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A taxonomic treatment of the violets (Violaceae) of the northeastern United States and adjacent Canada[1]

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Abstract. A taxonomic treatment is presented for the violets (Violaceae) confirmed in the range described in the second edition of Gleason and Cronquist's *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, in advance of the new treatment of this manual that is in preparation. Recent field, herbarium, and laboratory investigations of eastern North America's violet flora by the author and students have reexamined eastern North American violet taxa and utilized multiple sources of evidence filtered through modern species concepts to delimit taxa and assign appropriate taxonomic rank. Results have led to the recognition of 58 native and eight introduced species, one subspecies, one variety and one form, 10 informal variants, and 113 wild hybrids in our region, representing the genera *Cubelium*, *Pombalia*, and *Viola*. In *Viola*, two new species are described and three new combinations are made (one to species rank, one to subspecies, and one to forma), and eight names are typified. *Viola* taxa are distributed across five sections and nine subsections and are representative of most of the infrageneric taxonomic diversity in North America overall. Anomalous variants in *Viola emarginata*, *Viola palmata*, *Viola septentrionalis*, and *Viola sororia* currently lack sufficient information for taxonomic decisions but are presented to encourage study, collection, and documentation. Six potential taxa occur adjacent to or very near our region and may eventually be discovered in our area; they are included in the keys and briefly described with figures. The treatment includes introductory text, dichotomous keys, synonymy with some type information, detailed descriptions, and other information, as well as color figures of habit and plant structures and US county-level geographic distribution maps for nearly all included taxa.

Key words: northeastern North America, taxonomic treatment, Violaceae, violets

Many of us who live in boreal, temperate, or subtropical areas are familiar with the "true violets" of the genus *Viola*, with their white, yellow, purple, or multicolored flowers (Fig. 1). Sweet-smelling species such as English violet (*Viola odorata* L.) were prized in ancient Greece, and violets have played roles in folklore, literature, and drama (de Carvalho *et al*. 2013). The flowers and leaves of certain European species were described in early modern herbals as efficacious medicines for a wide range of internal and external ailments (Culpeper 1814), and the early name of "heart's ease" for the pansy reflects a herbalist's appreciation of its medical benefits. Violet fragrance is used in soaps, perfumes, and candies, and violet flowers are still used to make jellies and syrups and as adornments for cakes and salads, while the young leaves make a palatable potherb (Gibbons 1966). In describing *Viola palmata* L. var. *heterophylla* Elliott (now treated as *Viola edulis* Spach) from South Carolina and Georgia, Stephen Elliott (Elliott 1817) coined the name "salad violet," remarking that local people ate the leaves.

Viola is the largest of 27 recognized genera in the violet family (Violaceae) and, with 664 accepted species, it is one of the 40–50 largest

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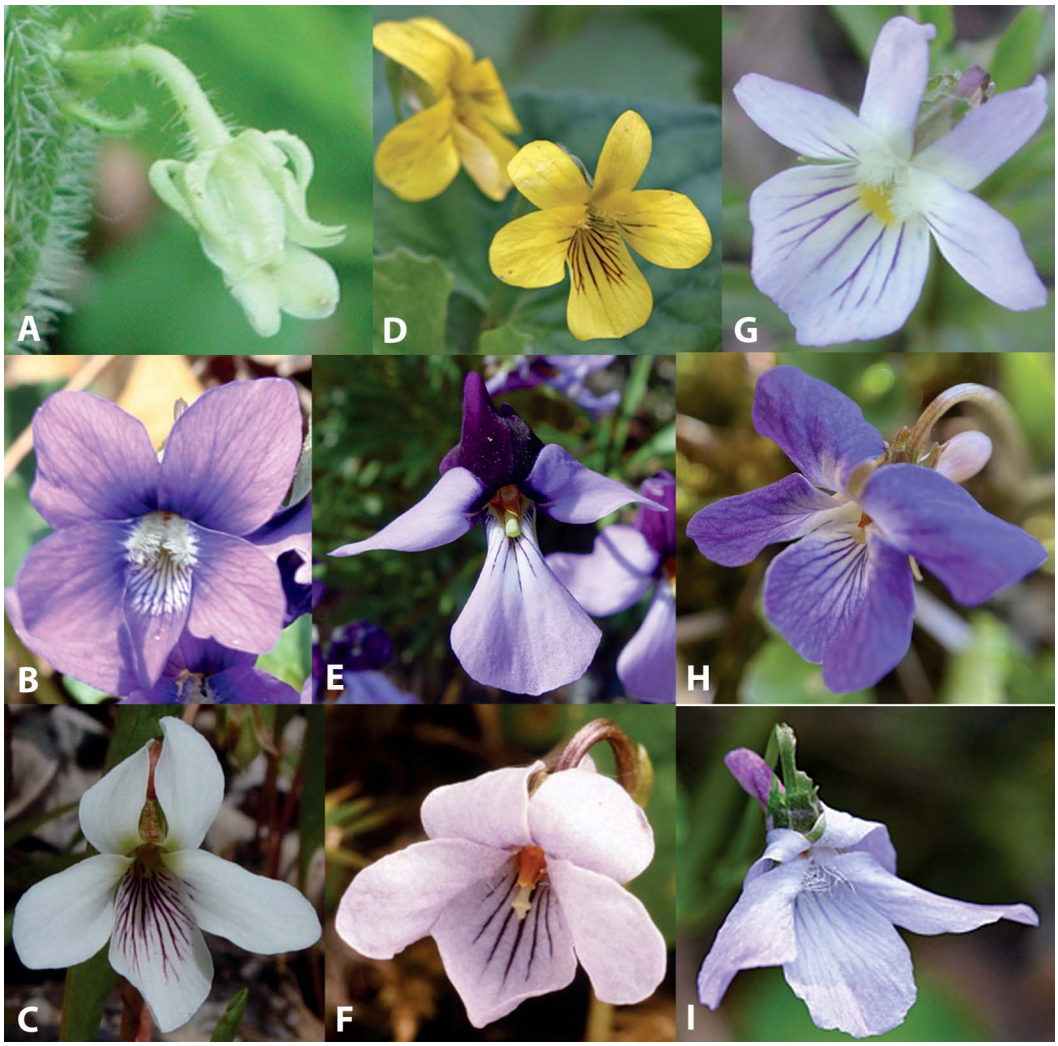

FIG. 1. Representative native violet species in our region. (A) *Cubelium concolor* (photo: D. Busemeyer). (B) *Viola sororia* (photo:Andrew Lane Gibson). (C) *Viola lanceolate* (photo: Arthur Haines. (D) *Viola eriocarpa* (photo: Andrew Lane Gibson). (E) *Viola pedata* (photo: Arthur Haines, Native Plant Trust). (F) *Viola suecica* (photo: Kim Blaxland). (G) *Viola rafinesquei* (photo: D. Busemeyer). (H) *Viola selkirkii* (photo: Adam Heikkila). (I) *Viola labradorica* (photo: Andrew Lane Gibson).

genera of angiosperms in the world (Frodin 2004 [*Viola* is not listed, as previously published species numbers were below 500]; Marcussen *et al*. 2022). Remarkably, its "sister" genera are South American *Noisettia* Kunth and *Schweiggeria* Spreng., each with a single species (Tokuoka 2008; Wahlert *et al*. 2014). The genus *Viola* is atypical in the family in a number of respects (Ballard *et al*. 2014). *Viola* consists almost entirely of annual or perennial herbs, where nearly all of the rest of the Violaceae are trees, (sub)shrubs, or woody vines. The genus is distributed in subtropical to boreal and arctic regions and also grows at higher altitudes in mountains of the tropics, whereas the majority of the other Violaceae are confined to low altitudes in the tropics. Most members of *Viola* maintain a mixed breeding system with showy chasmogamous cross-pollinated flowers and underdeveloped cleistogamous self-pollinated flowers; with one or two exceptions, the rest of the family is strictly chasmogamous. Many sublineages of *Viola* engage in hybridization, while the phenomenon is essentially unknown elsewhere in

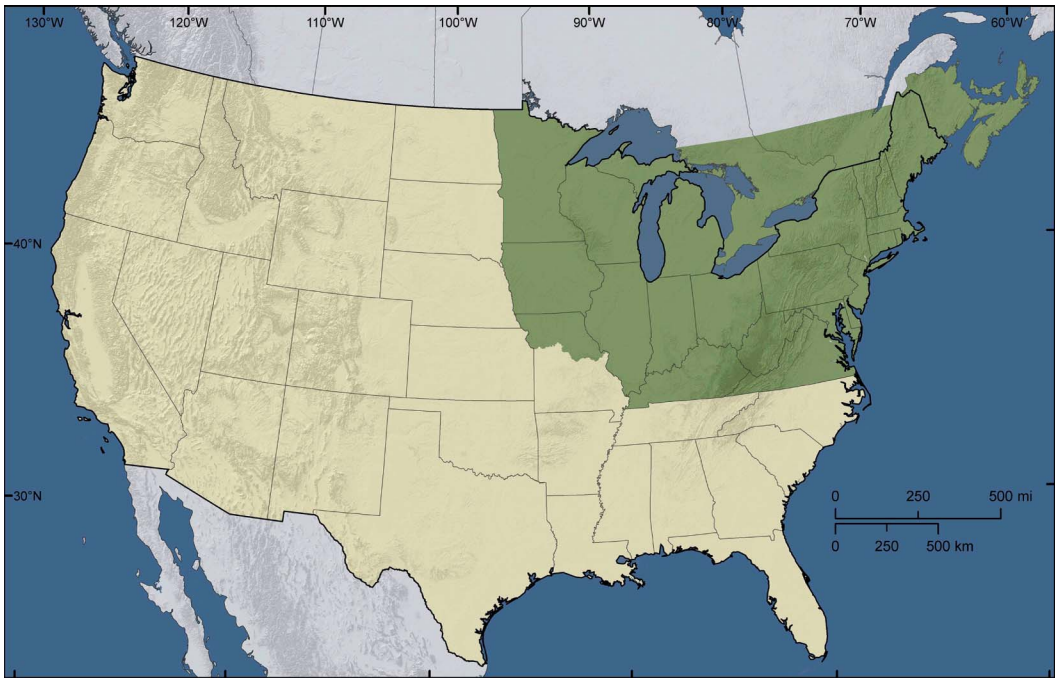

FIG. 2. Geographic region bounded by the "manual range" followed in this treatment. ©The New York Botanical Garden. Used with permission.

the Violaceae. *Viola* also differs from other genera in a number of inflorescence and floral traits.

Native *Viola* species in the United States and Canada (including Greenland), depending on the author, number 67 (Little and McKinney 2015), 75 (Brainerd 1921b), or 115 or more (H.E.B, unpublished data), while 6 (Little and McKinney 2015) to 8 (H.E.B, unpublished data) additional species are introduced. A few native species of two other genera are northern representatives of tropical violet lineages, previously placed in *Hybanthus* Jacq. They are green violet, *Cubelium concolor* (T.F.Forst.) Raf. ex Britton & A.Br., in the eastern United States and adjacent Canada; baby slippers or nodding green violet, *Pombalia verticillata* (Ortega) Paula-Souza, in the southern Great Plains and Southwest within a few counties of Missouri; and western green violet, *Pombalia attenuata* (Humb. & Bonpl. ex Willd.) Paula-Souza, in southern Arizona but also introduced in southern Florida. The violetilla, *Pombalia parviflora* (L.f.) Paula-Souza, has been sporadically introduced along the Atlantic Coast (and to other areas of the world) from Andean South America.

This treatment focuses on the native and introduced taxa of the Violaceae documented in the northeastern United States and adjacent Canada. The specific geographic region is delineated by the geographic region (Fig. 2) of the *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist 1991) and the new manual in preparation by Robert F. C. Naczi (Naczi 2016), in which a distillation of this treatment will be published.

A BRIEF TAXONOMIC HISTORY. Numerous authors have contributed to our present knowledge of the taxonomic diversity of, and geographic distributions and ecological niches occupied by, violets occurring in the region covered by this treatment. However, several in particular have made broader or more extensive contributions in the form of taxonomic studies of violets in a particular state or region or of a particular group, and these individuals are the focus here. Theses and dissertations found in a preliminary search representing taxonomic studies are also noted below. Taxonomic studies of violets elsewhere (such as western North America) are mentioned if taxa occurring in our region were included. Certain floras with geographic areas overlapping with or included in our region are referenced with respect to their treatment of individual taxa in the taxon

accounts. Similarly, authors of one tangential or narrower publication are mentioned with citations in the taxon accounts. Primarily ecological, reproductive, population genetic, developmental, physiological, molecular, or other types of studies are excluded.

The first taxonomic study for North American *Viola* was published two centuries ago by Lewis von Schweinitz (von Schweinitz 1822). His monograph provided a critical basis for violet taxonomy on our continent for the next 80 yr. Around the same time, Frédéric Gingins de la Sarraz produced the first treatment of the Violaceae (Gingins de la Sarraz 1823) and subsequently incorporated this new information into the family treatment for Alphonse de Candolle's monumental *Prodromus* (Gingins de la Sarraz 1824). John Leconte (who spelled his surname in various ways) shortly thereafter published his observations on North American violets (Leconte 1828), describing a number of new species and interpreting some of the currently applied names. Although he had intended for his handmade color plates to accompany his text, lack of funds forced him to exclude the watercolors. The original sets of the plates are rare (one set deposited in the Rare Books section of the University of Notre Dame Library) but are valuable for interpreting Leconte's names. Asa Gray published a two-part revision of North American violets in 1886, including several new species and some infraspecific combinations (Gray 1886a, b). He also postulated relationships or potential conspecificity in some instances in an attempt to bring order to the names applied to violets by North American and European botanists. Thus, most of the 19th century was marked by the major efforts of a very few individuals conducting comprehensive broad-scale studies.

A "renaissance era" in violet taxonomy was initiated by Edward Greene, whose many articles and treatises on violets from 1891 to 1914 (Greene 1891, 1896a, b, c, 1897a, b, 1898a, b, c, d, 1899a, b, 1900, 1901a, b, c, 1902a, b, c, 1903a, b, 1906a, b, c, 1910a, b, c, 1913, 1914) spanned the continent and generated over 170 published names for North American *Viola* (with 29 publications pertaining to taxa in our region). Greene was infamous for detecting subtle population-level variation and describing such phenotypes as distinct species. Some of his names are now treated as synonyms while others are known to represent hybrids (which he didn't acknowledge), and several others are still maintained as species today. A self-professed expert on various (especially western) genera of vascular plants, Greene is one of the most prolific botanical authors in terms of the number of taxa published (approximately 5,500), a record placing him among those who have accomplished worldwide floras (H. E. B., unpublished data). His efforts have had a major impact on violet taxonomy in North America and our region. Active during 1895 to 1913, Charles Pollard published six papers mainly on violets of the Atlantic coastal states, describing a few species, and contributed the *Viola* treatment to John Small's *Flora of the Southeastern United States* (Pollard 1895; 1896; 1897; 1898; 1902a, b; 1913). A contemporary of Pollard's, and similarly focusing on violets in the mid-Atlantic states, Eugene Bicknell (1904, 1913, 1914) published three articles to describe a small number of violet species and compare these with other familiar taxa. Ezra Brainerd, botanist and geologist, produced prodigious research from 1904 to 1924, focusing on native *Viola* taxa across North America (Brainerd 1904a, b, 1905, 1906a, b, c, 1907a, b, c, 1908a, b, 1909, 1910a, b, c, 1911a, b, 1912, 1913a, b, c, d, 1915, 1917a, b, 1921a, b, 1924). Nearly all of his papers encompassed violets occurring in our region, and his two tomes on violet hybrids and violets of North America are still used today as valuable continent-wide references. Brainerd attempted to reconcile numerous names with living taxa and accomplished a comprehensive taxonomic overhaul of violet taxa and the many hundreds of names cumulatively applied to them in North America. He annotated numerous collections and made many trips to areas throughout the eastern United States, but also had many correspondents send him pressed specimens and living plants. His several detailed studies of hybrids in a number of violet groups, ultimately documenting 80 different wild hybrids, inspired recognition of hybridization as a frequent to common phenomenon in North American *Viola*. During his career he maintained a common garden of thousands of living plants with most of the known violets represented, and grew hybrids found in the field and in many instances their F_3 and F_4 generations, to compare initial and later-generation hybrid morphology and reproductive behavior with those of their parental species. Brainerd published elaborate observations (for his time) documenting loss of chasmogamous repro-

duction in all observed hybrids, cleistogamous seed failure or capsule abortion in hybrids of most lineages, but commonly reduced viable seed set in cleistogamous capsules and "Mendelian" recombination of traits in cleistogamous progeny of interspecific hybrids involving *Borealiamericanae* violets. His scrutiny and detailed description of violets in his articles greatly extended the known "universe" of morphological traits distinguishing species. Through his studies he described several new species and resolved numerous nomenclatural debates. He is one of the earliest botanists to implicitly apply an integrative taxonomic approach with morphology, ecology, and reproductive behavior to delimit taxa, and his reach continues to today. Homer House, a contemporary of Brainerd's, published 12 articles involving violets in the eastern United States (House 1904, 1905, 1906a, b, 1907, 1914, 1917, 1923, 1924, 1925a, b), describing a few species and detailing ecological niches and local and regional distributions for many species, as well as providing formal binomials for many of Brainerd's unpublished hybrids in his later publications.

Alexander Gershoy (Gershoy 1928, 1934) published some of the earliest chromosome numbers for *Viola* and investigated style morphology of many North American violets in an attempt to organize taxa into the higher-level groupings proposed by Wilhelm Becker (1925) in the first comprehensive worldwide classification of *Viola*. Around the same time, Jens Clausen, whose career with violets stretched from 1927 to 1964, began his own research on chromosome numbers and style morphology to reevaluate infrageneric groups, and later to apply these and macromorphological features to understand western North American violets (Clausen 1927, 1929, 1964; Clausen *et al*. 1964). Milo Baker, a botanist working on western *Viola* and a contemporary and colleague of Clausen's, published several papers that provide information on certain violets in our region (Baker 1935, 1936, 1940, 1949a, b, c, 1957). He described several species and infrageneric taxa, made numerous chromosome counts to highlight polyploidy (including extensive allopolyploidy) as an active evolutionary process in some western violet groups, demonstrated the taxonomic utility of style morphology and chromosome number at the species level, and illuminated the taxonomic diversity of several lineages that had not received adequate attention. Viola Brainerd Baird, daughter of Ezra Brainerd, pursued studies on violets following Brainerd's passing and substantially extended his initial though incomplete observations on western violets. She published a popular book on North American violets and an article publicizing the existence of John Leconte's long-lost watercolor plates (Brainerd Baird 1938, 1942). In preparation for his magnum opus, *Gray's Manual*, Merritt Fernald (Fernald 1935, 1938, 1941, 1949) published two articles including various morphological traits of particular violets and describing a number of infraspecific taxa, and two others presenting range extensions of southern taxa into Virginia. Hannibal and Tyreeca Davis (Davis and Davis 1949) published a treatment of violets for West Virginia, and Hannibal Davis and Earl Core (Davis and Core 1949) followed that with new information on West Virginia violets in a broader article on flowering plants. Around the same time, Robert Platt (Platt 1950) published a report on two unusual Appalachian violets, with L. K. Henry (Henry 1953a, b) following up to describe one of those as a new species.

The next taxonomic "revolution" in violets was promoted by Norman Russell, who brought further order out of the morass of names and taxa generated by previous authors. He published 22 papers from 1952 to 1965 including keys or treatments of violets for Iowa, Louisiana, Minnesota, and Tennessee; analyses of hybrids and putative hybrid swarms; methods of morphological analysis; and interpretation of photoperiodic responses and their phenotypic effects in violets (Russell 1952, 1953, 1954a, b, 1955a, b, c, 1956a, b, c, d, 1958a, b, 1959, 1960, 1961, 1965; Russell and Cooperrider 1955; Russell and Graham 1958; Russell and Bowen 1960; Russell and Risser 1960; Russell and Crosswhite 1963). Russell was tasked with applying previous taxon concepts by Brainerd and his contemporaries onto eastern North American violets. His new interpretations, primarily utilizing leaf morphology and generally ignoring Brainerd's research on hybrid behavior, resulted in synonymy of some previously recognized taxa and attribution of a few others to hybrid status, but his efforts culminated in a "survey" of eastern North American violets that included a somewhat more sophisticated key, line drawings and range maps, and valuable commentary on each taxon he recognized—a far more "user-friendly" product than anything previously offered. In the process of

his extensive research, he annotated many thousands of collections from numerous herbaria, providing an ongoing valuable resource for later taxonomists and specialists. His efforts introduced eastern North American violets to a much broader professional audience than previous specialists had accomplished.

Several authors published one or two studies of violets in the 1950s through the 1970s, including an examination of hypothesized introgression in stemless white violets by Edgar Anderson (Anderson 1954), documentation of heterophylly in *Viola egglestonii* Brainerd by J. M. Shaver (Shaver 1959), the genera of the violet family in the southeastern United States by George Brizicky (Brizicky 1961), an overview of *Viola* largely focused on European taxa and evolutionary processes by David Valentine (Valentine 1962), the treatment of the Violaceae for the "Britton and Brown" flora by Edward Alexander (Alexander 1963), an overview of violets of Quebec by Lionel Cinq-Mars (Cinq-Mars 1966), a monographic revision of the caulescent yellow violets by L. Lévesque and Pierre Dansereau (Lévesque and Dansereau 1966), a cytogenetic and evolutionary study of Palustres violets by Marja Sorsa (Sorsa 1968), and a Masters thesis and taxonomic study of Intermountain caulescent yellow violets by Gerritt Davidse (Davidse 1968, 1976) that included *Viola nuttalli* Pursh and *Viola vallicola* A.Nelson. Several papers were published on the geography and ecology of *V. egglestonii* by Jerry and Carol Baskin (Baskin and Baskin 1970, 1972, 1975a, b, 1978) and with James Aldrich (Baskin *et al.* 1987). Gordon McPherson conducted a Masters thesis documenting two ploidy levels in *Viola adunca* Sm. (the tetraploid subsequently described as *Viola aduncoides* A.Löve & D.Löve) and published it with John Packer (McPherson 1972, McPherson and Packer 1974). Doretta Klaber (1976) published a book on violets of the United States.

Landon McKinney ushered in another period of taxonomic condensation and reevaluation, publishing his thesis on middle Tennessee violets, a revision of the stemless blue violets (*Borealiamericanae*), and other articles with collaborators, expanding to North American violets more broadly (McKinney 1977, 1992; McKinney and Blum 1978, 1981; McKinney and Russell 2002). He later joined forces with western *Viola* specialist John Little to prepare the Violaceae treatment for the *Flora of North America*. McKinney emphasized vegetative features in delimiting taxa, he considered many previously recognized taxa as products of phenotypic plasticity, and although acknowledging hybridization he didn't expressly accept it as a component of taxonomic diversity in violets. He synonymized many names and reduced others to infraspecific rank, recognizing fewer and more broadly delimited species in many instances.

The first author (H.E.B.), who is a contemporary of McKinney's, began studies of Midwestern violets in 1985 and gradually expanded his taxonomic studies to encompass the regional *Viola* flora. He later took on genus- and family-level phylogenetic analyses to examine relationships and higher-level groups, and biogeographic patterns. He produced violet treatments for Michigan, Missouri, and Pennsylvania; and published new hybrids and a number of new species, adopting similar taxon concepts to those of Russell. In 2012 he reexamined literature on evolutionary processes, species concepts, taxonomic approaches, and older violet literature. He also began fieldwork in the Appalachian Mountains and Piedmont of Virginia, where he discovered that a substantial amount of violet diversity was not accounted for by the prevailing taxonomic concepts and literature. He and his students redesigned their taxonomic approach to encompass a more rigorous integrative taxonomic reevaluation of eastern North American *Viola*. Their methods utilized Brainerd's common garden observations on morphology, hybrids and reproductive behavior, and intensive field studies; Gil-ad's precise and comprehensive approach to morphological characterization, and micromorphology of seed coats and lateral petal hairs; phenetic analyses of morphological and ecological data; analysis of ecological niche in soil factors; and genetic investigations in limited instances, to detect and delimit taxa and infer their evolutionary status and appropriate taxonomic rank. The results of their many ongoing studies are summarized in this treatment, which substantially expands the known taxonomic diversity and justification for recognition of many more species of *Viola* in our region and North America beyond previous treatments. Ballard completed a Masters thesis and Ph.D. dissertation and published 17 articles, some with coauthors, pertaining to violets in our region (Ballard 1985, 1987, 1990a, b, 1992, 1993, 1995, 1996, 2000, 2013, 2022; Ballard and Gawler 1994; Ballard and Wujek 1994; Ballard *et al.* 1999, 2001, 2014,

2020a, b). Publications include a family-wide overview of the Violaceae with Gregory Wahlert and Juliana Paula-Souza (see below), and a series of typifications for southeastern violets with doctoral students Rem Burwell (who is conducting a doctoral dissertation on the taxonomy and phylogenetic relationships of the Affinis and Edulis species groups), and Samuel Lockhart (who is studying the mixed breeding system in certain *Borealiamericanae*). D. Fabijan and colleagues (Fabijan *et al*. 1988) published a comprehensive taxonomic study of the Nuttalllianae species group, clarifying taxa and their nomenclature. John Little, a specialist on violets in the western states, began working with McKinney on the Violaceae on a continent-wide scale, publishing a number of new combinations (some with McKinney) and, eventually, produced the monumental treatment for the *Flora of North America* series (Little 1996, 2011; Little and McKinney 1992, 2010, 2015). The doctoral dissertation research of Nir Gil-ad (1995) focused on the most challenging group in *Viola*, the North American *Borealiamericanae*, which is legendary in its extensive hybridization and variation. Gil-ad pioneered detailed and precise morphological characterization and application of micromorphological techniques with seed coat sculpturing and lateral petal hairs (as a proxy for genetic data) to attempt to distinguish hybrids from "orthospecies." His research did much to demonstrate the ubiquitous nature of hybrids. Some of his conclusions dispensed with some previously accepted species as hybrid derivatives, while he accepted other taxa as distinct in expressing a unique reproductive and/or micromorphological trait or suite of traits. He completed his dissertation and published two impactful papers (Gil-ad 1995, 1997, 1998), which set a new standard for investigations of subsect. *Borealiamericanae* and other violet groups.

Arthur Haines, an astute New England botanist, published a number of newsletter notes and a treatment of the violets of Maine (Haines 2001). Wofford and colleagues (Wofford *et al*. 2004) reported the occurrence of Andean *Pombalia parviflora* (as *Hybanthus parviflora*) as an introduction to eastern North America. Min Feng completed her doctoral dissertation on flora development and molecular phylogenetic relationships in the Violaceae in 2005 (Feng 2005), revealing many new generic relationships and demonstrating extensive polyphyly in *Hybanthus* and *Rinorea* and later collaborated with Wahlert and others in publishing this research (Wahlert *et al*. 2014; see below). Steve Grund and Bonnie Isaac typified and corrected publication errors for *Viola appalachiensis* L.K.Henry, made a new varietal combination under *Viola walteri* House, and provided additional information on that species (Grund and Isaac 2007). Tokuoka (Tokuoka 2008) undertook a broader molecular phylogenetic study of genera in the Violaceae. Thomas Marcussen, a violet specialist originating from Europe who has published many taxonomic studies and treatments of violets in that region of the world, has conducted a broad range of regional and global taxonomic and phylogenetic studies on *Viola* and the Violaceae, as lead author and collaborator, that have greatly advanced our knowledge of taxon delimitation, relationships, and evolutionary processes in violets (Marcussen *et al*. 2011, 2012, 2015, 2022). Marcussen has spearheaded several major initiatives including violets in our region, the most recent publication being the second comprehensive worldwide classification of the genus *Viola* following Becker's (Marcussen *et al*. 2022), with the first author and other specialists in Europe and South America as coauthors. The infrageneric groups proposed in that publication are followed in this treatment. Kim Blaxland was an emerging violet specialist who published the new western North American species *Viola pluviae* Marcussen, H.E.Ballard & Blaxland (Blaxland *et al*. 2018) with Marcussen and the first author, and coauthored two publications with Marcussen, the first author, and others. Her copious and insightful taxonomic notes and illustrations, spectacular digital photographs, and extensive research on North American violets are captured in the "Botanikim" website (Blaxland 2022), maintained by her husband, Chris Blaxland. Gregory Wahlert later expanded sampling on Feng's phylogenetic work for his dissertation focused on Old World *Rinorea* and coauthored a comprehensive and well-sampled phylogenetic study and classificatory analysis of the Violaceae with Feng, Marcussen, Paula-Souza, and the first author (Wahlert *et al*. 2014). Bethany Zumwalde (Zumwalde 2015) conducted a Masters thesis with the first author consisting of an integrative taxonomic studies on the Pedatifida and Subsinuata species groups, elucidating the distinctions, conservation status, and ecology of the new shale

woodland species *Viola tenuisecta* Zumwalde & H.E.Ballard that had previously passed as *Viola pedatifida* G.Don. Jennifer Hastings (Hastings 2018) pursued a Masters thesis with the first author on integrative taxonomic studies of members of the Palmata and Subsinuata species groups in Virginia, revealing *Viola monacanora* J.L.Hastings & H.E.Ballard and *V. palmata* (*pseudostoneana* variant) as new overlooked taxa. *Viola monacanora* and *V. tenuisecta* are described as new species in the taxon accounts.

HYBRIDIZATION. Hybridization as an evolutionary process has been a frequent event throughout diversification of the *Viola*, given its fundamental role in the extensive allopolyploid evolutionary history of the genus (Marcussen *et al*. 2012, 2015, 2022). Hybridization continues to be a locally frequent event in most lineages of violets around the world, documented within many groups among numerous species. However, hybrids between locally sympatric species of most formally recognized infrageneric groups are unknown, while the very few documented hybrids are extremely rare.

Ezra Brainerd (Brainerd 1904b, 1906c, 1907a, b, 1909, 1910b, 1912, 1913a, 1924) exerted much of his research effort on detecting and analysing the morphology, ecology, and reproductive biology of hybrids in North American violets, publishing his major summary on 80 different hybrids in 1924. Based on extensive field studies, and observations on living plants transplanted to a common garden with numerous individuals of parental taxa and putative hybrids, he produced important data (mostly ignored) on the behavior of hybrids among taxa in different infrageneric groups. He documented that chasmogamous seed production fails in all hybrids of North American *Viola*, and that hybrids in all infrageneric groups except subsection *Borealiamericanae* do not produce viable cleistogamous seeds; in other words, all hybrids outside the *Borealiamericanae* are strictly F_1. He grew numerous progeny of *Borealiamericanae* hybrids from F_1 through F_3 generations using viable seeds from cleistogamous capsules (where these were produced) and studied their macromorphology and fertility. Brainerd found that in the *Borealiamericanae*, a few interspecific hybrids produce malformed cleistogamous capsules or capsules with no viable seeds, while most produced normal cleistogamous capsules with a substantially reduced percentage of viable seeds relative to either parental species (typically less than one third of ovules maturing to seeds, often 0–10%). However, in cases involving hybridization among *Viola emarginata* (Nutt.), *Viola fimbriatula* Sm., and *Viola sagittata* Aiton, he found little to no reduction in cleistogamous reproduction in the hybrids. He showed that the morphological traits of the parental species were expressed "codominantly" in the F_1, with the F_1 intermediate. The majority of hybrids he studied produced at least a small number of viable cleistogamous seeds, and he cultivated and observed seeds and mature reproductive plants in the subsequent F_2 through F_3 and occasionally F_4 generations. He found that the seeds in the cleistogamous capsules and the mature progeny germinated from those seeds expressed recombinant traits of the parents in typical "Mendelian" segregation ratios. He found no individuals out of thousands of hybrid progeny in which chasmogamous or cleistogamous fertility was fully restored. His field observations indicated that careful scrutiny can detect even later-generation hybrids, and that recognizable hybrids rarely grow very far from either or both of the parental species. Brainerd utilized ecological information and reproductive behavior (including the nearly universal limitation or obstruction to gene flow in interspecific hybrids) as criteria to recognize distinct species, and he was the only violet specialist until recently to (at least implicitly) adopt a modified biological species concept in species delimitation. The evolutionary and taxonomic implications of Brainerd's extensive research on North American violet hybrids have been all but ignored, although his documentation of hybridization as a frequent to common occurrence in most violet groups has been acknowledged. His scrutiny of morphological traits also pointed out that cleistogamous fruits and seeds exhibit a wealth of traits distinguishing species, a fact which some subsequent specialists have ignored. Many hybrid binomials were provided by Homer House (1924), basing most of them on descriptions and cited specimens of Brainerd's various publications.

Norman Russell (1952, 1954a, 1955a, 1956a; Russell and Bowen 1960; Russell and Cooperrider 1955; Russell and Risser 1960) conducted analyses of leaf traits to document several instances of hybridization in subsection (subsect.) *Stolonosae* and subsect. *Borealiamericanae*.

Harvey Ballard (1990a, b, 1992, 1993) conducted a thesis revising subsect. *Rostratae* in North

America and published three small papers highlighting hybrids among several of the species in subsect. *Rostratae*. He demonstrated that such hybrids are quite common and sterile, and given their presumed F_1 status are easily identified by their intermediate morphology relative to the parental species.

Nir Gil-ad (1995, 1997, 1998) studied subsect. *Borealiamericanae* during the 1990s for his dissertation research and later published a monographic revision and a paper focused on delimitation of species and hybrids. His initial premise, based on the extensive propensity for hybridization demonstrated by Brainerd and others, was that every plant could be a hybrid derivative unless evidence was found to the contrary. His primary goal was to distinguish and delineate "orthospecies" from potential hybrid derivatives. He used a modified minimum diagnosability criterion of the phylogenetic species concept, arguing that an accepted species must have at least one unique macromorphological trait in a reproductive structure and also must express unique micromorphological traits that cannot be construed as the product of hybridization between accepted orthospecies. He was the first to employ scanning electron microscopy as a proxy for genetic studies, to document species-specific micromorphological traits on cleistogamous seed coats and lateral petal trichomes. He characterized the traits of cleistogamous capsules and seeds more rigorously and precisely than Brainerd, and he grew a few plants of many taxa in the greenhouse in order to obtain mature cleistogamous seeds for investigation. He was the first to provide truly comprehensive and precise morphological descriptions of taxa he accepted as orthospecies and infraspecific taxa. He dismissed plants or taxa inferred as hybrid derivatives from further consideration if any evidence failed to reveal unique macromorphological or micromorphological reproductive structures.

Our field studies and those of others have demonstrated that taxa belonging to the same infrageneric group generally only grow near one another where their microhabitats make contact, typically at an ecotonal area between vegetation zones or broader plant communities, or where disturbance (natural or anthropogenic) has created a heterogeneous mosaic of microhabitats. These are also the most likely spots to find and observe hybrids. Conversely, taxa belonging to different taxonomic groups often co-occur as randomly dispersed, intermingling individuals at a site (*e.g.*, *Viola eriocarpa* Schwein. of the Nudicaules group and *Viola canadensis* L of the Canadenses group in section (sect.) *Chamaemelanium*; *Viola blanda* Willd. or *Viola incognita* Brainerd in subsect. *Stolonosae*; *Viola labradorica* Schrank, *Viola rostrata* Pursh and/or *Viola striata* Aiton in subsect. *Rostratae*; and *Viola sororia* Willd. species complex and others in subsect. *Borealiamericanae*), To date, 113 interspecific hybrids (including a few involving different infraspecific taxa representing one parent) have been documented in our region. Hybrids in sect. *Chamaemelanium* are very rare across the continent, with the only representative in our region being the rare hybrid of *V. canadensis* and *V. eriocarpa*. Hybrids in other groups are frequent to common. Individual hybrids are noted in the "Hybrids" section in each taxon account, referenced in both parental taxa. A list of hybrids, both by parental taxon formula and by binomial, is presented in the "Hybrids" section under "Accepted Taxa."

Collecting and Studying Violets. The following set of "best practices" is a summary of our experience in conducting field and herbarium research on violets over a number of decades. A brief check of the morphological traits we have used in the keys and presented in the taxon accounts of this treatment will demonstrate the need in many taxa to observe structures over the entire body of a violet in order to arrive at a confident identification. It is also necessary to preserve the habit and structures of representative specimens either digitally for a quality iNaturalist (https://www.inaturalist.org/) post, or (even more importantly) as pressed physical specimens to be deposited at a local or regional herbarium. A few violets are immediately distinct in any state, even as sterile plants, because of unusual habit, rhizome or stolon features, stipule or leaf blade traits. Accurate identification of most violets, however, requires plants with structures at the right stage, usually either in spring chasmogamous flower or in summer cleistogamous fruit with fully mature or naturally dehisced capsules and mature seeds (or chasmogamous capsules with seeds in *Viola pedata* L., the only strictly chasmogamous species in our region). A small number of taxa in the *Borealiamericanae* group are best identified with *both* chasmogamous flowers and cleistogamous capsules with seeds, from the same population. With practice and study of all the violets in one's

area, one may quickly learn how to identify the majority of taxa at any stage. A very generalized rule of thumb (with a few exceptions) is that, if plants of only one season are available to study and collect, caulescent species are best observed during spring chasmogamous flower, while acaulescent species are best observed during summer cleistogamous fruit. Many of our caulescent species have distinctive chasmogamous floral traits in addition to their vegetative differences. While they all can be distinguished vegetatively or in fruit, identification is far easier from flowering specimens. A few acaulescent species are most distinctive in chasmogamous flower (*e.g.*, native *V. pedata, Viola rotundifolia* Michx., and *Viola selkirkii* Pursh ex Goldie, and introduced *Viola inconspicua* Blume*, Viola japonica* Langsd. ex Ging., and *Viola patrinii* DC.), but many have important leaf traits that develop to their greatest extent in summer fruit, and these also have distinguishing features in the cleistogamous capsules and seeds. Some acaulescent taxa that are very similar and easy to confuse in chasmogamous flower are immediately distinct and easy to identify with confidence in cleistogamous fruit.

To aid in correct identification, the keys emphasize multiple traits wherever possible, and the descriptions are sufficiently complete that one could check several possible taxa before settling on the most likely name. It is possible that a challenging specimen is a hybrid derivative, especially if the site from which it came had multiple co-occuring species of the same infrageneric group. Although every effort has been made to characterize the morphological variation thoroughly in each taxon, it is also possible that another undocumented nonhybrid variant, or even a new taxon, may be found. Careful documentation and preservation of such plants is critically important. While iNaturalist posts are extremely useful if several clear images of all structures are included in the observations, well-pressed specimens with detailed labels that are donated to a herbarium expands access to your discovery to a much broader scientific audience. In this treatment we have used both types of material.

For studying living plants (by far the easiest with which to learn violets), one should visit the same violet population in full spring chasmogamous flower and in summer cleistogamous fruit, to examine all structures and note their characteristics during flower and fruit, as well as any changes in structures such as leaves that take place over the growing season. It is important to carefully examine several apparently conspecific plants across the population to understand the constancy and variability in individual traits of the taxon represented. Once traits defining a population of that taxon are clear, one can move to another observably different taxon at the same site, and so on. Examining violets plant by plant, population by population, at one particular site, then moving some distance away to continue the process, especially if the sites have different microhabitats or encompass multiple different plant communities, is the best way to make one familiar with the violet diversity of an area. The greater the heterogeneity of ecological niches and broader plant communities, the greater the taxonomic diversity of violets inhabiting the site(s) being visited.

While a good eye is sufficient to observe most features, a lighted 10 × or 20 × hand lens is very useful to examine hairs on foliage, cilia on sepals, the hairs of lateral petal beards, or the color pattern of seeds. For size of seeds, a dissecting microscope with strong light and an ocular micrometer for measurement is indispensable. An alternative used by the first author is a USB microscope, with seed or online herbarium specimen images in the presence of a centimeter ruler for scale; images are then opened in the freeware program ImageJ (https://imagej.net/ij/), calibrated against the scale, and features are measured on the images.

To make good collections, it is important to press several individuals between sheets of newspaper, ideally in a standard plant press (although a large book and some extra weights can be pressed into temporary service). Having an accomplice to manipulate plant parts into proper position is extremely useful. The belowground parts (which should always be collected), any stems, and leaves should be spread so that at least a few of the largest leaves are fully exposed on all sides, and the upper and lower surfaces are exposed on different leaves. Plants with many leaves overlapping can be pruned of some smaller leaf blades. Flowers should be arranged so that some are in profile view to expose the sepals and spur, while others are spread open to expose any petal beards and the throat. The thumb and thumbnail can be used with pressure to flatten leaves, pressing the thumbnail at the top of the petiole and lower portion of the leaf blade repeatedly to relax the tissues and spread the leaves; and the fingers can be used to spread some flowers open in

frontal view, the pad of the thumb then applied to flowers to flatten them temporarily to cover them with the newspaper sheet. It is good practice to pick several additional flowers with peduncles intact from other plants, and to press those along with whole plants, so that the extra flowers may be placed in a packet on the herbarium sheet later to be available for dissection and microscopy.

Seeds do not attain their full pigmentation pattern without being exposed to air following natural dehiscence. Pressing capsules before they have naturally dehisced usually preserves immature seeds, with the result that immature seeds for most species are usually pale with weak blotches, and are useless for identification purposes. If some fruiting plants have dehisced capsules still retaining their seeds after a couple of days, the seeds are usually fully pigmented. Those plants can be collected and immediately pressed. Care must be taken to keep the seeds of individual plants with their maternal plant. The seeds can be gently removed from the capsule and transferred into a small coin envelope labeled with the taxon name (if known), locality information, collector name and collection number, and date, pressing the envelope of seeds in the newspaper with the individual to which they belong. If no plants in the population have dehisced capsules with mature seeds, then more time-consuming measures must be implemented, including transference of a few living plants in heavy duty zip-top freezer bags with a ball of soil to a temporary garden to maintain them for the week to few weeks necessary for cleistogamous capsules to emerge, mature, and dehisce. Plants will survive for a few weeks with regular watering if a large fist-sized ball of soil from around the plant is included in the bag and the belowground parts are well covered. Fine mesh drawstring gift bags, 5×7.6 cm, are ideal for tying around the peduncle of a developing cleistogamous capsule to capture the seeds of the dehisced fruit. Care must be taken to tie the bag firmly so that no seeds escape, but not so tightly that the peduncle is strangled and the capsule withers before dehiscence. The first author routinely brings back several living plants per population for many taxa under study, then transfers them within a few days to pots with standard potting mix and some vermiculite added for better drainage. Pots are immediately labeled with key information on each taxon and collection including location, date, and collection number. Plants are observed every few days, and emerging fruits are bagged. Within a day or two of capsule dehiscence, bags are removed from the plants with the entire capsule plus peduncle pushed into the bag. If plants will not be observed very regularly, it is important to secure the ties of the seed bags to the soil next to the plant to which the bags belong, ideally with a large potting staple or other wire, as bags may fall off the plant with the capsule and seeds once dehiscence has taken place. While hybrids of most infrageneric groups will produce no viable cleistogamous seeds, those in the *Borealiamericanae* will usually produce a few mature seeds that will disperse from the capsule and will also have some abortive ovules that remain attached to the capsule wall; these appear as shriveled deflated balloons. A paper tag labeled with the same information as the plant pot tag is placed into the mesh bag, then the bag is tied tightly to secure the fruit and seeds. The capsule and seeds can be observed and imaged at a later date. Maintaining collections of living plants starting from chasmogamous flower is particularly valuable in order to examine morphological traits over the entire growing season on the same plants. Chasmogamous flowers and one or more midsized leaves can be removed in spring for pressing from a particular plant, while the whole fruiting plant can be pressed after harvesting capsules and seeds.

Occasionally, seeds from an apparently normally dehisced capsule may not achieve full pigmentation and remain pale with very weak blotches; or some seeds may be hollow, indicating inviability and failure to reach full development, as occurs in certain violet taxa in New York (D. Werier, New York Flora Association, personal communication) and elsewhere. Failure to achieve pigmentation has most often been observed in plants that either have been transplanted from their native habitat to a location quite far removed geographically, or have been subjected in cultivation to an unusual environmental stress such as frost or water deficiency. The production of hollow inviable seeds may also have multiple explanations, including hybrid origin. In studies of the reproductive biology of *Borealiamericanae* violets in southeastern Ohio, graduate student Samuel Lockhart (personal communication) has similarly observed significant levels of premature capsule dehiscence and "abortion" prior to full development of the seeds, and he is currently investigating the basis and consequences of this phenomenon.

Detailed label data for a specimen are immensely valuable. Basic information that should be recorded at the site include exact locality information (ideally including a latitude and longitude coordinate, easily obtained from a map app on one's smartphone) with driving or air mileage (specifying which) and directions from the nearest local landmark or landscape feature; habitat where the plants are growing, ideally noting the type of broader plant community and the specific microhabitat or niche including soils and a few associates; date; collector(s); and collector number if applicable. Additional information regarding ephemeral plant traits that will be lost upon pressing or drying (habit of plant, orientation of leaves or flowers, flower or foliage color, population size or frequency in the area, percentage in flower or fruiting in the population) are also very valuable. Noting other violet taxa, especially those of the same group, is useful to suggest possible parental taxa in case your collection is a hybrid derivative; if you suspect it is, then listing co-occurring taxa is particularly important.

Good quality iNaturalist observations are very valuable to document phenotypes or new taxa not yet captured in herbarium collections, and for expanding our understanding of phenology and distribution. One image for an observation is rarely sufficient or informative enough to make a quality observation for scientific purposes. As with identifying an unknown plant, the observer should make every effort to capture images (usually several) of overall habit, upper portion of stem with leaves if present, closeup of stem showing any indumentum, largest leaves, closeup of upper and lower leaf blade surfaces, chasmogamous flowers in front view and in profile view, chasmogamous capsule, cleistogamous capsule, and seeds if they are exposed on a dehisced capsule. The images must be sharp and in focus on a particular structure or feature in every case. One should learn to use the magnification feature on the smartphone to zoom in or out in order to capture important features such as fine hairs or cilia, pigmentation on stems, petioles, peduncles or sepals, purple tinge on the lower surface of leaf blades, and so on. A large percentage of current iNaturalist posts are difficult or impossible to confidently identify to species or infraspecific taxon because they are poor quality—either too few images to show all the necessary structures, or too blurry. It is important for us to remember the second word in the phrase "citizen science," and to make iNaturalist posts truly useful for scientific documentation.

Materials and Methods. HERBARIUM SPECIMENS AND iNATURALIST POSTS. For primary taxon delimitation and initial geographic distributions, herbarium specimens were examined in person or as online images at A, AQC, AUA, AUB, BH, BHO, BLH, BM, BRIT, CAN, CHRB, CM, DAO, DUKE, DUL, EKU, F, GH, GVSC, IA, ILL, ILLS, IND, K, LINN, LKHD, MAINE, MICH, MIN, MSC, MO, MT, NBM, NCU, NEBC, NDG, NHA, NY, NYS, OS, OSH, PAC, PENN, PH, TENN, TRT, UNB, US, UWGB, UWL, UWSP, VDB, VPI, VT, WILLI, WIS, WVA, and YU. Herbarium acronyms follow Thiers (2022). For certain taxa, including rare or introduced violets, iNaturalist was searched for potential observations. Confirmed observations were included in the geographic distributions.

FIELD STUDIES. Field studies spanning nearly 45 yr were conducted in Delaware, Indiana, Kentucky, Maine, Maryland, Michigan, Minnesota, New Jersey, New York, Ohio, Pennsylvania, Virginia, West Virginia, and Wisconsin. Fieldwork was particularly extensive in the Great Lakes region and the central Appalachian Mountains.

MORPHOLOGY. Many qualitative and quantitative traits of structures across the plant body were scrutinized and recorded for most taxa. For each well-studied taxon, macromorphological traits were recorded from many individuals across several to many populations or collections, and these data were summarized and utilized in preparation of the keys and taxon descriptions. Traits included belowground parts; habit and plant height; stems or stolons if present; foliage color, texture, and indument; stipule size, shape, texture, and margin; leaf orientation, size, and petiole color; leaf blade shape, texture, dissection, and margins in chasmogamous flower and cleistogamous fruit; chasmogamous peduncle height and color, chasmogamous flower size; calyx color and indument, size, and shape as well as indument and ciliation of sepals, size and shape of auricles in flower and fruit; corolla color pattern, petal margins, lateral and spurred petal indument, and spur color, length, and shape; (usually cleistogamous) peduncle orientation and color, capsule size, shape, and color; and seed size, shape, and color pattern. Some previous publications have utilized precise terms such as "sericeous," "villous,"

"strigose," or "hispidulous" to describe hairs (including cilia, all technically trichomes), the applications of which in violets are often difficult to interpret. We chose a simple three-term scheme that categorizes length, orientation, and density of hairs. We employed "hirsute" for longer hairs generally $>$ 1 mm long, "hirtellous" for shorter hairs between 0.25 and 1 mm long, and "puberulent" for very small hairs $<$ 0.25 mm long (these usually best seen with a hand lens). We used "spreading," "ascending," or "appressed" to describe the orientation of hairs (the default, if not specified, being "spreading"). We applied "sparse" or "weak" for widely spaced, interrupted, or scattered hair; "moderate" for closely spaced hairs not obscuring or covering the surface; and "dense" for hairs tightly spaced and mostly or completely obscuring or covering the surface. All taxa accepted here as worthy of formal recognition have yielded compelling evidence of producing uniform populations characterized by a distinctive suite of macromorphological features. In limited cases, micromorphological features of seed coats and lateral petal hairs were examined and provided additional evidence of taxon distinctions (H. E. B., unpublished data).

Reproductive Biology and Hybridization. Herbarium specimens and living plants were examined to determine the status of chasmogamous and cleistogamous reproduction, and to record chasmogamous flowering phenology. Taxa expressing full fertility in both breeding systems were deemed potentially distinct. Display of a shifted modal chasmogamous flowering time from related taxa was taken as further evidence of reproductive isolation, suggesting further limitation of cross-taxon pollination and gene flow. Plants in groups other than subsect. *Borealiamericanae* with morphologically intermediate traits and no successful chasmogamous or cleistogamous reproduction were treated as hybrids. Plants in the *Borealiamericanae* showing intermediate or recombinant traits in relation to other species with which they grew (where known) with no evidence of chasmogamous reproduction, and lacking cleistogamous reproduction or producing a reduced complement of seeds with recombinant features were treated as hybrids.

Ecology. Broader plant communities and microhabitats, as well as associated species, soil types, and moisture regimes were recorded from herbarium specimens and in the field from living populations, then summarized for taxon accounts. In a limited number of studies, soil factors such as texture, organic matter, and pH were analyzed from soil cores of study taxa and examined for statistical differences among taxa as evidence for ecological niche differentiation. Taxa within an infrageneric groups that grow consistently in a recognizable and modally distinct microhabitat from other taxa were recognized as potential species.

Geographic Distribution. The Biota of North America Program (BONAP, Kartesz 2022) maps display geographic distributions of taxa for the entire United States; while BONAP does not map Canadian records, the provinces where records are documented are highlighted in green. Maps prepared for this taxonomic treatment will be released to the BONAP website after publication of the treatment. Unless mentioned in the text, county records within our region are accepted with confidence, while in certain taxa some records outside our region are tentatively accepted and require future study. This is especially true of some predominately southern species which have not yet been subjected to recent taxonomic research. Nevertheless, the distributions as presented offer our best current understanding of the violets treated here.

Our collective efforts to examine or reexamine many thousands of physical herbarium specimens and images, and hundreds of iNaturalist posts, have resulted in new county-level maps representing our best understanding of geographic distributions for nearly all taxa presented. In certain taxa (especially those recently detected or resurrected from long-term synonymy) the geographic distribution is necessarily fragmentary, while in many others it is very complete. The ubiquity and taxonomic diversity of the genus *Viola* in particular is both a proverbial blessing and curse for a broad regional taxonomic treatment such as this, since even the smallest herbarium typically has hundreds of specimens, and a larger regional or national herbarium will typically have several thousands (too numerous for a loan of many taxa). In one case, the *V. sororia* complex, our knowledge is still so fragmentary regarding the two variants that one map is employed for the species complex. In three other cases, one involving *Viola glaberrima* (Ging. ex Chapm.) House and *Viola tenuipes* Pollard (south of our region), a second involving *V. palmata* var. *palmata* and var. *triloba*, and a third involving western *Viola suecica* Fr. and *Viola palustris* L. subsp. brevipes M.S.Baker, taxa have received

diverse treatments, and in the first and third cases usually being synonymized with other taxa. This has led to huge difficulties and countless hours in reexamining online specimens to reassign county records to particular taxa and create reliable geographic distribution maps. Our studies are still in progress. Our conservative approach with respect to these taxa has been to map the *V. glaberrima* complex including the distinct southeastern *V. tenuipes*, map *V. palmata* var. *palmata* and var. *triloba* together (but referencing Russell's 1965 distributions as guides), and map all western *V. suecica* and western *V. palustris* var. *brevipes* records with *V. palustris*, until such time as records can be disentangled and reliably reassigned to their correct taxa. We have invested an extraordinary amount of time in examining online specimens, visiting herbarium collections, and confirming iNaturalist posts, in order to reconfigure many earlier maps for taxa to the taxa as circumscribed in this treatment and to generate many maps for newly recognized taxa. In a few cases the maps are necessarily incomplete. In the majority of cases, the maps will provide a reasonable overall impression of the total range of the taxon concerned.

SPECIES CONCEPTS AND TAXON DELIMITATION. In all cases, an explicit morphological species concept has been applied initially to detect and delimit taxa. Further studies of the majority of taxa have generated additional evidence regarding potential ecological niche differentiation and reproductive isolation. Where multiple sources of evidence have become available, a modification of Kevin de Queiroz's "unified species concept" (de Queiroz 2007) has been employed (species are separately evolved metapopulations) to evaluate the distinctness and evolutionary status of taxa. Taxa represented by demonstrably distinct metapopulations under any phenotypic criterion, with "phenotypic" defined broadly, are recognized as separate evolutionary species. Recognizably distinct phenotypes that belong to a broader gene pool but show affinities with geologic formations or ecological zones are recognized as subspecies (the varieties in *V. palmata* have been left intact while ongoing studies evaluate their distinctness, so that additional unnecessary names are not created). The recommendation of Ellison *et al*. (2014) regarding adoption of the rank of subspecies for all infraspecific taxa worthy of formal recognition is followed here. Phenotypes that represent trivial single-trait polymorphisms occurring randomly in populations across the range of a species (*e.g.*, albino flowers in otherwise pigmented corollas, or the bicolorous *versus* concolorous corolla color pattern in *V. pedata*) without any relationship to other components of the natural history of the taxon are not recognized. Hybrids bring together the genomes of distinct taxa, do not reproduce successfully or generate bigenomic recombinants rather than genetically coherent populations, and thus do not fulfill the definition of a metapopulation.

Results. THIS TREATMENT. Expanded taxonomic investigations using a variety of evidence and a modified unified species concept has resulted in detection of greater taxonomic diversity than previously known, and acceptance of more taxa at species rank. All of the taxa accepted by Brainerd (1921b) have been supported, a number of additional species have been resurrected from taxonomic obscurity, two new species are described, and several variants are under evaluation. In this treatment we accept three genera with 58 native and 8 introduced species, 1 subspecies, 1 variety, and 1 form, plus 10 informal variants and 113 wild hybrids. Two new native *Viola* species are described below, while three new combinations (one species, one subspecies, and one form) are made. Six accepted names and two synonyms are typified. Six potential species have been documented within three counties of our region; they have been included in the keys and are discussed with figures briefly under the "Potential Taxa" section. Two species previously reported from our region are noted under the "Excluded Taxa" section on the basis of misidentifications and no confirmed specimens. Table 1 compares the disposition of taxa included in this treatment with those of previous regional and national treatments, from most recent to earliest (Little and McKinney 2015, Gleason and Cronquist 1991, Russell 1965, Alexander 1963, Fernald 1950, Brainerd 1921b). The general trend toward reduction and condensation of taxa from Brainerd's time to the present is apparent. Our recently initiated integrative taxonomic studies reverse that trend, revealing substantial unrecognized taxonomic diversity. A website maintained by the first author, "Violets of the Great Plains and eastern North America" (Ballard 2020), presents much of the information included in this treatment and for other taxa in the broader region.

Specimen lists are not included in this treatment, given that even limited state-level vouchers would

Table 1. Violet taxa included in this treatment and previous regional and national violet treatments. Forms are included only if they have been previously treated at higher rank. Names are arranged in alphabetical order, beginning with names employed in this treatment. NI, not included; NR, not recognized; *, introduced. Where a taxon was not explicitly named but attribution could be confidently made based on the text or annotated specimens, the probable name under which a presently accepted taxon was included is provided in parentheses. Potential taxa very near our region but not yet confirmed here are included in brackets and are not numbered. Fernald (1950) included *V. langloisii* and *V. villosa* from southern Virginia, and Fernald and Alexander (1963) included *V. lovelliana* from southern Missouri, but no verified specimens have been found to support these occurrences. Fernald's Virginia reports of *V. chalcosperma* are referred to *V. impostor*.

Ballard (2022)	Little and McKinney (2015)	Gleason and Cronquist (1991)	Russell (1965)	Alexander (1963)	Fernald (1950)	Brainerd (1921)
1. *Cubelium concolor*	*Hybanthus concolor*	*Hybanthus concolor*	NI	*Cubelium concolor*	*Hybanthus concolor*	NI
2. *Pombalia parviflora**	*Hybanthus parviflorus**	NI	NI	NI	NI	NI
[*Pombalia verticillata*]	[*Hybanthus verticillatus*]	NI	NI	NI	NI	NI
3. *V. adunca*	*V. adunca* var *adunca*	*V. adunca* var. *adunca*, var. *minor* (in part)	*V. adunca*	*V. adunca* var. *adunca*, var. *minor* (in part)	*V. adunca* var. *adunca*, var. *minor* (in part)	*V. adunca*
[*V. aduncoides*]	*V. adunca*	(*V. adunca*)	(*V. adunca*)	(*V. adunca*)	(*V. adunca*)	(*V. adunca*)
4. *V. affinis*	*V. affinis*	*V. sororia*	*V. affinis*	*V. affinis*	*V. affinis*	*V. affinis*
5. *V. appalachiensis*	*V. walteri* var. *appalachiensis*	NR	*V. conspersa* or hybrids	NR	NR	NR
6. *V. arcuata**	NI	NI	NI	NI	NI	NI
7. *V. arvensis**	*V. arvensis**	*V. arvensis**	*V. arvensis**	*V. arvensis**	*V. arvensis**	NI
8. *V. baxteri*	*V. brittoniana*	(*V. palmata* var. *palmata*)	(*V. palmata*)	(*V. palmata*)	(*V. palmata*)	(*V. palmata*)
9. *V. blanda*	*V. blanda*	*V. blanda*	*V. blanda*	*V. blanda*	*V. blanda*	*V. blanda*
10. *V. brittoniana*	*V. brittoniana*	*V. palmata* var. *palmata*	*V. brittoniana*	*V. brittoniana* var. *brittoniana*	*V. brittoniana*	*V. brittoniana*
11. *V. canadensis*	*V. canadensis* var. *canadensis*	*V. canadensis* var. *canadensis*	*V. canadensis* var. *canadensis*	*V. canadensis*	*V. canadensis*	*V. canadensis*
12a. *V. communis* f. *communis*	(*V. sororia*)	(*V. sororia*)	(*V. sororia*)	(*V. papilionacea* var. *papilionacea*)	(*V. papilionacea*)	(*V. papilionacea*)
12b. *V. communis* f. *priceana*	*V. sororia*	*V. sororia*	(*V. sororia*)	*V. papilionacea* var. *priceana*	*V. papilionacea* f. *albiflora*	*V. papilionacea*
13. *V. cucullata*	*V. cucullata*	*V. cucullata*	*V. cucullata*	*V. cucullata*	*V. cucullata*	*V. cucullata*
14. *V. domestica*	(*V. sororia*)	(*V. sororia*)	(*V. sororia*)	(*V. papilionacea*)	*V. papilionacea*	*V. papilionacea*
15. *V. edulis*	*V. palmata* var. *heterophylla*	*V. palmata* var. *palmata* [as *V. esculenta*]	*V. esculenta*	*V. esculenta*	*V. esculenta*	*V. esculenta*
16a. *V. egglestonii sensu stricto*	*V. egglestonii*	*V. palmata* var. *pedatifida*	*V. egglestonii*	*V. egglestonii*	*V. egglestonii*	*V. egglestonii*
16b. *V. egglestonii* (Canada variant)	NR	NR	NR	NR	NR	NR
17a. *V. emarginata sensu stricto*	*V. sagittata* var. *sagittata*	Hybrids with *V. sagittata*	*V. affinis* × *V. sagittata*	*V. emarginata*	*V. emarginata* var. *acutiloba*, var. *emarginata*	*V. emarginata*

Table 1. Continued.

Ballard (2022)	Little and McKinney (2015)	Gleason and Cronquist (1991)	Russell (1965)	Alexander (1963)	Fernald (1950)	Brainerd (1921)
17b. *V. emarginata* (Kentucky variant)	NR	NR	NR	NR	NR	NR
[*V. emarginata* (Lower Midwest variant)]	NR	NR	NR	*V. emarginata*	*V. emarginata*	*V. emarginata*
17c. *V. emarginata* (*phasmatifolia* variant)	NR	NR	NR	NR	NR	NR
17d. *V. emarginata* (*xiphophylla* variant)	NR	NR	NR	NR	NR	NR
18. *V. eriocarpa*	*V. pubescens* var. *scabriuscula*	*V. pubescens*	*V. pubescens* var. *eriocarpa*	*V. eriocarpa*	*V. pensylvanica* var. *leiocarpa*, var. *pensylvanica*	*V. eriocarpa*
19. *V. fimbriatula*	*V. sagittata* var. *ovata*	*V. sagittata*	*V. fimbriatula*	*V. fimbriatula*	*V. fimbriatula*	*V. fimbriatula*
20. *V. glaberrima*	*V. tripartita*	*V. tripartita*	*V. tripartita*	*V. tripartita* var. *glaberrima*	*V. tripartita* f. *tripartita*	*V. tripartita*
21. *V. grisea*	*V. novae-angliae*	*V. novae-angliae*	*V. novae-angliae*	*V. novae-angliae*, *V. septentrionalis*	*V. novae-angliae*, *V. septentrionalis* var. *grisea*	*V. novae-angliae*
22. *V. hastata*	*V. hastata*	NR	*V. hastata*	*V. hastata*	*V. hastata*	*V. hastata*
23. *V. hirsutula*	*V. hirsutula*	*V. villlosa*	*V. hirsutula*	*V. hirsutula*	*V. hirsutula*	*V. hirsutula*
[*V.* "*impostor*"]	NR	NR	NR	NR	*V. chalcosperma*	NR
24. *V. incognita*	*V. blanda*.	*V. blanda*	*V. incognita*	*V. incognita*	*V. incognita* var. *forbesii*, var. *incognita*	*V. incognita*
25. *V. inconspicua**	NR	NR	NR	NR	NR	NR
26. *V. japonica**	*V. japonica**	NR	NI	NI	NI	*V. chinensis**
27. *V. labradorica*	*V. labradorica*	*V. conspersa*, *V. adunca* var. *minor* (in part)	*V. conspersa*, *V. labradorica*	*V. conspersa*, *V. adunca* var. *minor* (in part)	*V. conspersa*, *V. adunca* var. *minor* (in part)	*V. conspersa*, *V. labradorica*
28. *V. lanceolata*	*V. lanceolata*	*V. lanceolata*	*V. lanceolata* var. *lanceolata*	*V. lanceolata*	*V. lanceolata* var. *lanceolata*	*V. lanceolata*
[*V. langloisii*]	*V. missouriensis*	*V. sororia*	NI in region	NI in region	*V. langloisii*	NI in region
29. *V. latiuscula*	*V. sororia*	*V. sororia*	NR	*V. latiuscula*	*V. latiuscula*	*V. latiuscula*
30. *V. minuscula*	*V. macloskeyi*	*V. macloskeyi*	*V. macloskeyi* subsp. *pallens*	*V. pallens*	*V. pallens*	*V. pallens*
31. *V. missouriensis*	*V. missouriensis*	*V. sororia*	*V. missouriensis*	*V. missouriensis*	*V. missouriensis*	*V. missouriensis*
32. *V. monacanora*	NR	NR	NR	NR	NR	NR
33. *V. nephrophylla*	*V. nephrophylla*	*V. nephrophylla*	*V. nephrophylla*	*V. nephrophylla*	*V. nephrophylla*	*V. nephrophylla*
34. *V. novae-angliae*	*V. novae-angliae*	*V. sororia*	*V. novae-angliae*	*V. novae-angliae*	*V. novae-angliae*	*V. novae-angliae*
35. *V. nuttallii*	*V. nuttallii*	*V. nuttallii*	*V. nuttallii*	*V. nuttallii*	NI	*V. nuttallii*

Table 1. Continued.

