.4 × 1.2–3.4 mm, glabrous, with or without glaucescence; calyx connate portion 0.2–1.0 mm long, lobes deltoid to ± hemispherical, 0.7–1.9 × 1.2–2.2 mm, with or without glaucescence, margin eciliate or slightly ciliate, apex acute to subrounded; corolla white, creamy white, green, greenish white, or yellowish white, often flushed or striped pink to red, short-campanulate to cylindrical-campanulate, 4.5–7.0 × 4.0–7.5 mm, glabrous both sides except very rarely with up to a few short eglandular trichomes on inner lobes; stamens 4.1–6.0 mm long; filaments 2.2–3.8 mm long, glabrous on surface, white-hirtellous marginally, trichomes to 0.20–0.44 mm long; anthers 2.7–3.8 mm long, cells 1.0–1.8 mm long, tubules 1.2–1.9 mm long, style exserted, 5–6 mm long, glabrous. **Fruits** at maturity black to blue, with or without glaucescence, subglobose, 4–10 mm diam. Figs. 9–11.

Chromosome Number—*Vaccinium simulatum* is a tetraploid ($2n = 4x = 48$).

Phenology—The species flowers from late March to early June, and fruits from late June to late August. Early expression of purple-red leaf spot caused by *Phyllosticta vaccinii* Earle (Ascomycota) is common in this species.

Distribution and Habitat—*Vaccinium simulatum* had been regarded as an Appalachian endemic (e.g., Weakley and Southeastern Flora Team 2023) but it is clear from our work that it also extends both east and west of the region (Fig. 11). Thus, the species is nearly endemic to the Southern Appalachian region, occurring in the Blue Ridge, Valley and Ridge, and Southwestern and Central Appalachian Ecoregions, with a few outlying localities. It ranges from southern Ohio and southern West Virginia to eastern and central Kentucky, south through eastern and central Tennessee to northeastern Mississippi and northeastern Alabama, east to far northern

Georgia, and north to far western South Carolina, western North Carolina, and western Virginia, occurring at elevations ranging from (160 to)300 to 1950 m, between 33°N and 39.5°N, and with the largest range of the three endemic species of *V.* sect. *Cyanococcus* in the Southern Appalachians (Fig. 11). Habitats encompass a variety of vegetation, terrain, and substrates, including wind-swept scrub, sandstone outcrops, shale bluffs, xeric talus slopes, dry exposed shale ridgetops, heath balds, heath thickets, cherty bedrock, moist rocky soils, seepy rocky areas, dry acidic forests, acidic cove forests, mixed forests, hemlock forests, granitic forests, oak forests, broadleaved forests, oak-hickory forests, oak-pine forests, edges of seepy forested areas, moist forests, low sandy forests, hollows, bottomland hardwood forests, swamp forests, high-elevation bogs, sandy floodplains, stream valleys, and stream thickets. It may occur in sympatry with *V. hirsutum* at lower elevations in the Central Appalachian Ecoregion and with *V. constablei* from 1100 to 1900 m in Blue Ridge Ecoregion.

***Proposed Common Name*—**Camp (1945) applied common names with the words "highbush" or "lowbush" rather freely to various species of *Vaccinium* sect. *Cyanococcus*, and Vander Kloet (1988, 2009) divided the section into "highbush" (> 1 m tall) and "lowbush" (< 1 m tall) types. However, in fact many of the species in the section show a range of heights that overlap these categories and as such do not fit appropriately into either. Furthermore, phylogenetic data from this and previous studies (Fritsch 2024b, Weakley et al. 2024, the present study) provide substantial evidence against monophyletic "highbush" and "lowbush" clades as these terms are traditionally applied. Of course, common names do not follow a strict set of rules for their use and application but it seems best that, whenever possible, they reflect some clear attribute of species. Therefore, we suggest that common names of the species of *V.* sect. *Cyanococcus* that incorporate the words "high," "highbush," "low," or "lowbush" should be used carefully. *Vaccinium simulatum* is one of the species with a range of heights that overlaps the "highbush" and "lowbush" categories (0.6–3.0 m tall) and so the common names recorded in Weakley and Southeastern Flora Team (2023) of "Mountain Highbush Blueberry" and Camp (1945) of "Upland Highbush Blueberry" are not ideal. Therefore, we propose the truncated common name of "Mountain Blueberry" for *V. simulatum*.

Notes—We opted to name this species conventionally (*Vaccinium simulatum*) as recommended for autopolyploids meeting criteria of various species concepts (Judd et al. 2007; Soltis et al. 2007; Eriksson et al. 2017), as opposed to other proposed naming schemes (see Soltis et al. 2007; Kadereit et al. 2012). In this case, the autotetraploid and its apparent diploid progenitor are each monophyletic, morphologically distinguishable, and have distinct geographic ranges. Each already has a species name, and so the addition of a prefix to the epithet ("diplo-" for the diploid, or "tetra-" for the tetraploid) cannot be readily conducted under the rules of nomenclatural priority.

Camp considered *Vaccinium carolinianum* Ashe to be a hybrid between *V. simulatum* and his concept of *V. altomontanum* but there is no good empirical morphological evidence for hybridization, not the least of which because the type of *V. altomontanum* is missing and the description is ambiguous. The type of *V. carolinianum* falls within the variation of *V. simulatum*. Because two collections were cited in the protologue, selection of a lectotype for *Vaccinium carolinianum* Ashe is warranted. We selected *W.W. Ashe 28* from NCU as the lectotype because we could not locate a specimen of the other collection cited, i.e., North Carolina, Transylvania Co., Pink Beds, 27 May 1916, *W.W. Ashe s.n.*

***Representative Specimens Examined*—USA.**—ALABAMA: Blount Co., Mullbery [Mulberry] Fork of Warrior River where crossed by Interstate hwy., 20 mi. S Cullman, 10 May

1966, *R. Kral 26632* (VDB BRIT110976). Cherokee Co., NE of Leesburg, ca. 2.7 mi. W of jct. AL 275 and Little River on AL 68, 25 Mar 1976, *R. D. Whetstone 7608* (NLU NLU0141024). DeKalb Co., N of Cedar Bluff, ca. 2 mi. S of AL 35 on Little River Canyon Parkway, 7 Apr 1976, *R. D. Whetstone 8248* (NLU NLU0140977). Jackson Co., S side Scottsboro, 3 Jun 1969, *R. Kral 34085* (VDB BRIT110722). Madison Co., Huntsville, Green Mt. NE side, 7 May 1977, *C. T. Bryson 1533* (VDB BRIT111017). St. Clair Co., Chandler Mountain, Fort Payne, Red Mt., near Lake Sumatanga, 4 Jun 1963, *P. E. Bostick 290-10* (NCU NCU00351217 [i]).

GEORGIA: Catoosa Co., Tennessee Army National Guard Training Facility, top of Recon Road on S-most portion of what might be the "backbone" of Sand Mt., 1215 ft., 31 May 2012, *J. Shaw and D. Estes s.n.* (GA GA086108, APSC APSC0015420 [i]). Chatooga Co., gorge of East Fork Little River, Camp Juliette Low, 22 Aug 1984, *N. C. Coile 24452* (GA GA058323). Dade Co., S of Lookout Point (in Tenn.) about 4 mi., 8 Jul 1931, *H. M. McKay s.n.* (GA GA058503, VDB BRIT311478). Dawson Co., Etowah River Basin, Dawson Forest Wildlife Management Area, Amicalola Tract, W side of Amicalola River, 1.1 mi. S of State Hwy. 53 Amicalola bridge, S side of promontory, near crest of slope, *L. Kruse 01-358* (GA GA058372). Fannin Co., NW of Winding Stair Gap, 12 Jul 1942, *W. H. Duncan 5496* (GA GA058771). Floyd Co., Horseleg Mt., Marshall Forest near Horseleg Creek Road, Rome, 10 Apr 1967, *L. Lipps 1-06* (SMU BRIT446568). Lumpkin Co., Woody's Gap, 3112 ft., 25 May 1932, *H. M. McKay s.n.* (GA GA058343, GA 058356, GA058370, GA058772, GA058773, NLU NLU0141202). Murray Co., Grassy Mt., along Mill Creek, near falls just downstream from Hichey Gap Campground, 1970 ft., 15 Apr 2001, *J. A. Moore 602* (GA GA058340). Rabun Co., below Rabun Bald, 18 May 1941, *W. H. Duncan 3272* (SMU BRIT427842). Towns Co., Just below summit of Brasstown Bald, 4760 ft., 1 Jun 1947, *W. H. Duncan 7621* (GA GA058774, VDB BRIT311460). Union

Co., 1.5 mi. N of Neels Gap between Dahlonega and Blairsville, 2800 ft., 1 May 1948, *A. Cronquist 5105* (SMU BRIT446562). Walker Co., WSW of LaFayette, Zahnd Natural Area Tract, off GA 157, *N. C. Coile 4054* (GA GA058320, NLU NLU0141207). Whitfield Co., Rocky Face Mt., 4 mi. NW of Dalton, 1500 ft., 24 Apr 1948, *A. Cronquist 5065* (SMU BRIT427841).

KENTUCKY: Bell Co., Fonde Surface-Mined Demonstration Area, 2.0 mi. ESE of Fonde from jct. KY 74 and KY 535, off adjacent haul road, 13 May 1989, *R. L. Thompson 89-877* (NLU NLU0140725). Boyle Co., Rose-Marie Roessler's Property off of Carpenter Creek Road, NE-facing slope of knob, 30 Apr 2013, *H. Braunreiter 89* (EKY 31234100808458). Breathitt Co., Hwy. 1812S 1 mi. W of mouth of Quicksand Creek, 800 ft., 23 Jul 1995, *H. Rice 56* (EKY 31234100408325). Carter Co., loop trail at Grayson Lake State Park, off Hwy. 7, ca. 10 mi. S of Grayson, 28 Apr 1996, *T. J. Weckman 2470* (EKY 31234100408358). Clark Co., near Oil Springs, 1.5 mi. NE of Indian Fields, 11 Jun 1942, *M. Wharton 6166* (EKY 31234100408366). Clay Co., Big Creek Quadrangle above Mill Branch, 18 May 1979, *R. Hannan and L. R. Phillippe 1850* (EKY 31234100409372). Clinton Co., Hancock Creek at Army Corps of Engineer's boundary, 9 Aug 1999, *M. A. Gorton 99-1052* (EKY 31234100408374). Edmonson Co., Nolin Lake Quad, Woods above Cubby Cove on SE side, 1 Sep 1979, *M. E. Medley 1621-79* (APSC APSC0086285 [i]). Elliott Co., end of Tree Farm Road, 5 Apr 2012, *M. Greene s.n.* (EKY 31234100408390). Estill Co., above Kentucky River floodplain, Hwy. 3329 (Old Landing Road), ca. 8.5 mi. SE of Irvine, 19 May 2006, *T. J. Weckman 10316* (EKY 31234100409398). Fleming Co., along Hwy. 3302, 3.7 mi. NE of Muses Mills, 20 Jul 1999, *R. C. Clark 25344* (EKY 31234100408416). Garrard Co., entrance to Maywoods Environmental and Educational Laboratory, 25 Jun 1984, *D. A. Godbey 662* (EKY 31234100408424). Harlan Co., Caney Creek, 10 Jun 1947, *A. J. Sharp and R. E. Shanks s.n.* (SMU BRIT446587). Jackson Co., Gravel Lick Creek, border between the old Land property and the Maupin property, Jul 1992, *J. Abner 92-2* (EKY 31234100408549). Knox Co., Hazel Fork Road, 13 Jul 1990, *R. Jones 6519* (EKY 31234100408580). Laurel Co., Rock Creek Research Natural Area, 30 km SW of London off KY 1193 and 0.7 km W on F.S. 131, 15 Jun 1985, *R. L. Thompson 85-378* (NLU NLU0140727). Lee Co., along Patterson-Logue Road, 0.8 mi. N of entrance to Cathedral Domain, 28 May 1993, *T. J. Weckman 280* (EKY 31234100408606). Letcher Co., Pine Mt., Little Shepherd Trail, 3 Jun 1983, *M. Medley and J. MacGregor 8031-83* (APSC APSC0086282 [i]). Lincoln Co., Black Shale Region, Chapel Gap Road, S of Crab Orchard, 5 Aug 1938, *M. E. Wharton 3395* (TENN TENN-V-0170506 [i]). Madison Co., Along Burnt Ridge Road (Madison-Rockcastle Co., line) ca. 2.5 mi. E of jct. road with KY 1617, ca. 2.8 mi. S of Berea, 1550 ft., 25 Jun 1982, *D. D. Taylor 1680* (NLU NLU0141198). Magoffin Co., 0.4 mi. up first paved side road to W of KY 30, this road 2.4 mi. S of KY 30-Kentucky Mountain Parkway interchange, 15 May 1965, *E. M. Browne and E. T. Brown, Jr. 9930* (TENN TENN-V-0169968 [i]). Martin Co., Chapman Sanctuary, above Wolf Creek, near Tug River, Lovely, 6 May 1961, *G. B. Rossbach et al. 2543 pro parte* (WVA WVA-V-0010546; mixed collection with *V. pallidum*). McCreary Co., 0.2 mi. N of River Bridge, on Trail 9, 21 Jun 1991, *W. Hess and N. Stoynoff 6748* (GA GA201349, NLU NLU0141195). Owsley Co., along Big Sturgeon Creek Road, ca. 2.6 mi. from jct. with Hwy. 30, 26 May 1996, *T. J. Weckman 2653* (EKY 31234100408705). Pike Co., KY 80, short distance W of KY-VA state line above Russel Fork of Big Sandy River, Breaks Interstate Park, 21 May 1964, *E. M. Browne and E. T. Browne, Jr. 8454* (EKY 31234100408721). Powell Co., S boundary of 74 at addition to Natural Bridge State Resort Park along Red River and Hwy. 11, Bryant-Henson tract, ca. 1.0 mi. SE of Slade exit, Mountain Parkway, 19 Apr 2005, *T. J.*

Weckman 9141 (EKY 31234100408762). Pulaski Co., along KY 192, 3 mi. E of Mount Victory, 23 May 1972, *H. W. Woodward 5102* (APSC APSC0086081 [i]). Rockcastle Co., Shearer Hollow, Berea College Forest, S of Burnt Ridge Road (Madison-Rockcastle Co. line) ca. 2.5 mi. W of jct. Burnt Ridge Road and US 421, 8 Aug 1981, *D. D. Taylor and C. Marsh 1110* (NLU NLU0140543). Rowan Co., Clack Mt., 23 May 1937, *E. L. Braun 1466* (NY 2548782 [i]). Russell Co., behind Mount Eden Church, Goose Creek drainage, 28 Jul 1988, *B. Hoagland 457* (EKY 31234100408804). Wayne Co., Pinnacle Mt., 19 Jun 1937, *D. Young s.n.* (APSC APSC0087064 [i]). Whitley Co., 10337 Cumberland Falls Hwy., 11 Apr 1994, *A. Carter 36* (EKY 31234100408812). Wolfe Co., along Wildcat Trail (US Forest Service Trail 228, ca. 1 mi. W of Swift Camp Creek, 21 Aug 1991, *R. C. Clark 22616* (EKY 31234100776671).

