Understanding the systematics and evolution of *Vaccinium* sect. *Cyanococcus* (Ericaceae): progress and prospects

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ABSTRACT. The true blueberries (*Vaccinium* sect. *Cyanococcus*; Ericaceae) comprise a clade of about nine to 24 species distributed mainly in eastern temperate North America, with one species reaching farther west. Despite extensive study, the systematics and evolution of the group are still poorly understood. Limited morphological variation, multiple ploidy levels of uncertain origin, and natural hybridization all contribute to the challenge. Questionable analytical methods, such as the use of phenetics and an overemphasis on crossing experiments, have further impeded progress. Here we review the history of research on the systematics and evolution of *V.* sect. *Cyanococcus* with the aim of clarifying and summarizing hypotheses of species origins and diversification, especially in relation to polyploidy. We also present recent progress from our own work and, on that basis, offer promising lines of investigation with morphological and molecular data. We anticipate that these avenues of research will ultimately clarify patterns of natural species diversity in *V.* sect. *Cyanococcus* with benefits for biodiversity studies, conservation, and crop breeding.

Key words: biosystematics, blueberries, hybridization, morphology, North America, polyploidy, systematics, taxonomy

Vaccinium section *Cyanococcus* A. Gray, the true blueberries (Ericaceae: Vaccinioideae Arn.: Vaccinieae Rchb.; henceforth "*Cyanococcus*"), is a polyploid complex of ca. nine to 24 primarily outcrossing diploid (2x), tetraploid (4x), and/or hexaploid (6x) species distributed across much of temperate North America (Camp 1945; Song and Hancock 2011; Vander Kloet 1988; Figure 1). The species of this group are of immense ecological and economic value. They form a ubiquitous component of heathlands and acidophilic plant communities and serve as a critical food source for wildlife. They also comprise the wild progenitors of most of the blueberry cultivars that form the basis of a vibrant and growing multi-billion-dollar agroindustry. Blueberries represent one of only a handful of major crop plants originating in North America.

Although the sectional limits of *Cyanococcus* are clear, the number of accepted species and their boundaries vary dramatically among the key published taxonomic treatments. Considered the current standard, the treatment in the *Flora of North America* (Vander Kloet 2009) is undoubtedly flawed, yet alternatives produced concomitantly or since cover only limited geographic regions or are largely recapitulations of prior work that is itself questionable. The unresolved taxonomy of *Cyanococcus* has led to confusion and inconsistency in species identification and the application of names by researchers across biological fields. It has also resulted in ambiguity in the names of *Cyanococcus* cultivars. For example, the name *Vaccinium* *corymbosum* L. has been used liberally for both “Highbush” and “Southern Highbush” cultivars more than one meter tall, in northern and southern climates, respectively, despite differences in genetic composition revealed through artificial hybridization with various species (Galleta and Ballington 1996).

Progress in understanding the systematics and evolution of *Cyanococcus* has thus far been reviewed primarily from the perspective of horticulture and crop breeding (e.g., Galleta and Ballington 1996; Luby et al. 1991; Song and Hancock 2011). Here we provide a review with the focus placed primarily on natural populations. We first address the taxonomic establishment and circumscription of the section and discuss the key morphological characters used in taxonomic treatments. This is followed by an overview of the two seminal monographs of *Cyanococcus*, i.e., those of W.H. Camp (1945) and S.P. Vander Kloet (1988), comparing them to each other and to more recent, mainly regional treatments, with the aim of providing clarity on the rich set of hypotheses developed by *Cyanococcus* researchers over the last eight decades that can be tested with new data. Relevant evolutionary studies conducted after the work of Vander Kloet are then summarized. We end with our own preliminary findings based on fieldwork and examination of herbarium material and offer prospects for resolving the systematics and evolution of the group. The terminology of morphological characters and evolutionary concepts used in cited works has been updated and standardized, with changes from the original terms and concepts noted where appropriate. Phylogenetic relationships are addressed at only a cursory level here because the published data are still sparse, are primarily based on phenetics, and do not incorporate ploidy or hybridization into the analyses. We plan to focus more fully on these topics in future publications.

ESTABLISHMENT, RANK, POSITION, AND CIRCUMSCRIPTION OF *CYANOCOCCUS*

Cyanococcus was first published at the rank of section under *Vaccinium* L. (Gray 1848). It was then raised to the level of subgenus (Klotzsch 1851), and then to genus (Rydberg 1917, although as the illegitimate name *Cyanococcus* (A. Gray) Rydb. non *Cyanococcus* A. Hansgirg publ. 1905; International Plant Names Index 2021). The latter rank was accepted by Small (1933), but Camp (1945) considered it to "probably [merit] the rank of subgenus under *Vaccinium*." The key treatments that include *Cyanococcus* published since have all recognized it as a section of *Vaccinium* (e.g., Sleumer 1941; Stevens 2004; Vander Kloet 1983, 1988; Vander Kloet and Dickinson 2009). Nonetheless, *Vaccinium* has been considered "wildly polyphyletic" (Stevens 2004), and the available molecular phylogenetic data have supported para- or polyphyly for the genus (Powell and Kron 2002). This has led to proposals that divide *Vaccinium* into various numbers of genera, many corresponding to current sections. In the most extreme of these proposals, *Vaccinium* would be reduced to the single species *V. uliginosum* L. (W.S. Judd, University of Florida, pers. comm.), in which case *Cyanococcus* would be recognized again at the level of genus (although with a new name). However, much greater taxon sampling and improved molecular phylogenetic data will need to be generated and analyzed before seriously contemplating such changes.

Cyanococcus fits easily into the tribe Vaccinieae within the Ericaceae by its inferior ovary (Stevens 2004). Other characters that, in combination, place the section in this tribe are abortive pseudoterminal vegetative buds (versus non-abortive), presence of anther tubules (versus absence), and baccate fruits (versus dry; Stevens 2004). The phylogenetic placement of *Cyanococcus* within the Vaccinieae is currently unclear and, as with rank, will require much more extensive sampling within the tribe and improved molecular data than has thus far been applied.

As to circumscription, Gray (1859, 1860) and Sleumer (1941) placed several Japanese and northeastern Asian species in *Cyanococcus*, and Sleumer (1941) erected *Vaccinium* sect. *Pseudocyanococcus* Sleumer for the strongly evergreen species *V. myrsinites* Lam.; these placements have been rejected by subsequent authors. Odell et al. (1989) presented strong evidence for the current circumscription of the section based on the unique characters within *Vaccinium* of eruptive periderm development resulting in distinctive elongate diamond-shaped bark patterns and raised branchlet stomata rendering the branchlets verrucose (Figure 2A, 2B). Several other characters in combination also serve to diagnose the section, e.g., dimorphic vegetative and flowering buds, flowering buds with more than two overlapping scales, flowers in short racemes, the presence of an articulation between the pedicel apex and hypanthium (ovary), well-developed calyx lobes, the absence of anther spurs, and a pseudo-10-locular ovary (Camp 1945; Vander Kloet 1983; Figure 2C–H). A phylogenetic study based on DNA sequence data from the nuclear ITS and plastid *matK* and *ndhF* regions, which included samples of many sections of *Vaccinium*, supports the monophyly of the section, albeit with only two species of *Cyanococcus* sampled (Powell and Kron 2002). Phylogenomic analysis based on high-throughput DNA sequence data with more species of *Cyanococcus* included also supports the monophyly of the section (Crowl et al. 2022; A.A. Crowl et al., unpubl. data).

MORPHOLOGICAL CHARACTERS USED IN THE TAXONOMY OF *CYANOCOCCUS*

One of the main challenges in resolving the systematics and evolution of *Cyanococcus* has been the relative paucity of distinct morphological characters for use in species delimitation.

The characters that have been used to delimit taxa often overlap from taxon to taxon and some are often tightly correlated (e.g., the color of the leaves, pedicels, and hypanthium). The key morphological characters that have generally been used in taxonomic treatments of *Cyanococcus* are as follows. Habit: plant height, shape; extent of clonality (single above-ground stems vs. several stems together or many stems forming colonies). Branchlet: density; color; angularity; presence, arrangement, and length of surface trichomes. Vegetative bud: color; size. Leaf: persistence. Leaf blade: color on abaxial and adaxial surfaces; sheen on the abaxial surface; shape; dimensions; presence, density, and length of simple trichomes on the abaxial surface; presence of stipitate-glandular trichomes on the abaxial surface; presence, orientation, and length of trichomes on midvein on the abaxial surface; presence and regularity of (stipitate-glandular-tipped) serrations on the margin. Flower: density per inflorescence. Pedicel and calyx: color; presence of simple and stipitate-glandular trichomes. Corolla: color; shape; dimensions; presence of stipitate-glandular trichomes on the abaxial surface. Stamens: presence and arrangement of simple trichomes on the filaments; diameter of pollen tetrads. Fruit: color; sheen; dimensions; presence and quantity of surficial wax (“bloom”); seed weight.

Most of these characters are fully retained on herbarium specimens. For those that are not, we implore collectors to supply field information with the specimen. Particularly important are the following: plant clonality and diameter of the clone when present (care should be taken to distinguish among physically overlapping clones as assessed by, e.g., consistently different leaf blade shapes); plant height, and the number of basal stems; colors of various organs (branchlets, leaves, calyx, corolla [note any patterns such as lines], fruit); corolla shape, which can be distorted on dried specimens through, e.g., the splitting of campanulate or urceolate corollas; the presence or absence, and degree of, wax deposits on the calyx and fruit (“bloom”); fruit sheen (dull or glossy); and the orientation of flowers and fruit. It is also important to indicate plant species associates, especially the presence of other species of *Cyanococcus* growing with the collected plant. Separate collections should be made to document local variation in morphology, or suspected hybrids or introgressants. Collections of the same plant should ideally be made at different times of the season because flowers and fruits typically occur asynchronously in populations, and flowering often occurs prior to full leaf expansion. Finally, care should be taken to note whether any suckering branchlets have been collected because the leaves on these branchlets can differ from those on normal branchlets in at least shape and dimensions.

TAXONOMIC TREATMENTS

Critical taxonomic work on *Cyanococcus* can be divided into three segments roughly corresponding to time intervals. Before this work, the only group-wide treatments of *Cyanococcus* were produced as part of general floristic accounts for all or part of North America (e.g., Britton and Brown 1913; Chapman 1897; Gray 1908; Small 1933). The first two comprise the *Cyanococcus*-wide works of W.H. Camp in the 1940s and S.P. Vander Kloet mainly in the 1970s through 1990s. Both of these investigators conducted their research in the overall context of crop improvement, applying data from experimental crossing studies, genetics, and cytology to questions of species delimitation and the evolution of natural populations. These individuals produced a wealth of research that has advanced the knowledge of *Cyanococcus* substantially, although the focus on horticulture appears to have too strongly favored evidence relevant for crop breeding such as crossing information and fruit quality. The third segment consists of treatments of *Vaccinium*, including *Cyanococcus*, for specific U.S. states, written partly in response to those of Camp and/or Vander Kloet.

W.H. Camp. Comprehensive taxonomic study of *Cyanococcus* began in earnest with the work of W.H. Camp (Figure 3A) while he was an herbarium curator at the New York Botanical Garden. Although lesser known than some of the other botanists contributing to the evolutionary synthesis such as G.L. Stebbins and E. Anderson, Camp was nonetheless influential in the development and promulgation of biosystematics, i.e., the study of taxonomy and classification based directly on evolutionary principles and processes, as applied to botany (Kleinman 2009). Under the tenets of the biological species concept (Mayr 1942, 1963), the plant biosystematists used data from morphology, experimental crossing studies, genetics, and cytology to assess the reproductive isolation of individuals and populations emphasized for species delimitation, as well as to disentangle genetic from environmental influences on morphology and physiology. Although the theory of phylogenetic classification had yet to be fully developed, biosystematic classifications can be considered phylogenetically based; e.g., species were placed along or terminating lines of descent.

Based on prior studies (Camp 1942; Camp and Gilly 1943; Darrow and Camp 1945) but with much new information, Camp (1945) developed the first comprehensive taxonomic treatment of *Cyanococcus*; this was also one of the early taxonomic products of the plant biosystematists. *Cyanococcus* was divided into 24 species, with many earlier species and varietal names placed into synonymy (Table 1; Supplementary Data). Hypotheses were proposed only for the origins of most of the tetraploids and hexaploids; the origins of the diploids and the tetraploid *Vaccinium hirsutum* Buckley were left unspecified. Camp strongly emphasized estimates of ploidy derived from chromosome squashes to delimit species boundaries. No species possesses more than one ploidy level in the treatment, and species often form an ancestor-descendant diploid (2x, with $x = 12$)–tetraploid (4x)–hexaploid (6x) series (the "euploidion" of Camp and Gilly 1943) that either branches or converges with other species or series and thus form reticulate patterns of relationship (the "polyploid complex" of Grant 1981). Some species were thought to have originated through autopolyploidy and others through allopolyploidy (terms as in, e.g., Grant 1981; Spoelhof et al. 2017; Stebbins 1950), and two (the tetraploid *V. corymbosum* and hexaploid *V. ashei* J.M. Reade) were considered to combine parts of the genomes of several ancestral species.

Today the categories "highbush" and "lowbush" are applied to various *Cyanococcus* species in the horticultural literature, usually with the additional category "rabbit-eye" included and "highbush" often divided into "southern highbush" and "northern highbush" (e.g., Galletta and Ballington 1996; Luby et al. 1991; Vander Kloet 1983; Weakley 2020). However, Camp generally avoided the term "lowbush" and applied "highbush" only to those species more than one meter tall that he considered being involved in the evolution of *Vaccinium corymbosum*. An exception is the use of "lowbush" in the general key to species, but it appears that Camp used it merely as an artificial means of identification, with the division at one meter. Camp also referred frequently to "halfhigh" plants, which supposedly resulted from various crosses of "lowbush" and "highbush" types.