Ballard (2022)	Little and McKinney (2015)	Gleason and Cronquist (1991)	Russell (1965)	Alexander (1963)	Fernald (1950)	Brainerd (1921)
36. *V. odorata**	*V. odorata**	*V. odorata**	*V. odorata**	*V. odorata**	*V. odorata**	NI
37a. *V. palmata* var. *palmata*	*V. palmata* var. *palmata*	*V. palmata* var. *palmata*	*V. triloba* var. *dilatata*	*V. triloba* var. *dilatata*	*V. triloba* var. *dilatata*	*V. triloba* var. *dilatata*
37b. *V. palmata* var. *triloba*	*V. palmata* var. *palmata*	*V. palmata* var. *palmata*	*V. triloba* var. *triloba*	*V. triloba* var. *triloba*	*V. triloba* var. *triloba*	*V. triloba* var. *triloba*
37c. *V. palmata* (*avipes* variant)	NR	NR	NR	NR	NR	NR
37d. *V. palmata* (*pseudostoneana* variant)	NR	NR	NR	NR	NR	NR
38. *V. palustris*	*V. palustris*	*V. palustris*	*V. palustris*	*V. palustris*	*V. palustris*	*V. palustris*
39. *V. patrinii**	NR	NR	NR	NR	NR	NI
40. *V. pectinata*	*V. brittoniana*	*V. palmata* var. *palmata*	*V. brittoniana*	*V. brittoniana* var. *pectinata*	*V. pectinata*	*V. brittoniana*
41a. *V. pedata* subsp. *cuneatiloba*	NR	NR	NR	NR	*V. pedata* f. *cuneatiloba*	NR
41b. *V. pedata subsp. pedata*	*V. pedata* var. *pedata*	*V. pedata*	*V. pedata*	*V. pedata* var. *lineariloba*, var. *pedata*	*V. pedata* var. *lineariloba*, var. *pedata*	*V. pedata*
42. *V. pedatifida*	*V. pedatifida*	*V. palmata* var. *pedatifida*	*V. pedatifida*	*V. pedatifida*	*V. pedatifida*	*V. pedatifida*
43. *V. pratincola*	*V. nephrophylla*	*V. sororia*	*V. pratincola*	NR	*V. papilionacea*	*V. papilionacea*
44. *V. primulifolia*	*V. primulifolia* var. *primulifolia*	*V. primulifolia*	*V. primulifolia*	*V. primulifolia*	*V. primulifolia* var. *acuta*, var. *primulifolia*, var. *villosa*	*V. primulifolia*
45. *V. pubescens*	*V. pubescens* var. *pubescens*	*V. pubescens*	*V. pubescens* var. *pubescens*	*V. pubescens*	*V. pubescens*, var. *peckii*, var. *pubescens*	*V. pubescens*
46. *V. rafinesquei*	*V. bicolor*	*V. rafinesquii*	*V. rafinesquii*	*V. rafinesquii*	*V. kitaibeliana var. rafinesquii*	*V. rafinesquii*
47. *V. renifolia*	*V. renifolia*	*V. renifolia*	*V. renifolia*	*V. renifolia*	*V. renifolia* var. *brainerdii*, var. *renifolia*	*V. renifolia*
48. *V. retusa*	*V. nephrophylla*	NR	NR	NR	NR	NR
49. *V. rostrata*	*V. rostrata*	*V. rostrata*	*V. rostrata*	*V. rostrata*	*V. rostrata*	*V. rostrata*
50. *V. rotundifolia*	*V. rotundifolia*	*V. rotundifolia*	*V. rotundifolia*	*V. rotundifolia*	*V. rotundifolia*	*V. rotundifolia*
51. *V. rugulosa*	*V. canadensis* var. *rugulosa*	*V. canadensis* var. *rugulosa*	*V. canadensis* var. *rugulosa*	*V. rugulosa*	*V. rugulosa*	*V. rugulosa*

Table 1. Continued.

Ballard (2022)	Little and McKinney (2015)	Gleason and Cronquist (1991)	Russell (1965)	Alexander (1963)	Fernald (1950)	Brainerd (1921)
52. *V. sagittata*	*V. sagittata* var. *sagittata*	*V. sagittata*	*V. sagittata*	*V. sagittata*	*V. sagittata*	*V. sagittata*
53. *V. selkirkii*	*V. selkirkii*	*V. selkirkii*	*V. selkirkii*	*V. selkirkii*	*V. selkirkii*	*V. selkirkii*
54. *V. septemloba*	*V. septemloba*	*V. palmata* var. *palmata*	*V. septemloba*	*V. septemloba*	*V. septemloba*	*V. septemloba*
55a. *V. septentrionalis sensu stricto*	*V. sororia*	*V. sororia*	*V. septentrionalis*	*V. septentrionalis*	*V. septentrionalis*	*V. septentrionalis*
55b. *V. septentrionalis* (Upper Midwest variant)	NR	NR	NR	NR	NR	NR
56a. *V. sororia sensu stricto*	*V. sororia*	*V. sororia*	*V. sororia*	*V. sororia*	*V. sororia*	*V. sororia*
56b. *V. sororia* (glabrous variant)	NR	NR	NR	NR	NR	NR
56c. *V. sororia* (*hirsutuloides* variant)	NR	NR	NR	NR	NR	NR
57. *V. stoneana*	*V. palmata* var. *palmata*	*V. palmata* var. *palmata*	hybrids	*V. stoneana*	*V. stoneana*	*V. stoneana*
58. *V. striata*	*V. striata*	*V. striata*	*V. striata*	*V. striata*	*V. striata*	*V. striata*
59. *V. subsinuata*	*V. subsinuata*	*V. palmata* var. *palmata*	*V. palmata*	*V. palmata*	*V. palmata*	*V. palmata*
60. *V. suecica*	*V. epipsila* subsp. *repens*	*V. palustris*	(*V. palustris)*	(*V. palustris)*	(*V. palustris)*	(*V. palustris)*
61. *V. tenuisecta*	*V. pedatifida*	(*V. palmata* var. *pedatifida*)	NR	NR	NR	NR
62. *V. tricolor**	*V. tricolor* *	*V. tricolor* *	*V. tricolor* *	*V. tricolor* *	*V. tricolor* *	NI
63. *V. tripartita*	*V. tripartita*	*V. tripartita*	*V. tripartita*	*V. tripartita* var. *tripartita*	*V. tripartita* f. *tripartita*	*V. tripartita*
[*V. vallicola*]	[*V. vallicola*]	[*V. nuttallii*]	[*V. nuttallii*]	NI	NI	[*V. nuttallii*]
64. *V. viarum*	*V. palmata* var. *palmata*	*V. palmata* var. *palmata*	*V. viarum*	*V. viarum*	*V. viarum*	*V. viarum*
65. *V. vittata*	*V. lanceolata*	*V. lanceolata*	*V. lanceolata* var. *vittata*	*V. vittata*	*V. lanceolata* var. *vittata*	*V. vittata*
66. *V. walteri*	*V. walteri* var. *walteri*	*V. walteri*	*V. walteri*	*V. walteri*	*V. walteri*	*V. walteri*

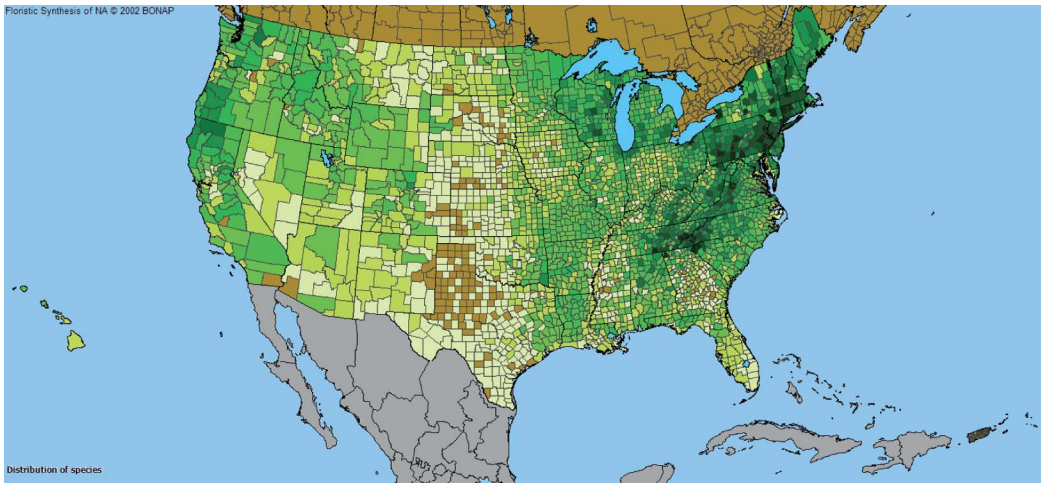

FIG. 3. United States county-level distribution map of species richness for Violaceae in North America (photo: the Biota of North America Program).

add a substantial number of pages to this manuscript. Lists of vouchers and other supporting evidence are available upon request.

BIOGEOGRAPHY AND ENDEMISM. Our violet taxa express some interesting biogeographic patterns. Collectively, Violaceae mapped at the county level over the United States (Fig. 3) reveal highest species richness east of the Mississippi River in the Appalachian Mountains and associated uplands northward into New England, and in the Great Lakes region. When taxa in our region are categorized by generalized biogeographic regions, more specific patterns emerge. Biogeographic areas were delineated that loosely follow the Level III ecoregions defined by the US Environmental Protection Agency and other federal agencies (US Environmental Protection Agency 2022). After excluding urban and suburban *Viola domestica* E.P.Bicknell, presumed adventive or planted populations of *Viola communis* Pollard in the western portion of its range, and *V. egglestonii* (Canada variant) restricted to plantings and lawns, the remaining violet taxa were either placed into the "widespread" category or assigned to a biogeographic region that largely or fully encompassed their range (Table 2). Twenty-eight taxa were widespread, occurring over multiple biogeographic regions. The other 38 taxa were interpreted as regional or local endemics. Reflecting the national species richness map for the Violaceae overall, the biogeographic region with the largest taxonomic diversity by far was the Appalachian Mountains and associated uplands, with 14 taxa; four taxa were interpreted as very narrowly endemic to a small portion of the region. The Boreal/northern and Coastal Plain biogeographic regions encompassed seven taxa, while the Great Plains/western Midwest region harbored six taxa. Outside of the Appalachian Mountain region, the only other biogeographic region with a narrowly endemic taxon was the Piedmont. In some widespread taxa, a recognizable biogeographic pattern could be detected, one of the most common being ranges that encompassed the Appalachian Mountains, northeast or boreal regions, and the Great Lakes.

CLASSIFICATION. Of the three genera found in our region and North America, only *Viola* has formally recognized infrageneric groups. The *Viola* taxa are distributed across five sections and nine subsections. Group-level diversity in our region is representative of most of the infrageneric diversity in North American *Viola* overall (Table 3). The largest formal infrageneric group by species number is subsect. *Borealiamericanae* in sect. *Nosphinium* (acaulescent blue violets, with several informal groups) with 31 species, followed by sect. *Chamaemelanium* (caulescent and acaulescent yellow violets) and subsect. *Stolonosae* (mostly stoloniferous white and purple violets) with nine species each. For additional information on classification and infrageneric groups in *Viola* worldwide, see the new classification of the genus by Marcussen *et al*. (2022).

Table 2. Biogeography and endemism of native Violaceae accepted in our region; * indicates very limited range within its biogeographic region. *Viola domestica*, *Viola egglestonii* (Canada variant), and adventive or cultivated populations of *Viola communis* west of Kentucky and Ohio are excluded from consideration due to their restriction to anthropogenic environments.

Widespread species (28 taxa)
- *Cubelium concolor* (eastern North America)
- *Viola affinis* (eastern North America)
- *Viola canadensis* (eastern North America)
- *Viola communis* (eastern Great Lakes, Appalachian Mountains)
- *Viola cucullata* (eastern North America)
- *Viola emarginata* (Kentucky variant) (Interior Low Plateau, Gulf states)
- *Viola eriocarpa* (northeastern North America)
- *Viola fimbriatula* (Appalachian Mountains, northeastern, Great Lakes)
- *Viola incognita* (Appalachian Mountains, Boreal/northern, Great Lakes)
- *Viola labradorica* (Appalachian Mountains, Boreal/northern, Great Lakes)
- *Viola lanceolata* (eastern North America)
- *Viola minuscula* (Appalachian Mountains, Boreal/northern, Great Lakes, West)
- *Viola nephrophylla* (Boreal/northern, Great Lakes, Great Plains and western Midwest, West)
- *Viola palmata* var. *palmata* (eastern North America)
- *Viola palmata* var. *triloba* (eastern North America)
- *Viola pedata* L. subsp. *pedata* (eastern North America)
- *Viola primulifolia* (Appalachian Mountains, Coastal Plain, Piedmont, Southeast)
- *Viola pubescens* (eastern North America)
- *Viola rafinesquei* (eastern North America)
- *Viola rostrata* (Appalachian Mountains, Great Lakes)
- *Viola sagittata* (eastern North America)
- *Viola septentrionalis sensu stricto* (Appalachian, Boreal/northern)
- *Viola septentrionalis* (Upper Midwest variant) (western Great Lakes/Upper Midwest)
- *Viola striata* (eastern North America)
- *Viola subsinuata* (Appalachian Mountains, Interior Low Plateau)
- *Viola sororia* (eastern North America)
- *Viola viarum* (Lower Midwest, Great Plains & western Midwest)
- *Viola walteri* (Appalachian Mountains, Southeast)

Regional endemics

Great Plains and western Midwest (6 taxa)
- *Viola missouriensis*
- *Viola nuttallii* (barely extending into western Minnesota from Great Plains)
- *Viola pedatifida* (Midwest Prairie Peninsula, slightly disjunct in northern Ohio and southern Ontario)
- *Viola pratincola*
- *Viola retusa* (disjunct in eastern Minnesota)
- *Viola rugulosa* (also Rocky Mountains)

Interior Low Plateau (1 taxa)
- *Viola egglestonii*

Table 2. Continued.

Boreal/northern (6 taxa)
- *Viola adunca*
- *Viola novae-angliae* (New York, Maine, and maritime Canada)
- *Viola palustris* (just reaching into Maine and New Hampshire from Canada)
- *Viola renifolia*
- *Viola selkirkii*
- *Viola suecica* (just reaching into northern Michigan and northern Minnesota from Canada)

Eastern Great Lakes (1 taxon)
- *Viola baxteri*

Great Lakes/Upper Midwest (1 taxon)
- *Viola grisea*

Appalachian Mountains (14 taxa)
- *Viola appalachiensis* (central and southern Appalachians)
- *Viola blanda* (Appalachian Mountains and adjacent uplands)
- **Viola emarginata* (*xiphophylla* variant) (Ridge and Valley of southwestern Virginia and southwestern North Carolina]
- *Viola glaberrima* (central and southern Appalachian Mountains and adjacent uplands)
- *Viola hastata*
- *Viola hirsutula* (Appalachian Mountains and adjacent uplands)
- *Viola latiuscula* (northern Appalachians, New York, and New England)
- *Viola monacanora* (Blue Ridge Mountains)
- **Viola palmata* (*avipes* variant) (Virginia Ridge and Valley)
- *Viola palmata* (*pseudostoneana* variant) (central Ridge and Valley)
- **Viola pedata* subsp. *cuneatiloba* (Shale Barrens region of mid-Atlantic states)
- *Viola rotundifolia* (Appalachian Mountains and adjacent uplands)
- **Viola tenuisecta* (in portions of adjacent Alleghany and Bath counties, Virginia)
- *Viola tripartita* (southern Appalachian Mountains, disjunct in Ohio and West Virginia)

Piedmont (3 taxa)
- *Viola emarginata sensu stricto*
- **Viola emarginata* (*phasmatifolia* variant) (Piedmont of southern Virginia and central North Carolina)
- *Viola stoneana* (around "fall line" of mid-Atlantic states, slightly disjunct in North Carolina)

Coastal Plain (6 taxa)
- *Viola brittoniana* (Atlantic Coastal Plain)
- *Viola edulis* (eastern and southern Atlantic Coastal Plain)
- [*Viola* "*impostor*" (southeastern Atlantic Coastal Plain)]
- *Viola pectinata* (Atlantic Coastal Plain)
- *Viola septemloba* (as historical record, just reaching into southeastern Virginia from southeast)
- *Viola vittata* (southeastern Coastal Plain to southeastern Virginia, slightly disjunct in Delaware and New Jersey)

Table 3. Classification of Violaceae included in this treatment. Genera and infrageneric groups represented in our region are in bold and organized alphabetically, with species within groups arranged alphabetically. Introduced taxa are denoted by an asterisk (*). Potential taxa very near our region but not yet confirmed here are included in brackets and are not numbered.

- Genus *Cubelium* Raf. ex Britton & A.Br.
  - *Cubelium concolor* (T.F.Forst.) Raf. ex Britton & A.Br.
- Genus *Pombalia* Vand.
  - *Pombalia parviflora* (L.f.) Paula-Souza*
  - [*Pombalia verticillata* (Ortega) Paula-Souza]
- Genus *Viola* (all taxa below in subgenus *Viola*)
  - Section *Chamaemelanium* Ging.
    - Canadenses group
      - *Viola canadensis* L.
      - *Viola rugulosa* Greene
    - Nudicaules group
      - *Viola eriocarpa* Schwein.
      - *Viola glaberrima* (Ging. ex Chapm.) House
      - *Viola hastata* Michx.
      - *Viola pubescens* Aiton
      - *Viola tripartita* Elliott
    - Nuttallianae group
      - *Viola nuttallii* Pursh
      - [*Viola vallicola* A.Nelson]
    - Orbiculatees group
      - *Viola rotundifolia* Michx.
  - Section *Melanium* Ging.
    - Subsection *Bracteolatae* Kupffer
      - *Viola arvensis* Murray*
      - *Viola tricolor* L.*
    - Subsection *Cleistogamae* Marcussen & Danihelka
      - *Viola rafinesquei* Greene
  - Section *Nosphinium* W.Becker
    - Subsection *Borealiamericanae* (W.Becker) Gil-ad
      - Affinis group
        - *Viola affinis* Leconte
        - [*Viola* "*impostor*"]
        - [*Viola langloisii* Greene]
        - *Viola missouriensis* Greene
      - Cucullata group
        - *Viola communis* Pollard
        - *Viola cucullata* Aiton
        - *Viola domestica* E.P.Bicknell
        - *Viola nephrophylla* Greene
        - *Viola pratincola* Greene
        - *Viola retusa* Greene
      - Edulis group
        - *Viola edulis* Spach
      - Palmata group
        - *Viola palmata* L. species complex
        - *Viola stoneana* House
      - Pedatifida group
        - *Viola brittoniana* Pollard
        - *Viola pectinata* E.P.Bicknell
        - *Viola pedatifida* G.Don
      - Sagittata group
        - *Viola emarginata* (Nutt.) Leconte species complex
        - *Viola fimbriatula* Sm.
        - *Viola sagittata* Aiton
        - *Viola septemloba* Leconte
      - Sororia group
        - *Viola grisea* (Fernald) H.E.Ballard
        - *Viola hirsutula* Brainerd
        - *Viola latiuscula* Greene
        - *Viola novae-angliae* House
        - *Viola septentrionalis* Greene species complex
        - *Viola sororia* Willd. species complex
      - Subsinuata group
        - *Viola baxteri* House
        - *Viola monacanora* J.L.Hastings & H.E.Ballard
        - *Viola subsinuata* (Greene) Greene
        - *Viola tenuisecta* Zumwalde & H.E.Ballard
      - Viarum group
        - *Viola egglestonii* Brainerd
        - *Viola viarum* Pollard
    - Subsection *Pedatae* (Pollard ex W.Becker) Bricicky ex Marcussen & H.E.Ballard
      - *Viola pedata* L.
  - Sect. *Plagiostigma* Godr.
    - Subsect. *Bilobatae* (W.Becker) W.Becker
      - *Viola arcuata* Blume*
    - Subsect. *Patellares* (Boiss.) Rouy & Foucaud
      - *Viola inconspicua* Blume*
      - *Viola japonica* Langsd. ex Ging.*
      - *Viola patrinii* DC.*
      - *Viola selkirkii* Pursh ex Goldie
    - Subsect. *Stolonosae* (Kupffer) Kupffer
      - Blandae group
        - *Viola blanda* Willd.
        - *Viola incognita* Brainerd
      - Palustres group
        - *Viola palustris* L.
        - *Viola suecica* Fr.
      - Stolonosae group
        - *Viola lanceolata* L.
        - *Viola minuscula* Greene
        - *Viola primulifolia* L.
        - *Viola renifolia* A.Gray
        - *Viola vittata* Greene
  - Section *Viola*
    - Subsection *Rostratae* (Kupffer) W.Becker
      - *Viola adunca* Sm.
      - [*Viola aduncoides* A.Löve & D.Löve]
      - *Viola appalachiensis* L.K.Henry
      - *Viola labradorica* Schrank
      - *Viola rostrata* Pursh
      - *Viola striata* Aiton
      - *Viola walteri* House
    - Subsection *Viola*
      - *Viola odorata* L.*

Keys to Violaceae

KEY A. GENERA

1. Plant acaulescent or caulescent, if caulescent then leafy nodes typically ≤ 8 per stem; leaf blades of many species about as broad as long or broader, base cordate; flowers solitary; peduncle not articulated, bearing a pair of bracteoles; sepals with basal auricles; bottom petal spurred at base, blade distinctly shorter than lateral and upper petals . . . . . *Viola*, Key C
1. Plant caulescent, leafy nodes > 10 per stem; leaf blades much longer than broad, base narrowly cuneate; flowers solitary or in few-flowered reduced cymes; peduncle/pedicel articulated, lacking bracteoles; sepals lacking basal auricles; bottom petal saccate at base, blade slightly to greatly exserted beyond lateral and upper petals 2

2(1). Stem unbranched; leaves strictly alternate; leaf blades oblanceolate, entire or with 1–2 irregular coarse teeth on either margin; flowers 1–3 in reduced cymes; corolla uniformly green; bottom petal < 1.3 × as long as others, blade slightly expanded, retuse; capsule 15–23 mm long; seeds 4.5–5.0 × 3.5–4.8 mm, subglobose, tan; native to rich mesic and lowland forests in eastern North America. . . . . *Cubelium*
2. Stem branched from base or lower nodes; upper leaves alternate and lower (sub)opposite; leaf blades narrowly linear or linear-lanceolate and entire, or lanceolate or elliptic to rhombic-lanceolate and uniformly crenate-serrate; flowers solitary; corolla white, violet, or greenish to dull yellow tinged with violet, throat yellow; bottom petal > 1.3 × as long as others, blade somewhat to very much expanded, emarginate or broadly rounded; capsule < 10 mm long; seeds < 2 mm broad, flattened, black; one species native to grasslands and desert scrub in Great Plains and North America (not yet recorded from our region), one Latin American species introduced in New Jersey and Georgia . . . . . *Pombalia*, Key B

KEY B. *POMBALIA*

1. Leaves subtending flowers or fruits much reduced; leaf blades lanceolate or elliptic to rhombic-lanceolate, margins prominently crenate-serrate; apex of bottom petal blade bilobate; native of South America, introduced to New Jersey and Georgia. . . . . 2. *Pombalia parviflora* (L.f.) Paula-Souza
1. Leaves subtending flowers or fruits not reduced; leaf blades narrowly linear to (ob)lanceolate, margins entire; apex of bottom petal broadly rounded; native of grasslands and open xeric sites, southwestern North America and Great Plains (not yet documented in our region, see "Potential Taxa"). . . . . *Pombalia verticillata* (Ortega) Paula-Souza

KEY C. *VIOLA*

1. Plant caulescent, producing aerial stems bearing leaves and flowers or capsules at nodes 2
1. Plant acaulescent, with leaves and flowers or fruits arising directly from the rootstock (yellow-flowered *V. rotundifolia* is acaulescent during spring flowering but produces a stolon-like prostrate stem with 0–1 leaf and 1–3 capsules in summer, and is inserted in Keys C and D) 3

2(1). Corolla yellow or white with a yellow throat (occasionally fading or drying to lavender), ventral surface of petals commonly pink- or purple- to brown-tinged); stipules membranous or partially to wholly herbaceous, margins entire or erose . . . . . Key D
2. Corolla cream or pale blue or multicolored (violet to purple with orange or yellow) with a yellow throat, or cream-white, pale blue, or violet to purple with a white throat, ventral surface not differently tinged; stipules herbaceous, margins fringed or deeply lobed. . . . . Key E

3(1). Plant growing from horizontal stoloniform rhizome, producing surficial or subsurficial leafy stolons especially in summer, rhizome and/or stolons < 3 mm in diameter (rhizome ≥ 3 mm in summer fruiting *V. rotundifolia*, stolons lacking in *Viola renifolia* A.Gray, stolons absent or present and with few leaves in *Viola vittata* Greene); corolla white, white tinged with violet, or violet, with greenish-white throat and mostly < 1 cm long (in *V. suecica and V. palustris*), or uniformly white or purple and > 1 cm (in *V. odorata*) . . . . . Key F
3. Plant growing from ascending to vertical thickish, occasionally branched, rhizome commonly ≥ 3 mm in diameter, lacking stolons; corolla blue or violet to purple (white with blue, blue-gray, or purple eyespot in *V. communis* f. *priceana*, white in rare albinos of various species), > 1 cm long (yellow and up to 1.4 cm in *V. rotundifolia*) . . . . . Key G

KEY D. CAULESCENT VIOLETS WITH WHITE OR YELLOW FLOWERS, AND ENTIRE OR EROSE STIPULES

1. Corolla white with a yellow center, ventral surface of petals pink- or violet-tinged, dorsal surface of aging flowers fading to pink or violet; stipules mostly membranous and occasionally deciduous, long-triangular, narrowly attenuate, entire 2
1. Corolla yellow, ventral surface of petals often brown-tinged; stipules mostly or wholly herbaceous, ovate to narrowly ovate, entire or erose 3
2(1). Plants not densely colonial, rhizome short, lacking an elongate stoloniform extension (southern Appalachian plants occasionally produce a stoloniform rhizome); foliage nearly glabrous or upper portion of stem, petioles, and lower surface of leaf blades sparsely hirtellous, peduncles glabrous; upper leaf blades long-acuminate at apex, lower subacuminate; basal leaf blades shallowly cordate; calyx glabrous and eciliate, sepals linear-lanceolate; North America east of the Great Plains . . . . . 11. *V. canadensis* L.
2. Plants commonly densely colonial, rhizome continuing in an elongate stoloniform extension that often terminates in a plantlet; foliage and peduncles moderately to densely hirtellous; upper leaf blades subacuminate to acute at apex, lower acute to obtuse; basal leaf blades deeply cordate; calyx typically hirtellous and ciliate, sepals lanceolate; western Great Lakes region, northern Great Plains and Rocky Mountains . . . . . 51. *V. rugulosa* Greene
3(1). One or more cauline leaf blades deeply 3- or 5-lobed or -divided; nectar-guide lines of chasmogamous flower extending $>$ 2/3 length of the spurred petal . . . . . 63. *V. tripartita* Elliott
3. Leaf blades unlobed; nectar-guide lines extending $\leq$ 1/2 length of spurred petal 4
4(3). Larger cauline leaf blades as broad as long or broader than long 5
4. Larger cauline leaf blades distinctly longer than broad 6
5(4). Stems (1)2–5(6), spreading to decumbent at base during chasmogamous flowering or occasionally strongly ascending to erect in chasmogamous flower (especially in plants with few stems), becoming erect in fruit; basal leaves usually 1–3 per stem, uncommonly none; all nodes with fully developed leaves or infrequently the lowest node leafless, the 4–5 cauline leaves distributed over 1/2–4/5 of the stem; larger cauline leaf blades ovate to triangular-ovate, shallowly to moderately cordate at base, narrowly acute to abruptly acuminate at apex, the uppermost fully expanded leaf blade (typically at the second node) bearing 5–15 marginal teeth per side; foliage usually medium green, glabrous to moderately hirtellous on upper portion of stems and leaves, peduncles glabrous or uncommonly sparsely hirtellous; stipules highly variable, lanceolate to ovate, often cordate-auriculate on outer side; widely distributed over eastern North America . . . . 18. *V. eriocarpa* Schwein.
5. Stems 1(2), erect; basal leaves none (very rarely 1) per stem; lowest 1–2 nodes leafless, the 2–3 cauline leaves clustered in the upper 1/5–1/3 of the stem; larger cauline leaf blades broadly ovate or broadly deltate-ovate to (deltate-)reniform, broadly cuneate to truncate at base, abruptly acute or subacuminate (in chasmogamous flower) to broadly obtuse (in fruit) at apex, the uppermost fully expanded leaf blade (typically at the second node) bearing 13–26 marginal teeth per side; foliage gray-green, stems (at least in upper portion), leaves and peduncles densely spreading-hirsute; stipules broadly ovate, rarely ovate-lanceolate, cuneate at base on both sides; restricted to Applachian Mountains and associated uplands, Northeast and Great Lakes region . . . . . 45. *V. pubescens* Aiton
6(4). Rhizome whitish; leaf blades hastate, base subcordate to deeply cordate with basal lobes parallel or divergent; upper surface of leaf blades in living material frequently bicolorous, silvery-green between the contrasting darker green veins . . . . . 22. *Viola hastata* Michx.
6. Rhizome brown; leaf blades lanceolate, ovate- or rhombic-lanceolate, to narrowly ovate, base truncate, rounded or cuneate; leaf blade surfaces uniformly gray-green or green 7
7(6). Foliage green; leaf blades narrowly ovate or lance-triangular to rhombic-lanceolate, margins crenate-serrate; forests of eastern North America . . . . . 20. *V. glaberrima* (Ging. ex Chapm.) House
7. Foliage gray-green; leaf blades linear-lanceolate to narrowly ovate, margins subentire; grasslands and desert scrub of Great Plains and western North America 8
8(7). Largest leaf blades linear-lanceolate to lanceolate, $\geq 3.5\times$ as long as wide, base narrowly cuneate; just entering our range in Minnesota from the Great Plains . . . . . 35. *V. nuttallii* Pursh
8. Largest leaf blades narrowly ovate or elliptical, $< 2.6\times$ as long as wide, base broadly cuneate to truncate (not yet documented in our region, see "Potential Taxa") . . . . . *V. vallicola* A.Nelson

KEY E. CAULESCENT VIOLETS WITH WHITISH TO PALE BLUE, VIOLET, PURPLE OR MULTICOLORED FLOWERS, AND FRINGED OR LOBED STIPULES

1. Corolla strongly frontally flattened in living material; petals cream or pale blue to purple, red to orange or multicolored with yellow throat; spur short, up to 3 mm long; stipules deeply pinnately lobed with few to many lateral segments, the terminal lobe resembling the leaf blades; leaf blades linear-lanceolate to elliptical, base cuneate to truncate; plants annual or biennial, with slender rootstock 2
1. Corolla not strongly frontally flattened in living material; petals cream, pale blue, or violet to purple with white throat; spur longer, 3–20 mm long; stipules subentire to irregularly lacerate or laciniate but not deeply lobed with leaf-like terminal lobe; leaf blades ovate to reniform, base cordate; plants perennial, with thickish rootstock 5
2(1). Petals shorter than the sepals or scarcely surpassing them by 1–2 mm, cream-white; sepals nearly or fully concealing capsule; native of Eurasia, sparingly cultivated but introduced widely . . . . . 7. *V. arvensis* Murray
2. Petals well surpassing sepals, pale blue to violet (infrequently cream-white) or multicolored; sepals neither surpassing nor concealing capsule 3
3(2). Leaves all cauline; petals pale blue to violet or cream-white; terminal lobe of stipules slightly larger than lateral lobes, similar in shape, with 0–3 crenations per margin; quadrate stems recurved-puberulent or -hispidulous on face directly above a leaf node but essentially glabrous on the other faces; capsules $<$ 6 mm; seeds 1.2–1.5 $\times$ 0.6–0.8 mm; cleistogamous flowers produced; native of diverse situations, especially in alkaline floodplains . . . . . 46. *V. rafinesquei* Greene
3. Leaves cauline and basal; petals variously colored, distal half of upper pair of petals purple-black or borders of all petals black; terminal lobe of stipules much larger and differently shaped than lateral lobes, with (2–)4 or more crenations per margin; quadrate stems recurved-puberulent on the angles or glabrous; capsules 6–10 mm long; seeds 1.4–1.7 $\times$ 0.8–0.9 mm; cleistogamous flowers lacking; cultivated plants of abandoned homesteads, roadsides, and cemeteries 4
4(3). Flowers $\leq$ 1.5 cm long; corolla commonly with lower 3 petals cream-white or with yellow, and upper 2 violet, reddish-purple, purple or purple-black at least in distal half; native of Eurasia, widely cultivated and escaped . . . . . 62. *V. tricolor* L.
4. Flowers $>$ 1.5 cm long; all petals variously colored, often with broad black border; barely persistent following cultivation (see 62. *V. tricolor*) . . *V.* ×*wittrockiana* Gams ex Nauenb. & Buttler
5(1). Plants mat-forming, the current year's stems ascending at chasmogamous flowering time and persistent through winter to become prostrate and root at the nodes 6
5. Plants not mat-forming, the current year's stems ascending to erect at chasmogamous flowering time through fruiting, deciduous through winter (basal portion of stems occasionally rooting at the nodes in rare introduced *Viola arcuata* Blume) 7
6(5). Foliage glabrous except for small scattered subappressed hairs on upper surface of leaf blades (especially near the margins), peduncles and stems glabrous; upper surface of leaf blades uniformly green; stipules weakly lacerate, with marginal processes $<$ 1/4 as long as the stipule; moist loam of riverbanks and lawns, northern and central Appalachians, Pennsylvania, Maryland, and West Virginia, disjunct in western North Carolina . . . . . 5. *V. appalachiensis* L.K.Henry
6. Foliage, peduncles, and stems densely puberulent; upper surface of leaf blades silvery- to gray-green with darker green veins; stipules deeply laciniate with marginal processes $>$ 1/2 as long as the stipule; sandy loam, commonly on dolomite ledges in dry-mesic and mesic forests in the northern part of the range and under dry oak-pine forests southward, southeastern USA and sporadic northward into the central Appalachians, Western Allegheny Plateau, and Interior Lowland Plateau . . . . . 66. *V. walteri* House
7(5). Corolla pale violet with purple-black eyespot surrounding throat formed by dense and coalescing nectar-guide lines; spur 10–15 mm, as long as to longer than blade of bottom petal; all petals glabrous; stipules oblong- to linear-lanceolate, $>$ 3 $\times$ as long as broad, weakly lacerate; margins of leaf blade remotely crenate-serrate . . . . . 49. *V. rostrata* Pursh
7. Corolla blue to purple, or white to cream-white, nectarguide-lines fine and inconspicuous (dense, extensive and blackish nectar-guide lines on spurred petal in *V. arcuata*), lacking a dark eyespot; spur short or elongate but distinctly shorter than blade of bottom petal; lateral petals bearded;

stipules lanceolate to ovate, < 3 × as long as broad, weakly to strongly lacerate or laciniate; margins of leaf blades closely crenulate, crenate or subentire 8

8(7). Corolla white (rarely pale violet), spurred petal with extensive dense nectar-guide lines; spur short, 1–2 mm; cauline leaf blades broader than long, ovate- to deltate-reniform; stipules subentire or minutely toothed; native of temperate eastern and tropical Asia, introduced to New Jersey and New York . . . . . 6. *V. arcuata* Blume

8. Corolla cream-white, blue or purple, spurred petal with few fine inconspicuous nectar-guide lines ; spur moderately short to elongate, 3–7 mm; cauline leaves longer than broad to broader than long but not deltate; stipules weakly to strongly lacerate or fimbriate 9

9(8). Corolla cream-white; calyx ciliate; auricles prominent and quadrate; margins of leaf blades closely crenulate; stipules strongly lacerate to fimbriate . . . . . 58. *V. striata* Aiton

9. Corolla blue to purple; calyx eciliate (midvein of sepals occasionally puberulent in *V. adunca*); auricles short and rounded; margins of leaf blade subentire, rounded-dentate or (sub)crenate; stipules minutely toothed or lacerate to strongly laciniate 10

10(9). Foliage, stems, and peduncles puberulent (very rarely glabrous in boreal populations); margins of leaf blades subentire to subcrenate, commonly revolute; stipules strongly laciniate 11

10. Foliage glabrous except for small scattered subappressed hairs on upper and/or lower surface of leaf blades; stems and peduncles glabrous; stipules subentire to weakly lacerate . . . . . 27. *V. labradorica* Schrank

11(10). Style abruptly expanding just below head; projections on head (when present) commonly dense, narrowly cylindrical, their length up to 1/6 the width of the style head, tip below stigmatic orifice abruptly bent upward at 90°; hairs of foliage and peduncle (when present) up to 0.3 mm long; guard cells 22–30 μm long; pollen grains 3.2–4.6 μm in diameter; transcontinental, north and east of Lake Superior in the Great Lakes and Northeast, mostly south of the US-Canadian border in the West . . . . . 3. *V. adunca* Sm.

11. Style uniformly cylindrical or gradually expanding to head; projections on head (when present) sparse, conical or globular, their length up to 1/10 the width of the style head, tip below stigmatic orifice gradually bent upward at 45°; hairs of foliage and peduncle (when present) up to 0.22 mm long; guard cells 25–36 μm long; pollen grains 4.1–4.9 μm in diameter; virtually restricted to central and western Canada, from northern shore of Lake Superior west to Yukon and Vancouver Island, British Columbia (not yet documented in our region, see "Potential Taxa") . . . . . *V. aduncoides* A.Löve & D.Löve

Key F. Acaulescent Violets with Horizontal Stoloniform Rhizomes and/or Stolons (Stolons Lacking in *V. renifolia*, Commonly Lacking in *V. vittata*), and White or Purple Flowers (Yellow-Flowered *V. rotundifolia* is Included Here in its Summer Fruiting State, its Prostrate Stems Often Misinterpreted as a Stolon)

1. Corolla violet (often white in *V. odorata*); flower > 1 cm long; plant forming a distinct rosette and producing greenish leafless nonreproductive stolons terminating in a plantlet, or plant not forming a distinct rosette but growing from a creeping rhizome with lateral stolons, the leaves inserted individually along the length of the rhizome and stolons near the apex (flowers and fruits arising from the leaf axils); leaf blades orbiculate to reniform 2

1. Corolla white; flower mostly ≤ 1 cm long; plant forming a distinct rosette and producing leafy summer stolons with leaves and cleistogamous fruits along their length (stolons lacking in *V. renifolia*, stolons leafless and nonreproductive but terminating in a plantlet in *V. incognita*, stolons commonly lacking or nonreproductive with few leaves in *V. vittata*); leaves narrowly linear to reniform 4

2(1). Plant rosulate, growing from vertical or stoloniform rhizome with pale to greenish subherbaceous stipules, producing leafless and nonreproductive, greenish, cordlike stolons; foliage puberulent; corolla white or violet; style of chasmogamous flower with a pronounced downward-pointing hook; cleistogamous capsule purple-spotted or blotched, hirtellous; native of Eurasia, widely cultivated and also escaped to lawns, roadsides and urban woodlots. . . . . 36. *V. odorata* L.

2. Plant growing from a creeping pale, occasionally branching, rhizome with pink or brownish membranous stipules, producing leaves, flowers, and capsules along its length; foliage essentially

glabrous; style of chasmogamous flower lacking a pronounced downward-pointing hook; cleistogamous capsule unspotted, glabrous; natives of bogs and sedge meadows in arctic and boreal North America, south to Maine, Vermont, Michigan, and Minnesota; Colorado, Arizona, and northern California 3

3(2). Leaves during chasmogamous flower 2–5, blades 25–50 mm long, glabrous; bracts positioned at or below middle of peduncle; lateral petals glabrous within; spur *ca*. 2.0 mm long, 1.5 × as long as auricles; style and stamen appendages weakly exserted and scarcely visible in living material; seeds very dark brown to black, unspotted; southward from eastern Canada in our region to Maine and New Hampshire . . . . . 38. *V. palustris* L.

3. Leaves during chasmogamous flower 1–2, blades 8–25 mm long during chasmogamous flower, glabrous or lower surface with fine hairs along proximal veins; bracts positioned above the middle, often near the apex of the peduncle; lateral petals sparsely bearded within; spur *ca*. 1.5 mm long, 2–3 × as long as auricles; style and stamen appendages prominently exserted and fully visible in living material; seeds dark gray to olive-green, blotched; southward from eastern Canada in our region to Michigan and Minnesota. . . . . 60. *V. suecica* Fr.

4(1). Leaf blades distinctly longer than broad (1.5–15 × as long as broad), ovate-lanceolate to ovate-triangular, or lanceolate to linear 5

4. Leaf blades usually as broad as long or broader than long (< 1.2 × as long as broad), ovate or orbiculate to reniform. 7

5(4). Largest leaf blades ovate-lanceolate to ovate-triangular, 1.5–2 × as long as broad, base broadly rounded to subcordate . . . . . 44. *Viola primulifolia* L.

5. Largest leaf blades lanceolate to linear-lanceolate in early chasmogamous flower, narrowly lanceolate to linear in fruit, 3–15 × as long as broad, base cuneate 6

6(5). Largest leaf blades narrowly elliptical to lanceolate, 3–6(8) × as long as broad, (5)7–29 mm broad, abruptly tapering to the petiole; gland of marginal teeth appressed to incurved, margins appearing subentire, low-serrate or shallowly (sub)crenate; summer plants producing surficial leafy stolons with 1–few cleistogamous capsules in the leaf axils; lowest sepals of chasmogamous flowers narrowly triangular to ovate-triangular, acuminate; foliage glabrous (rarely sparsely hirtellous in extreme southern populations); seeds obovoid, 1.1–1.4 × 0.8–1.0 mm, dark olive-brown; widespread in northeastern and central North America but absent from the extreme southeast Atlantic Coastal and Gulf Coastal Plains . . . . . 28. *V. lanceolata* L.

6. Largest leaf blades linear to linear-lanceolate, 8–15 × as long as broad, (2)4–9(13) mm broad, tapering gradually to the petiole; gland of marginal teeth ascending to spreading, margins commonly appearing denticulate; summer plants rarely producing surficial stolons, if present these leafless and nonreproductive (occasionally terminating in a plantlet); lowest sepals of chasmogamous flowers linear-lanceolate to lance-triangular, acuminate to attenuate; foliage glabrous to moderately hirtellous; seeds 1.0–1.2 × 0.7–0.9 mm, broadly obovoid, dull gray-brown; central and southern Atlantic and Gulf Coastal Plains. . . . . 65. *V. vittata* Greene

7(4). Plant growing from a vertical twisted rhizome, lacking stolons; leaf blades broadly ovate or suborbiculate to reniform, widely spreading or more often prostrate on the substrate in living material, especially during fruit, either glabrous or wholly densely hirsute or one or both leaf blade surfaces densely hirsute; lateral petals beardless (rarely sparsely bearded) within; cleistogamous capsule purple-spotted, on short prostrate peduncle; seeds orange-brown to brown . . . . . 47. *V. renifolia* A.Gray

7. Plant growing from a horizontal stoloniform rhizome, producing surficial or subsurficial stolons especially during summer fruit (rhizome vertical and "stolon" a horizontal surficial stem in *V. rotundifolia*); leaf blades elevated and spreading in living material, glabrous to variously pubescent (prostrate on the substrate in living material, especially during fruit, in *V. rotundifolia*); lateral petals beardless or bearded; cleistogamous capsule unspotted on erect peduncle, or purple-spotted to blotched on prostrate peduncle; seeds tan or medium to dark brown or blackish-brown 8

8(7). Rhizome vertical, ≥ 3 mm in diameter; leaf blades thickish in living material, broadly elliptical to orbiculate; stipules entire along margins; stolon-like summer stem(s) bearing 0–1 leaf and terminating in a reduced cyme of 1–3 purple-spotted or blotched cleistogamous capsules; seeds ivory to light orange-brown . . . . . 50. *V. rotundifolia* Michx., in part

8. Rhizome horizontal and stoloniform, < 3 mm in diameter; leaf blades thin in living material, variously shaped; stipules glandular-fringed along margins; stolons leafless or bearing leaves and/

or cleistogamous capsules at nodes along their length, occasionally terminating in a plantlet; cleistogamous capsules unspotted or spotted to blotched; seeds light brown to olive-brown or blackish 9

9(8). Leaf blades uniformly green on both surfaces (lower surface occasionally drying orange-tinged), glabrous (petioles may be glabrous or pubescent), orbiculate, mostly broadly rounded at apex, margins subentire to shallowly crenate; cleistogamous capsules green, unspotted, on erect peduncles; seeds 0.8–1.4 × 0.7–0.8 mm, medium to dark olive-brown or brownish-black, with minute black spots. . . . . 30. *Viola minuscula* Greene

9. At least some leaf blades broader than long, bicolorous with darker green upper surface and paler lower surface, usually pubescent on one or both surfaces, obtuse to acute (acuminate) at apex, blade margins most often shallowly serrate; cleistogamous capsules with dense fine purple spots, on prostrate to arching peduncles; seeds 1.2–2.2 × 0.7–1.3 mm, brown or brownish-blackish, unspotted 10

10(9). Leaves glabrous except for scattered appressed hairs on upper surface of leaf blades, peduncles glabrous; largest leaf blades with proportionally short basal lobes < 1/4 of total length of blade, sinus narrow with inner edges of basal lobes attingent or overlapping in living material, acute at apex, margins shallowly crenate; petioles and peduncles commonly red-tinged or -spotted; all petals glabrous; cleistogamous capsules 6.5–8 mm long; seeds 1.2–1.3 × 0.7–0.8 mm, brownish-black; primarily Appalachian Mountains and adjacent uplands, common at higher elevations . . . . . 9. *V. blanda* Willd.

10. Petioles and/or one or both surfaces of leaf blades glabrous or sparsely to densely hirsute, peduncles glabrous to hirsute; largest leaf blades with proportionally longer basal lobes > (1/4–)1/3 of total length of blade, sinus broad with basal lobes well separated or divergent in living material, typically obtuse to rounded at apex, margins low-serrate with noticeable teeth (check at widest point of leaf); petioles and peduncles not red-tinged or -spotted; lateral petals bearded; cleistogamous capsules 7–14 mm long; seeds 1.6–2.2 × 1.0–1.3 mm, light to medium brown; widely distributed in Appalachians, Northeast and Great Lakes regions, in central and southern Appalachians most common at lower elevations. . . . . 24. *V. incognita* Brainerd

KEY G. ACAULESCENT VIOLETS LACKING STOLONS, WITH BLUE OR VIOLET TO PURPLE FLOWERS (YELLOW IN *V. ROTUNDIFOLIA*, WHITE OR WEAKLY VIOLET-TINGED IN *V. PATRINII*, WHITE WITH BROAD BLUE, BLUE-GRAY, OR PURPLE EYESPOT IN *V. COMMUNIS* F. *PRICEANA*)

1. Corolla yellow; leaf blades broadly elliptical to orbiculate, nearly or completely prostrate on substrate, especially during fruit . . . . . 50. *V. rotundifolia* Michx., in part

1. Corolla blue or violet to purple (white with broad blue, blue-gray, or purple eyespot in *V. communis* f. *priceana*, rarely white in sporadic albinos of various species); leaf blades various (commonly prostrate on substrate during fruit in *Viola hirsutula* Brainerd, at least the outer leaves prostrate in *V. fimbriatula*) 2

2(1). At least the largest leaf blades notched, incised, coarsely toothed, lobed or dissected, or bearing linear marginal processes. 3

2. All leaf blades undivided, margins merely crenate or serrate (pectinately serrate in *Viola pectinata* E.P.Bicknell; occasional *V. edulis* in early chasmogamous flower without lobed leaf blades may key to *Viola langloisii* Greene just south of our range but has ovate-triangular sepals acuminate from the middle and shorter broader auricles < 2 mm long). 27

3(2). All petals glabrous within; corolla concolorous blue or lower 3 petals blue and upper pair purple-black; stipules long-adnate to petiole; rhizome erect, barrel-like; cleistogamous flowers absent; dry sandy, gravelly, or rocky soils in oak or oak-pine forests, barrens and sand prairies, and slopes 4

3. Lateral petals bearded within, occasionally the spurred petal also; corolla concolorous except for expanded white area from the throat in a few species; stipules free; rhizome horizontal or ascending, occasionally branching, not barrel-like; cleistogamous flowers produced; diverse substrates and habitats. 5

4(3). Largest leaf blades deeply "triternately" dissected, with secondary divisions on each primary lobe deeply divided into multiple crowded narrowly linear ultimate segments; endemic to Shale Barrens region, southwestern New Jersey and Pennsylvania to Virginia and eastern West Virginia . . . . . 41a. *V. pedata* L. subsp. *cuneatiloba* (Brainerd ex Fernald) H.E.Ballard

4. Largest leaf blades deeply pedately divided, with primary lobes undivided or with a short subapical tooth on one or both sides (blades rarely obrhombic or obovate with 1–2 shallow apical crenations or short broadly rounded lobes due to partial fusion of leaf segments); widespread in eastern North America . . . . . .41b. *V. pedata* L. subsp. *pedata*

5(3). Plant homophyllous, all blades lobed or dissected (plants with largest leaf blades shallowly lobed are frequent where *V. sororia* and other species with unlobed leaf blades are locally sympatric with species producing deeply divided leaves and are *de novo* hybrids; they will not key readily and must be inferred by association with the parent species) 6

5. Plant heterophyllous, producing leaf blades with lobes, coarse teeth, or incisions during chasmogamous flowering and cleistogamous fruiting, and undivided leaf blades in very early spring and late autumn (often retaining one or more undivided blades) 11

6(5). Petioles glabrous, leaf blades sparsely appressed-hirtellous on veins, margins appressed-ciliolate; spurred petal densely bearded; lowest sepals lanceolate, sharply acute; auricles prominent, elongating in fruit to 6 mm; cleistogamous capsules green drying tan, unspotted, on erect peduncles nearly or fully as long as petioles; seeds 1.3–2.0 × 0.9–1.3 mm, narrowly obovoid, medium brown to orange-brown, unspotted 7

6. Foliage glabrous, or petioles and at least lower surface of leaf blades hirsute, margins often ciliate; spurred petal glabrous; lowest sepals oblong to ovate, obtuse to rounded at apex (lance- to ovate-triangular and acuminate in *V. monacanora*); auricles short and rounded, not elongating in fruit; cleistogamous capsules purple-spotted, on prostrate or arching peduncles shorter than petioles; seeds 1.6–2.4 × 1.1–1.7 mm, various but not medium brown to orange-brown, mostly spotted or blotched 8

7(6). Largest leaf blades narrowly to broadly ovate in outline, base subtruncate to cordate, biternately divided into 7 or 9 ultimate lanceolate segments, terminal ultimate segment of terminal primary division commonly distinctly broader and well surpassing lateral segments; sepals eciliate (auricles infrequently irregularly ciliolate); seeds 1.3–1.9 × 0.9–1.3 mm; moist to wet sandy or peaty soils of brackish marshes, banks of streams and rivers, ditches along fields and in meadows, and forest clearings, Atlantic Coastal Plain . . . . . 10. *V. brittoniana* Pollard

7. Largest leaf blades reniform in outline, base broadly rounded to subcordate, triternately divided into (13)17–25 narrowly linear ultimate segments, terminal ultimate segment of terminal primary division neither distinctly broader nor longer than lateral segments; calyx usually ciliate; seeds 1.7–2.0 × 1.1–1.3 mm; rich mesic loam of blacksoil prairies and savanna openings in the Midwest to the Great Plains and southwestern North America, slightly disjunct in southern Ontario and northern Ohio. . . . . 42. *V. pedatifida* G.Don

8(6). Foliage glabrous (petioles uncommonly sparsely hirsute in *V. monacanora*); calyx eciliate; lowest sepals acuminate; montane North Carolina and Virginia 9

8. Foliage moderately to densely hirsute; calyx ciliate; lowest sepals ovate-lanceolate to broadly ovate, obtuse to broadly rounded (occasionally acute in *Viola baxteri* House). 10

9(8). Largest leaf blades during chasmogamous flower narrowly ovate-triangular and palmatifid to subbiternate, blades in fruit ovate, biternately divided into 9–11(13) usually slightly falcate ultimate lobes, these becoming asymmetrically angulate at apex in fruit, outer margins of lobes with 1–3 incurved teeth, primary divisions not narrowed or constricted at base; lower surface of leaf blade not distinctly paler than upper, purple-tinged; lowest sepals lance- to ovate-triangular, acute or acuminate; seeds 1.8–2.1 × 1.2–1.4, blackish with minute raised black reticulations; moist loam soils in rich mesic rocky woodlands in the Blue Ridge Mountains of western Virginia and northwestern North Carolina . . . . . 32. *V. monacanora* J.L.Hastings & H.E.Ballard

9. Largest leaf blades during chasmogamous flower ovate and deeply bi- to subtriternately divided, blades in fruit orbiculate to reniform and tri- to tetraternately dissected into 17–27 narrowly linear ultimate lobes, these narrowly rounded at apex, margins entire or with a minute subapical tooth on either margin, primary divisions distinctly constricted at base into a very slender elongate "petiolule"; lower surface of blade distinctly paler than upper, not purple-tinged; lowest

sepals ovate-lanceolate to narrowly ovate, broadly acute to obtuse; seeds 1.7–2.4 × 1.1–1.5 mm, gray, gray-brown, or light to medium (reddish-)brown, unspotted or with sparse to dense minute raised black spots; dry sandy shale-derived soils of woodland borders surrounding shale barrens in Allegany and Bath counties, Virginia . . . . . 61. *V. tenuisecta* Zumwalde & H.E.Ballard

10(8). Largest leaf blades biternately to subtriternately divided into 9–13(15) narrowly linear-lanceolate lobes < 3 mm wide (in chasmogamous flower), the lateral second-order lobes of the terminal primary division attached medially, second-order lobes usually with a prominent slender spreading sharply acute tooth or short lobe on each side; primary divisions commonly narrowed at base to slender "petiolules"; foliage and peduncles not purple-tinged; lowest sepals acute or obtuse; seeds ivory, unspotted, or occasionally with small weak light brown blotches or streaks; limestone prairies and prairie-like openings; lower elevations in eastern Great Lakes region, western New York to southwestern Ontario and southeastern Michigan, south to southwestern Pennsylvania, southwestern Ohio, and northeastern Indiana . . . . . 8. *V. baxteri* House

10. Largest leaf blades (sub)biternately divided into 7 or 9 broadly linear or lanceolate lobes > 3 mm wide (in chasmogamous flower), the second-order lobes of the terminal primary division attached medially or basally, second-order lobes entire or with 1–2 inconspicuous short appressed or incurved teeth on each side; primary divisions not distinctly narrowed at base; lower surface of leaf blades, petioles, and peduncles often purple-tinged; lowest sepals obtuse to rounded; seeds light brown with small prominent dark orange-brown streaks, or light to medium gray with small prominent darker gray blotches or streaks; dry-mesic woodlands, not consistently associated with limestone; widely distributed in Appalachian Mountains (almost exclusively Ridge and Valley province in central Appalachians), northeastern and southeastern Piedmont, Interior Lowland Plateau southward, Massachusetts and Vermont to New York, south to northern Georgia and western Tennessee . . . . . 59. *Viola subsinuata* (Greene) Greene

11(5). At least some petioles prominently winged; lowest sepals linear-lanceolate to lance-triangular, acuminate; spurred petal bearded within; cleistogamous capsule unspotted, on erect peduncle (declined in *V. fimbriatula*); auricles prominent, elongating in fruit to 3 mm or more; in dry acidic sandy or gravelly soils in oak or oak-pine forests, barrens, and forest borders, in the Atlantic Coastal Plain and Piedmont, Appalachian Mountains and southern Great Lakes regions 12

11. Petioles not winged; lowest sepals lanceolate to (more commonly) ovate-lanceolate, oblong or ovate, acuminate to rounded; spurred petal glabrous or bearded within; cleistogamous capsule unspotted or purple-spotted or -blotched, on erect or declined to prostrate peduncle; auricles short and rounded or prominent, remaining short or weakly to strongly elongating in fruit; in diverse substrates and habitats, in various places in our region 15

12(11). Foliage densely hirtellous, uniform green; at least the outer leaves widely spreading or prostrate on the substrate in living material; petioles shorter than (in chasmogamous flower) to 2 × longer (in fruit) than blades; largest leaf blades broadly elliptical to narrowly oblong-ovate or narrowly ovate-triangular in outline, in fruit developing 1–2(3) coarse apically oriented teeth at base on each side; peduncle hirtellous; calyx ciliate; corolla purple, petals broadly rounded, spurred petal not medially compressed; peduncle of cleistogamous capsule declined; seeds 1.4–1.9 × 0.9–1.3 mm, medium to dark brown or gray-brown, unspotted or with small weak darker blotches . . . . . 19. *V. fimbriatula* Sm., in part

12. Foliage glabrous or surfaces of leaf blades sparsely appressed-hirsute, blue-green, lower surface of blades, petioles, and peduncles tinged with purple; leaves erect in living material; petioles > 2 × as long as leaf blades; largest leaf blades either with terminal division long and narrowly linear to oblong-linear and 2–4 elongate linear lobes or processes at the base or distributed along the margin on each side, or ovate- or lance-triangular with 1–3 short broadly triangular basal lobes on each side; peduncle glabrous; calyx eciliate; corolla violet, petals commonly emarginate, spurred petal commonly medially compressed; peduncle of cleistogamous capsule erect; seeds 1.4–2.2 × 0.9–1.5 mm, pinkish-gray to dark gray with prominent darker streaks and spots 13

13(12). Largest leaf blades with terminal primary division ovate- to lance-triangular, with 1–3 short broadly triangular basal lobes on each side; Atlantic Coastal Plain in the northern portion of its range, the upper Atlantic Coastal Plain and Piedmont in Virginia and the Carolinas, Massachusetts south to Georgia . . . . . 17a. *V. emarginata sensu stricto*,) in part

13. Largest leaf blades either with terminal division long and narrowly linear to oblong-linear and 2–4 elongate linear lobes or processes at the base or distributed along the margin on each side; Piedmont and Appalachian Mountains in southern Virginia to western South Carolina 14

14(13). Largest leaf blades resembling a walkingstick insect (*e.g.*, *Diapheromera femorata* (Say)), each side with 2–4 long slender variously bent processes distributed along its length; south-central Virginia and central North Carolina . . . . . 17c. *V. emarginata* (*phasmatifolia* variant)

14. Largest leaf blades resembling a sword, each side with 1–2 long slender spreading falcate-linear processes at the base, occasionally with an additional process on one side a little above the base; bimodal and sporadic in the Appalachian Mountains, southwestern Virginia, and southwestern North Carolina and adjacent northwestern South Carolina .17d. *V. emarginata* (*xiphophylla* variant)

15(11). Largest leaf blades distinctly longer than broad (blade length:width ratio $\geq$ 1.3) 16

15. Largest leaf blades slightly longer than broad to broader than long (blade length:width ratio $<$ 1.3) 18

16(15). Leaves erect in living material; leaf blades narrowly elliptical or ovate-lanceolate with small basal teeth or lobes during chasmogamous flower, sagittate or lance-triangular with larger slender basal teeth or linear-falcate lobes during fruit, teeth or lobes $\leq$ 1/4 length of the midrib; foliage glabrous or (more commonly) sparsely to moderately hirtellous; lowest sepals linear-lanceolate to lance-triangular; spurred petal densely bearded within; inhabiting upland or wetland sites in dry to seasonally moist acidic sandy soils in sand prairies and oak barrens, interdunal swales, and lakeshores; widespread throughout much of eastern North America, mostly absent from Atlantic and Gulf Coastal Plains . . . . . 53. *V. sagittata* Aiton, in part

16. Leaves erect or widely spreading in living material; leaf blades narrowly ovate-triangular to narrowly ovate or broadly oblong-lanceolate, lateral lobes short and angulate during chasmogamous flower but elongating to $\geq$ 1/4 length of the midrib in fruit (in *V. edulis*), or variously short and elliptical or longer and linear and $\geq$ 1/4 length of the midrib (in *Viola viarum* Pollard); foliage glabrous; lowest sepals linear-lanceolate to ovate-triangular; spurred petal glabrous or sparsely bearded within; inhabiting diverse substrates of bottomland sites along streams and rivers of the Atlantic Coast or central and lower Midwest 17

17(16). Leaves widely spreading in living material; leaf blades narrowly ovate-triangular, lateral lobes short and angulate during chasmogamous flower and elongating during fruit; lowest sepals ovate-triangular; spurred petal glabrous within; inhabiting floodplains of streams and rivers along the Atlantic and Gulf Coastal Plains . . . . . 15. *V. edulis* Spach, in part

17. Leaves ascending to erect in living material; leaf blades ovate-triangular to narrowly ovate, slender lateral lobes already 1/4–1/2 midrib length during chasmogamous flower; lowest sepals linear-lanceolate to lanceolate; spurred petal sparsely bearded within; inhabiting thin alluvial soils amid limestone gravel or rubble or cracks in limestone bedrock along streams and rivers, mainly in the northern Ozarks and Missouri River drainage of the central and lower Midwest, east to northern Illinois and north to southeastern South Dakota. . . . 64. *V. viarum* Pollard, in part

18(15). Foliage glabrate to hirsute (occasionally essentially glabrous in *Viola stoneana* House); peduncles glabrous or sparsely to moderately hirsute; calyx eciliate or ciliate; lowest sepals linear-lanceolate to ovate, acuminate to rounded; auricles short and rounded and not elongating in fruit (prominent and weakly elongating in fruit in *V. stoneana*); cleistogamous capsule finely to heavily purple-spotted or -blotched, on initially prostrate peduncle arching upward just before dehiscence, peduncle much shorter than petioles (peduncle ascending to erect and as long as to longer than shorter petioles in *V. stoneana*) 19

18. Foliage glabrous; peduncles glabrous; calyx eciliate, lowest sepals acute or acuminate (calyx occasionally ciliate, sepals obtuse to rounded in *V. egglestonii sensu stricto*); auricles short and not elongating in fruit, or prominent and elongating in fruit; cleistogamous capsule unspotted or finely to heavily spotted or blotched with red, reddish-purple, or purple, on erect or suberect peduncle, peduncle as long as to longer than shorter petioles (prostrate or arching upward or ascending, much shorter than petioles in *V. egglestonii sensu stricto* and *V. egglestonii* [Canada variant]) 23

19(18). Largest lobed leaf blades biternately divided, the terminal primary division bearing lateral lobes (veins of these lateral lobes will connect with the midrib or with veins of the terminal primary division) 20

19. Largest lobed leaf blades pedately divided, the terminal primary division lacking lateral lobes (any shorter intermediary lobes between the terminal and lateral primary divisions will have veins connecting to the veins of the lateral primary divisions) 21

20(19). Central and lateral lobes of terminal primary division linear-lanceolate to lanceolate, lateral lobes inserted at or just above the base of the central lobe, strongly ascending; base of primary divisions not or only weakly constricted to a long slender "petiolule"; petioles and lower surface of leaf blades sparsely to densely hirtellous or hirsute, margins of blades ciliate; chasmogamous and cleistogamous peduncles glabrous or hirsute; calyx ciliate; lowest sepals relatively short, lanceolate or lance-triangular to ovate, acuminate to obtuse or rounded; seeds pale golden-yellow or tan to light red-brown with small weak or prominent streaks and blotches; Ridge and Valley province of the Appalachian Mountains, southern Pennsylvania south to North Carolina and eastern Tennessee . . . . . 37d. *V. palmata* (*pseudostoneana* variant)

20. Central and lateral lobes of terminal primary division rhombic-lanceolate, lateral lobes inserted well above the base of the central lobe, widely divergent; base of terminal and lateral primary divisions usually constricted to a long slender "petiolule"; foliage essentially glabrous, or petioles and lower surface of leaf blades sparsely hirsute and margins of blades sparsely ciliolate; chasmogamous and cleistogamous peduncles glabrous; calyx eciliate; lowest sepals lance-triangular, acuminate; seeds ivory to tan or light gray-brown, unspotted or with weak brown rectangular blotches; rich mesic forests along "fall line" between lower Piedmont and upper Atlantic Coastal Plain, New Jersey south to central Virginia, disjunct in east-central North Carolina . . . . . 57. *V. stoneana* House

21(19). Larger leaf blades shallowly to moderately divided into 3 or 5 lobes, central lobe of terminal primary division narrowly ovate or ovate-triangular, significantly larger than lateral primary lobes or intermediary lobes between terminal and lateral primary divisions, primary divisions separated by sinuses not usually $>$ 2/3 the distance to petiole summit (shallowly lobed plants in the range of *V. palmata* var. *dilatata* are probable *de novo* hybrids with *V. sororia* and other species with unlobed leaf blades); peduncles essentially glabrous or sparsely hirsute; northeastern USA and southern Ontario southward into the southern Appalachian Mountains and associated uplands, mostly absent from Lower Piedmont and southeastrn Atlantic Coastal Plain, the southern limit in the Gulf States and Lower Midwest unclear . . . . . 37b. *V. palmata* L. var. *triloba* (Schwein.) Ging.