MISSISSIPPI: Monroe Co., beside US 278 E of Buttahatchee Creek, 16 Apr 1968, *R. D. Thomas 7050* (NLU NLU0456482).

NORTH CAROLINA: Alexander Co., near Hiddenite on Co. Road 1427, 10 May 1983, *E. Herron s.n.* (WILLI 75889). Alleghany Co., Cranberry Township, Citron, along the Blue Ridge Parkway at Alligator Back/Bluff Mt. (Doughton Park Recreation Area) along Bluff Mt. Trail, 29 May 2009, *D. B. Poindexter 09-453* (NCU NCU00315063 [i]). Ashe Co., Jefferson, Mt. Jefferson State Natural Area and environs, S.R. 1152, ca. 0.2 mi. past first overlook on left, 3500–4683 ft., 25 May 2005, *D. B. Poindexter 05-347* (NCU NCU00086145 [i]). Avery Co., Beech Mt., vicinity of the Ponds of Beech, 5000 ft., 21 May 1981, *J. L. Collins* 5230 (VDB BRIT313007). Buncombe Co., edge of parking area on Blue Ridge Parkway, N of Asheville, 1 Jul 2000, *R. Pappert 15* (GA GA201268). Burke Co., near top of Hawksbill Mt., S off NC 181, S of Jonas Ridge Community, 4030 ft., 30 Apr 1977, *T. L. Mellichamp 2507* (UNCC UNCC_11412 [i]). Caldwell Co., 1.2 mi. SE of Blowing Rock on US 321, 18 Jun 1958, *H. E.*

Ahles 43951 (NCU NCU00330121 [i]). Cherokee Co., Nantahala National Forest, along Upper Tellico River Four-Wheel Drive roads E of Cherokee National Forest and the Tennessee state line E of Tellico Plains, 20 Jul 1996, *R. D. Thomas and B. R. Thomas 150013* (NLU NLU0141033). Clay Co., W of the city of Franklin, 0.64 km (0.4 mi.) W of the Macon Co line on US Rte. 64, then 3.5 km (2.2 mi.) S on US Forest Service Road along Buck Creek, 900 m, 18 May 1980, *D. E. Boufford 22086* (USF 163452 [i]). Graham Co., Stratton Meadows, Tellico Plains, ca. 4800 ft., 17 Aug 1970, *K. E. Rogers 4160-B* (SMU BRIT61670). Haywood Co., vicinity of Cove Creek, Teaberry Ridge, Pat and Charlie Davis property, 3200 ft., May 1991, *W. K. George 91-12* (VDB BRIT312815). Henderson Co., about 5 mi. NE of Brevard on US Rte. 64, 12 Jun 1964, *R. L. Wilbur 7106* (DUKE DUKE10100311 [i]). Jackson Co., 2 mi. W of Cashiers on US 64, 25 May 1972, *J. L. Collins 537* (VDB BRIT312121). Macon Co., 1.3 mi. N of Wayah Gap, 23 Aug 1952, *A. E. Radford 1479* (SMU BRIT446578). Madison Co., 8.4 mi. W of State Rte. 209 on the Forest Service road to Max Patch, 1140 m, 11 Aug 1994, *J. S. Miller and N. Snow 8334* (VDB BRIT311247). McDowell Co., Lick Log Ridge, ca. 1.5 mi. ENE of Green Knob Lookout on Blue Ridge Parkway, 1 Sep 1956, *H. E. Ahles 17695* (NCU NCU00330915 [i]). Mitchell Co., Appalachian Trail Road 0.2 mi. NE of Indian Grave Gap, 3 Jul 1986, *Q. V. Ma 86-84* (NLU NLU0141028). Polk Co., Green River Watershed, road along Cove Creek or Little Cove Creek, 1100–1600 ft., 14 May 1974, *J. W. Hardin 13531* (NCSC NCSC00085483 [i]). Rutherford Co., Chimney Rock Park along Skyline Trail W of Exclamation Point, 9 May 1983, *E. Feil 424* (UNCC UNCC_16569 [i]). Swain Co., Spruce Heath Bog, 1 mi. NE of Blazed Gap, 3800 ft., 21 Aug 1952, *A. E. Radford 6402* (SMU BRIT446573). Transylvania Co., Pisgah National Forest, Hwy. 276, 2–5 mi. S of Blue Ridge Parkway, 19 May 1991, *E. Sundell 9902* (NLU NLU0141034). Watauga Co., Rich Mt. NW of the city of Boone, 36°14’ N, 81°43’ W, 1500 m, 16 May 1979, *E. W. Wood 4157* (VDB BRIT311466). Wilkes Co., Joe’s field, near Sunland Orchards, Brushy Mts., 13 Jun 1938, *L. Stewart s.n.* (NCU NCU00330278 [i]). Yancey Co., Mt. Mitchell, 16 Aug 1939, *H. W. Youngken s.n.* (SMU BRIT528947).

OHIO: Adams Co., without specific locality, 14 Mar 1965, *F. Bartley s.n.* (OS 81795 [i]). Highland Co., Fort Hill, 25 Jun 1933, *E. S. Thomas s.n.* (OS 28901 [i]). Jackson Co., White’s Gulch, Liberty Twp., 30 May 1933, *F. Bartley and L. L. Pontius s.n.* (OS 28899).

SOUTH CAROLINA: Greenville Co., S side Caesar’s Head, 17 May 1976, *R. Kral 58131* (GA GA201252, VDB BRIT311260). Oconee Co., Fodderstack Mt., 29 Jul 1934, *T. G. Harbison s.n.* (NCU NCU00096494 [i]). Pickens Co., 1.8 mi. N from US Rte. 178 on Sassafras Mt. Road, 8 Jun 1956, *H.E. Ahles 14321* (NCU NCU00096485 [i]).

TENNESSEE: Anderson Co., near Savages Garden on Coal Creek behind store opposite Gardens, 7 May 1958, *A. J. Sharp et al. 23100* (TENN TENN-V-0169191 [i]). Bledsoe Co., Fall Creek Falls State Park, on old trail/road behind horses stables that are located ca. 0.8 km N of Newton Ford Picnic Area on Hwy. 284, ca. 3.0 km SE of stables near intersection with Upper Loop Trail, Sampson Quad, 550 m, 12 Jun 2001, *C. A. Fleming and K. Bowman FCF-710* (NLU NLU0141275). Blount Co., near Cades Cove, 10 Jul 1936, *J. Barkesdale 13469* (SMU BRIT446563). Campbell Co., Ed Faust’s place, Cove Creek, 11 Jul 1934, *L. R. Hesler et al. 1842* (TENN TENN-V-0169198 [i]). Carter Co., Heaton Creek Ridge, above Sugar Hollow Road, 15 Jul 1978, *P. Somers 1249* (VDB BRIT113011). Cocke Co., Cosby Low Gap Trail, 6 Jun 1935, *H. M. Jennison 321* (GSMNP GSMNP11386 [i]). Coffee Co., Rutledge Falls near Tullahoma, 3 Jul 1947, *A. J. Sharp et al. 3723* (VDB BRIT113014). Cumberland Co., Drippy Spring Road, 0.6 mi. off Hwy. 24/70, 400 yds to S along timber road, 3 Jun 1987, *R. L. Jones*

4831 (VDB BRIT113016). DeKalb Co., Center Hill Lake where crossed by US 70S, E of Smithville, 15 Apr 1968, *R. Kral 30098* (GA GA201685). Fentress Co., off Hwy. 127, across from stockyards S of Jamestown, 1 Aug 1989, *R. L. Jones 6180* (EKY 31234100408952). Franklin Co., Carter Mt. along gravel drive 0.8 mi. from Rowe Gap Church, Hwy 16, Pither Ridge Quad, 4 Jun 1987, *R. L. Jones 4843* (EKY 31234100408945). Greene Co., near top of Camp Creek Bald, 4500 ft., 22 May 1966, *R. D. Thomas 41355* (TENN TENN-V-0169019 [i]). Grundy Co., Big Fiery Gizzard Cove, Grundy State Forest, 4 Jul 1975, *R. Kral 56067* (VDB BRIT113022). Hamilton Co., Big Soddy Creek Gorge, vicinity of pond, 35.32721°, −85.18303°, 4 May 2015, *Z. Irick s.n.* (MO). Hickman Co., Pickett Hollow, SE of Centerville off Hwy. TN 50, just N of Bond, 4 May 1983, *R. Carter 3604* (VDB BRIT113026). Jackson Co., Cummins Falls, 4 May 1987, *Weedeaters 114* (HTTU HTTU007863 [i]). Johnson Co., Holston Mt., 20 May 1934, *J.K. Underwood 801* (IND IND-0097229 [i]). Marion Co., along TN 108, ca. 2 mi. above Whitwell, 9 May 1973, *R. Kral 49884* (GA GA201280, VDB BRIT113025). Maury Co., Rattlesnake Falls, trailside, 21 Apr 2002, *R. Carrico 59* (MTSU MTSU017713 [i]). McMinn Co., Englewood, Cherokee National Forest, Bullet Creek wetland, 30 Jun 2021, *J. Shaw 5-208* (UCHT UCHT045106). Monroe Co., Cherokee National Forest, ridge top near Beech Gap, 30 May 1940, *A. J. Sharp 710* (GA GA201285, TENN TENN-V-0169260 [i]). Morgan Co., Lansing [Lancing] Quad (p.r. 1980), outcrop overlooking Lily [Lilly] Bridge and Clear Creek, 1250 ft., 11 Jun 1993, *C. Bullington 93-67* (NLU NLU0141272). Overton Co., along Muddy Pond Road, near E Branch of Obey River, 6 May 1993, *V. E. McNeilus 93-503* (TENN TENN-V-0169275 [i]). Pickett Co., Ball Tract, trail to Chimney Rock, Sharp Place Quad, 21 Jun 1994, *M. Pyne 94-159*, (VDB BRIT311491). Polk Co., ca. 1.0 km NW of Chimneytop, Big Creek Trail, Caney Creek Quad, 790 m, 7 May 1983, *Z. E. Murrell and B. Jacobs 68* (NLU

NLU0140974). Putnam Co., ca. 1.1 mi. E Monterey by TN 62, 21 May 1971, *R. Kral 42807* (GA GA201248, VDB BRIT113031). Rhea Co., W of Dayton, 1 May 1941, *S. L. Meyer 1394* (TENN TENN-V-0169289). Roane Co., 3 mi. E of Rockwood on road to Kingston, 11 Aug 1935, *M. B. Wilson 4239* (TENN TENN-V-0169292 [i]). Scott Co., Big South Fork, Honey Creek area, 24 Apr 2015, *C. Mausert-Mooney 15-12* (APSC APSC0132486 [i]). Sequatchie Co., along TN 108 NW of Barkertown just inside county, 10 May 1989, *R. Kral 76186* (VDB BRIT110848). Sevier Co., along trail from Hotel Place to Bogle Springs and Baker Place on Chilhowee Mt. NW of Pigeon Forge, 6 Aug 1994, *R. D. Thomas and AIBS Field Trip Group* (NLU NLU0141271). Sullivan Co., near the gap on Holston Mt., 17 Jun 1934, *A. J. Sharp and J. K. Underwood 988* (TENN TENN-V-0169299 [i]). Unicoi Co., vicinity of Nolichucky River ca. 1 mi. W of Erwin, 13 Jun 1969, *A. J. Sharp et al. 43102* (VDB BRIT446593). Van Buren Co., Fall Creek Falls State Park, base of Can Creek Falls, along Cane Creek, ca. 20 m downstream from falls, Spencer Quad, 460 m, 11 Jul 2001, *C. A. Fleming FCF-1049* (VDB BRIT110851). White Co., S of Todd Town, N bank of Tarklin Ford, downstream of the ford just as the river bends to the north, [35.87694°, −85.22472°], 27 Jul 2014, *M. Brock 558* (APSC APSC0072915 [i]).