Camp ascribed his observations of wide variation within and among the species of *Cyanococcus* mainly to hybridization and introgression, and less commonly to segmental allopolyploidy. Based largely on the observation that viable hybrids are freely produced experimentally from parental species with the same ploidy level (either diploid, tetraploid, or hexaploid; Darrow and Camp 1945), Camp concluded that natural hybridization among the species of *Cyanococcus* is rampant and assumed that morphological similarity between experimentally produced hybrid progeny and wild individuals demonstrated that the latter are hybrids. Camp also thought that at least some of the allopolyploidization events produced “segregative allopolyploids” (± equivalent to “segmental allopolyploids” of e.g., Grant 1981; Mason and Wendel 2020; Stebbins 1950), i.e., allopolyploids in which the morphology of progeny tends toward that of one or the other parent through genetic recombination. Individuals with morphology ranging outside the norm of a species and resulting from hybridization, introgression (although not termed as such), and/or segmental allopolyploidization were designated as “elements” or “phases,” e.g., “the ‘simulatoid’ element of *Vaccinium corymbosum*” or “the ‘alto-montanoid’ element of *V. constablaei*” A. Gray. Camp also considered the boundary corresponding to the edge of the ice sheet during the last glacial maximum to have significantly influenced the current geographic distribution of the “highbush” species of *Cyanococcus*, such that distributional information relative to this boundary was included in the “Key to the basic populations” of species, sometimes to the exclusion of morphology. Camp proposed that interbreeding does not swamp species boundaries in *Cyanococcus* because hybrid establishment mainly occurs in habitats modified by humans, whereas in undisturbed areas the species were considered to be more fully separated by habitat and thus tend to breed true.

Camp’s treatise is at once comprehensive, groundbreaking, and thought-provoking. The work offers a wealth of information, including an abundance of hypotheses on *Cyanococcus* species boundaries and evolution that can be further refined and tested with new data. Despite the significant advance represented by Camp’s treatment, the overall value of the work is nonetheless compromised in several ways, which must be noted for a complete understanding of its implications. (1) Other than types, herbarium specimens are not cited; this renders the (somewhat abbreviated) species descriptions, discussions, and figures as the only means for the reader to obtain information on species boundaries, infraspecific and interspecific variation, hybridization, and introgression. Furthermore, the few figures in the treatment consist merely of low-resolution photographs of some of the species in the living condition. (2) If one is to assume that the work of Darrow et al. (1944) represents the entirety of the count data on which the species chromosome numbers are based, then the determination of ploidy is apparently based on only one to several counts for each species. Moreover, Darrow et al. (1944) do not clearly distinguish between chromosome counts made from cultivated versus wild-collected material. (3) Three of the species are provided with an indication of a ploidy level (all tetraploids) that is merely a prediction based on morphology versus an empirical chromosome count; thus, the hypothesized origin of these species, and even their very existence, must be questioned. (4) Assertions of natural hybridization and introgression are inadequately documented, i.e., presented without supporting data. (5) The evolutionary origin and diversification of many of the species are too often presented as substantiated fact when the evidence was scant at best, including highly speculative movements of ancestral species in response to climatic and glaciation events.

S.P. Vander Kloet. The work of Camp was used as the basis for further investigating the taxonomy and evolution of *Cyanococcus* by S.P. Vander Kloet, professor of biology at Acadia University and curator of its E.C. Smith Herbarium (Figure 3B). Like Camp, Vander Kloet relied heavily on experimental crossing studies as a basis for taxonomic conclusions in *Cyanococcus*. In contrast to Camp, he employed morphological phenetic analyses based on the principles of numerical taxonomy (Sneath and Sokal 1973); as such, he rejected the use of phylogenetics in estimating lines of descent and delimiting species boundaries a priori. After contributing numerous publications on the taxonomy and evolution of *Cyanococcus* (Vander Kloet 1976a, 1976b, 1977a, 1977b, 1978a, 1978b, 1980, 1983), Vander Kloet produced a culminating treatment of the group as part of a monograph of *Vaccinium* in North America, recognizing nine species of *Cyanococcus* (Vander Kloet 1988). Like the works of Camp, those of Vander Kloet often suffer from inadequate evidence-based conclusions. This applies particularly to assertions of natural hybridization and introgression but extends to species circumscription as well, because only rarely are herbarium specimens cited. The data from experimental crosses are too often presented anecdotally and backed neither by published data nor cited herbarium vouchers. For example, the published works often lack the data sets on which phenetic analyses are based.

The most prominent element of Vander Kloet's revisionary work (see particularly Vander Kloet 1980) based on the above approaches was the conclusion that all *Cyanococcus* species more than one meter tall ("highbush") form a "compilospecies," i.e., a genetically aggressive species that acquires the heredities of closely related sympatric species through hybridization and introgression (Harlan and deWet 1963). Vander Kloet proposed that this compilospecies, *Vaccinium corymbosum*, originated from hybridization between *V. darrowii* Camp and *V. tenellum* Aiton, and that it subsequently acquired and is still acquiring characters from the other diploid "lowbush" blueberries in his treatment, i.e., *V. boreale* I.V. Hall & Aalders, *V. pallidum* Aiton, and *V. myrtilloides* Michx., through repeated crossing, introgression, and polyploidization where they contact each other. As such, *V. corymbosum*, now the sole "highbush" species in *Cyanococcus*, was considered a highly variable species both morphologically and genetically, arising through multiple origins and comprising diploids, tetraploids, and hexaploids. Consequently, 12 of Camp's species were placed in synonymy (Table 1).

As evidence for justifying this concept of *Vaccinium corymbosum*, Vander Kloet cited the clustering of the "highbush" samples in his phenetic analysis relative to the "lowbush" samples, as well as the general lack of internal resolution within the "highbush" cluster. Because the character matrix for this analysis was not provided in the publication, it is difficult to independently assess these conclusions. Vander Kloet considered the findings of significantly fewer stainable pollen tetrads in "highbush" tetraploids versus "lowbush" diploids, and progeny from seed collected in the field from a single open-pollinated shrub that only partially resembled the parent, further evidence of a hybrid origin of *V. corymbosum*. It is unfortunate that of the 56 populations collected, Vander Kloet detailed only one example of the latter observation—a hybrid between plants corresponding to the diploids *V. atrococcum* A. Heller and *V. caesariense* Mack. sensu Camp (1945). The rest of the data are merely summarized by the statement "Similar results were obtained from the other seed collections acquired and treated in the same way as described above...." Vander Kloet's discussion implies that tetraploid individuals and populations of *V. corymbosum* have been repeatedly produced from the "lowbush" diploids, and hexaploids from tetraploid × diploid crosses, although the crossing data from hexaploids were sparse and therefore excluded from the study.

Based on observed habitat and phenological differences between *Vaccinium angustifolium* Aiton and *V. corymbosum*, Vander Kloet (1976) suggested that the other members of *Cyanococcus*, although still hybridizing in nature, are sufficiently isolated reproductively so as to be regarded as species. Thus, in at least one instance, Vander Kloet used ploidy to distinguish between morphologically similar species (diploid *V. boreale* versus tetraploid *V. angustifolium*; Vander Kloet 1977a). This may be one reason why, in contrast to Camp, Vander Kloet (1977b) asserted that "...the frequency of naturally occurring hybrids in areas of sympatry is much lower than expected from...experimental data. Indeed,...hybrids are rare," which ironically seems to contradict his concept of *V. corymbosum* as a compilospecies formed through hybridization.

In addition to recircumscribing *Vaccinium corymbosum*, Vander Kloet modified the concepts of *V. angustifolium*, *V. pallidum*, and *V. myrsinites* sensu Camp (see Supplementary Data). *Vaccinium angustifolium* is generally equivalent to Camp's concept of *V. lamarckii* Camp as altered to become the sole species throughout the geographic range encompassing Camp's *V. brittonii* Porter ex E.P. Bicknell and *V. lamarckii* at the tetraploid level, whereas *V. boreale* is reserved for plants that are morphologically similar to *V. angustifolium* but diploid. Aalders and Hall (1963) showed that the diagnostic characters of *V. brittonii* (i.e., glaucous stems and leaves) are controlled by a single gene and exposure to sunlight (Aalders and Hall 1963), and Vander Kloet (1978a) demonstrated that the characters defining *V. brittonii* and *V. lamarckii* do not breed true and co-occur extensively without phenological differences (Vander Kloet 1978a).

As reviewed in Luby et al. (1991), Aalders and Hall (1962) documented a positive correlation between leaf stomatal size and ploidy in *Vaccinium angustifolium* and their recently described species *V. boreale*. They measured the lengths of stomata in 12 individuals each of diploids and tetraploids consistent with *V. angustifolium* in morphology, finding a positive correlation between stomatal length and ploidy. They then measured the (presumed) average stomatal length from the type specimen of *V. angustifolium*, finding that it occurred well outside the range of stomatal lengths of the diploids but within the range of the tetraploids (the statistical basis for this conclusion was not presented). Thus, tetraploidy was ascribed to the type of *V. angustifolium*, which justified the continued recognition of their new species *V. boreale* based on its diploid ploidy level and several morphological characters, i.e., corolla length (3.0–3.5 mm versus 5–7 mm), pollen tetrad size (35–40 µm versus 40–43 µm), and a higher degree of branching (Hall and Aalders 1961). They stated that other vegetative characters could be found to distinguish these species with confidence.

Vander Kloet (1988) recognized *Vaccinium boreale* but, in contrast to Hall and Aalders (1961), he only used smaller plant height and smaller leaf blade size in his key to distinguish it from *V. angustifolium* with morphology; this is despite the clearly different corolla lengths presented in his descriptions (3–4 mm versus 4–6 mm, respectively). Vander Kloet (1977a) asserted that vegetative characters could be used to distinguish the two species but we consider the data presented too imprecise for properly assessing this claim. In particular, the extent to which the plants used for the morphological measurements were assessed for ploidy is unclear. This species sensu Vander Kloet can be considered equivalent to *V. angustifolium* sensu Camp except for a much more restricted geographic range, occurring only in far eastern Canada south through the northern border area of the northeastern United States (see Supplementary Data). In related research, Vander Kloet (1977a) cited the similarity of progeny to *V. angustifolium* in experimental crosses between *V. boreale* (2x) and *V. pallidum* (2x) in proposing that tetraploid *V. angustifolium* originated from hybridization between these two species, albeit the progeny of the crosses were all diploid.

Vander Kloet (1978b) presented convincing evidence from morphology and crossing experiments for placing *Vaccinium vacillans* Kalm ex Torr. into the synonymy of *V. pallidum*. In sampling the ploidy of individuals from several populations, he found that, out of 119 individuals sampled for chromosome number, 93% were diploid and 7% tetraploid. He thus confirmed the presence of tetraploid individuals in *V. pallidum*-like individuals as found by Camp (1945; no herbarium vouchers or images of chromosome squashes were cited). However, Vander Kloet chose to synonymize the tetraploids under *V. pallidum*, unlike Camp, who apparently recognized them as *V. altomontanum* Ashe (the application of the name *V. altomontanum* is unresolved because its type appears to be missing). Vander Kloet found no morphological characters to distinguish the tetraploids from the diploids and no evidence to indicate that the tetraploids behave ecologically as a distinct species. Although Vander Kloet did not specify a hypothesized origin of the tetraploids, it appears that he agreed with Camp that they have been produced as polyphyletic autoploids of the diploids.

The main difference in the concept of *Vaccinium myrsinites* from that of Camp is that both the diploid and tetraploid levels are cited, without explanation, in Vander Kloet (2009), although only the diploid level is cited in Vander Kloet (1983, 1988). Vander Kloet apparently considered the tetraploid level to have originated in the same way as did Camp, i.e., from a cross between *V. darrowii* and *V. tenellum*.

Vander Kloet's taxonomic view of *Cyanococcus* is currently considered the standard, having been adopted by the U.S. Department of Agriculture, plant breeders, and many local and regional floras, including the *Flora of North America* (Vander Kloet 2009). A key consequence is that the terms "highbush" and "lowbush" have become firmly established in distinguishing *Cyanococcus* species on the basis of plant height, i.e., generally more than one meter tall (*Vaccinium corymbosum* and any segregates) versus less than one meter tall (remaining species; e.g., Weakley 2020). Despite his assertion of widely occurring hybridization among the diploid "lowbush" members of *Cyanococcus* resulting in the polymorphic and polyphyletic *V. corymbosum*, Vander Kloet (1983, 1988) considered the diploids to have largely parapatric geographic distributions, with each of the species flanked by only one or two others.

Key Treatments for U.S. States. Just prior to and since the time of Vander Kloet's work, two researchers with field and herbarium experience in *Vaccinium* each produced a taxonomic treatment of *Cyanococcus* for a U.S. state as part of a more extensive treatment of

Vaccinium. Although constrained by geography, their studies often address more general taxonomic problems in *Cyanococcus* and thus achieve relevance here.