21. Larger leaf blades deeply divided into (3)5 or 7 lobes, lobes approximately equal in size and length, primary divisions separated by sinuses nearly or fully to petiole summit; peduncles moderately hirsute; western Virginia, or Piedmont, Atlantic and Gulf Coastal Plains, and Lower Midwest 22

22(21). Uppermost lobes of lateral primary divisions (or longest axis of lateral primary divisions if not deeply cleft or divided) spreading to ascending, lateral primary divisions occasionally scarcely to weakly cleft and appearing falcate, lunate or "dilated", the smallest lowest lobes at the base of the lateral primary division (if any) not usually overlapping in living material; foliage, peduncles and calyces gray-green to medium green, commonly lacking red-purple or purple pigmentation; chasmogamous and cleistogamous peduncles and calyces green; widespread at lower elevations of Piedmont and Atlantic and Gulf Coastal Plains in southeastern USA, and Lower Midwest . . . . . 37a. *V. palmata* L. var. *palmata*

22. Uppermost lobes of lateral primary divisions widely divergent, lateral primary divisions always deeply bilobate into 2 major lobes, the lowest major lobe with a third small lobe near the base, these smallest lobes overlapping in living material; foliage color gray- or blue-green, lower surface of leaf blades strongly tinged with purple, peduncles and calyces strongly spotted with red-purple or purple; sporadic and rare in Ridge and Valley province of the Appalachian Mountains in western Virginia . . . . . .37c. *V. palmata* (*avipes* variant)

23(18). Largest leaf blades deeply biternately divided nearly to petiole summit into (5)7 or 9 lobes (biternately divided leaf blades occasionally produced by *Viola septemloba* Leconte, which is keyed out in 24a), the terminal primary division narrowly lanceolate and not much broader than its lateral lobes or the lobes on the lateral primary divisions; lowest sepals oblong-lanceolate to ovate, obtuse to broadly rounded; auricles short and rounded, not elongating in fruit; spurred

petal sparsely to densely bearded within; cleistogamous capsule unspotted, on prostrate to arching peduncle much shorter than petioles; seeds 2.2–2.7 × 1.5–1.7 mm, medium to dark brown, unspotted; upland limestone cedar glades of Interior Highlands region, southern Indiana south to northwestern Georgia and northern Alabama . . . 16a. *V. egglestonii* Brainerd *sensu stricto*

23. Largest leaf blades shallowly to deeply pedately divided into 3, 5, or 7(9) lobes (rarely biternately divided in *V. septemloba*), the terminal primary division broadly lanceolate or ovate-lanceolate, oblong or ovate to rhombic-ovate, distinctly to much broader than any intermediary lobes between the terminal and lateral divisions as well as the lobes of the lateral primary divisions (rarely all lobes somewhat narrowly linear in *V. septemloba*); lowest sepals linear-lanceolate to ovate-triangular, acuminate from near base or middle to a sharply acute apex (rarely obtuse in *V. egglestonii* [Canada variant]); auricles prominent, weakly to strongly elongating to 3 mm in fruit; spurred petal glabrous within (sparsely bearded in *V. viarum*, densely bearded in *V. septemloba*); cleistogamous capsules unspotted, on ascending to erect peduncles as long as to longer than the petioles (much shorter than the petioles in *V. egglestonii* [Canada variant]); seeds dark bronze and unspotted, or brown with minute black spots or reticulations (seeds unknown in *V. egglestonii* [Canada variant]); inhabiting pine savannas (*V. septemloba*), bottomland sites along streams and rivers in the Atlantic and Gulf Coastal Plains and lower Midwest Missouri River drainage (*V. edulis* and *V. viarum*), or plantings and lawns in suburban areas in and near Ottawa, ON, and Montreal, QC (*V. egglestonii* [Canada variant]) 24

24(23). Largest leaf blades moderately to deeply pedately divided into (3)5 or 7(9) lobes (rarely biternaly divided), terminal primary division narrowly oblong-linear to broadly elliptical or rhombic-ovate, lateral lobes commonly much narrower and linear-lanceolate to lanceolate, lobes divergent on blades with 5 or more lobes, lowest lobe downward-pointing; blade margins entire or subentire; spurred petal densely bearded; cleistogamous capsule unspotted, on tall erect peduncle surpassing some petioles; seeds (1.5)1.9–2.5 × 1.4–1.6 mm, brownish-black, unspotted; dry to seasonally moist sand of frequently burned long-leaf pine savannas . . . . . 54. *V. septemloba* Leconte

24. Largest leaf blades shallowly to deeply pedately divided with 3, 5, or 7 lobes, terminal primary division linear-oblong, lanceolate or narrowly lance-triangular to narrowly oblong-ovate, smaller lobes linear-lanceolate, oblong or falcate-angulate and ascending to spreading, lateral primary divisions lacking a distinct downward-pointing lobe; blade margins prominently incurved-serrate or crenate-serrate; spurred petal glabrous (*V. edulis, V. egglestonii* [Canada variant]) or sparsely bearded within (*V. viarum*); cleistogamous capsule unspotted (*V. edulis, V. egglestonii* [Canada variant]) or finely to heavily spotted or blotched with red or purple (*V. edulis*), on ascending to erect peduncle surpassing some petioles (*V. edulis*) or on prostrate peduncle much shorter than petioles (*V. egglestonii* [Canada variant], *V. viarum*); seeds various; bottomland sites in diverse substrates along rivers and streams or swamps (*V. edulis*, *V. viarum*) or or plantings and lawns in suburban areas (*V. egglestonii* [Canada variant]) 25

25(24). Leaves widely spreading to ascending in living material; leaf blades shallowly 3- to 5-lobed, lobes of lateral primary divisions comparatively short and broad, trapezoidal to ovate-lanceolate; lowest sepals oblong to ovate-triangular, acuminate from the middle; spurred petal glabrous within; cleistogamous capsule unspotted, on ascending to erect peduncle equaling or surpassing petioles; inhabiting sandy or silty soils of floodplains, swamps and hammocks on the Atlantic Plain . . . . . 15. *V. edulis* Spach, in part

25. Leaves ascending to erect in living material; leaf blades deeply 5-lobed, lobes of lateral primary divisions comparatively long and slender, linear-oblong or narrowly lanceolate; lowest sepals linear-lanceolate to lanceolate, acuminate from near the base; spurred petal glabrous (*V. egglestonii* [Canada variant]) or sparsely bearded (*V. viarum*) within; cleistogamous capsule unspotted, on ascending peduncle much shorter than petioles (*V. egglestonii* [Canada variant]) or finely spotted with red or purple, on ascending to erect peduncle equaling or surpassing shorter petioles (*V. viarum*) 26

26(25). Spurred petal glabrous within; lateral petal beards very short, not obscuring the throat; cleistogamous capsule unspotted, on ascending peduncle much shorter than petioles; plantings and lawns in and around Ottawa, ON, and Montreal, QC, also adventive in Europe and Korea . . . . . 16b. *V. egglestonii* (Canada variant)

26. Spurred petal sparsely bearded within; lateral petal beards moderately long, obscuring the throat; cleistogamous capsule finely spotted with red or purple, on ascending to erect peduncle equaling or surpassing shorter petioles; inhabiting thin alluvial soils amid limestone gravel or rubble or cracks in limestone bedrock along streams and rivers, mainly in the northern Ozarks and Missouri River drainage of the central and lower Midwest, east to northern Illinois and north to southeastern South Dakota. . . . . 64. *V. viarum* Pollard, in part

27(2). At least some petioles narrowly or broadly winged along much or all of their length; largest leaf blades distinctly longer than broad; lowest sepals linear-lanceolate, acuminate; auricles prominent, elongating in fruit, erose (auricles short and entire, remaining $<$ 1 mm in fruit in *V. patrinii*); cleistogamous capsule unspotted, on declined or erect peduncle; in dry acidic sandy or gravelly soils of oak or oak-pine forests, barrens, and forest borders (sidewalk cracks or mulch of gardens in *V. patrinii*) 28

27. Petioles not noticeably winged; largest leaf blades longer than broad to broader than long; lowest sepals lanceolate to (more commonly) ovate-lanceolate, oblong or ovate, acuminate to rounded; auricles inconspicuous and remaining short and rounded, or prominent and elongating in fruit and often erose; cleistogamous capsule unspotted or spotted, on prostrate, declined or erect peduncle; in diverse substrates and habitats 32

28(27). Petioles and lower surface of leaf blades moderately to densely hirtellous (rarely glabrous); at least the outer leaves widely spreading or prostrate on the substrate in living material; petioles shorter than leaf blades (chasmogamous flower) to 2 $\times$ as long as blades (cleistogamous fruit); largest leaf blades elliptical or narrowly oblong-ovate in outline; peduncle hirtellous; calyx ciliate; corolla purple, petals broadly rounded, spurred petal not medially compressed; peduncle of cleistogamous capsule declined; seeds medium to dark brown or gray-brown, unspotted or with small weak darker blotches . . . . . 19. *V. fimbriatula* Sm., in part

28. Foliage glabrous or surfaces of leaf blades sparsely appressed-hirsute near margins and margins ciliate; leaves ascending to erect in living material; petioles $>$ 2 $\times$ as long as leaf blades (shorter in long-leaved *V. patrinii*); largest leaf blades narrowly oblong- or ovate-triangular, triangular or deltate-triangular; peduncle glabrous; calyx eciliate; corolla white or weakly violet-tinged to violet; petals occasionally emarginate and spurred petal commonly medially compressed; peduncle of cleistogamous capsule erect; seeds pinkish-gray to dark gray with streaks and spots (*V. emarginata*) or yellow-brown to dark brown (*V. patrinii*) 29

29(28). Stipules 2/3-adnate to petiole; petioles broadly winged, especially in distal half; corolla white or weakly tinged with violet; spurred petal glabrous within; spur slender and cylindrical, $>$ 2–3 $\times$ as long as tall; lateral petal beards short, exposing throat in living material; auricles of cleistogamous capsule short and narrowly rounded or ovate-triangular, $\leq$ 1 mm long; seeds yellow-brown to dark brown; native of Asia, introduced through plantings to Connecticut and New York . . . . . 39. *V. patrinii* Ging.

29. Stipules free; petioles narrowly winged; spurred petal glabrous or bearded within; corolla violet; spur stout, $\leq$ 1.5 $\times$ as long as tall; lateral petal beards long, mostly obscuring throat in living material; auricles of cleistogamous capsule elongate to 3 mm or longer; seeds pinkish-gray to dark gray with streaks and spots; native to dry oak and oak-pine woodlands or wet prairies . . . 30

30(29). Petals commonly emarginate; spurred petal commonly medially compressed; at least some petioles broadly winged; dry sandy soils of open dry oak and oak-pine woodlands and forest edges on the Piedmont and Atlantic Coastal Plain . . . . . 17a. *V. emarginata sensu stricto*, in part

30. Petals broadly rounded; spurred petal not medially compressed; at least some petioles narrowly winged; various habitats in the Lower Midwest 31

31(30). Outline of largest leaf blades concavely tapering to narrowly acuminate or narrowly rounded apex; open dry oak and oak-pine woodlands and forest edges, Central and Lower Midwest, West Virginia and southern Ohio, south to northern Alabama, Louisiana, and northern Arkansas . . . . . 17b. *V. emarginata* (Kentucky variant)

31. Outline of largest leaf blades convexly tapering to (broadly) rounded apex; low wet prairies, southern Missouri and eastern Kansas south to southeastern Oklahoma (not yet documented in our region, see "Potential Taxa") . . . . . *V. emarginata* (Lower Midwest varian)

32(27). All petals glabrous within (lateral petals densely bearded within in *V. inconspicua*); spur $\geq$ 2 $\times$ as long as thick, cylindrical or club-shaped; stipules at least half-adnate to petioles 33

32. Lateral petals bearded within, spurred petal in some species bearded; spur $< 1.5 \times$ as long as thick, rounded; stipules free 35

33(32). Leaf blades narrowly ovate to ovate, base deeply cordate with inner edges of basal lobes commonly overlapping in living material; petiole and lower surface of leaf blades glabrous, upper surface of blades with scattered subappressed hairs; circumboreal, Greenland and Newfoundland and Labrador to Alaska, south to Rhode Island, Pennsylvania, Wisconsin, northern Minnesota, and northwest Rocky Mountains; disjunct in South Dakota and Colorado; Eurasia . . . . . 53. *V. selkirkii* Pursh ex Goldie

33. Leaf blades linear-oblong or narrowly ovate-triangular to narrowly deltate-triangular, base cuneate to cordate with non-overlapping or divergent lobes; leaves glabrous or puberulent; native to Asia, introduced in North America 34

34(33). Spur 1–3 mm long; lateral petals densely bearded within; leaves glabrous (blades and/or petioles rarely puberulent); largest leaf blades narrowly deltate-triangular, base broadly cordate with divergent basal lobes, margins concavely tapering from widest point on leaf blade to the apex; native of Asia, introduced to southeastern USA and Maine . . . . . 25. *V. inconspicua* Blume

34. Spur 3–8 mm long; lateral petals glabrous (rarely sparsely bearded) within; leaf blades sparsely puberulent (rarely glabrous); largest leaf blades narrowly ovate, base subcordate to shallowly cordate with downward-pointing basal lobes, margins mostly convexly tapering from widest point on leaf blade to the apex; native of Asia, introduced to northeastern U.S. . . . . 26. *V. japonica* Langsd. ex Ging.

35(32). Leaves spreading to prostrate on the substrate in living material; upper surface of leaf blades silvery- or gray-green with contrasting dark green or red-purple veins, lower surface purple-tinged; foliage glabrous except for conspicuous stiff ascending or spreading hairs uniformly distributed over upper surface of leaf blade; calyx eciliate; lowest sepals oblong to ovate, obtuse to rounded; spurred pet densely bearded; cleistogamous capsule purple-spotted, on initially prostrate peduncle shorter than petioles; seeds $1.5–2.1 \times 1.1–1.4$ mm, light brown, commonly with slightly darker streaks and spots . . . . . 23. *V. hirsutula* Brainerd

35. Leaves strongly ascending to erect in living material (at least outer leaves widely spreading to prostrate in *V. fimbriatula*); upper surface of leaf blades uniformly green, lower surface green or purple tinged; foliage glabrous or variously pubescent, if hairs confined to upper surface of leaf blade, then these are very small, scattered, and subappressed; calyx and lowest sepals, cleistogamous capsule and seeds various 36

36(35). Margins of largest leaf blades closely pectinately serrate, surfaces glabrous or sparsely appressed-hirtellous; chasmogamous flowers held above the leaves; lowest sepals linear-lanceolate, acuminate; auricles prominent, elongating to 3 mm in fruit; sporadic along Atlantic Coastal Plain . . . . . 40. *V. pectinata* E.P.Bicknell

36. Margins of largest leaf blades merely crenate to serrate, various in indument; chasmogamous flowers held above or among the leaves; lowest sepals and auricles various; most species absent from or rare on the Atlantic Coastal Plain 37

37(36). Plant in chasmogamous flower. 38

37. Plant in cleistogamous fruit 60

38(37). Largest leaf blades approx. as broad as long to broader than long (length:width ratio < 1.2), broadly ovate or orbiculate to deltate or reniform. 39

38. Largest leaf blades distinctly longer than broad (length:width ratio ≥ 1.2). 50

39(38). Spurred petal sparsely to densely bearded within; lower surface of leaf blades commonly purple-tinged (blades uniformly green in *Viola pratincola* Greene and *Viola retusa* Greene) 40

39. Spurred petal glabrous within; foliage green (foliage blue-green, petioles, midrib on upper surface of leaf blades, lower surface of leaf blades, peduncle, and calyx purple-tinged in *V. sororia* [*hirsutuloides* variant]) 44

40(39). Foliage and peduncle sparsely to densely hirsute, leaf blade margins spreading-ciliate with hairs commonly long; calyx glabrous or appressed-hirtellous, ciliate to apex with hairs commonly long; auricles prominent, quadrate . . . . . 55. *V. septentrionalis* species complex, in part

40. Foliage and peduncle glabrous or upper surface of leaf blades with small scattered subappressed hairs, blade margins eciliate; calyx glabrous, eciliate; auricles short and rounded or prominent and quadrate 41

41(40). Largest leaf blades broadly ovate, orbiculate or reniform, broadly obtuse to rounded at apex; lowest sepals oblong to ovate, convexly tapering to obtuse to rounded apex; dry or wet calcareous open sites, transcontinental, Northeast, Great Plains, and the West . . . . . 33. *Viola nephrophylla* Greene, in part

41. Largest leaf blades ovate to broadly deltate-triangular, acute to short-acuminate at apex; lowest sepals lanceolate to linear-lanceolate, acuminate from near base or middle to sharply acute apex (oblong-lanceolate to ovate-lanceolate and usually acute in *Viola latiuscula* Greene) 42

42(41). Petals broadly obovate, broadly rounded; lowest sepals > 2 mm wide, oblong-lanceolate to ovate-lanceolate, acute (occasionally narrowly obtuse); auricles short and rounded; lower surface of leaf blades commonly tinged with purple; summit of petioles commonly papillate, granular, or minutely puberulent; dry sandy woodland soils and dry ledges, northeastern endemic, Vermont to southeastern Ontario, south to Connecticut and New York . . . . 29. *V. latiuscula* Greene, in part

42. Petals narrowly to broadly obovate, broadly rounded (*V. pratincola*) or upper commonly retuse (*V. retusa*); lowest sepals < 2 mm wide, linear-lanceolate to oblong-lanceolate, acuminate from near base or middle to sharply acute apex; auricles prominent, quadrate; leaves uniformly green; petioles smooth; moist to wet soils of wet prairies, bottomlands, and stream- and riverbanks in Great Plains and western Midwest 43

43(42). Largest leaf blades ovate to broadly ovate; petals broadly obovate, broadly rounded; lowest sepals oblong-lanceolate, acuminate from middle to sharply acute apex; wet prairies, stream banks and bottomlands, lawns, and railroad rights-of-way, in western Midwest and eastern Great Plains . . . . . 43. *V. pratincola* Greene, in part

43. Largest leaf blades ovate or broadly deltate-triangular; petals narrowly obovate, upper commonly retuse; lowest sepals linear-lanceolate to lance-triangular, acuminate from near base to sharply acute apex; gravel alluvium and riparian zones in the Great Plains, North Dakota, and southern Wyoming south to Oklahoma and New Mexico; slightly disjunct in southeastern Minnesota . . . . . 48. *V. retusa* Greene, in part

44(39). Lowest sepals oblong to ovate, convexly tapering to obtuse to rounded apex; auricles not prominent, short and rounded or truncate 45

44. Lowest sepals linear-lanceolate or oblong-lanceolate to ovate-triangular, acuminate from base or middle to sharply acute apex (convexly tapering to acute apex in *V. domestica*); auricles prominent, narrowly linear to trapezoidal (somewhat prominent and truncate in *V. domestica*) 47

45(44). Foliage sparsely to densely hirsute; chasmogamous and cleistogamous peduncles sparsely to moderately hirsute; calyx ciliate; widespread in eastern North America westward into the eastern Great Plains . . . . . 56a. *V. sororia sensu stricto*, in part

45. Foliage strictly or essentially glabrous, upper surface of leaf blades in some taxa with scattered small to minute subappressed hairs (petioles occasionally sparsely hirtellous in *V. sororia* [*hirsutuloides* variant]); chasmogamous and cleistogamous peduncles glabrous; calyx eciliate 46

46(45). Foliage, peduncles, and calyx uniformly medium green; apex of leaf blades obtuse or abruptly acutish; margins incurved-serrate or closely serrulate; lowest sepals oblong to narrowly ovate (uncommonly broadly so), obtuse to rounded at apex . . . 56b. *V. sororia* (glabrous variant), in part

46. Foliage, peduncle, and calyx blue-green; midrib of upper leaf blade surface, lower surface of leaf blades, petioles, peduncle, and calyx tinged with purple; apex of leaf blades broadly rounded; margins shallowly crenate; lowest sepals ovate, broadly rounded at apex (occasionally narrowly so) . . . . . 56c. *V. sororia* (*hirsutuloides* variant), in part

47(44). Corolla pale blue or violet with purple eyespot; lowest sepals linear-lanceolate, acuminate from near base to narrowly sharply acute apex; lateral petal beards very short, exposing throat in living material, hairs (especially those on the perimeter of the beard) strongly clavate or reniform to "doorknob-shaped"; leaf blades narrowly ovate to ovate, narrowly rounded to obtuse at apex, medium to light green, dull on both surfaces in living material; upper leaf blade surface with scattered easily visible appressed hairs; auricles commonly prominent, rectangular, entire; wet soils in marshes, swamps, lakeshores, stream- or riverbanks, and ditches . . . . . 13. *Viola cucullata* Aiton, in part

47. Corolla uniformly violet to purple (white with broad blue, blue-gray, or purple eyespot in *V. communis* f. *priceana*); lowest sepals ovate-triangular, acuminate from middle to sharply acute apex (convexly tapering to acute apex in *V. domestica*); lateral petal beards long, obscuring

throat in living material, hairs filiform or slightly clavate; leaf blades suborbiculate or deltate-ovate to reniform, broadly rounded to abruptly obtuse-angulate at apex, light to medium or deep green, dull or glossy on both surfaces in living material; foliage glabrous or upper leaf blade surface with scattered minute appressed hairs requiring magnification; auricles weakly prominent, trapezoidal, and commonly erose or quadrate and truncate; native to moist loamy soils in floodplains and bottomlands, often spreading or persisting in moist lawns in the eastern states, adventive or planted in suburbs and cities west of Kentucky and Ohio in *V. communis*) or almost exclusively cultivated (*V. domestica*). 48

48(47). Foliage light to medium green with upper leaf blade surfaces scarcely glossy to dull in living material; largest leaf blades broadly ovate to reniform, margins somewhat coarsely crenate-serrate, angulate to obtuse or broadly acute apex; lowest sepals oblong-lanceolate, convexly tapering to acute apex; cultivated, perhaps barely escaping . . . . . 14. *V. domestica* E.P.Bicknell, in part

48. Foliage deep green, occasionally with basal half of petioles and peduncles purple-tinged, with upper leaf blade surfaces glossy; largest leaf blades suborbiculate to deltate-ovate, margins closely and uniformly crenate-serrate; lowest sepals ovate-triangular, acuminate from middle to sharply acute apex; native to stream terraces, ecotones between mesic forest slopes and floodplains, and often escaping into lawns, mostly central and eastern USA, cultivated and escaped west of Kentucky and Ohio 49

49(48). Corolla violet to purple, lacking a conspicuously contrasting eyespot . . . . . 12a. *V. communis* Pollard f. *communis*

49. Corolla white with broad blue, blue-gray, or purple eyespot. . . . . .12b. *V. communis* Pollard f. *priceana* (Pollard) H.E.Ballard

50(38). Spurred petal sparsely to densely bearded within 51

51. Spurred petal glabrous within 57

51(50). Foliage sparsely to densely hirsute; lowest sepals oblong to ovate, convexly tapering to narrowly or broadly rounded apex; calyx eciliate or cili(ol)ate. 52

51. Foliage glabrous, or upper surface of leaf blades bearing small, scattered, subappressed hairs (foliage occasionally sparsely to moderately hirtellous in *V. sagittata*); lowest sepals linear- to oblong-lanceolate or lance-triangular, acuminate from near base or middle to sharply acute apex; calyx eciliate 54

52(51). Largest leaf blades narrowly ovate, convexly tapering to narrowly rounded or acute apex, margins commonly ciliate with long hairs; sepals ciliate nearly or fully to apex with commonly long hairs; dry to moist woodlands, often associated with limestone or igneous rock outcrops, boreal, interruptedly transcontinental, primarily boreal, Appalachian, Northeast, Upper Midwest, and northern Rocky Mountains, Newfoundland and Labrador to Saskatchewan and British Columbia, south to western North Carolina and eastern Tennessee; eastern Iowa, western Montana, and eastern Washington . . . . . .55. *V. septentrionalis* species complex, in part

52. Largest leaf blades narrowly ovate-triangular, convexly tapering or acuminate from near base to sharply acute apex, margins sparsely to moderately ciliate with short hairs; various habitats, almost strictly boreal 53

53(52). Leaves and peduncles moderately to densely hirsute; margins of leaf blades with 10–(avg. 14)–21 teeth on each side, ciliate; calyx often pubescent, margins uniformly ciliate (often with long hairs) to apex; lowest sepals 2.7–3.8 mm wide, length:width ratio $\leq$ 2.1; western Great Lakes region, northern Michigan to southeastern Manitoba, south to central Wisconsin and central Minnesota, disjunct in Hastings Co. in southeastern Ontario . . . . . .21. *Viola grisea* (Fernald) H.E.Ballard, in part

53. Petioles glabrous or sparsely hirsute below middle, leaf blades and peduncles glabrous; margins of leaf blades with 10–(avg. 11)–14 teeth on each side, eciliate; calyx glabrous, eciliate; lowest sepals 1.9–2.7 mm wide, length:width ratio $>$ 2.1; Maine and New Brunswick, disjunct in eastern New York. . . . . .34. *Viola novae-angliae* House, in part

54(51). Largest leaf blades narrowly elliptical, ovate-lanceolate, lance-triangular, or sagittate; base narrowly (sub)cordate; foliage glabrous or sparsely to moderately hirtellous; flowers overtopping leaves; auricles prominent and quadrate; in dry to moist sand of sand barrens and dry prairies, and lakeshores. . . . . 52. *V. sagittata* Aiton, in part

54. Largest leaf blades narrowly ovate- to deltate-triangular; foliage glabrous or upper surface of leaf blades bearing scattered, small, subappressed hairs; flowers held among the leaves; auricles short and rounded (*V. affinis*) or prominent (*V. pratincola* and *V. retusa*); in sandy, silty or muck soils of floodplains, drainages, and swamps, or in gravel or sand along riverbanks 55

55(54). Largest leaf blades narrowly ovate-triangular; upper surface of leaf blades bearing scattered, small, subappressed hairs; upper petals broadly obovate, broadly rounded; auricles short and rounded; spurred petal densely bearded; stream and river terraces, floodplains, and swamps, widely distributed, mostly east of the Mississippi River . . . . . 4. *V. affinis* Leconte, in part

55. Largest leaf blades narrowly ovate to narrowly deltate-triangular; leaves glabrous; upper petals narrowly or broadly obovate, broadly rounded or retuse; auricles typically prominent, quadrate; spurred petal sparsely to densely bearded; riverbanks, riparian wet prairies, bottomlands, Wisconsin and Illinois westward 56

56(55). Largest leaf blades narrowly ovate to ovate, acute at apex; petals broadly obovate, broadly rounded; lowest sepals oblong-lanceolate, acuminate from middle to sharply acute apex; spurred petal sparsely bearded; wet prairies, terraces bordering streams and rivers, and streambanks in swampy woods, often invading (or persisting in) low-lying lawns, railroad rights-of-way, and other anthropogenic sites. . . . . 43. *V. pratincola* Greene, in part

56. Largest leaf blades narrowly deltate-ovate or deltate-triangular, shortly acuminate at apex; petals narrowly obovate, upper commonly retuse; lowest sepals linear-lanceolate to lance-triangular, acuminate from near base to sharply acute apex; spurred petal densely bearded; gravel and sand alluvium along rivers in the Great Plains, North Dakota, and southern Wyoming south to Oklahoma and New Mexico; slightly disjunct in southeastern Minnesota. . . . . 48. *V. retusa* Greene, in part

57(50). Calyx ciliolate (populations in Upper Midwest commonly eciliate); lowest sepals oblong to ovate-lanceolate, gradually or abruptly tapering to a narrowly obtuse to rounded apex; auricles short and rounded . . . . . 31. *Viola missouriensis* Greene, in part

57. Calyx eciliate (some northern populations of *V. cucullata* with sparsely ciliate margins); lowest sepals linear-lanceolate to ovate-triangular, acuminate from near base or middle to sharply acute apex; auricles prominent to elongate 58

58(57). Corolla pale blue or violet with purple eyespot; lowest sepals linear-lanceolate; lateral petal beards very short, with strongly clavate to reniform hairs; widely distributed over eastern North America, mostly absent on the southeastern Atlantic and Gulf Coastal Plains . . . . . 13. *V. cucullata* Aiton, in part

58. Corolla violet, lacking purple eyespot but with flush of dark purple at base of lateral petals; lowest sepals lance- to ovate-triangular; lateral petal beards long, with slightly clavate hairs; southern Atlantic and Gulf Coastal Plains 59

59(58). Leaves strongly ascending in living material; petioles, lower surface of leaf blades, peduncle, and calyx commonly tinged or finely spotted with purple; auricles prominent to very elongate, 1.5–4 mm long; frequently flooded sandy and silty soils along streams and rivers on the southern lower Atlantic Coastal Plain, North Carolina south to southeastern Georgia (not yet documented in our region, see "Potential Taxa") . . . . . *Viola* "*impostor*", in part

59. Leaves widely spreading in living material; foliage, peduncle, and calyx green; auricles prominent, to $\leq$ 1.5 mm long; Gulf Coastal Plain, eastern Texas to western Florida panhandle, north to southeastern Missouri (not yet documented in our region, see "Potential Taxa"). . . . . *V. langloisii* Greene, in part

60(37). Largest leaf blades substantially longer than broad (length:width ratio $\geq$ 1.2), lance-triangular or sagittate to narrowly ovate-triangular 61

60. Largest leaf blades about as long as broad to broader than long (length:width ratio $<$ 1.2), broadly ovate or broadly deltate-triangular to reniform 63

61(60). Leaf blades lance-triangular or sagittate; foliage glabrous or sparsely to moderately hirtellous; peduncle glabrous; cleistogamous capsule unspotted, on erect peduncle; calyx eciliate; sepals lanceolate to lance-triangular, acuminate; auricles elongating to 3 mm or more; distributed almost exclusively south of the boreal region . . . . . 52. *V. sagittata* Aiton, in part

61. Leaf blades narrowly ovate-triangular; foliage glabrate or sparsely to densely hirsute; peduncle glabrous or hirsute; cleistogamous capsule heavily purple-spotted or blotched, on prostrate

peduncle arching upward just prior to dehiscence; calyx eciliate or ciliate; sepals oblong to ovate, narrowly to broadly rounded; auricles weakly elongating to 2 mm; confined to the boreal region . 62

62(61). Petioles and lower surface of leaf blades moderately to densely hirsute; peduncle hirsute; margins of leaf blades with 10–(avg. 14)–21 teeth on each side, ciliate; calyx often pubescent, margins uniformly ciliate (often with long hairs) to apex; sepals 2.7–3.8 mm wide, length:width ratio $\leq$ 2.1; Western Great Lakes region, northern Michigan to southeastern Manitoba, south to central Wisconsin and central Minnesota, disjunct in Hastings Co. in southestern Ontario . . . . . 21. *V. grisea* (Fernald) H.E.Ballard, in part

62. Petioles glabrous or sparsely hirsute below middle, leaf blades glabrous; peduncle glabrous; margins of leaf blades with 10–(avg. 11)–14 teeth on each side, eciliate; calyx glabrous, eciliate; sepals 1.9–2.7 mm wide, length:width ratio $>$ 2.1; Maine and New Brunswick, disjunct in eastern New York. . . . . 34. *V. novae-angliae* House, in part

63(60). Petioles and lower surface of leaf blades hirsute; peduncle hirsute; calyx ciliate. 64

63. Foliage glabrous or upper surface of leaf blades with scattered small to minute subappressed hairs (petioles occasionally sparsely hirtellous in *V. sororia* [*hirsutuloides* variant]); peduncle glabrous; calyx eciliate (ciliolate in *V. missouriensis*) 66

64(63). Margins of leaf blades ciliate with short ascending hairs; sepals ciliate in proximal 1/2(2/3) with short hairs; auricles short and rounded; seeds 1.5–2.6 $\times$ 0.9–1.6 mm, dark gray to dark grayish-brown or blackish, unspotted or with small usually weak blackish streaks; inhabiting drier to moist loamy, sandy, or clayey soils in upland and lowland forests in much of eastern North America . . . . . .56a. *V. sororia sensu stricto*, in part

64. Margins of leaf blades ciliate with spreading often long hairs; sepals ciliate to apex, cilia often long; auricles prominent, quadrate and/or erose, elongate to 2 mm; seeds 1.2–2.3 $\times$ 0.8–1.2 mm, light-medium brown to dark brown, unspotted or with small weak darker streaks or spots; inhabiting limestone and dolomite-associated soils in the boreal region of northern North America and southward at higher elevations into the southern Appalachian Mountains, igneous rocks and acidic soils in the Upper Midwest 65

65(64). Foliage sparsely to densely hirsute; sepals ovate-triangular and acuminate from middle to oblong-ovate or ovate and obtuse to rounded, sparsely to densely ciliate; seeds 1.2–2.3 $\times$ 0.8–1.2 mm, narrowly obovoid, light-medium brown to dark brown, unspotted; in dryish to moist forests, commonly on or near limestone, across boreal Canada, south into the northwestern Rocky Mountains and New England and at higher elevations into the southern Appalachian Mountains. . . . . 55a. *V. septentrionalis sensu stricto*

65. Foliage uniformly densely hirsute; sepals ovate and obtuse to rounded, uniformly densely ciliate; seeds 1.9–2.1 $\times$ 1.2–1.3 mm, broadly obovoid, red-brown, with small weak darker streaks or darker raised spots; on or near igneous outcrops in Thunder Bay area, Ontario, south to Minnesota and eastern Iowa. . . . . .55b. *V. septentrionalis* (Upper Midwest variant)

66(63). Capsule unspotted 67

67. Capsule finely spotted, or heavily purple-spotted or blotched 73

67(66). Peduncle declined 68

67. Peduncle ascending to erect (initially prostrate and coiled then elongating to become sinuous-erect in *V. communis*, arching to ascending in *V. domestica*). 69

68(67). Petioles and leaves widely spreading in living material; leaf blades deltate-triangular, broadly acute or right-angled at apex; sepals lanceolate, acuminate; auricles prominent, elongating to 2 mm; seeds yellow-brown, unspotted; silt or sand in floodplains of streams and rivers in Gulf Coast region and Florida, north to southeastern Missouri (not yet documented in our region, see "Potential Taxa"). . . . . *V. langloisii* Greene, in part

68. Petioles ascending in living material; leaf blades reniform, broadly obtuse to rounded at apex; sepals oblong to ovate, obtuse to rounded; auricles short and rounded; seeds medium brown to dark olive-brown, unspotted or rarely with minute raised darker spots; dry or wet calcareous open sites, transcontinental, Northeast, Great Plains, and the West . . . . . 33. *V. nephrophylla* Greene, in part

69(67). Cleistogamous peduncle relatively short, ascending to erect or eventually arching to sinuous-erect, not reaching petioles; sepals oblong- to ovate-lanceolate or ovate-triangular, $<$ 1/2 as long as the capsule, convexly tapering to an acute apex or acuminate from the middle to a sharply

acute apex; auricles weakly elongate; seeds medium brown or olive- to brownish-black or blackish, with minute raised black spots; ecotonal thickets, stream terraces and floodplains (*V. communis*), wet prairies, and streambanks in swampy woods (*V. pratincola*), and escaping into lawns or railroad rights-of-way, or cultivated and perhaps barely escaping (*V. domestica*) 70

69. Cleistogamous peduncle tall and erect, often reaching or surpassing petioles; sepals linear-lanceolate to lanceolate, > 1/2 as long as the capsule, acuminate from near base to a sharply acute apex; auricles weakly or strongly elongate; seeds medium to dark brown or reddish-brown, unspotted or spotted; intermittently or permanently wet soils of wetlands, swamps, and riverbanks, not cultivated or escaping to lawns and other anthropogenic sites. 72

70(69). Foliage glabrous except for upper surface of leaf blades with scattered minute appressed hairs requiring magnification; largest leaf blades suborbiculate to deltate-reniform, base shallowly to deeply cordate and not noticeably cuneate-decurrent onto summit of petiole, apex broadly obtuse to rounded, both surfaces glossy in living material, margins closely and uniformly crenate-serrate; peduncle initially prostrate and coiled but eventually becoming sinuous-erect; sepals ovate-triangular, acuminate from middle to sharply acute apex; auricles trapezoidal, commonly erose; in moist clay or loam soils of thickets, grassy banks and meadows, slope-floodplain transitions, floodplains, lawns, roadsides, and suburban woodlots . . . . . .12. *V. communis* Pollard, in part

70. Foliage glabrous; largest leaf blades broadly deltate-ovate to deltate-reniform, base shallowly cordate or subtruncate and shortly cuneate-decurrent onto summit of petiole, apex broadly and abruptly obtuse-angulate to subacuminate, both surfaces dull or upper surface scarcely glossy in living material, margins conspicuously incurved-crenate-serrate; peduncle arching or ascending; sepals oblong-lanceolate and convexly tapering to acute apex (*V. domestica*) or ovate-lanceolate and acuminate from the middle to a sharply acute apex, < 1/2 as long as capsule; auricles quadrate, truncate 71

71(70). Largest leaf blades broadly deltate-reniform, base subtruncate and shortly cuneate-decurrent onto summit of petiole, apex broadly and abruptly obtuse-angulate, both surfaces dull or upper surface scarcely glossy in living material; peduncle arching or ascending; sepals oblong-lanceolate, convexly tapering to acute apex; seeds 1.9–(avg. 2.0)–2.2 × 1.2–(avg. 1.26)–1.3 mm; planted, possibly rarely escaping . . . . . .14. *V. domestica* E.P.Bicknell, in part

71. Largest leaf blades deltate-ovate, base cordate and not noticeably decurrent onto summit of petiole, apex abruptly acute to subacuminate, both surfaces dull; peduncle ascending; sepals ovate-lanceolate, acuminate from middle to a sharply acute apex; seeds 1.4–(avg. 1.8)–2.1 × 0.8–(avg. 1.1)–1.3 mm; wet prairies, stream banks and bottomlands, lawns, and railroad rights-of-way, in western Midwest and eastern Great Plains . . . . . 43. *V. pratincola* Greene, in part

72(69). Auricles strongly elongate, 3–8 mm; seeds 1.4–1.9 × 0.8–1.3 mm, dark brown to dark reddish-brown, unspotted; open or forested wet sites including marshes, sedge meadows, seeps, bog forests, and swamps throughout most of eastern North America, mostly east of the Great Plains . . . . . 13. *V. cucullata* Aiton, in part

72. Auricles weakly elongate to 1.5(–2) mm; seeds 1.7–2.2 × 1.0–1.3 mm, medium brown with dense minute raised black spots; gravel and sand alluvium along streams and rivers in the Great Plains, North Dakota, and southern Wyoming south to Oklahoma and New Mexico; slightly disjunct in southeastern Minnesota . . . . . 48. *V. retusa* Greene, in part

73(66). Sepals oblong- to ovate-lanceolate or ovate, convexly tapering to a narrowly or broadly obtuse to rounded apex. 74

73. Sepals linear-lanceolate to ovate-triangular, acuminate (acute to narrowly rounded in *V. latiuscula*) 76

74(73). Calyx ciliolate; seeds 1.5–2.2 × 1.0–1.3 mm, medium orange-brown, unspotted or with small weak darker streaks, blotches, and spots; sandy or silty soils of bottomland forests, in western Midwest, Lower Midwest, and Great Plains. . . . . 31. *V. missouriensis* Greene, in part

74. Calyx eciliate; seeds 1.5–2.0 × 1.0–1.3 mm (limited measurements, upper ranges may be larger), light to medium gray or gray-brown with small prominent gray or gray-brown streaks (seeds of *V. sororia* [*hirsutuloides* variant] unknown); various substrates, especially in rich mesic upland forests, in the Appalachian Mountains and associated uplands 75

75(74). Foliage, peduncles, and calyx uniformly medium green; largest leaf blades deltate-reniform, base cordate to subcordate, apex obtuse or abruptly acutish; margins incurved-serrate or closely

serrulate; sepals oblong to narrowly ovate (uncommonly broadly so), obtuse to rounded at apex . . . . . 56b. *V. sororia* (glabrous variant), in part

75. Foliage, peduncles, and calyx blue-green, midrib of upper leaf blade surface often purple, lower surface of leaf blades, petioles, peduncles, and calyx tinged with purple; largest leaf blades broadly ovate to reniform, base deeply cordate, apex broadly rounded or apiculate; margins shallowly crenate; sepals ovate, narrowly to broadly rounded at apex . . . . . 56c. *V. sororia* (*hirsutuloides* variant), in part

76(73). Peduncle declined, or initially prostrate and coiled but becoming erect-sinuous; auricles prominent, weakly to strongly elongate, 1.5–4 mm; seeds olive-brown or brownish-black to black, unspotted or with minute black spots 77

76. Peduncle initially prostrate, arching upward prior to capsule dehiscence; auricles short and rounded or truncate; seeds yellow- to orange-brown or purple-black and unspotted, or light red-brown with dark brown or red-brown blotches 78

77(76). Largest leaf blades broadly obtuse to rounded at apex, both surfaces glossy in living material; peduncle stout, initially prostrate and coiled, elongating to become erect-sinuous prior to dehiscence; calyx green; auricles triangular-trapezoidal, weakly elongate to 1.5(2) mm; capsule finely spotted to heavily blotched with dark purple; seeds 1.5–2.5 × 0.9–1.5 mm, olive-brown, brownish-black to black with dense minute raised spots or rarely unspotted; in moist clay or loam soils of thickets, grassy banks and meadows, slope-floodplain transitions, floodplains, lawns, roadsides, and suburban woodlots, widespread in eastern North America, rare on the Atlantic Coastal Plain, populations west of Ohio and Kentucky planted and escaped . . . . . 12. *V. communis* Pollard, in part

77. Largest leaf blades (abruptly) acute at apex, neither surface glossy in living material; peduncle slender, declined or ascending from the beginning, gently curved; calyx purple-pigmented (rarely green); auricles narrowly linear, strongly elongate, (1.5)2–4 mm; capsule finely purple-spotted at least at base; seeds 1.3–1.8 × 0.9–1.2 mm, dark brown with white raphe, unspotted; frequently flooded sandy and silty soils along streams and rivers on the southern lower Atlantic Coastal Plain, North Carolina south to southeast Georgia (not yet documented in our region, see "Potential Taxa") . . . . . *V.* "*impostor*," in part

78(76). Largest leaf blades approx. as broad as long, ovate- to deltate-triangular, 37–69 mm wide, broadly acute at apex, shallowly to moderately cordate at base; petioles smooth throughout; sepals linear-lanceolate or lanceolate, acuminate, ≥ 1/2 as long as mature or dehisced cleistogamous capsule; cleistogamous capsules frequently hirtellous; seeds light to medium yellow- or orange-brown, unspotted; moist to wet soils of swamps, floodplains, and riverside meadows over much of eastern North America east of the Great Plains, mostly absent from the central and southern Atlantic Coastal Plain, absent from the Gulf Coastal Plain . . . . . 4. *V. affinis* Leconte, in part

78. Largest leaf blades much broader than long, broadly deltate-reniform, 34–145 mm wide, abruptly obtuse to acute at apex, truncate to subcordate at base; summit of petioles granular or papillate-puberulent; sepals oblong-lanceolate to ovate-lanceolate, acute or acutish, mostly < 1/2 as long as mature or dehisced cleistogamous capsule; cleistogamous capsules glabrous; seeds purplish-black, with very weak darker blotches, spots, or streaks; dry sandy soils in upland forests or dry ledges, northeastern endemic, Northeastern endemic, Vermont to southeastern Ontario, south to Connecticut and New York . . . . . 29. *V. latiuscula* Greene, in part

Taxonomic Treatment. Included taxa are those confirmed in our region. For ease of use, taxa are presented alphabetically by genus and species, with species numbered and infraspecific taxa lettered sequentially. Some names have type information provided, and for a few names types are newly designated. Infraspecific taxa (both formally recognized taxa and variants under study) are cited near the top of the account for their inclusive species or species complex and also have separate taxon accounts immediately following the account of the inclusive species or species complex. The descriptions in the taxon accounts for species or species complexes with infraspecific taxa are fully characterized and embrace all included variation, and include all common names applied to their infraspecific taxa, but they do not include synonyms. Infraspecific taxa have their own common names and synonyms, and are more briefly discussed, primarily highlighting where

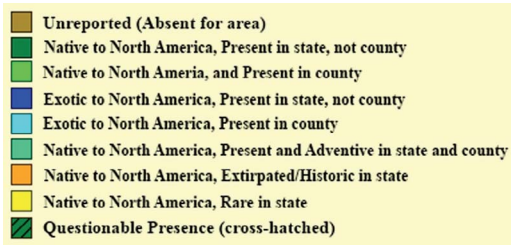

FIG. 4. Color legend representing status of a taxon in provinces, states and counties.

they differ from the typical infraspecific taxon or species *sensu stricto*. Each taxon account has synonyms (if any) listed below the accepted scientific name, followed by the common name(s), description, similar species, ecology, distribution, rarity, phenology, affinities, hybrids, and comments. Nearly all taxa have a plate of figures depicting plants or particular structures, and nearly all taxa have their own geographic distribution map (see Fig. 4 for color legend). In a case where an infraspecific taxon does not differ from the inclusive species or species complex for a particular section, this is noted (*e.g.*, "Same as the species"). Distribution is a short phrase briefly delineating the overall range of the taxon, using US states and Canadian provinces but often including biogeographic provinces or regions if these are obvious and useful. Rarity status includes all states and provinces that include the taxon on a current list of "rare" plants for that area, without regard to actual status (or lack of it). Two new species, *V. monacanora* and *V. tenuisecta*, are described in their respective taxon accounts. These accounts deviate from the standard format by the addition of a type statement, diagnosis, and a "Paratypes" section to comply with requirements of the International Code of Nomenclature (Turland *et al*. 2018) for new taxon descriptions.

Below "Included Taxa" is the short section "Potential Taxa," with brief discussion of six taxa occurring within three counties of our region that may someday be found here. After that is the "Excluded Taxa" section with two previously reported species, for which no documented evidence has been found to support their existence in our region. The "Uncertain Names" section lists 26 names, the taxonomic status of which has not been determined. Finally, the treatment ends with the "Hybrids" section.

INCLUDED TAXA

1. ***Cubelium concolor*** (T.F.Forst.) Raf. ex Britton & A.Br., Ill. Fl. N. U.S. 2: 456. 1897; *Viola concolor* T.F.Forst., Trans. Linn. Soc. London 6: 309. 1802; *Cubelium concolor* (T.F.Forst.) Raf., First Cat. Gard. Transylv. Univ.: 13. 1824 [*nomen nudum*]; *Solea concolor* (T.F.Forst.) Ging. ex DC., Prodr. 1: 306. 1824; *Hybanthus concolor* (T.F.Forst.) Spreng., Syst. Veg. 1: 805. 1825 ["1824"]; *Ionidium concolor* (T.F.Forst.) Benth. & Hook.f. ex S.Watson, Bibl. Index N. Amer. Bot.: 81. 1878; *Calceolaria concolor* (T.F.Forst.) Kuntze, Revis. Gen. Pl. 1: 41. 1891. Type. England. Mr. Forster's garden from N. America, 1791, [no collector] (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2). 218): LINN-HS1380-26 (*n.v.*), internet image). Fig. 5.

Solea stricta (Vent.) Spreng., Pl. Min. Cogn. Pug. 1: 22. 1813 [misapplied, Sprengel makes the new combination *Solea stricta* based on *Ionidium strictum* Vent. [= *P. linearifolia*], cites Muhlenberg's *nomen nudum* (= *C. concolor*), incorrectly applying his new combination in this publication to *C. concolor*]; *Viola stricta* Muhl., Trans. Am. Phil. Soc. 3: 178. 1793 [*nomen nudum*].

Viola sprengeliana (Roem. & Schult.) Steud., Nom. Bot.: 887. 1821; *Ionidium sprengelianum* Roem. & Schult., Syst. Veg., ed. 15, 5:401. 1819.

Noisettia acuminata DC., Prodr. 1:290. 1824.

Cubelium concolor (T.F.Forst.) Raf. f. *subglabrum* Eames, Rhodora 32:141. 1930; *Hybanthus concolor* (T.F.Forst.) Spreng. f. *subglaber* (Eames) Zenkert, Flora of the Niagara Frontier Region: 202. 1934.

Common Name. Eastern green violet.

Description. Caulescent perennial, erect from thick horizontal rhizome with branched roots, $\leq$ 9 dm tall; glabrescent to hirsute; stipules very small, free, linear, entire; leaves several to many, spreading, alternate, blades oblanceolate to narrowly obovate, base cuneate, apex abruptly attenuate, margins entire or irregularly serrate to dentate with 1–2(3) coarse teeth per margin, $\leq$ 140 $\times$ 55 mm, petioles $<$ 1 cm; pedicels 3–10 mm; chasmogamous flower 3–6 mm; sepals narrowly linear, attenuate; corolla green; bottom petal slightly longer than other, blade slightly expanded, retuse at apex; chasmogamous and cleistogamous capsules 15–23 mm long, obovoid, green drying

FIG. 5. *Cubelium concolor*. (A) Stem (photo: Andrew Lane Gibson). (B) Chasmogamous flower (photo: D. Busemeyer). (C) Cleistogamous fruit (photo: Paul Rothrock).

tan, unspotted; seeds 4.5–5.0 × 3.5–4.8 mm, subglobose, tan, unspotted; 2n = 48.

Similar Species. None. This species is distinctive in our region.

Ecology. Nutrient-rich mesic forests and stabilized floodplains, especially over calcareous limestone or dolomite substrates, also in drier forest microsites where the substrate is alkaline.

Distribution. Widespread in eastern North America, Vermont, and southern Ontario to southeastern Minnesota, south to northern Florida and eastern Oklahoma. Fig. 6.

Rarity. State-listed (as *Hybanthus concolor*) in Connecticut, Delaware, Iowa, Maryland, Michigan, Minnesota, New Jersey, Ontario, and Vermont.

Phenology. Chasmogamous flower April–May, chasmogamous fruit May–July, cleistogamous fruit May–October.

Affinities. Recent comprehensive phylogenetic investigations of the Violaceae family demonstrated that broadly circumscribed *Hybanthus* was extensively polyphyletic, and that the sole trait of a bottom petal that was saccate at base failed to delineate natural evolutionary groups (Feng 2005; Tokuoka 2008; Wahlert *et al*. 2014). The majority of New World hybanthoids formed a well-supported clade and were subsequently segregated into the resurrected genus *Pombalia* on the basis of differences in floral and seed features and

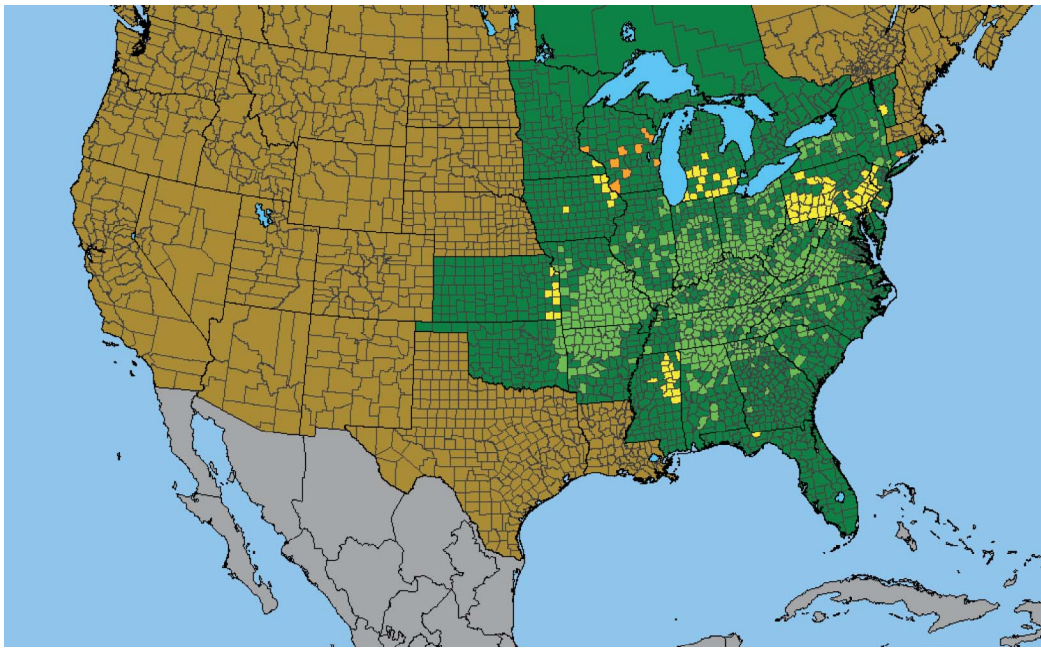

FIG. 6. United States county distribution of *Cubelium concolor* (map: Biota of North America Program).

anatomical traits (Paula-Souza and Ballard 2014). Our temperate eastern North American native hybanthoid now belongs to the resurrected monotypic genus *Cubelium*, with the genus and species first validly published by Britton and Brown (1897). It is sister to the very small genus *Hybanthus sensu stricto* from Mesoamerica and the West Indies, that consists of three species of shrubs and treelets.

Hybrids. None.

Comments. Forster did not cite a type specimen in the protologue but stated that he had grown a plant in Royal Botanic Garden at Kew for more than 14 yr. He also noted that his observations were made on living material and specimens in the Banks Herbarium. His detailed plate illustrated structures of the new species. A 1791 sheet at LINN (LINN-HS1380-26) has a handwritten notation, "Mr. Forster's garden from N. America", suggesting that it is original material. That specimen was designated by Ballard *et al*. (2020a) as the lectotype.

The genus and species under *Cubelium* were first validly published by Britton and Brown (1897). It has been accepted as a species under the genus *Hybanthus* by Fernald (1950), Henry (1953a), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1995, 2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015), and under *Cubelium* by Alexander (1963). Scoggan (1978) recognized f. *subglaber* but others have synonymized it. Our eastern green violet differs from *Hybanthus sensu stricto* in herbaceous habit, highly reduced cymose inflorescence, and several unique floral, fruit, seed, and anatomical features. This violet is quite nondescript, frequently forming sizeable populations that are nevertheless easily overlooked. We are following Little and McKinney (2015) in using the common name "eastern green violet" to distinguish *Cubelium concolor* from the vegetatively superficially similar "western green violet," *Pombalia attenuata*.

2. ***Pombalia parviflora*** (L.f.) Paula-Souza, in Paula-Souza and H.E.Ballard, Phytotaxa 183(1): 10. 2014; *Viola parviflora* L.f., Suppl. pl.: 360. 1782 ["1781"]; *Ionidium parviflorum* (L.f.) Vent., in Vent. & Redouté, Jard. Malmaison 1(5): pl. 27. 1803; *Solea parviflora* (L.f.) Spreng., Syst. veg. 1: 804. 1825 ["1824"]; *Ionidium glutinosum* Vent. var. *parviflorum* (L.f.) Eichler, Fl. bras. 13(1): 374. 1871; *Calceolaria parviflora* (L.f.) Kuntze, Revis.

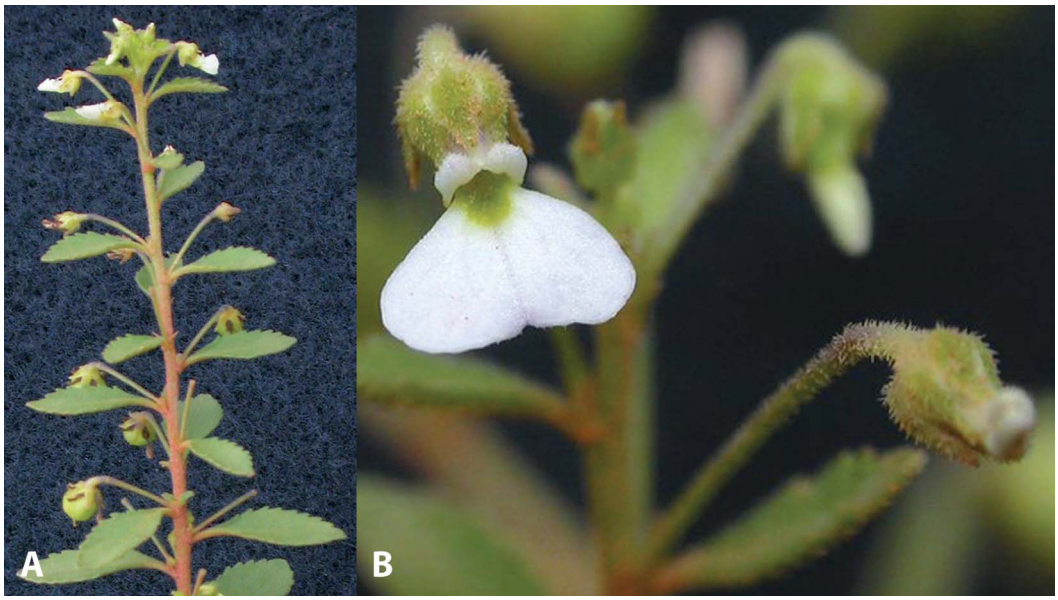

FIG. 7. *Pombalia parviflora*. (A) Upper stem (photo: Juliana Paula-Souza). (B) Chasmogamous flower (photo: Juliana Paula-Souza).

gen. pl. 3(2): 8. 1898. Type: "Habitat in Americae meridionalis calidioribus regionibus" [protologue], [no date], *Mutis s.n*. (holotype: LINN1052-25). Fig. 7.

Ionidium marcucii Bancr., Jam. Phys. J. 2: 338. 1835.

Calceolaria parviflora (L.f.) Kuntze f. *glabra* Kuntze, Revis. gen. pl. 3(3): 8. 1898.

Calceolaria parviflora (L.f.) Kuntze f. *viscosa* Kuntze, Revis. gen. pl. 3(3): 8. 1898.

Calceolaria parviflora (L.f.) Kuntze var. *normalis* Kuntze, Revis. gen. pl. 3(2): 8. 1898.

Hybanthus parviflorus (L.f.) Baill. var. *glutinosus* (Vent.) Hassl., Bull. Soc. Bot. Genève, Sér. II, 1: 214. 1909; *Hybanthus glutinosus* (Vent.) Taub., in Engl. & Prantl, Nat. Pflanzenfam., ed. 1, 3(6): 333. 1895; *Calceolaria glutinosa* (Vent.) Kuntze, Revis. gen. pl. 1: 41. 1891; *Solea glutinosa* (Vent.) Spreng., Syst. veg. 1: 804. 1825 ["1824"]; *Viola glutinosa* (Vent.) Poir., Encyc. 8: 647. 1808; *Ionidium glutinosum* Vent., in Vent. & Redouté, Jard. Malmaison 1(5): pl. 27. 1803.

Hybanthus parviflorus (L.f.) Baill. var. *angustifolius* (Eichler) Hassl., Bull. Soc. Bot. Genève, Sér. II, 1: 214. 1909; *Calceolaria parviflora* (L.f.) Kuntze var. *angustifolia* (Eichler) Kuntze, Revis. gen. pl. 1: 41. 1891; *Ionidium glutinosum* Vent. var. *angustifolium* Eichler, Fl. bras. 13(1): 374. 1871.

Hybanthus parviflorus (L.f.) Baill. var. *latifolius* (Eichler) Hassl., Bull. Soc. Bot. Genève, Sér. II, 1: 214. 1909; *Ionidium glutinosum* Vent. var. *latifolium* Eichler, Fl. bras. 13(1): 374. 1871.

Hybanthus parviflorus (L.f.) Baill. f. *microphyllus* (Kunth) Schulze-Menz, Bot. Jahrb. Syst. 67: 485. 1936; *Hybanthus microphyllus* (Kunth) Baill., Traité bot. méd. phan. 2(3): 841. 1884 ["1883-1884"]; *Ionidium microphyllum* Kunth, in Humb., Bonpl. & Kunth, Nov. gen. sp. 5(23)[quarto]: 374, pl. 495. 1823.

Hybanthus parviflorus (L.f.) Baill. f. *membranaceus* Schulze-Menz, Bot. Jahrb. Syst. 67: 485. 1936.

Hybanthus parviflorus (L.f.) Baill. var. bangii (Rusby) Sparre, Lilloa 23: 535. 1950; *Calceolaria bangii* Rusby, Mem. Torrey Bot. Club 3(3): 6. 1893.

Hybanthus parviflorus (L.f.) Baill. var. *chamaedrifolius* (C.Presl) Sparre, Lilloa 23: 535. 1950; *Ionidium chamaedrifolium* C.Presl, Reliq. haenk. 2(2): 96. 1831–1835.

Hybanthus parviflorus (L.f.) Baill. var. *argentinensis* Sparre, Lilloa 23: 535, fig. 1a, pl. 1. 1950

Viola venezuelensis Steyerm., Fieldiana, Bot. 28: 403, Fig. 84A-J. 1952.

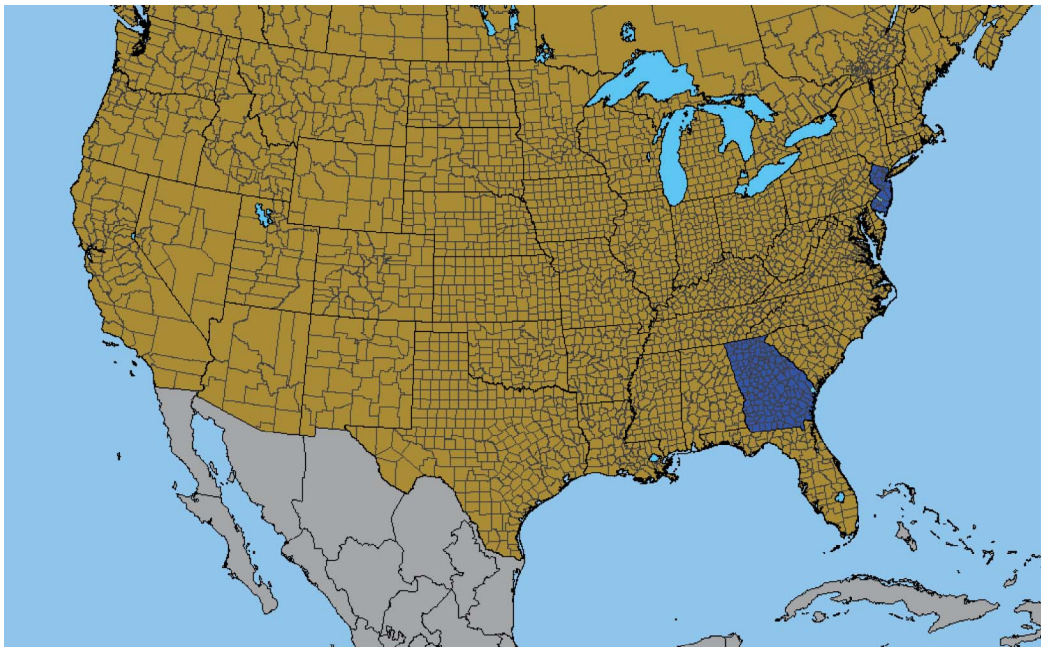

FIG. 8. United States county distribution of *Pombalia parviflora* (map: Biota of North America Program).