VIRGINIA: Alleghany Co., Hexagon No. 3707968, Subplot 1, Quadrat 1, 24 Jun 1992, ID code XIVACCIGIBD, *G. Parker s.n.* (CLEMS CLEMS0045063 [i]). Augusta Co., Flint Mtn., Big Levels, 3400 ft., 20 Jun 1997, *C.E. Stevens 25883* (WILLI 81959). Bland Co., Big Ridge off East River Mt., S of Bluefield, 3800 ft., 7 Jun 2005, *T. F. Wieboldt 11605* (VDB BRIT446591). Dickenson Co., Towers Overlook, 20 Jun 2009, *J. B. Clark and J. Mooreleghen 734* (EKY 31234100409026). Giles Co., Salt Pond Mt., 0.3 mi. NE jct. 668 on Rte. 613, 11 Jun 1974, *L. J. Uttal 10424* (ODU 00020983). Grayson Co., Highlands State Park, Twin Pinnacles Trail, 29

May 2008, *D. Atha 6302* (MO MO-38888403; ODU ODU00020982). Halifax Co., Difficult Creek Natural Area Preserve, ca. 16 km NE of South Boston and 2.5 km N of Dryburg, transmission right-of-way 0.5 km S of its intersection with Allens Mill Road (VA 719), 26 Apr 2018, *J. F. Townsend 5857* (WILLI 83509). Lee Co., Cumberland Gap National Historical Park, Plot 5, 18 Jun 1974, *R. Hinkle s.n.* (EKY 31234100410164). Russell Co., Saltville along Tumbling Creek, 13 May 1997, *J. A. Churchill 97072* (NLU NLU0141259). Scott Co., High Knob (VA 619), above Devil's Fork, ca. 3500 ft., 17 May 1973, *L. J. Uttal 9700* (CLEMS CLEMS0045151 [i]). Smyth Co., 16 mi. N Marion, 2 Aug 1960, *R. Kral 10888* (SMU BRIT446570). Tazewell Co., along Laurel Bed Creek, ca. 2 mi. above Laurel Bed Lake and 7 mi. N of Saltville, 3750 ft., 21 Jun 1986, *T. F. Wieboldt 6114* (WILLI 50988). Washington Co., Brumely Mt., 4000 ft., 28 Jun 1962, *R. Kral 14777* (VDB BRIT311448). Wise Co., High Knob, 4000 ft., 11 Jul 1950, *B. Mikula 6509* (NLU NLU0140384).

WEST VIRGINIA: Mercer Co., US 52, Pinnacle Rock State Park, Bramwell, 2772 ft., 11 Sep 2021, *K. Campbell KC10490* (WVA 182158). Monroe Co., Peters Mountain, Jefferson National Forest, Appalachian Trail, vegetation plot JENF.11, 19 Jul 2012, *J. Vanderhorst 7646* (NCU NCU00446746 [i]). Nicholas Co., near Summersville, 11 Jul 1933, *P. D. Strausbaugh s.n.* (WVA 54632).

Unresolved Name—*Vaccinium altomontanum* Ashe, Rhodora 33: 196 (1931). TYPE: NORTH CAROLINA. Macon Co.: Fodderstock Mt., 22 June 1924, *W.W. Ashe s.n.* (type material not found). Camp (1945) considered this a tetraploid derivative of his concept of *V. vacillans* Kalm ex Torr., a diploid. Camp treats this as a wide-ranging taxon from the central and Southern Appalachians to southern Ohio, central Kentucky, Missouri, and Arkansas growing in uplands, whereas Vander Kloet (1988, 2009) and others (e.g., Luteyn et al. 1996; Weakley 2020) treated it as a synonym of *V. pallidum* Aiton, a diploid. This name has also been applied occasionally to the species we are recognizing as *V. constablei* on herbarium material. At least from the time of Camp (1945), the type material of *V. altomontanum* has been missing, and despite an extensive search at the NCU herbarium by Bruce Sorrie (pers. comm.) and our search on the SERNEC and JStor Global Plants web portals, type material has not been located. The description in the protologue states "Frutex 3−10 dm alta..." suggesting either *V. pallidum* or *V. constablei*, but this height range also overlaps with that of low individuals of *V. simulatum*. We have opted not to neotypify this name because the protologue information is too vague to know whether the species is *V. constablei*, *V. pallidum*, or *V. simulatum*, and in any case under our taxonomy the name will be a heterotypic synonym no matter which species it belongs to. Therefore, in following Recommendation 9B of the *ICNAFP* (Turland et al. 2025), we treat this name as unplaced to species.

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Author Contributions

PSM developed the project, acquired financial support, conceived the research plan, participated in fieldwork, provided photographs, and prepared the manuscript. AAC developed the project, acquired financial support, conceived the research plan, participated in fieldwork, conducted data analyses, elaborated the figures, provided photographs, and prepared the manuscript. GPT conducted data analysis and reviewed the manuscript. PWF developed the project, acquired financial support, conceived the research plan, participated in fieldwork, conducted the herbarium work and was the primary author of the taxonomic treatment, elaborated the figures, provided photographs, and prepared the manuscript.

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TABLE 1. Comparison of morphological differences among *Vaccinium constablei*, *V. hirsutum*, and *V. simulatum*.

Character	*V. constablei*	*V. hirsutum*	*V. simulatum*
Height (m)	0.3–2.1	0.4–0.6	0.6–3.0
Length of vegetative bud scales (mm)	1.5–2.5	2.3–3.9	1.3–2.4
Leaf blade margin pubescence	At least sparsely ciliate-pubescent on at least some leaves	Ciliate-pubescent	Usually glabrous distally beyond base
Leaf blade margin	Revolute throughout at least on some leaves or rarely planar	Revolute on at least some leaves	Planar distally beyond base at least on some leaves or rarely slightly revolute
Leaf blade sessile marginal gland presence	Present on at least some leaves	Present on most leaves	Often absent
Leaf blade marginal teeth	With generally straight outer edges and	Absent	With generally outcurved outer edges and deep

	shallow narrow sinuses		and broad sinuses
Leaf blade apex	Acute to short-acuminate	Obtuse to acuminate	Short-acuminate to acuminate
Inflorescence bracts	White often flushed pink, cucullate	Green, planar, leaf-like	White often flushed pink, cucullate
Stipitate glands on pedicels, hypanthium, calyx, corolla, and fruit	Absent	Present	Absent

APPENDIX 1. Specimen vouchers of samples used for assessing ploidy in the polyploid species of *Vaccinium* sect. *Cyanococcus* endemic to the Southern Appalachians. All vouchers deposited at BRIT with a duplicate set at DUKE.

***Vaccinium constablei*—USA.**—GEORGIA. Rabun Co., Rabun Bald, trail from Beegum Gap, at summit, 34.965663°, -83.308632°, 18 May 2021, *P. S. Manos CY-430*; ibid., *P. S. Manos CY-431* (DNA). NORTH CAROLINA. Buncombe Co., Blue Ridge Parkway, Craggy Gardens, Picnic area, 35.700027°, -82.392045°, 22 Jun 2023, *P. S. Manos CY-509*; Jackson Co., along trail to Goat Knob, 35.118887°, -83.181903°, 24 Jun 2018, *P. S. Manos CY-092* (DNA); Whiteside Mountain, 29 May 2019, *P. S. Manos CY-241* (DNA); Devil's Courthouse, Whiteside Mountain, 35.088512°, -83.134049°, 2 Jun 2019, *P. S. Manos CY-252* (DNA); ibid., *P. S. Manos CY-253*; Blue Ridge Parkway, Richland Balsam Mountain, base of trail, near parking area, 4 Jun 2019, *P. S. Manos CY-257*; Macon Co., Highlands, Sunset Rock, 35.046755°, -83.186772°, 16 Jun 2017, *P. S. Manos CY-060*; Satulah Mountain, 30 May 2019, *P. S. Manos CY-242*; ibid., *P. S. Manos CY-243*; ibid., *P. S. Manos CY-244*; trail from Shortoff Mountain to Cole Gap, 35.109372°, -83.186663°, 31 May 2019, *P. S. Manos CY-246*; ibid., *P. S. Manos CY-248*; ibid., *P. S. Manos CY-249*; ibid., *P. S. Manos CY-250*; Shortoff Mountain, trail to Yellow Mountain, first rock outcrop facing E, 35.109617°, -83.187395°, 1 Jul 2023, *P. S. Manos CY-511*; ibid., *P. S. Manos CY-512*; Sunset Rock, Highlands, 35.046765°, -83.187128°, 12 Aug 2023, *P. S. Manos CY-513*; ibid., *P. S. Manos CY-514*. Mitchell Co., Roan Mountain, trail to Round Bald Scattered wind-swept shrubs, 36.107477°, -82.105841°, 24 May 2021, *P. S. Manos CY-442* (DNA); ibid., *P. S. Manos CY-443*. Transylvania Co., Yellow Mountain, W of peak, along trail to Cold Gap, 35.153428°, -82.991911°, 10 Jun 2017, *P. S. Manos CY-048*. Watauga Co., Elk Knob State Park, summit, 36.327442°, -81.676517°, 26 Jun 2020, *P. S. Manos CY-339*; ibid., *P. S. Manos CY-340*. VIRGINIA. Giles Co., Aiton Pembroke, Bald Knob, above Mountain Lake Lodge, 37.349804°, -80.538229°, 19 Jul 2019, *P. S. Manos CY-283*; ibid., *P. S. Manos CY-284*.

***Vaccinium hirsutum*—USA.**—TENNESSEE. Monroe Co., Cherohala Skyway (Rte. 165), 0.5 km E of Hemlock Road turnoff, 35.362685°, -84.144888°, 4 Jun 2018, *A. A. Crowl CY-077* (DNA) (no voucher); ibid., *A. A. Crowl CY-078* (DNA).

***Vaccinium simulatum*—USA.**—ALABAMA. DeKalb Co., E side Desoto Parkway NE (AL-89), ca. 0.90 mi. SSW of jct. Co. Road 89 and Co. Road 165, DeSoto State Park at the entrance sign, 34.49281°, -85.62061°, 466 m elev., 30 Apr 2022, *P. W. Fritsch 2419*. GEORGIA. Rabun Co., Rabun Bald, trail from Beegum Gap on trail down W of the summit, near the summit by the campsites, 34.965663°, -83.308632°, 18 May 2021, *P. S. Manos CY-434*. NORTH CAROLINA. Ashe Co., Mount Jefferson State Park, starting at parking lot near upper trails, Rhododendron Loop Trail to Luther Rock, 36.396944°, -81.460401°, 27 Jun 2020, *P. S. Manos CY-346*; ibid., *P. S. Manos CY-347*. Avery Co., Grandfather Mountain Trail to Grandfather Gap, 36.105119°, -81.818703°, 15 May 2017, *P. S. Manos et al. CY-043*. Buncombe Co., Blue Ridge Parkway, Craggy Gardens, Picnic area, 35.700027°, -82.392045°, 22 Jun 2023, *P. S. Manos CY-508*; Graham Co., western finger of Santeetlah Lake, near Joyce Kilmer Memorial Forest entrance, western edge of dock parking lot, 35.372318°, -83.906382°, 4 Jun 2018, *A. A. Crowl CY-079* (DNA). Jackson Co., Richland Balsam, near summit, 35.367191°, -82.990479°, 13 Jun 2017, *P. S. Manos CY-054*; along trail to Goat Knob, 35.118887°, -83.181903°, 24 Jun 2018, *P. S. Manos CY-094*; Blue Ridge Parkway, Richland Balsam Mountain, base of trail, near parking area, 4 Jun 2019, *P. S. Manos CY-256*. Macon Co., Highlands, Sunset Rock, 35.046765°, -83.187128°, 16 Jun 2017, *P. S. Manos CY-059*; Shortoff Mountain, ridge trail, 35.109372°, -

83.186663°, 24 Jun 2018, *P. S. Manos CY-089*; ibid., *P. S. Manos CY-090*; Satulah Mountain, 30 May 2019, *P. S. Manos CY-245* (DNA); trail from Shortoff Mountain to Cole Gap, 35.109372°, -83.186663°, 31 May 2019, *P. S. Manos CY-247*; Sunset Rock, Highlands, down the trail, 35.046765°, -83.187128°, 12 Aug 2023, *P. S. Manos CY-515*; ibid., *P. S. Manos CY-516*. Watauga Co.: Elk Knob State Park, trail to the summit, near or on the summit, 36.327442°, -81.676517°, 26 Jun 2020, *P. S. Manos CY-338*; Blue Ridge Parkway, trail to Line Cove starting at mile post 299, Cold Prong Pond Overlook, 36.135053°, -81.757098°, 27 Jun 2020, *P. S. Manos CY-341*; ibid., *P. S. Manos CY-342*; ibid., *P. S. Manos CY-343*; ibid., *P. S. Manos CY-344*. Yancey Co., Mt. Mitchell State Park, 0.25 mi. S of park headquarters, 35.749929°, -82.276471°, 22 Jun 2023, *P. S. Manos CY-505*; ibid., *P. S. Manos CY-506*; ibid., *P. S. Manos CY-507*.

APPENDIX 2. Accession data for samples of *Vaccinium* sections *Cyanococcus* and *Oxycoccus* (*V. macrocarpon*) used in genetic analyses including species, library ID from sequencing runs, collector, herbarium voucher location, ploidy, and BioSample Accession number (NCBI).