D.B. Ward of the University of Florida (Figure 3C) published a treatment of *Vaccinium* for the state of Florida (Ward 1974). Ward compared his work to that of Camp (1945) and others (Correll and Johnston 1970; Rehder 1940; Small 1933; Vander Kloet had not yet begun to publish on *Vaccinium*). Ward summarized the contrast between his conclusions and those of Camp with the statement that *Cyanococcus* is "...difficult but not in any way an irresolvable tangle of intergrading populations." Nonetheless, Ward seems to have oversimplified Camp's taxonomy by not addressing issues regarding potential variation in ploidy among morphologically similar plants. Ward recognized *V. amoenum* Aiton, *V. ashei*, *V. australe* Small, *V. darrowii*, *V. elliottii* Chapm., *V. fuscatum* Aiton, *V. myrsinites*, and *V. tenellum* for Florida. Differences from Camp's treatment are noted below. Ward did not habitually indicate ploidy for the species entries; ploidy is thus indicated only when noted in the treatment.

Ward agreed with Camp in distinguishing *Vaccinium amoenum* (6x) from *V. virgatum* Aiton (4x; not occurring in Florida to Ward), differentiating the two by the larger habit, leaves, and flowers of *V. amoenum*, as well as inflorescences that are limited to no more than two or three successive axils per branchlet (versus small paniculate clusters in the axils of many successive leaves per branchlet) and more widely separated from each other.

Ward considered *Vaccinium ashei* sensu Camp to be "...perhaps less of a taxonomic category than it is a philosophical concept," yet Ward recognized it, apparently in deference to Camp. It was distinguished from *V. amoenum* by leaves with abaxial surfaces that are glabrous or pubescent only along the midvein and that are more sparsely stipitate glandular.

Vaccinium arkansanum Ashe and *V. atrococcum* were combined with *V. fuscatum*, with Ward stating that although ploidy differs within this group, on a practical basis (we suppose meaning morphologically) the species cannot be distinguished. Ward differentiated *V. fuscatum* from *V. australe* by pubescent leaves and branchlets and black non-glaucous fruit (versus glabrous leaves and branchlets and blue-glaucous fruit) without commenting on or distinguishing among ploidy levels. Apparently, Ward did not consider *V. fuscatum* to be a hybrid of *V. atrococcum* and *V. darrowii* (unlike Camp), because at the end of the entry for *V. fuscatum* he stated that "Hybrids of *V. fuscatum* with...*V. darrowi*[*i*] are rather frequent," yet *V. atrococcum* was placed in synonymy with *V. fuscatum*.

There is essentially no difference in Ward's concept of *Vaccinium tenellum* from that of Camp, although Ward and Lyrene (2007) provided evidence to show that *V. tenellum* does not occur in Florida. They stated that prior herbarium specimen documentation of the species from the state was based on misidentifications of *Gaylussacia dumosa* (Andrews) A. Gray.

L.J. Uttal of Virginia Polytechnic Institute and State University (Virginia Tech; Figure 3D) published a treatment of *Vaccinium* for the state of Virginia. The treatment was produced partly to counter the concept of Vander Kloet's circumscription of the single highly variable species of "highbush" blueberry *V. corymbosum* (Uttal 1987), although Uttal readily adopted other species of Vander Kloet and their circumscriptions. Uttal agreed with Ward (1974) in segregating *V. elliottii*, *V. virgatum* (although thought not to occur in Virginia), and other species recognized by Camp (1945) from *V. corymbosum*. Uttal's work was based entirely on morphology and for the most part did not include quantitative data. Below we summarize and comment on the species of *Cyanococcus* in Virginia sensu Uttal.

There are essentially no differences between Uttal's and Camp's concepts of *Vaccinium caesariense* (2x), *V. elliottii* (2x), *V. myrtilloides* (2x), *V. simulatum* Small (4x), and *V. tenellum* (2x).

Vaccinium angustifolium (4x). Uttal adopted Vander Kloet's concept of this species.

Vaccinium corymbosum (4x). This species sensu Uttal best fits the concept of Camp except that *V. constablaei* (6x) is placed in synonymy. Uttal considered *V. constablaei* not to occur in Virginia, but considered it unreliably distinguishable from *V. corymbosum* with morphology.

Vaccinium formosum Andrews (4x). This species corresponds to Camp's concept of *V. australe*. We presume that Uttal considered *V. formosum* to be the earlier and thus correct name, although this is not clarified by Uttal.

Vaccinium fuscatum (2x, 4x). Uttal differed from Vander Kloet in recognizing this species as distinct from *V. corymbosum*. However, he also diverged from Camp (and apparently agreed with Ward [1974]) in adopting it as a species versus a hybrid between *V. atrococcum* (which he placed in the synonymy of *V. fuscatum*) and *V. darrowii*. He based this decision on the type material of *V. atrococcum*, which he asserted could not have been collected any farther south than South Carolina, whereas Camp's concept of *V. fuscatum* applies exclusively to plants from southern Georgia and Florida. According to Uttal, if the latter plants referred to by Camp merit recognition then they require a new name. Ironically, however, Uttal mentioned that the small leaves of the type of *V. holophyllum* (Small) Uphof suggest a hybrid between *V. fuscatum* and *V. darrowii*, which would in fact match Camp's concept of *V. fuscatum* as (an allotetraploid) hybrid between *V. atrococcum* and *V. darrowii*.

Vaccinium ×*marianum* P. Watson. Uttal employed a nothospecies name for this hybrid while leaving other recognized hybrids unnamed, apparently because morphological intermediates of *V. formosum* and *V. fuscatum* are the most common hybrids in the Virginia flora. Whereas Camp specified *V. marianum* as an allotetraploid of diploid *V. caesariense* (2x) and *V. atrococcum* (2x), Uttal clarified neither the ploidy level(s) at which hybridization occurred, nor the resulting ploidy level post-hybridization. Because Uttal considered *V. fuscatum* to comprise both 2x and 4x individuals, this aspect of *V.* ×*marianum* remains unresolved in his treatment.

Vaccinium pallidum. There is essentially no difference in the concept in this species from that of Vander Kloet, with both diploids and tetraploids included. *Vaccinium altomontanum*, apparently sensu Camp (1945; 4x), was placed in synonymy, as was *V. vacillans*.

Other Treatments. Taxonomic studies of *Cyanococcus* published after Uttal's treatment provide additional insights but are limited in scope. Three principal regional treatments of *Cyanococcus* focusing on the southeastern U.S. largely reflect the concepts of one or more of the prior global or state treatments above. The treatment of Godfrey (1988) for northern Florida and adjacent Georgia and Alabama followed "with not a little reluctance" Vander Kloet's (1988) treatment except that *Vaccinium elliottii* was considered distinct enough morphologically to warrant separate species recognition. The treatment of Luteyn et al. (1996) for the whole of the southeastern U.S. entirely reflects Vander Kloet's treatment, undoubtedly because, according to the Acknowledgments section, Vander Kloet was responsible for the treatment of *Vaccinium* in that work. The treatment of Weakley (2020) for the southeastern U.S. comprises elements of Camp, Vander Kloet, and Uttal, while also according with Ward's observation that hybrids, while indeed occurring, are not nearly as frequent as asserted by Camp and Vander Kloet.

Weakley's treatment recognizes 15 species, including *V. angustifolium*, *V. caesariense*, *V. corymbosum*, *V. darrowii*, *V. elliottii*, *V. fuscatum*, *V. formosum*, *V. hirsutum*, *V. myrsinites*, *V. myrtilloides*, *V. pallidum*, *V. tenellum*, and *V. virgatum*. The treatment deviates from prior treatments in also recognizing *V. altomontanum* and *V. simulatum*, while placing *V. constablaei* in synonymy with *V. corymbosum*. The differences among treatments generally in the latter regard, at least in part, likely result from the missing type of *V. altomontanum* together with misapplications of one or more of these names, but careful study will be needed to address this problem.

In other work, Luby et al. (1991) and Galleta and Ballington (1996) stated that sufficient morphological and ecological separation exists to recognize *Vaccinium elliottii*, and possibly *V. constablaei* and *V. simulatum*, all sensu Camp (1945), while leaving the rest of *V. corymbosum* sensu Vander Kloet (1983, 1988) intact. Luby et al. (1991) thought it best to consider the state of knowledge of the taxonomy of *Cyanococcus* (at the time) preliminary, urging further studies with multiple approaches. Various blueberry breeders have considered *V. fuscatum* (defined as diploid, in contrast to Camp 1945) and *V. ashei* (6x but "more properly denoted *V. virgatum*") to be sufficiently distinct from *V. corymbosum* sensu Vander Kloet to justify their recognition (Song and Hancock 2011).

EVOLUTIONARY STUDIES ON *CYANOCOCCUS* AFTER VANDER KLOET

Various studies investigating the nature of polyploidy and species relationships in *Cyanococcus* have been conducted since the time of Vander Kloet. These are addressed in turn below.

Ploidy. The original observation of Camp and others that *Vaccinium* species of the same level of ploidy can generally be crossed successfully under artificial conditions has been corroborated (with some exceptions; see Ballington and Galletta [1978]). Because of the strong triploid and pentaploid block in *Cyanococcus*, crosses among species of differing ploidy are only rarely successful (Hancock 1998; Lyrene et al. 2003; Ortiz et al. 1999). Nonetheless, the rare exceptions, thought to result from the production of unreduced gametes at low frequency (Ortiz et al. 1992a, 1992b), are exploited in blueberry breeding in the development of new cultivars (Hancock 1998). This suggests a means by which ploidy might increase in natural populations.

Allozyme and random amplified polymorphic DNA studies of progeny from tetraploid *Cyanococcus* cultivars found a clear pattern of tetrasomic inheritance, which is expected in autopolyploids (Krebs and Hancock 1989; Qu and Hancock 1997; Qu et al. 1998). Based on reanalyzed data from Hall and Aalders (1963), Hokanson and Hancock (1993) suggested that *Vaccinium angustifolium* shows tetrasomic inheritance and is thus an autotetraploid, contrary to the view of Vander Kloet (1977a), who considered it an allopolyploid hybrid of the diploid parents *V. boreale* and *V. pallidum*. On the basis of the results from Hokanson and Hancock (1993) and other less definitive studies, all polyploidy in *Cyanococcus* has been proposed to be derived through autopolyploidization (Lyrene et al. 2003; Soltis et al. 2007).

We emphasize, however, that variation in the definition of auto- and allopolyploidy affects the interpretation of these conclusions. In a taxonomic or mode-of-origin definition, autopolyploids arise from within a single species, whereas allopolyploids arise from interspecific hybridization. Conversely, in a genetic or cytological definition, autopolyploids display multivalent nonpreferential pairing of chromosomes during meiosis and allopolyploids display bivalent pairing (Doyle and Egan 2010; Ramsey and Schemske 2002). These two definitions will often lead to the same conclusion but sometimes a taxon may be classified as an autopolyploid under one definition and an allopolyploid under the other. In groups with highly conserved chromosome evolution, for example, hybridization between highly divergent taxa (i.e., clearly distinct species) might still result in the nonpreferential pairing of chromosomes. Conversely, divergence at individual loci could impair the ability to detect tetrasomic inheritance. Further confusing the issue is that there is no explicit criterion as to the threshold of genetic divergence above which two entities should be considered distinct species, versus populations of a single species, not to mention the related issues involving the application of various species concepts. Depending on the group under study and research goals, both definitions can nonetheless be useful. We advocate that studies explicitly state the definition used when deciding to label a taxon as an auto- or allopolyploid. Regardless, whether autopolyploidy is the sole or primary mode of polyploidization, versus allopolyploidy as proposed by earlier authors, has not yet been assessed in natural populations of *Cyanococcus*.

Hummer et al. (2015) used U.S. Department of Agriculture germplasm stock, including many of the original species in Vander Kloet's living collection and other living material, to measure ploidy levels with flow cytometry in samples of many *Vaccinium* species. The ploidy levels in the species of *Cyanococcus* largely matched those reported for the same species in prior work.

Poster et al. (2017) achieved a critical breakthrough in understanding the prevalence and significance of ploidal variation in natural populations of *Cyanococcus*. By carefully documenting diploid and tetraploid individuals of *Vaccinium corymbosum* (apparently sensu Vander Kloet) in sympatry in New Jersey with flow cytometry, they found ploidy to be significantly correlated with both flower size and phenology, with the tetraploids having larger flowers and a peak flowering period ca. one week later than the diploids. The significant difference in flower phenology suggests an isolating mechanism between the diploids and tetraploids, although the overlap also indicates that individuals of different ploidy levels can potentially crossbreed. The strong triploid block in *Cyanococcus* would presumably result in hybrid infertility, but unreduced gametes in diploids could result in unidirectional gene flow into the tetraploid phase. Whether morphological characters beyond flower size correlate with the two ploidal segments of the population remained unaddressed in the study.

Stomatal density and size. Stomatal density and size on the abaxial surfaces of leaves have been correlated with ploidy in many plant groups (e.g., Beck et al. 2003; Padoan et al. 2013; Sax and Sax 1937; Tan and Dunn 1973). When patterns are detected, stomatal size is most often positively correlated with ploidy, and stomatal density is negatively correlated. In some studies, these stomatal characters have consistently predicted the level of ploidy.

Darrow et al. (1944) were the first to suggest that stomatal size and/or density could be used to estimate ploidy in *Vaccinium*. They initially considered the method to show promise for determining ploidy in the genus, but later concluded that the method was likely confounded by the complex lines of descent common in the genus. Nonetheless, as noted earlier, Aalders and Hall (1962) used stomatal length to estimate ploidy for the nomenclatural type of *V. angustifolium*. Subsequently, Chavez and Lyrene (2009) and Dweikat and Lyrene (1991) found that stomatal guard cells (and pollen tetrad diameter) were significantly longer in colchicine-derived tetraploid leaf tissue of *V. elliottii* and *V. darrowii* than in the untreated diploids from the same genetic line.