Common Name. Violetilla.

Description. Caulescent herb, stems branched, erect or ascending rhizomes, $\leq$ 3 dm tall; stems, petioles, lower surface of leaf blades, pedicels, and sepals glabrous to (glandular-)puberulent or (glandular-)hirtellous; stipules small, herbaceous, free, narrowly lanceolate, entire; leaves many, spreading, lowest frequently opposite, middle and upper alternate, blades (ob)lanceolate or oblong to elliptic or (ob)ovate, base attenuate or acute to rounded, apex acute to obtuse, margins crenate-serrate, $\leq$ 30(–35) $\times$ 10(–15) mm, short-petiolate; flowers axillary or in poorly defined racemose inflorescences; pedicels 3–11(–24) mm, weakly deflexed beyond the articulation; chasmogamous flower (1.5–)3.0–3.7 mm; sepals narrowly lanceolate or rarely ovate to suborbiculate, acuminate or rarely subobtuse to rounded; corolla white, frequently with purplish nectar guides on bottom petal and yellow-green throat; bottom petal much longer than others, blade moderately expanded distally, obdeltate, apex broadly rounded to truncate and weakly emarginate; chasmogamous capsules 3–4 mm long, ovoid to globose, green drying tan, unspotted; seeds *ca*. 1.5 $\times$ 1.0–1.2 mm.

Similar Species. This is distinctive among our *Pombalias* in its lanceolate to elliptic prominently crenate-serrate leaf blades and abundant small flowers and fruits. There are no similar species.

Ecology. In its native South America, it occurs in open sites, often behaving as a weed along roadsides and pastures; inhabiting railroad ballast in our region.

Distribution: Widespread in South America but mainly Andean; reported as a sporadic waif in New Jersey and established in eastern Georgia (Wofford *et al*. 2004). Fig. 8.

Rarity. None.

Phenology. Chasmogamous flower April, chasmogamous fruit July–October.

Affinities. Recent comprehensive phylogenetic investigations of the Violaceae family demonstrated that broadly circumscribed *Hybanthus* was extensively polyphyletic, and that the sole trait of a bottom petal which was saccate at base failed to delineate natural evolutionary groups (Feng 2005; Tokuoka 2008; Wahlert *et al*. 2014). The majority of New World hybanthoids formed a well-supported clade and were subsequently segregated into the resurrected genus *Pombalia* on the basis of differences in floral and seed features and anatomical traits (Paula-Souza and Ballard 2014).

FIG. 9. *Viola adunca*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Chasmogamous flowers profile view (photo: Arthur Haines, Native Plant Trust).

Hybrids. None.

Comments. The description borrows heavily from Wofford *et al*. (2004), supplemented by herbarium specimens at MO and NY. This species appears quite able to disperse long distances, presumably via human transport. In addition to its rare and sporadic occurrence in the USA, it has been confirmed as an accidental introduction in South Africa (specimens at K) and India (Parthipan 2019).

3. ***Viola adunca*** Sm., in Rees, Cycl. 37: no. 63. 1817-1818; *Viola canina* Walter var. *adunca* (Sm.) A.Gray, Bot. Gaz. 11(11): 292. 1886; *Lophion aduncum* (Sm.) Nieuwl. & Lunell, Amer. Midl. Naturalist 4: 478. 1916. Type: West coast of North America, 1803, *Menzies s.n*. (holotype: LINN1380.53 (*n.v.*), image; duplicates: BM (*n.v.*), UC-photo). Fig. 9.

Viola muhlenbergiana Ging. var. *albiflora* Hook., Fl. bor.-amer. 1: 78. 1830.

Viola diversifolia Nutt., Gen. N. Amer. Pl.: 140. 1838.

Viola longipes Nutt., in Torr. & A.Gray, Fl. N. Amer. 1: 140. 1838; *Viola adunca* Sm. var. *longipes* (Nutt.) Rydb., Mem. New York Bot. Gard. 1: 263. 1900.

Viola muhlenbergii Torr. var. *pubescens* A.Gray, Amer. J. Sci. Arts 33: 404. 1862.

Viola canina Walter var. *oxyceras* S.Watson, in W.H.Brewer & S.Watson, Bot. California 1: 56. 1876; *Viola oxyceras* (S.Watson) Greene, Pittonia 3: 255. 1897; *Viola adunca* Sm. subsp. *oxyceras* (S.Watson) Piper, Contr. U.S. Natl. Herb. 11: 395. 1906; *Viola adunca* Sm. var. *oxyceras* (S.Watson) S.Watson ex Jeps. [no bibliographic data available].

Viola canina Walter var. *puberula* S.Watson, in S.Watson & J.M.Coult., Manual, ed. 6: 81. 1890; *Viola silvestris* var. *puberula* (S.Watson) E.Sheld., Bull. Geol. Nat. Hist. Surv. 9: 17. 1894.

Viola silvatica Fr. ex Hartm.f. var. *adunca* (Sm.) Kurz, Bot. Jahrb. Syst. 19: 364. 1894.

Viola subvestita Greene, Erythea 5: 39. 1897.

Viola albertina Greene, Pittonia 4: 288. 1901.

Viola bellidifolia Greene, Pittonia 4: 292. 1901; *Viola adunca* Sm. var. *bellidifolia* (Greene) H.D.Harr., Man. Pl. Colorado: 377, 641. 1954.

Viola cardaminifolia Greene, Pittonia 4: 289. 1901.

Viola demissa Greene, Pl. baker. 3: 10. 1901.

Viola desertorum Greene, Pittonia 4: 291. 1901.

Viola filipes Greene, Pittonia 4: 289. 1901.

Viola fulcrata Greene, Pittonia 4: 285. 1901.

Viola inamoena Greene, Pl. baker. 3: 11. 1901.

Viola oreocallis Greene, Pittonia 4: 288. 1901.
Viola petrophila Greene, Pittonia 4: 286. 1901.
Viola stenantha Greene, Pl. baker. 3: 10. 1901.
Viola unguiculata Greene, Pittonia 4: 291. 1901.
Viola anisopetala Greene, Leafl. bot. observ. 2(2): 97. 1910–1912; *Lophion anisopetalum* (Greene) Nieuwl. & Lunell, Amer. Midl. Naturalist 4: 478. 1916.
Viola centellifolia Greene, Leafl. bot. observ. 2(2): 98. 1910–1912.
Viola cordulata Greene, Leafl. bot. observ. 2(2): 33. 1910–1912.
Viola huronensis Greene, Leafl. bot. observ. 2(2): 96. 1910–1912.
Viola oxysepala Greene, Leafl. bot. observ. 2(2): 34. 1910–1912.
Viola uncinulata Greene, Leafl. bot. observ. 2(2): 97. 1910–1912; *Viola adunca* Sm. var. *uncinulata* (Greene) Applegate, Amer. Midl. Naturalist 22: 282. 1939; *Viola adunca* Sm. var. *uncinulata* (Greene) C.L.Hitchc., Vasc. Pl. Pacific NorthW. 3: 440. 1961.
Viola verbascula Greene, Leafl. bot. observ. 2(2): 32. 1910–1912.
Viola adunca Sm. var. *glabra* Brainerd, Rhodora 15: 109. 1913; *Lophion aduncum* Nieuwl. & Lunell var. *glabrum* (Brainerd) Nieuwl. & Lunell, Amer. Midl. Naturalist 4: 478. 1916; *Viola adunca* Sm. f. *glabra* (Brainerd) G.N.Jones, Univ. Wash. Publ. Biol. 5: 194. 1936.
Viola adunca Sm. subsp. *ashtonae* M.S.Baker, Madroño 3: 233, pl. 11, figs. 4, 7. 1936.
Viola adunca Sm. subsp. *radicosa* M.S.Baker, Madroño 3: 234, pl. 11, fig. 5. 1936.
Viola adunca Sm. subsp. *typica* M.S.Baker, Madroño 3: 233. 1936.
Viola adunca Sm. f. *albiflora* Vict. & J.Rousseau, Contr. Inst. Bot. Univ. Montreal 36: 20. 1940.
Viola bellidifolia Greene subsp. *typica* M.S.Baker, Madroño 5: 223. 1940.
Viola bellidifolia Greene subsp. *valida* M.S.Baker, Madroño 5: 223, pl. 21, 22, fig. 8. 1940.
Viola adunca Sm. f. *candida* Lepage, Naturaliste Canad. 79: 180. 1942.
Viola cascadensis M.S.Baker, Leafl. W. Bot. 5: 173. 1949; *Viola adunca* Sm. var. *cascadensis* (M.S.Baker) C.L.Hitchcock, Vasc. Pl. Pacific NorthW. 3: 440. 1961.
Viola adunca Sm. var. *kirkii* V.G.Duran, Leafl. W. Bot. 10: 319. 1966.

Common Name. Hook-spurred violet.

Description. Caulescent perennials from somewhat slender rhizome, stems ascending in flower but commonly reclining in fruit, commonly > 2, < 16 cm tall; stems, foliage, and peduncles blue-green, puberulent (very rarely glabrous in our region) with hairs up to 0.30 mm long, guard cells 22–30 μm long; leaves cauline and basal, cauline distributed along stem; stipules free, deeply incised; leaves ascending to spreading, leaf blades undivided, largest $\leq 33 \times 28$ mm, narrowly ovate-triangular to narrowly ovate, base broadly rounded to subcordate, margins subcrenate to subentire and often revolute, ciliolate (rarely eciliate), apex narrowly rounded; chasmogamous flower ≤ 16 mm; calyx glabrous or sepals puberulent along midvein, eciliate; lowest sepals linear-lanceolate to lanceolate, acute; auricles short and entire or prominent and erose, not elongating in fruit; corolla medium to dark blue, throat white; spur elongate, slender, 5–7 mm, blue to white; lateral petals densely bearded with filiform hairs, spurred petal glabrous; style abruptly expanded into head; projections on head (when present) cylindrical, lengths up to 1/6 the width of the head; tip below stigmatic orifice abruptly bent upward at *ca*. 90°; pollen grains 3.2–4.6 μm in diameter; cleistogamous flowers produced after chasmogamous; capsule 6–9 mm, green drying tan, unspotted or with fine red spots, glabrous; seeds $1.5–2.0 \times 0.9–1.0$ mm, medium to dark brown, unspotted; $2n = 20$.

Similar Species. This caulescent northern species and the mat-forming southern *V. walteri* share the unusual feature of densely puberulent foliage. It is very similar to the boreal tetraploid *V. aduncoides* (not yet confirmed in our region) but can be distinguished by the several style features and shorter foliage puberulence as noted in the key. It is immediately distinct from *V. labradorica* and other nonpuberulent caulescent species by its dark blue-green typically puberulent foliage, narrowly ovate leaf blades with subentire to shallowly crenate and often revolute margins, and deeply lacerate stipules.

Ecology. Dry sandy and rocky ground in forests and parklands, rock crevices or talus.

Distribution. Transcontinental, Greenland to Alaska, south to Connecticut, Wisconsin, and northwestern Nebraska, widespread in the Rocky Mountains south to the Mexico border. Fig. 10.

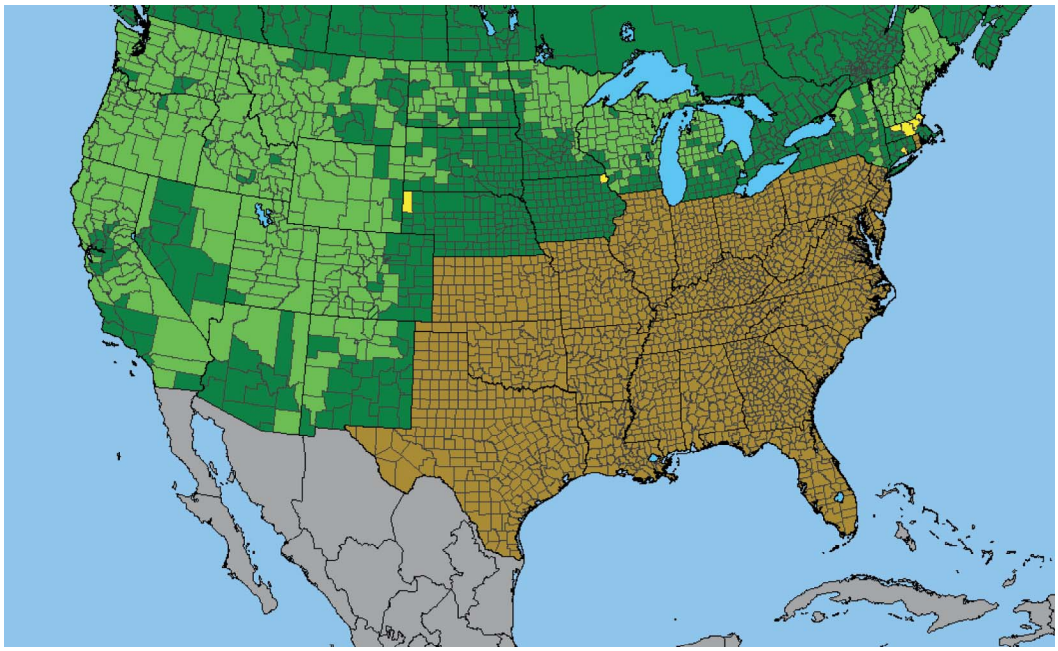

FIG. 10. United States county distribution of *Viola adunca* (map: Biota of North America Program).

Rarity. Listed in Connecticut, Iowa, and Massachusetts.

Phenology. Chasmogamous flower May–June, chasmogamous fruit June–July, cleistogamous fruit July–September.

Affinities. This species belongs to the Rostrate Violet lineage, sect. *Viola*, subsect. *Rostratae* (Kupffer) W.Becker.

Hybrids. Hybridizes with *V. adunicoides* (McPherson and Packer 1974) and *V. labradorica* (Brainerd 1924; Ballard 1992, 1995; Haines *et al*. 2011). According to McPherson and Packer (1974) and Brainerd (1924), both hybrids are sterile, neither reproducing by chasmogamous flowers nor producing viable cleistogamous seeds. The first author has observed the hybrid with *V. labradorica* and have found the features of chasmogamous flowers and foliage to be precisely intermediate, although Brainerd reports some variation.

Comments. Smith's protologue in Rees' *Cyclopedia* states that the plants on which the description is presumably based were "Brought by Mr. Menzies from the west coast of North America." Stafleu and Cowan (1985) state that Smith's herbarium was bought by the Linnean Society from the Smith estate in 1829, and that the types are at LINN; the types have been digitized. Other material is at several other herbaria. There is a single sheet, LINN1380.53, imaged in the the Smith Herbarium of the online LINN database, labeled by hand as collected by Archibald Menzies in 1803, with the same information as the protologue. There is sufficient evidence to accept this as the holotype. A photo of an isotype at BM has also been seen.

This species and *V. aduncoides* are immediately distinguishable from other rostrate violets by their blue-green foliage color, subentire leaf blades, and (commonly in our region) densely puberulent indument. Brainerd (1921b), Brainerd Baird (1942), Russell (1965), Ballard (1995), Haines *et al*. (2011), Voss and Reznicek (2012), and Little and McKinney (2015) accepted *V. adunca* as a distinct, broadly delimited species (implicitly including *V. aduncoides*) separate from *V. labradorica*, while Fernald (1950), Alexander (1963), and Scoggan (1978) treated the present species as var. *adunca* and segregated glabrous plants of *V. adunca* together with boreal and alpine populations of *V. labradorica* as *V. adunca* var. *minor* (Hook.) Fernald, following Fernald's (1949) initial taxonomic error of treating the two taxa as equivalent (see *V. labradorica* for clarification on this). Gleason and Cronquist (1991) synonymized

both under *V. adunca*. *Viola adunca* as a species complex is quite variable across its range, with more than 50 names attributed to that variability. Typical *V. adunca sensu lato*, with densely puberulent foliage, is the ubiquitous form in our region. Glabrous plants across the range of *V. adunca sensu lato* have received various names, including var. *glabra* Brainerd (type material from Bonaventure, Quebec, which could be assumed to belong to *V. adunca sensu stricto*). Glabrate to glabrous plants in our region invariably grow intermingled with puberulent ones in exposed sites such as conglomerate Great Lakes shorelines or windswept bluffs, where immediate environmental conditions could obviously abrade the foliage epidermis or hairs. Indument loss in this case is probably a phenotypic response rather than a genetically fixed trait, and taxonomic recognition of glabrous or glabrate plants in our region seems unwarranted. Conversely, in western North America such plants often proliferate uniform populations separate from puberulent populations, often at higher elevations, and additionally express other foliage and floral differences from typical *V. adunca* or *V. aduncoides*. Some of these (*e.g.*, *V. bellidifolia* Greene) very likely deserve taxonomic recognition at the species level (R. McCauley, Fort Lewis College, personal communication).

McPherson and Packer (1974) documented fertile diploid ($2n = 20$) and tetraploid ($2n = 40$) cytotypes, and a sterile triploid ($2n = 30$) cytotype assumed to be the hybrid. They observed that the style head of the diploids bore longer, more crowded cylindrical projections, longer hairs on the foliage (when present), shorter guard cells, and smaller pollen grains. Photographs of the styles also suggest that the diploid style abruptly expands near the head and the tip containing the stigmatic orifice is abruptly bent upward at *ca*. 90°, while the tetraploid style remains nearly uniformly cylindrical to the head and the tip containing the stigmatic orifice is angled upward at *ca*. 45°, although the authors made no comment on this. Diploids comprised all specimens and study populations north and east of Lake Superior, as well as south of the USA-Canadian border in western North America, with only sporadic occurrences northward in the range of the tetraploid. The tetraploid was confined to the region of Canada west-northwest from the north shore of Lake Superior. The authors noted that the diploid differed slightly biochemically, flowered 2 wk earlier than the tetraploid in the greenhouse, and was further isolated by the absolute sterility of the triploid hybrids. Although the type of *V. adunca* Sm. was likely collected by Menzies in a region dominated by diploids and could be assumed to be diploid, McPherson and Packer (1974) hesitated to provide a name to one of the cytotypes because the status of the type was not yet confirmed with certainty. That did not stop Löve and Löve (1976) from publishing the name *V. aduncoides* for the tetraploid, based on a type from Winnipeg, Manitoba. Mauer *et al*. (1978) later studied the cytotypes physiologically but found no statistical differences in their behavior. Ballard (1992) examined macromorphological traits of flowers and leaves across the range of *V. adunca* and was unable to separate macromorphological taxa in *V. adunca sensu lato* based on leaf morphology alone; nevertheless, the two cytotypes are morphologically differentiated in style morphology and indument, and foliage indument; they express a phenological shift in chasmogamous flowering suggesting some degree of physiological differentiation, are reproductively isolated by ploidy level, and have largely allopatric distributions. They are recognized here as distinct evolutionary species, applying the name *V. aduncoides* for the tetraploid. According to McPherson and Packer's distribution map, our northeastern populations are *V. adunca*, while those in the Thunder Bay region and northwest are mostly *V. aduncoides*.

4. ***Viola affinis*** Leconte, Ann. Lyceum Nat. Hist. New York 2: 138. 1828 ["1826"]; *Viola sororia* Willd. var. *affinis* (Leconte) L.E.McKinney, Sida, Bot. Misc. 7: 39. 1992 [without basionym]; *Viola sororia* Willd. subsp. *affinis* (Leconte) R.J.Little, Phytologia 72(2): 78. 1992; *Viola sororia* Willd. subsp. *affinis* (Leconte) R.J.Little, Phytologia 80(4): 295. 1996. Type: J. E. Leconte, plate number 24 of Leconte's unpublished watercolors, call number QK 495 V811 L496f, University of Notre Dame Libraries, Department of Special Collections, Section of Rare Books (lectotype (designated by Nir Gil-ad, Boissiera 53: 51. 1997): ND; isolectotype: K). Fig. 11.

Viola papilionacea Pursh, Fl. Amer. sept. 1: 173. 1813–1814 [requires proposal for rejection].

Viola nepetifolia Greene, Pittonia 5: 92. 1902.

Viola affinis Leconte var. *subarctica* J.Rousseau, Canad. J. Res. 28, sec. C: 245. 1952 ["1950"].

Viola affinis Leconte f. *albiflora* L.K.Henry, Castanea 18: 45. 1953.

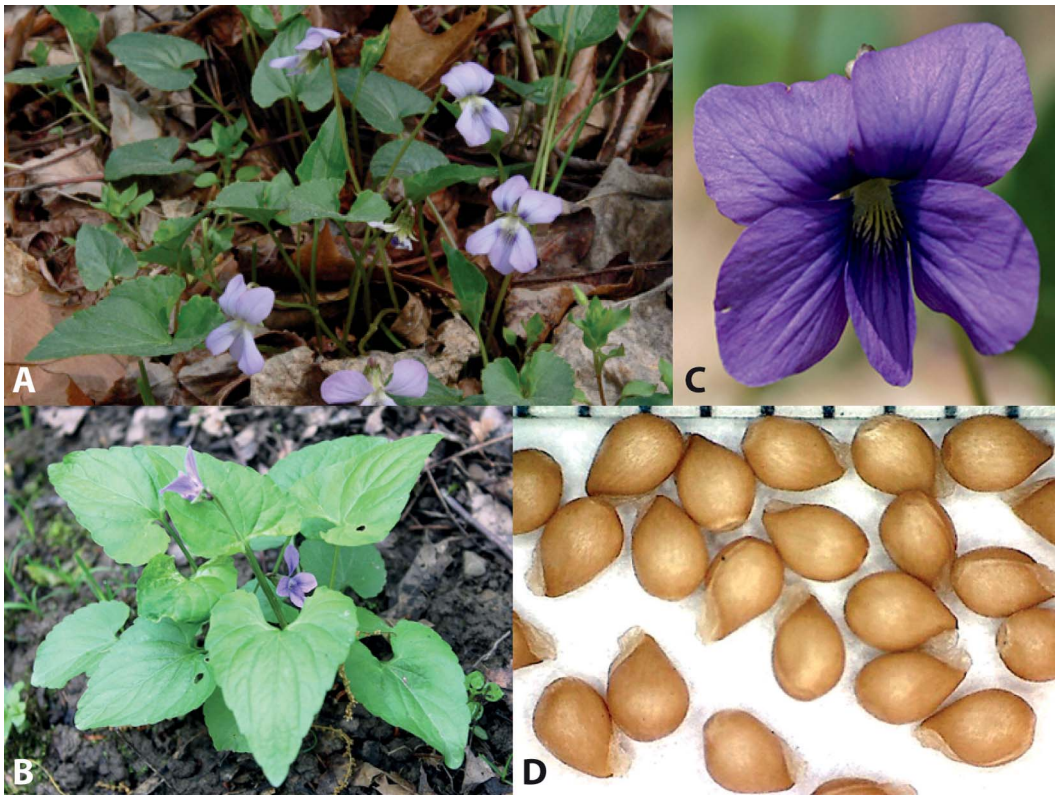

FIG. 11. *Viola affinis*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Leaves during chasmogamous flower (photo: Jack Pierce). (C) Chasmogamous flower front view (photo: Andrew Lane Gibson). (D) Seeds from herbarium specimen: transplanted from North Carolina, Cumberland Co., H. *Ballard et al. 15-005F* (BHO).

Common Names. Leconte's violet, sand violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 23 cm; foliage and peduncles green, glabrous except for scattered, small, subappressed hairs on upper surface of leaf blades; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest $\leq 72 \times 68$ mm, in spring distinctly longer than broad and narrowly ovate-triangular, apex acute to narrowly rounded, in summer broadening to about as broad as long or broader and broadly ovate-triangular, apex acute to obtuse, base shallowly to deeply cordate, margins crenate but becoming more remote and shallow near apex, eciliate; chasmogamous peduncle held among the leaves, glabrous; chasmogamous flower $\leq$ 23 mm; calyx glabrous, eciliate; lowest sepals narrowly oblong-lanceolate to lanceolate, acute; auricles short and entire, not elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to slightly clavate hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles and arching just before capsule dehiscence; cleistogamous capsule 6–10 mm, yellow-green drying tan with purple spots or blotches, often hirtellous; seeds 1.4–2.0 $\times$ 0.9–1.4 mm, light to medium yellow- or orange-brown, unspotted; $2n = 54$.

Similar Species. This species has the distinction of being the only *Borealiamericanae* violet to have frequently hirtellous cleistogamous capsules; the only other acaulescent eastern North American violet with hirtellous capsules is the often-cultivated and escaped European *V. odorata*. In chasmogamous flower, with its narrowly ovate leaf blades longer than broad, this species can be distinguished from *V. cucullata* by its short rounded auricles, lack of a conspicuously contrast-

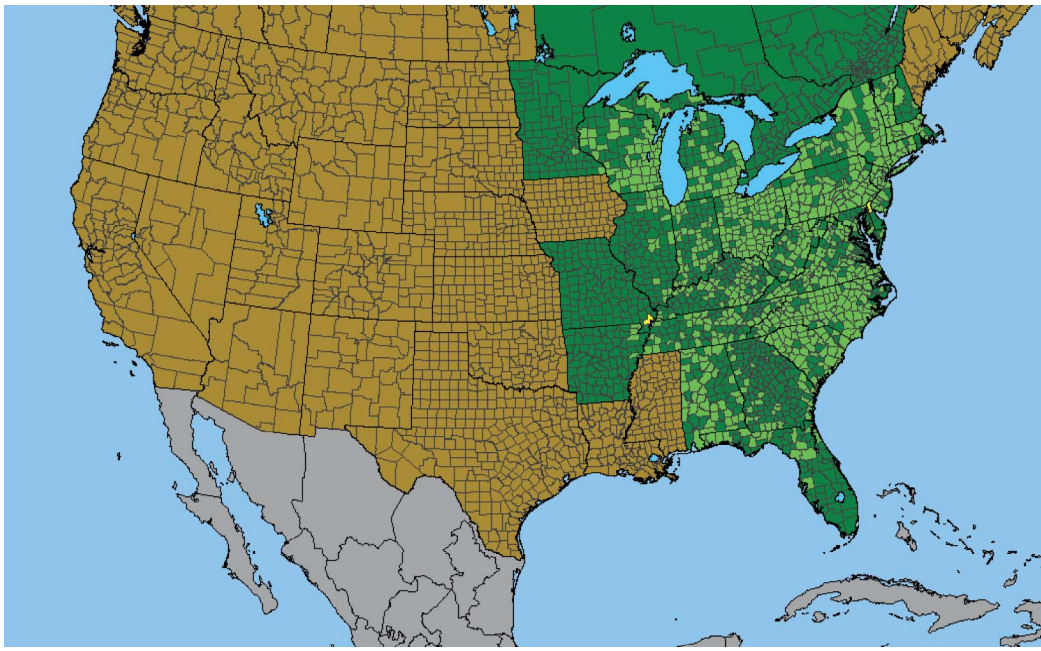

FIG. 12. United States county distribution of *Viola affinis* (map: Biota of North America Program).

ing dark purple eyespot around the throat, long narrowly linear to weakly clavate hairs in the lateral petal beards, and densely bearded spurred petal; from *V. langloisii* (not yet confirmed in our region) by its strongly ascending to erect leaves, short rounded auricles, and densely bearded spurred petal; from *V. missouriensis* by leaves with the upper surface bearing scattered subappressed hairs, lanceolate to linear-lanceolate acuminate eciliate sepals, and densely bearded spurred petal; and from *V. pratincola* and *V. retusa* by its leaves with upper surface bearing scattered subappressed hairs, and short rounded auricles. In cleistogamous fruit, once its leaves have broadened substantially, it can be separated from *V. communis*, *V. cucullata*, *V. langloisii*, *V. pratincola*, and *V. retusa* by the heavily spotted or blotched (and occasionally hirtellous) cleistogamous capsule on a prostrate peduncle; from *V. sororia* (glabrous and *hirsutuloides* variants) by its narrow sharply acute sepals and yellow- to orange-brown seeds. It is distinct from *V. missouriensis* in its leaves with upper surfaces bearing scattered subappressed hairs, and lanceolate to linear-lanceolate acuminate eciliate sepals.

Ecology. Damp to saturated or inundated, often sandy soils bordering vernal pools, streams, and rivers in mesic to wet forests, and on terraces in floodplains and swamp borders.

Distribution. Widely distributed in eastern North America, Massachusetts and Quebec to southeastern Minnesota, south to Florida, Alabama, and northeastern Arkansas (Gulf Coast range currently being disentangled from *V. langloisii* and other taxa). Fig. 12.

Rarity. Listed in Missouri.

Phenology. Chasmogamous flower April–May, chasmogamous fruit June, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium*, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Affinis species group.

Hybrids. Hybridizes with *V. baxteri* (Brainerd 1924; Haines *et al*. 2011), *V. brittoniana* (Dowell 1910; Brainerd 1924; House 1924), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (House 1906b, 1924; Brainerd 1924), *V. cucullata* (Brainerd 1906c, 1924; House 1924; Gaiser and Moore 1966; Haines *et al*. 2011), *V. emarginata sensu stricto* (Brainerd 1924), *V. fimbriatula* (Dowell 1910; Brainerd 1924; House 1924; Haines *et al*. 2011), *V. hirsutula* (Brainerd

1906c, 1924; House 1906b, 1924; Dowell 1910), *V. nephrophylla* (Brainerd 1906c, 1924; House 1924; Haines *et al*. 2011), *V. palmata* var. *triloba* (Brainerd 1924), *V.* "*palmata pseudostoneana*" (Hastings 2018; H.E.B., personal observation), *V. sagittata* (Brainerd 1906c, 1910b, 1924; House 1924; Russell and Risser 1960; Russell 1965), *V. septentrionalis* (Brainerd 1904b, 1907b, 1924; House 1924), *V. sororia sensu stricto* (Brainerd 1904b, 1924; House 1924; Gaiser and Moore 1966; Haines *et al*. 2011), and *V. subsinuata* (Dowell 1910; Brainerd 1924; House 1924). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). Hybrids fail to reproduce by chasmogamous flowers, and the cleistogamous capsules either abort or produce a substantially reduced proportion of viable seeds.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Ballard (1995, 2000), Gil-ad (1995, 1997, 1998), Haines *et al*. (2011), Voss and Reznicek (2012), and Weakley *et al*. (2012) maintained this species (although Haines *et al*. included *V. latiuscula*, and Ballard included *V. langloisii*, *V. missouriensis*, and *V. rosacea*); and Scoggan (1978) referred all Canadian material to var. *subarctica* Rousseau. Gleason and Cronquist (1991) synonymized it under *V. sororia* as a form with the spurred petal bearded. McKinney (1992) interpreted that *V. affinis* Leconte and *V. nephrophylla* Greene were synonymous, then made the (illegitimate) new combination *V. sororia* Willd. var. *affinis* (Leconte) McKinney to accommodate the collective taxon. Little and McKinney (2015) later reinstated the two as separate species. Extensive field studies and abundant herbarium collections support recognition of the two as wholly distinct evolutionary species, and consultation of protologues and types confirm the traditional application of names as correct. Although Brainerd (1921b) and others have included *V. crenulata* Greene and *V. venustula* Greene as synonyms of this species, some of the traits observed on type material indicate that these are better considered *de novo* hybrids with *V. nephrophylla*. This species is widely distributed in our region east of the Great Plains and western Midwest states but is commonly misidentified as the more commonly encountered *V. cucullata* or *V. sororia*. While it may form large linear populations in floodplains of larger river systems, it typically occurs as scattered solitary plants along smaller stream terraces and swamp borders, and it is likely overlooked. Scattered records of *V. affinis* from northwestern Illinois and southern Wisconsin in the region of overlap with *V. missouriensis* have been confirmed. Contrary to Russell's (1965) statement that the two taxa intergrade with each other and with other taxa of the *V. affinis* complex, field and herbarium studies demonstrate that all members of the complex consistently maintain their many morphological distinctions, and each taxon simply "drops out" at the limits of their geographic range, presumably as ecological conditions become inhospitable to their persistence. Due to previous confusion and synonymization of this species with *V. langloisii* and other taxa south of our region, the Gulf Coast portion of the range of *V. affinis* is uncertain, and the map for this species south of our region must be regarded as tentative. This and other members of the Affinis species group are currently under study by Remington Burwell at Ohio University.

5. ***Viola appalachiensis*** L.K.Henry, Castanea 18: 131. 1953 [replacement name for *V. allegheniensis*]; *Viola allegheniensis* L.K.Henry [homonym of *V. alleghanensis* Roem. & Schult. (1819)], Castanea 18: 53, pl. 2. 1953; *Viola walteri* House var. *appalachiensis* (L.K.Henry) L.E.McKinney ex S.P.Grund & B.L.Isaac, Castanea 72(1): 59. 2007. Type: USA Pennsylvania, Somerset Co.: 2.5 mi SE of Somerset on Rt. 219, along Kimberly Run, 13 May 1950, *L. K. Henry & W. E. Buker s.n.* (lectotype (designated by Grund & Isaac, Castanea 72: 59. 2007): CM107915; isolectotype, CM0064). Fig. 13.

Common Names. Appalachian violet, Henry's violet.

Description. Caulescent mat-forming perennials from somewhat slender rhizome, flowering stems short and ascending, later prostrate, persistent and node-rooting, commonly ≥ 2, ≤ 7 cm tall; stems, foliage, and peduncles green, glabrous except for scattered hairs on upper leaf blade surfaces; leaves cauline and basal, cauline distributed along stem; stipules free, weakly lacerate with marginal processes $< 1/4$ as long as the stipule; leaves ascending to spreading, leaf blades undivided, largest $\leq 35 \times 37$ mm, broadly ovate to reniform,

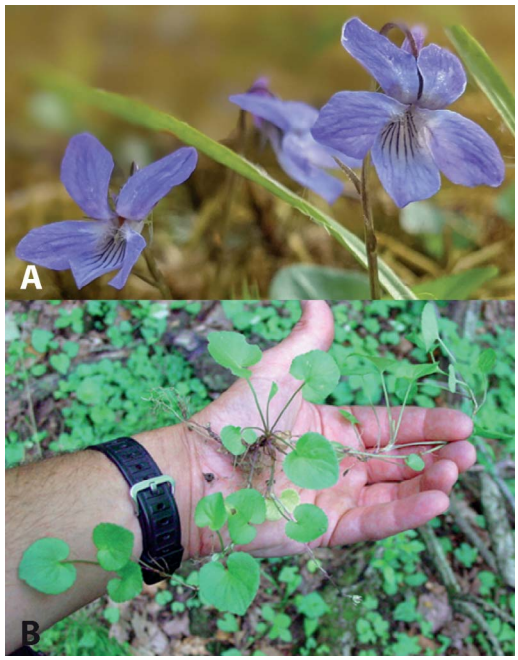

FIG. 13. *Viola appalachiensis*. (A) Chasmogamous flowers (photo: Chris Poling). (B) Stolons (photo: James Henderson).

base deeply cordate, margins crenate, eciliate, apex broadly rounded; chasmogamous flower $\leq$ 16 mm; calyx glabrous, eciliate; lowest sepals lanceolate, acute; auricles short and entire, not elongating in fruit; corolla pale blue, with white throat extending onto base base of lateral and spurred petal, throat white; spur moderately elongate, slender, 4–5 mm, blue to white; lateral petals densely bearded with filiform hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 4.5–5 mm, green drying tan, unspotted or with fine red spots, glabrous; seeds *ca*. 1.5 mm long, light brown, unspotted.

Similar Species. This species and *V. walteri* are our only mat-forming members of subsect. *Rostratae*. This species could be mistaken for *V. labradorica* in flower or fruit if the mat-forming habit with node-rooting stolons were ignored. It differs from *V. striata* by its mat-forming habit and pale blue corolla. It is distinct from *V. walteri* in foliage lacking pubescence except for scattered subappressed hairs on the upper surface of leaf blades, uniformly green leaves, weakly lacerate stipules, and other features as noted in the key. The herbaceous lacerate stipules with nonglandular processes would distinguish it in fruit from stoloniferous members of subsect. *Stolonosae*.

Ecology. Moist loam on stream terraces in mesic forests, rich cove forests, and on mafic or ultramafic rocks especially in seepage, serpentine, and olivine barrens, and in disturbed sites such as stream- or lakeside lawns and old roadbeds through coves.

Distribution. Northern and central Appalachians, Pennsylvania, Maryland, and West Virginia; disjunct in western North Carolina. Fig. 14.

Rarity. Listed in Maryland and Pennsylvania.

Phenology. Chasmogamous flower May–June, chasmogamous fruit June, cleistogamous fruit September.

Affinities. This species belongs to the Rostrate Violet lineage, sect. *Viola*, subsect. *Rostratae* (Kupffer) W.Becker.

Hybrids. Hybridizes with *V. striata* (Ballard 1992, 1993). Hybrids with *V. labradorica* and *V. rostrata* should be sought, as *V. appalachiensis* and the latter species occasionally grow in local sympatry. Hybrids fail to reproduce by chasmogamous flowers, and cleistogamous capsules fail to produce viable seeds.

Comments. Henry's publication of *Viola alleghaniensis* erroneously states "...flood-plain of Kimberly Run, 2.5 mi. southwest of Somerset (type locality), May 15, 1950, and Sept. 6, 1952, LKH, WEB", doesn't mention Route 219, and gives an incorrect spring flowering date, as well as citing two different collections. Grund and Isaac (2007) later corrected the errors concerning collections noted in Henry's (1953a) publication, designated a lectotype from the three collections Henry presented as types.

Davis and Davis (1949) discovered a mat-forming, node-rooting rostrate violet in West Virginia, which they initially identified as *V. labradorica*, then considered an alpine and boreal species. Platt (1950) studied such anomalous populations in West Virginia, Pennsylvania, and Maryland and reported that these did not match *V. labradorica*, rather they differed in several macromorphological features from *V. walteri*. Henry (1953a, b) promptly studied the taxon and named it *V. alleghaniensis* (an illegitimate homonym of the same name applied earlier to *V. sagittata*), then later provided the new name *V. appalachiensis*

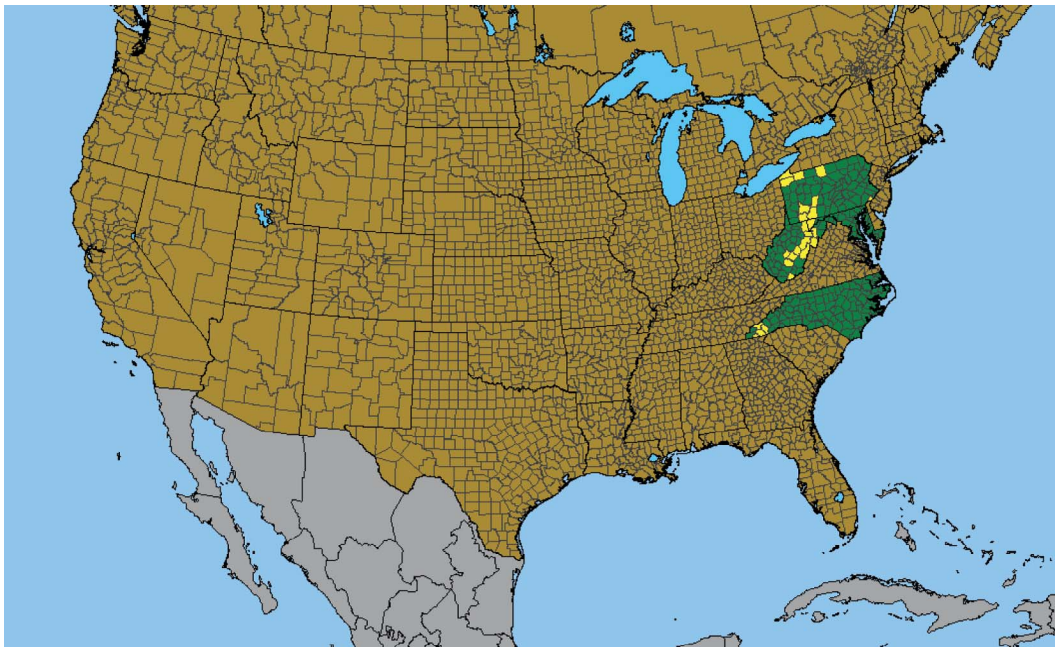

FIG. 14. United States county distribution of *Viola appalachiensis* (map: Biota of North America Program).

with the same type. Russell (1965) examined field populations and herbarium specimens and concluded that the violet represented depauperate *V. labradorica* ("*V. conspersa*") or *V. walteri* transitioning to the former. Strausbaugh and Core (1978) and Ballard (2000) maintained it as a species distinct from *V. walteri*. McKinney and Russell (2002) produced an invalid varietal combination for it under *V. walteri*. Grund and Isaac (2007) later provided a valid varietal combination as well as additional information on the rarity of this regional endemic. Weakley *et al.* (2012) and Little and McKinney (2015) maintained the present taxon as a variety under *V. walteri*. Ballard (1992) and Ballard and Wujek (1994) demonstrated that this violet is fully distinct macromorphologically, micromorphologically, and ecologically from *V. walteri*, that it inhabits a geographic range nearly allopatric from the latter, and that it is deserving of species rank. This species and *V. walteri* are the only two North American species in the subsect. *Rostratae* that are mat-forming through persistent node-rooting stems. The single shared trait of persistent mat-forming stems seems to have driven repeated efforts to subsume both species into one despite the many other consistent differences; but nobody has suggested the converse proposal of sinking all the other rostrate violets into a single species because of their shared aerial stems. The present species shares certain traits with *V. labradorica* and others with *V. walteri*. The shared traits and the low reproduction in terms of mature capsules and viable seeds urged Ballard and Wujek to propose that *V. appalachiensis* might be the product of hybrid speciation involving the other two species. It is nevertheless a stable and distinct entity deserving of species rank.

6. ***Viola arcuata*** Blume, Bijdr.: 58. 1826 ["1825"]. Fig. 15.

Viola notoniana Wall., Numer. List: no. 1449. 1829 [not validly published].

Viola distans Wall., Trans. Med. Soc. Calcutta 7: 227. 1835.

Viola alata Burgersd., F.A.W.Miquel, Pl. Jungh.: 121. 1852.

Viola verecunda A.Gray, Mem. Amer. Acad. Arts, n.s., 6: 382. 1858; *Viola alata* Burgersd. subsp. *verecunda* (A.Gray) W.Becker, Beih. Bot. Centralbl. 34(2): 227. 1916.

Viola wightiana Wall. var. *glabra* Thwaites, Enum. Pl. Zeyl.: 20. 1858.

Viola excisa Hance, J. Bot. 6: 296. 1868.

Viola metziana Hohen. ex Hook.f., Fl. Brit. India 1: 184. 1872 [not validly published].

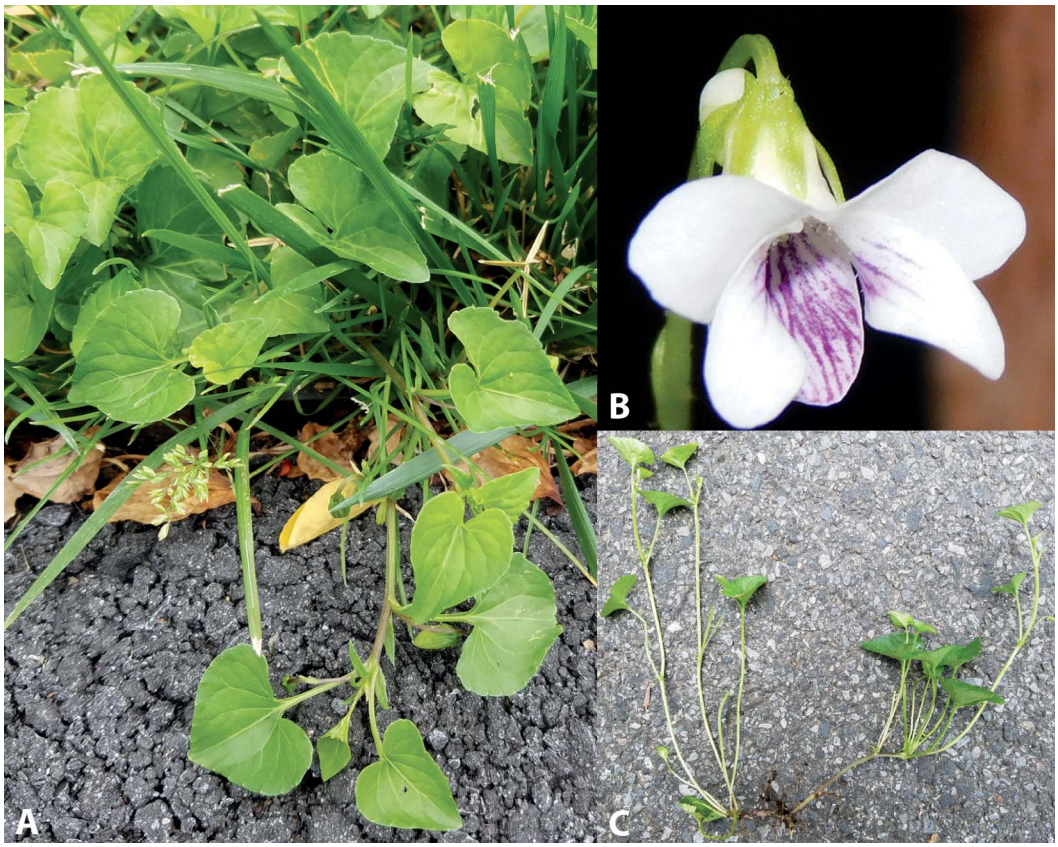

FIG. 15. *Viola arcuata*. (A) Summer vegetative habit (photo: Harvey Ballard). (B) Chasmogamous flower (photo: Tyler Fishman). (C) Prostrate node-rooting stems (photo: Harvey Ballard).

Viola verecunda A.Gray var. *semilunaris* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 23: 335. 1877; *Viola semilunaris* (Maxim.) W.Becker, Beih. Bot. Centralbl. 34(2): 231. 1916.

Viola japonica var. *decumbens* Franch. & Sav., Enum. Pl. Jap. 2(2): 287. 1878.

Viola japonica var. *pusilla* Franch. & Sav., Enum. Pl. Jap. 2(2): 287. 1878.

Viola japonica var. *subaequiloba* Franch. & Sav., Enum. Pl. Jap. 2(2): 287. 1878.

Viola verecunda A.Gray var. *excisa* (Hance) Maxim., Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 9: 750. 1886.

Viola alata W.Becker, Beih. Bot. Centralbl. 20(2): 125. 1906 [homonym of *V. alata* Burgersd. (1852)].

Viola toppingii Elmer, Leafl. Philipp. Bot. 2: 504. 1908.

Viola verecunda A.Gray f. *radicans* Makino, Bot. Mag. (Tokyo) 27: 153. 1913.

Viola fibrillosa W.Becker, Beih. Bot. Centralbl. 34(2): 229. 1916.

Viola hupeiana W.Becker, Beih. Bot. Centralbl. 34(2): 232. 1916.

Viola lunata Ridl., Trans. Linn. Soc. London, Bot. 9: 17. 1916.

Viola arcuata Blume f. *radicans* (Makino) Nakai, Bot. Mag. (Tokyo) 36: 88. 1922.

Viola arcuata Blume var. *verecunda* (A.Gray) Nakai, Bot. Mag. (Tokyo) 36: 88. 1922.

Viola excisa Hance var. *subaequiloba* (Franch. & Sav.) Nakai, Bot. Mag. (Tokyo) 36: 85. 1922.

Viola yakusimana Nakai, Bot. Mag. (Tokyo) 36: 35. 1922.

Viola carlesii Nakai, Bot. Mag. (Tokyo) 42: 557. 1928.

Viola verecunda A.Gray f. *hensoaensis* Kudô & Sasaki, Rep. (Annual) Taihoku Bot. Gard. 1: 37. 1931.

Viola semilunaris W.Becker var. *divaricata* Honda, Bot. Mag. (Tokyo) 46: 677. 1932.

Viola herbivaga Ridl., J. Bot. 73: 17. 1935.

Viola verecunda A.Gray var. *fibrillosa* (W.Becker) Ohwi, Bull. Natl. Sci. Mus. Tokyo 33: 80. 1953.

Viola verecunda A.Gray var. *yakusimana* (Nakai) Ohwi, Bull. Natl. Sci. Mus. Tokyo 33: 80. 1953.

Viola verecunda A.Gray f. *divaricata* (Honda) F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 221. 1954.

Viola verecunda A.Gray var. *subaequiloba* (Franch. & Sav.) F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 221. 1954.

Viola verecunda A.Gray f. *violascens* Hiyama ex F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 221. 1954.

Viola verecunda A.Gray f. *variegata* Honda, Nom. Pl. Jap., ed. emend.: 389. 1957.

Viola verecunda A.Gray f. *candidissima* M.Mizush. ex E.Hama, J. Jap. Bot. 51: 340. 1976.

Common Names. None in English.

Description. Caulescent perennials from somewhat slender prostrate rhizome, reportedly also stoloniferous, stems bra7.nched and decumbent in their basal half and commonly rooting at lower nodes, the distal portions ascending, $\leq$ 35 cm tall; stems, cauline leaves and peduncles light to medium green, basal leaves deeper green, glabrous or the lower surface sparsely puberulent along veins; leaves cauline and basal, cauline distributed along stem; stipules free, entire to remotely denticulate; leaves ascending or spreading, leaf blades undivided, largest $\leq 30 \times 55$ mm, reniform-deltate, base shallowly and broadly cordate, margins shallowly crenate or low-serrate, eciliate, apex broadly rounded to obtuse (leaf blades thus lunate); chasmogamous flower $\leq$ 8 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate, acuminate; auricles very short and entire, not elongating in fruit; corolla white to pale violet, throat white; spur short, slender, *ca*. 2 mm, white to pale violet; lateral petals sparsely bearded with narrowly linear hairs or glabrous, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 6–8 mm, green drying tan, unspotted, glabrous; seeds *ca*. 1.5×1.0 mm, yellowish, unspotted, with a basal membranous wing on one side; $2n = 24$.

Similar Species. This species is distinctive in its broadly reniform-deltate cauline leaves with somewhat remotely low-serrate margins, but the occasionally white corolla, short spur, and basally reclining stems could be confused with *V. striata* if the proportionally broader leaf blades were ignored. The commonly node-rooting basal portion of the stems and slender entire to remotely denticulate stipules would distinguish this species.

Ecology. In its native range this species is said to inhabit "Moist and marshy places, grasslands, grassy places on mountain slopes, thickets, forest margins, fields, alongside houses" (Chen *et al*. 2007); in and around The New York Botanical Garden the violet is common in moister well-watered areas of lawns; in a park farther south in New York City and another park along Skyline Drive in New Jersey the violet grows in planting beds or pots, presumably brought in with nursery stock or bedding plants.

Native to east temperate and tropical Asia, confirmed in New York and New Jersey as the first Western Hemisphere reports by Rob Naczi and Harvey Ballard in 2022 from observed populations and iNaturalist posts. Fig. 16.

Rarity. None.

Phenology. Chasmogamous flower in May (in our region), fruiting data not available.

Affinities. This species belongs to sect. *Plagiostigma*, subsect. *Bilobatae* (W.Becker) W.Becker.

Hybrids. None.

Comments. Although this is a newly discovered introduction, it is well established in lawns in and around The New York Botanical Garden and in planting beds and pots elsewhere in New York City and a park along Skyline Drive in New Jersey. These are the first reports of the species in the New World. The description was composed from plants observed in the lawn at The New York Botanical Garden, specimens in New York, and from Chen *et al*. (2007). The *Plants of the World Online* website (Royal Botanic Gardens, Kew 2022) calls this species *V. hamiltoniana* D.Don, placing the name *V. arcuata* Blume into synonymy.

7. ***Viola arvensis*** Murray, Prodr. stirp. gott.: 73. 1770; *Viola tricolor* L. subsp. *arvensis* (Murray) Gaudin, Fl. Helv. 2: 210. 1828; *Viola tricolor* L. var. *arvensis* (Murray) Boiss., Fl. Orient. 1: 465. 1867 (illegitimate homonym of *V. tricolor* var. *arvensis* (Murray) DC. (1824)]; *Viola tricolor* L. proles *arvensis* (Murray) Rouy & Foucaud, Fl. France 3:

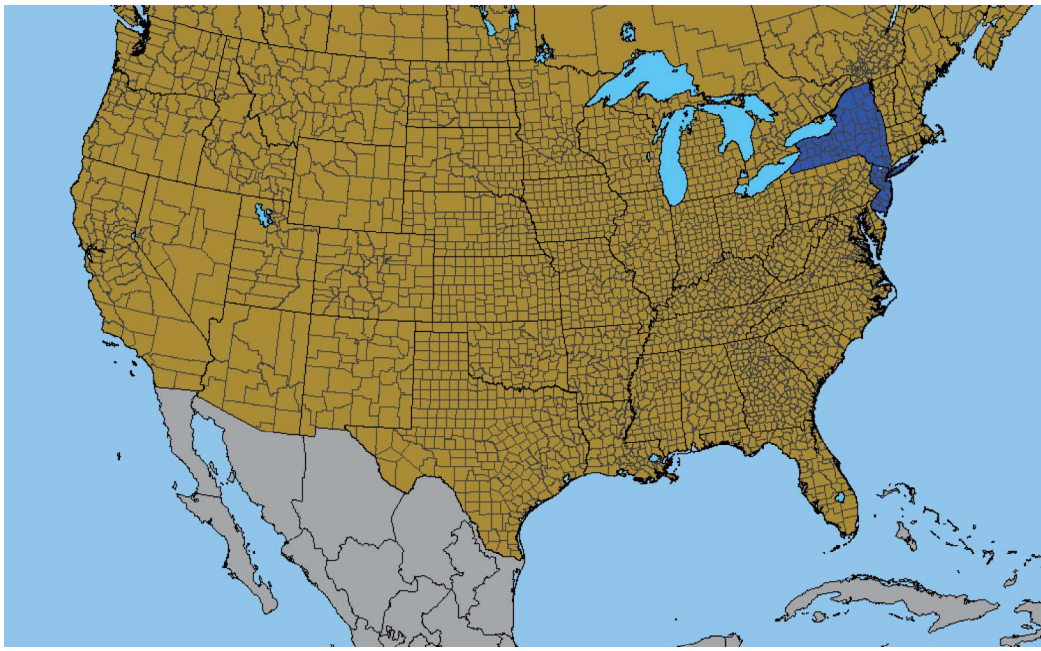

FIG. 16. United States county distribution of *Viola arcuata* (map: Biota of North America Program).

44. 1896; *Mnemion arvense* (Murray) Nieuwl., Amer. Midl. Naturalist 3: 217. 1914. Fig. 17.

Viola arvensis Murray f. *subpatens* C.G.Westerl., Bot. Not. 1906: 23. 1906.

Viola tricolor L. var. *montana* Lázaro Ibiza, Revista Real Acad. Ci. Madrid 17: 402, 404. 1919.

Viola arvensis Murray f. *timbalii* (Jord.) Font Quer, Treb. Mus. Ci. Nat. Barcelona, Sèr. Bot. 5(5): 19. 1924.

Common Name. European field pansy.

Description. Caulescent annuals from slender taproot, stems declined at base but erect distally, commonly ≥ 2, ≤ 41 cm tall; stems, foliage and peduncles green, stems glabrous or sparsely to moderately recurved-puberulent or -hirtellous, leaves sparsely to moderately hirtellous, peduncles glabrous; leaves cauline and commonly basal; stipules free, deeply pinnatifid, terminal lobe linear-lanceolate (upper leaves) to broadly elliptical (lower leaves) with 2–6 crenations on each side; leaves ascending, leaf blades undivided, upper $\leq 33 \times 10$ mm (including indistinguishable petiole), linear-lanceolate to lanceolate, base narrowly cuneate, lower $< 21 \times 16$ mm, narrowly ovate to orbiculate, base broadly rounded to truncate, margins conspicuously crenate or serrate, ciliate, apex rounded or occasionally acute; chasmogamous flower $\leq$ 19.5 mm, distinctly shorter than sepals or surpassing them by 1–2 mm; calyx glabrous or hirtellous, usually ciliate; lowest sepals broadly lanceolate to ovate-lanceolate, sharply acute; auricles prominent, entire or erose, not elongating in fruit; corolla cream, occasionally with upper petals purple-black apically (this trait possibly the result of hybridization with *V. tricolor*), throat yellow; spur elongate, slender, extending beyond the auricles; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers lacking; capsule 5–10 mm, green drying tan, unspotted, glabrous; seeds 1.5–1.7 $\times$ 0.8–1.0 mm, medium orange-brown, unspotted; $2n = 34$.

Similar Species. This species is easily distinguished from *V. rafinesquei* by the petals nearly or fully surpassed by the sepals (the latter often largely concealing the mature capsule), the cream-white corolla (which is rare in the latter), and pinnatifid stipules with the terminal leaf-like lobe much larger and broader than the lateral lobes and having 4 or more crenations per side. It differs from *V. tricolor* by the pinnately divided stipules, sepals nearly equaling to fully surpassing the petals, and the cream-colored petals.

Ecology. Disturbed sites such as railroad rights-of-way, roadsides, and crop fields.

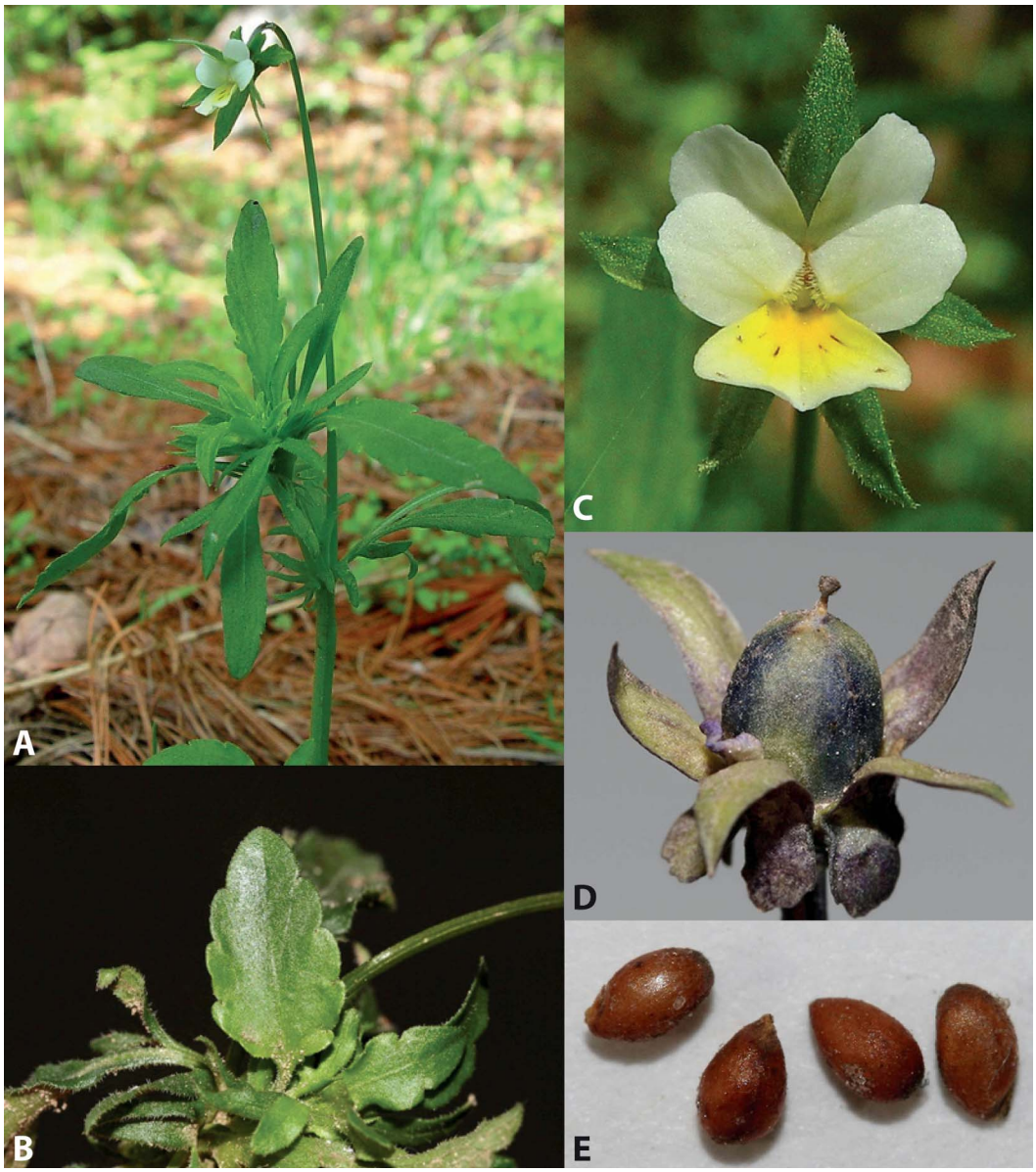

FIG. 17. *Viola arvensis*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Leaves (photo: Paul Busselen). (D) Chasmogamous fruit (photo: Paul Busselen). (E) Seeds (photo: Paul Busselen).

Distribution. Transcontinental, widely distributed across Canada, and in the eastern and western USA but largely absent in the Great Plains region; surely more common than range maps indicate. Fig. 18.

Rarity. None.

Phenology. Chasmogamous flower March–July (August), chasmogamous fruit May–June (August).

Affinities. This species belongs to the Pansy lineage, sect. *Melanium* Ging.

Hybrids. Hybridizes with *V. tricolor*, based on occasional plants in the field and on herbarium specimens with intermediate floral characteristics, such as distally purple-black upper petals but sepals about equaling the petals (Voss and Reznicek 2012; H.E.B., personal observation).

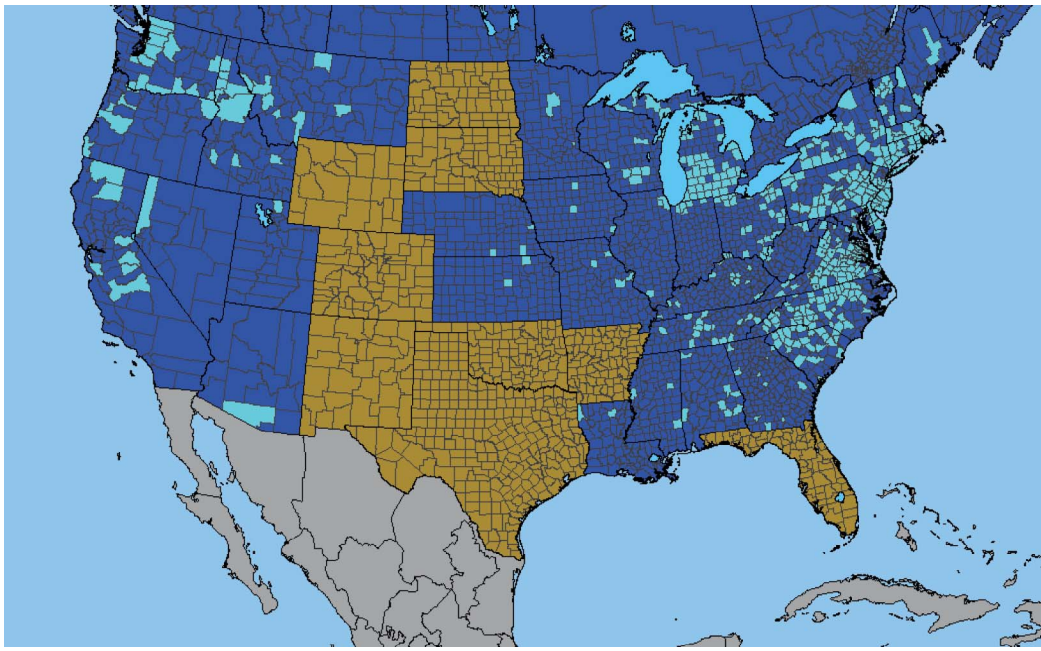

FIG. 18. United States county distribution of *Viola arvensis* (map: Biota of North America Program).

Comments. This naturalized European species has been noted by Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1995, 2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney (2015). It is distinctive among the pansies occurring in North America in having the sepals longer than to scarcely shorter than the petals, which in fruit largely conceal the chasmogamous capsule. Occasional plants with lateral petals surpassing sepals and with upper petals dark blue or purple distally are probable hybrids with *V. tricolor*.