Library_ID	Collector Name and Number	Herbarium	Species	Location	Ploidy	BioSample Accession
SL410052_V_boreale_CY113	A.A. Crowl CY-113	BRIT	*Vaccinium boreale*	ME. Hancock Co.; Mt. Desert Island; Acadia National Park, Cox Protectorate	2x	SAMN29441129
SL410055_V_boreale_CY122	P.S. Manos CY-122	BRIT	*Vaccinium boreale*	NH. Grafton Co.; Mount Lafayette, ridge trail	2x	SAMN29441132
431_altomontanum_6x	P.S. Manos CY-431	BRIT	*Vaccinium constablei*	GA. Rabun Co.; Rabun Bald, trail from Beegum Gap, at summit to the summit, collections from the summit, east facing slope; 1431 m	6x	
442_altomontanum_6x	P.S. Manos CY-442	BRIT	*Vaccinium constablei*	NC. Mitchell Co; Roan Mt., collections from trail to Round Bald, scattered wind-swept shrubs	6x	
SL410051_V_altomontanum_CY092_6x	P.S. Manos CY-092	BRIT	*Vaccinium constablei*	NC. Jackson Co.; Along trail to Goat Knob	6x	
SL441692_V_altomontanum_CY241_6x	P.S. Manos CY-241	BRIT	*Vaccinium constablei*	NC. Jackson Co.; Whiteside Mt., North Carolina	6x	
SL441695_V_altomontanum_CY252_6x	P.S. Manos CY-252	BRIT	*Vaccinium constablei*	NC. Jackson Co.; Devil's courthouse, Whiteside Mt.	6x	
2308_darrowii_2x	P.W. Fritsch WF-2308	BRIT	*Vaccinium darrowii*	LA.; Tangipahoa Co.; Ca. 13 meters W of LA-1054, ca. 0.1 mi. S of entrance to	2x	

				Camp Whispering Pines		
SL410066_V_darrowii_CY191	A.A. Crowl CY-191	BRIT	*Vaccinium darrowii*	FL. Alachua Co.; Gainesville; woods at 7830 SW 90th Lanenext to Walt Judd's house	2x	SAMN29441141
SL410068_V_darrowii_CY205	A.A. Crowl CY-205	BRIT	*Vaccinium darrowii*	FL. Liberty Co.; Apalachicola National Forest, along Hwy. 65, across from Forest, NF Road 105 pullout.	2x	SAMN29441145
SL441683_V_darrowii_CY221	A.A. Crowl CY-221	BRIT	*Vaccinium darrowii*	FL. Charlotte Co.; Port Charlotte, Tippecanoe Environmental Park	2x	SAMN29441149
2328_elliottii_2x	P.W. Fritsch WF-2328	BRIT	*Vaccinium elliottii*	LA.; Union Co.; Along E side of Canaan Church Road (Parish Road 3355), ca. 0.15 mi. N of Parish Road 3353, ca. 0.1 mi. (direct) E of LA-558 (Iron Mountain Road)	2x	
SL410061_V_elliottii_CY172	P.S. Manos & A.A. Crowl CY-172	BRIT	*Vaccinium elliottii*	NC. Harnett Co.; Raven Rock State Park, Raven Rock Loop Ttrail	2x	SAMN29441136
SL410070_V_elliottii_CY207	A.A. Crowl CY-207	BRITDUKE	*Vaccinium elliottii*	FL. Liberty Co.; Telogia, along Hwy 65, 100 m North of Telogia Baptist Church	2x	SAMN29441146
SL441659_V_elliottii_CY201	A.A. Crowl CY-201	BRIT	*Vaccinium elliottii*	GA. Bleckley Co.; Cochran, Red Dog Farm Road (dirt road)	2x	SAMN29441144

				near junction with Magnolia Road		
2267_fuscatum_xx	P.W. Fritsch PWF-2267	BRIT	*Vaccinium fuscatum*	TX. Nacogdoches Co.; Ca. 18 meters N of Farm to Market Road 1087 (Camp Tonkawa Road), ca. 4 mi. E of TX-259	-	
2358_fuscatum_2x	P.W. Fritsch & J. Reed WF-2358	BRIT	*Vaccinium fuscatum*	AR. Poinsett Co.; Ca. 90 meters N of Mink Road along S bank of creek, ca. 0.5 mi. W of AR-163, Crowley's Ridge	2x	
2359_fuscatum_2x	P.W. Fritsch & J. Reed PWF-2359	BRIT	*Vaccinium fuscatum*	AR. Poinsett Co.; Ca. 90 meters N of Mink Road along S bank of creek, ca. 0.5 mi. W of AR-163, Crowley's Ridge	2x	
372_caesariense_2x	A.A. Crowl CY-372	BRIT	*Vaccinium fuscatum*	GA. Ware Co.; N of Laura S Walker Lake, W of Hwy-117 on Sam's Road (dirt road); edge of pine plantation	2x	
404_fuscatum_2x	P.S. Manos CY-404	BRIT	*Vaccinium fuscatum*	NJ. Union Co.; Watchung Reservation, along shore of Surprise Lake	2x	
SL410050_V_fuscatum_CY082	P.S. Manos & A.A. Crowl CY-082	BRIT	*Vaccinium fuscatum*	NC. Durham Co.; Duke Forest off of Gate 10 entrance.	2x	SAMN29441126
SL410060_V_fuscatum_CY145	P.S. Manos CY-145	BRIT	*Vaccinium fuscatum*	NJ. Middlesex Co.; Cheesequake State Park, trail to Hooks Creek Lake, yellow trail	2x	SAMN29441134

SL410064_V_fuscatum_CY190	A.A. Crowl CY-190	BRIT	*Vaccinium fuscatum*	FL. Alachua Co.; Aalong Gainesville-Hawthorn trail	2x	SAMN29441140
SL441581_V_caesariense_CY175	P.S. Manos & A.A. Crowl CY-175	BRIT	*Vaccinium fuscatum*	NC. Harnett Co. Raven Rock State Park, Raven Rock Loop Trail	2x	SAMN29441138
SL441625_V_fuscatum_CY194	A.A. Crowl CY-194	BRIT	*Vaccinium fuscatum*	SC. Kershaw Co.; Dr. Humphries Road just before junction with Rte. 34	2x	SAMN29441142
SL441679_V_fuscatum_CY211	A.A. Crowl CY-211	BRIT	*Vaccinium fuscatum*	FL. Duval Co.; Racetrack Road near intersection with FL-9B	2x	SAMN29441147
SL441680_V_fuscatum_CY214	A.A. Crowl CY-214	BRIT	*Vaccinium fuscatum*	FL. Nassau Co.; Yulee, Mentoria Road near junction with Rte. 200	2x	SAMN29441148
SL441696_V_fuscatum_CY254	P.S. Manos CY-254	BRIT	*Vaccinium fuscatum*	NC. Jackson Co.; West edge of Dulany Bog, west edge, Bull Pen Road, near Highlands	2x	
SL441697_V_fuscatum_CY084	P.S. Manos & A.A. Crowl CY-084	BRITDUKE	*Vaccinium fuscatum*	NC. Durham Co.; Duke Forest off of Gate 10 entrance.	2x	SAMN29441127
SL410047_V_hirsutum_CY077_4x	A.A. Crowl CY-077	BRITDUKE	*Vaccinium hirsutum*	TN. Monroe Co.; Cherohala Skyway (Rte. 165); 0.5 km E of Hemlock Road turnoff; roadside	4x	
SL441658_V_hirsutum_CY078_4x	A.A. Crowl CY-078	BRIT	*Vaccinium hirsutum*	TN. Monroe Co. Cherohala Skyway (Rte. 165); 0.5 km E of Hemlock Road turnoff; roadside	4x	
SL410075_V_macrocarpon_CY234	A.A. Crowl CY-234	BRIT	*Vaccinium macrocarpon*	OH. Portage Co.; Triangle Lake Bog State Nature Preserve	2x	SAMN29441155

SL410053_V_myrtilloides_CY114	A.A. Crowl CY-114	BRIT	*Vaccinium myrtilloides*	ME. Hancock Co.; Mt. Desert Island, Acadia National Park; Cox Protectorate	2x	SAMN29441130
SL419999_V_myrtilloides_CY258	A.A. Crowl CY-258	BRIT	*Vaccinium myrtilloides*	MI. Gogebic Co.; University of Notre Dame Environmental Research Center (UNDERC-East), Tender BogUpper Peninsula; UNDERC Field Station; Tender Bog	2x	SAMN29441158
SL441685_V_myrtilloides_CY227	A.A. Crowl CY-227	BRIT	*Vaccinium myrtilloides*	WV. Tucker Co.; Canaan Valley; Freeland Bboardwalk	2x	SAMN29441153
SL441730_V_myrtilloides_CY105	A.A. Crowl CY-105	BRIT	*Vaccinium myrtilloides*	NH. Carroll Co. White Mountains; below Silver Cascade Falls	2x	SAMN29441128
SL441752_V_myrtilloides_CY120	P.S. Manos CY-120	BRITDUKE	*Vaccinium myrtilloides*	NH. Grafton Co. White Mountains; north N of Echo Lake along trail to Artists Bluff	2x	SAMN29441131
2363_pallidum_2x	P.W. Fritsch & T. Marisco WF-2363	BRIT	*Vaccinium pallidum*	AR. Greene Co.; Along Dancing Rabbit Trail, 0.26 mi. (direct) SE of AR-168 N, Crowley's Ridge State Park, Crowley's Ridge	2x	
SL441694_V_pallidum_CY251	P.S. Manos CY-251	BRIT	*Vaccinium pallidum*	NC. Macon Co.; Trail from Shortoff Mt. to Cole Gap	2x	SAMN29441157
SL410059_V_pallidum_CY141	P.S. Manos CY-141	BRIT	*Vaccinium pallidum*	NJ. Middlesex Co.; Cheesequake State Park; trail to Hooks	2x	SAMN29441133

				Creek Lake, Yellow trail		
SL410062_V_pallidum_CY178	P.S. Manos & A.A. Crowl CY-178	BRIT	*Vaccinium pallidum*	NC. Harnett Co.; Raven Rock State Park; Raven Rock Loop Trail	2x	SAMN29441139
SL410073_V_pallidum_CY223	A.A. Crowl CY-223	BRIT	*Vaccinium pallidum*	VA. Augusta Co. A; along Blue Ridge Parkway	2x	SAMN29441150
SL410074_V_pallidum_CY224	A.A. Crowl CY-224	BRIT	*Vaccinium pallidum*	VA. Augusta Co.; Blue Ridge Parkway, Ravens Roost Overlook	2x	SAMN29441151
SL441684_V_pallidum_CY226	A.A. Crowl CY-226	BRIT	*Vaccinium pallidum*	VA. Rockingham Co.; Riven Rock Park, Harrisonburg; along Rawley Pike Road.	2x	SAMN29441152
SL441686_V_pallidum_CY080	A.A. Crowl CY-080	BRIT	*Vaccinium pallidum*	TN. Monroe Co.; Cherohala Skyway (Rte. 165); 0.5 km E of Hemlock Roadd turnoff; roadside	2x	SAMN29441124
SL441688_V_pallidum_CY231	A.A. Crowl CY-231	BRIT	*Vaccinium pallidum*	OH. Portage Co.; West Branch State Park; along Alliance Road	-	SAMN29441154
SL441691_V_pallidum_CY240	P.S. Manos CY-240	BRIT	*Vaccinium pallidum*	NC. Jackson Co.; Bull Pen Road, North Carolina, Slick Rock	-	SAMN29441156
SL410048_V_simulatum_CY079_4x	A.A. Crowl CY-079	BRIT	*Vaccinium simulatum*	NC. Graham Co. western finger of Santeetlah Lake; western finger of lake, near Joyce Kilmer Memorial Forest entrance, western edge of dock parking lot.	4x	

SL441693_V_simulatum_CY245_4x	P.S. Manos CY-245	BRIT	*Vaccinium simulatum*	NC. Macon Co.; Satulah Mt.	4x	
346_simulatum_4x	P.S. Manos CY-346	BRIT	*Vaccinium simulatum*	NC. Ashe Co.; Mt. Jefferson State Park, starting at parking lot near upper trails, Rhododendron Loop Trail to Luther Rock	4x	
435_simulatum_4x	P.S. Manos CY-435	BRIT	*Vaccinium simulatum*	GA. Rabun Co., Rabun Bald, trail from Beegum Gap to the summit, collected half-way down to Beegum gap, near the summit by the campsites; 1200 m	4x	
SL410049_V_tenellum_CY081	P.W. Manos & A.A. Crowl CY-081	BRIT	*Vaccinium tenellum*	NC. Durham Co.; Duke Forest off of Gate 10 entrance.	2x	SAMN29441125
SL441570_V_tenellum_CY174	P.S. Manos & A.A. Crowl CY-174	DUKE	*Vaccinium tenellum*	NC. Harnett Co.; Raven Rock State Park; Raven Rock Loop Trail	2x	SAMN29441137
SL441701_V_tenellum_CY299	P.S. Manos & A.A. Crowl CY-299	BRIT	*Vaccinium tenellum*	NC. Randolph Co.; Uwharrie National Forest; Birkhead Trail	2x	SAMN29441159
SL441702_V_tenellum_CY314	A.A. Crowl CY-314	BRIT	*Vaccinium tenellum*	NC. New Hanover Co. Halyburton City Park	2x	SAMN29441161

Figure Legends

Figure 1. Phylogenetic tree from a concatenated maximum-likelihood analysis of DNA sequence data based on the Angiosperms353 probe set (left) and PCA plots (right) for diploid species of *Vaccinium* sect. *Cyanococcus*, with each of the three endemic Southern Appalachian polyploid species of the section added separately. A. *V. constablei*. B. *V. hirsutum*. C. *V. simulatum*.