Species relationships. Bruederle and Vorsa (1994) conducted an allozyme study with 25 natural populations of diploid *Cyanococcus*. Based on phenetic analysis with genetic identity values and the unrooted pair group method with arithmetic mean (UPGMA) algorithm combined with an assessment of morphological distinctness, they delimited seven diploid species, i.e., *Vaccinium boreale*, *V. corymbosum*, *V. darrowii*, *V. elliottii*, *V. myrtilloides*, *V. pallidum*, and *V. tenellum*. They anecdotally mentioned that all of their samples of *V. pallidum* from Arkansas were found to be tetraploid and thus excluded from the study. Based on genetic similarity and (anecdotally presented) overlapping variation in fruit color and leaf vestiture within populations, they treated *V. atrococcum* and *V. caesariense* as conspecific with the caveat that only three populations were sampled. Both species were referred to the more inclusive but variable concept of *V. corymbosum* sensu Vander Kloet (1988) with *V. elliottii* excluded. *Vaccinium elliottii* was considered a species distinct from *V. corymbosum* by habit, leaf and branchlet morphology, flowering phenology, and ecological distribution (but again without presenting data). Based on their field observations of morphology, they anecdotally considered hybridization in *Cyanococcus* to be “widespread,” although we note that the allozyme data seem not to have uncovered instances of hybridization.

Rowland et al. (2022) conducted phenetic UPGMA and neighbor-joining analyses of 50 mainly cultivated accessions of *Cyanococcus* with 249 expressed sequence tag-polymerase chain reaction markers. They found that tetraploid *Vaccinium corymbosum* grouped most closely with the diploids *V. caesariense* and *V. fuscatum*, followed by diploid *V. elliottii*. Tetraploid *V. angustifolium* grouped with the diploids *V. boreale* and *V. myrtilloides*, and hexaploid *V. virgatum* grouped most closely with *V. tenellum*. They considered the data to support the recognition of *V. elliottii* as a distinct species. The implications of the work for natural populations are limited by the lack of a clearly stated taxonomic framework and the use of cultivated material unspecified as to origin.

CURRENT STATUS, NEW DATA, AND FUTURE DIRECTIONS

We feel that progress in understanding the systematics and evolution of *Cyanococcus* over the past 80 years has been slower than might be expected, even after Luby et al. (1991) urged more comprehensive work on the group. Addressing the taxonomic problems in *Cyanococcus* from a primarily horticultural perspective has been a recurring motif. Given the tremendous economic potential of the group for blueberry breeding, we consider this understandable. However, such a perspective has often resulted in misleading extrapolation of studies based on cultivated material of unknown or imprecisely documented sources to natural variation and the limits of species. The problem is exacerbated by the inconsistent application of both scientific and common species names to cultivated samples and cultivars, the latter of which in any case may or may not correspond to species in nature. It is also compounded by the relative lack in many studies of samples vouchered with herbarium specimens, which limits the interpretation and impact of such studies. Over-reliance on crossing experiments to assess the origins of species and polyploids has also hindered the field. The morphological similarity of experimentally generated progeny to any particular species, which has been taken as de facto evidence of the origin of that species, may be mere coincidence and, in any case, has not been adequately documented with data in the instances proposed. Finally, assessment of ploidy has relied on far too few samples with which to base chromosome numbers, which often have been assumed too freely to define an entire species over its geographic range.

Our assessment of the current state of *Cyanococcus* systematics differs little from that of Luby et al. (1991), now over 20 years old. We feel that the treatment of Vander Kloet (2009), generally considered the current standard, to be flawed by an over-aggregation of species. Such "lumping" risks masking taxonomically significant diversity, obscures the origins of the cultivated blueberries, and leads to confusion in the field and in breeding programs. Conversely, the treatment of Camp (1945) likely has over-divided the section, as seems clear, for example, in the case of *Vaccinium pallidum* versus *V. vacillans*.

In this context, we have undertaken a multi-year collaborative project to address the longstanding issues in the systematics and evolution of *Cyanococcus* with new perspectives and data sources. We are integrating field- and herbarium-based research on samples collected from natural populations across the geographic range of *Cyanococcus* with data from DNA sequencing for phylogenetic analysis and flow cytometry to estimate ploidy. The sequence data will be used to assemble phylogenomic datasets from target enrichment and whole-genome data to infer evolutionary relationships, and a data pipeline will be designed to test hypotheses regarding the origins and mode of polyploidization and identification of diploid progenitors. Based on the sum of data, a comprehensive taxonomic revision of *Cyanococcus* will be produced. We ask the following questions to address the systematics and evolution of *Cyanococcus*: How many species are there, and what are their morphological definitions, geographic boundaries, and habitat distinctions? How is diversity generated through polyploidization? How evolutionarily labile is polyploidy—does it arise sparingly or frequently from diploidy? What is the prevalence of autopolyploidy versus allopolyploidy and their relative roles, if any, in species formation? Can morphology be used to help assess species, and is it correlated with ploidy? How prevalent is mixed ploidy within a locality ("population")? Is hybridization rampant in the group, as initially thought, and what is its role in the group's evolution?

Although we have only recently initiated our project, already ca. 3000 herbarium specimens of *Cyanococcus* have been examined from the combined BRIT-SMU, -VDB, and -NLU herbaria, and 550 leaf samples have been collected from across much of the range of the section for DNA sequence and flow cytometry analysis. Herbarium vouchers and photographs of the living plants in the field have been taken for most of the molecular and flow cytometry samples. Sampling multiple individuals in sympatry from each locality is a key distinguishing feature of our strategy. The aim is to identify morphological characters within and among localities that correlate with ploidy and phylogenetic data to discern evolutionary units (i.e., species). Although it is too early in the project to draw firm conclusions, particularly regarding our DNA sequence and flow cytometry data, we feel confident enough about the most salient of our observations on morphology in the field and herbarium specimen examination to report preliminarily on them here, accompanied by images of some of the species variation observed in the field and herbarium material (Figures 4–7). We caution that the names used below should be considered tentative, subject to change based on the critical examination of types and the results of further morphological examination of other herbarium material, ploidy assessment, and phylogenomics.

1. Consistent with the observations of Bruederle and Vorsa (1994), Camp (1945), Godfrey (1988), Luby et al. (1991), Uttal (1987), and Ward (1974), *Vaccinium elliottii* appears to be easily separated from the rest of Vander Kloet's "highbush blueberry" concept (Figures 4F–H and 6D). In places where *V. amoenum*/*V. virgatum* and other "highbush" blueberries occur (see below), plants with the morphology of *V. elliottii* sensu Camp appear to be distinct. One character in particular appears to easily separate *V. elliottii* from the remaining species of *Cyanococcus*, i.e., a style that is included within the corolla (versus exserted; Figure 4F). It is

ironic and rather inexplicable that Vander Kloet (1998) noted the existence of this character in a paper re-emphasizing the supposed indistinctness of *V. elliottii* from other "highbush" blueberries. Lyrene (1994), apparently independently of Vander Kloet, observed it in five cultivated selections from the wild identified as *V. elliottii*. Whether the short style of *V. elliottii* is a consequence of selection for or against increased selfing, or related in some way to dicliny, has not been adequately tested. Other characters in combination that can serve to distinguish *V. elliottii* are relatively small leaves that are usually not stipitate-glandular abaxially and a fruit with a persistent calyx of relatively narrow width.

2. In contrast to Vander Kloet (1983, 1988) and consistent with Ward (1974) and Uttal (1987), the abaxially stipitate-glandular-leaved plants corresponding to the Coastal Plain *Vaccinium amoenum*/*V. virgatum* sensu Camp (1945) appear to be distinct from the rest of Vander Kloet's (1983, 1988) "highbush blueberry" concept. These plants grow together with other typically non-stipitate-glandular species and are easily distinguished in the field by this character, along with a combination of usually serrate leaf blade margins and (when in flower) strongly exerted styles (Figures 5F, 5G and 6C). The correlation of their ploidy (*V. virgatum* [4x] and/or *V. amoenum* [6x]) with morphology and geography, as predicted by Camp (1945) and Ward (1974), has yet to be assessed. Also evident is that these plants can vary from less than to more than one meter tall and thus do not follow the "highbush" pattern that the treatment of Vander Kloet implies. Our preliminary findings suggest that variation in height is not categorical (which might otherwise imply a link with ploidy) but instead continuous.

3. A third species often growing with *Vaccinium amoenum*/*V. virgatum* and *V. elliottii* in areas where no other species of *Cyanococcus* are thought to occur (e.g., east Texas) corresponds to some version of *V. atrococcum* or *V. arkansanum* sensu Camp (1945), depending on ploidy, or

V. fuscatum sensu Uttal (1987; Figure 5A, 5B). When these plants occur together with those of *V. amoenum*/*V. virgatum* and *V. elliottii*, we find a dry to wet microhabitat trend, with *V. amoenum*/*V. virgatum* in the driest habitats and *V. atrococcum*/*V. arkansanum* in the wettest (but at most seepy), with *V. elliottii* found in intermediate habitats.

4. The stipitate glands on the abaxial leaf surfaces of *Vaccinium tenellum* and *V. myrsinites* differ from those of all other species of *Cyanococcus* in which such glands occur by having elongate versus subglobose heads (Figure 6). This is easily observed in herbarium material at 64× and is in fact depicted in Vander Kloet (1983: Figures 15–17), yet neither Vander Kloet nor others have apparently noted this distinction. The hypothesis in which *V. amoenum*/*V. virgatum* is derived from *V. tenellum* through autoploidy, at least on the assumption of homology of these glands alone, should thus be questioned, although their shared presence could still indicate close relationship. Conversely, the morphological similarity of these glands in *V. tenellum* and *V. myrsinites* supports the alloploid derivation of *V. myrsinites* from *V. darrowii* × *V. tenellum* as first proposed by Camp (1945).

5. The synonymy of *Vaccinium vacillans* under *V. pallidum* (Figure 5D) as proposed by Vander Kloet (1978b, 1988) and supported by Uttal (1987) seems well justified on the basis of morphology, with the few ill-defined characters used by Camp such as margin serration appearing to be taxonomically trivial. Whether *V. altomontanum* can be considered a synonym as well, as in Vander Kloet (1988) and Uttal (1987), will depend on resolution of typology, ploidy assessment, and delimitation of its geographic range, i.e., whether it is an Appalachian endemic or, as Camp suggested, extending as far as Ohio and Arkansas.

6. The treatment of *Vaccinium lamarckii* and *V. brittonii* as synonyms of *V. angustifolium* (4x), as distinct from *V. boreale* (2x), appears to be well documented in the literature and

justified on morphology (Aalders and Hall 1962, 1963; Hall and Aalders 1961; Vander Kloet 1977a, 1978a; Figure 4A–C). More study is needed to confirm the difference in corolla size between *V. angustifolium* and *V. boreale*.

7. Vander Kloet (1980) observed variation in the presence and quantity of fruit "bloom" (glaucescence) for the wild-collected F_1 progeny of two individuals of "highbush" blueberries corresponding most closely to *Vaccinium atrococcum* of Camp, and also for the wild-collected F_1 progeny of *V. angustifolium* (Vander Kloet 1978a). We have observed variation in this character within each of *V. atrococcum*, *V. elliottii*, and *V. amoenum*/*V. virgatum* in Arkansas and Louisiana (e.g., cf. Figure 4G, 4H). This character will require careful evaluation as to its taxonomic utility. We suspect that it has been overemphasized in taxonomic treatments because of the focus on fruit qualities in blueberry breeding programs. This is likely true also for fruit flavor and degree of sweetness.

8. Assertions of hybridization in *Cyanococcus* have invariably suffered from inadequate documentation in the literature. Claims are based either on anecdotal morphological observations, i.e., those without precise backing data, or vaguely defined similarity of natural variants or species to experimentally crossed hybrids. More rigorous documentation and analyses based on morphological and genetic data are required before the prevalence of natural hybridization in *Cyanococcus* can be assessed appropriately.

Nonetheless, we agree with others (Uttal 1987; Vander Kloet 1977b; Ward 1974; Weakley 2020) that the prevalence of hybridization and introgression in natural populations of *Cyanococcus*, at least as asserted by Camp (1945), appears to have been overstated. In our field work, we have thus far only infrequently encountered plants that exhibit some form of intermediacy between other species that occur in the same area. Moreover, in at least some of these cases, we speculate that such intermediates represent simple infraspecific variation of morphological characters at one ploidy level having nothing to do with species reticulation.

One example worthy of further study is the presence or absence of subglobose-headed stipitate glands on the abaxial surface of leaves. Such glands clearly can occur in species (sensu Camp) other than those considered to be defined by the presence of this character (*Vaccinium amoenum*/*V. virgatum*, *V. myrsinites*, and *V. tenellum*). They are clearly present occasionally in specimens of *V. atrococcum* and *V. elliottii* (Figure 6A, 6D). In these cases, the stipes are usually longer than those seen in *V. amoenum*/*V. virgatum*; in *V. atrococcum* they occur most frequently on the leaves of sterile branchlets. Camp (1945) considered the presence of such glands in plants that are otherwise morphologically consistent with *V. elliottii* evidence of hybridization of *V. elliottii* and *V. tenellum*. However, we have only observed subglobose-headed glands in *V. elliottii*, not elongate-headed glands, which might be expected in at least some of the hybrids. Rather than the result of hybridization with a glandular species, the presence or absence of such glands likely represents mere variation within these species. The same variation in the presence or absence of stipitate glands on the leaves abaxially is evident in species of *Vaccinium* in other sections, e.g., *V. arboreum* Marshall in *V.* sect. *Batodendron* (Nutt.) A. Gray, and *V. stamineum* of *V.* sect. *Polycodium*; it would thus not be surprising if this type of variation occurs in species of *Cyanococcus* as well.