8. ***Viola baxteri*** House, Bull. New York State Mus. Nat. Hist. 254: 500. 1924. [replacement name for *Viola perpensa* sensu House non Greene]. Type: USA New York, Ontario Co.: Fishers, 3 Jun 1916, *H. D. House & M. Baxter s.n*. (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14[2]: 219): NYS33489 (*n.v.*), image). Fig. 19.

Common Name. Baxter's violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 24 cm tall; foliage and peduncles green, not purple-tinged, mostly moderately to densely hirsute; stipules free, irregularly glandular-fimbriate; homophyllous, leaves ascending, smallest leaf blades palmatifid, largest deeply biternately to subtriternately divided into 9–13(15) narrowly linear-lanceolate lobes $<$ 3 mm wide (in chasmogamous flower), the lateral lobes of the terminal primary division attached medially, most ultimate lobes with a prominent slender spreading sharply acute tooth or short lobe on each side, primary divisions commonly narrowed at base to slender "petiolules," $\leq$ 69 $\times$ 82 mm, outline narrowly ovate to ovate during chasmogamous flower but broadening to broadly ovate or reniform in fruit, base (sub)cordate, margins of the lateral and often central second-order segments of the terminal primary division and occasionally of the lateral primary divisions with a prominent spreading slender sharply acute tooth or short lobe on each side, eciliate or ciliate, apex acute to obtuse; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 21 mm; calyx glabrous, ciliate; lowest sepals oblong to ovate, obtuse to rounded (rarely broadly acute); auricles short and entire, not or scarcely elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous (occasionally sparsely

FIG. 19. *Viola baxteri*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower profile view (photo: Andrew Lane Gibson). (C) Seeds from herbarium specimen: Transplanted from Michigan, Washtenaw Co., *Ballard et al. 15-045Y* (BHO).

bearded); chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle prostrate, arching just before dehiscence, shorter than petiole; cleistogamous capsule 6–7 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.6–2.3 × 1.1–1.6 mm, ivory, unspotted or with small weak light brown streaks or blotches.

Similar Species. The most extreme form of this species has the leaf blades biternate with the ultimate leaf divisions or segments narrowly linear and nearly as slender as those found in *V. pedatifida*. It shares with *V. stoneana* (a heterophyllous member of the Palmata species group) the unusual feature in *Borealiamericanae* violets of pale unspotted or weakly blotched seeds. It is most similar to other homophyllous cut-leaved taxa in the Pedatifida and Subsinuata species groups. Aside from the pale seeds, this species can be separated from *V. brittoniana* and *V. pedatifida* by its densely hirsute foliage, short rounded auricles, oblong or narrowly ovate ciliate obtuse to rounded sepals, glabrous spurred petal, and heavily spotted cleistogamous capsule on short prostrate peduncle. It differs from *V. monacanora* in its densely hirsute foliage, and oblong or narrowly ovate ciliate obtuse to rounded sepals. It can be distinguished from *V. subsinuata* by the several features of leaf dissection noted in the key, as well as the seed features. It is easily separated from *V. tenuisecta* in its densely hirsute foliage, biternately divided leaf blades, and oblong or narrowly ovate ciliate obtuse to rounded sepals.

Ecology. Sandy or rocky loam of limestone prairies and prairie-like openings, often surrounded by richer mesic or swamp forest.

Distribution. Endemic to the eastern Great Lakes region, central New York and southwestern

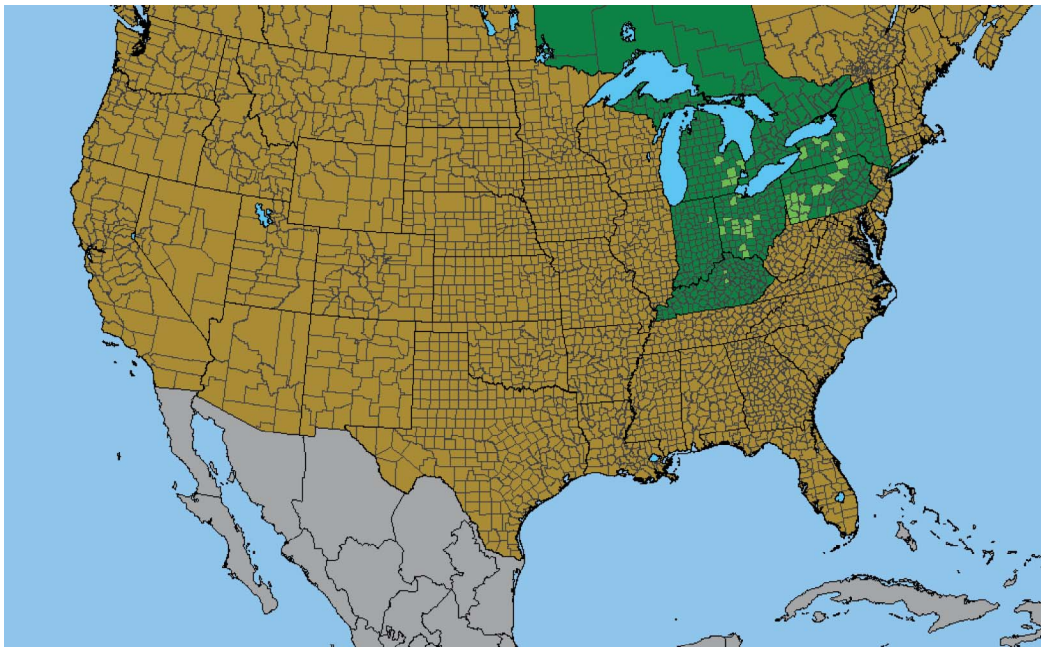

FIG. 20. United States county distribution of *Viola baxteri* (map: Biota of North America Program).

Ontario to southeastern Michigan, south to Pennsylvania, northern Kentucky, and eastern Indiana. Fig. 20.

Rarity. Listed in Indiana and Ohio.

Phenology. Chasmogamous flower April–May (July), chasmogamous fruit May–June, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium*, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Subsinuata species group.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1924; Haines *et al*. 2011), *V. fimbriatula* (House 1917, 1924; Brainerd 1924 in part), *V. sagittata* (H.E.B., personal observation), and *V. sororia* (Brainerd 1924; H.E.B., personal observation). Other hybrids are surely possible over the broad regional zone of sympatry and should be sought. Hybrids studied thus far have intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). They fail to reproduce by chasmogamous flowers, and cleistogamous capsules produce a substantially reduced proportion of viable seeds.

Comments. House (1917) initially identified plants "On shaded hillsides and moist woodlands which become dry in summer" from Rochester, NY, as *V. perpensa* Greene and cited two separate collections. Later (House 1924) he noted that that name *V. perpensa* represented midwestern hybrids of *V. pedatifida* and *V. sororia*, and he provided the replacement name *V. baxteri* for the New York plants. Subsequently, he cited an earlier article (House 1921) in support of his new species, but that actually referred to his new *Veronica baxteri*, not *V. baxteri*. Nevertheless, House (1924) did refer back to to his 1918 publication of *V. perpensa*, providing a clear reference to that published description and types. McKinney incorrectly annotated sheet NY97505 (June 2, 1916) as the holotype, but House stated the date as June 3 for the chasmogamous flowering collection. NY97505 is probably original material but is not considered a type. The NYS33489 sheet was designated as lectotype by Ballard *et al*. (2020a), being the most morphologically representative of the taxon and matching the protologue information.

This is a regional endemic subsumed until recently (at least as herbarium specimens) in a broadly delimited *V. palmata* by Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry

(1953a), Alexander (1963), Russell (1965), and Scoggan (1978); later called *V. subsinuata* by McKinney (1992), Ballard (2000), and Little and McKinney (2015). Ballard (1995) included *V. pedatifida* × *V. sororia* hybrids in western Michigan and specimens resembling them in the absence of *V. pedatifida* in southeastern Michigan as *V.* ×*subsinuata*, interpreting the latter as a relict hybrid swarm. Gil-ad (1995, 1997, 1998) dismissed the predominately Appalachian populations of *V. palmata sensu* Brainerd and Russell as hybrid derivatives. Voss and Reznicek (2012) recognized one broadly circumscribed "*V. palmata*" that included *V. baxteri* and *V. triloba* (*V. palmata* var. *triloba* in this treatment). Specimens of *V. baxteri* have thus generally been referred to *V. palmata*/*subsinuata* taxonomically. However, the name *V. baxteri* was placed into synonymy under *V. brittoniana* by Gil-ad (1997), McKinney (1992), and Little and McKinney (2015), who evidently failed to consider the many differences of *V. baxteri* from the latter species, such as hirsute foliage, broad obtuse sepal shape, beardless spurred petal, purple-spotted or -blotched cleistogamous capsule on prostrate peduncle, and pale weakly spotted or unspotted seeds. Brainerd (1921b) referred to plants of *V. baxteri* as a "Great Lakes ecotype" but did not treat it formally, believing that it transitioned into two other ecotypes farther east and south; however, he seems to have examined very few specimens and makes no mention of growing or studying it. Plants in chasmogamous flower can be difficult to separate from some individuals or populations of *V. subsinuata* with extreme leaf dissection; confident identification relies on summer-fruiting plants with mature cleistogamous seeds, as well as careful note of its characteristically more open, alkaline habitat (often in the presence of outcropping limestone).

Populations observed and herbarium specimens collected under closed-canopy forests in eastern Ohio, western Pennsylvania, and central New York are atypical in their shallowly divided leaf blades with broader lobes and seeds approaching those of *V. sororia*; they are virtually identical with subfertile *de novo* hybrids found in intimate association with both *V. baxteri* and *V. sororia* and are treated as hybrids here. Approximately 10 extant populations (some quite small) have been confirmed of typical *V. baxteri* in western Ohio. Many historical localities in western New York, southwestern Pennsylvania, and southern Ontario should be sought and reexamined to determine the current status of this species.

9. ***Viola blanda*** Willd. non Salisb. (1796), Hort. Berol. [Willdenow] 1(2): pl. 24. 1804. Type: [illustration] Willdenow, Hort. Berol.: pl. 24. 1804 (lectotype designated by T. Y. S. Choo *et al*., Taxon 63(3): 690. 2014). Fig. 21.

Viola pallens T.F.Forst. ex Schult., in Roem. & Schult., Syst. veg. 5: 359. 1819.

Viola leconteana G.Don, Gen. hist. 1: 324. 1831.

Viola burtonii Reeks, List Fl. Pl. Ferns Newfoundland: 2. 1873.

Viola alsophila Greene, Pittonia 4: 7. 1899 [replacement name for *V. amoena* Leconte (1828) non T.F.Forst. (1798)]; *Viola amoena* Leconte, Ann. Lyceum Nat. Hist. New York 2: 144. 1828 ["1826"]; *Viola blanda* Willd. var. *amoena* (Leconte) Britton, Sterns & Poggenb., Prelim. Cat.: 6. 1888.

Common Name. Sweet white violet.

Description. Acaulescent stoloniferous perennials from slender rhizome, stolons surficial, colonial from surficial stolons produced in summer, stolons bearing multiple nodes each with a leaf and cleistogamous capsule, ≤ 17 cm tall; foliage and peduncles pale gray-green with upper surface of leaf blades darker, with petioles, peduncles, and calyx commonly red-tinged or -spotted, leaves glabrous except for scattered hairs on upper leaf blade surfaces, peduncles glabrous; stipules free, glandular-fimbriate; leaves spreading, leaf blades undivided, largest ≤ 69 × 62 mm, narrowly ovate, base deeply cordate with narrow sinus, basal lobes ≤ 1/4 as long as total leaf blade length, inner edges of lobes attingent or overlapping in living material, margins crenate, eciliate, apex acute; chasmogamous peduncle held among the leaves; chasmogamous flower ≤ 11.0 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate to ovate, acutish to rounded; auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; all petals glabrous; chasmogamous capsule green or with fine red spots; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles, arching upward and occasionally surpassing petioles just before capsule dehiscence; cleistogamous capsule 6–8 mm, green drying tan with red-purple to purple spots or blotches, glabrous; seeds 1.2–1.3 ×

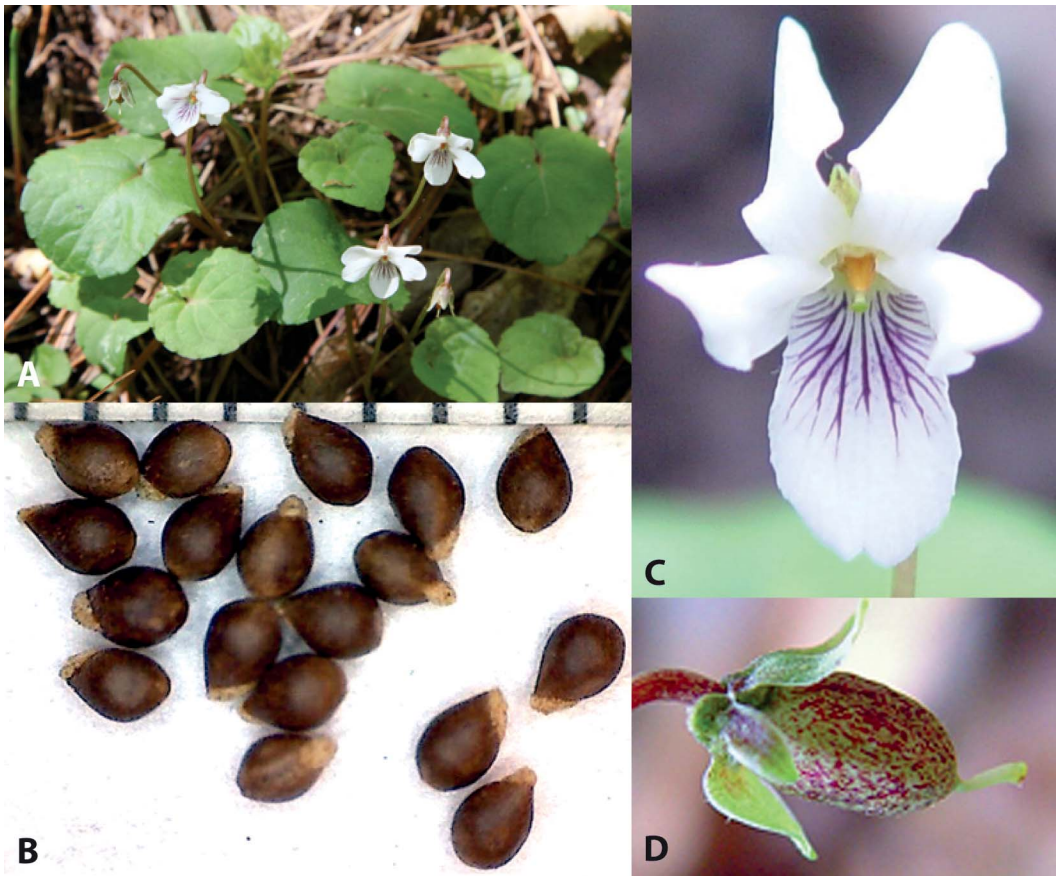

FIG. 21. *Viola blanda*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Chasmogamous fruit (photo: Arthur Haines, Native Plant Trust). (D) Seeds from herbarium specimen: Connecticut, New London Co., *C. A. Weatherby s.n.* (CBS17933).

0.7–0.8 mm, brownish-blackish, unspotted; 2n = 44.

Similar Species. This species can be distinguished from *V. incognita* by its commonly red-tinged petioles and peduncles, pubescence (if present) restricted to subappressed hairs on the upper surface of the leaf blades, largest leaf blades narrowly ovate and deeply cordate with narrow sinus, the short basal lobes with inner edges commonly touching or overlapping, acute apex and crenate margins (check this at the widest point on the leaf blade), glabrous lateral petals, summer stolons with leaves and cleistogamous capsules distributed along their length, and smaller broadly obovoid dark brown seeds. The narrower leaf blade shape (especially in younger chasmogamous flowering plants) and shallowly crenate blade margins are similar to *V. minuscula*, but it differs in the upper surface of the leaf blades commonly bearing subappressed hairs, glabrous petioles, and heavily spotted cleistogamous capsule on a prostrate peduncle. It is different from some coastal and southeastern populations of *V. primulifolia* with subcordate or shallowly cordate leaf bases in having the leaf blade base deeply and narrowly cordate with inner edges of the basal lobes touching or overlapping, glabrous foliage or hairs limited to the upper surface of the leaf blades, and heavily spotted cleistogamous capsule on a prostrate peduncle. It is easily distinct from *V. renifolia* in the elevated narrowly ovate leaf blades with acute apex, pubescence (if present) restricted to short subappressed hairs on the upper surface of the leaf blades, and broadly obovoid dark brown seeds.

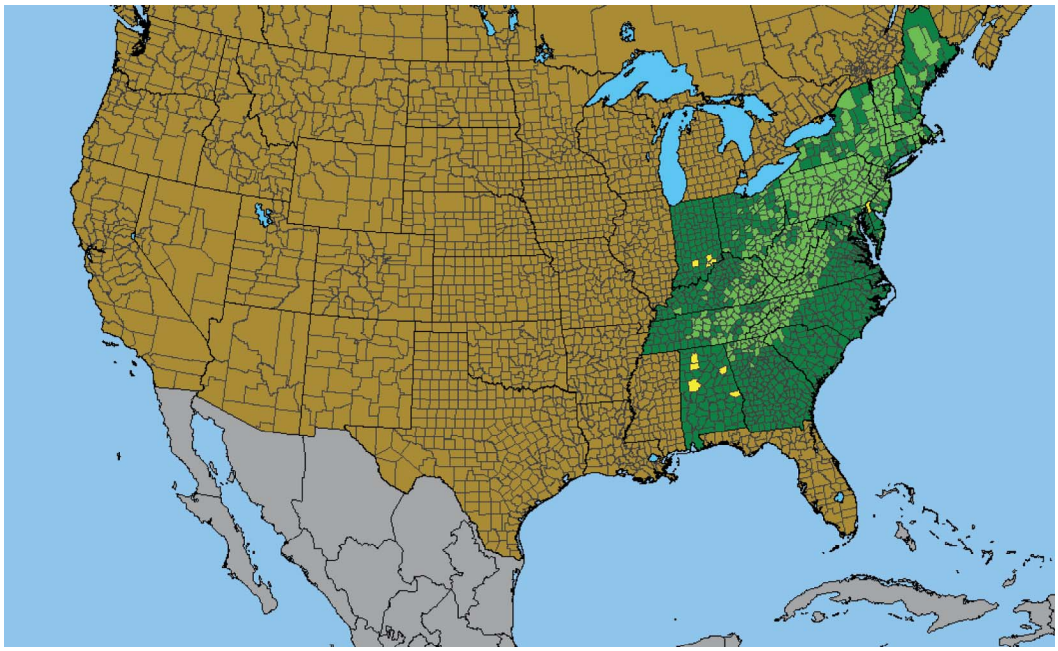

FIG. 22. United States county distribution of *Viola blanda* (map: Biota of North America Program).

Ecology. Moist organic loamy or sandy loam soils in mesic northern hardwood forests, base of slopes with seepage in drier forests, along streams, often under conifers (*e.g.*, *Tsuga*), at higher elevations or northern microclimates.

Distribution. Appalachian Mountains and associated uplands, Maine to southern Indiana, south to northwestern South Carolina and Alabama (reports from the western Great Lakes are misidentifications). Fig. 22.

Rarity. None.

Phenology. Chasmogamous flower April–June, chasmogamous fruit June–July, cleistogamous fruit June–Septembter.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. incognita* (Russell 1954a, 1955c, 1965); hybrids are probably much more common than the very limited reports suggest. Hybrids with *V. minuscula* and *V. renifolia* should be sought, given the overlaps in range in the Appalachian Mountains and adjacent uplands (for the former) and the more northeasterly portion of our region (for the latter), and occasional to frequent local sympatry. Hybrids would fail to reproduce by chasmogamous flowers, would have sterile pollen, and would very likely produce abortive cleistogamous capsules or capsules with no viable seeds, simply due to the difference in ploidy level. Hybrids with *V. incognita* would presumably fail to reproduce chasmogamously and might also express reduced cleistogamous seed output. Studies are needed to confirm these predictions.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Russell (1955c, 1965), Alexander (1963), Scoggan (1978), Strausbaugh and Core (1978), and Weakley *et al*. (2012) maintained this as a distinct species separate from *V. incognita*. Haines *et al*. (2011) merged the two but maintained two varieties, var. *blanda* and var. *palustriformis* Brainerd, while Gleason and Cronquist (1991), Ballard (1995, 2000), Voss and Reznicek (2012), and Little and McKinney (2015) synonymized *V. incognita* under *V. blanda* without infraspecific recognition. Brainerd, Fernald, Alexander, and Scoggan erroneously reported the range extending west to Wisconsin, Minnesota, and Illinois, whereas Russell and others pointed out that typical *V. blanda* is virtually confined to the Appalachian highlands and associated uplands and does not range further west than southern Indiana, with reports from outside that narrower region

representing misidentifications of other species. Nearly glabrous plants of *V. incognita* formerly called var. *forbesii* Brainerd, with indument restricted to the upper surface of leaf blades, can occasionally appear similar to *V. blanda* when chasmogamous flower and cleistogamous fruit characters are ignored. The shape of the largest leaf blades and coloration of the foliage and peduncles are somewhat variable and less reliable during chasmogamous flower, and best interpreted on summer fruiting plants. The trait of twisted *versus* nontwisted petals as a distinguishing feature used in some keys has been elusive to the first author, who has preferentially relied more heavily on other features presented in the keys. As yet unclear levels of within-population and regional variation in *V. blanda* and *V. incognita* render determination of the extent of hybridization difficult, but (surprisingly) studies of hybridization are lacking. The extremes, which are very common, are highly divergent in several features of foliage, chasmogamous flowers, and seeds, and are thus treated as distinct evolutionary species. Chasmogamous flowering plants of this species with leaves not fully expanded can be particularly difficult to identify with confidence from *V. incognita*, whereas cleistogamous fruiting plants in summer express quite conspicuous differences in foliage and peduncle color, leaf shape and indument, and cleistogamous seeds. Choo *et al*. (2014) have proposed conservation of the widely used name *V. blanda* Willd. (1804) against the earlier neglected name *V. blanda* Salisb. (1796, now a synonym of the European pansy *V. cornuta* L.).

10. ***Viola brittoniana*** Pollard, in Britton, Man. fl. n. states, ed. 1: 635. 1901 [replacement name for *V. atlantica* Britton (1897)]; *Viola atlantica* Britton, Bull. Torrey Bot. Club 24: 92. 1897 [illegitimate homonym of *V. atlantica* Pomel (1874)]; *Viola pedatifida* G.Don subsp. *brittoniana* (Pollard) L.E.McKinney, Sida, Bot. Misc. 7: 22. 1992; *Viola pedatifida* G.Don var. *brittoniana* (Pollard) R.J.Little & L.E.McKinney, J. Bot. Res. Inst. Texas 4(1): 225. 2010. Type: USA New York, Staten Island, along salt meadows, 8 Jun 1888, *N. L. Britton s.n*. (lectotype (incorrectly designated as holotype by Landon McKinney, Sida, Bot. Misc. 7: 22. 1992; corrected to lectotype by Nir Gil-ad. 1997. Boissiera 53: 53): NY00095712, isolectotype: US00479254, internet image). Fig. 23.

Common Names. Britton's violet, northern coast violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 26 cm tall; foliage and peduncles green with lower surface of leaf blades often tinged purple, petioles and peduncles glabrous, leaf blades finely appressed-hirtellous along veins and ciliolate; stipules free, irregularly glandular-fimbriate; homophyllous, leaves ascending, smallest leaf blades palmatifid, largest deeply biternately divided into 7 or 9 lanceolate lobes, central lobe of terminal primary division commonly distinctly broader and longer than its lateral lobes, $\leq 75 \times 95$ mm, outline narrowly to broadly ovate, base subtruncate to cordate, margins entire proximally and usually irregularly serrulate distally, ciliolate, apex broadly acute to obtuse; chasmogamous peduncle often held among the leaves; chasmogamous flower $\leq$ 20 mm; calyx glabrous, eciliate or auricles infrequently irregularly ciliolate; lowest sepals linear-lanceolate to lanceolate, acuminate; auricles usually prominent and entire or erose, elongating to 3 mm in fruit; corolla blue to purple, throat white; lateral petals bearded with filiform to narrowly linear hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, on erect peduncle commonly a little shorter than the petioles; capsule 9–18 mm, yellow-green drying tan, unspotted, glabrous; seeds 1.3–1.9 $\times$ 0.8–1.3 mm, medium brown to orange-brown, unspotted; $2n = 54$.

Similar Species. This homophyllous cut-leaved species has been most frequently confused with other members of the Pedatifida and Subsinuata species groups. It differs from *V. pedatifida* in its ovate cordate biternately divided leaf blades and with other features noted in the key, sepals eciliate (but auricles occasionally ciliolate), and slightly smaller seeds. It is easily separated from *V. baxteri* and *V. subsinuata* by its glabrous petioles and peduncle, leaf blades appressed-hirtellous along veins and ciliolate along margins, lanceolate to linear-lanceolate acuminate sepals and prominent auricles, densely bearded spurred petal, unspotted cleistogamous capsule on tall erect peduncle, and unspotted brown to orange-brown seeds. Both this and *V. septemloba* grow along the Atlantic Coastal Plain, with almost non-overlapping local ranges, but the two have been misidentified for each other. This species differs from the heterophyllous *V. septemloba* in all leaf blades being divided, the largest thinner and biternately divided with the terminal lobe of the terminal primary division

FIG. 23. *Viola brittoniana*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust). (D) Seeds from herbarium specimen: Transplanted from North Carolina, Columbus Co., *H. Ballard et al. 15-004Y* (BHO).

usually narrow, blade surfaces appressed-pubescent along veins, and ciliolate margins, the chasmogamous peduncle often held among the leaves, often smaller flower, and smaller medium brown seeds.

Ecology. Moist to seasonally inundated sandy, peaty or mucky soils of seeps, bogs, brackish marshes, streambanks, and river shores, persisting in ditches bordering fields, moist meadows, trail edges, and forest clearings.

Distribution. Typically near the Atlantic coast in the northern half of its range but shifting inland to the upper Coastal Plain and "fall line" in the Carolinas; Massachusetts and eastern New York south to South Carolina. Fig. 24.

Rarity. Listed in most states in its northern range: Connecticut, Massachusetts, New Jersey, New York, and Pennsylvania.

Phenology. Chasmogamous flower April–June, chasmogamous fruit May–July, cleistogamous fruit July–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Pedatifida species group.

Hybrids. Hybridizes with *V. affinis* (Dowell 1910; Brainerd 1924; House 1924), *V. communis* or possibly the glabrous or *hirsutuloides* variants of *V. sororia* (Dowell 1910; Brainerd 1924; House 1924), *V. cucullata* (Bicknell 1904; House 1905; Brainerd 1906c, 1907a, 1924; Haines *et al*. 2011), *V. emarginata sensu stricto* (House 1906b; Brainerd 1906c, 1924; House 1924), *V. fimbriatula* (Pollard 1902b, Brainerd 1906c, 1907b, 1924; Dowell 1910; Haines *et al*. 2011), *V. lanceolata* (Forbes 1909; Brainerd 1924; Haines *et al*. 2011), *V. palmata* var. *triloba* (Brainerd 1906c, 1924), *V.*

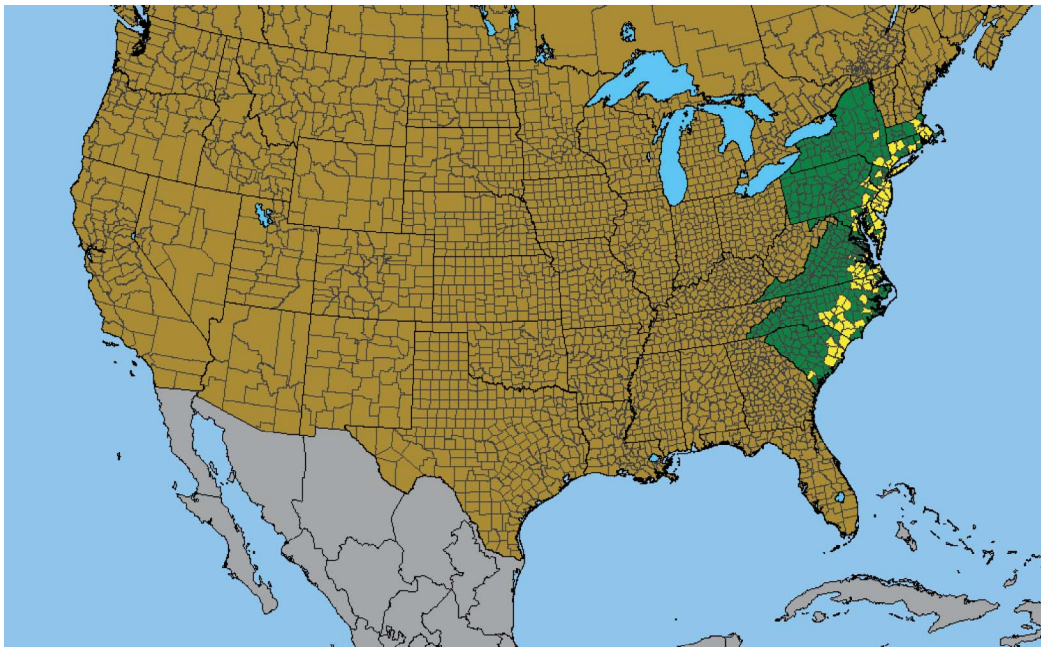

FIG. 24. United States county distribution of *Viola brittoniana* (map: Biota of North America Program).

pectinata (Brainerd 1906c, 1924; Haines *et al*. 2011; H.E.B., personal observation), *V. sagittata* (Brainerd 1906c, 1924; House 1906b, 1924), *V. sororia sensu stricto* (Brainerd 1924; House 1924; Haines *et al*. 2011), and *V. subsinuata sensu stricto* (Brainerd 1906c; House 1924). Brainerd reported that the hybrids he observed exhibited intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort); failed to reproduce by chasmogamous flowers; and produced cleistogamous capsules that were largely abortive or yielded a substantially reduced proportion of viable seeds. Individuals of *V. brittoniana* × *V. pectinata*, which we transplanted from multiple sites in New Jersey and North Carolina, did not manifest significant reduction of mature cleistogamous seeds.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), Gil-ad (1995, 1997), Ballard (2000), Haines *et al*. (2011), and Weakley *et al*. (2012) maintained *V. brittoniana* as a distinct species; however, McKinney (1992) subsumed it as a subspecies under *V. pedatifida*, and Gleason and Cronquist (1991) lumped it and several other taxa in a very broadly delimited *V. palmata* var. *pedatifida*. Little and McKinney (2015) later reinstated the present taxon to species status (synonymizing *V. baxteri* and *V. pectinata* under it). Gil-ad (1995, 1997, 1998) and Zumwalde (2015) provided compelling empirical evidence to support recognition of *V. brittoniana* and *V. pedatifida* as distinct species. The circumscription applied here excludes *V. pectinata*; for comments see that species. Two potentially misleading sources of information have probably contributed to the erroneous reports of *V. septemloba* on the Atlantic Coastal Plain north of Virginia: Brainerd's earliest misnaming of *V. brittoniana* as *V. septemloba* before he and others accepted two distinct species, and herbarium specimens of occasional hybrids between *V. brittoniana* and *V. sagittata* that superficially resemble *V. septemloba*.

11. ***Viola canadensis*** L., Sp. pl., ed. 1, 2: 936. 1753; *Lophion canadense* (L.) Spach, Hist. Nat. Vég. (Spach) 5: 517. 1836. Type: Canada [locality and date unknown], [*Peter*] *Kalm s.n*. (lectotype (designated by H. O. Juel, Rhodora 33: 179. 1931): Herb. Burser XI: 8 (UPS (*n.v.*)); presumed isolectotype: LINN1052-14 (*n.v.*), internet image)). Fig. 25.

Viola canadensis L. var. *corymbosa* Nutt. ex Torr. & A.Gray, in Torr. & A.Gray, Fl. N. Amer. 1(1): 143. 1838.

Viola discurrens Greene, Pittonia 5: 26. 1902.

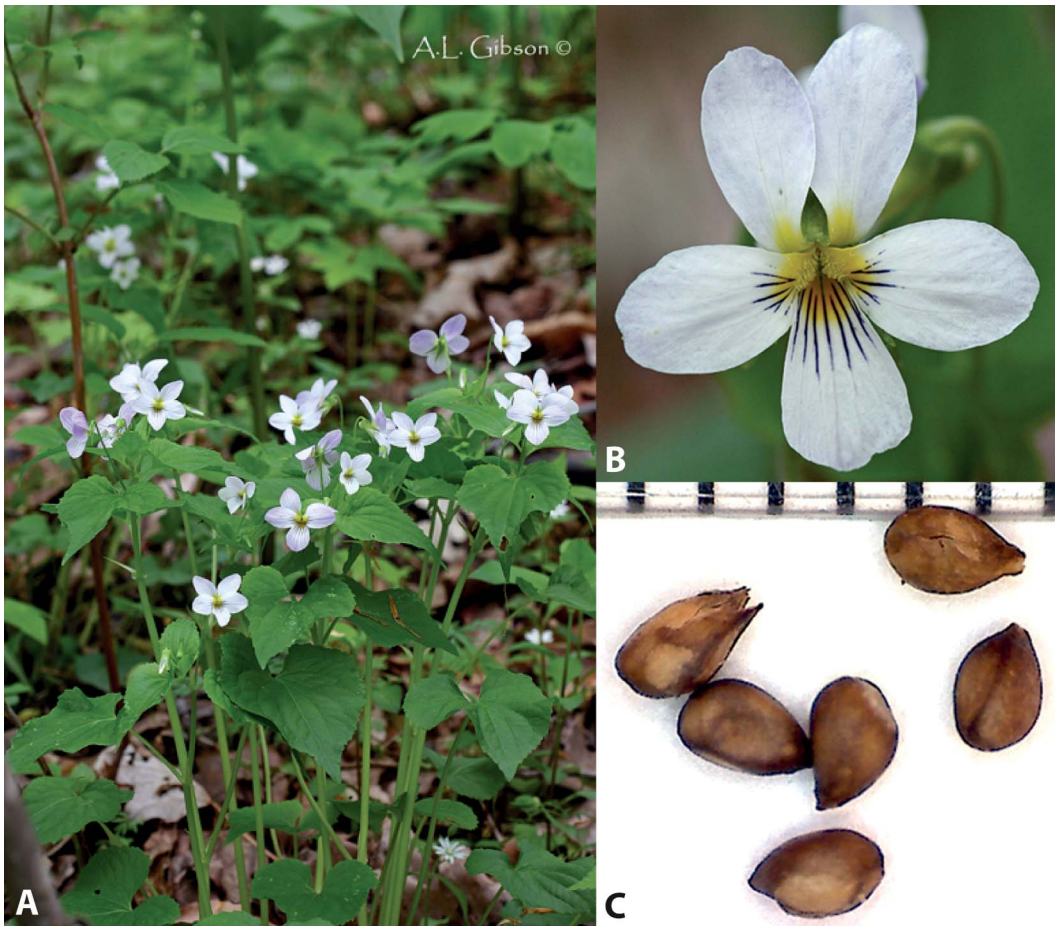

FIG. 25. *Viola canadensis*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: Andrew Lane Gibson). (C) Seeds from herbarium specimen: Ohio, 17 Jun 1964, *E. M. Herrick s.n.* (OS75045).

Viola eurybiifolia Greene, Pittonia 5: 25. 1902.

Viola canadensis L. var. *pubens* Farw., Rep. (Annual) Michigan Acad. Sci. 19: 248. 1917.

Common Names. Canada violet, eastern tall white violet.

Description. Caulescent perennials from somewhat thick rhizome (some southern Appalachian populations have stoloniform extensions and are mat-forming or colonial), stems erect, solitary or multiple, $\leq$ 40 cm tall; stems, foliage, and peduncles gray-green, upper surface of leaf blades darker than lower, glabrous or sparsely hirtellous on either surface; leaves cauline and basal, cauline distributed along stem; stipules membranous and commonly deciduous in fruit, free, lance-attenuate, entire; leaves ascending or spreading, leaf blades undivided, largest $\leq 78 \times 71$ mm, upper narrowly ovate with long-acuminate apex, middle and lower ovate to subreniform with subacuminate apex, base cordate, margins crenate-serrate, eciliate; chasmogamous flower $\leq$ 18 mm; calyx glabrous or sparsely hirtellous, eciliate or ciliate; lowest sepals linear-lanceolate, acuminate; auricles short and entire, not elongating in fruit; corolla white gradually fading to pink or pale purple on dorsal surface of petals, ventral surface of petals pink- or violet-tinged, throat yellow; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 4–8.5 mm, green drying tan, unspotted, papillate-puberulent or hirtellous to sparsely hirsute (infrequently gla-

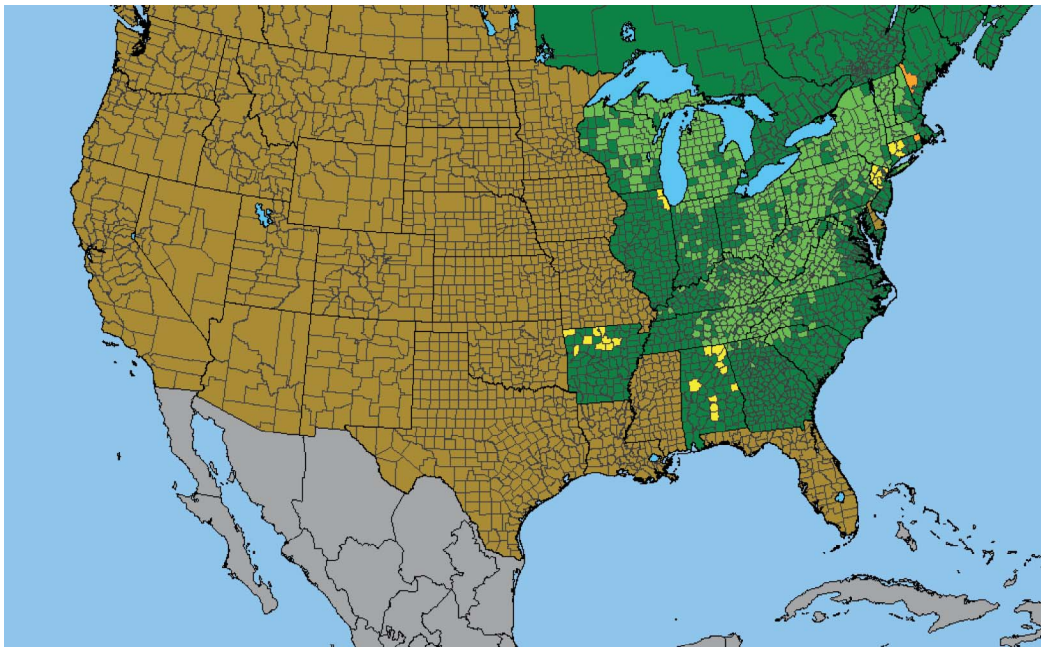

FIG. 26. United States county distribution of *Viola canadensis* (map: Biota of North America Program).

brous); seeds 1.5–2.2 × 1.2–1.5 mm, medium brown, unspotted, caruncle obsolete; 2n = 24.

Similar Species. This species and *V. rugulosa* appear to be the only species in our region with the usually conspicuous seed caruncle obsolete, as well as the only species besides the pansies of sect. *Melanium* to have two-toned corollas (white petals with yellow throat). This species will most often be confused with *V. rugulosa*, which appears not to grow at the same sites where their ranges slightly overlap in the western Midwest, and also with *V. eriocarpa* and *V. striata*, with which it often grows. It differs from *V. rugulosa* in usually lacking long-creeping stoloniform rhizomes (thus, it is not colonial or mat-forming) (some southern Appalachian populations of *V. canadensis* do display this but are otherwise identical to *V. canadensis*), glabrous to sparsely hirtellous foliage, glabrous peduncles, long-acuminate upper leaf blades, shallowly cordate basal leaf blades, and lanceolate usually eciliate sepals. It can be distinguished from the other two species with which it often grows, from *V. striata* in its membranous attenuate entire stipules which are commonly deciduous in summer, remotely crenate-serrate leaf blade margins, very short rounded auricles, and yellow corolla throat. It can be separated in fruit from *V. eriocarpa*, with which it often grows, in the commonly deciduous membranous attenuate entire often deciduous stipules.

Ecology. Rich loamy and rocky soils of mesic forests, and on lower slopes and terraces of coves and floodplains.

Distribution. Eastern North America, north-south to northwestern Ontario and Wisconsin, south to northern South Carolina, Alabama, and western Kentucky; slightly disjunct in Arkansas. Fig. 26.

Rarity. Listed in Connecticut, Illinois, Maine, New Jersey, and Rhode Island.

Phenology. Chasmogamous flower April–July, chasmogamous fruit May–July, cleistogamous fruit July–August.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging.

Hybrids. Hybridizes very rarely with *V. eriocarpa* (Henry 1953a), and the hybrid is probably overlooked. The characteristics of chasmogamous flowers and foliage would presumably be approximately intermediate or perhaps somewhat more similar to *V. canadensis* (a tetraploid). Given the difference in ploidy level, the hybrid would fail to reproduce by chasmogamous flowers and would

presumably produce abortive cleistogamous capsules or capsules lacking viable seeds. Studies are needed to confirm these predictions.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Russell (1959), Alexander (1963), and Swink and Wilhelm (1979) treated this and *V. rugulosa* as distinct species. Strausbaugh and Core (1978), Ballard (1995, 2000), and Voss and Reznicek (2012) simply accepted *V. canadensis*, given that *V. rugulosa* was out of their flora range. Russell (1965), Gleason and Cronquist (1991), Weakley *et al*. (2012), and Little and McKinney (2015) treated the two taxa as varieties under *V. canadensis*. Plants in the southern Appalachians occasionally have short stoloniform rhizome extensions similar to the elongate extensions of *V. rugulosa* and have been misidentified as the latter, but the Appalachian plants are otherwise identical to typical *V. canadensis*. Greene (1902b) segregated several species from *V. canadensis*; *V. discurrens* clearly applies to the "stoloniferous" Appalachian phenotype of *V. canadensis* and is a synonym of the present species, but phenotypes in the West are somewhat different (*e.g*., puberulent rather than hirtellous foliage, different leaf shape and marginal serration, different sepal shape) and deserve further study. At least some of the specimens we have examined in western North America that have belowground parts have stoloniform rhizomes like *V. rugulosa*, and all the western records are tentatively attributed to *V. rugulosa* until further studies are made to sort out this larger species complex. This leaves *V. canadensis* as circumscribed here restricted to eastern North America, and the remainder of populations previously subsumed under *V. canadensis* in the West transferred tentatively to *V. rugulosa*. In northern Illinois and southern Wisconsin, where the ranges of *V. canadensis* and *V. rugulosa* overlap, the two taxa do not occupy the same woodlands (at least according to herbarium specimens), suggesting some degree of ecological separation. Moreover, in Wisconsin confirmed herbarium specimens of *V. rugulosa*, some of which were visited in person, were found on talus slopes or cliffs bordering lakes or larger river systems, habitats quite different from the rich mesic and bottomland forest habitats of *V. canadensis*. While collections of *V. canadensis* are nearly all from southeastern, central, and northeastern counties in Wisconsin, *V. rugulosa* sites were scattered across the southern half of the state. Despite Russell's (1965) assertion that the two intergrade, they maintain their morphological distinctions in the region of sympatry in Illinois and Wisconsin. Given several divergent morphological traits between the two, geographic and ecological separation, absence of confirmed hybrids, and morphological integrity maintained in the zone of sympatry, the northern Great Plains and western Midwest *V. rugulosa* is segregated from *V. canadensis* here as a distinct evolutionary species (see additional comments under *V. rugulosa*). The rather cumbersome common name "eastern tall white violet" has been proposed to distinguish this species from *V. rugulosa*; since both species occur in Canada, the euphonious common name "Canada violet" unfortunately does not distinguish this from *V. rugulosa*.

The *V. canadensis* complex of the Canadenses species group, including *V. canadensis* and *V. rugulosa*, is tetraploid ($2n = 24$), as compared to the caulescent yellow-flowered members of the Nudicaules species group. Other diploid (and possibly tetraploid) species of the Canadenses are distributed largely allopatrically in the West and in Mexico; further cytogenetic studies on the Canadenses should be conducted.

12. ***Viola communis*** Pollard

Infraspecific taxa belonging to this species include the following:

12a. *Viola communis* f. *communis*

12b. *Viola communis* f. *priceana* (Pollard) H.E.Ballard

Common Names. Common blue violet, confederate violet, dooryard violet, hooded blue violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 20 cm tall; foliage and peduncles deep green, both surfaces of leaf blades glossy, lower surface occasionally purple-tinged, glabrous or upper surface of leaf blades with scattered minute appressed hairs (may need hand lens to visualize); stipules free, irregularly glandular-fimbriate; leaves spreading, leaf blades undivided, largest $\leq$ 92 $\times$ 92 mm, in spring suborbiculate or broadly deltate-ovate, in summer broadening to deltate-reniform, base cordate to shallowly cordate, margins closely and uniformly crenate-serrate to the broadly obtuse (rarely broadly acute) to rounded apex, eciliate; chasmogamous peduncles held among the leaves (occasionally above the leaves in regularly mowed

lawns and roadsides); chasmogamous flower $\leq$ 21 mm; calyx eciliate; lowest sepals lance- to ovate-triangular, acuminate; auricles prominent, usually erose, weakly elongating in fruit to 2 mm; corolla blue to purple, or white with a broad blue-gray eyespot surrounding the throat formed from coalescing nectar-guide lines (f. *priceana*), throat white; spur short-globose; lateral petals densely bearded with filiform to slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous, on prostrate and curved or coiled peduncle gradually elongating to become upright and sinuous-straight but shorter than petioles (held among or above the leaves in mowed or disturbed sites); cleistogamous capsule 8–12 mm, green drying tan, unspotted or with fine to heavy purple spots or blotches, glabrous; seeds 1.5–2.5 $\times$ 0.9–1.5 mm, olive- or brownish-black to blackish seeds, commonly with minute raised black spots.

Similar Species. The undivided deep green and essentially glabrous glossy orbiculate to broadly deltate-ovate or deltate-reniform leaf blades with margins closely and uniformly crenate, apex broadly obtuse to rounded, render this species unmistakable. It is most similar to *Borealiamericanae* taxa with glabrous foliage and leaf blades as broad as to broader than long, as well as species with leaf blades broadening substantially in fruit. Besides the vegetative features noted above, this species differs in chasmogamous flower from *V. nephrophylla* in its glabrous spurred petal, sepals with acute apices and prominent auricles; and from *V. domestica*, *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) in its shorter stature, ovate-triangular sepals acuminate from the middle, and prominent auricles. *Viola communis* f. *communis* differs from *V. cucullata* in the flowers held among the leaves, ovate-triangular sepals acuminate from the middle, blue to purple corolla lacking a conspicuously contrasting eyespot around the throat, and lateral petal beards with long filiform to slightly clavate hairs concealing the throat; f. *priceana* shares a conspicuously contrasting eyespot around the throat with *V. cucullata* but diverges in its usually white to very pale violet petals, as well as the other traits mentioned for f. *communis*. In cleistogamous fruit, it can be separated from *V. affinis* and *V. missouriensis* in its often unspotted cleistogamous capsule on gradually erect-sinuous peduncle, ovate-triangular acuminate eciliate sepals, weakly elongating auricles, and blackish unspotted or minutely spotted seeds. It is distinguished from *V. langloisii*, *V. pratincola*, and *V. retusa* in its its glossy orbiculate to deltate-reniform leaf blades with apex obtuse to rounded, margins closely and uniformly crenate, and shorter and broader ovate-triangular sepals acuminate from the middle rather than from the base.

Ecology. Moist loamy and clayey soils of floodplains, thickets, transitions between forested slopes and swamp or wetland borders, suburban woodlots, and disturbed sites such as lawns, forest edges, and roadsides representing formerly natural habitats.

Distribution. Widely distributed in eastern North America (likely to be discovered in southern Canada), Maine to Minnesota, south to Alabama and Missouri (distribution incomplete). Fig. 27.

Rarity. See infraspecific taxa.

Phenology. Chasmogamous flower March–June (September–October), chasmogamous fruit April–July, cleistogamous fruit July–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Cucullata species group.

Hybrids. See *V. communis* f. *communis*.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Strausbaugh and Core (1978), and Swink and Wilhelm (1979) included this and other glabrous or glabrate taxa with undivided leaf blades nearly as broad as to broader than long into a broadly defined *V. papilionacea* Pursh. Russell (1965) took a different approach, maintaining western Midwest and Great Plains *V. pratincola* Greene but subsuming all eastern glabrate and glabrous populations into *V. sororia*. Gleason and Cronquist (1991), Ballard (1995, 2000, 2013), Haines *et al*. (2011), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney (2015) included all such taxa in a broadly delimited *V. sororia*, while McKinney (1992) placed these in *V. sororia* var. *sororia*, recognizing several other taxa only at the varietal level. Gil-ad (1995, 1997, 1998) examined specimens identified or annotated by Brainerd as *V. papilionacea* and reported a wealth of diversity in seed macro- and micromorphologies; he dismissed

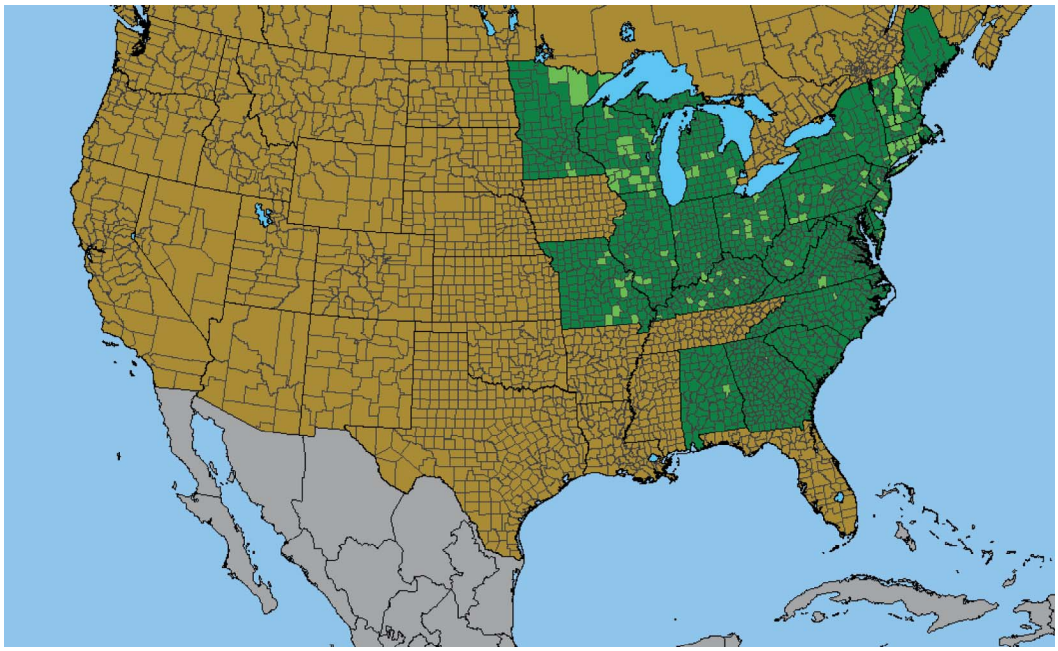

FIG. 27. United States county distribution of *Viola communis* (map: Biota of North America Program).

the lot as an array of hybrids involving *V. affinis*, *V. cucullata*, and *V. sororia*. However, the locations of Gil-ad's study samples suggest that he included multiple taxa as delimited here, such as *V. communis* Pollard, *V. pratincola*, *V. sororia* (glabrous variant), and *V. sororia* (*hirsutuloides* variant), as well as advanced-generation hybrids. The first three taxa have highly uniform seed morphologies within and across populations, but the seeds are noticeably different among the taxa; no opportunity to observe the seeds of *V. sororia* (*hirsutuloides* variant) has presented itself. The present species has been extracted and delineated narrowly from the various changing compositions of the heterogeneous *V. sororia* species complex based on several consistent vegetative and reproductive features, as well as its modally different habitat. This species is the only violet in our region that produces both unspotted cleistogamous capsules and purple-spotted or -blotched capsules, although the latter are less frequent overall and are typically found in anthropogenic situations, perhaps reflecting past hybridization with species such as *V. affinis* and *V. sororia* (which have been documented). Other characteristics of plants with the two types do not obviously diverge, and the two capsule types occur fully intermingled in populations in lawns. It is common in lawns and urban woodlots—anthropogenic situations resembling its favored natural habitats of thickets and terraces along stream floodplains, and woodland slope-floodplain transitions. Other glabrous phenotypes are tentatively included in the *V. sororia* complex as broadly circumscribed in this treatment (see "Comments" under that species), pending further study. The only validly published name that unequivocally applies to this taxon is used here. Some years after Pollard (1898) published his new species, Greene—whom Pollard had initially consulted about the violet—returned to the situation and provided a detailed and rather scathing critique of Pollard's description, offering up his own more detailed and "correct" description with a new name, *Viola familiaris* Greene, and a new type. Although Greene asserted that the latter name applied to *V. communis* only "in part," it is clear from the publication text that Greene simply provided an extensively emended and extended description of the same taxon, making *V. familiaris* Greene a *nomen superfluum*.

Two floral color forms comprise this species, the typical f. *communis* with violet to purple corollas and indistinct purple nectarguides, and the confederate violet. The latter was first described as *V. priceana* Pollard and was recognized first as a species, then as a variety under *V. papilionacea*,

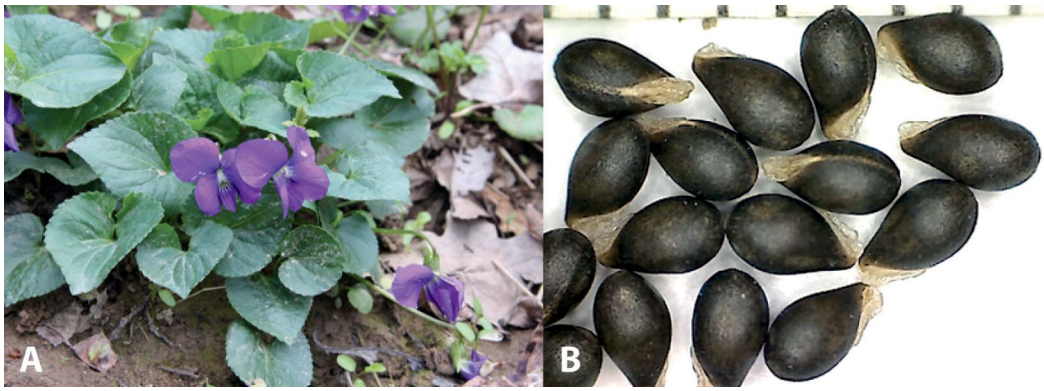

FIG. 28. *Viola communis* f. *communis*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Seeds from herbarium specimen: Transplanted from Ohio, Athens Co., *H. Ballard 17-023B* (BHO).

and more recently by Cooperrider (1984) as a form under *V. sororia*. The new combination for *V. priceana* under *V. communis* is published in the account for f. *priceana*. The two floral forms are indistinguishable except for corolla color pattern and flower size (f. *priceana* is typically a bit larger, perhaps a pleiotropic effect of the partial albinism) but are commonly found growing together.

12a. *Viola communis* Pollard f. ***communis***, Bot. Gaz. 26: 336. 1898; *Viola familiaris* Greene, Cybele Columb. 1: 14. 1914 [*nomen superfluum*]; *Viola domestica* E.P.Bicknell var. *communis* (Pollard) Farw., Pap. Michigan Acad. Sci. 2: 30. 1923 [“1922”]. Type: unknown. Fig. 28.

Viola papilionacea sensu Brainerd, Russell and others, in part.

Common Names. Common blue violet, dooryard violet, hooded blue violet.

Description. Same as the species, but corolla blue to purple, lacking a conspicuous contrasting eyespot around the throat.

Ecology. Same as the species.

Distribution. Same as the species.

Rarity. None.

Phenology. Same as the species.

Hybrids. Reports of hybrids involving “*V. papilionacea*” and other species probably refer to this (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*). They include hybrids with *V. affinis* (House 1906b, 1924; Brainerd 1924), *V. brittoniana* (Dowell 1910; Brainerd 1924; House 1924), *V. cucullata* (Brainerd 1906c, 1924; House 1924), *V. emarginata* (House 1906b, 1924; Brainerd 1924), *V. fimbriatula* (Stone 1903; Brainerd 1906c, 1924; House 1924), *V. hirsutula* (House 1906b; Brainerd 1907a, b, 1924; Henry 1953a), *V. nephrophylla* (Brainerd 1924), *V. palmata* var. *triloba* (Brainerd 1912, 1924), *V. sagittata* (Brainerd 1906c, 1924; House 1924), *V. sororia sensu stricto* (Dowell 1910; Greene 1914; Brainerd 1924; Henry 1953a), *V. stoneana* (Brainerd 1912, 1924), and *V. subsinuata* (Dowell 1910; Brainerd 1912, 1924; House 1924). The actual parentage of these hybrids (with regard to which *V. sororia* variant was involved) needs to be established beyond doubt. Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All hybrids fail to reproduce by chasmogamous flowers, and the cleistogamous capsules are abortive or produce a drastically diminished proportion of viable seeds. The first author has seen frequent hybrids of the present taxon with *V. affinis* and with *V. sororia sensu stricto* sporadically throughout Athens Co., OH. These exhibit the traits Brainerd reported in nearly all other hybrids of acaulescent blue violets.

Comments. Pollard’s protologue cited no types or specimens, providing a replacement name for “*V. obliqua* and *V. cucullata* of recent authors; not of Hill nor of Aiton.” Stafleu and Cowan (1983) state that Pollard’s herbarium and types are at US, with duplicates elsewhere. The US specimen database yielded no specimens of *V. communis*

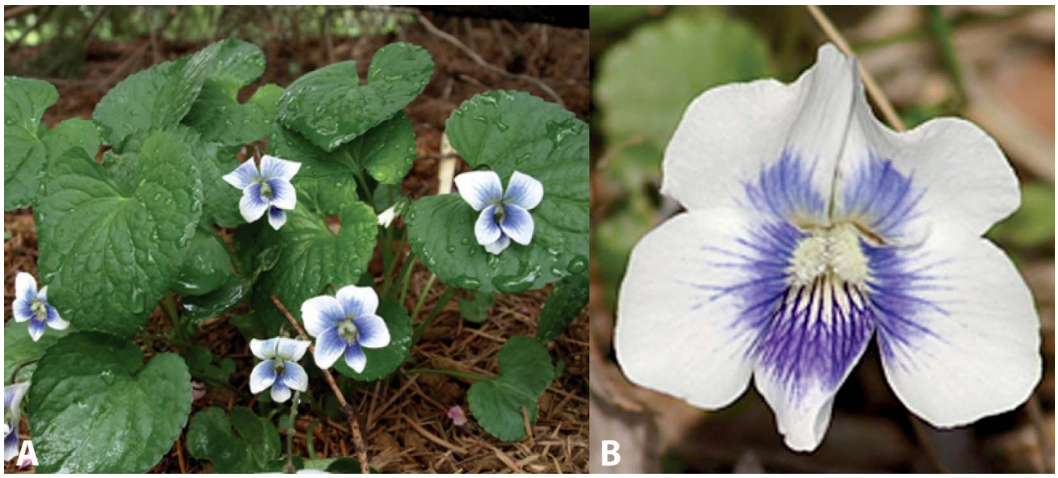

FIG. 29. *Viola communis* f. *priceana*. (A) Chasmogamous flowering habit (photo: Rob Broekhuis). (B) Chasmogamous flower front view (photo: Ivy Main).

either collected by or annotated by Pollard. The species thus far remains untypified.

12b. *Viola communis* Pollard f. ***priceana*** (Pollard) H.E.Ballard, **comb. nov.** *Viola priceana* Pollard, Proc. Biol. Soc. Washington 16: 127. 1903; *Viola papilionacea* Pursh var. *priceana* (Pollard) Alexander, in Gleason, New Ill. fl. n. U.S. 2: 555. 1952; *Viola sororia* Willd. f. *priceana* (Pollard) T. S. Cooperr., Mich. Bot. 23(4): 167. 1984. Type: USA Kentucky, Bowling Green, In Lawns, 4 Jun 1900, *S. F. Price s.n.* (lectotype (**designated here**): US03013737 (*n.v.*); isolectotypes: US03013734 (*n.v.*), US03013735 (*n.v.*), US03013736 (*n.v.*); all internet images). Fig. 29.

Common Name. Confederate violet.

Description. Same as the species, but corolla white or very pale violet with dense coalescing nectar-guide lines forming a conspicuously contrasting broad blue, blue-gray, or purple eyespot around the throat.

Ecology. Same as the species.

Distribution. Same as the species.

Rarity. None.

Phenology. Same as the species.

Hybrids. Hybridizes with f. *communis* (H.E.B., personal observation).

Comments. In his protologue, Pollard wrote "In rich soil, various stations around Bowling Green, Kentucky. The description is drawn from a clump of plants in my garden, sent to me in May, 1901, by Miss Sadie F. Price; these flowered rather sparsely in April, 1902, but more freely in 1903, and were conspicuous when in bloom on account of the contrast between the purple margins and pale ground color of the corolla. Miss Price reported it as very constant in its characters, and as easily distinguishable from other violets with which it grew. A herbarium specimen taken from these living plants and deposited in the United States National Herbarium, is the type." An in-person search of collections at US and of the herbarium specimen database yielded no specimens collected by Pollard. However, five specimens from Miss Price were found: one collected in 1899 by Miss Price (USA, Kentucky, Bowling Green, yards, 1 Apr 1899, US03012900) and four duplicates collected in 1900 by her (USA, Kentucky, Bowling Green, In Lawns, 4 Jun 1900, S. F. Price s.n. [US03013734, US03013735, US03013736, and US03013737]). These presumably constitute original material. Since Pollard's type has not been found, a lectotype is designated here.