Figure 2. Genetic clustering analysis with STRUCTURE analysis for diploid species of *Vaccinium* sect. *Cyanococcus*, with each of the three endemic Southern Appalachian polyploid species added separately, $K = 4$ through 7. A. *V. constablei*. B. *V. hirsutum*. C. *V. simulatum*.

Figure 3. *Vaccinium constablei*. A. Stem. B. Vegetative bud and leaf base. C. Leaf blade surface. D. Leaf blade margin. E. Inflorescence bracts and bracteoles. F. Flower. Scale bars, A, B, D–F = 2 mm; C = 500 µm. All images from dried herbarium specimens. A, *P. S. Manos CY-018* (BRIT BRIT698715); B, *P. S. Manos CY-096* (BRIT BRIT698651); C, *P. S. Manos CY-024* (BRIT BRIT698718); D, *P. S. Manos CY-097* (BRIT BRIT698652); E, *P. S. Manos CY-399* (BRIT BRIT792872); F, *P. S. Manos CY-400* (BRIT BRIT792873).

Figure 4. *Vaccinium constablei*. A. Clonal habit (red-leaved shrubs, in autumn), Big Fodderstack, Highlands, NC; B. Habit (red-leaved shrubs, in autumn); Big Fodderstack, Highlands, NC; C. Branchlet showing adaxial leaf surfaces. D. Inflorescence. E. Fruiting branchlet. F. Fruit. All images in situ, with the following herbarium vouchers. A, *P. S. Manos*

CY-500 (BRIT BRIT914510); B, *P. S. Manos CY-501* (BRIT BRIT914511); C, *P. S. Manos CY-513* (BRIT BRIT1082255). D, *P. S. Manos CY-439* (BRIT BRIT792909), modified from Fritsch et al. (2024b); E, F, *P. S. Manos CY-513* (BRIT BRIT1082255). All photographs by P. S. Manos.

FIGURE 5. Geographic distribution of *Vaccinium constablei* with resolution to the level of county. The shaded area corresponds to the Southern Appalachian region as described in the text.

FIGURE. 6. *Vaccinium hirsutum*. A. Stem. B. Vegetative bud and leaf base. C. Leaf blade surface. D. Leaf blade margin. E. Inflorescence bracts and bracteoles. F. Flower. Scale bars, A, B, D–F = 2 mm; C = 500 µm. All images from dried herbarium specimens. A, *W. H. Duncan 5311* (SMU BRIT424374); B, C, *R. D. Thomas s.n.* (SMU BRIT424380); D, F, *A. A. Crowl CY-078* BRIT BRIT698702); E, *H. E. Ahles 13147* (SMU BRIT 424377).

FIGURE 7. *Vaccinium hirsutum.* A. Habit, flowering upright stem. B. Branchlet showing adaxial leaf surfaces. C. Leaf, abaxial surface. D. Inflorescence; E. Immature infructescence. F. Infructescence with mature fruit (shiny black). All images in situ, with the following sources or herbarium vouchers. A, B, D, *A. A. Crowl CY-078* (BRIT BRIT698702); C, F, © Ashley M. Bradford, some rights reserved (CC-BY-NC), via iNaturalist; available at https://www.inaturalist.org/observations/225246296, ashley_bradford and https://www.inaturalist.org/observations/231541257; E, *A. A. Crowl CY-078* (BRIT BRIT698702). Photographs A, B, D, E by A. A. Crowl; C, F by Ashely Bradford.

FIGURE 8. Geographic distribution of *Vaccinium hirsutum* with resolution to the level of county. The shaded area corresponds to the Southern Appalachian region as described in the text.

FIGURE 9. *Vaccinium simulatum*. A. Stem. B. Vegetative bud and leaf base. C. Leaf blade surface. D. Leaf blade margin. E. Inflorescence bracts and bracteoles. F. Flower. Scale bars, A, B, D-F = 2 mm; C = 500 µm. All images from dried herbarium specimens. A, *P. W. Fritsch 2420* (BRIT BRIT698871); B, *A. A. Crowl CY-079* (BRIT BRIT 698703); C, F, *P. W. Fritsch 2419* (BRIT BRIT698870); D, *P. S. Manos CY-345A* (BRIT BRIT698858); E, *P. S. Manos CY-425* (BRIT BRIT792898).

FIGURE 10. *Vaccinium simulatum*. A, B. Habit, Satulah Mountain, NC. A. Clumped individual. B. Clonal individual or individuals. C. Branchlet showing raised stomata (dots). D. Branchlet showing abaxial surfaces of leaves. E. Branchlet showing adaxial surfaces of leaves. F, G. Inflorescences. F, greenish white flowers. G. Pale yellow flowers strongly flushed pink. H. Infructescences. All images in situ, with the following herbarium vouchers. A, *P. S. Manos CY-245* (BRIT BRIT698791); B, vicinity of *P. W. Fritsch 2412* (BRIT BRIT698863); C, *P. W. Fritsch 2413* (BRIT BRIT698864); D–F, *P. W. Fritsch 2412*; G, *P. S. Manos CY-425* (BRIT792898); H, *P. S. Manos CY-515* (BRIT1082257). Photographs A, B–F by P. W. Fritsch; B, C, G, H by P. S. Manos.

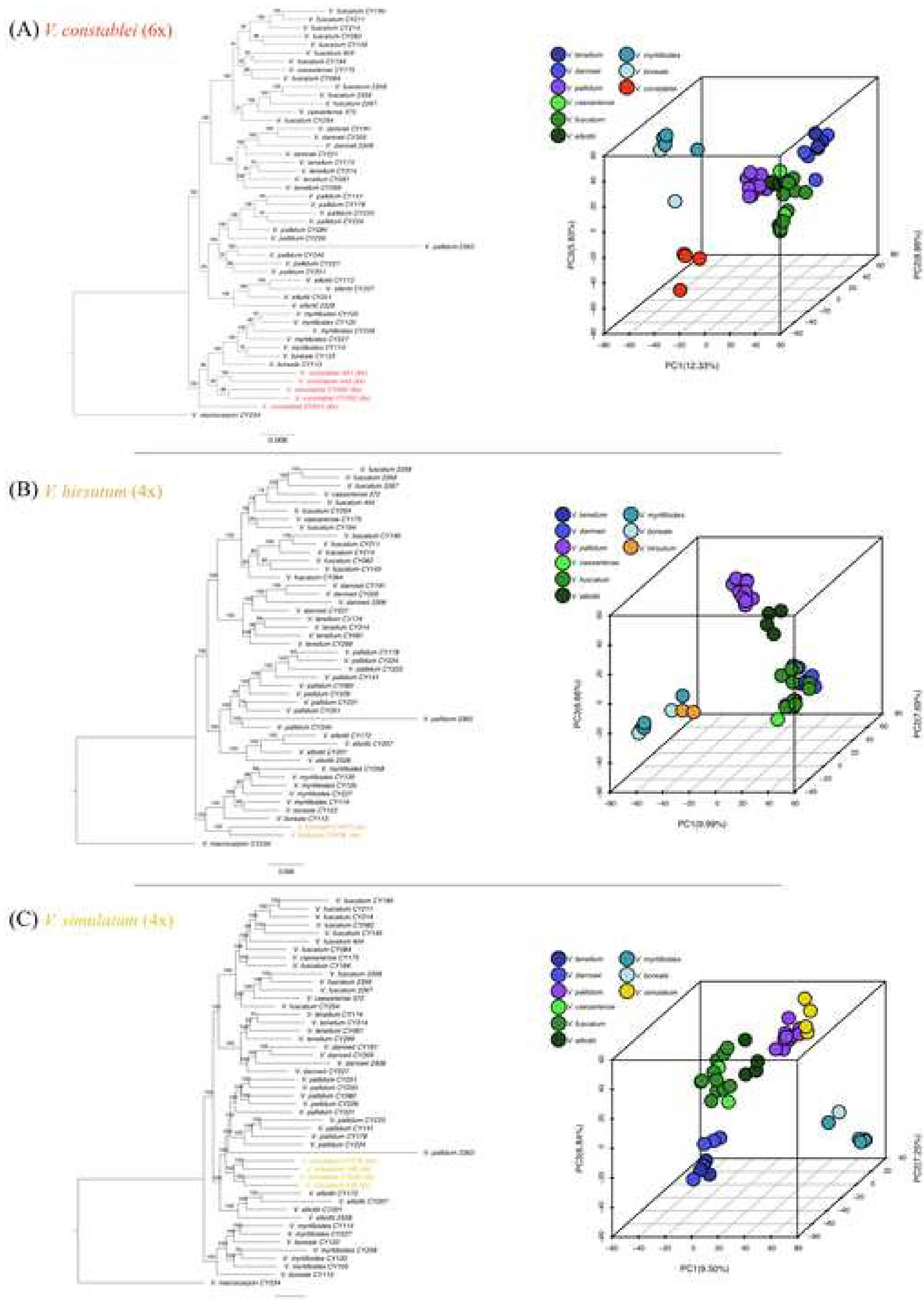
FIGURE 11. Geographic distribution of *Vaccinium simulatum* with resolution to the level of county. The shaded area corresponds to the Southern Appalachian region as described in the text.

SUPPLEMENTARY FIGURE 1. Phylogenetic tree, principal component plot, and STRUCTURE plots with the three polyploid species of *Vaccinium* sect. *Cyanococcus endemic* to the Southern Appalachian region included with the diploids of the section. (A) Best tree from maximum-likelihood analysis based on DNA sequences of the Angiosperms353 probe set. Bootstrap values are indicated above the branches. (B) Principal component analysis plot. (C) STRUCTURE plots, $K = 4$ through 8.

SUPPLEMENTARY FIGURE 2. Phylogenetic trees from ASTRAL gene-tree analyses based on DNA sequences of the Angiosperms353 probe set, with the three polyploid species of *Vaccinium* sect. *Cyanococcus* endemic to the Southern Appalachian region each added separately or together to the diploid species phylogeny. Numbers on branches indicate posterior probability support values. (A) Diploids plus *V. constablei*. (B) Diploids plus *V. hirsutum*. (C) Diploids plus *V. simulatum*. (D) Combined analysis of diploids plus all three polyploids.

fig 1

Click here to access/download;Figure;Fig_1_summary_PCA_PHYLOGENY.tif



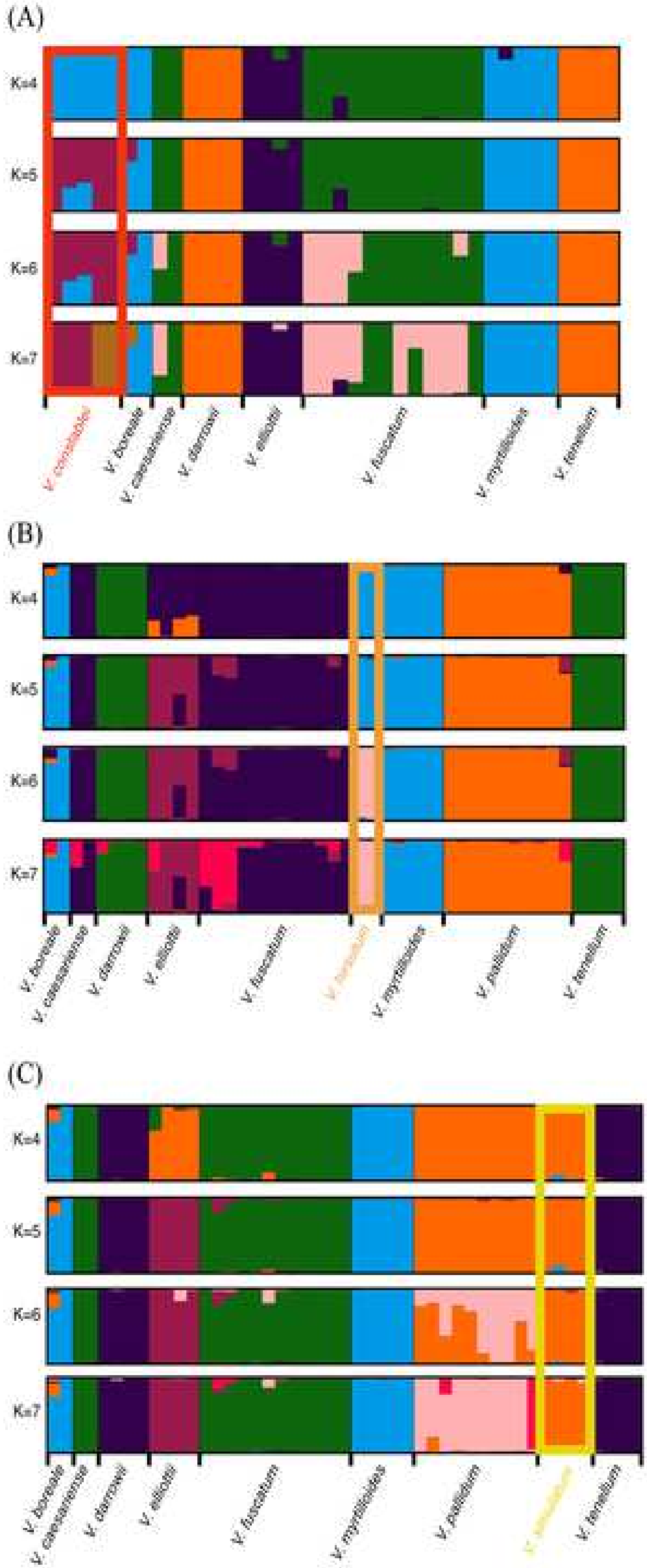

(A)
K=4
K=5
K=6
K=7
V. constablei
V. boreale
V. caesariense
V. darrowii
V. elliottii
V. fuscatum
V. myrtilloides
V. tenellum
(B)
K=4
K=5
K=6
K=7
V. boreale
V. caesariense
V. darrowii
V. elliottii
V. fuscatum
V. myrtilloides
V. pallidum
V. tenellum
(C)
K=4
K=5
K=6
K=7
V. boreale
V. caesariense
V. darrowii
V. elliottii
V. fuscatum
V. myrtilloides
V. pallidum
V. tenellum