Another confounding factor potentially leading to an overestimation in the prevalence of natural hybridization in *Cyanococcus* may be the escape of cultivars from plantings into natural environments. Such escapes have already been anecdotally noted by Camp (1945) and Ballington et al. (1982) and have been postulated in northern Florida (P.M. Lyrene, pers. comm.). In a forest in Smith County, Texas, an area considered out of range for native

Cyanococcus species, we observed a single 2.4 m tall shrub with pale leaves and calyces and sparsely scattered stipitate glands on the leaves abaxially (*Fritsch 2259* [BRIT, DUKE]). In a clearing on the same property, we observed cultivated blueberry plants (*Fritsch 2260* [BRIT]) with the same (vegetative only) characters as the plant in the forest, suggesting that the forest plant is progeny from the cultivated plants. In the Watson Native Plant Preserve in Tyler County, Texas, we observed a single plant with the same morphology as the plant above with larger fruits than those from the typical plants of *Vaccinium amoenum*/*V. virgatum* growing in the same preserve (6 × 10 mm versus 4–5 × 5–6 mm in sicco) and of clearly different appearance (e.g., glaucous versus green leaves and calyces; *Fritsch 2271* (BRIT, DUKE) and *Fritsch 2270* (BRIT, DUKE), respectively; Figure 5H). Blueberry farms are scattered throughout Tyler County. Another out-of-range plant similar in morphology to the Texas plants above has been collected in the Occoneechee Mountain State Natural Area in Orange County, North Carolina (*Manos & Crowl CY-321* [BRIT, DUKE]), and others with similar morphology have been collected in Liberty County, Florida (*Crowl CY-203*, *CY-204*, and *CY-206* [all BRIT]). Thus it seems clear that escapes from cultivation do occur at least sporadically, but the extent to which such plants have been conflated with naturally occurring hybridization has not been previously considered. We hypothesize that escape from cultivation into natural habitats of “rabbit-eye,” “northern highbush,” and other cultivars, which today are often complex hybrids developed through crop breeding programs (Song and Hancock 2011), at least in part explain Camp’s observations in wild *Cyanococcus*, e.g., those concerning *V. ashei* and *V. corymbosum* sensu Camp. Assessing the occurrence and prevalence of the intermixing of such escapes with natural populations will require the application of DNA sequence and flow cytometry data.

9. Despite the promise shown by studies for the use of stomatal density and size as an indicator of ploidy in *Cyanococcus* (Aalders and Hall 1962; Chavez and Lyrene 2009; Darrow et al. 1944; Dweikat and Lyrene 1991), apparently none since Aalders and Hall (1962) have assessed these characters as a proxy for estimating ploidy in natural populations of the group. In this regard, it may be fortuitous that in *Cyanococcus* the verrucose stems that define the section in *Vaccinium* result from raised stomata, where each stomate occurs atop a wart-like projection. Stem stomatal size and density can be roughly estimated with a stereomicroscope at 64×. We have used second-year stem morphology with other characters (e.g., stem color, corolla color and shape, and plant height) and flow cytometry to consistently distinguish individuals of *V. pallidum* (2x), *V. simulatum* (4x), and *V. constablaei* (6x; all sensu Camp 1945), all growing together in the Southern Appalachian Mountains, from each other (Figure 7). The relationship also appears to exist among *V. atrococcum* (2x), *V. corymbosum* (4x), and *V. formosum* (4x), all sensu Camp (Figure 7). This correlation, if substantiated on more rigorous investigation and particularly if the variation is found to be discontinuous and tied to ploidy, would greatly aid in the identification of *Cyanococcus* species in the Appalachians and elsewhere. Studies on this topic would be most impactful if pollen tetrad diameter were also included.

10. *Vaccinium simulatum*, endemic to the Southern and Central Appalachians, appears to be separable by the combination of height more than 1 m, broadly urceolate to campanulate corollas, and the stomate size and density associated with tetraploid plants (Figure 5E). Luby et al. (1991) also suggested distinct species status for *V. simulatum* but proposed more highly variable leaf morphology than indicated in Camp (1945). Separation of *V. simulatum* and *V. corymbosum* must be more carefully assessed (see below).

11. Once *Vaccinium amoenum*/*V. ashei*/*V. virgatum*, *V. elliottii*, and *V. simulatum* and are excluded from the concept of the “highbush” blueberry, the remaining variation in the group encompasses Camp’s *V. caesariense* and *V. atrococcum* (or *V. fuscatum*, depending on currently unresolved nomenclature) at the diploid level, and *V. arkansanum*, *V. corymbosum*, *V. formosum* (= *V. australe*), and *V. marianum* at the tetraploid level. We present the following working hypothesis to explain the morphological variation among the entities in this “residual highbush” group for testing with DNA sequence and flow cytometry data. (A similar hypothesis was proposed by Luby et al. [1991] in more abbreviated form.) We propose that diploid *V. atrococcum* and *V. caesariense* are two ends of a continuous spectrum of leaf pubescence (densely pubescent versus glabrous, respectively) where intermediates merely reflect morphological variation within a single diploid species. Similarly, tetraploid *V. arkansanum* and *V. formosum* comprise a single species with the same patterns of morphological variation (the named intermediate tetraploid *V. marianum* sensu Camp would be a synonym). This hypothesis would be consistent with the variation in progeny observed anecdotally by Vander Kloet (1980) and in the field by Ballington et al. (1980, 1982), the overall genetic similarity in diploid *V. atrococcum* and *V. caesariense* observed in the allozyme study of Bruederle and Vorsa (1994), and the study of Poster et al. (2017) documenting diploids and tetraploids in a natural population of *V. corymbosum* sensu Vander Kloet. The tetraploids could have originated from a diploid progenitor once or multiple times. The latter would render the tetraploids polyphyletic, and even then, they might cross among themselves locally or panmictically.

The remaining element of the “residual highbush” group to be considered is *Vaccinium corymbosum*, the name Camp applied to the widespread “highbush” blueberry in wetlands throughout the northeastern and north-central United States, and southeastern Canada. In origin and evolution, this entity may be the most enigmatic of those in the entire *Cyanococcus* clade. It could stand by itself as a tetraploid of these northern forests (whether or not, as Camp asserted, its southern boundary corresponds to that of the maximal extent of the last ice sheet). Alternatively, as proposed by Camp (1945), it could intergrade with various other species such as *V. simulatum* if both are found to be consistently tetraploid, and possibly even with tetraploid *V. arkansanum* sensu Camp, in which case it would extend across the entire eastern United States. It may even have been derived polyphyletically from diploid ancestors, then resembling Vander Kloet's compilospecies concept but with a narrower set of ancestors and/or descendants.

We hope and anticipate that this and the other hypotheses put forward in the literature and here will be addressed in the coming years through estimates of ploidy from flow cytometry, phylogenetic relationships from high-throughput DNA sequence data, and intensive study of morphology, all densely sampled from throughout the geographic range of *Cyanococcus*. With these data in hand, we are optimistic that the complex evolution of this ecologically and economically important group of plants can finally be disentangled, with benefits for biodiversity studies, conservation, and crop breeding.

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Table 1. Comparison of the two major taxonomic treatments of *Vaccinium* sect. *Cyanococcus*, that of Camp (1945) and Vander Kloet (2008), with their hypotheses for the origin of the tetraploids (4x) and hexaploids (6x) indicated. The terms "highbush" and "lowbush" are used in the sense of Vander Kloet as > 1 m tall versus < 1 m tall, respectively; auto = autopolyploid; allo = allopolyploid. See Supplementary Data for additional notes.

Camp (1945) species	Camp hypotheses	Vander Kloet (2008) species	Vander Kloet hypotheses
"Lowbush"			
V. myrtilloides Michx. (2x)	–	*V. myrtilloides* (2x)	
V. angustifolium Aiton (2x)	–	*V. angustifolium* (4x)	Allo of *V. boreale* and *V. pallidum*
V. brittonii Porter ex E. P. Bicknell (4x)	Auto of *V. angustifolium* or sister of *V. lamarckii*	*V. angustifolium* (4x)	"
V. lamarckii Camp (4x)	Auto of *V. angustifolium*	*V. angustifolium* (4x)	"
Not treated	–	*V. boreale* I.V.Hall & Aalders (2x)	–
V. pallidum Aiton (2x)	–	*V. pallidum* (2x)	–
V. vacillans Kalm ex Torr. (2x)	–	*V. pallidum* (2x)	–
V. altomontanum Ashe (4x)	Polyphyletic auto of *V. vacillans*	*V. pallidum* (4x)	No hypothesis indicated
V. darrowii Camp (2x)	–	*V. darrowii* (2x)	–
V. myrsinites Lam. (4x)	Segmental allo of *V. darrowii* × *V. tenellum*	*V. myrsinites* (2x, 4x)	4x is allo of *V. tenellum* × *V. darrowii*
V. tenellum Aiton (2x)	–	*V. tenellum* (2x)	

V. hirsutum Buckley (4x)	No hypothesis specified	*V. hirsutum* (4x)	No hypothesis specified
“Highbush”			
V. elliottii Chapm. (2x)	–	*V. corymbosum* (2x, 4x, 6x)	Complex allo of “lowbush” diploids; a “compilospecies”
V. virgatum Aiton (4x)	Auto of *V. tenellum*	*V. corymbosum* (2x, 4x, 6x)	"
V. amoenum Aiton (6x)	Auto of *V. tenellum*/*V. virgatum*	*V. corymbosum* (2x, 4x, 6x)	"
V. ashei J. M. Reade (6x)	Complex allo of five tetraploids	*V. corymbosum* (2x, 4x, 6x)	"
V. corymbosum L. (4x)	Complex allo of six tetraploids	*V. corymbosum* (2x, 4x, 6x)	"
V. atrococcum A. Heller (2x)	–	*V. corymbosum* (2x, 4x, 6x)	"
V. arkansanum Ashe (“probably 4x”)	Theoretical auto of *V. atrococcum*	*V. corymbosum* (2x, 4x, 6x)	"
V. caesariense Mack. (2x)	–	*V. corymbosum* (2x, 4x, 6x)	"
V. australe Small (= *V. formosum* Andrews; 4x)	Auto of *V. caesariense*	*V. corymbosum* (2x, 4x, 6x)	"
V. constablaei A. Gray (6x)	Allo of *V. altomontanum* × *V. simulatum*	*V. corymbosum* (2x, 4x, 6x)	"
V. fuscatum Aiton (“probably 4x”)	Theoretical allo of *V. atrococcum* × *V. darrowii*	*V. corymbosum* (2x, 4x, 6x)	"
V. marianum P. Watson (“probably 4x”)	Theoretical allo of *V. atrococcum* × *V. caesariense*	*V. corymbosum* (2x, 4x, 6x)	"
V. simulatum Small (4x)	Auto of *V. pallidum*	*V. corymbosum* (2x, 4x, 6x)	"

Figure Legends

Figure 1. Geographic distribution of *Vaccinium* sect. *Cyanococcus*, endemic to North America.