Henry (1953a) accepted this as a distinct species closely related to *V. communis* or *V. sororia* (glabrous variant) (which he collectively called *V. papilionacea*). Brainerd Baird (1942) and Alexander (1963) accepted the present taxon as *V. papilionacea* var. *priceana*; and Ballard (2013) treated it as *V. sororia* f. *priceana*. Brainerd (1921b) did not distinguish it from *V. papilionacea*, while Russell (1965), Ballard (2000), Voss

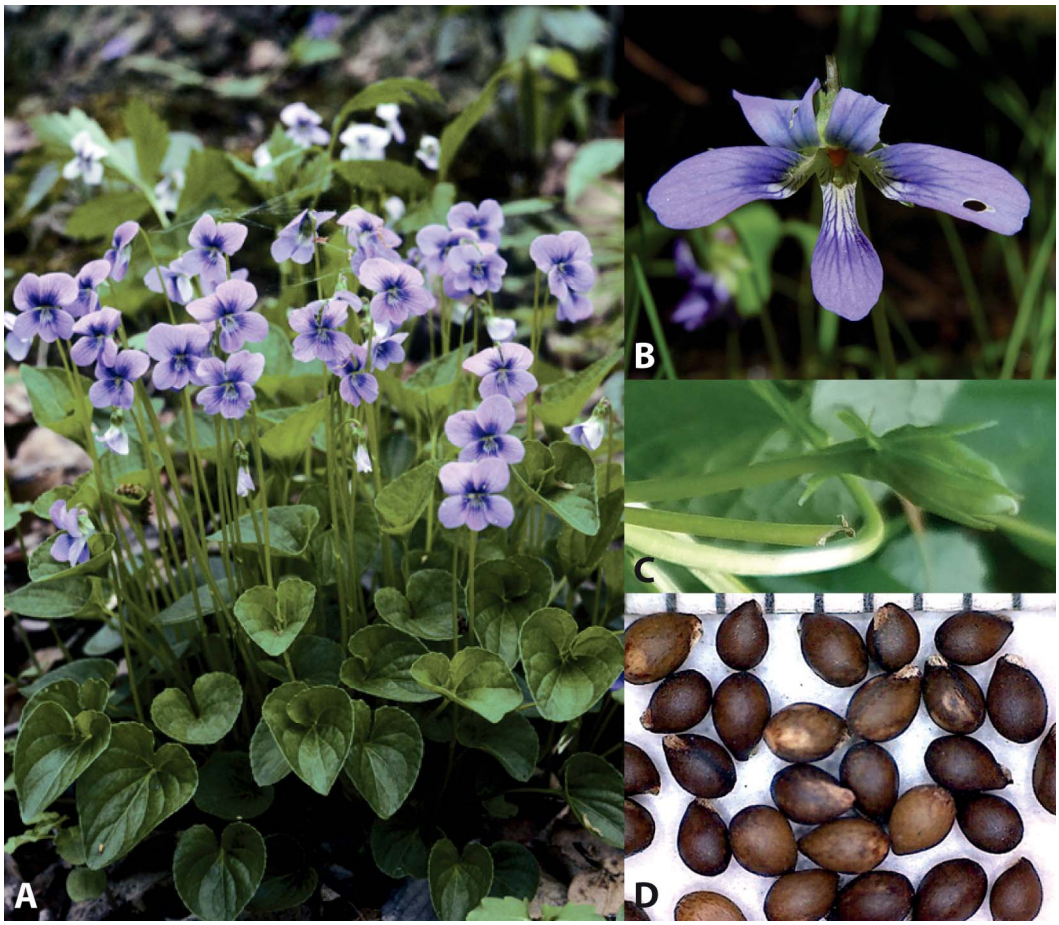

FIG. 30. *Viola cucullata*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Cleistogamous fruit (photo: Harvey Ballard). (D) Seeds from herbarium specimen: Transplanted from North Carolina, *E. Brainerd 33* (NY).

and Reznicek (2012), and Weakley *et al*. (2012) implicitly or explicitly included it in *V. sororia*, and McKinney (1992) and McKinney and Russell (2002) synonymized it under *V. sororia* var. *sororia*. Fernald (1950) and Strausbaugh and Core (1978) inaccurately treated it as a synonym of *V. papilionacea* f. *albiflora*, ignoring that the latter is a true albino lacking nectar-guide lines while the former is a "partial" albino retaining the pigmentation of the nectar-guide lines. The new combination at the rank of forma is made here for the partial albino, placing it under the species with which it belongs morphologically and ecologically. The "confederate violet" and garden varieties developed from it are cultivated due to its attractive corolla color pattern and often escape locally, but ostensibly wild populations often grow quite remote from human habitation. The corollas in f. *priceana* tend to be larger than those of f. *communis*.

13. ***Viola cucullata*** Aiton, Hort. Kew., ed. 1, 3: 288. 1789; *V. palmata* L. var. *cucullata* (Aiton) A.Gray, Bot. Gaz. 11: 254. 1886. Type: "Hort. Kew 1778" (holotype: BM001134389, internet image, MICH-photo (*n.v.*)). Fig. 30.

Viola obliqua Aiton, Hort. Kew., ed. 1, 3: 288. 1789.

Viola cucullata Aiton f. *albiflora* Britton, Bull. Torrey Bot. Club 17: 124. 1890.

Viola watsonii Greene, Pittonia 4: 5. 1899.

Viola consors Greene, Pittonia 5: 100. 1902.

Viola leptosepala Greene, Pittonia 5: 98. 1902; *Viola cucullata* Aiton var. *leptosepala* (Greene)

W.Stone, Proc. Acad. Nat. Sci. Philadelphia 1903: 674. 1903.

Viola macrotis Greene, Pittonia 5: 97. 1902.

Viola prionosepala Greene, Pittonia 5: 99. 1902; *Viola cucullata* Aiton f. *prionosepala* (Greene) Brainerd, Rhodora 15: 112. 1913.

Viola planifolia Greene, Leafl. Bot. Observ. 2(2): 41. 1910–1912.

Viola cucullata Aiton var. *microtitis* Brainerd, Rhodora 15: 112. 1913.

Common Name. Blue marsh violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 26 cm tall; foliage and peduncles light to medium green, glabrous or upper surface of leaf blades with small scattered subappressed hairs; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest $\leq$ 100 $\times$ 64 mm, narrowly ovate to broadly ovate, base cordate, margins crenate-serrate with apical teeth remote and shallow, eciliate, apex acute to narrowly obtuse; chasmogamous peduncle held well above the leaves; chasmogamous flower $\leq$ 23 mm; calyx glabrous, eciliate (frequently sparsely ciliate in northeastern boreal populations); lowest sepals linear-lanceolate to lanceolate, acuminate; auricles prominent, entire or erose, elongating to 7 mm in fruit (auricles scarcely elongate in northeastern boreal populations); corolla pale violet with heavy dark purple eyespot around throat, throat white; spur short-globose; lateral petals densely bearded with short clavate to reniform hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous, on erect peduncle slightly shorter to longer than petioles; capsule 10–15 mm, green drying tan, unspotted, glabrous; seeds 1.4–1.9 $\times$ 0.8–1.3 mm, dark brown to dark reddish-brown, unspotted; $2n = 54$.

Similar Species. In chasmogamous flower, only *V. communis* f. *priceana* could be mistaken for this species, since both produce pale corollas with a conspicuously contrasting dark eyespot around the throat, and have a glabrous spurred petal and prominent auricles; *V. cucullata* differs from *V. communis* f. *priceana* in having flowers strongly overtopping the leaves, linear to linear-lanceolate sepals acuminate from the base, and short lateral petal beards with strongly clavate to doorknob-shaped hairs that do not obscure the throat of the corolla. In cleistogamous fruit this species is distinct from several other glabrous uncut-leaved taxa, such as *V. affinis*, *V.* "*impostor*" (see "Potential Taxa" section), *V. latiuscula*, *V. missouriensis*, and *V. sororia* in producing unspotted cleistogamous capsules on tall erect peduncles. Among taxa with unspotted capsules on ascending to erect peduncles, it differs from *V. communis*, *V. domestica*, *V.* "*impostor*", *V. pratincola*, and *V. retusa* in the taller peduncles reaching or exceeding the petioles, longer auricles, and unspotted dark brown to reddish-brown seeds.

Ecology. Circumneutral to acidic saturated sandy, peaty, or mucky soils in seeps, springs, marshes, swamps, bog forests, and wet borders of streams, rivers, and lakes.

Distribution. Widely distributed across eastern North America, Newfoundland to northwestern Ontario, south to northwestern Florida and Mississippi. Fig. 31.

Rarity. None.

Phenology. Chasmogamous flower April–July, chasmogamous fruit June–July, cleistogamous fruit July–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Cucullata species group.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1906c, 1924; House 1924; Gaiser and Moore 1966; Haines *et al*. 2011), *V. brittoniana* (Bicknell 1904; House 1905; Brainerd 1906c, 1907b, 1924; Haines *et al*. 2011), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Brainerd 1906c, 1924; House 1924), *V. fimbriatula* (Pollard 1897; Brainerd 1904b, 1905, 1924; House 1924; Henry 1953a; Haines *et al*. 2011), *V. nephrophylla* (Brainerd 1906c, 1924; House 1924; Haines *et al*. 2011), *V. palmata* var. *triloba* (Brainerd 1906c, 1913c, 1924; House 1924; Haines *et al*. 2011), *V. pectinata* (Brainerd 1924), *V. primulifolia* (Bicknell 1904, Brainerd 1906c [initially mistaken as hybrid with *V. emarginata sensu stricto*], 1909, 1924; House 1924), *V. sagittata* (Brainerd 1906c, 1924; House 1924), *V. septentrionalis sensu stricto* (Brainerd 1904b, 1924; House 1924; Russell 1955a), *V. sororia sensu stricto* (Brainerd 1904b, 1924; House 1924; Henry 1953a; Haines *et al*. 2011), *V. subsinuata* (Brainerd 1913c, 1924; House 1924; Haines *et al*. 2011), and *V. viarum* (Brainerd 1924). Brainerd

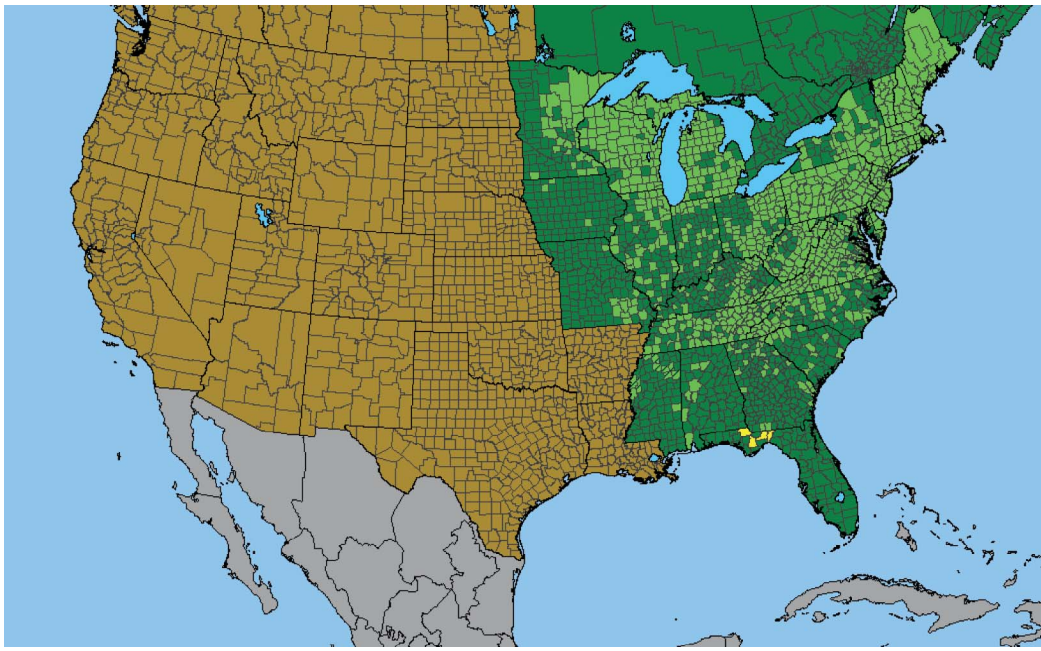

FIG. 31. United States county distribution of *Viola cucullata* (map: Biota of North America Program).

reported that the hybrids involving only acaulescent blue violet taxa express intermediate or recombinant traits in foliage, chasmogamous flowers, cleistogamous capsules, and seeds (when these do not abort). All hybrids fail to reproduce by chasmogamous flowers, and the cleistogamous capsules are abortive or produce extremely few viable seeds. The situation surrounding *V.* ×*lavandulacea* E.P.Bicknell is interesting. Bicknell (1904) published it as a species. Brainerd (1906c) shortly thereafter interpreted its characters to indicate a hybrid of *V. cucullata* with *V. emarginata sensu stricto*, resisting Bicknell's insistence that *V. primulifolia* in the vicinity could be the other parent. In 1909, Brainerd rethought his position, inspired in that year by Forbes's discovery of a remarkable hybrid between *V. brittoniana* and *V. lanceolata*. Brainerd's later enumeration of intermediate features supported *V. primulifolia* as the second parent. House (1924) mentioned the hybrid and its taxonomic history, remarking that Brainerd's original assessment of *V. emarginata* as the second parent seemed more likely. The first author's examination of the holotype image reveals very short auricles and rather short merely acute sepals that would be unlikely on a hybrid involving *V. cucullata* and *V. emarginata sensu stricto*, two species with very prominent auricles and long-acuminate sepals in chasmogamous flower. Examination of pollen fertility and morphology of the style would provide convincing evidence; the pollen stainability of acaulescent blue hybrids is generally 50% to 90%, whereas a hybrid involving two very different ploidy levels would presumably have essentially 100% abortive pollen, and members of the *Borealiamericanae* and *Stolonosae* groups have noticeably different style morphologies.

Comments. Brainerd (1921), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), McKinney (1992), Ballard (1995, 2000, 2013), Gil-ad (1995, 1997, 1998), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney 2015) have recognized this distinctive taxon at species rank. Strausbaugh and Core referred Tosh's (1942) report and a second unidentified 1945 report of *V. missouriensis* from West Virginia to this species. While many other acaulescent blue species have long hairs in the lateral petal beards that are often weakly clavate, the very short beard hairs in this species are strongly clavate to reniform ("doorknob-shaped") and expose the

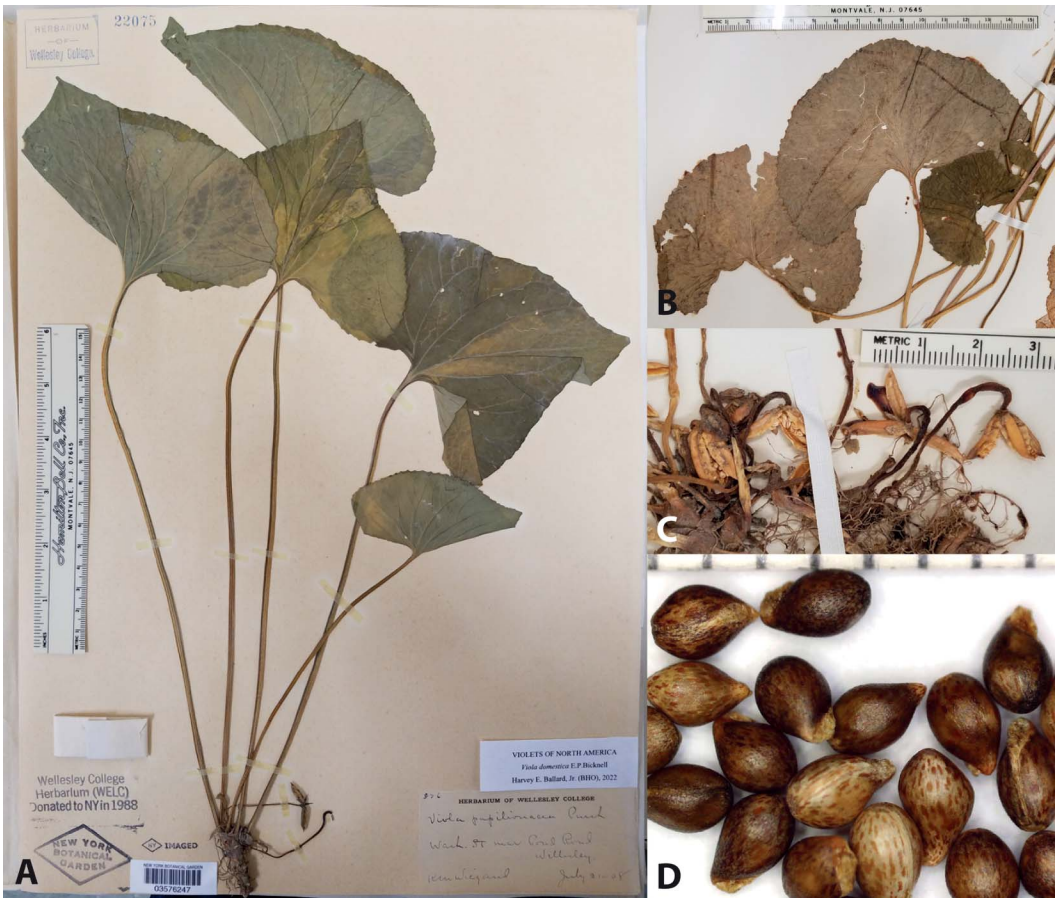

FIG. 32. *Viola domestica*. (A) Cleistogamous fruiting habit from herbarium specimen: Massachusetts, Wellesley, 21 July 1908, *K. M. Wiegand 876* (NY03576247). (B) Leaves during cleistogamous fruit from herbarium specimen: Massachusetts, Martha's Vineyard, 10 Oct 1911, *E. P. Bicknell 6178* (NY04298243). (C) Cleistogamous fruit from herbarium specimen: Massachusetts, Martha's Vineyard, 10 Oct 1911, *E. P. Bicknell 6178* (NY04298243). (D) Seeds from herbarium specimen: New York, The New York Botanical Garden, *W. W. Eggleston 21288* (NY04298237).

interior of the throat in living material. Populations from the boreal region of extreme northeastern North America, from Maine eastward into maritime Canada, possess shorter sepals and short auricles that scarcely elongate or don't at all in fruit. Authors from Brainerd (1921) through Scoggan (1978), but excepting Russell (1965), segregated these northern variants as var. *microtitis* Brainerd, but they do not differ in any other observable respect from typical *V. cucullata* farther south and are no longer formally recognized. Occasional plants with pubescent foliage and/or a sparsely ciliate calyx are invariably found in the vicinity of *V. septentrionalis* or *V. sororia* and are *de novo* hybrids. Most of the specimens previously identified as *V. cucullata* from the southeastern Lower Atlantic Coastal Plain are the newly detected *V.* "*impostor*," noted in the "Potential Taxa" section.

14. ***Viola domestica*** E.P.Bicknell, Britton & Brown, Illust. Fl. US & Canada 3 [Appendix]: 519. 1898; *Viola papilionacea* Pursh var. *domestica* (E.P.Bicknell) Pollard, in Britton, Man. fl. n. states, ed. 1: 636. 1901. Type: USA New York. [New York Co.] Fort Washington, 7 Aug 1897, *E.P. Bicknell s.n.* (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 220.): NY00097529, internet image). Fig. 32.

Common Name. Yard violet.

Description. Acaulescent rosulate perennials from thick rhizome, ≤ 38 cm tall; foliage and peduncles light to medium green, dull (occasionally the upper surface of leaf blades slightly glossy), glabrous; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest ≤ 126 × 90 mm, in spring broadly ovate to deltate-ovate, in summer broadening to deltate-reniform and often reaching very large size, base cordate to shallowly cordate but in summer nearly or quite truncate and shortly cuneate-decurrent to the summit of the petiole, margins conspicuously incurved-crenate-serrate to the abruptly obtuse-angulate apex, eciliate; chasmogamous peduncles held among the leaves; chasmogamous flower ≤ 18 mm; calyx eciliate; lowest sepals oblong-lanceolate, convexly tapering to acute apex; auricles slightly prominent, quadrate, weakly elongating in fruit to 1.5 mm; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous, on short arching to ascending peduncle much shorter than petioles; cleistogamous capsule 11–14 mm, green drying tan, unspotted, glabrous; seeds 1.9–2.2 × 1.2–1.3 mm, medium to dark brown (occasionally with weak orange-brown blotches), commonly with dense small raised dark spots.

Similar Species. Among *Borealiamericanae* taxa with strictly or essentially glabrous foliage and leaf blades as broad as to broader than long (including some *V. cucullata*), *V. domestica* differs from *V. nephrophylla* in its glabrous spurred petal, sepals with acute apices and slightly prominent auricles, short ascending to erect cleistogamous peduncle, and commonly spotted seeds; from *V. communis* in its taller stature, light to medium green foliage with dull leaf blade surfaces, proportionally broader ovate leaf blades broadening to reniform-deltate with broadly and shallowly cordate to truncate base and prominently incurved-serrate margins, and proportionally more slender and merely acute sepals; from *V. cucullata* in shorter and less acuminate sepals with shorter auricles, no conspicuously contrasting dark purple eyespot on the corolla, lateral petal beards with long slender hairs, shorter cleistogamous peduncle, and commonly spotted seeds; and from *V. sororia* (glabrous and *hirsutuloides*variant) in its slender acute sepals with slightly prominent auricles, unspotted cleistogamous capsule on an ascending to erect peduncle, and commonly spotted seeds. In cleistogamous fruit, it can be separated from *V. affinis* and *V. missouriensis* in its acute eciliate sepals, slightly prominent auricles, unspotted cleistogamous capsule on an ascending to erect peduncle, and brown commonly spotted seeds; and from *V. langloisii* (not yet confirmed in our region), *V. pratincola*, and *V. retusa* in its proportionally broader leaf blades with subcordate to truncate base shortly cuneate-decurrent onto the petiole, prominently incurved-serrate leaf blade margins, and merely acute sepals with weakly prominent auricles.

Ecology. Found only in relatively rich loamy soils in garden plantings and other actively disturbed sites.

Distribution. Probably very incomplete, frequently cultivated and presumably barely escaping in urban and suburban areas; few herbarium records sporadic over the eastern USA. Fig. 33.

Rarity. None.

Phenology. Not yet known.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Cucullata species group.

Hybrids. None yet confirmed, although occasional plants with sparsely hirsute foliage may reflect hybridization; this bears investigation.

Comments. Bicknell published the name in the Appendix to Britton and Brown's (1897) *Illustrated Flora* and provided a broad geographic range and habitat, stating that it was "Apparently always in cultivated soil, especially about buildings, southern New York, New Jersey and Pennsylvania." Bicknell designated no types and cited no herbaria. According to Stafleu and Cowan (1976), Bicknell's herbarium and types are at NY. The NY00097529 sheet constitutes original material. McKinney annotated this sheet incorrectly as a holotype, but in his 1992 publication he designated a different sheet (USA, New York, Manhattan Island, 11 Jun 1993, T. Maring s. n., NY) that does not appear to be original material. Sheet NY00097529 is representative of the taxon based on Bicknell's description and was selected by Ballard *et al*. (2020a) as the lectotype.

After a few references to the name earlier in the last century, this violet has since been ignored or

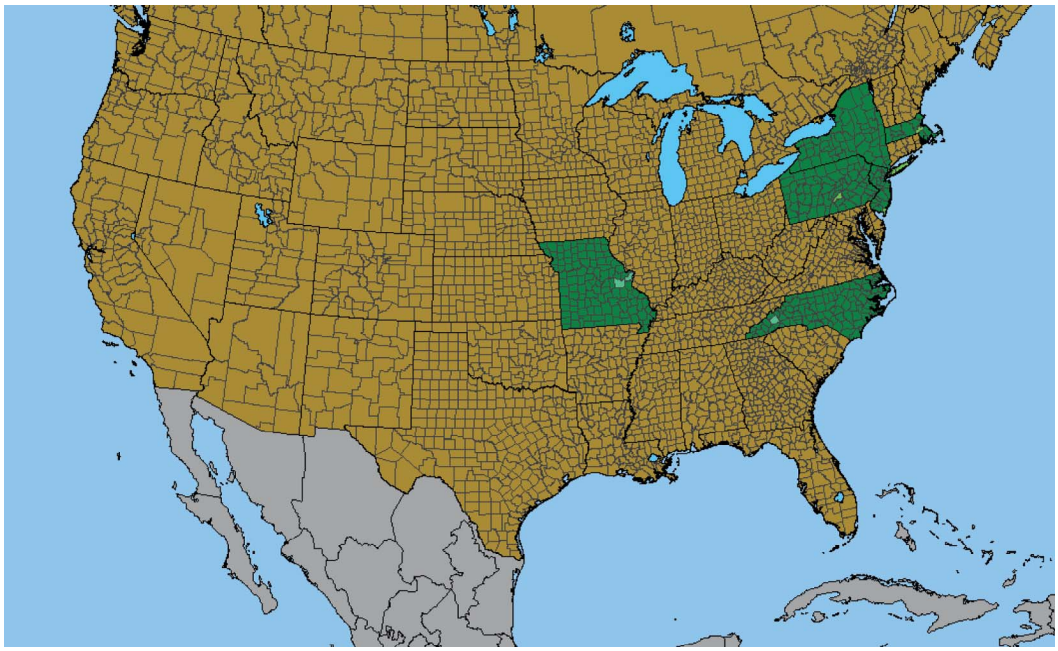

FIG. 33. United States county distribution of *Viola domestica* (map: Biota of North America Program).

synonymized under the name *V. sororia* Willd., which recently has been treated in a very broad sense. However, the morphological features of leaves, chasmogamous flowers, cleistogamous capsules, and seeds are not similar to the glabrous variants of *V. sororia*, being much closer to other members of the Cucullata species group, especially *V. communis* and *V. pratincola*. Many of its morphological features appear to be somewhat intermediate between or shared by either *V. communis* and *V. sororia*, and this taxon is almost undoubtedly a cultigen of plant breeders, perhaps descending from hybrids between both of those species but more similar to *V. communis*. It seems virtually confined to heavily cultivated sites, seeming scarcely to escape from where it was planted and only then to other nearby plantings or actively disturbed microsites.

15. ***Viola edulis*** Spach, Hist. Nat. Vég. (Spach) 5: 508. 1836 [replacement name at species rank for *V. palmata* L. var. *heterophylla* Elliott]; *Viola palmata* L. var. *heterophylla* Elliott, Sketch bot. S. Carolina 1(3): 300. 1817; *Viola heterophylla* Leconte, Ann. Lyceum Nat. Hist. New York 2: 139. 1828 ["1826"] [illegitimate homonym of *Viola heterophylla* (Vent.) Poir. (1808) and of *Viola heterophylla* Bertol. (1810)]; *Viola esculenta* Elliott ex Greene, Pittonia 3: 314. 1898; *Viola palmata* L. var. *esculenta* Elliott ex D.B.Ward, Phytologia 88: 244. 2006 [nomen superfluum]. Type: [USA Georgia] Ogeechee river in udis etian in Pennsyl. Flor. April [no year], [*S. Elliott s.n.*] (holotype: CHARL). Fig. 34.

Common Name. Atlantic Coast salad violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm tall; foliage and peduncles light to medium green, glabrous throughout; stipules free, irregularly glandular-fimbriate; heterophyllous, leaves spreading, largest leaf blades in mid- to late chasmogamous flower into fruit shallowly to moderately pedately divided into 3 or 5 lobes, $\leq 70 \times 60$ mm, outline in spring narrowly ovate-triangular, in summer broadening to broadly ovate, base cordate, margins serrate to sporadically so, eciliate, apex acute; earliest chasmogamous peduncle held above the leaves; chasmogamous flower $\leq$ 21 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate to ovate-triangular, acuminate; auricles prominent, entire or erose, elongating to 3 mm and erose in fruit; corolla light blue, white of throat extending onto exposed basal portion of spurred petal; spur short-globose; lateral petals densely bearded with narrowly linear to slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced

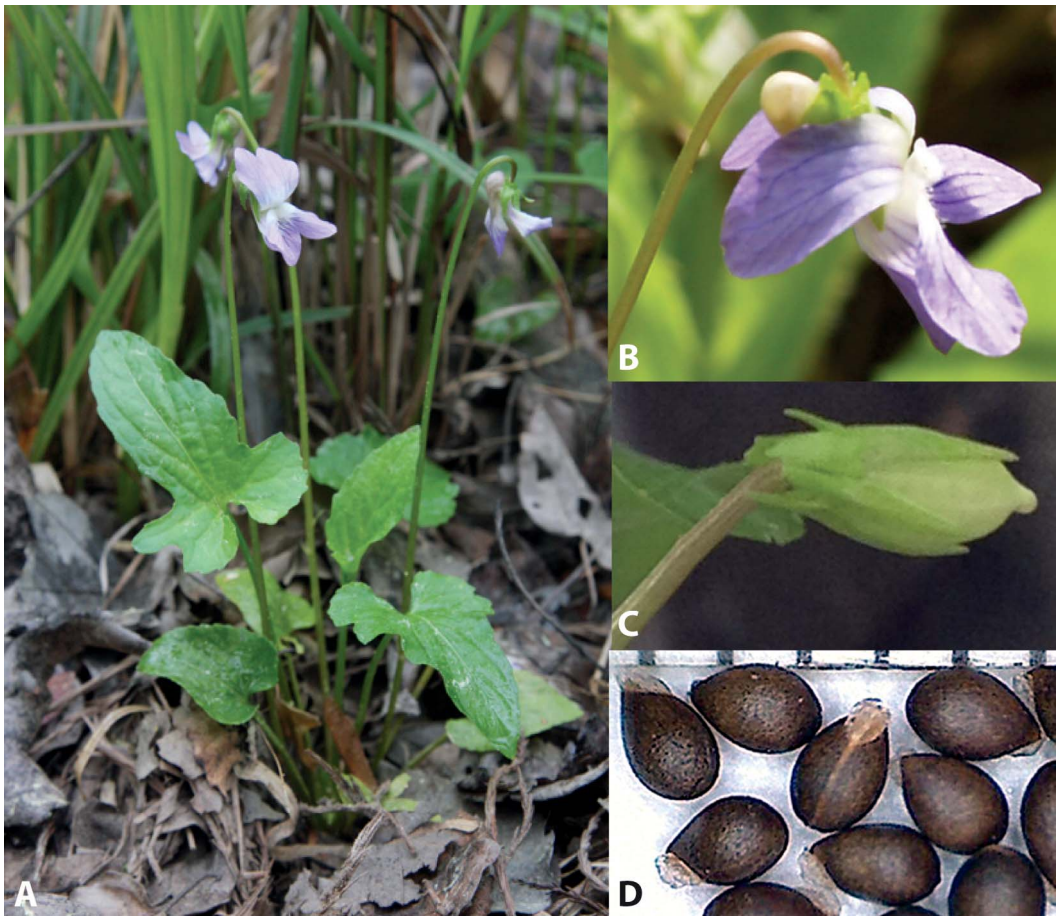

FIG. 34. *Viola edulis*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Chasmogamous flower profile view (photo: Harvey Ballard). (C) Cleistogamous fruit (photo: Harvey Ballard). (D) Seeds from herbarium specimen: Transplanted from Georgia, Bulloch Co., *H. Ballard et al. 16-030* (BHO).

during or after chasmogamous, on erect peduncle equaling or surpassing petioles; capsule 8–10 mm, green drying tan, unspotted, glabrous; seeds 1.5–1.9 × 1.0–1.2 mm, medium to dark brown or purplish-brown with dense minute raised black spots or reticulations (these occasionally sparse, seeds then appearing medium brown overall).

Similar Species. This species is most likely to be confused with the few other heterophyllous taxa with glabrous foliage, namely *V. egglestonii* and *V. viarum* in the Viarum species group. It differs from those two species in its less deeply divided leaf blades with 3–5 lobes, the lateral shorter and broader, glabrous spurred petal, unspotted cleistogamous capsule on rather tall erect peduncle, sharply acute sepals, elongate auricles, brown seeds with dense minute black spots or reticulations, and restriction to riparian bottomland forests on the Atlantic Coastal Plain.

Ecology. Sandy, silty, or mucky alluvial soils of low terraces and frequently inundated floodplain zones along blackwater streams and rivers, and in swamps.

Distribution. Eastern Atlantic Coastal Plain, extending to just above the "fall line" in the Carolinas, Maryland south to southeastern Georgia. Fig. 35.

Rarity. Listed in Maryland (as *V. esculenta*).

Phenology. Chasmogamous flower February–May, chasmogamous fruit February–May, cleistogamous fruit April–August.

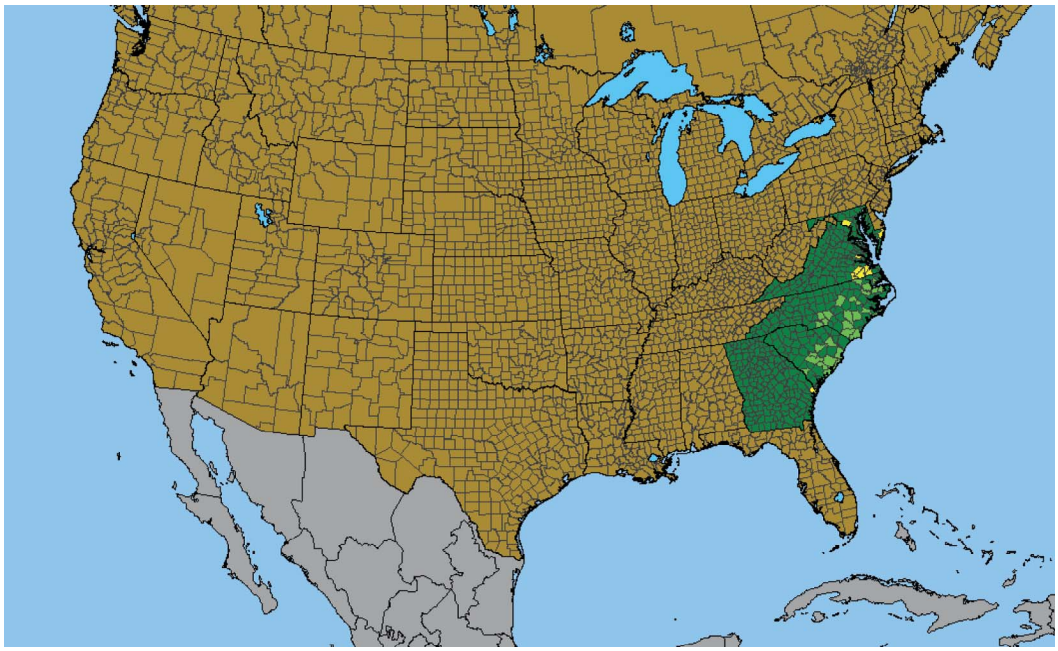

FIG. 35. United States county distribution of *Viola edulis* (map: Biota of North America Program).

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium*, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Edulis species group.

Hybrids. The first author has collected hybrids with *V.* "*impostor*" (see "Potential Taxa"), growing intermingled with both parent species, at Elwell Ferry in Bladen Co., NC. This is apparently the first report of hybridization involving *V. edulis*. No information is available on hybrid reproduction, although the hybrids mostly expressed intermediate traits in foliage characteristics.

Comments. Elliott's protologue does not reference a type or cite a particular collection, and it does not designate a herbarium. However, he does note the species is common along the Ogeechee River in Georgia, flowering in March and April. Stafleu and Cowan (1976) acknowledged Charleston Museum as the depository for Elliott's collection. A thorough in-person search revealed only one sheet, bearing a plant with an attached label, which matches the protologue. The sheet is accepted as the holotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), and Weakley *et al*. (2012) recognized a broadly circumscribed and geographically widely distributed coastal plain *V. esculenta*. Gleason and Cronquist (1991), McKinney (1992), and McKinney and Russell (2002) included it in a very broadly delimited *V. palmata*. Gil-ad (1995, 1997, 1998) reviewed the macromorphological features mentioned by others for distinguishing it and concluded that the taxon had no unique vegetative or reproductive traits. He reported that the seeds revealed no unique micromorphological features, and that some features resembled those of *V. missouriensis*, suggesting that as one parent of the putative hybrid origin of this taxon. Given the heterophylly, leaf blade division and southern distribution, he suggested the other parent species may have been *V. septemloba* or *V. triloba* (= *V. palmate*). Gil-ad concluded that the present taxon most likely originated by hybridization or introgression and dismissed it. Ward (2006) examined this taxon and determined that too few characters separated it from the broadly defined *V. palmata* in the region, and he published the unfortunate superfluous name *V. palmata* L. var. *esculenta* Elliott ex D.B.Ward. Little and McKinney (2015) reinstated a broadly defined taxon equivalent to Brainerd's and Russell's *V. esculenta* and followed Ward's (2006) reduction to variety under *V. palmata*, using the already available name var. *heterophylla* Elliott. We have collected and studied

over a dozen populations along the eastern Atlantic Coastal Plain, from southern Maryland to eastern Georgia (19 km upstream on the Ogeechee River from the likely type locality of Elliott's plantation). The macromorphological traits of leaves, chasmogamous flowers, cleistogamous capsules, and seeds are highly uniform across populations, as are the dimensions and color patterns of the seeds. The micromorphologies of the seed coats are also uniform, and all plants are fully fertile. They differ collectively in several to many characteristics from other similar taxa. No populations have been confirmed, either in the field or as herbarium specimens, south or west of the Atlantic Coastal Plain of southeastern Georgia. This taxon is recognized as a distinct, narrowly circumscribed species of the Atlantic Coastal Plain. Specimens identified as "*V. esculenta*" off the Coastal Plain have invariably proven to be other taxa, and plants superficially resembling the present taxon in Florida and the Gulf Coast display different macromorphological features of leaves, chasmogamous flowers, cleistogamous fruits, and seeds; these likely constitute yet another undescribed species. A substantial proportion of the herbarium specimens labeled or annotated as *V. esculenta* are other taxa. Notwithstanding the universal application of *V. esculenta* Elliott ex Greene for this at species rank, the earliest correct name is *V. edulis* Spach. We have provided a more specific common name for this species to distinguish it from the undescribed *Viola* in the Gulf states. Russell's (1965) illustration is actually *V. septemloba*, which frequently produces three-lobed leaf blades. This and other members of the Edulis species group are currently under study by Remington Burwell at Ohio University.

16. ***Viola egglestonii*** **species complex**

Infraspecific taxa belonging to this species include the following:

16a. *Viola egglestonii* Brainerd *sensu stricto*

16b. *Viola egglestonii* (Canada variant)

Common Name. Eggleston's violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm tall; foliage and peduncles green, occasionally slightly subsucculent, upper surface of leaf blades occasionally darker, glabrous throughout; stipules free, irregularly glandular-fimbriate; heterophyllous, leaves ascending, largest leaf blades moderately to deeply biternately divided into 7 or 9 lobes, terminal primary division narrowly or broadly oblong to oblong-lanceolate, distinctly narrowing proximally with the central lobe not much broader than its lateral lobes (*V. egglestonii sensu stricto*), or terminal primary division not distinctly narrowing proximally and noticeably broader than the laterals (*V. egglestonii* [Canada variant]), $\leq$ 120 $\times$ 114 mm, outline ovate to subreniform, base broadly cuneate to subcordate, margins of lobes entire proximally and serrate distally, eciliate, apex sharply acute to obtuse; chasmogamous peduncle held among or above the leaves; chasmogamous flower $\leq$ 17 mm; calyx glabrous, eciliate or sparsely ciliate; lowest sepals lanceolate to ovate-lanceolate and obtuse to broadly rounded (*V. egglestonii sensu stricto*), or linear-lanceolate and acuminate from near the base to a narrowly sharply acute (rarely obtuse) apex (*V. egglestonii* [Canada variant]); auricles short and entire, not elongating in fruit (*V. egglestonii sensu stricto*), or prominent and quadrate, elongating somewhat in fruit (*V. egglestonii* [Canada variant]); corolla blue to purple, white of throat extending onto lateral petals and halfway down spurred petal; lateral petals densely bearded with narrowly long linear to slightly clavate hairs that at least partially obscure the throat, and spurred petal sparsely to densely bearded (*V. egglestonii sensu stricto*), or lateral petals densely bearded with very short clavate hairs that do not obscure the throat, and spurred petal glabrous within (*V. egglestonii* [Canada variant]); chasmogamous capsule green, unspotted; cleistogamous flowers produced after chasmogamous, the peduncle prostrate, arching just before capsule dehiscence (*V. egglestonii sensu stricto*) or ascending (*V. egglestonii* [Canada variant]), much shorter than petioles; capsule 12–18 mm, ovoid, green drying tan, unspotted, glabrous; seeds (1.8)2.7–3.3 $\times$ 1.3–1.7 mm, medium to dark brown, unspotted (seeds of *V. egglestonii* [Canada variant] unknown).

Similar Species. Among heterophyllous taxa, this species complex is most similar to others with glabrous foliage in our region, namely *V. edulis* in the Edulis species group and *V. viarum* in the Viarum species group. It differs in its more deeply biternately divided leaf blades with 7–9 comparatively longer narrow lobes, the central lobe oblong to oblong-lanceolate and nearly or quite as narrow as or somewhat broader than the lateral ones, linear-lanceolate and acuminate sepals or lanceolate to

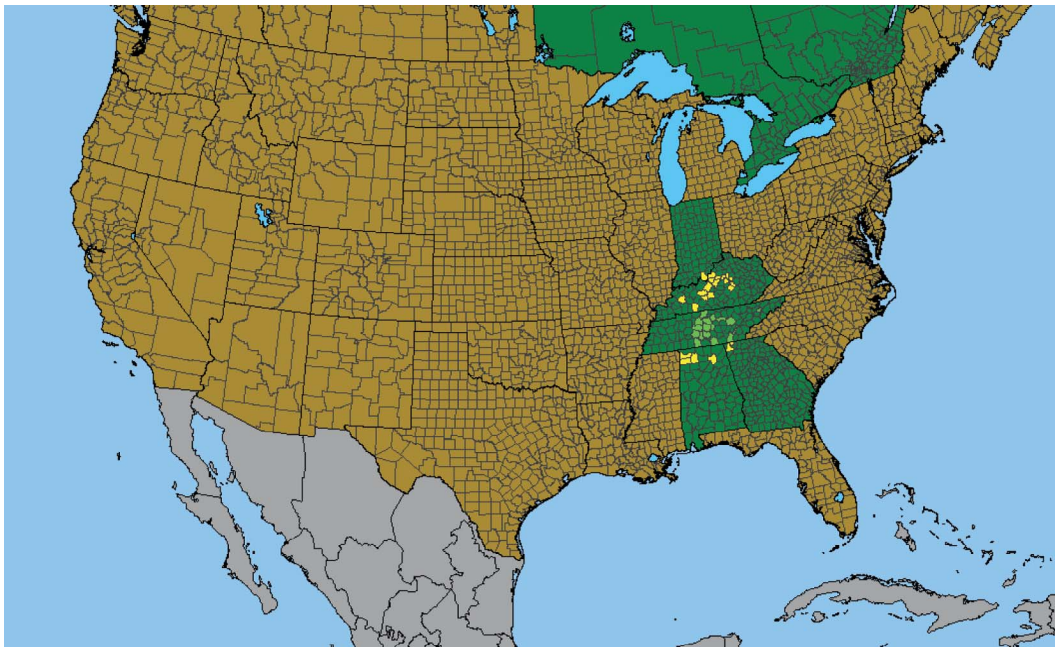

FIG. 36. United States county distribution of *Viola egglestonii* species complex (map: Biota of North America Program).

ovate-lanceolate rounded sepals, glabrous or bearded spurred petal, unspotted cleistogamous capsule on short prostrate to ascending peduncle, short to weakly elongating auricles, unspotted brown seeds, and its habitat in limestone cedar glades of the Interior Low Plateau or in grassy areas (*e.g.*, lawns) overlying limestone.

Ecology. Dry rock crevices of limestone cedar glades (calcareous barrens), occasionally persisting in more disturbed sites overlying limestone such as pastures and roadsides (*V. egglestonii sensu stricto*). Also recently documented in lawns and plantings in cities and suburbs in southeastern Canada (*V. egglestonii* [Canada variant]) and in lawns as an introduction in Europe.

Distribution. Interior Lowland Plateau, southern Indiana south to northwestern Georgia and northern Alabama (*V. egglestonii sensu stricto*); southern Ontario and Quebec, and apparently introduced into Europe (*V. egglestonii* [Canada variant]) (Vitek *et al*. 2012; Cheon *et al*. 2019). Fig. 36.

Rarity. See infraspecific taxa.

Phenology. Chasmogamous flower April–May, chasmogamous fruit May–June, cleistogamous fruit July.

Affinities. This species complex belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Viarum species group.

Hybrids. See infraspecific taxa.

Comments. Brainerd cited one specific collection as the type but did not reference a particular sheet. Gil-ad (1995, 1997) pointed out that Brainerd noted his intentions to supply types to NY; nevertheless, searches by Director Barbara Thiers, McKinney, Gil-ad, and Ballard have failed to produce specimens at that herbarium. Gil-ad attributed the sole specimen to an isotype, but there is no indication that Brainerd ultimately distributed other specimens elsewhere. Since only the UVMVT024585 sheet exists, Ballard *et al*. (2020a) accepted the sheet as the holotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), and Gil-ad (1995, 1997, 1998) accepted this narrow regional and edaphic endemic as a distinct species. Gleason and Cronquist (1991) synonymized it under *V. palmata* var. *pedatifida* (G.Don) Cronquist, while McKinney (1992) treated this as a subspecies under *V. septemloba* on the basis of similar leaf morphology. Little and McKinney

(2015) later reinstated it at species rank. Although they look superficially similar, the two differ in certain vegetative features and many features of chasmogamous flowers and cleistogamous fruits and seeds, diverge in micromorphological features of the seeds, and have very different ecological niches. The two are maintained as separate species here.

Native populations occupy limestone cedar glades of the Interior Lowland Plateau as a regional endemic. Although it appears to persist in degraded limestone cedar glades, no information is currently available on whether the species expresses weedy tendencies or a proclivity for escaping into anthropogenic sites. However, populations we tentatively refer to this species complex have been documented recently on iNaturalist at several sites in eastern Ontario and southwestern Quebec; see "Comments" under *V. egglestonii* (Canada variant). Shaver (1959) investigated leaf development and the heterophyllous nature of this species. Baskin and Baskin (1970, 1972, 1975a, b, 1978) and Baskin *et al*. (1987) examined its seed germination, ecology, and the geographic distribution.

16a. *Viola egglestonii* Brainerd ***sensu stricto***, Bull. Torrey Bot. Club 37: 526, pl. 34, 35. 1910; *Viola septemloba* Leconte subsp. *egglestonii* (Brainerd) L.E.McKinney, Sida, Bot. Misc. 7: 33. 1992. Type: USA Tennessee, [Davidson Co.] West Nashville, limestone barrens, 23 May 1909, *W. W. Eggleston 4421* (holotype: UVMVT024585, internet image). Fig. 37.

Common Name. Eggleston's violet.

Description. Habit, foliage, and stipules same as the species complex; largest leaf blades with terminal primary division distinctly narrowing proximally, the central lobe not much broader than its lateral lobes; calyx eciliate or sparsely ciliate; lowest sepals lanceolate to ovate-lanceolate, obtuse to broadly rounded; auricles short and entire, not elongating in fruit; lateral petals densely bearded with narrowly linear to slightly clavate hairs that partially or completely obscure the throat, spurred petal sparsely to densely bearded; cleistogamous peduncle prostrate, arching just before capsule dehiscence; other flower, capsule, and seed traits same as species complex.

Similar Species. Among heterophyllous taxa, this species is most similar to others with glabrous foliage in our region, namely *V. edulis* in the Edulis species group and *V. viarum* in the Viarum species group. It differs in its more deeply biternately divided leaf blades with 7–9 long narrow lobes, the central lobe nearly or quite as narrow as the lateral ones, rounded sepals, bearded spurred petal, unspotted cleistogamous capsule on short prostrate peduncle, short auricles, unspotted brown seeds, and its habitat in limestone cedar glades of the Interior Low Plateau.

Ecology. Dry rock crevices of limestone cedar glades (calcareous barrens), occasionally persisting in more disturbed sites overlying limestone such as pastures and roadsides.

Distribution. Interior Lowland Plateau, southern Indiana south to northwestern Georgia and northern Alabama. Fig. 38.

Rarity. Listed in Indiana and Kentucky (as *V. septemloba* var. *egglestonii*).

Phenology. Same as the species complex.

Affinities. Same as the species complex.

Hybrids. The first author has identified a herbarium specimen at CM from Rutherford Co., TN, as a hybrid with *V. sororia*. It displayed intermediate characteristics of foliage traits. This is the first report of hybridization for *V. egglestonii sensu stricto*. No information is available on hybrid reproduction.

Comments. Brainerd cited one specific collection as the type but did not reference a particular sheet. Gil-ad (1995, 1997) pointed out that Brainerd noted his intentions to supply types to NY; nevertheless, searches by Director Barbara Thiers, McKinney, Gil-ad, and Ballard have failed to produce specimens at that herbarium. Gil-ad attributed the sole specimen to an isotype, but there is no indication that Brainerd ultimately distributed other specimens elsewhere. Since only the UVMVT024585 sheet exists, Ballard *et al*. (2020a) accepted the sheet as the holotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), and Gil-ad (1995, 1997, 1998) accepted this narrow regional and edaphic endemic as a distinct species. Gleason and Cronquist (1991) synonymized it under *V. palmata* var. *pedatifida* (G.Don) Cronquist, while McKinney (1992) treated this as a subspecies under *V. septemloba* on the basis of similar leaf morphology. Little and McKinney

FIG. 37. *Viola egglestonii sensu stricto*. (A) Chasmogamous flowering habit (photo: Alan Cressler). (B) Chasmogamous flower front view (photo: Alan Cressler). (C) Seeds from herbarium specimen: Transplanted from Tennessee, Davidson Co., *E. Brainerd 44* (NY).

(2015) later reinstated it at species rank. Although they look superficially similar, the two differ in certain vegetative features and many features of chasmogamous flowers and cleistogamous fruits and seeds, they diverge in micromorphological features of the seeds, and have very different ecological niches. The two are maintained as separate species here.

Native populations occupy limestone cedar glades of the Interior Lowland Plateau as a regional endemic. Although it appears to persist in degraded limestone cedar glades, no information is currently available on whether the species expresses weedy tendencies or a proclivity for escaping into anthropogenic sites. Populations treated here as *V. egglestonii* (Canada variant) are

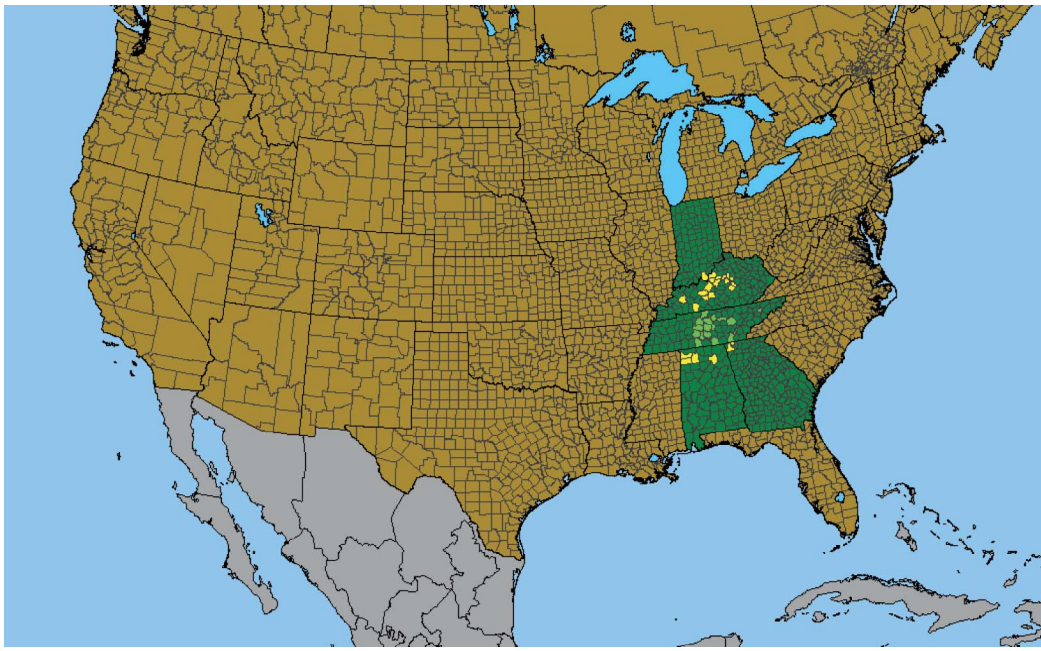

FIG. 38. United States county distribution of *Viola egglestonii sensu stricto* (map: Biota of North America Program).

morphologically divergent in a number of respects as noted in the key, and they inhabit lawns or garden plantings in urban and suburban environments in a region of southeastern Canada overlying limestone. They are tentatively placed here out of convenience but appear distinct and require further study. See "Comments" under that variant.

Shaver (1959) investigated leaf development and the heterophyllous nature of this species. Baskin and Baskin (1970, 1972, 1975a, b, 1978) and Baskin *et al*. (1987) examined its seed germination, ecology, and geographic distribution.

16b. *Viola egglestonii* (Canada variant), Fig. 39.

Common names. None.

Description. Habit, foliage, and stipules same as the species complex; largest leaf blades with terminal primary division not distinctly narrowing proximally, the central lobe somewhat broader than its lateral lobes, calyx eciliate; lowest sepals

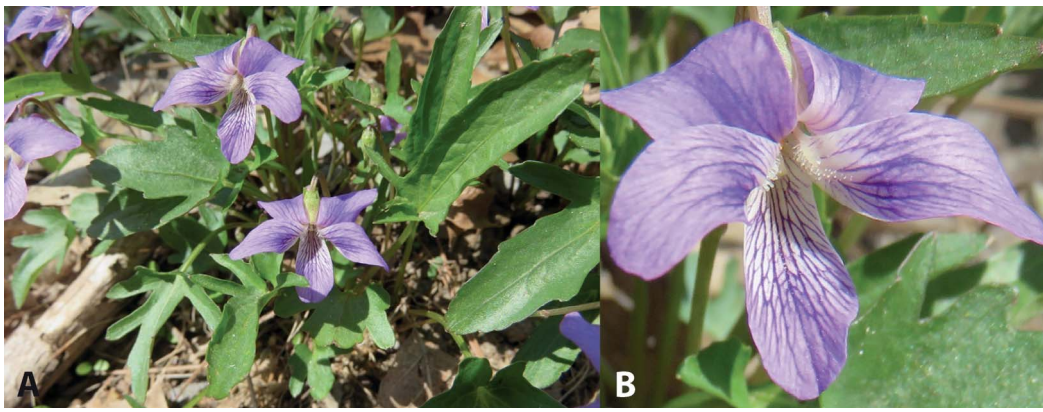

FIG. 39. *Viola egglestonii* (Canada variant). (A) Chasmogamous flowering habit (photo: Annie Bélair). (B) Chasmogamous flower front view (photo: Annie Bélair).

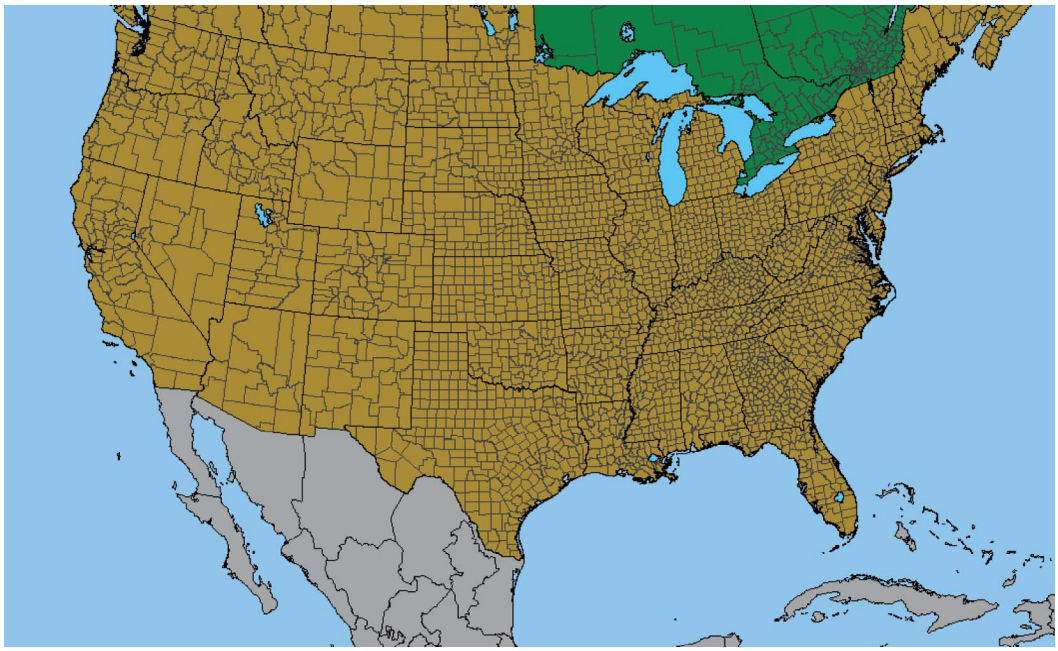

FIG. 40. United States county distribution of *Viola egglestonii* (Canada variant) (map: Biota of North America Program).

linear-lanceolate, acuminate from near the base to a narrowly sharply acute (rarely obtuse) apex; auricles prominent and quadrate, elongating somewhat in fruit; lateral petals densely bearded with very short clavate hairs exposing the throat, spurred petal glabrous within; cleistogamous peduncle ascending; other flower and capsule traits same as species complex; seeds unknown.

Similar Species. Same as species complex.

Ecology. Lawns and plantings in cities and suburbs.

Distribution. Southern Ontario and Quebec, and apparently introduced (as *V. palmate*) into Europe (Vitek *et al*. 2012) and Korea (Cheon *et al*. 2019); Fig. 40.

Rarity. None.

Phenology. Same as species complex.

Affinities. Same as species complex.

Hybrids. An apparent hybrid involving nearby *V. communis* has been confirmed from an iNaturalist post. No information is available on hybrid reproduction.

Comments. Populations belonging to this variant have been documented recently on iNaturalist at several sites in eastern Ontario and southwestern Quebec. Plants show considerable morphological variation but appear to represent one taxon, growing in city plantings and urban and suburban lawns, occasionally forming substantial populations and occasionally hybridizing with *V. communis*. The plants diverge morphologically from *V. egglestoniii sensu stricto* in several respects including the shape of the central lobe of the terminal primary division of the largest leaf blades, the shape of the sepals, relative elongation and shape of the auricles, length and shape of lateral petal trichomes, glabrous spurred petal, and ascending peduncle. This rather mysterious Canadian taxon requires further study. Recent reports of *V. palmata* introduced into Europe (Vitek *et al*. 2012; Cheon *et al*. 2019) match this taxon and are not *V. palmata*. Mention by Cheon *et al*. of pubescent foliage and ciliate sepals suggests that the introduction included hybrids with *V. septentrionalis* or *V. sororia*.

17. ***Viola emarginata*** **species complex**

Infraspecific taxa belonging to this species include the following:

17a. *Viola emarginata* (Nutt.) Leconte *sensu stricto*

17b. *Viola emarginata* (Kentucky variant)

17c. *Viola emarginata* (*phasmatifolia* variant)

17d. *Viola emarginata* (*xiphophylla* variant)

Common Name. Triangle-leaved violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm; foliage and peduncles dark blue-green, lower surface of leaf blades commonly purple-tinged, glabrous, or infrequently sparsely pubescent on either surface of leaf blades, leaf blades thick and subsucculent in living material; stipules free, irregularly glandular-fimbriate; largest leaf blades $\leq$ 84 $\times$ 75 mm, outline during chasmogamous flower narrowly ovate-triangular, oblong, oblong-ovate, or narrowly deltate-triangular, during cleistogamous fruit deltate-triangular to broadly so, base truncate to subcordate, margins crenate, eciliate (occasionally ciliate), apex acute to narrowly rounded; six divergent phenotypes included in this species complex, the first four with prominentaly winged petioles and commonly with lateral and upper petal apices emarginate and spurred petal laterally compressed in living material, the last two with slender less prominent petiole wings, nonemarginate petals and noncompressed spurred petal: *V. emarginata sensu stricto*, widespread on Atlantic Coastal Plain and Piedmont, consisting of plants (at least in chasmogamous flower) producing uncut leaf blades (more common on the northeastern Atlantic Coastal Plain) or heterophyllous plants producing larger blades pedately divided with 1–2 basal incisions or 1–3 large broadly triangular or oblong basal lobes per margin; *V. emarginata* (deltate variant) in the Piedmont of central North Carolina, a puzzling taxon unknown in chasmogamous flower or mature cleistogamous fruit, with summer leaf blades broadly deltate to deltate-reniform, terminal primary division excluding lobes lanceolate, bearing 1–2 short medial lobes on each side of terminal primary division, each primary lateral division with 3–4 short oblong lateral lobes; *V. emarginata* (*phasmatifolia* variant) in south-central Virginia and central North Carolina, with leaf blades resembling a walkingstick insect (*e.g.*, *Diapheromera femorata*), the central axis narrowly oblong-linear, each margin with 2–4 long slender variously bent processes; *V. emarginata* (*xiphophylla* variant) in the "Gorges" region of southwestern montane North Carolina and adjacent South Carolina, also somewhat disjunct in Kelly Flats area of Giles Co., VA, with the leaf blade commonly fancifully resembling a medieval sword, the undivided terminal primary division very long and slender (in a few individuals with a short oblong lateral lobe near the base on each side), the lateral divisions linear-falcate or often oriented perpendicular to the terminal division; *V. emarginata* (Lower Midwest variant) in wet prairies of southern Missouri and northeastern Oklahoma, with undivided narrowly ovate leaf blades convexly tapering to an obtuse apex; and *V. emarginata* (Kentucky variant) in dry oak and pine woodlands in southern Ohio south to northern Alabama and northern Louisiana., with undivided or very slightly basally incised narrowly ovate-triangular blades tapering uniformly from near the widest point to a sharply acute apex; chasmogamous peduncle mostly held above the leaves; chasmogamous flower $\leq$ 17 mm; calyx glabrous, eciliate; lowest sepals linear-lanceolate to lance-triangular, acuminate; auricles prominent, entire to erose, elongating to 5 mm in fruit; corolla violet, throat white; lateral petals densely bearded with filiform hairs, spurred glabrous or sparsely to densely bearded; cleistogamous flowers produced after chasmogamous, the peduncle erect and mostly equaling or surpassing petioles; capsule 8–12 mm, green drying tan, unspotted, glabrous; seeds 1.4–2.2 $\times$ 0.9–1.5 mm. pinkish-gray to dark gray with prominent darker streaks and spots (at least in *V. emarginata sensu stricto*); 2n = 54.

Similar Species. The various phenotypes of this species could resemble several different violets with glabrous to glabrate foliage and leaf blades longer than broad. The whole complex has usually been subsumed under *V. sagittata*, while the phenotypes lacking cut leaf blades have occasionally been confused with *V. fimbriatula*. All phenotypes differ from most other similar species except for *V. fimbriatula* in their narrowly to prominently winged petioles, and from *V. fimbriatula* in their erect glabrous to glabrate leaves, glabrous peduncle, eciliate sepals, and cleistogamous capsule on an erect peduncle.

Ecology. Somewhat acidic, well-drained sandy soils in oak and oak-pine forests, and open sites along forest borders and roadsides adjacent to open woodlands (*V. emarginata sensu stricto*, *V. emarginata* [*phasmatifolia* variant], *V. emarginata* [Kentucky variant], and possibly *V. emarginata*

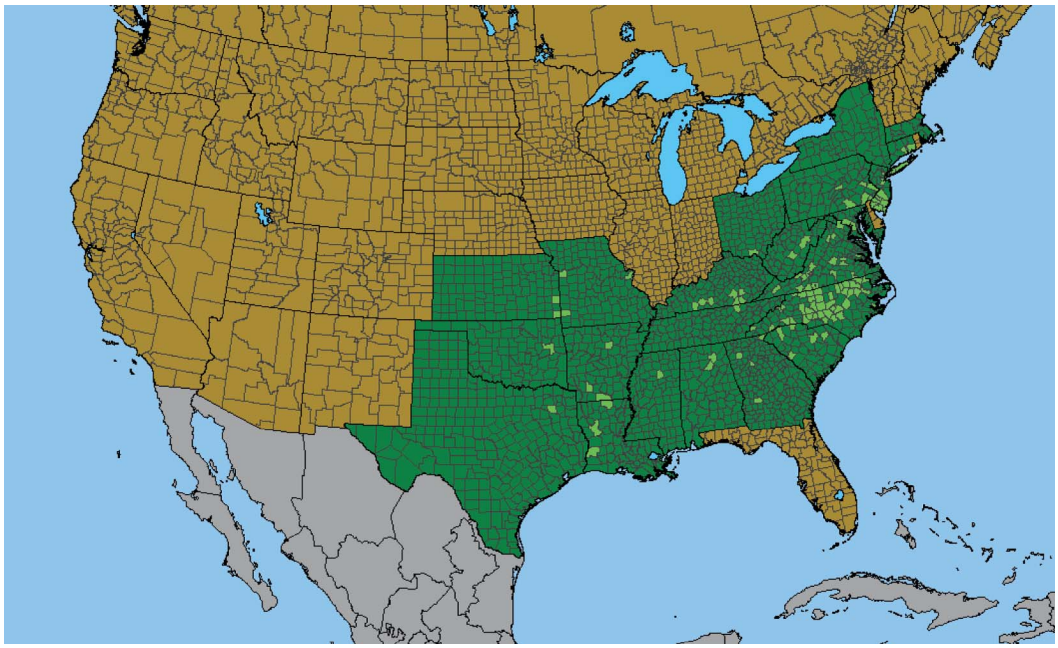

FIG. 41. United States county distribution of *Viola emarginata* species complex (map: Biota of North America Program).

[*xiphophylla* variant]), rich mesic deciduous forest slopes (*V. emarginata* [deltate variant] in central North Carolina), and wet prairies (*V. emarginata* [Lower Midwest variant] immediately south and southwest of our region).