fig 3

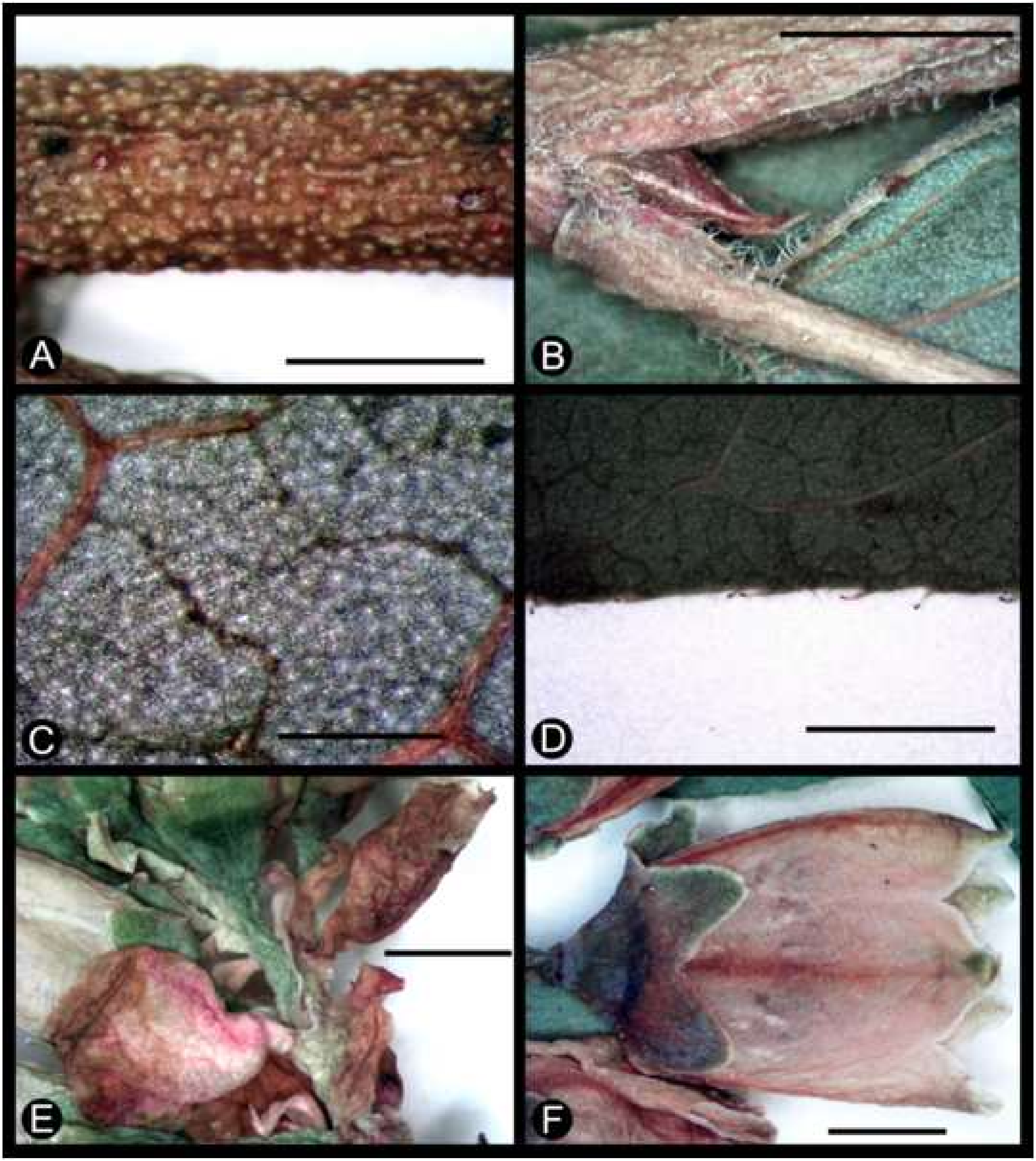


fig 4

Click here to access/download;Figure;Fig_4_constab_living_plate.tiff

fig 5

Click here to access/download;Figure;Fig_5_county_map_constab.tiff

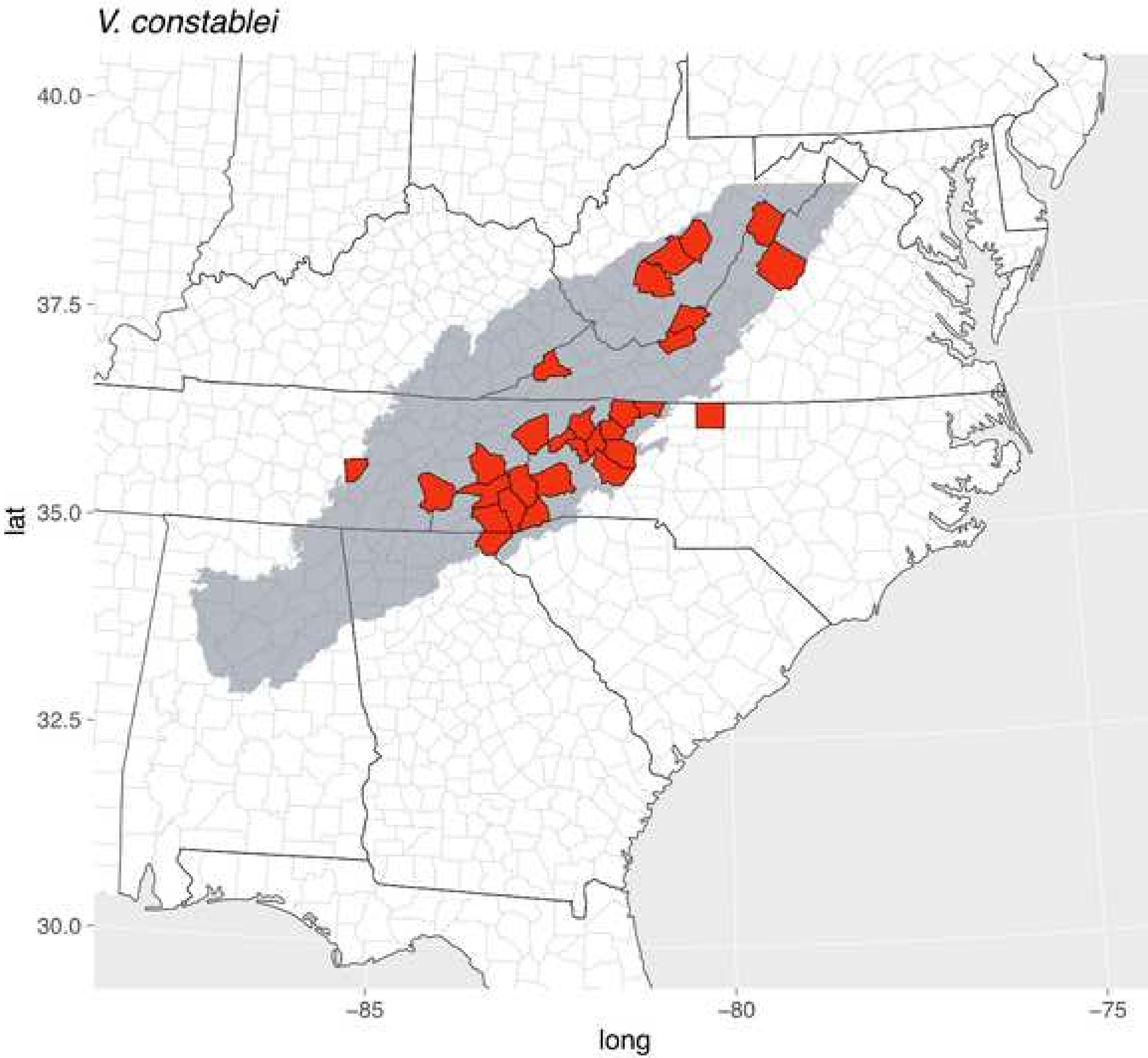


fig 6

Click here to access/download;Figure;Fig_6_hirsut_microchars_plate.tiff

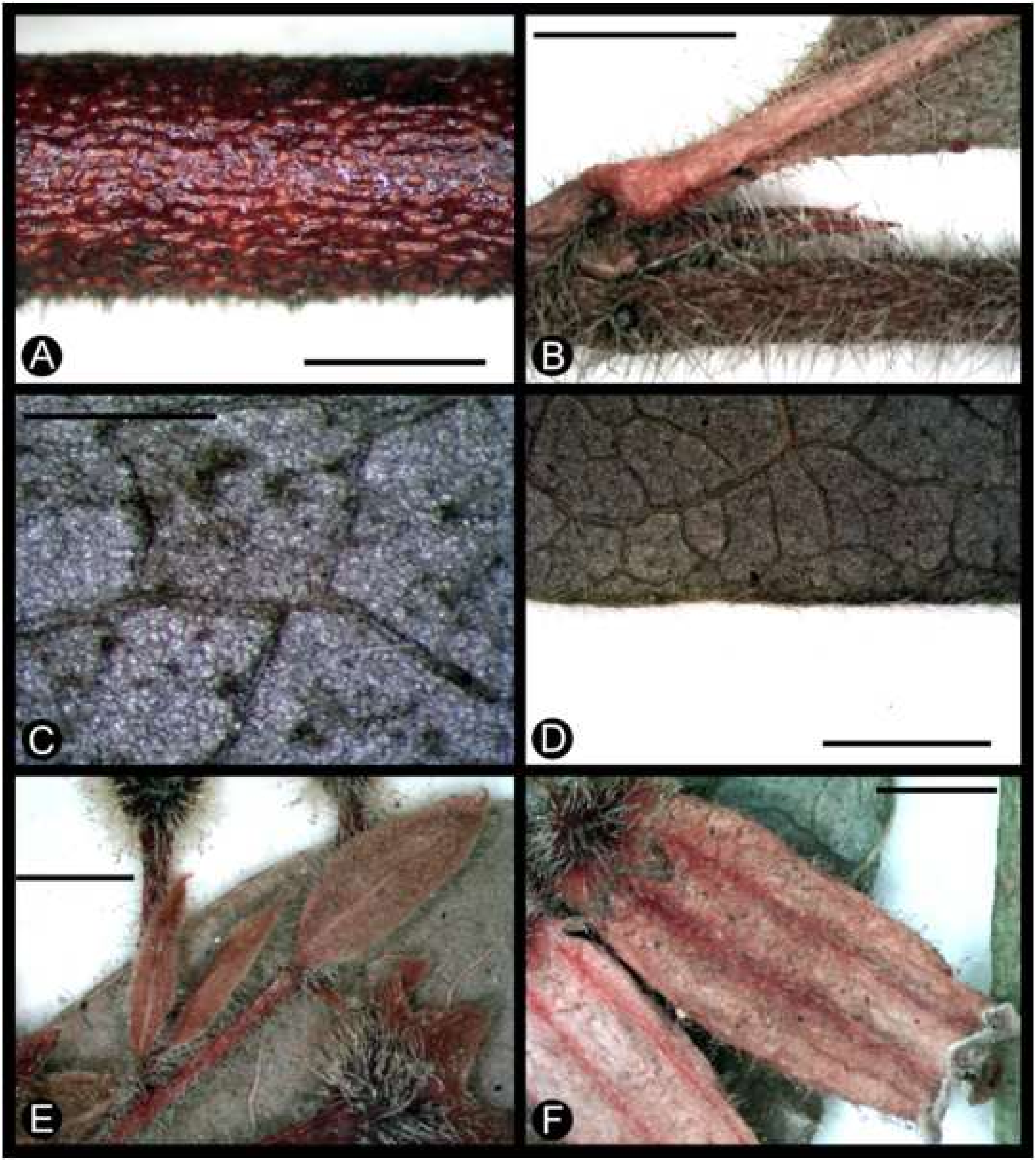


fig 7

Click here to access/download;Figure;Fig_7_hirsutum_living_plate.tiff