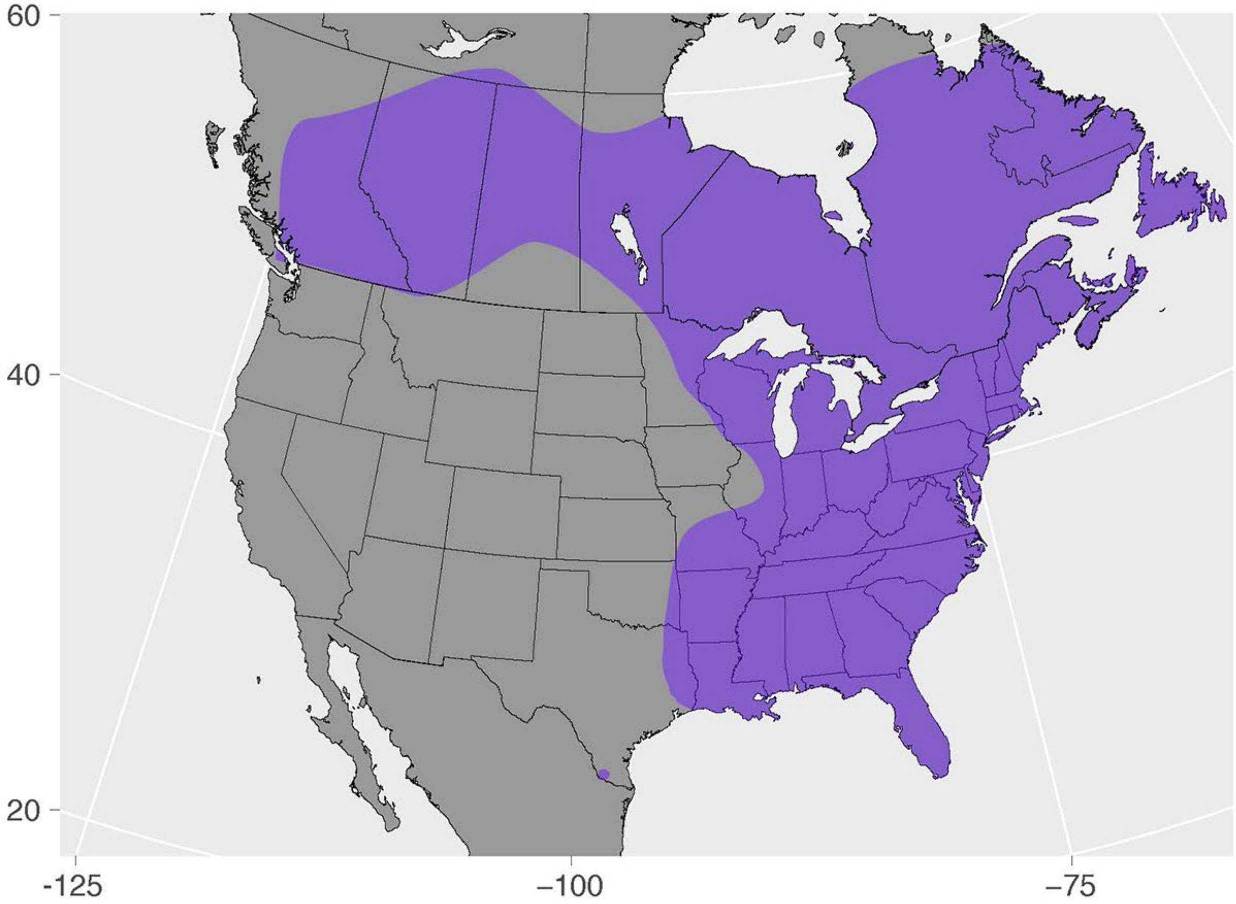

Figure 2. Some diagnostic morphological characters of *Vaccinium* sect. *Cyanococcus*. Species names are tentative, approximating those of Camp (1945). (A) Eruptive periderm on the bark of a cultivated plant of *V.* sect. *Cyanococcus*. (B) Raised stomata on the second-year stems of a cultivated plant of *V.* sect. *Cyanococcus*. (C) Dimorphic buds on a cultivated plant of *V.* sect. *Cyanococcus*. The four larger more distal buds are reproductive buds and the smaller more proximal buds are vegetative. (D) Flowering bud showing multiple overlapping bud scales. (E) *V. tenellum*, showing multi-flowered inflorescences. (F) Infructescence of *V. amoenum*/*V. virgatum* showing the articulation between the pedicel apex and hypanthium, and well-developed calyx lobes. (G) Stamens of *V. constablaei*. Note the absence of dorsal anther spurs. *Manos CY-442* (BRIT, DUKE). Scale bar = 2 mm. (H) Cross section of young fruit of *V. amoenum*/*V. virgatum* with upper immature seeds removed showing architecture of pseudo-10-locular ovary. The five septa alternate with five invaginations from the outer wall. *Fritsch 2282* (BRIT, DUKE). Scale bar = 2 mm. Photos: A–C by Anna Becker, used with permission; D, derivative of https://www.inaturalist.org/observations/41521073 by Nathaniel Sharp licensed under CC BY-NC 4.0; E by A.A. Crowl; F–H by P.W. Fritsch.

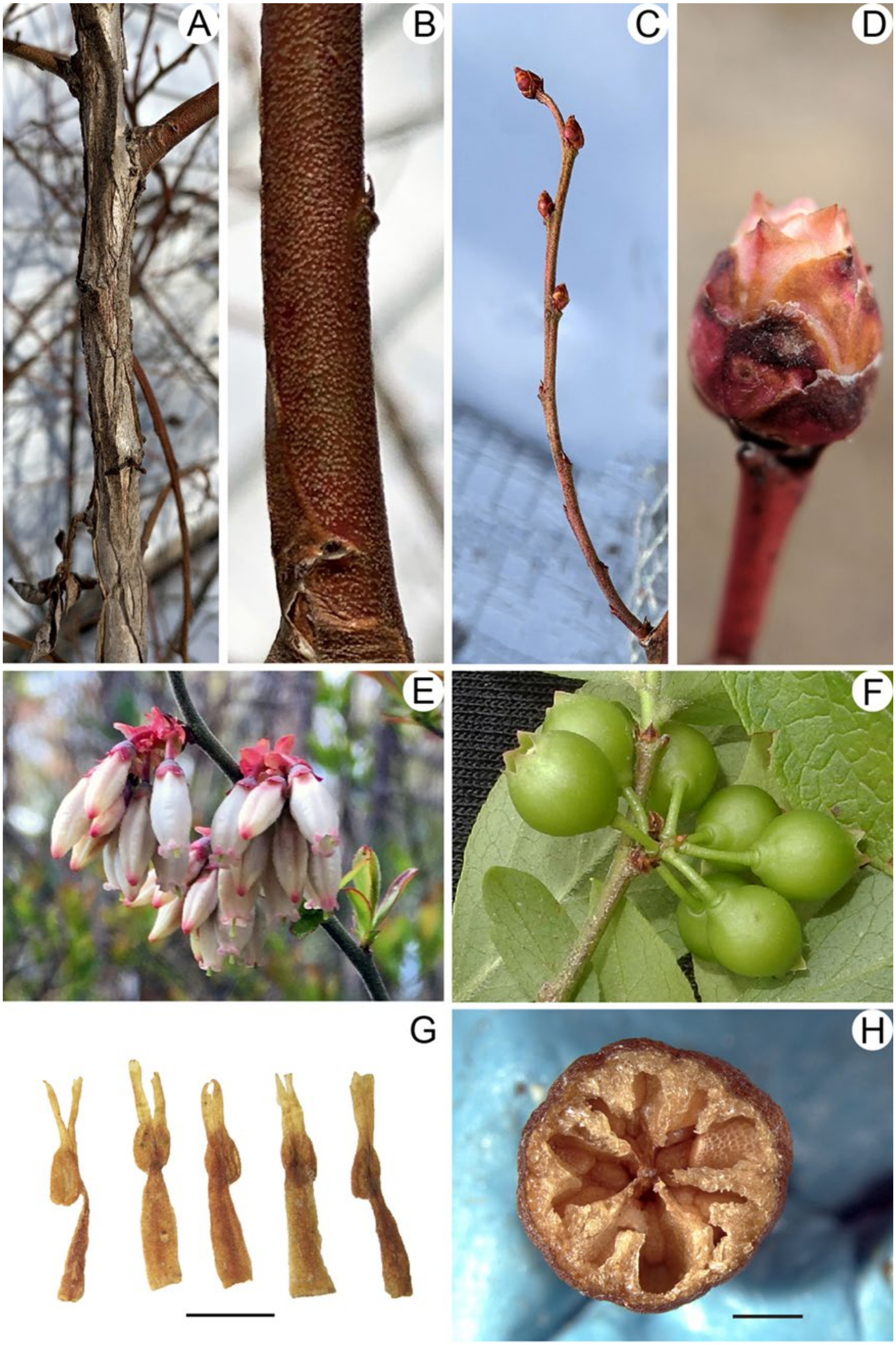
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Figure 3. Authors of key taxonomic treatments of *Vaccinium* sect. *Cyanococcus*. (A) W.H. Camp. (B) S.P. Vander Kloet. (C) D.B. Ward. (D) L.J. Uttal. A, courtesy of the Archives of the New York Botanical Garden; B, courtesy of Melanie Priesnitz, used by permission; C, courtesy of Gordon Ward, used by permission; D, courtesy of Jeannie Uttal Breeden, used by permission.

Figure 4. Field images of *Vaccinium* sect. *Cyanococcus*. Species names are tentative, approximating those of Camp (1945). (A) Flowering plant of *V. angustifolium*. Cultivated, University of California Botanical Garden 78.0093 (origin: Nova Scotia, Canada). (B) Fruiting plant of *V. angustifolium. Fritsch 2371* (BRIT, DUKE). (C) Pallid-leaved form of *V. angustifolium. Fritsch 2373* (BRIT, DUKE). (D) Inflorescence of *V. constablaei*. *Manos CY-439* (BRIT, DUKE). (E) Fruiting plant of *V. darrowii*. *Fritsch 2310* (BRIT, DUKE). (F) Flowering branchlet of *V. elliottii*. Note lack of exserted style. *Crowl CY-368* (BRIT). (G) *V. elliottii* with glossy black fruits. *Fritsch 2295* (BRIT, DUKE). (H) *V. elliottii* with glaucous fruit. *Fritsch 2333* (BRIT, DUKE).Photos: A–C, E, G, H by P.W. Fritsch; D by P.S. Manos; F by A.A. Crowl.

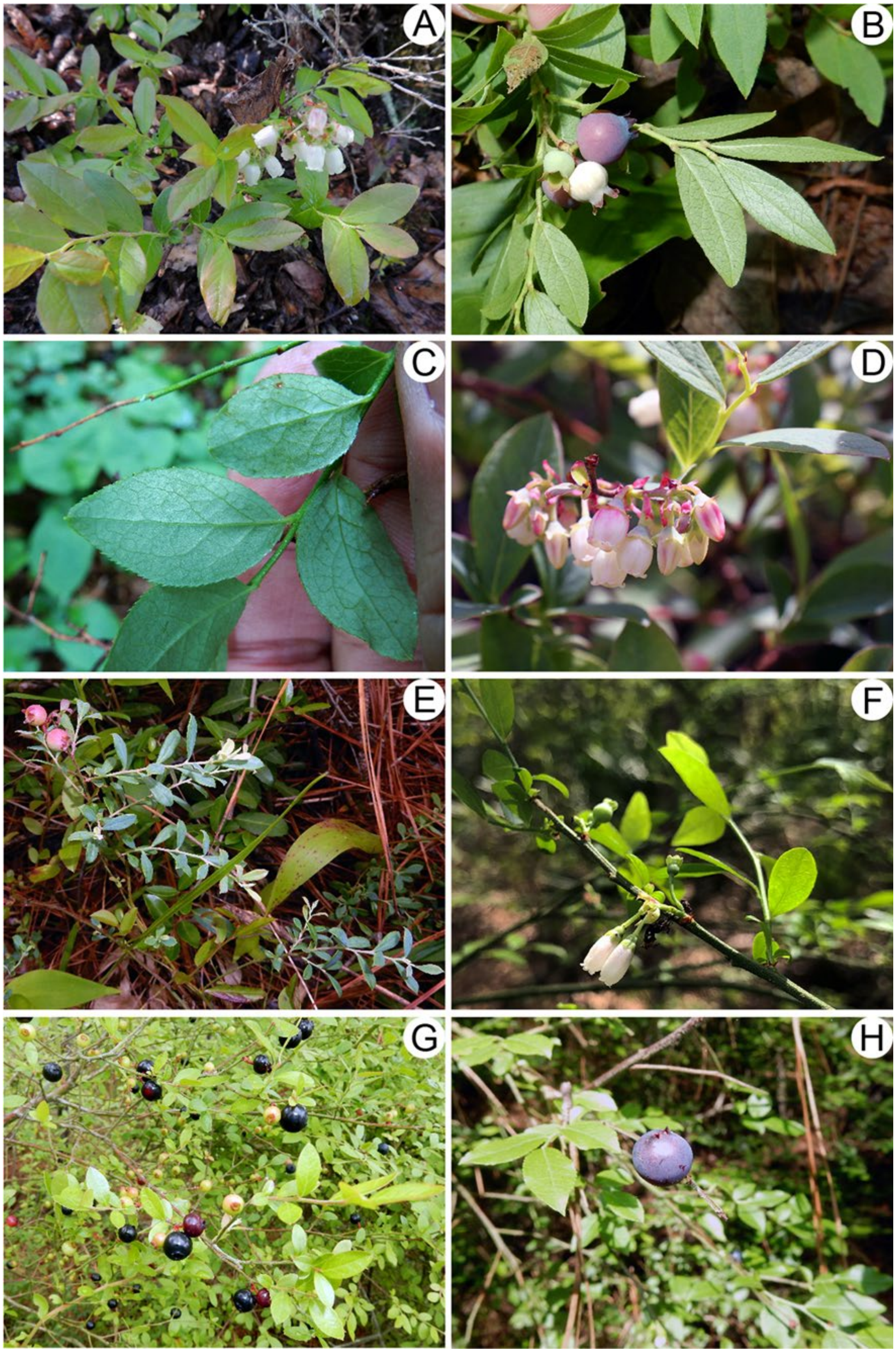
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Figure 5. Field images of *Vaccinium* sect. *Cyanococcus*. (A) Flowering branchlet of *V. atrococcum*/*V. fuscatum*. *Crowl CY-375* (BRIT). (B) Fruiting branchlet of *V. atrococcum*/*V. fuscatum*. *Fritsch 2351* (BRIT, DUKE). (C) Fruiting branchlet of *V. myrtilloides*. *Fritsch 2241* (BRIT, DUKE). (D) Fruiting branchlets of *V. pallidum* (including *V. vacillans*). *Fritsch 2354* (BRIT, DUKE). (E) Inflorescence of *V. simulatum*. *Manos CY-397* (BRIT, DUKE). (F) Inflorescences of *V. amoenum*/*V. virgatum*. *Crowl. CY-374* (BRIT). (G) Fruiting branchlet of *V. amoenum*/*V. virgatum*. *Fritsch 2270* (BRIT, DUKE). (H) Likely “rabbit-eye” escape from cultivation. *Fritsch 2271* (BRIT, DUKE). Species names are tentative, approximating those of Camp (1945). Photos: A, F by A.A. Crowl; B–D, G, H, by P.W. Fritsch; E by P.S. Manos.