Distribution. Atlantic Coastal Plain and lower Piedmont west to Lower Midwest and southeastern Great Plains, Massachusetts to eastern Kansas, south to Georgia and northeastern Texas. Fig. 41.

Rarity. See infraspecific taxa.

Phenology. Chasmogamous flower March–May, chasmogamous fruit April–June, cleistogamous fruit May–September.

Affinities. This species complex belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sagittata species group.

Hybrids. See *V. emarginata sensu stricto*.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), and Strausbaugh and Core (1978) accepted this species (or rather, implicitly accepted *V. emarginata sensu stricto* plus *V. emarginata* [Lower Midwest variant]); and Fernald and Alexander recognized var. *acutiloba* Brainerd. Russell and Risser (1960) and Russell (1965) misapplied the name to hybrids between *V. affinis* and *V. sagittata* (the type specimen is quite different), and Russell (1965) excluded the name on the basis of its inferred hybrid status. Gleason and Cronquist (1991), McKinney (1992), Ballard (2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015) synonymized it under *V. sagittata*. Gil-ad (1995, 1997) dismissed it as a hybrid derivative based on Russell and Risser's interpretation and the reported absence of unique traits. Nevertheless, botanists in Kentucky and New Jersey have continued to recognize *V. emarginata* as a distinct species, noting that it is obviously very different from *V. fimbriatula* and *V. sagittata*. Herbarium specimens of *V. emarginata* have usually been misidentified as *V. sagittata*. While *V. emarginata* shares certain features with *V. fimbriatula* and others with *V. sagittata*, it differs from both in a number of traits in the foliage, chasmogamous flower, and seeds as noted in the keys, and has a modally different habitat especially from the haunts of *V. sagittata*. These observations are based on numerous herbarium specimens at more than a dozen herbaria, extensive field studies

on the Atlantic Coastal Plain and Piedmont from New Jersey to North Carolina, and supplemental confirmed observations on iNaturalist. Populations and specimens studied constitute highly uniform, fully fertile taxa represented by a consistent suite of macromorphological traits including erect leaves, at least some petioles prominently winged, glabrous, or sparsely appressed-hirtellous leaf blades, lower surface of blades often tinged with purple, the largest of which in chasmogamous flower through midsummer fruit are typically deltate-triangular and either unlobed or variously lobed (in *V. emarginata sensu stricto*), with eciliate calyx, linear-lanceolate to lance-triangular acuminate sepals, auricles prominent and somewhat elongating in fruit, occasionally glabrous or more often sparsely to densely bearded spurred petal, upper and lateral petal apices frequently emarginate and spurred petal occasionally laterally compressed (except in the Kentucky and Lower Midwest variants), green cleistogamous capsule on erect peduncle, and brown seeds usually larger than those found in related species (*e.g.*, *V. fimbriatula* and *V. sagittata*). Brainerd reported that hybrids with the latter were variously nearly sterile to subfertile.

While quite distinct from other *Borealiamericanae* species, this complex encompasses considerable diversity of phenotypes, at least insofar as vegetative features express; aside from *V. emarginata sensu stricto*, which has been reasonably well studied, the other five taxa remain poorly understood. The four taxa east of the spine of the Appalachian Mountains, *V. emarginata sensu stricto*, *V. emarginata* (*phasmatifolia* variant), *V. emarginata* (*xiphophylla* variant), and *V. emarginata* (deltate variant) in North Carolina, have more prominently broad-winged petioles, as well as flowers commonly with emarginate lateral and upper petals and a laterally compressed spurred petal; the first three phenotypes prefer dry sandy soils in oak and oak-pine forests, while the few specimens of the peculiar *V. emarginata* (deltate variant) were collected on richer mesic forest slopes. The two taxa distributed west of the Appalachian Mountains, *V. emarginata* (Kentucky variant) and *V. emarginata* (Lower Midwest variant), have inconspicuously narrowly winged petioles, and flowers with rounded lateral and upper petals and a noncompressed spurred petal. The Kentucky variant is found in dry sandy soils in oak and oak-pine forests similar to most phenotypes east of the Appalachian Mountains, while *V. emarginata* (Lower Midwest variant) has only been taken in wet prairies. All of these ecological niches are quite different from those frequented by *V. sagittata*, with which *V. emarginata sensu lato* has previously been merged. The assemblage is treated here as a distinct evolutionary species complex. The variants are currently under study to determine whether subspecies or species status is appropriate.

17a. ***Viola emarginata*** (Nutt.) Leconte ***sensu stricto***, Ann. Lyceum Nat. Hist. New York 2: 142. 1828 [“1826”]; *Viola sagittata* Aiton var. *emarginata* Nutt., Gen. N. Amer. Pl.: 147. 1818. Type: “Viola sagittata β emarginata” [protologue] [no date], [*T. Nuttall s.n.*] (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 221): PH00029288 (*n.v.*), internet image). Fig. 42.

Common Name. Triangle-leaved violet.

Description. Growth form, foliage, and peduncle color and indument same as the species; leaf blade outline during chasmogamous flower narrowly ovate-triangular or narrowly deltate-triangular, during cleistogamous fruit deltate-triangular to broadly so, base truncate to subcordate, margins crenate, eciliate (occasionally ciliate), apex acute to narrowly rounded, plants (at least in chasmogamous flower) producing uncut leaf blades (more common on the northeastern Atlantic Coastal Plain) or heterophyllous plants producing larger blades pedately divided with 1–2 basal incisions or 1–3 large broadly triangular or oblong basal lobes per margin; chasmogamous flowers, cleistogamous fruits and seeds same as the species.

Similar Species. See the species complex.

Ecology. Somewhat acidic, well-drained sandy soils in oak and oak-pine forests, and open sites along forest borders and roadsides adjacent to open woodlands.

Distribution. Atlantic Coastal Plain in the northern portion of its range, the upper Atlantic Coastal Plain and Piedmont in Virginia and the Carolinas, Massachusetts south to Georgia. Fig. 43.

Rarity. None.

Phenology. Same as the species complex.

Affinities. Same as the species complex.

FIG. 42. *Viola emarginata sensu stricto*. (A) Chasmogamous flowering habit (cut leaf blades) (photo: Harvey Ballard). (B) Chasmogamous flowering habit (uncut leaf blades) (photo: Harvey Ballard). (C) Chasmogamous flower front view (photo: Harvey Ballard). (D) Chasmogamous flower profile view (photo: Harvey Ballard). (E) Seeds from herbarium specimen: Transplanted from North Carolina, Cumberland Co., Fort Bragg, *H. Ballard et al. 15-006Y* (BHO).

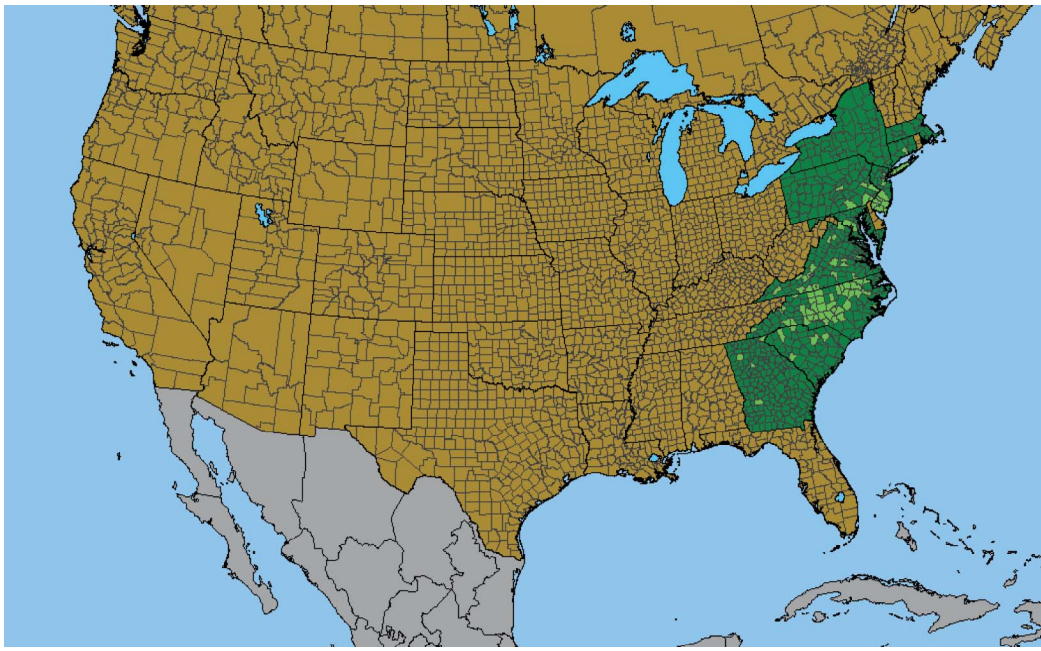

FIG. 43. United States county distribution of *Viola emarginata* sensu stricto (map: Biota of North America Program).

Hybrids. Hybridizes with *V. affinis* (Brainerd 1924), *V. brittoniana* (Brainerd 1906c, 1924; House 1906b, 1924), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (House 1906b, 1924; Brainerd 1924), *V. fimbriatula* (Brainerd 1906c, 1924; House 1924; H.E.B., personal observation), *V. hirsutula* (House 1906b; Malte and Macoun 1915; House 1924), *V. sagittata* (Brainerd 1906c, 1924), *V. septemloba* (House 1914; Brainerd 1924), *V. sororia sensu stricto* (Brainerd 1924), and *V. stoneana* (Brainerd 1924). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). Hybrids do not reproduce by chasmogamous flowers. Most produce either abortive cleistogamous capsules or capsules with substantial to highly reduced proportions of viable seeds. However, the hybrid with *V. fimbriatula* reportedly was fully fertile with no loss of viable cleistogamous seeds, while various hybrid plants with *V. sagittata* ranged from nearly sterile (almost no viable seeds) to scarcely subfertile (most ovules fertilized as viable seeds).

Comments. In describing the basionym, Nuttall's protologue stated the violet was found "In the sandy fields of New Jersey near Philadelphia, and also on the banks of the Schuylkill [in Pennsylvania]." His statement appears to refer collectively to *V. sagittata*, not just to his new var. *emarginata*. Nuttall cited no specific type specimens. Stafleu and Cowan (1981) noted that Nuttall's collections leading up to the 1818 publication of his *Genera of North American Plants* were presented to PH. Two sheets in the JSTOR Global Plants database, one at BM and one at PH, are labeled as types of *V. sagittata* var. *emarginata* and are attributed to Nuttall. McKinney (1992) incorrectly annotated the whole PH sheet and designated both collections as the holotype. Given that only PH00029288 (excluding the leaf of *V. sagittata*) matches the protologue, McKinney's designation was corrected and restricted in a second-stage lectotypification by Ballard *et al*. (2020a).

Brainerd (1921b) mentioned that specimens in the southern part of the Atlantic Coastal Plain range and the Lower Midwest of *V. emarginata* (he didn't separate *V. emarginata sensu stricto* from *V. emarginata* [Lower Midwest variant]) lacked emarginate petals, but we have not found this to be true from examinations of numerous herbarium specimens and several populations in the field in the central and southern Atlantic Coastal Plain. At least in chasmogamous flower, plants with all leaf

FIG. 44. *Viola emarginata* (Kentucky variant). (A) Chasmogamous flowering habit from herbarium specimen: Louisiana, Seale, *E. Brainerd 47* (NY). (B) Cleistogamous fruiting plant from herbarium specimen: Kentucky, Pulaski Co., *M. Medley et al. 17744-87* (APSC0093939).

blades unlobed predominate in populations in New Jersey, whereas plants with leaf blades well lobed predominate in populations in North Carolina, with a rough trend of increasing proportions of lobed-leaved plants from north to south. Additionally, the species *sensu stricto* is widely distributed and relatively common on the northern Atlantic Coastal Plain region in Washington, D.C., northward to New Jersey, whereas the range of the species shifts upward onto the Piedmont and is mostly absent from the Atlantic Coastal Plain in the Carolinas southward. Bicknell (1914) discussed the local occurence of this species on Staten Island and Long Island in New York, and in Martha's Vineyard area of Massachusetts, the northermost confirmed site. Brainerd published var. *acutiloba* for plants in the Washington, D.C., area exhibiting prominently lobed leaf blades during early chasmogamous flower. Although this name has been applied to plants with lobed leaf blades farther south (*e.g.*, the Carolinas, by Radford *et al*. 1968), specimens identified or annotated as var. *acutiloba* in Washington, D.C., and Maryland show features suggesting they are hybrids of *V. brittoniana* and *V. sagittata*, and the name is excluded here. The lobed-leaved plants are otherwise identical to unlobed-leaved ones, the two occur together in mixed populations throughout the range of *V. emarginata sensu stricto*, and they appear to represent a population-level leaf development polymorphism. No formal recognition seems required. Strausbaugh and Core (1978) noted that Davis and Core (1940) provided the first report of the present taxon from West Virginia, and that it had previously been misidentified as *V. novae-angliae*.

17b. *Viola emarginata* (Kentucky variant). Fig. 44.

Common Name. None.

Description. Growth form, foliage, and peduncle color and indument same as the species; petioles narrowly winged; leaf blade outline narrowly ovate-triangular, uniformly tapering from the widest point of the blade to a narrowly and sharply acute apex, all blades undivided; petal apices broadly rounded; spurred petal not laterally compressed in living material; corolla color and

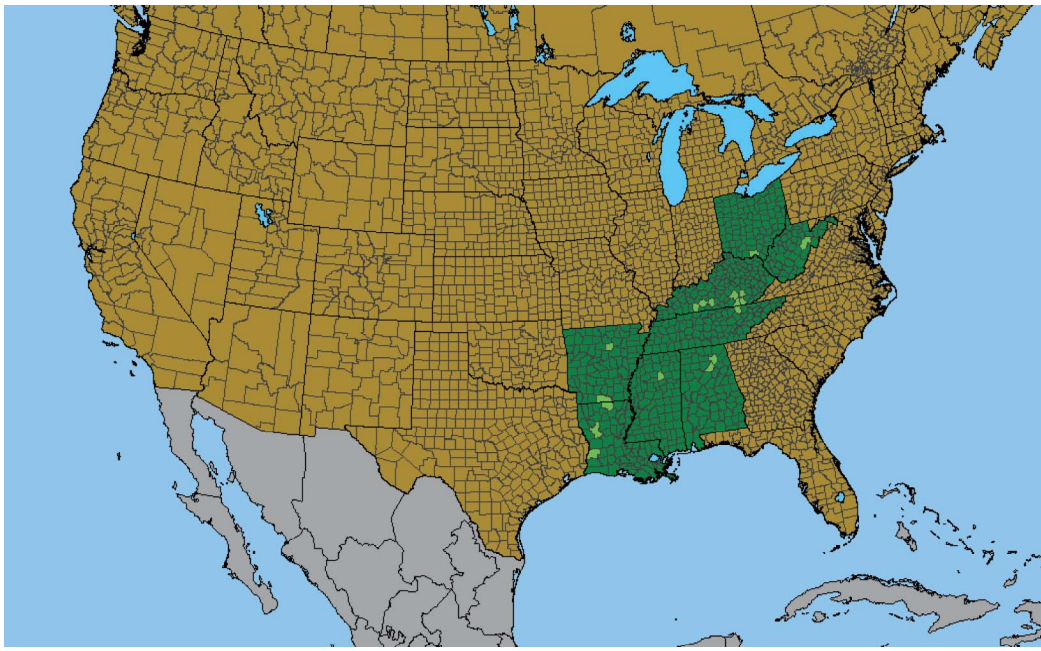

FIG. 45. United States county distribution of *Viola emarginata* (Kentucky variant) (map: Biota of North America Program).

other features as in the species; cleistogamous fruits and seeds unknown.

Similar Species. See the species complex.

Ecology. Dry sandy soils in oak and oak-pine woodlands, similar to phenotypes on the eastern Piedmont and upper Atlantic Coastal Plain.

Distribution. Lower Midwest, West Virginia, and southern Ohio, south to northern Alabama, Louisiana, and northern Arkansas. Fig. 45.

Rarity. None.

Phenology. Chasmogamous flower April–May, chasmogamous fruit April, cleistogamous fruit May.

Affinities. Same as the species complex.

Hybrids. None.

Comments. This regionally endemic variant has been misidentified and overlooked as undivided-leaved *V. sagittata*. It should be sought in mature cleistogamous fruit, which is currently unknown.

17c. *Viola emarginata* (*phasmatifolia* variant). Fig. 46.

Common Name. None.

Description. Growth form, foliage, and peduncle color and indument same as the species; petioles prominently winged; leaf blade outline broadly oblong, leaf blades of some plants resembling a walkingstick insect (*e.g.*, *Diapheromera femorata*), the central axis narrowly oblong-linear, each margin with 2–4 long slender variously bent processes; chasmogamous flowers same as the species, cleistogamous fruits and seeds unknown.

Similar Species. See the species complex.

Ecology. Somewhat acidic, well-drained sandy soils in oak and oak-pine forests, and open sites along forest borders and roadsides adjacent to open woodlands.

Distribution. Piedmont of south-central Virginia south to central North Carolina. Fig. 47.

Rarity. None.

Phenology. Same as the species complex.

Affinities. Same as the species complex.

Comments. This narrow regionally endemic variant is highly distinctive vegetatively. It should be sought in mature cleistogamous fruit to

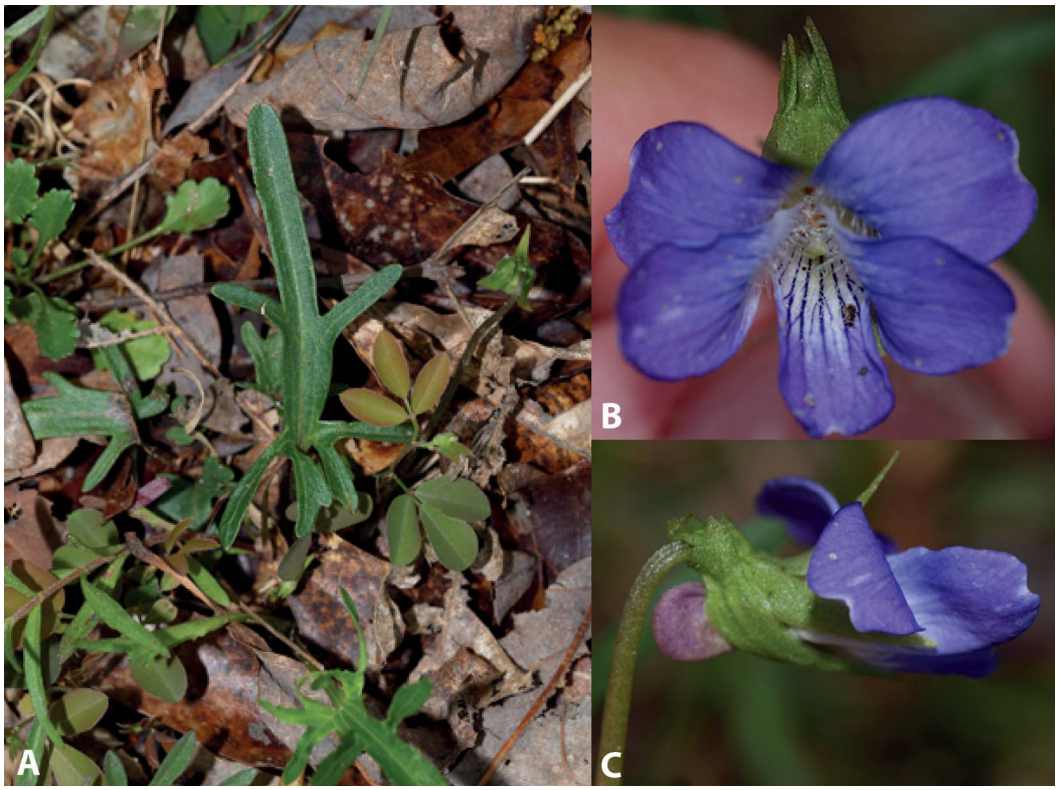

FIG. 46. *Viola emarginata* (*phasmatifolia* variant). (A) Chasmogamous flowering habit (photo: Harvey Ballard). (B) Chasmogamous flower front view (photo: Harvey Ballard). (C) Chasmogamous flower profile view (photo: Harvey Ballard).

document capsule and seed morphology. Needs further study.

17d. *Viola emarginata* (*xiphophylla* variant). Fig. 48.

Common Name. None.

Description. Growth form, foliage, and peduncle color and indument same as the species; leaf blade outline narrowly long-triangular, leaf blades resembling a sword, the central axis narrowly oblong-linear without lobes or occasionally a shorter narrowly linear-falcate lobe near the base on one or both sides, the lateral primary divisions reduced to 1–2 close linear-falcate lobes; chasmogamous flowers same as the species, cleistogamous fruits and seeds unknown.

Similar Species. See the species complex.

Ecology. Limited information suggests sandy or rocky soils in montane oak and oak-pine forests, or dry open oak barrens.

Distribution. Central and southern Appalachian Mountains, two disjunct areas in western Virginia and southwestern North Carolina. Fig. 49.

Rarity. None.

Phenology. Same as the species complex.

Affinities. Same as the species complex.

Comments. This narrow regionally endemic variant is distinctive, and it should be sought in mature cleistogamous fruit. Needs further study.

18. ***Viola eriocarpa*** Schwein., Amer. J. Sci. 5: 75. 1822; *Crocion eriocarpum* (Schwein.) Nieuwl. & Kaczm., Amer. Midl. Naturalist 3: 214. 1914; *Viola pubescens* Aiton var. *eriocarpa* (Schwein.) N.H.Russell, Sida 2: 78. 1965 [*nomen superfluum*]. Type: USA, [North Carolina, Salem, no date, *von Schweinitz s.n.*], (lectotype (**designated here**): PH00029084 (*n.v.*), internet image). Fig. 50.

Viola pubescens Aiton var. *scabriuscula* Schwein. ex Torr. & A.Gray, Fl. N. Amer. 1(1):

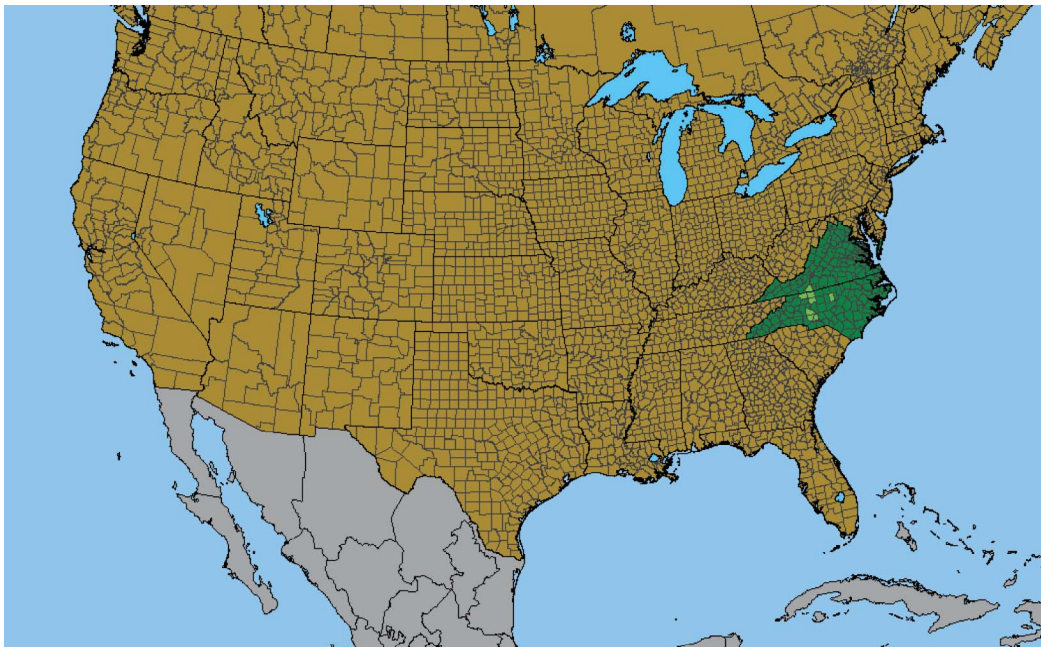

FIG. 47. United States county distribution of *Viola emarginata* (*phasmatifolia* variant) (map: Biota of North America Program).

142. 1838; *Viola scabriuscula* (Torr. & A.Gray) Shafer [nomen superfluum], Ann. Carnegie Mus. 1(1): 27. 1901; *Crocion scabriusculum* (Schwein. ex Torr. & A.Gray) Nieuwl. & Kaczm., Amer. Midl. Naturalist 4: 75. 1915.

Viola achlydophylla Greene, Pittonia 5: 87. 1902; *Crocion achlydophyllum* (Greene) Kaczm., Amer. Midl. Naturalist 4: 74. 1915; *Viola pubescens* Aiton f. *achlydophylla* (Greene) Farw., Amer. Midl. Naturalist 12: 127. 1930.

Viola dasyneura Greene, Leafl. Bot. Observ. 2(2): 96. 1910–1912.

Viola eriocarpa Schwein. var. *sessilis* Clute, Amer. Bot. (Binghamton) 30: 32. 1914.

Viola eriocarpa Schwein. var. *leiocarpa* Fernald & Wiegand, Rhodora 23: 275. 1921; *Viola pubescens* Aiton f. *leiocarpa* (Fernald & Wiegand) Farw., Pap. Michigan Acad. Sci. 2: 33. 1923 ["1922"]; *Viola eriocarpa* Schwein. f. *leiocarpa* (Fernald & Wiegand) Deam, Fl. Indiana: 691. 1940; *Viola pensylvanica* Michx. var. *leiocarpa* (Fernald & Wiegand) Fernald, Rhodora 43: 617. 1941; *Viola pubescens* Aiton var. *leiocarpa* (Fernald & Wiegand) B.Boivin, Phytologia 15: 435. 1967.

Viola eriocarpa Schwein. var. *typica* Grover, Ohio J. Sci. 39: 145. 1939 [*nomen invalidum*].

Common Name. Smooth yellow violet.

Description. Caulescent perennials from thick rhizome, (1)2–5(6), spreading to decumbent at base during chasmogamous flowering or occasionally strongly ascending to erect in chasmogamous flower (especially in plants with few stems), becoming erect in fruit, $\leq$ 35 cm tall; stems, foliage, and peduncles usually medium green (uncommonly pale green), foliage glabrous to rather densely hirtellous, peduncles glabrous to sparsely hirtellous; leaves cauline and typically basal, basal leaves 1–3 per stem (rarely none), the most common form usually with 2–5 stems each bearing 4–5 leaves distributed over the upper 1/2–4/5 of the stem and the lowest node leafless or leafy, the less frequent form usually with 1–2(3) stems each bearing 2–3 leaves clustered in upper 1/3–1/2 of the shoot and the lowest 1– 2 nodes leafless; stipules free, narrowly lanceolate or oblong-lanceolate to ovate, often cordate-auriculate on the outer side, entire or weakly erose; leaves ascending to spreading, leaf blades undivided, largest $\leq 64 \times 73$ mm, larger cauline leaf blades ovate to triangular-ovate, shallowly to moderately cordate at base, narrowly acute to abruptly acuminate at apex, the uppermost fully expanded leaf blade (typically at the second node)

FIG. 48. *Viola emarginata* (*xiphophylla* variant). Summer vegetative habit (photo: Janie Marlow).

bearing 5–15 marginal teeth per side, margins eciliate or ciliate; chasmogamous flower ≤ 12 mm; calyx glabrous, eciliate or ciliate; lowest sepals linear-lanceolate to lanceolate, acute to obtuse; auricles short and entire, not elongating in fruit; corolla wholly yellow with purple-black lines at base of petals and purple-tinged on backs of petals; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 7–13 mm, green drying tan or brown, unspotted, glabrous or densely tomentose; seeds 2.1–2.7 × 1.4–1.7 mm, medium orange-brown, unspotted; 2n = 12.

Similar Species. In chasmogamous flower, the most likely species to be confused with this are yellow-flowered *V. glaberrima* and *V. pubescens*. It differs from both species in commonly producing multiple stems (these commonly declined at base or curved in chasmogamous flower, especially in plants with 2 or more stems) and 1 or more basal leaves per stem; from *V. glaberrima* in cauline leaf blades broader and subcordate to cordate at base; and from *V. pubescens* in glabrous to hirtellous foliage and peduncles, leaves commonly 4 or more and inserted along most of the stem length, the first fully expanded leaf (at the second node) with 5–15 marginal teeth per side, and lanceolate to ovate stipules that are often cordate-auriculate on the outer side. In fruit, besides the above distinguishing traits, it can be separated from *V. canadensis* and *V. rugulosa* by the fewer coarser crenate-serrate or incurved-serrate teeth on the leaf blade margins, and shorter mostly or wholly herbaceous stipules. Its entire or irregularly erose stipules set it apart from the caulescent rostrate violets often growing with it (*V. labradorica*, *V. rostrata*, and *V. striata*).

Ecology. Moist to wet loam or silt soils of low-lying mesic forests, floodplains, and swamp borders or better-drained slopes under mesic forest cover.

Distribution. Widely distributed in eastern North America and eastern Great Plains, Nova Scotia to North Dakota and northeastern Wyoming, south to northern Georgia and northeastern Texas. Fig. 51.

Rarity. Listed in Rhode Island.

Phenology. Chasmogamous flower March–May, chasmogamous fruit April–June, cleistogamous fruit May–August.

Affinities. This species complex belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Nudicaules species group.

Hybrids. Hybridizes very rarely with *V. canadensis* (Henry 1953a), or it is overlooked. The hybrid with *V. canadensis* would presumably be roughly intermediate in characteristics of chasmogamous flowers and foliage or might be more similar to tetraploid *V. canadensis*. Given the difference in ploidy level with tetraploid *V. canadensis*, the triploid hybrid would fail to reproduce by chasmogamous flowers and would presumably produce abortive cleistogamous capsules or capsules lacking viable seeds. Studies are needed to test this hypothesis. Many reports of "extensive" hybridization with *V. pubescens*, the erroneously inferred "intergradation" often used as ammunition to merge the two (Russell 1965;

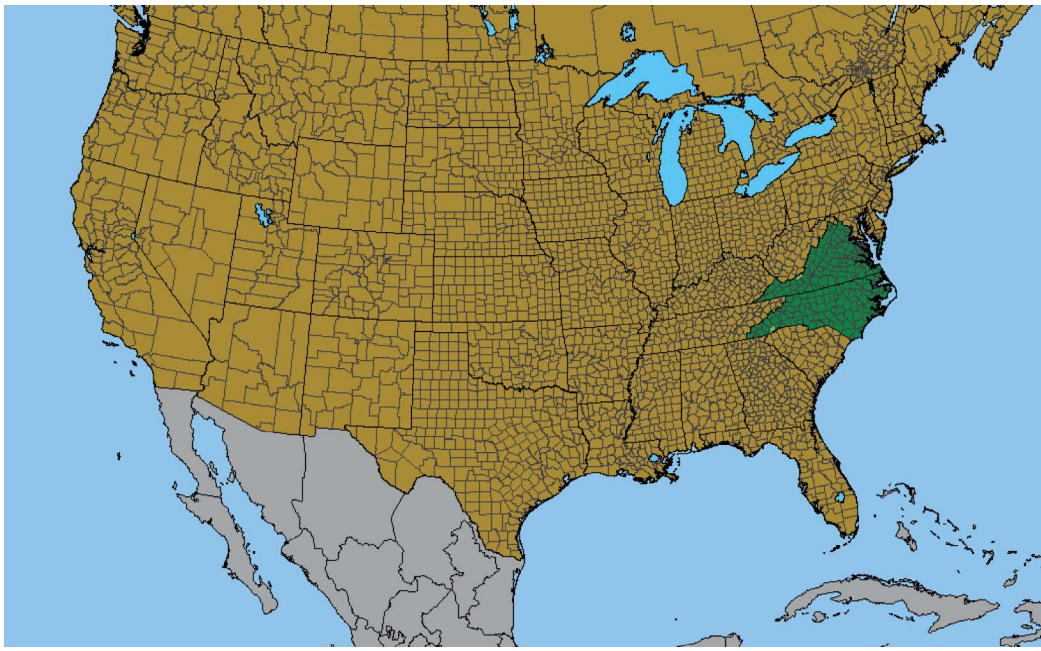

FIG. 49. United States county distribution of *Viola emarginata* (*xiphophylla* variant) (map: Biota of North America Program).

Scoggan 1978), but our recent studies have uncovered significantly greater morphological variation than previously known (see "Comments" below for further details).

Comments. Although von Schweinitz devoted considerable text in the protologue to describing this species in detail and contrasting many features as different from *V. pubescens*, he made no

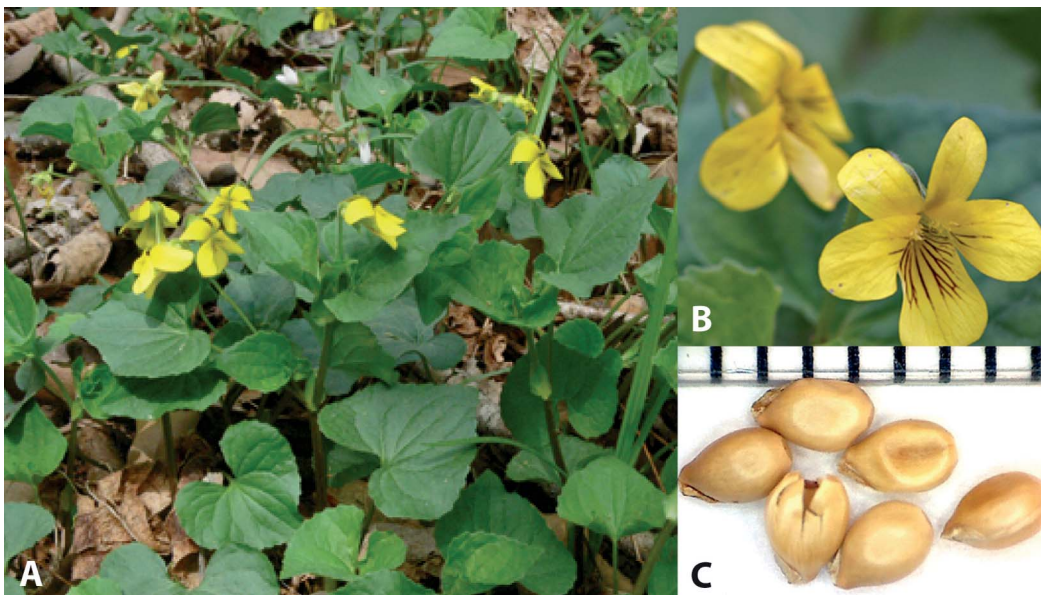

FIG. 50. *Viola eriocarpa*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Chasmogamous flower front view (photo: Andrew Lane Gibson). (C) Seeds from herbarium specimen: 2 Aug 1942, *H. N. Moldenke 1684* (OS48907).

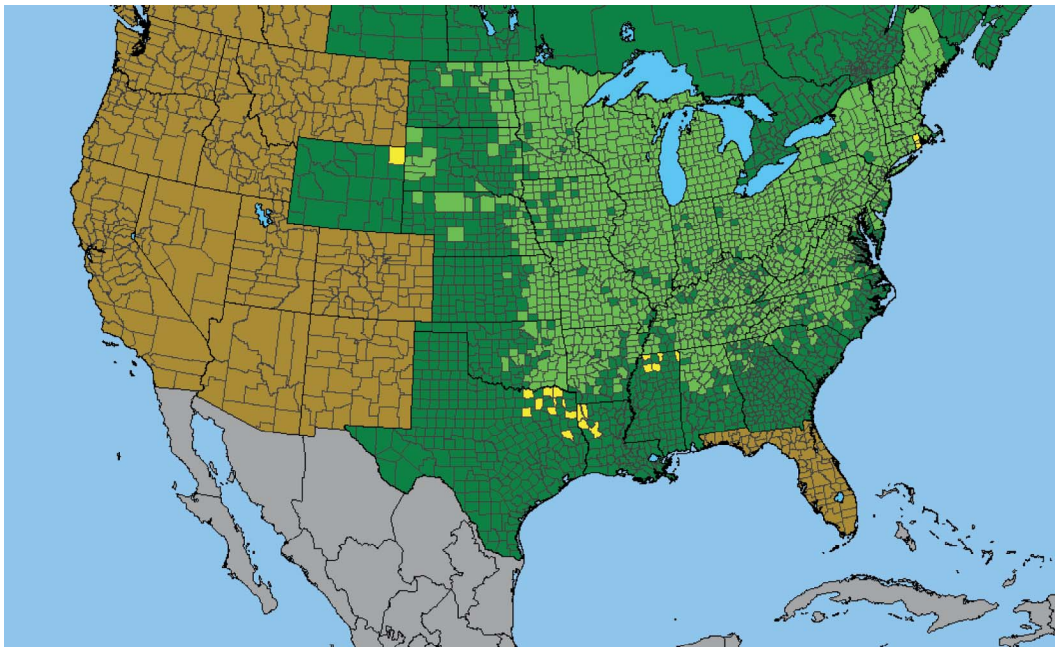

FIG. 51. United States county distribution of *Viola eriocarpa* (map: Biota of North America Program).

reference to a particular collection or location, and designated no type. Stafleu and Cowan (1985) note that von Schweinitz's herbarium is at PH. A sheet at PH is notated as "Type collection" and has two separate barcoded collections on it. The PH00029084 collection consists of three plants and has "*Viola scabriuscula* NOBIS *eriocarpa*" written in pen by one hand above the specimens and immediately beneath that "Herb. Schweinitz" in pen by another hand. Below the specimens is the annotation "Salem [North Carolina]" in pen by a third hand with an arrow pointing to the specimens. The PH00029085 collection is also *V. eriocarpa* but bears a discordant paper label below it with "*Viola pubescens*" in pen in one hand, "*V. scabriuscula*" in pen by a second hand, and "N. W. Territory," "J. N. Nicollet," and "400" in pencil by a third hand. The pencil annotation for a northwestern location is obviously in error. The second sheet is not considered a type. The PH00029084 sheet is designated here as a lectotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), and Weakley *et al*. (2012) maintained this as a distinct species. Fernald, Henry, and Alexander additionally recognized var. *leiocarpa* to distinguish plants with glabrous rather than tomentose capsules. Brainerd, Brainerd Baird, Alexander, and Scoggan applied the name *V. eriocarpa* Schwein. to the present taxon; while Fernald, Henry, Strausbaugh and Core, Swink and Wilhelm, and Weakley *et al*. used *V. pensylvanica* Michx.—a name that Jones (1959) correctly pointed out is based on a description unambiguously referring to *V. pubescens* Aiton. Russell (1965) argued that *V. pubescens* and *V. eriocarpa* frequently intergraded where their habitats met and published the new and unfortunately superfluous name *V. pubescens* var. *eriocarpa* (Schwein.) N.H.Russell, while var. *scabriuscula* Schwein. ex Torr. & A.Gray was already available. Adding to the confusion, Nuttall previously published *V. pubescens* var. *eriocarpa* (corrected from the originally published *eriocarpon*) based on material of typical *V. pubescens*. Lévesque and Dansereau (1966) conducted extensive studies on the Nudicaules species group, including *V. eriocarpa* and *V. pubescens*, and published an elaborate monograph, providing a wealth of morphological taxonomic differences upholding the two species and refuting the reports of extensive intergradation. They also provided detailed nomenclatural and ecological information. However, virtually all floras and treatments since

Russell's 1965 publication have treated the present taxon as *V. pubescens* var. *scabriuscula* Schwein. ex Torr. and A.Gray, including Ballard (1995, 2000), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), and Little and McKinney (2015). Gleason and Cronquist (1991) and Ballard (2013) synonymized this species under *V. pubescens*.

Capsule indument in this species and *V. pubescens* is clearly a simple allelic phenotype uncorrelated with other, taxonomically significant, traits, and glabrous and tomentose capsules are commonly found growing in mixed populations of otherwise identical plants. Infraspecific taxa in both species that refer to capsule indument have necessarily been abandoned.

We have delimited *V. pubescens* very narrowly, and upon reexamining the remainder of the *V. eriocarpa*-*V. pubescens* assemblage we have found more extensive local variation and weaker regional variation in *V. eriocarpa* than previously documented. Most fixed differences in *V. pubescens* vary substantially in *V. eriocarpa*, but they do not show coordinated variation to converge on *V. pubescens* as previously believed. Populations can be observed over most of the range of *V. eriocarpa* but especially more commonly in the south and west portions, with 1 to few erect stems in chasmogamous flower, no or 1(2) basal leaves per stem, consistently more marginal teeth per side on leaf blades and these more prominent into the apex, more slender stems, glabrous to glabrate foliage, and narrow lanceolate stipules cuneate at the base. This divergent phenotype, according to label information, may grow more often on slopes and ridgetops than typical *V. eriocarpa*. Such plants deserve further study over the range of the species. Many of these plants have been attributed to *V. pubescens*, and in fact Russell's (1956) treatment of Minnesota depicts this "slender few-stemmed" phenotype as *V. pubescens*. Numerous other specimens of *V. eriocarpa* show wide variation in stipule shape (occasionally as broad as the most extreme *V. pubescens*) and foliage indument; many plants of *V. eriocarpa* bearing broad stipules and/or densely hirtellous foliage have been misidentified as *V. pubescens*. Specimens of *V. eriocarpa* are easiest to differentiate from *V. pubescens* in chasmogamous flowering condition, as stems of fruiting plants that had previously been declined at base or curved become erect, and leaves broaden somewhat, plants thus appearing to converge toward *V. pubescens*.

In an unpublished study with limited sampling, Theresa Culley at the University of Cincinnati found distinctly different microsatellite alleles in *V. eriocarpa* and *V. pubescens*. Further genetic study would be illuminating.

19. ***Viola fimbriatula*** Sm., in Rees, Cycl. 37: 16. 1817. Type: North America, "dry hills from Canada to Virginia", 1817, F. Boott s.n. (holotype: Herb. Smith no. *1380.11*, LINN (*n.v.*), internet image; photo: MICH [*n.v.*]). Fig. 52.

Viola primulifolia Pursh non L. (1753), Fl. Amer. sept. 1: 173. 1813.

Viola ovata Nutt., Gen. N. Amer. Pl.: 148. 1818; *Viola sagittata* Aiton var. *ovata* (Nutt.) Torr. & A.Gray, Fl. N. Amer. 1(1): 138. 1838.

Viola alleghanensis Schult., Syst. veg. 5: 360. 1819.

Viola ovata Nutt. var. *belvisiana* Ging., in DC., Prodr. 1: 294. 1824.

Viola sagittata Aiton var. *hicksii* Pollard, Bot. Gaz. 20: 326. 1895; *Viola ovata* Nutt. var. *hicksii* (Pollard) Pollard, Proc. Biol. Soc. Washington 10: 92. 1896.

Viola amorphophylla Pollard, Proc. Biol. Soc. Washington 13: 129. 1900.

Viola fimbriatula Sm. f. *albescens* Farw., Amer. Midl. Naturalist 11: 66. 1928.

Viola fimbriatula Sm. f. *glabrata* Pennell, Bartonia 12: 19. 1931.

Viola fimbriatula Sm. f. *umbelliflora* Fernald, Rhodora 51: 56. 1949; *Viola sagittata* Aiton f. *umbelliflora* (Fernald) Scoggan, Fl. Canada pt. 1: 52. 1978.

Common Names. Northern downy violet, ovate-leaved violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 19 cm tall; foliage and peduncles green (lower surface of leaf blades occasionally tinged purple), densely hirtellous; subheterophyllous, at least the outer leaves spreading or prostrate, leaf blades during chasmogamous flower undivided, in fruit often with 1–2(3) short coarse apically oriented basal teeth on each side; stipules free, irregularly glandular-fimbriate; largest leaf blades $\leq$ 80 $\times$ 30 mm, oblong-ovate to narrowly ovate, in summer becoming ovate-triangular, base truncate to subcordate, margins crenate, ciliate, apex acute to obtuse; chasmog-

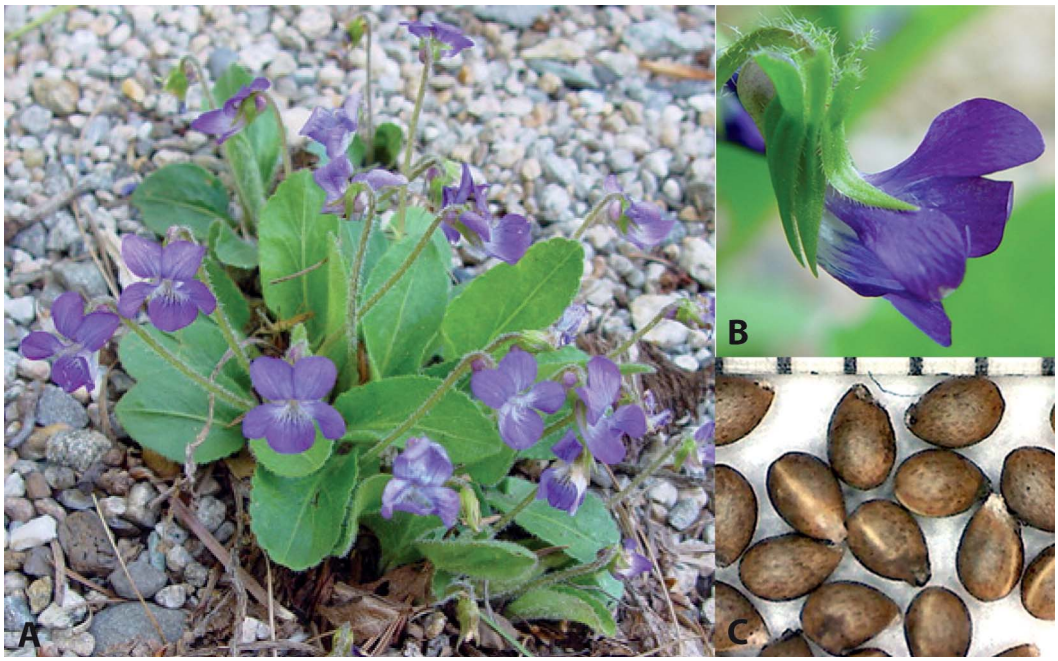

FIG. 52. *Viola fimbriatula*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust). (C) Seeds from herbarium specimen: Transplanted from Ohio, Guernsey Co., *H. Ballard & J. Larson 15-054W* (BHO).

amous peduncle held above the leaves; chasmogamous flower $\leq$ 20 mm; calyx glabrous, ciliate; lowest sepals ovate-lanceolate to ovate, acute; auricles short to somewhat prominent and entire, elongating to 4 mm in fruit and becoming erose; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, the peduncle declined and shorter than or equaling petioles; capsule 7–11 mm, green drying tan, unspotted, glabrous; seeds 1.3–1.9 $\times$ 0.8–1.3 mm, medium to dark brown or gray-brown, unspotted or with small weak darker blotches; 2n = 54.

Similar Species. The distinctive habit of the spreading to prostrate leaves in living plants of this species, resembling a primrose rosette, and the proportionally short(er) petiole relative to the leaf blade distinguish it from the most similar species *V. emarginata* and *V. sagittata* in the Sagittata species group, which also share the densely spurred petal, sharply acute sepals, prominent elongating auricles, and unspotted cleistogamous capsules. It shares winged petioles with *V. emarginata*, but differs from *V. emarginata* and *V. sagittata* in its densely hirtellous foliage and chasmogamous peduncles, ciliate sepals, and declined cleistogamous peduncle. Young flowering plants of this species are occasionally troublesome to separate from midwestern *V. sagittata*, given that the commonest phenotype in the latter exhibits sparsely to moderately hirtellous foliage and occasionally sparsely hirtellous peduncles and sparsely ciliate sepals; however, the erect leaf habit, proportionally longer petioles, and absence of prominent petiole wings in *V. sagittata* will separate the two. It could also potentially be mistaken for *V. grisea*, a northern Great Lakes species, if the distinctive "primrose-rosette" is ignored, differing in its winged petioles, sharply acute sepals, prominent elongating auricles, and unspotted cleistogamous capsule on a declined peduncle.

Ecology. Somewhat acidic, well-drained sandy and gravelly soils in glades, prairie openings in oak barrens and savannas, and on sparsely vegetated slopes of oak forests; occasionally persists in droughtier microsites of old pastures and other areas that were former barrens and prairies.

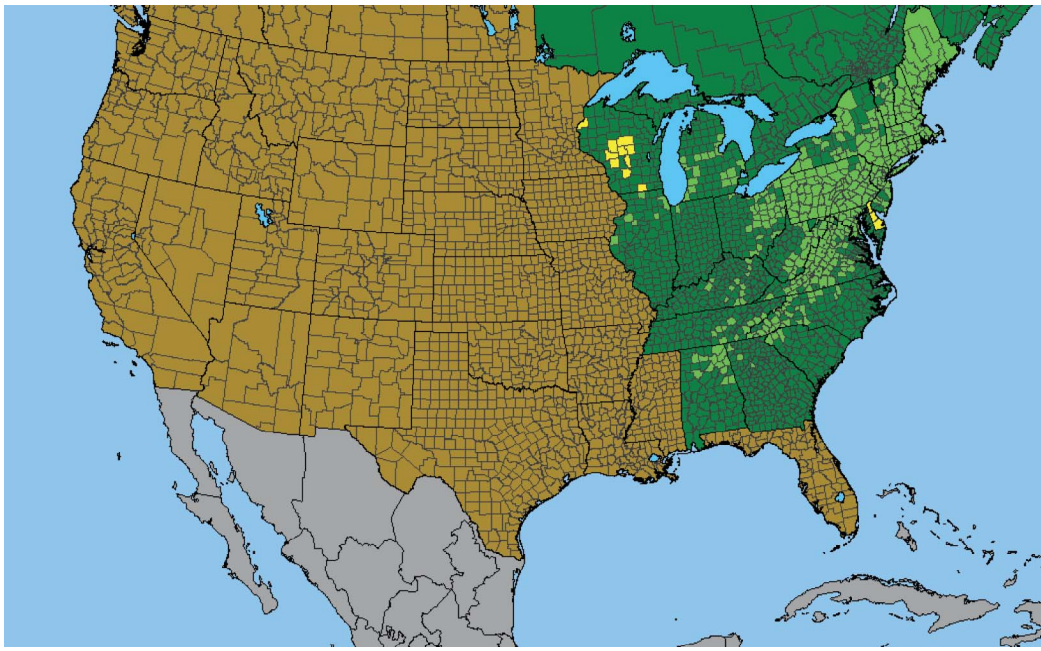

FIG. 53. United States county distribution of *Viola fimbriatula* (map: Biota of North America Program).

Distribution. Restricted to higher elevations of the Appalachian Mountains and associated uplands, and at lower elevations in the southern Great Lakes region, Nova Scotia to Wisconsin, south to northern Alabama and northern Illinois. Fig. 53.

Rarity. Listed in Quebec (as *V. sagittata* var. *ovata*) and Wisconsin.

Phenology. Chasmogamous flower April–May, chasmogamous fruit May–June, cleistogamous fruit July–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sagittata species group.

Hybrids. Hybridizes with *V. affinis* (Dowell 1910; Brainerd 1924; Haines *et al*. 2011), *V. baxteri* (House 1917, 1924; Brainerd 1924 in part), *V. brittoniana* (Pollard 1902b; Brainerd 1906c, 1907b, 1924; Haines *et al*. 2011), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Stone 1903; Brainerd 1904b, 1906c, 1924; House 1924), *V. cucullata* (Brainerd 1904b, 1905, 1924; Henry 1953a; Haines *et al*. 2011), *V. emarginata sensu stricto* (Brainerd 1906c, 1924; House 1924; H.E.B., personal observation), *V. hirsutula* (Dowell 1910; Brainerd 1924; Henry 1953a), *V. latiuscula* (Brainerd 1924; House 1924), *V. palmata* var. *triloba* (Brainerd 1906c, 1924; Haines *et al*. 2011), *V. sagittata* (Brainerd 1906c, 1907b, 1924; House 1924; Cinq-Mars 1966; Haines *et al*. 2011), *V. septentrionalis sensu stricto* (Brainerd 1904b, 1905, 1924; House 1924), *V. sororia sensu stricto* (Brainerd 1904b, 1924; House 1924; Henry 1953a; Haines *et al*. 2011), and *V. subsinuata* (Brainerd 1913c, 1924; House 1924; Haines *et al*. 2011). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All hybrids fail to reproduce by chasmogamous flowers. Many hybrids produce abortive cleistogamous flowers or capsules, while most others generate a substantially to highly reduced proportion of viable seeds. Hybrids involving *V. emarginata* and *V. sagittata* are more variable, some plants nearly sterile and others nearly fully fertile in their viable seed output.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Gleason and Cronquist (1963), Russell (1965), and Strausbaugh and Core (1978) recognized *V. fimbriatula* at species rank. McKinney (1992), Ballard (1995, 2000), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and

McKinney (2015) demoted it to *V. sagittata* Aiton var. *ovata* (Nutt.) Torr. & A.Gray, while Gleason and Cronquist (1991) synonymized it under *V. sagittata*. Gil-ad (1995, 1997, 1998) documented unique macromorphological features and consistent micromorphological differences in petal trichomes. However, he noted that micromorphological features of the seed coat were similar in many respects to *V. sagittata* and could not be used to support species status separate from the latter. He tentatively maintained *V. fimbriatula* as a species pending further studies testing a hypothesis of hybrid speciation involving *V. sagittata* and another unidentified species. Gil-ad also pointed out that at least some plants studied ecologically under the name of this species were probably hybrids of *V. fimbriatula* and *V. sagittata*. This is true of studies by Yost (1987) to examine effects of light on petiole length, as the photographs of living plants subjected to environmental treatments diverge from *V. fimbriatula* in several vegetative and reproductive traits. This species can easily be distinguished from *V. sagittata* (including commonly sparsely to moderately hirtellous plants which have caused confusion in the Midwest) by its primrose-like habit of the rosette, in which at least the outer rosette leaves are widely spreading or lying prostrate on the substrate (typically all of them during cleistogamous fruit), proportionally short winged petioles, densely hirtellous indument, ciliate sepals, coarse basal teeth on leaf blades of summer fruiting plants, and declined cleistogamous peduncles (Gil-ad designated these as "prostrate," but in several typical populations over the range of this taxon we have observed them to be declined rather than horizontal). The macromorphology of the seeds is subtly different, and its typical habitats are more xeric and soils are more gravelly than is usual for *V. sagittata*. Moreover, Gil-ad's documentation of consistent micromorphological differences from *V. sagittata* in the petal trichomes and in the seed coat (regardless of suggestions of hybrid origin) provide additional evidence that it is not conspecific with *V. sagittata*. Rare glabrous plants or populations have been collected in the Appalachian Mountains but they are otherwise identical to typical *V. fimbriatula*. A peculiar leaf morph described from Tryon, NC, with the main axis of the blade lanceolate, bearing a basal elongated process on each side, has been named *V. amorphophylla* Pollard and was discussed at length by Brainerd (1911a). Although distinctive and peculiar in blade dissection, it is identical in all other respects to typical *V. fimbriatula* and included without formal recognition. The range of the species is primarily Appalachian but extends into the southwestern Great Lakes region through northern Ohio and southern Ontario to southern Michigan, then is slightly disjunct in the "Driftless Area" of southwestern Wisconsin. It ranges northeastward into New England and adjacent Canada, where *V. sagittata* is virtually absent.

20. ***Viola glaberrima*** (Ging. ex Chapm.) House, Torreya 6: 172. 1906; *Viola hastata* Michx. var. *glaberrima* Ging. [not validly published], in DC., Prodr. 1: 300. 1824; *Viola hastata* Michx. var. *glaberrima* Ging. ex Chapm., Fl. South. U.S., ed. 3: 34. 1897; *Viola tripartita* Elliott var. *glaberrima* (Ging.) R.M.Harper, Bull. Torrey Bot. Club 27: 337. 1900; *Viola tripartita* Elliott f. *glaberrima* (Ging.) Fernald, Rhodora 51: 52. 1949; *Viola tripartita* Elliott f. *glaberrima* (Ging.) H.Lév., Naturaliste Canad. 93: 501. 1966 [illegitimate homonym]; Type: unknown. Fig. 54.

Common Name. Northern wedge-leaved violet.

Description. Caulescent perennials from thick rhizome, stems erect, solitary, $\leq$ 36 cm tall; stem, foliage, and peduncles green, glabrous, or sparsely to moderately hirtellous with easily visible hairs; leaves cauline (rarely 1 basal), clustered in upper 1/4 of stems; stipules free, usually strongly erose; leaves spreading, leaf blades undivided, largest $\leq 92 \times 90$ mm, upper narrowly ovate-lanceolate, middle and lower narrowly ovate-triangular to broadly ovate-lanceolate, broadest well above the base, base cuneate to broadly rounded, margins conspicuously serrate to the tip, eciliate or appressed-ciliate, apex short- to long-acuminate; chasmogamous flower $\leq$ 14 mm; calyx glabrous or hirtellous along midvein, eciliate or ciliate; lowest sepals lanceolate, acute; auricles short and entire, not elongating in fruit; corolla wholly yellow with purple-black lines at base of petals and purple-tinged on backs of petals; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 6–14 mm, green drying brown, unspotted, usually glabrous; seeds 2.7–2.8 $\times$ 1.8 mm, tan to light brown, unspotted.

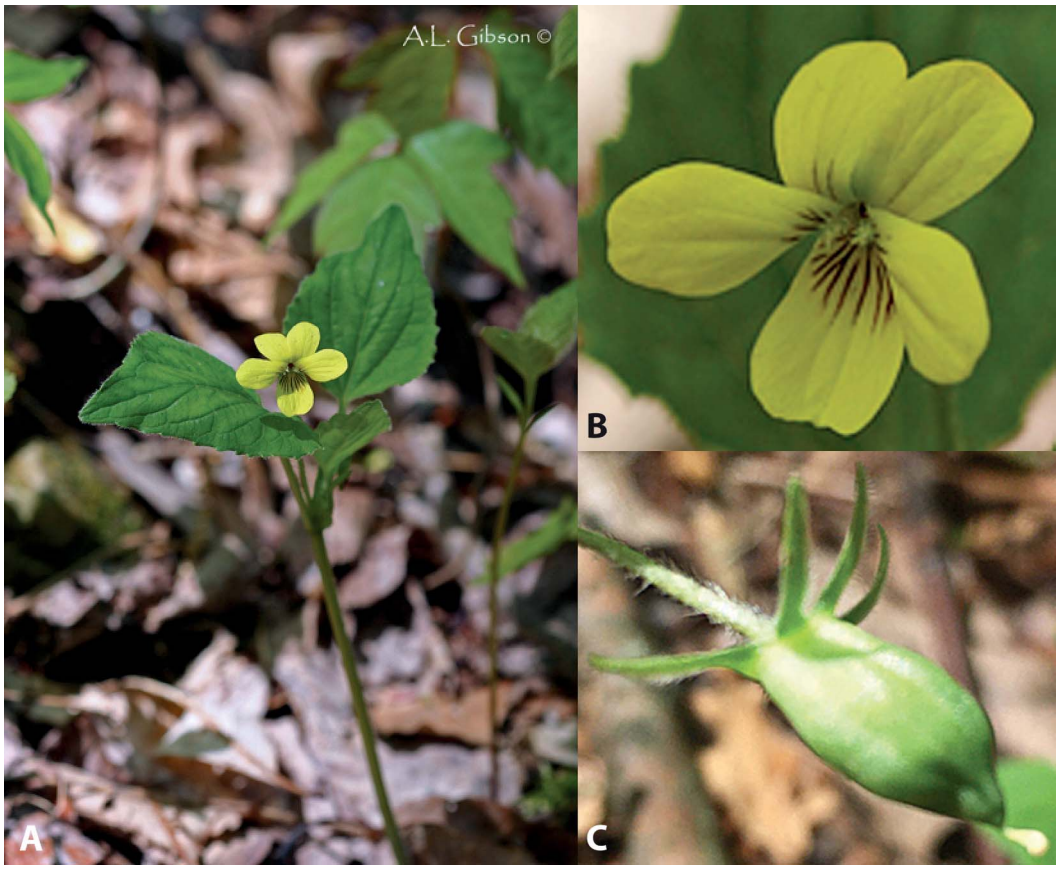

FIG. 54. *Viola glaberrima*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: Andrew Lane Gibson). (C) Chasmogamous fruit (photo: Bonnie Isaac).

Similar Species. In chasmogamous flower, this species might be confused with other caulescent yellow-flowered species with leaf blades longer than broad, such as occasional specimens of *V. eriocarpa* and *V. hastata*. It differs from *V. eriocarpa* in its solitary stems with 1 or no basal leaves, cauline leaves clustered in the uppermost fourth of the plant, and cauline leaf blades with rounded to cuneate base; and from *V. hastata* in leaf blades rhombic-ovate or ovate with a cuneate to rounded base and uniformly green upper leaf surface. In fruit, besides the above distinctions, it can be separated from *V. canadensis* and *V. rugulosa* by the fewer crenate-serrate teeth on the leaf blade margins, and the small herbaceous stipules. Its solitary stem with leaves clustered at the top, and entire stipules distinguish it from the caulescent rostrate violets often growing with it (*V. labradorica*, *V. rostrata*, and *V. striata*).

Ecology. Rich mesic to wet-mesic forests on lower slopes and bottomlands, especially over mafic or calcareous rocks.

Distribution. Southwestern Pennsylvania to southeastern Indiana, south to northwestern Florida and northeastern Mississippi (includes southeastern *V. tenuipes*, currently being disentangled from *V. glaberrima*). Fig. 55.

Rarity. Listed in Ohio and Virginia (as *V. tripartita* var. *glaberrima*), Pennsylvania (as *V. tripartita*), and West Virginia (included in *V. tripartita*).

Phenology. Chasmogamous flower March–May, chasmogamous fruit April–June, cleistogamous fruit July–August.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Nudicaules species group.

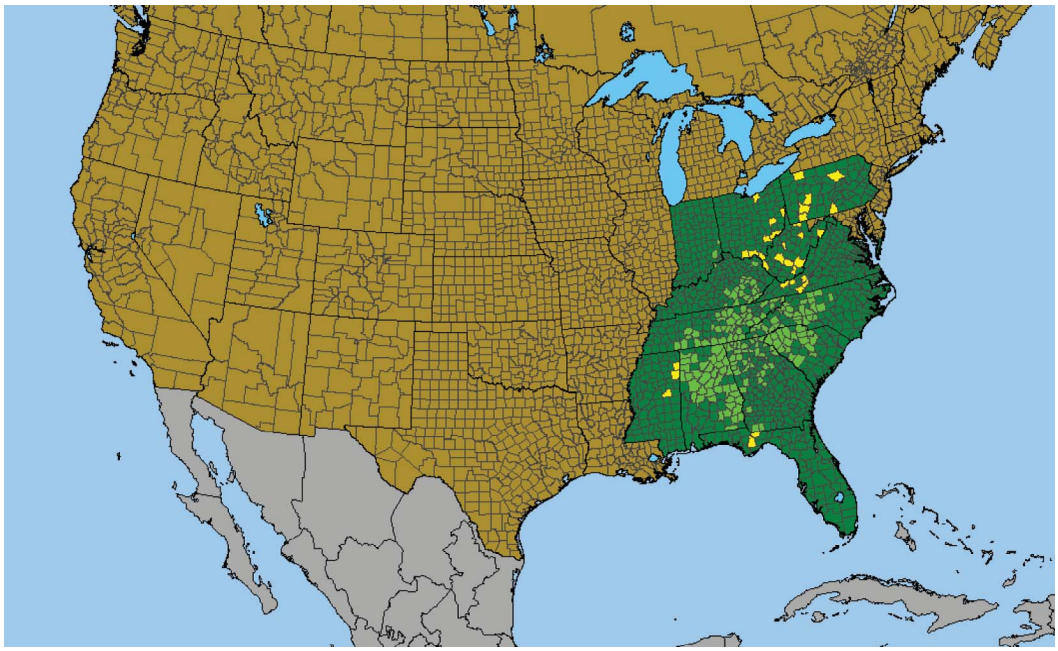

FIG. 55. United States county distribution of *Viola glaberrima* species complex, including southern *V. tenuipes* (map: Biota of North America Program).

Hybrids. None.