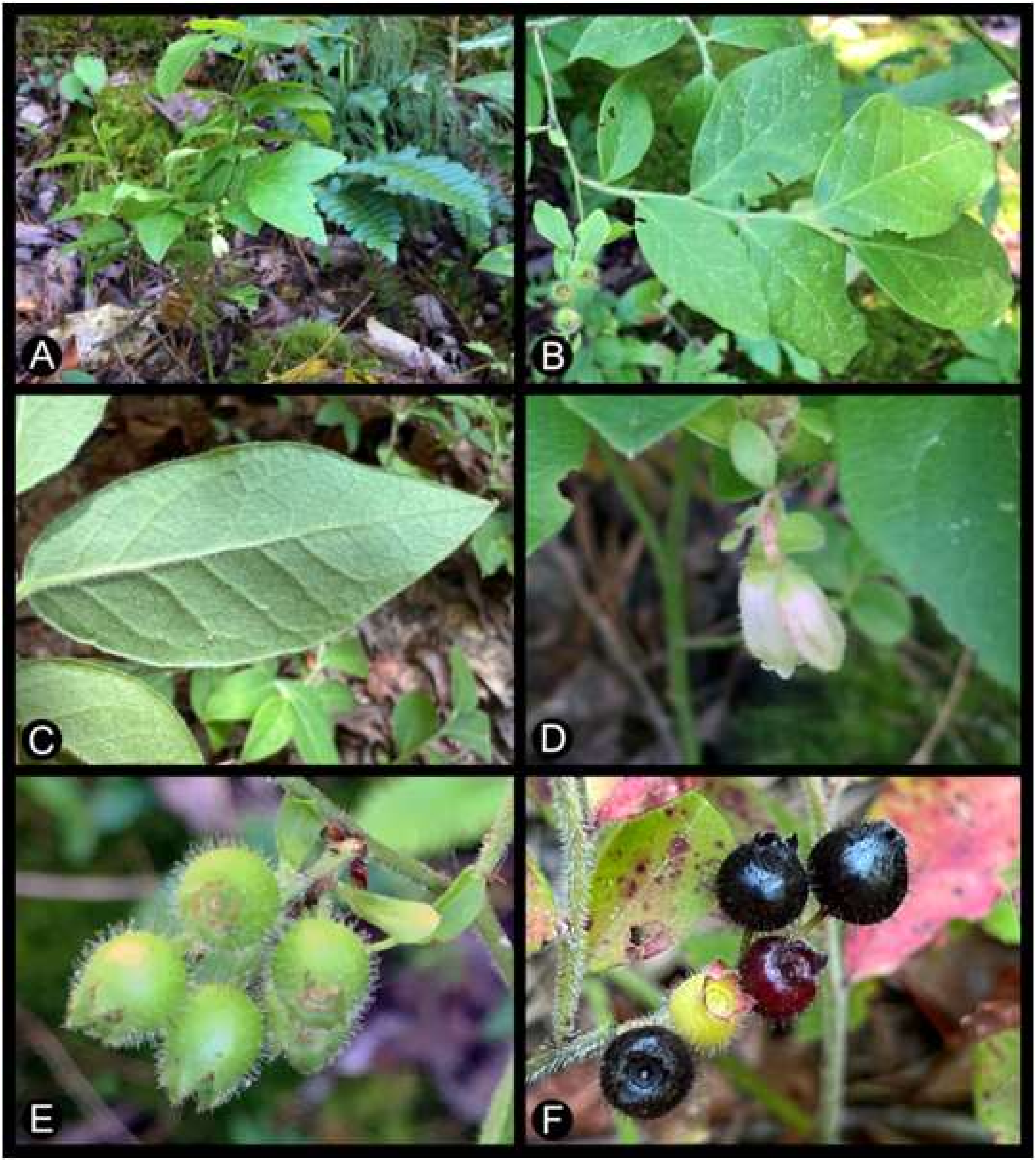


fig 8 Click here to access/download;Figure;Fig_8_county_map_hirsutum.tiff

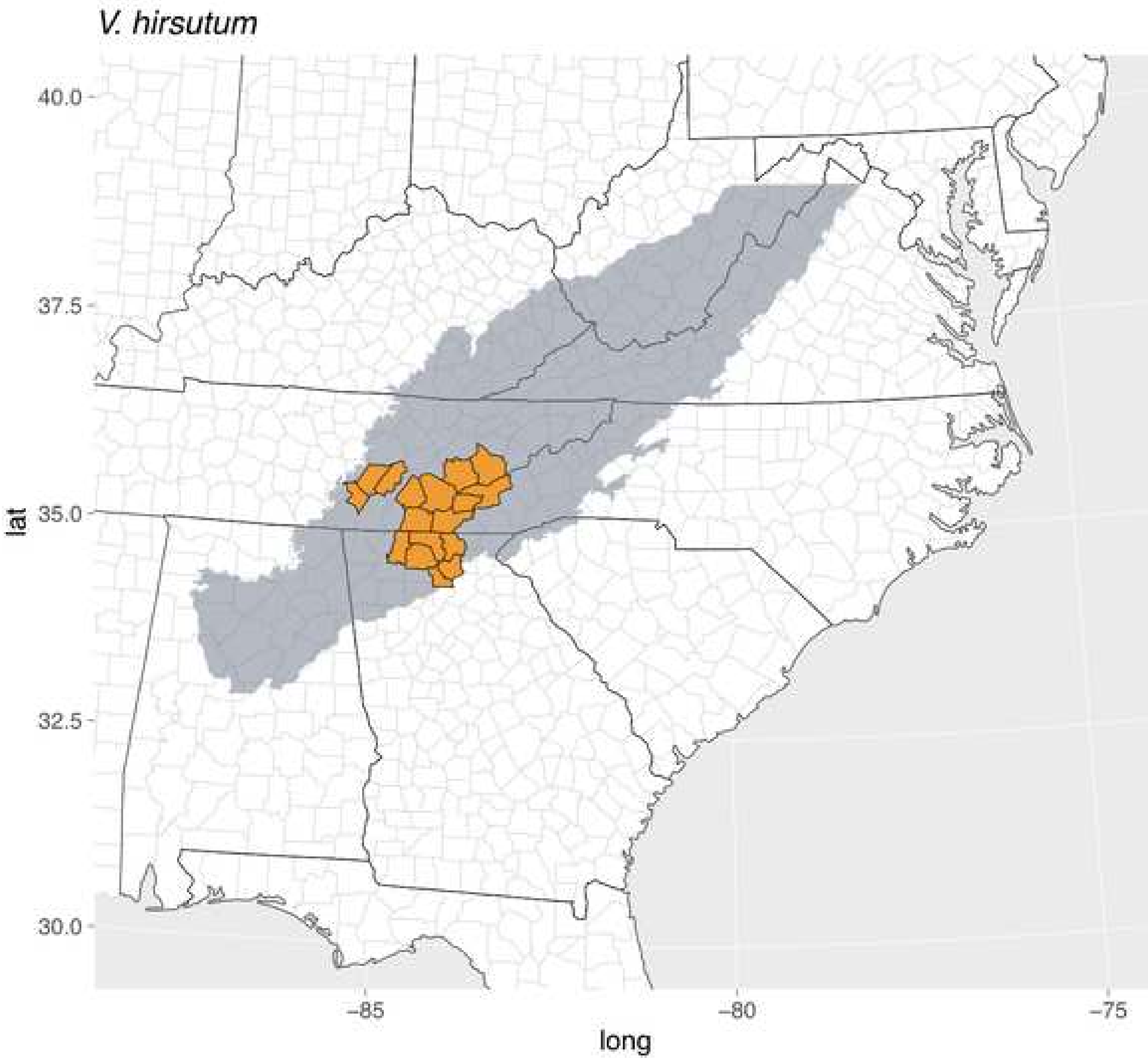


fig 9

Click here to access/download;Figure;Fig_9_sim_microchars_plate.tiff

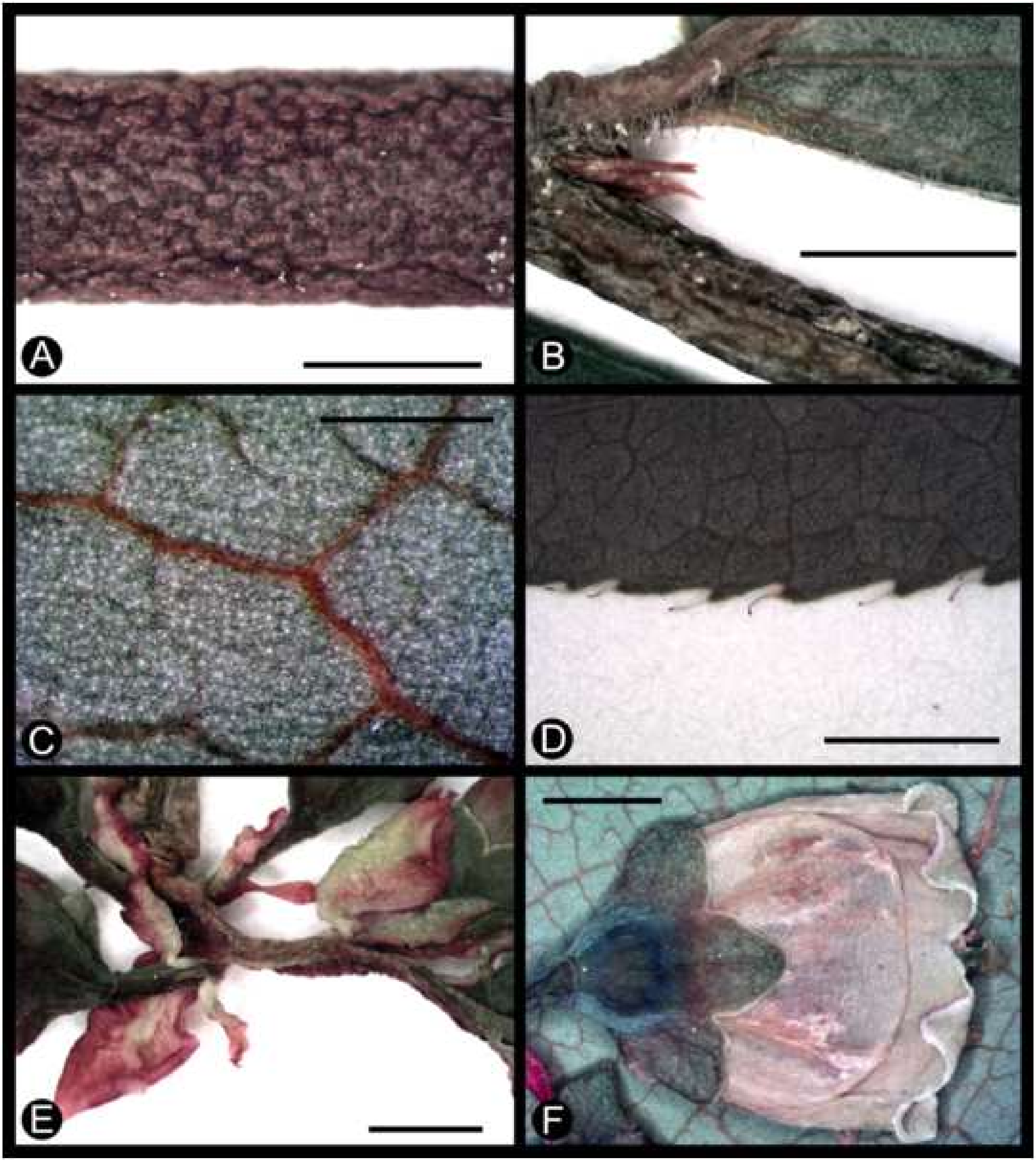


fig 10

Click here to access/download;Figure;Fig_10_simulatum_living_plate.tiff

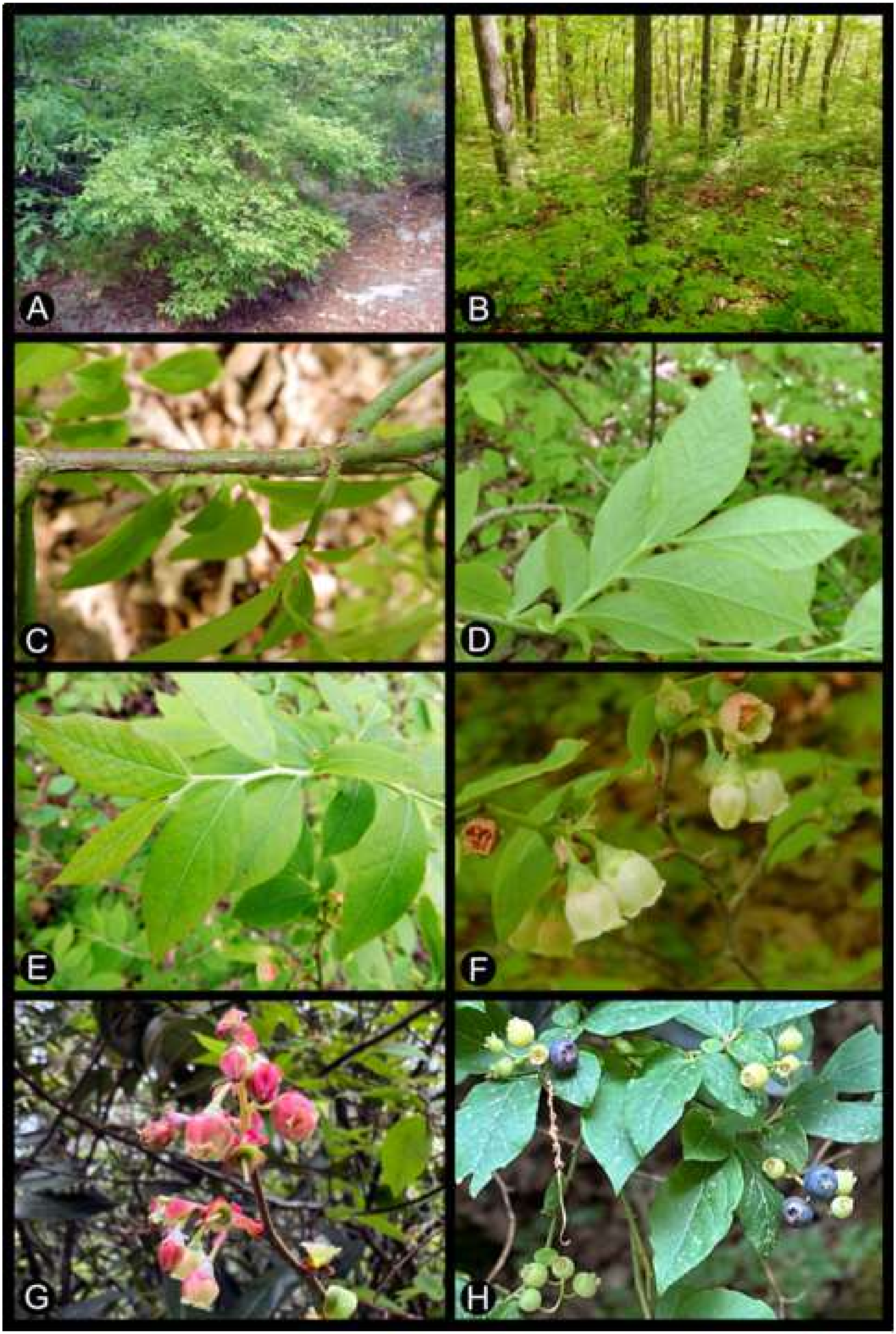
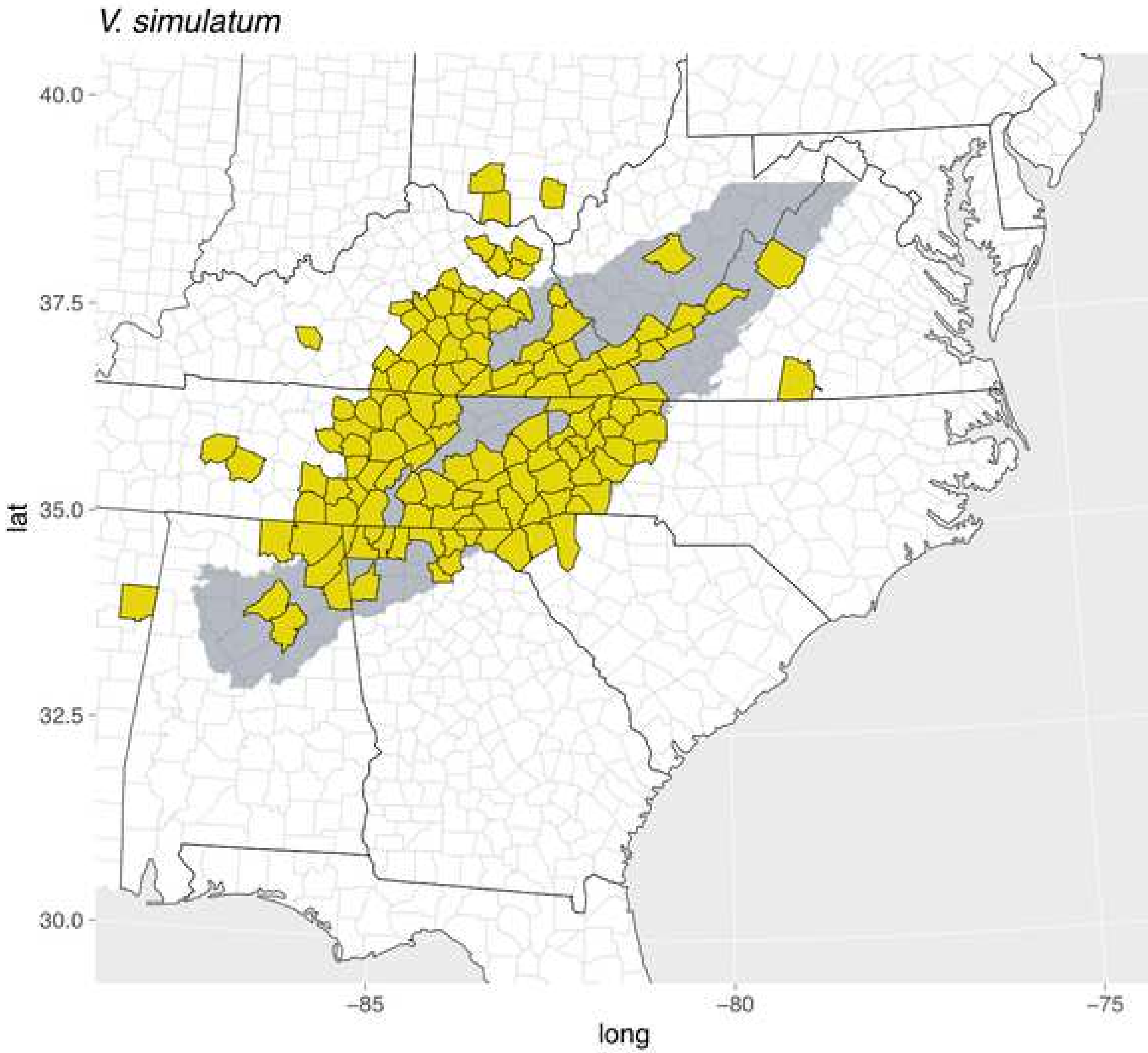