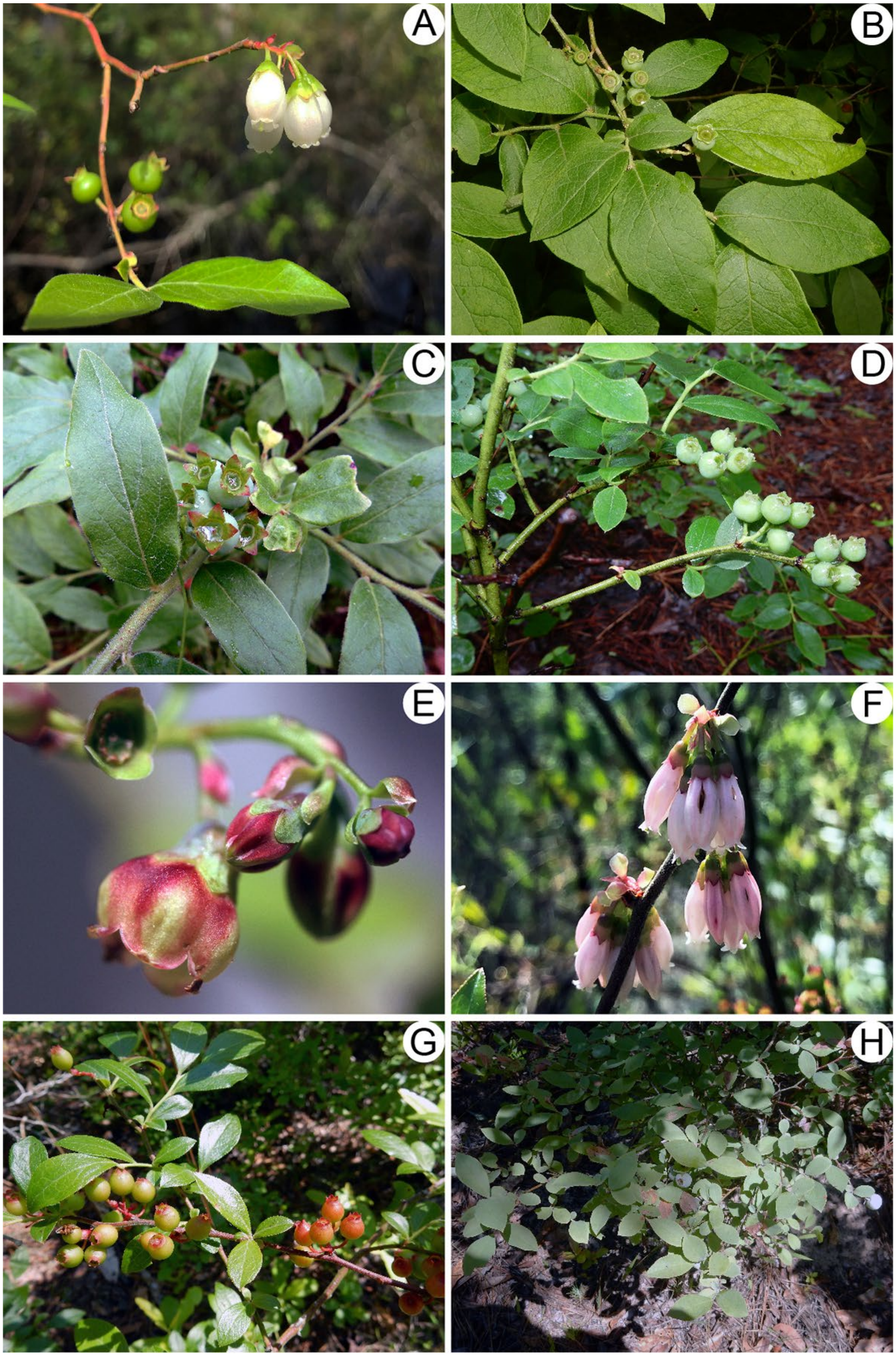
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Figure 6. Stipitate-glandular trichomes on the abaxial surface of the leaf blades in *Vaccinium* sect. *Cyanococcus*. Species names are tentative, approximating those of Camp (1945). (A) *V. atrococcum*/*fuscatum*, secondary veins. *Whitehouse 3159* (BRIT). (B) *V. myrsinites*. *Crowl 188* (BRIT), secondary veins and surface. Note the elongated heads relative to the globose heads in the other subfigures. (C) *V. amoenum*/*virgatum*, tertiary veins and surface. *Fritsch 2263* (BRIT, DUKE). (D) *V. elliottii*, base of midvein. *Fritsch 2280* (BRIT, DUKE). Scale bars = 300 µm.

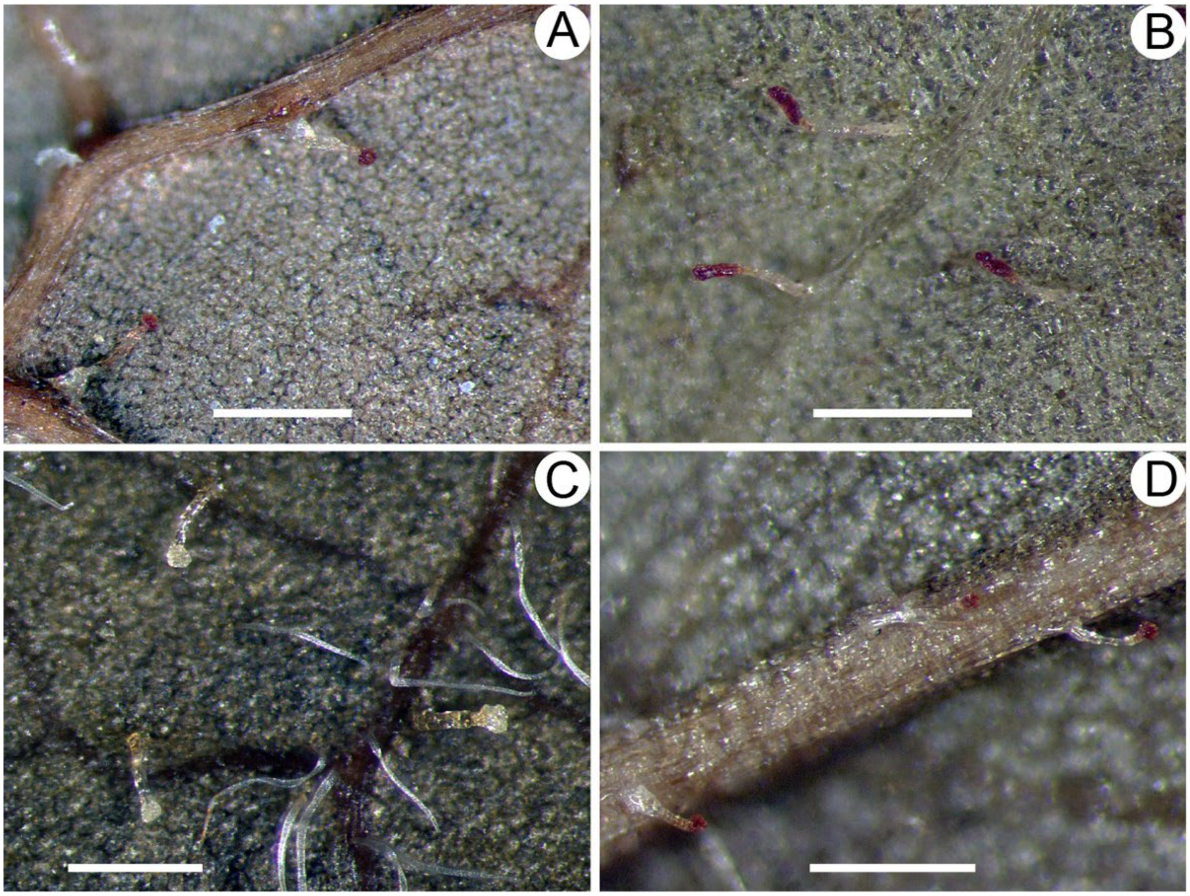
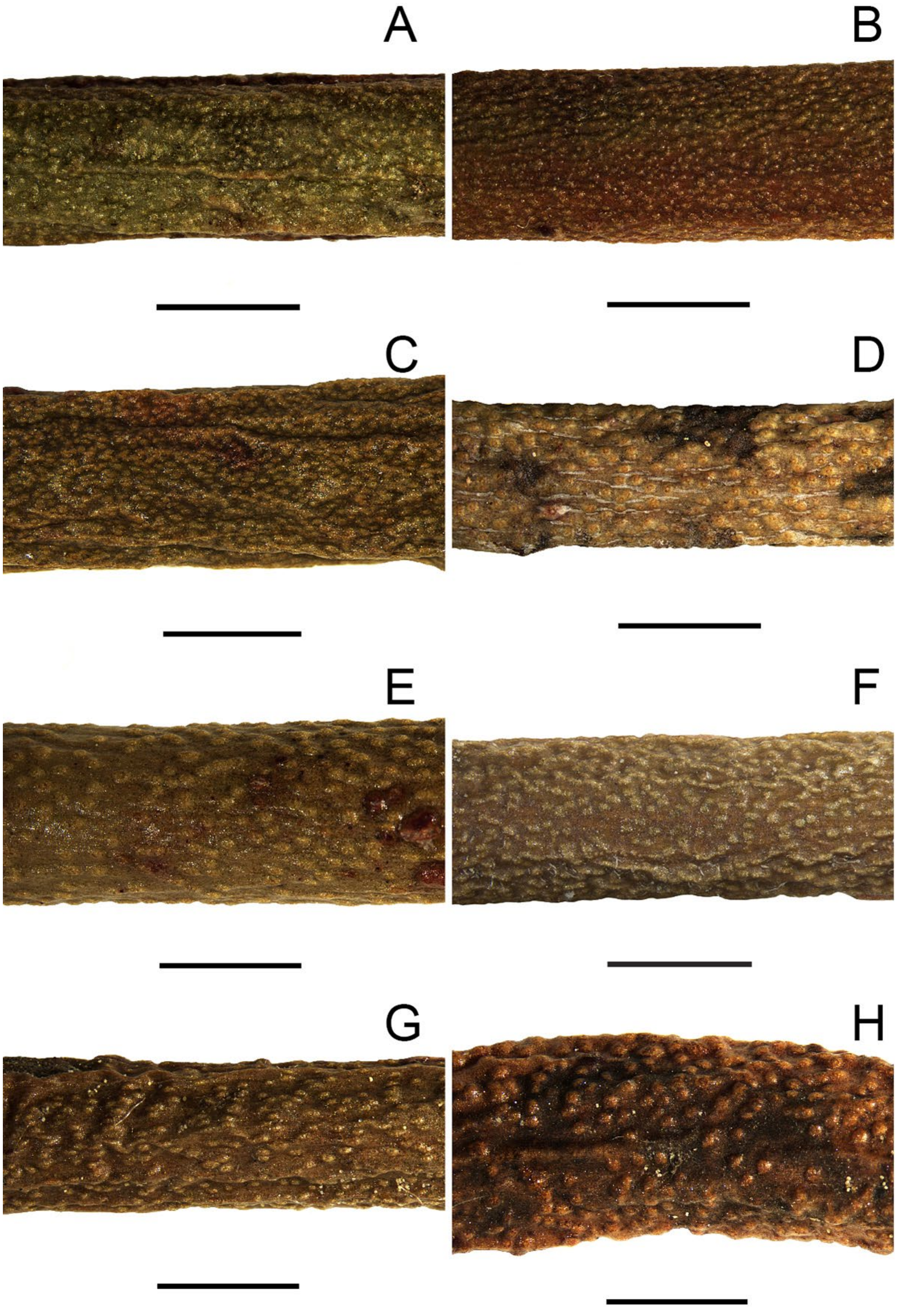


Figure 7. Raised stomata on second-year stems of *Vaccinium* sect. *Cyanococcus*. The size and density of the stomata are thought to be positively and negatively correlated with ploidy, respectively. Species names approximate those sensu Camp (1945) except where noted. (A) *V. atrococcum* (2x). *Manos CY-070* (BRIT). (B) *V. atrococcum* (2x). *Manos CY-326* (BRIT, DUKE). (C) *V. pallidum* including *V. vacillans* (2x). *Manos CY-052* (BRIT, DUKE). (D) *V. australe* (4x; = *V. formosum*). *Crowl CY-235* (BRIT). (E) *V. arkansanum* (4x). *Manos CY-155* (BRIT). (F) *V. simulatum* (4x). *Manos CY-059* (BRIT, DUKE). (G) *V. corymbosum* (4x). *Shaw CY-333* (BRIT, DUKE). (H) *V. constablaei* (6x). *Manos CY-028* (BRIT). Species names are tentative, approximating those of Camp (1945). Scale bars = 2 mm.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SUPPLEMENTARY DATA

SUMMARY OF THE 24 SPECIES OF *VACCINIUM* SECT. *CYANOCOCCUS* RECOGNIZED BY CAMP (1945) ARRANGED BY PLOIDY

Descriptions have been modified from the original for consistency. Geographic distribution and habitats of the species are essentially as originally presented. See Table 1 for Camp's hypothesized origins of the tetraploid and hexaploid species; additional comments are presented here for some species.

Diploids

Vaccinium angustifolium Aiton. Plants deciduous, to 0.2 m tall; leaves 1–3 × 0.4–1.0 cm, abaxial surface green, shining, glabrous or rarely pubescent, not stipitate-glandular, margin serrate; corolla usually white, cylindrical, 3–5 mm long; fruit blue, 5–7 mm diam. Newfoundland and Labrador west to Minnesota and south to New Jersey, and in the Appalachian Mountains to Virginia and West Virginia. Open rocky uplands or dry sandy areas, or sometimes on hummocks in swampy areas.