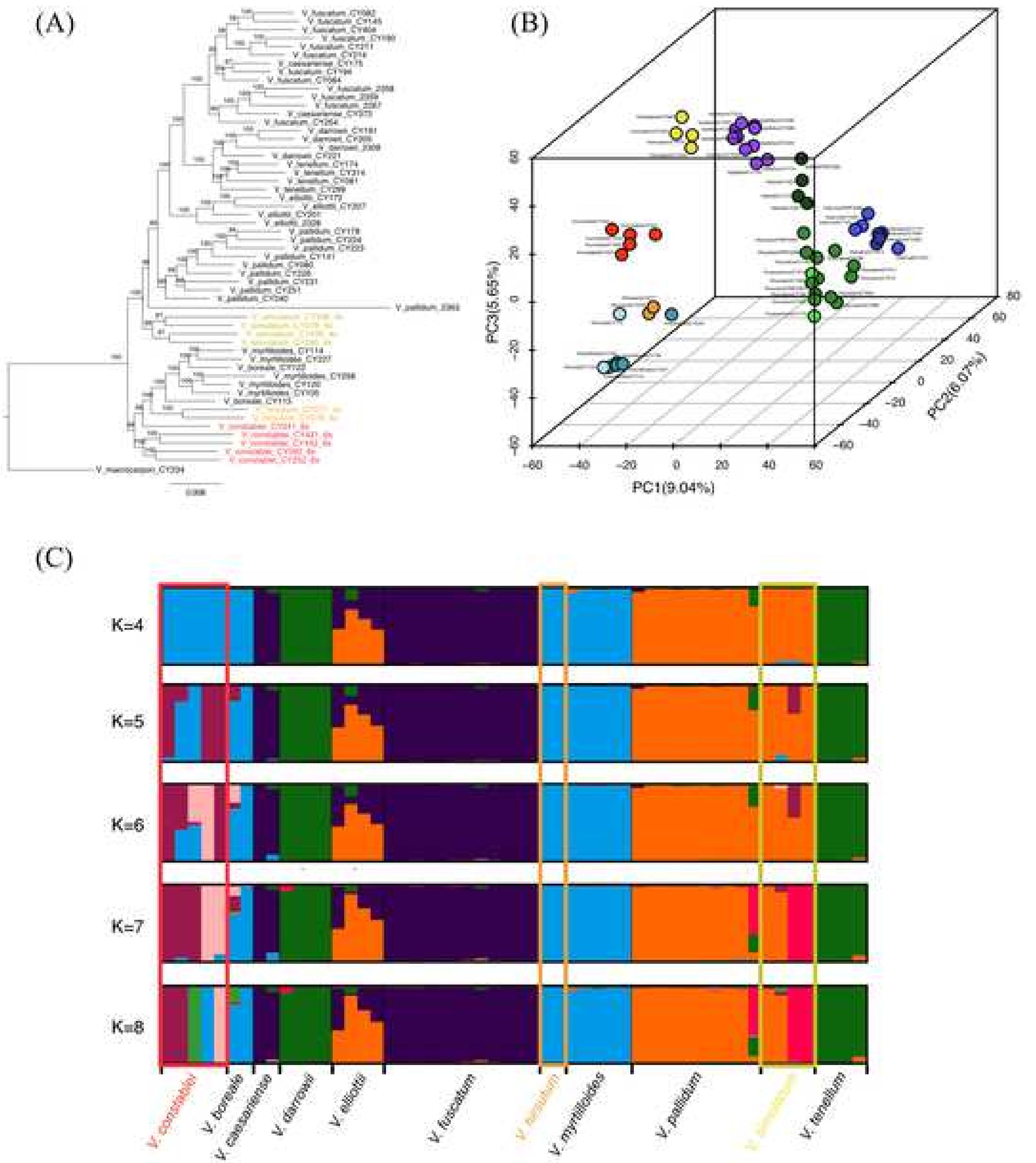
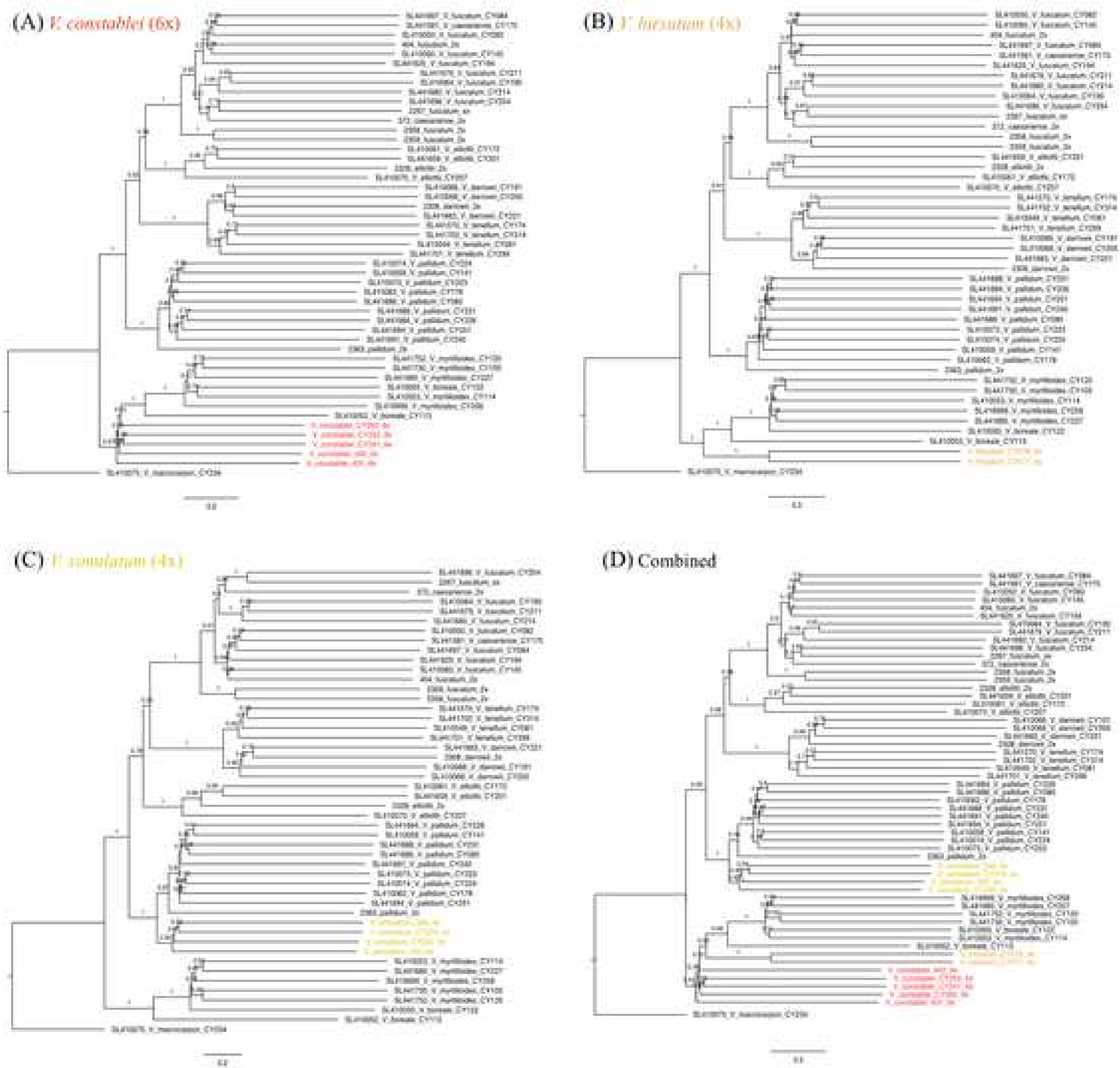


fig 11 Click here to access/download;Figure;Fig_11_county_map_simulatum.tiff



Suppfig 1


(A)
(B)
PC1(9.04%)
PC2(6.07%)
PC3(5.65%)
(C)
K=4
K=5
K=6
K=7
K=8
V. constablei
V. boreale
V. caesariense
V. darrowii
V. elliottii
V. fuscatum
V. hirsutum
V. myrtilloides
V. pallidum
V. simulatum
V. tenellum


(A) V. constablei (6x)
(B) V. hirsutum (4x)
(C) V. simulatum (4x)
(D) Combined