Vaccinium atrococcum A. Heller. Plants deciduous, 1.5–3.0 m tall; leaves 3–6 × 1.5–3.0 mm, abaxial surface green, pubescent, non-stipitate-glandular, margin entire; corolla greenish or yellowish white, often flushed pink, urceolate, 5–6 mm long; fruit black, 5–8 mm diam. Western Tennessee and Arkansas south to the Gulf, east to northern Florida, north to central New York and Maine; possibly southern Canada and the Great Lakes region. Coastal plain swamps, along rivers, seepages, occasionally fairly dry ground.

Vaccinium caesariense Mack. Plants deciduous, 1.5–2.0 m tall; leaves 3–6 × 1.5–2.5 cm, abaxial surface whitish green, glabrous, non-stipitate-glandular, margins entire; corolla white, urceolate, 5–6 mm long; fruit blue, 5–7 mm diam. Northern Florida to southern Maine; central New York. Coastal Plain swamps, inland in boggy areas, occasionally on open wooded slopes nearby.

Vaccinium darrowii Camp. Plants evergreen, to 0.4 m tall; leaves 0.8–1.5 × 0.3–0.5 cm, abaxial surface whitish green (especially when young), glabrous or pubescent, stipitate-glandular, margin entire; corolla pink to red, urceolate, 5–6 mm long; fruit blue, 4–6 mm diam. Louisiana to Florida. Usually on dry sandy soil.

Vaccinium elliottii Chapm. Plants deciduous, 2–4 m tall; leaves 1.5–3.0 × 0.8–1.5 mm, abaxial surface green, shining, glabrous to pubescent, non-stipitate-glandular, margin serrate or occasionally entire; corolla usually pink, urceolate, 6–7 mm long; fruit black or occasionally glaucous, 5–8 mm diam. or occasionally larger. Southeastern Virginia south to Florida west to Louisiana and Arkansas. Open flatwoods and ravines, cleared river bottoms, rarely swampy areas.

Vaccinium myrtilloides Michx. Plants deciduous, to 0.5 m tall; leaves 1.5–3.0 × 0.75–1.50 cm, abaxial surface green, shining, pubescent, margin entire; corolla white or rarely flushed pink, cylindrical-campanulate, 4–5 mm long; fruit blue, 4–7 mm diam. Montana, southeastern British Columbia to Northwest Territories, east to Labrador and Newfoundland south to New York, Pennsylvania, Indiana, and West Virginia. Muskeg or boggy areas, uplands, mountain meadows.

Vaccinium pallidum Aiton. Plants deciduous, to 1 m tall; leaves 3–5 × 1.5–2.5 cm, abaxial surface usually whitish green, glabrous or occasionally pubescent, non-stipitate-glandular, margin serrate; corolla greenish white often flushed pink, urceolate or cylindrical-campanulate, 4–6 mm long; fruit blue or black, 5–7 mm diam. Northern Georgia and northern Alabama, north to West Virginia, Kentucky, Pennsylvania, and New York; also Ozark Mountains in Arkansas and Missouri, and Kansas. Dry upland woods and brushy areas.

Vaccinium tenellum Aiton. Plants deciduous, to 0.4 m tall; leaves 2–4 × 0.5–1.5 cm, abaxial surface green, glabrous or pubescent, stipitate-glandular, margin serrate; corolla pink to red, urceolate, 4–6 mm long; fruit black, 5–8 mm diam. Southeastern Virginia to Georgia and Alabama. Open forests and meadows.

Vaccinium vacillans Kalm ex Torr. Plants deciduous, to 0.5 m tall; leaves 2.0–3.5 × 1.5–2.0 cm, abaxial surface usually whitish green, glabrous or pubescent, non-stipitate-glandular, margin entire or serrate; corolla white or greenish white often flushed red, urceolate to campanulate, 4–6 mm long; fruit glaucous to dull or black, 5–8 mm diam. Minnesota and southern Ontario to Maine, south to Missouri, Tennessee, and Georgia; probably in northern Alabama, northern Mississippi, and Arkansas. Usually in dry open woods, rocky ledges, or abandoned farmland.

Tetraploids

Vaccinium altomontanum Ashe. Plants deciduous, to 1 m tall; leaves 3–5 × 1.5–3.0 cm, abaxial surface whitish green, glabrous, non-stipitate-glandular, margin entire; corolla white or greenish white often flushed pink, urceolate to cylindrical-campanulate, 5–7 mm long; fruit glaucous to dull or black, 7–10 mm diam. Northern Georgia and Alabama north to Virginia, eastern Tennessee; possibly Kentucky, southern Ohio, Missouri, and Arkansas. Usually open woods and rocky uplands, mountains.

Vaccinium arkansanum Ashe ("probably 4x"). Plants deciduous, 2–4 m tall; leaves 6–8 × 3–4 cm, abaxial surface green, pubescent, non-stipitate-glandular, margin entire; corolla greenish white often flushed pink, urceolate, 6–8 mm long; fruit usually black, occasionally slightly glaucous, 7–10 mm diam. Northern Florida, west to Texas and Arkansas. Sandy lake and stream margins, swamps, occasionally open flatwoods or low ridges. No chromosome count was obtained for this species. Camp presumed its existence as a tetraploid based on the proposed parallel autotetraploid derivation of *V. australe* from the diploid *V. caesariense* (both similar in morphology to *V. arkansanum* and *V. atrococcum* but with glabrous versus pubescent leaves), as well as the supposed taller habit and larger size of the flowers and fruits relative to the diploid *V. atrococcum*.

Vaccinium australe Small. Plants deciduous, 2–5 m tall; leaves 5–8 × 2.5–4.0 cm, abaxial surface whitish green, usually glabrous, non-stipitate-glandular, margin entire; corolla white occasionally flushed pink, cylindrical, 8–11 mm long; fruit blue, 7–12 mm diam. Southeastern Alabama, northern Florida, north to New Jersey; mixed with *V. corymbosum* in Maine, central New York, and southern Canada. Coastal Plain marshes and swamps, inland in boggy areas. This species is equivalent in circumscription to *V. formosum* Andrews of later authors.

Vaccinium brittonii Porter ex E.P. Bicknell. Plants deciduous, to 0.35 m tall; branchlets of current season glaucous; leaves 1.5–4.0 × 1.0–1.5 cm, abaxial surface whitish green, glabrous, non-stipitate-glandular, margin serrate; corolla white, cylindrical-campanulate, 5–6 mm long; fruit dark, black, or slightly glaucous, 8–12 mm diam. Labrador and Newfoundland to Minnesota south to New Jersey and the mountains of West Virginia. Usually in open rocky uplands or dry sandy areas, or occasionally on hummocks or borders of swamps.

Vaccinium corymbosum L. Plants deciduous, 1–4 m tall; leaves 4–8 × 2–3 cm, abaxial surface green to whitish green, glabrous or pubescent, non-stipitate-glandular, margin entire or serrate; corolla white often flushed pink, urceolate or occasionally slightly campanulate or slightly globose, 6–10 mm long; fruit blue, dull, or black, 5–10 mm diam. Michigan east to Nova Scotia south to the glacial boundary. Usually in swamps and boggy areas, or along lake and stream margins, occasionally in moist sandy areas or hillside seepages. A complex tetraploid developed through repeated hybridization and backcrossing among the tetraploids *V. arkansanum*, *V. australe*, *V. brittonii*, *V. lamarckii*, *V. marianum*, and *V. simulatum*. Camp proposed that the overall morphology of *V. corymbosum* will generally trend toward one or more of these species in the areas where they occur; we presume that he considered this to result from hybridization and introgression, and perhaps also segmental allopolyploidization.

Vaccinium fuscatum Aiton ("probably 4x"). Plants evergreen, 1.5–3.0 m tall; leaves 3.5–5.0 × 1.5–2.5 cm, abaxial surface green or occasionally slightly whitish green, pubescent, non-stipitate-glandular, margin entire or occasionally serrate; corolla pink or red, urceolate, 7–9 mm long; fruit dark, dull, or slightly glaucous, 6–10 mm diam. Southern Georgia, Florida. Usually in sandy flatwoods and bottomlands or along streams and lakes. No chromosome count was obtained for this species.

Vaccinium hirsutum Buckley. Plants deciduous, 0.4–0.7 m tall; leaves 2.5–5.5 × 1.5–2.5 cm, abaxial surface green, pubescent, non-stipitate glandular, margin entire; pedicels and hypanthium stipitate-glandular; corolla urceolate, 7–10 mm long; fruit black, 6–10 mm diam., stipitate-glandular. North Carolina and Tennessee in the Appalachian Mountains. Dry ridges and mountain meadows (balds). A vague reference was made to a possible cross between *V. vacillans* and one of the stipitate-glandular forms of *V. stamineum* L. of *V.* sect. *Polycodium* Rehder.

Vaccinium lamarckii Camp. Plants deciduous, to 0.4 m tall; leaves 1.5–3.0 × 1.0–1.5 cm, abaxial surface green, shining, glabrous or occasionally pubescent, non-stipitate-glandular; corolla usually white, cylindrical, 4–8 mm long; fruit blue, 8–12 mm diam. Labrador and Newfoundland west to Minnesota south usually in the uplands and mountains to West Virginia and North Carolina. Open rocky uplands or dry sandy areas, or sometimes on hummocks in swampy areas.

Vaccinium marianum P. Watson ("probably 4x"). Plants deciduous, 2–3 m tall; leaves 5–7 × 2–3 cm, abaxial surface green or slightly whitish green, glabrous to pubescent, non-stipitate glandular, margin entire; corolla white, cylindrical, 6–8 mm long; fruit black to slightly glaucous, 6–10 mm diam. North Carolina north to Long Island, New York. Habitats of *V. caesariense* and *V. atrococcum* where they grow together. No chromosome count was obtained for this species. The recognition of this species accommodated plants similar to *V. australe* but with some pubescence on the leaves, shorter corollas, and/or with slightly less glaucescence on the fruit than normal.

Vaccinium myrsinites Lam. Plants evergreen, to 1 m tall; leaves 0.7–1.5 × 0.3–0.8 cm, abaxial surface green or slightly whitish green, shining or dull, glabrous or pubescent, usually stipitate-glandular, margin entire or slightly serrate; corolla white to pink, urceolate, 5–7 mm long; fruit dark to subglaucous, 5–7 mm diam. Florida, southern Alabama, southern Georgia, coastal South Carolina. Dry sandy areas.

Vaccinium simulatum Small. Plants deciduous, 1.5–4.0 m tall; leaves 5–7 × 2–3 cm, abaxial surface pale green to slightly whitish green, glabrous or pubescent, non-stipitate-glandular, margin serrate or subentire; corolla greenish white often flushed pink, cylindrical-campanulate, 5–6 mm long; fruit usually dark, occasionally black or slightly glaucous, 6–10 mm diam. Northern Alabama and northern Georgia, north in the Appalachian Mountains to Kentucky and Virginia. Open mountain slopes and meadows, and along streams.

Vaccinium virgatum Aiton. Plants deciduous, 0.3–0.5 m tall; leaves 3–5 × 1–2 cm, abaxial surface green, glabrous or pubescent, stipitate-glandular, margin serrate; corolla white flushed pink, urceolate, 4–6 mm long; fruit usually shining black, 6–10 mm diam. South Carolina(?), Georgia, Alabama, northern Florida west to Texas and Arkansas. Open forests and meadows.

Hexaploids

Vaccinium amoenum Aiton. Plants deciduous, 1.5–2.5 m tall; leaves 4–5 × 1.5–2.5 cm, abaxial surface green or rarely slightly whitish green, pubescent, stipitate-glandular, margin serrate; corolla often pink, urceolate, 10–12 mm long; fruit black or dark, 8–10 mm diam. South Carolina to northern Florida west to Texas and Arkansas. Uplands and open woods, brushy areas, margins of streams, lakes, and swamps. Autohexaploid terminating the lineage of diploid *V. tenellum* and tetraploid *V. virgatum*. Camp mentioned that "...occasional pentaploids are also known."

Vaccinium ashei J.M. Reade. Plants deciduous or occasionally evergreen, 1.5–7.0 m tall; leaves 4–8 × 1.5–3.5 cm, abaxial surface glabrous to pubescent, stipitate-glandular (occasionally sparsely so), margin serrate to entire; corolla pink or occasionally white or red, urceolate, 8–12 mm long; fruit black to dull or glaucous, 8–18 mm diam. Georgia, southern Alabama, and northern Florida; possibly South Carolina and Mississippi. Various habitats: along streams and lakes, open woods, abandoned agricultural areas. Segmental allopolyploid generated by a series of southern hybrid complexes from the tetraploids *V. arkansanum*, *V. australe*, *V. fuscatum*, *V. myrsinites*, and *V. virgatum*, with one or more of these variously predominating in the genetic composition of populations, apparently also in part through hybridization and introgression.

Vaccinium constablaei A. Gray. Plants deciduous, 0.5–8.0 m tall; leaves 4–7 × 2–4 cm, abaxial surface pale green to whitish green, glabrous or pubescent, non-stipitate-glandular, margin serrate or entire; corolla white or white flushed green or pink, cylindrical-campanulate, 6–8 mm long; fruit glaucous or slightly glaucous or rarely dark, 7–12 mm diam. Mountain tops and upper slopes of western North Carolina and eastern Tennessee. Balds and slicks, ericaceous meadows. Polyphyletic allohexaploid of *V. altomontanum* and *V. simulatum*. Camp considered this species a particularly compelling example of a segregative allopolyploid based on its high morphological variation toward one or the other of the two parental species.