Comments. In de Gingins's protologue, under *V. hastata* he presents "β? *glaberrima*, foliis rhomboideo - lanceolatis.–In sylvis et collibus Carolinae septentrion. *V. hirta* Lewis l. c. non auctorum. An spec. ?" Kanchi Gandhi (Harvard University Herbaria & Libraries, personal communication) has pointed out that the font and presentation of this name is different from the other accepted infraspecific taxa and suggests that de Gingins did not accept it, rendering the name invalidly published. Chapman was the first to publish it, attributing it to de Gingins. Searches online, both in the JSTOR Global Plants Database and in the online database of the Geneva Herbarium, have failed to yield original material consulted by de Gingins that could serve as a lectotype. The name may need neotypification.

Many specimens of this species from southern states are inexplicably misidentified as *V. pubescens*, a violet which (as we circumscribe it here) is very rare in North Carolina and Tennessee at the southern edge of its range. It differs from *V. pubescens* in many traits, as one can surmise from scrutinizing the key. Brainerd (1921b), Russell (1965), Lévesque and Dansereau (1966), Gleason and Cronquist (1991), McKinney and Russell (2002), and Little and McKinney (2015) synonymized the present species under *V. tripartita* as a mere leaf morph. Fernald (1950) maintained it as *V. tripartita* f. *glaberrima*; Alexander (1963), Brainerd Baird (1942), Ballard (2000), and Weakley *et al.* (2012) recognized it as var. *glaberrima*. In all cases the present species has implicitly included *V. tenuipes* Pollard, a name forgotten as soon as it was published for a species in the southeastern states. Brainerd (1921b) reported visiting three southeastern localities, Biltmore Estate and Tryon, NC, and Tuscaloosa, AL, where he found *V. tripartita* and *V. glaberrima* (including *V. tenuipes*) "often associated and intergrading," and he used these observations as the basis for synonymizing all unlobed-leaved and lobed-leaved populations under *V. tripartita*. Russell (1965) mapped specimens with unlobed leaf blades and lobed or divided leaf blades, presenting a map with very few instances of county-level cooccurrence and a much broader, lower-elevation range for the unlobed-leaved populations, yet he argued that the two grow sympatrically and intergrade. Lévesque and Dansereau (1966) found no features to separate the taxa besides leaf dissection. Nevertheless, an as yet unpublished morphometric study of foliage and flower characteristics in the *V. tripartita* species

complex by undergraduate researcher Nick Chilson and Ballard (unpublished data), currently being expanded by undergraduate researcher Colin McClurkin, have documented a number of statistically significant quantitative stem and leaf traits as well as other qualitative distinctions and tendencies in indument and leaves, plus blade dissection distinguishing *V. tripartita*, and a floral difference in degree to which the nectar-guide lines extend beyond the middle of the spurred petal blade, to separate *V. glaberrima*, southeastern *V. tenuipes*, and *V. tripartita* (see traits used in the keys). Examinations of numerous collections from 15 herbaria across the eastern USA revealed very few herbarium specimens with *V. glaberrima* (or *V. tenuipes*) taken from the same locality as *V. tripartita*, indicating a low frequency of local sympatry, and only a handful of sheets bore mixed collections to suggest (but not prove) cooccurrence. With several macromorphological distinctions and additional divergent tendencies among the three taxa in mind, no specimens displayed convincing evidence of "intergradation" or hybridization. Specimens from three locations in Georgia and Tennessee exhibited peculiar shallow leaf division that is intermediate between a deeply 3- or 5-lobed state and an entire leaf, but these were otherwise identical to typical *V. tripartita sensu stricto* in the area and appeared clearly to be a case of developmental arrest in leaf division, not hybridization with *V. glaberrima* (or *V. tenuipes*). An unpublished survey by Awl *et al*. (unpublished data) of protected plant species on the Oak Ridge National Laboratory Reservation documented occurrences of *V. glaberrima* and *V. tripartita* on the tract but noted that the two taxa occupy different ecological niches and did not intergrade there. Our limited field observations corroborated comprehensive herbarium collections to indicate that this is the norm over the bulk of the range of the *V. tripartita* species complex, in which the three taxa grow in separate populations over the majority of their overlapping ranges, only rarely commingling, and the three taxa inhabit modally different ecological niches. This evidence overwhelmingly supports recognition of three distinct evolutionary species. The known northern extent of the range of *V. glaberrima* has been substantially expanded with recent herbarium collections and reidentifications of specimens previously attributed to *V. eriocarpa* or *V. pubescens*. Even as late as 1963, Alexander noted that it had not yet been reported (as var. *glaberrima*) from northeastern North America. We have recently begun separating county records of *V. glaberrima* from *V. tenuipes* for mapping, and much additional research is necessay to complete the process. The map presented includes both *V. glaberrima* and southeastern *V. tenuipes*.

Three violet complexes, *V. glaberrima/tenuipes/tripartita*, *V. brittoniana/pectinata*, and the *Viola lobata* complex in California and Oregon have been held up as examples of infraspecific leaf dimorphism. The *V. tripartita* species complex has clearly been misinterpreted. Our preliminary evidence on the *V. brittoniana* species complex indicates that the situation is also more complicated than simple allelic dimorphism can accommodate. A preliminary study by undergraduate researcher Tristan Kinnison on several herbarium collections for the *V. lobata* complex also reveals the presence of multiple potentially distinct evolutionary taxa, similar to the situation in the *V. tripartita* species complex. Current evidence would suggest that there are no legitimate instances of dimorphism in North American *Viola* except in corolla color of *V. pedata*, and that examples previously proposed as dimorphism were simply the consequence of inadequate empirical study. The common name proposed here distinguishes *V. glaberrima* from *V. tenuipes*, which occurs south of our range.

21. ***Viola grisea*** (Fernald) H.E.Ballard, **comb. nov.** *Viola septentrionalis* Greene var. *grisea* Fernald, Rhodora 37: 301, pl. 375. 1935; *Viola novae-angliae* House subsp. *grisea* (Fernald) Gil-ad, Boissiera 53: 68. 1997; *Viola sororia* Willd. var. *grisea* (Fernald) L.E.McKinney, J. Bot. Res. Inst. Texas 4(1): 226. 2010. Type: USA Michigan. Schoolcraft Co., dry sandy plain near Driggs, 2 Jul 1934, *M. L. Fernald & H. S. Pease 3430* (holotype: GH00032648; isotypes: MICH, US). Fig. 56.

Common Name. Great Lakes violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 27 cm tall; foliage and peduncles green, upper surface of leaf blades often darker, lower surface commonly purple-tinged, moderately to densely hirsute; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest $\leq$ 89 $\times$ 51 mm, narrowly triangular-ovate in chasmogamous flower, scarcely broadening in fruit, base subcordate to deeply cordate, margins crenate to serrate with 10–(avg. 14)–21 teeth on each side, ciliate, apex

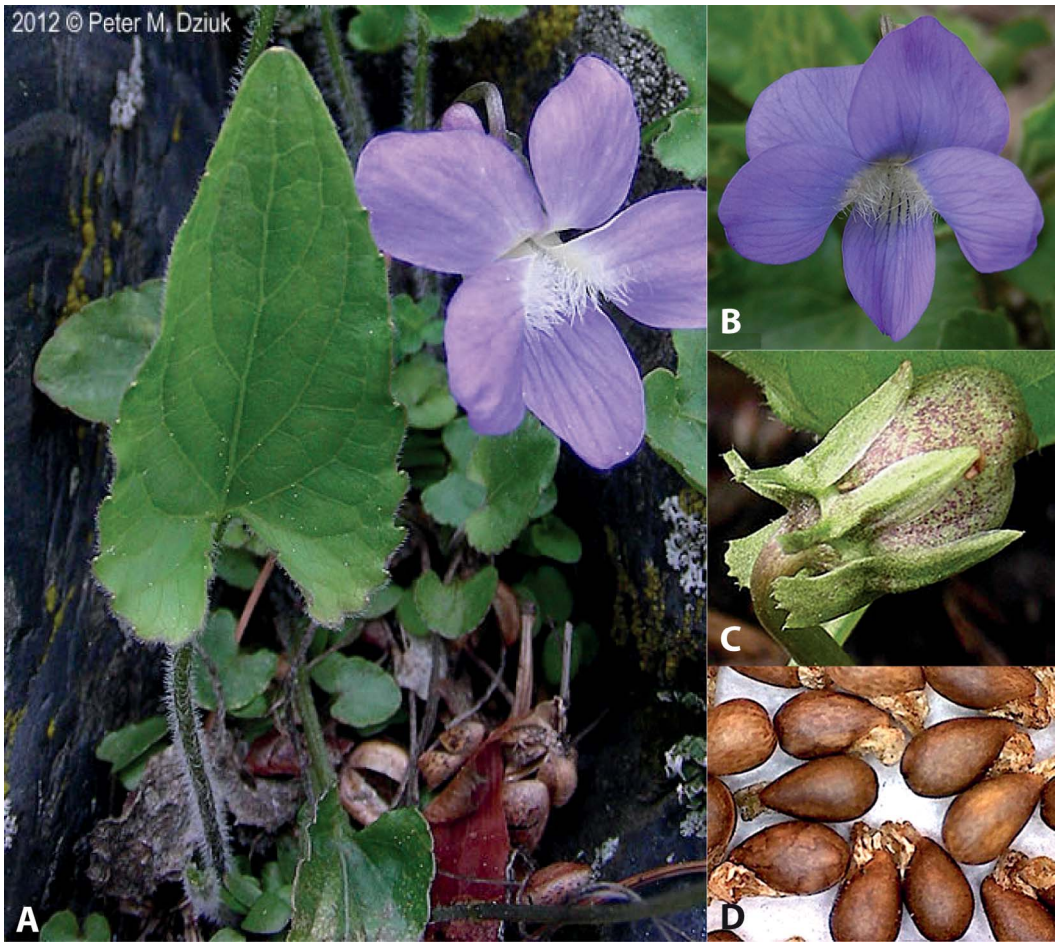

FIG. 56. *Viola grisea*. (A) Chasmogamous flowering habit (photo: Peter M. Dziuk). (B) Chasmogamous flower front view (photo: Peter M. Dziuk). (C) Cleistogamous fruit (photo: Peter M. Dziuk). (D) Seeds from herbarium specimen: Transplanted from Wisconsin, Mercer, Dr. Ogden donor, *E. Brainerd 89* (NY).

acuminate to narrowly obtuse; chasmogamous peduncle held among or above the leaves, moderately to densely hirsute especially in the lowest 2/3; chasmogamous flower $\leq$ 25 mm; calyx glabrous or pubescent, ciliate to apex, often with long hairs; lowest sepals ovate, 2.7–3.8 mm wide, length:width ratio $\leq$ 2.1, broadly rounded; auricles short to somewhat prominent and entire, elongating in fruit to 2 mm; corolla blue to purple, throat white; spur short-globose; lateral and spurred petal densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, the peduncle prostrate, arching just before dehiscence, shorter than petioles; cleistogamous capsule 5–11 mm, green drying to tan with purple spots or blotches, glabrous; seeds 1.6–2.0 $\times$ 1.0–1.4 mm, medium yellow-brown to dark brown, unspotted.

Similar Species. The most similar species likely to be confused with the present violet are *V. novae-angliae* and *V. septentrionalis*, *Borealiamericanae* violets with pubescent foliage, undivided narrowly ovate or narrowly ovate-triangular leaf blades the largest of which are longer than broad (at least some of the time), oblong to ovate ciliate obtuse to rounded sepals, prominent auricles, a densely bearded spurred petal, a heavily spotted or blotched cleistogamous capsule on a prostrate peduncle, and unspotted brown seeds. This species differs from *V. novae-angliae* in its moderately to densely hirsute petioles, leaf blades, and peduncles, commonly proportionally broader leaf blades

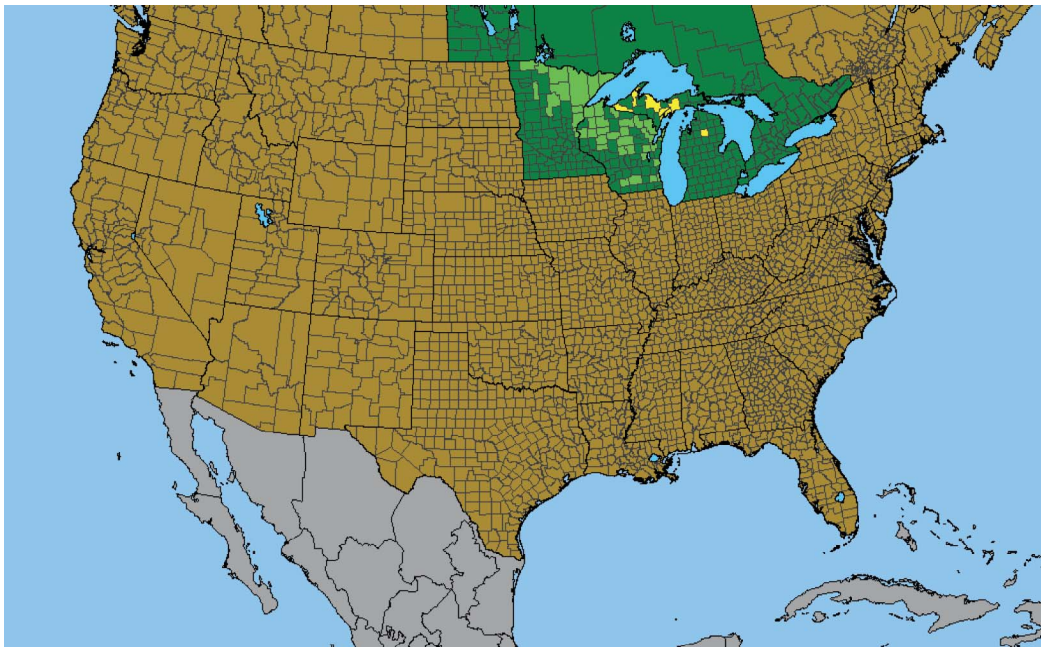

FIG. 57. United States county distribution of *Viola grisea* (map: Biota of North America Program).

with more numerous marginal teeth, and commonly broader densely ciliate sepals; and from *V. septentrionalis* by its consistently narrowly ovate-triangular leaf blades, consistently rounded ciliate sepals, and more broadly ovoid unspotted seeds.

Ecology. Thin soil on mostly granitic rock outcrops and other acidic rock substrates along rivers, moist sand of lakeshores and borders of mesic sand prairies, rarely on limestone alvar (in central Upper Peninsula of Michigan, southeastern Ontario).

Distribution. Western Great Lakes region, northern Michigan to southeastern Manitoba, south to central Wisconsin and central Minnesota, disjunct in Hastings Co. in southeastern Ontario. Fig. 57.

Rarity. Listed in Michigan and Ontario (both as *V. novae-angliae*).

Phenology. Chasmogamous flower May–June, chasmogamous fruit June, cleistogamous fruit July–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sororia species group.

Hybrids. Occasional specimens with intermediate foliage characteristics were inferred as hybrids with *V. sororia* during field studies in Minnesota and Wisconsin leading to the publication by Ballard and Gawler (1994). No information is available on hybrid reproduction.

Comments. The *V. novae-angliae* species complex was collectively treated as *V. novae-angliae* by Brainerd (1921b), Brainerd Baird (1942), Alexander (1963), Russell (1965), Scoggan (1978), Ballard and Gawler (1994), Ballard (1995), Haines *et al*. (2011), and Little and McKinney (2015). Fernald (1950) circumscribed *V. novae-angliae* to be a geographically bimodal taxon including northeastern populations and western Great Lakes populations, but he segregated northern Michigan *V. septentrionalis* var. *grisea* from the Driggs area, Schoolcraft Co., that he had described a year before (Fernald 1949). In studying the *V. novae-angliae* complex and *V. septentrionalis*, Gil-ad (1995, 1997, 1998) concluded that *V. septentrionalis* var. *grisea* Fernald shared many vegetative and reproductive traits as well as micromorphological features of petal trichomes and seed coats with *V. novae-angliae*, and he transferred *grisea* to the latter species. He documented a number of differences between the *grisea* taxon (to which he added specimens from

Crawford Co. in Michigan's Lower Peninsula) and typical *V. novae-angliae*. On the basis of few study samples from the western Upper Great Lakes range of the complex, Gil-ad made the new combination *V. novae-angliae* subsp. *grisea* to accommodate the latter and referred all other western Great Lakes populations plus northeastern populations to *V. novae-angliae* subsp. *novae-angliae*. Voss and Reznicek (2012) have followed this treatment. In the last several years I have studied numerous specimens from several herbarium collections from the western Great Lakes region, New England, and maritime Canada (including all relevant sheets examined by Gil-ad), as well as the first author' (H.E.B.'s) own field-collected chasmogamous flowering specimens from Crawford Co., and chasmogamous flowering and cleistogamous fruiting population samples from northern Minnesota provided by Lynden Gerdes. The much-increased sampling of specimens and study material (but still few fruiting specimens of northeastern populations) permitted extended cumulative observations and conduct morphometric studies of leaves, chasmogamous flowers, cleistogamous capsules, and seeds. Results obliterated the distinctions proposed by Gil-ad between the Crawford and Schoolcraft county subsp. *grisea versus* material from the rest of the western Great Lakes region and have compelled us to treat all specimens from the western Upper Great Lakes region under the *grisea* taxon. The 1971 specimen from Schoolcraft Co. (D. Henson 53) previously assigned to *V. novae-angliae* exhibited macromorphological features verging toward *V. nephrophylla* and was reinterpreted as a hybrid between *V. grisea* and *V. nephrophylla*. Broader comparisons between Great Lakes *V.grisea* and northeastern *V. novae-angliae sensu stricto* yielded some statistically significant quantitative differences, a few qualitative distinctions, and a number of additional tendencies that collectively separated the two geographically distinct sets of populations. Gil-ad's micromorphological studies provided additional indications that the two taxa could not be considered morphologically identical at the species level. Label information, field studies, and floristic treatments also suggested a substantial degree of habitat differentiation, with *grisea* occupying primarily circumneutral to somewhat acidic substrates and *novae-angliae* inhabiting primarily alkaline substrates. We treat the two taxa here as different evolutionary species, and we publish the new combination at species rank above for the regionally endemic western Great Lakes taxon. The common name of Great Lakes violet is proposed as an appropriate moniker.

22. ***Viola hastata*** Michx., Fl. bor.-amer., ed. 1, 2: 149. 1803. Type: [USA, North or South Carolina] in altis montibus Carol., [no date], [*A.*] *Michaux* [*s.n.*] (lectotype (**designated here**): MNHN-P-P04643848 [Richard Herbarium] (*n.v.*); isolectotype: MNHN-P-P04643826 (*n.v.*) [barcode refers to the whole sheet of three separate collections, isolectotype is probably the bottom left plant]; internet images). Fig. 58.

Common Names. Halberd-leaved violet, silver-leaved violet, spear-leaved yellow violet.

Description. Caulescent perennials from thick whitish rhizome, stems erect, solitary (very rarely 2), $\leq$ 30 cm tall; stems, foliage, and peduncles pale gray-green, upper surface of leaf blades frequently bicolorous or "variegated" with silvery-green lamina between the constrasting darker green veins, glabrous throughout or the upper leaf blade surface with short appressed hairs; leaves usually cauline only (occasionally with one basal leaf), clustered in upper 1/5 of shoot; stipules free, shallowly incised with 2–5 short processes especially on longer side; leaves spreading, leaf blades undivided, largest $\leq$ 86 $\times$ 58 mm, narrowly or broadly ovate-triangular to hastate, base subcordate to deeply cordate with basal lobes parallel or divergent, margins serrate at widest point, shallowly serrate to subentire distally, eciliate, apex acuminate; chasmogamous flower $\leq$ 12 mm; calyx glabrous, eciliate; lowest sepals lanceolate, sharply acute; auricles short and entire, not elongating in fruit; corolla wholly yellow with purple-brown tinge on back of petals; spur short-globose, barely exserted beyond auricles; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 7–9 mm, dark green drying brown, unspotted, glabrous; seeds 2.0–2.5(3.5) $\times$ 1.3–1.6(2.0) mm, brown, unspotted; $2n = 12$.

Similar Species. This caulescent species is unique in its long hastate leaf blades, which are often bicolorous ("variegated") on the upper surface with the gray- or silvery-green lamina separating the darker green veins. With its solitary stem, few or no basal leaves, and long leaf blades, this species could only be mistaken for *V.*

FIG. 58. *Viola hastata*. (A) Chasmogamous flowering habit (photo: Dan Nydick). (B) Chasmogamous fruiting habit (photo: Suzanne Caldwell).

glaberrima, but differs from that in the hastate leaf blades with short but deeply cordate base, and the frequently "variegated" upper surface. The variegated leaf blades are an unusual feature shared with *V. hirsutula* and *V. villosa* (in the southeastern states) in subsect. *Borealiamericanae*, and *V. walteri* in subsect. *Rostratae*.

Ecology. Rich rocky or sandy loam in somewhat acidic dry-mesic to mesic forests, cove and bluff forests, and bases of rock ledges.

Distribution. Primarily Appalachian Mountain highlands and associated uplands but extending southward to Gulf Coast, Pennsylvania to northeastern Ohio, south to Florida panhandle and eastern Mississippi. Fig. 59.

Rarity. None.

Phenology. Chasmogamous flower March–May, chasmogamous fruit May–June, cleistogamous fruit June–August.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Nudicaules species group.

Hybrids. None.

Comments. Following the description, Michaux's protologue added "Hab. in altis montibus Carolinae." He cited no specimens or types. According to Stafleu and Cowan (1981), Michaux's North American herbarium is at P as a separate historical collection, with some duplicates in Herb. Richard. The herbarium database at P has images and data for two sheets presumed to be original material, all matching the protologue information. Sheet MNHN-P-P04643826 has three labels indicating three separate collections. The upper right label is unambiguously associated with a plant of this species by Lowrie in the 1850s from Pennsylvania and is not original material. The two lower labels are in a somewhat ambiguous position relative to the two plants, one label with printed and handwritten information denoting an 1873 collection by Parker in Pennsylvania that is also not original material. The third is a handwritten label with "*Viola hastata*" and "In montibus altioribus Carolinae" and "Legit Michaux," and the label seems most likely to be associated with the bottom left plant on the sheet. Sheet MNHN-P-P04643848 has six plants with one label. The label has "*Viola hastata*," "Michaux," and "in altis montibus Carol." written in one hand, and "Herbarium Richard" at the top in another hand. None of the labels for the presumed original material on the two sheets closely match the handwriting of Michaux. With a more representative sampling of plants and unambiguous determination of provenance, sheet MNHN-P-P04643848 is selected here as the lectotype.

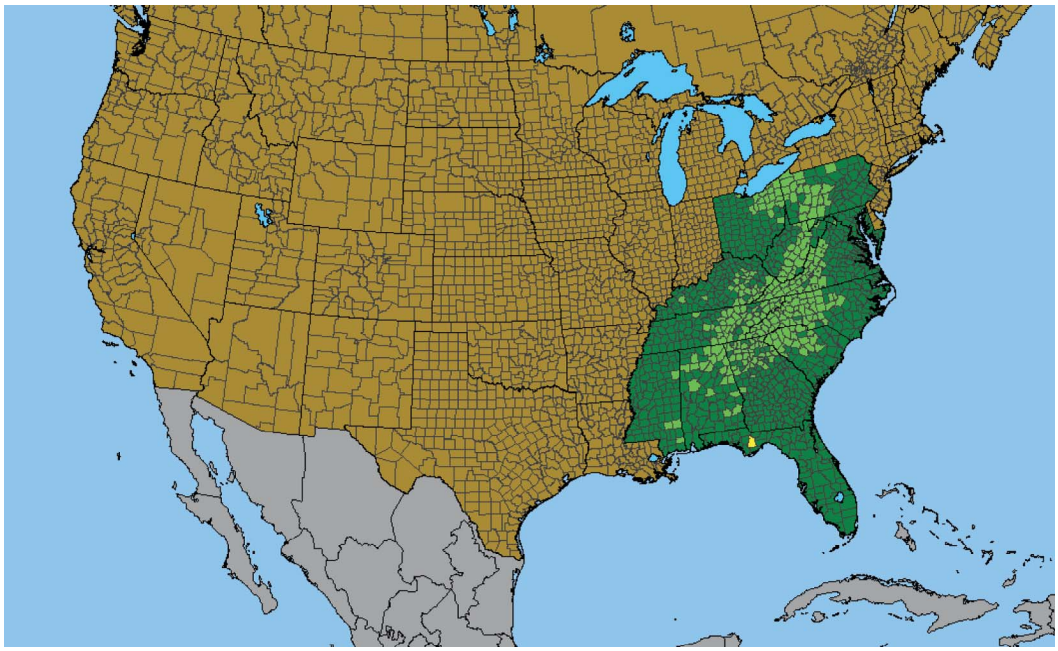

FIG. 59. United States county distribution of *Viola hastata* (map: Biota of North America Program).

This distinctive species has been accepted without controversy in all Violaceae treatments and floras, including Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Strausbaugh and Core (1978), Gleason and Cronquist (1991), Ballard (2000), McKinney and Russell (2002), Weakley *et al*. (2012), and Little and McKinney (2015). Nevertheless, specimens are not infrequently confused with *V. glaberrima* or *V. tenuipes* (south of our range), and less often with *V. eriocarpa*, when the whitish rhizome, conspicuous hastate leaf blades with parallel or divergent basal lobes, and frequently bicolorous or "variegated" upper surface of the blades are ignored. Botanists have debated whether the present species occurs in Florida, but a number of herbarium specimens and online images misidentified as "*V. tripartita*" *sensu lato* or as "*V. tripartita* var. *glaberrima*" are this species from the state's panhandle, supporting its occurrence there.

23. ***Viola hirsutula*** Brainerd, Rhodora 9: 98. 1907 [replacement name for *Viola villosa* Nutt.]; *Viola villosa* Nutt. non Walter (1788), Gen. N. Amer. Pl.: 148. 1818. Type: USA, North Carolina, Tryon, Rich open woodland, 14 Apr 1909, *E. Brainerd 64* (neotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 222.): GH00067133; isoneotype: NO0109933 (*n.v.*); internet images. Fig. 60.

Viola ciliata Willd. ex Schult., Syst. veg. 5: 360. 1819 (needs a proposal for rejection).

Viola hirsutula Brainerd f. *albicans* L.K.Henry, Castanea 18: 46. 1953.

Common Name. Southern wood violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 16 cm tall; foliage and peduncles dark green, upper surface of leaf blades light gray- or silvery-green with dark green or reddish-purple veins, lower surface of blades and peduncles often purple-tinged, all glabrous except for uniformly distributed conspicuous spreading or erect hairs on upper surface of leaf blades; stipules free, irregularly glandular-fimbriate; leaves spreading to prostrate (commonly lying on substrate during summer fruit), leaf blades undivided, largest $\leq$ 55 $\times$ 45 mm, ovate to suborbiculate, base cordate, margins crenate to serrate, eciliate, apex acute to rounded; chasmogamous peduncle held above the leaves; chasmogamous flower $\leq$ 18 mm; calyx glabrous, eciliate; lowest sepals ovate (uncommonly ovate-lanceolate), obtuse to rounded; auricles short and entire, not elongating in fruit; corolla blue to purple or reddish-purple, throat white; spur short-globose; lateral petals densely

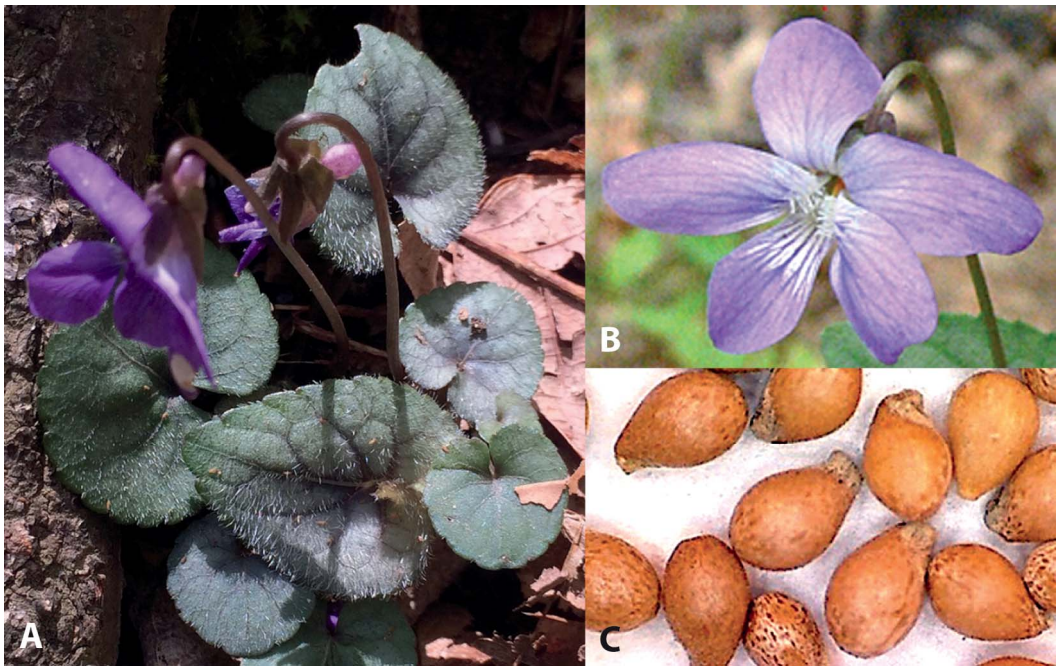

FIG. 60. *Viola hirsutula*. (A) Chasmogamous flowering habit (photo: Jessica Champagne). (B) Chasmogamous flower front view (photo: Bruce Sorrie). (C) Seeds from herbarium specimen: Indiana, *C. C. Deam 20567* (NY).

bearded with filiform to narrowly linear hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle initially prostrate but arching just before capsule dehiscence and shorter than petioles; cleistogamous capsule 6.5–12 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.5–2.1 × 1.1–1.4 mm, very light brown to orange-brown, unspotted or with weak to prominent brown streaks and spots; $2n = 54$.

Similar Species. This species is distinctive in its spreading to prostrate leaves, the upper surface bicolorous ("variegated") with the silvery-green lamina divided by deep green or red-purple veins and beset with erect hispid hairs. On the basis of the relatively short broad variegated leaves alone, it could be misidentified as *V. walteri* (which is mat-forming by node-rooting stolons) or the acaulescent southern *V. villosa* that does not enter our region, but the foliage and peduncle are glabrous except for the small hispid hairs on the upper leaf blade surface.

Ecology. Sandy soils on ridgetops, slopes of dry or dry-mesic oak and oak-pine or conifer forests, moist slopes or bottomlands, and clearings in former natural wooded habitats.

Distribution. Primarily Appalachian Mountain highlands and associated uplands but extending southward, Connecticut and New York to eastern Ohio, south to northern Florida and eastern Mississippi. Fig. 61.

Rarity. Listed in Connecticut, Indiana, New Jersey, and New York.

Phenology. Chasmogamous flower February–May, chasmogamous fruit May, cleistogamous fruit May–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sororia species group.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1906c, 1924; House 1906b, 1924; Dowell 1910), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (House 1906b; Brainerd 1907a, b, 1924; Henry 1953a), *V. emarginata sensu stricto* (House 1906b; Malte and Macoun 1915; House 1924), *V. fimbriatula*

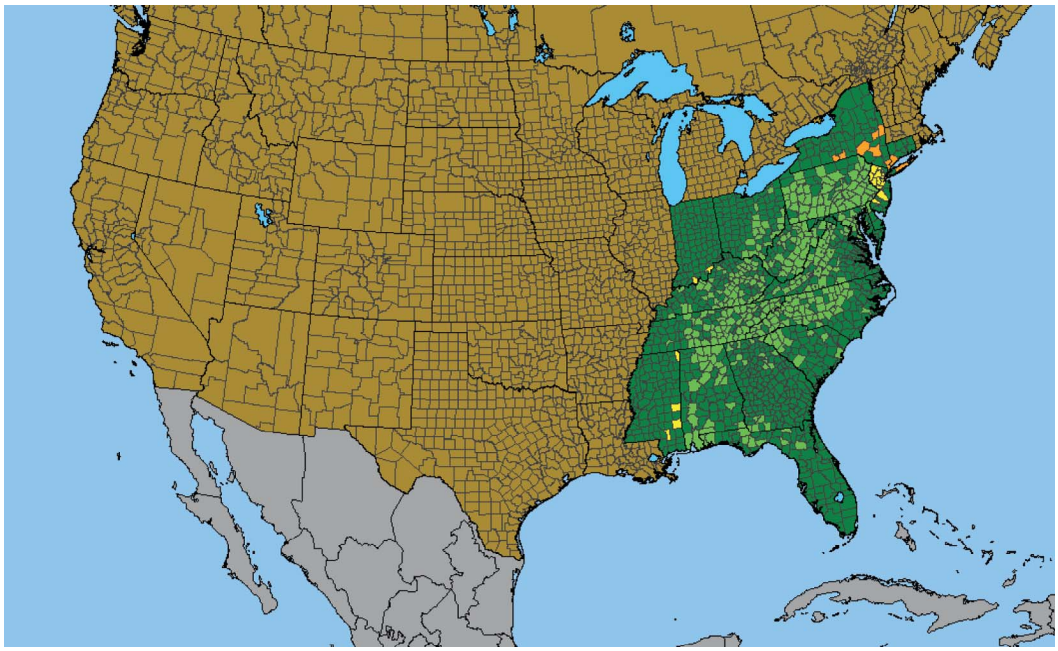

FIG. 61. United States county distribution of *Viola hirsutula* (map: Biota of North America Program).

(Dowell 1910; Brainerd 1924; Henry 1953a), *V. palmata* var. *triloba* (Brainerd 1906c, 1912, 1924; House 1924), *V. sagittata* (Henry 1953a), *V. sororia sensu stricto* (Brainerd 1924; Henry 1953a), *V. stoneana* (House 1906b; Brainerd 1912, 1924), and *V. subsinuata* (Brainerd 1906c, 1912, 1924). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). None of the hybrids reproduce by chasmogamous means. Some hybrids produce abortive cleistogamous flowers or capsules, while the remaining hybrids produce normal cleistogamous capsules but with substantial to dramatic reduction in the proportion of viable seeds.

Comments. Brainerd cited no type in the protologue, but following publication of the name he distributed specimens under his No. 64. No earlier collections named by him have been found. McKinney (1992) incorrectly annotated the GH00067133 sheet as the holotype but later stated the type as "unknown." JSTOR Global Plants includes the GH sheet and a NO sheet of Brainerd 64, but the collections postdate Brainerd's publication and are therefore not original material. In the absence of original material from which to select a lectotype, Ballard *et al*. (2020a) designated the GH and NO sheets as neotype and isoneotype, respectively. The name *V. ciliata* Willd. ex Schult. was published in 1819, long before Brainerd published the name *V. hirsutula*. Schultes's protologue clearly describes the present species, and the type material in the Willdenow Herbarium in Berlin are an exact match for what has passed as *V. hirsutula*. Since Schultes' name *V. ciliata* has been published, it has been essentially absent from the literature. It requires a proposal for rejection.

This species has been recognized by Brainerd (1924), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Strausbaugh and Core (1978), McKinney (1992), Ballard (2000), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015). In their extensive merger, Gleason and Cronquist (1991) synonymized it under *V. villosa*. Gil-ad (1995, 1997, 1998) conducted field studies and examined three samples for micromorphological traits; seeds from Brainerd's original material were not available. He discovered no unique micromorphological features, with some suggestive of *V. affinis*, *V. missouriensis*, or *V. sororia*. He argued that the taxon possessed no unique macromorphological features, noting that the foliage coloration could be attributed to *V. nephrophylla*, the pubescence

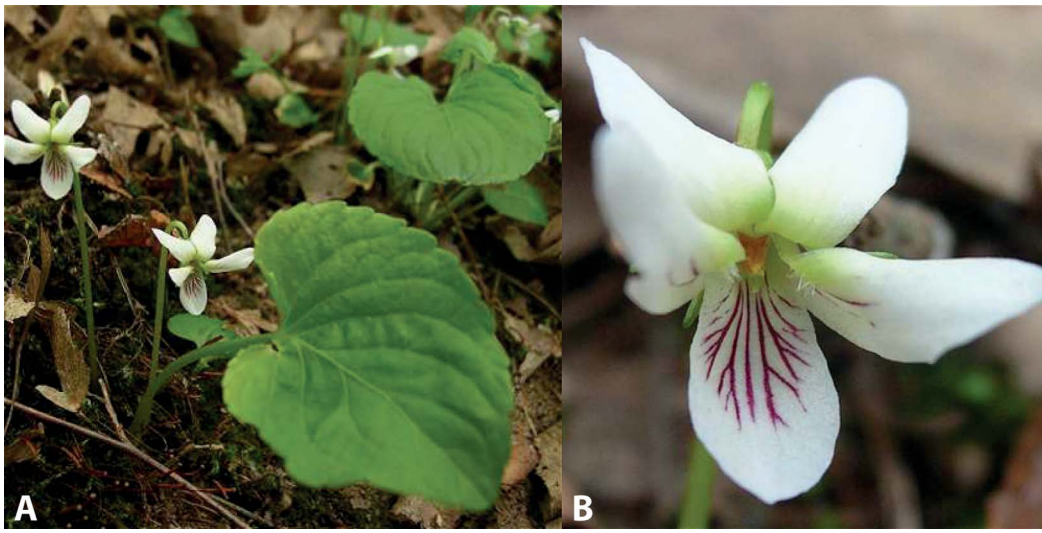

FIG. 62. *Viola incognita*. (A) Chasmogamous flowering habit (photo: Merel Black). (B) Chasmogamous flower front view (photo: Merel Black).

pattern is similar to that of *V. cucullata* and other species, and that reproductive characters resembled those of other species. He pointed out the variable habitats occupied by the species as final evidence that this species is of hybrid origin and should be abandoned. His micromorphological sampling, as cited in the dissertation, is both sparse and problematic; one study sample was collected from Taberville Prairie in Missouri, nearly 640 km west of the confirmed western limit of this species in Calloway and Henderson counties of Kentucky. Ballard (2013) made no mention of the presence of *V. hirsutula* in Missouri. The first author has examined mature cleistogamous seeds from Alabama (Brainerd 65), Indiana (Deam 20567), Maryland (House 1002), North Carolina (Ballard 15-012), and elsewhere and found them quite uniform in dimensions and color pattern. Herbarium specimens from throughout the primarily Appalachian range of the species, when not adulterated by frequent hybridization, are also highly uniform in traits of foliage, chasmogamous flowers, and cleistogamous fruits. The dry to dry-mesic woodland habitat, often in the vicinity of *V. palmata* and *V. sororia sensu stricto*, with which it commonly hybridizes, is as narrowly defined as any other woodland violet. The suite of macromorphological features that distinguishes this species is unique in the lineage, and its woodland ecological niche is different from most other species (although it makes contact with a few other species regularly). Under the unified species concept, the uniformity of morphological traits within and across populations over its range, the suite of consistent vegetative and reproductive differences separating it and other species, and reduced fertility of hybrids with other species, provide compelling evidence for recognizing *V. hirsutula* as a distinct species. It is distinctive vegetatively, with foliage glabrous except for the conspicuous spreading to erect hairs on the upper surface of the leaf blades, the bicolorous upper surface with gray- to silvery-green lamina between contrasting dark green or red-purple primary veins, and the tendency of the leaves (especially in fruit) to be horizontally oriented and eventually lie flat on the substrate. Hybrids express the striking bicolorous color pattern and the conspicuous spreading to erect hairs of the upper leaf blade surface; the frequent hybrid with *V. palmata* is particularly beautiful.

24. ***Viola incognita*** Brainerd, Rhodora 7: 248. 1905. Type: USA, Vermont, Forest at base of Moosalamoo Mt., Salisbury, pubescent form [originally identified as *Viola blanda*], 5 May 1903, *E. Brainerd s.n.* (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 222.): GH00067134). Fig. 62.

Viola blanda Willd. var. *palustriformis* A.Gray, Bot. Gaz. 11: 255. 1886.

Viola incognita Brainerd var. *forbesii* Brainerd, Bull. Torrey Bot. Club 38: 8. 1911.

Common Names. Common sweet white violet, large-leaved white violet.

Description. Acaulescent stoloniferous perennials from slender rhizome, colonial from surficial stolons produced in summer, stolons naked or with 1 to very few leaves (but not cleistogamous capsules) along their length and terminating in a plantlet, $\leq$ 14 cm tall; foliage and peduncles gray-green, upper surface of leaf blades darker than lower, petioles and/or one or both surfaces glabrous or sparsely to moderately hirsute, peduncles often hirsute; stipules free, glandular-fimbriate; leaves ascending or spreading, leaf blades undivided, largest $\leq 61 \times 72$ mm, ovate to deltate-ovate or reniform, base deeply cordate at base with broad sinus, basal lobes $>$ (1/4–)1/3 as long as total leaf blade length and mostly divergent in living material (aberrant Labrador populations have narrow sinus and basal lobes attingent or slightly overlapping in living material), margins low-serrate, eciliate, apex usually obtuse to broadly rounded (occasionally broadly acute); chasmogamous peduncle held above the leaves; chasmogamous flower $\leq$ 13 mm long; calyx glabrous, eciliate; lowest sepals lanceolate to ovate-lanceolate, narrowly obtuse to rounded; auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; lateral petals bearded with slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles and arching upward just before capsule dehiscence; cleistogamous capsule 5–9 mm, green drying tan with purple spots or blotches, glabrous; seeds (1.6)1.9–2.2 $\times$ 1.0–1.3 mm long, light to medium brown, unspotted; $2n = 44$.

Similar Species. Nonreproductive plants and younger chasmogamous flowering plants of this species can be particularly challenging to distinguish from *V. blanda*, and from *V. renifolia* if the rhizome and any stolons present are not collected. This species is most similar to other *Stolonosae* violets with leaf blades nearly as broad as to broader than long. In chasmogamous flower it differs from *V. palustris* and *V. suecica* in its noncreeping rhizome, leaves forming a discrete rosette, and white corolla; from *V. blanda* in its occasionally hirsute petioles and lower surface of leaf blades, and densely bearded lateral petals; from *V. minuscula* in its occasionally hirsute leaf laminas and noticeably serrate leaf blade margins, and from *V. renifolia* by its threadlike stolons, foliage often sparsely hirsute, leaves ascending, leaf blades commonly ovate to broadly ovate, and lateral petals densely bearded. It can be distinguished in cleistogamous fruit from *V. minuscula*, *V. palustris*, and *V. suecica* by the rhizome and foliage characters noted above as well as its heavily purple-spotted or -blotched cleistgamous capsules and brown seeds; from *V. blanda* in producing summer stolons mostly lacking leaves and fruits along its length (but terminating in a plantlet), petioles and lower surface of leaf blades occasionally hirsute, leaf blades more broadly ovate to ovate-deltate with deeper broader basal sinus and obtuse apex, and seeds larger, more narrowly obovoid and lighter brown; and from *V. renifolia* by its horizontal stoloniform rhizomes and threadlike stolons, foliage often sparsely hirsute, ascending leaves, and leaf blades commonly ovate to broadly ovate.

Ecology. Moist to wet somewhat acidic loamy, sandy, or peaty soils in mesic to wet forests, at bases of slopes and swamp margins, rarely on rock ledges.

Distribution. Northeastern North America, Newfoundland to Saskatchewan, south to North Carolina, Tennessee, and eastern Iowa. Fig. 63.

Rarity. Listed in Illinois (as *V. blanda*), New Jersey, and West Virginia (as *V. blanda* var. *palustriformis*).

Phenology. Chasmogamous flower April–June, chasmogamous fruit June, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. blanda* (Russell 1954a, 1955c, 1965), *V. lanceolata* (Ballard 1995), *V. minuscula* (Scoggan 1978; Ballard 1995), and *V. renifolia* (Russell 1954a; Ballard 1995). Hybrids with *V. blanda* might fail to reproduce by chasmogamous flowers, and cleistogamous capsules might express reduced viable seed output, while hybrids with the other species (being lower in ploidy) would definitely fail to reproduce

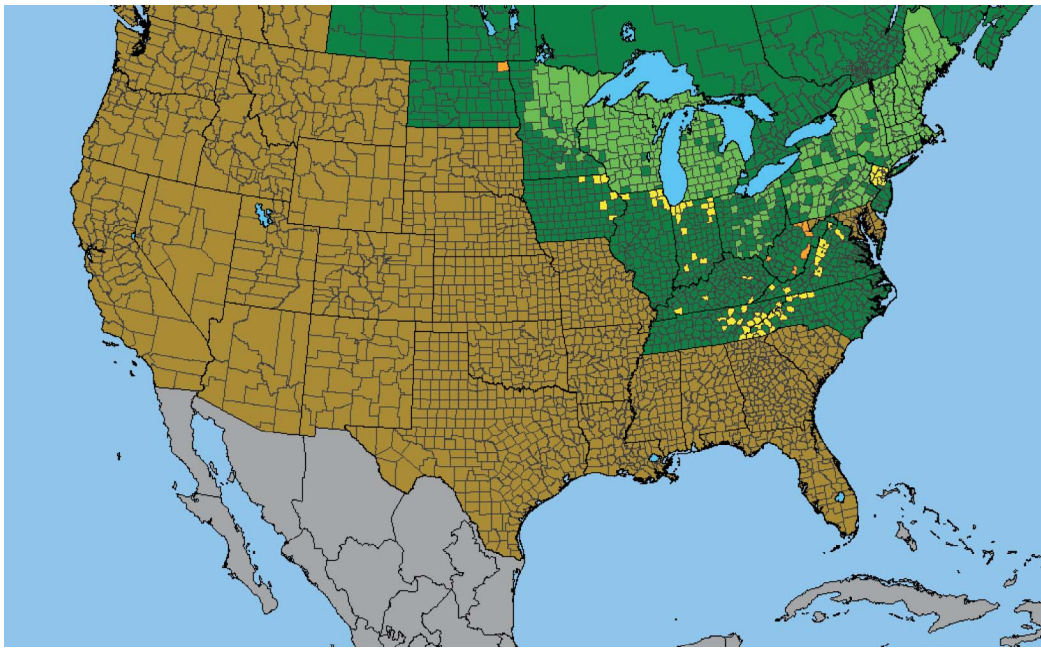

FIG. 63. United States county distribution of *Viola incognita* (map: Biota of North America Program).

chasmogamously and would produce either abortive cleistogamous capsules or no viable seeds. Studies are needed to confirm these predictions.

Comments. Brainerd's protologue mentioned "Type in Hb. Gray from wooded slopes of Moosalamoo Mountain, Salisbury, Vermont, May 5, 1903, and August 14, 1905." The sheet GH00067134 represents the cited May-flowering collection, but August-fruiting specimens have not been found. Brainerd's second handwritten label on the GH sheet states "*Viola incognita*, Brainerd, n. sp.,", indicating that the sheet was intended as a type. Ballard *et al*. (2020a) designated the GH sheet as the lectotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Russell (1955c), Alexander (1963), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), and Weakley *et al*. (2012) maintained this as a species separate from *V. blanda*. Gleason and Cronquist (1991), Ballard (1995, 2000), McKinney and Russell (2002), Voss and Reznicek (2012), and Little and McKinney (2015) synonymized it under *V. blanda*, while Haines *et al*. (2011) maintained it as *V. blanda* var. *palustriformis* A.Gray. Brainerd, Fernald, Henry, Alexander, Scoggan, and Swink and Wilhelm also recognized var. *forbesii* Brainerd, distinguished by pubescence confined to the upper surface of the leaf blades similar to the condition in *V. blanda*. Such plants, scattered over much of the western portion of the range of the present species, may at least partly explain reports of *V. blanda* in the western Great Lakes region. It has been synonymized under *V. incognita* by later taxonomists, or under *V. blanda* when only one species was recognized.

This species and *V. blanda* are allo-octoploid derivatives of ancient hybridization between a *V. minuscula*–like ancestor of the *Stolonosae* lineage and *V. renifolia* (Marcussen *et al*. 2012, Blaxland *et al*. 2018). Allopolyploidy and long-term regional differentiation may partly explain the perplexing variation in the Appalachian region and also much of the morphological similarity and frequent confusion between *V. incognita* and *V. renifolia*, as well similarity in certain foliage features between *V. blanda* and *V. minuscula* and occasional confusion over identification. Within-population variation in certain features such as foliage indument and pigmentation (or lack of it) in either species, and relative leaf expansion, makes identification more challenging in chasmogamous material. Over much of its range, typical *V. incognita* varies from nearly glabrous or glabrate to quite hirsute on one or both leaf surfaces, petioles, and peduncles, individual leaves on the same plant commonly with wholly

FIG. 64. *Viola inconspicua*. (A) Chasmogamous flowering habit (photo: Floyd Griffith). (B) Chasmogamous flower front view (photo: Floyd Griffith). (C) Chasmogamous flower profile view (photo: Floyd Griffith).

divergent pubescene patterns. Some populations of *V. blanda* and the less frequent *V. incognita* in the Appalachian highlands express perplexing local variation, perhaps in part due to ongoing hybridization between *V. blanda* and *V. incognita* as suggested by Russell (1954a, 1955c, 1965). The two species diverge most conspicuously in morphological characters during cleistogamous fruit; the seeds are then available to provide additional differences. Hybrids with *V. renifolia* are frequent in boreal North America and are commonly misidentified as *V. renifolia* when the stolons inherited from *V. incognita* and the infertile cleistogamous capsules are not noted. Populations of the present species in Labrador are unusual in leaf blades with a narrow basal sinus and basal lobes attingent or overlapping in living material but are otherwise typical of *V. incognita* in all other respects (S. Meade, Flora of Newfoundland and Labrador Project, personal communication). Russell (1954b) conducted analyses of variation in leaf pubescence over the ranges of this species and *V. renifolia*; in *V. incognita* he found some evidence for segregation of plants with pubescence limited to the upper leaf blade surface (previously called var. *forbesii*) to the southern portion of the species range but concluded that is was inadvisable to recognize a taxon based on a single trait.

25. ***Viola inconspicua*** Blume, Cat. Gew. Buitenzorg (Blume): 57. 1823. Fig. 64.

Viola apetala Roxb. non Gilib. (1782) nec F.W.Schmidt (1791), Fl. Ind. 2: 449. 1824.

Viola confusa Champ. ex Benth., Hooker's J. Bot. Kew Gard. Misc. 3: 260. 1851.

Viola patrinii Ging. var. *minor* Makino, Bot. Mag. (Tokyo 16: 126. 1902.

Viola minor (Makino) Makino, Bot. Mag. (Tokyo 26: 151. 1912.

Viola philippica Cav. subsp. *malesica* W.Becker, Beibl. Bot. Jahrb. Syst. 120: 178. 1917.

Viola mandshurica W.Becker subsp. *nagasakiensis* W.Becker, Beih. Bot. Centralbl. 40(2): 161. 1923.

Viola hunanensis Hand.-Mazz., Symb. Sin. 7: 376. 1931.

Viola minor Makino var. *albescens* Taken., J. Nat. Hist. Soc. Fukuoka 2(5): 195. 1938.

Viola minor Makino f. *ciliata* Taken., J. Nat. Hist. Soc. Fukuoka 2: 190, 195. 1938.

Viola minor Makino var. *ciliata* Taken., J. Nat. Hist. Soc. Fukuoka 2(5): 189, 195. 1938.

Viola minor Makino var. *serratodentata* Taken., J. Nat. Hist. Soc. Fukuoka 2: 189. 1938.

Viola angustistipulata C.C.Chang, Bull. Fan Mem. Inst. Biol., n.s., 1: 250. 1949.

Viola pseudomonbeigii C.C.Chang, Bull. Fan Mem. Inst. Biol., n.s., 1: 251. 1949.

Viola confusa Champ. ex Benth. subsp. *nagasakiensis* (W.Becker) F.Maek. & T.Hashim., J. Jap. Bot. 43: 161. 1968.

Viola confusa Champ. ex Benth. f. *pilosa* (F.Maek.) F.Maek. & T.Hashim., J. Jap. Bot. 43: 161. 1968.

Viola confusa Champ. ex Benth. f. *leucantha* E.Hama, Violets of Japan: 181. 1987.

Viola inconspicua Blume subsp. *nagasakiensis* (W.Becker) J.C.Wang & T.C.Huang, Taiwania 35: 41. 1990.

Viola confusa Champ. ex Benth. f. *albiflora* S.S.Ying, Coloured Ill. Fl. Taiwan 4: 783. 1992.

Viola confusa Champ. ex Benth. var. *lanyuensis* S.S.Ying, Coloured Ill. Fl. Taiwan 4: 18. 1992.

Viola inconspicua Blume var. *minor* (Makino) S.S.Ying, Coloured Ill. Fl. Taiwan 4: 26. 1992.

Viola inconspicua Blume f. *pilosa* (F.Maek.) Yonek., J. Jap. Bot. 80: 326. 2005.

Common Name. None in English.

Description. Acaulescent rosulate perennials from somewhat thick rhizome, $\leq$ 20 cm tall; foliage, peduncles, and calyces green, proximal portion of petioles, peduncles, and calyces finely spotted with reddish-purple, upper surface of leaf blades dark green, plant glabrous throughout; stipules adnate to petiole for up to 3/4 their length, fimbriate-dentate; petioles not winged; leaves spreading to prostrate, leaf blades undivided, largest $\leq$ 90 $\times$ 70 mm, ovate-triangular, base shallowly to moderately deeply cordate, margins crenate, eciliate, apex acuminate; chasmogamous peduncle held above leaves; chasmogamous flower $\leq$ 12 mm; calyx glabrous, eciliate or ciliate; lowest sepals lanceolate to ovate-lanceolate, acuminate; auricles prominent and erose, not elongating in fruit; corolla pale blue to purple with proximal 1/2 of spurred petal white, throat white; spur cylindrical, 2–4(4.5) mm, pale green spotted with reddish-purple; lateral petals densely bearded; chasmogamous capsule green, 8–10 mm; cleistogamous flowers produced after chasmogamous, cleistogamous capsule features not reported; seeds 1.0–1.5 $\times$ ca. 0.8 mm, deep green, unspotted; $2n = 24, 48, 72$.

Similar Species. This species and others most similar to it belong to the predominately Asian subsect. *Patellares*, which consists of acaulescent nonstoloniferous violets with stipules at least half-adnate to their petioles, somewhat to very elongate spurs, and mostly violet to purple corollas. Three species in the subsection that are introduced in our region, including this one, have leaf blades longer than broad. This species differs from *V. japonica* in its glabrous foliage, proportionally shorter petioles, shorter spur, and densely bearded lateral petals. It is distinct from *V. patrinii* in lacking broad wings on the proportionally longer petioles, and in its violet to purple corolla.

Ecology. In Asia, growing in grasslands, forest margins, fields, and along paths (Chen *et al*. 2007); in North America, inhabiting nurseries, lawns, and roadsides.

Distribution. Temperate and tropical Asia; introduced and apparently naturalized in Florida and Georgia (L. Anderson, personal commication), also in Texas and Maine. Fig. 65.

Rarity. None.

Phenology. Chasmogamous flower November–April in its native range (Chen *et al*. 2007), chasmogamous fruit December–May (September), cleistogamous fruit throughout the year(?).

Affinities. This species belongs to sect. *Plagiostigma* Godr., subsect. *Patellares* (Boiss.) Rouy & Foucaud.

Hybrids. None.

Comments. Besides the species and their differences noted in the "Similar Species" section, a third introduced Asian species of subsect. *Patellares* west of our region in Kansas and Nebraska, *V. philippica* Cav., is not all that similar. That species has linear-lanceolate to lanceolate leaf blades cuneate to subtruncate at the base but glabrous lateral petals. It has been reported from lawns, roadsides, and river bottoms in Kansas and Nebraska. The present Asian introduction was initially brought to our attention by Loran

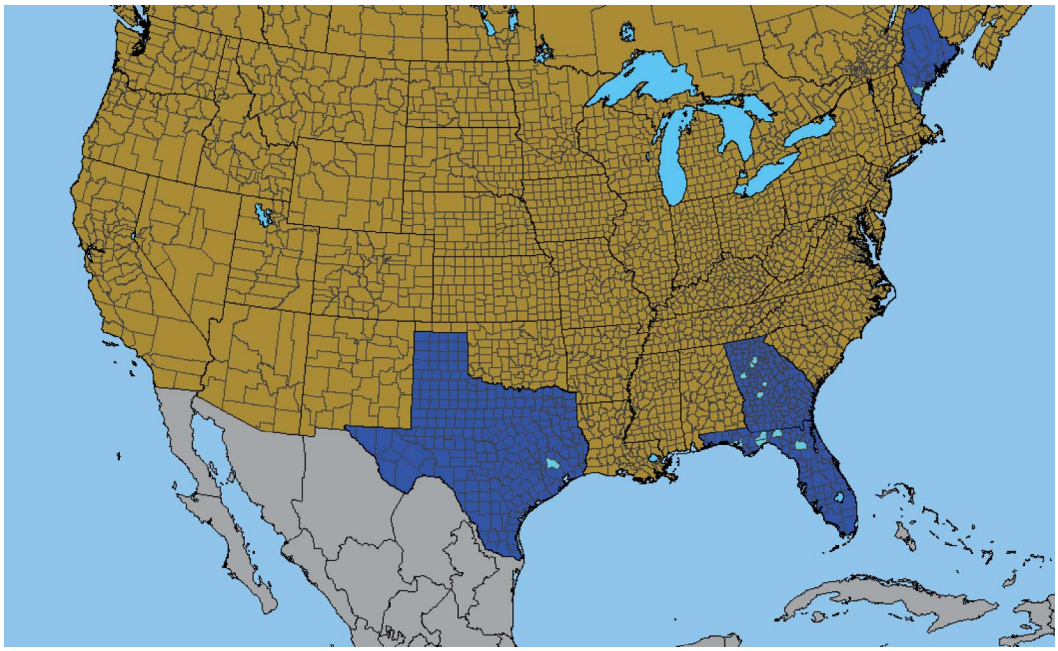

FIG. 65. United States county distribution of *Viola inconspicua* (map: Biota of North America Program).

Anderson and Floyd Griffith in Florida; several other iNaturalist posts indicate that the violet has spread in the Southeast as far west as Texas. A recent iNaturalist post from Maine has been confirmed, where the species was found in mulch among nursery plants; in the short time since posting, the plants have already disappeared. Chen *et al*. (2007) suggest that the violet is somewhat weedy in its native range and often occupies lawns, roadsides, sidewalk cracks, and other anthropogenic sites. The description was composed from images from a Florida population provided by Griffith and from Chen *et al*. (2007).

26. ***Viola japonica*** Langsd. ex Ging., in DC., Prodr. 1: 295. 1824. Fig. 66.

Viola kapsanensis Nakai in Bot. Mag. (Tokyo) 36: 35. 1922.

Viola kapsanensis Nakai var. *albiflora* Nakai in Bot. Mag. (Tokyo) 36: 36. 1922.

Viola metajaponica Nakai in Bull. Soc. Bot. France 72: 192. 1925.

Viola japonica Langsd. ex Ging.var. *variegata* Hatus. in Exp. Forest. Kyushu Imp. Univ. 5: 132. 1934.

Viola metajaponica Nakai f. *barbara* Hiyama in J. Jap. Bot. 26: 157. 1951.

Viola japonica Langsd. ex Ging.f. *albida* F.Maek. in H.Hara, Enum. Spermatophytarum Japon. 3: 205. 1954 (not validly published).

Viola japonica Langsd. ex Ging.f. *barbara* (Hiyama) F.Maek. in H.Hara, Enum. Spermatophytarum Japon. 3: 205. 1954.

FIG. 66. *Viola japonica*. Chasmogamous flowering habit (photo: Xiao Yanli).

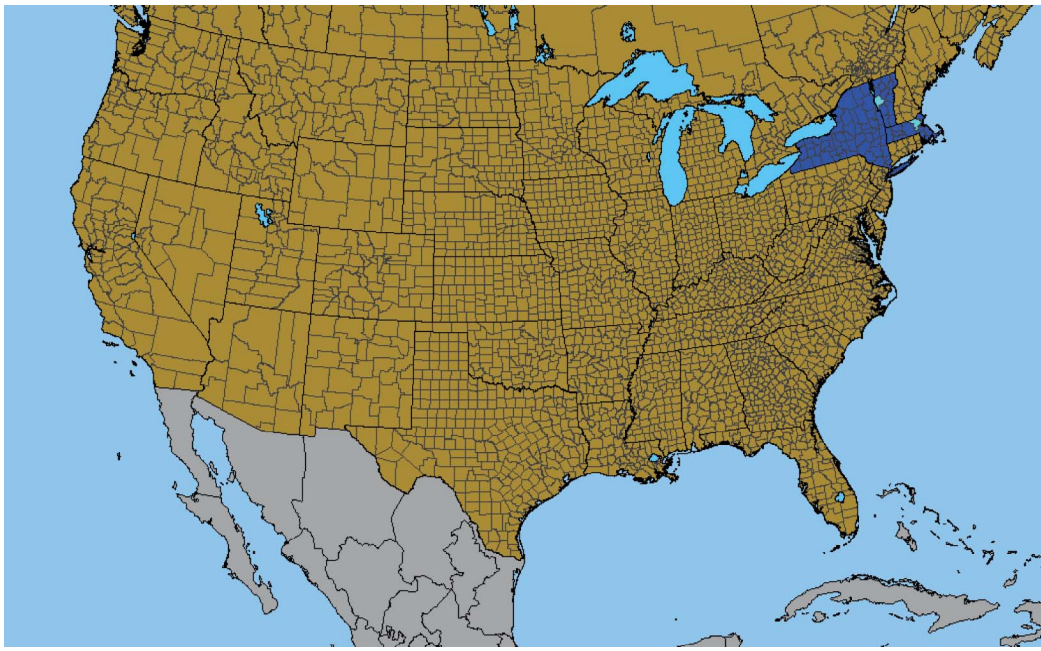

FIG. 67. United States county distribution of *Viola japonica* (map: Biota of North America Program).

Viola japonica Langsd. ex Ging.f. *variegata* (Hatus.) F.Maek. in H.Hara, Enum. Spermatophytarum Japon. 3: 205. 1954.

Viola japonica Langsd. ex Ging.f. *pallescens* Sugim. in J. Geobot. 16: 50. 1968.

Common Name. None in English.

Description. Acaulescent rosulate perennials from somewhat thick rhizome, $\leq$ 22 cm tall; foliage, peduncles, and calyces green, upper surface of leaf blades slightly darker than lower, both surfaces sparsely puberulent or rarely glabrate; stipules adnate to petiole for *ca*. 2/3 their length, remotely serrulate; petiole not winged, nearly to quite equalling leaf blade during chasmogamous flower, elongating to much longer than blade in fruit; leaves erect, leaf blades undivided, largest $\leq$ 110 $\times$ 50 mm, narrowly ovate, base moderately deeply cordate with basal lobes pointing downward, margins crenate, eciliate, apex acute; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 12 mm; calyx glabrous, eciliate or ciliate; lowest sepals broadly lanceolate, acuminate; auricles prominent and truncate or erose, elongating in fruit to 3 mm; corolla pale violet to violet, throat white; spur cylindrical, 6–8 mm, white to violet; lateral petals glabrous to sparsely bearded; chasmogamous capsule green, 8–10 mm; cleistogamous flowers produced after chasmogamous, cleistogamous capsule ellipsoid, *ca*. 1 cm; seeds not reported; 2n = 24, 48, 72.

Similar Species. This species and others most similar to it belong to the predominately Asian subsect. *Patellares*, which consists of acaulescent nonstoloniferous violets with stipules at least half-adnate to their petioles, somewhat to very elongate spurs, and mostly violet to purple corollas. Three species in the subsection that are introduced in our region, including this one, have leaf blades longer than broad. This species differs from *V. inconspicua* in its sparsely puberulent leaves, much longer spur, and glabrous to sparsely bearded lateral petals. It is distinct from *V. patrinii* in lacking prominent wings on the proportionally longer petioles, and in its violet to purple corolla.

Ecology. In Asia it grows in "sunny or half shaded places in lowlands" (Chen *et al*. 2007); in the USA, plants inhabit lawns and plantings.

Distribution. Native to Taiwan, Japan, and South Korea; introduced in Argentina, Washington, D.C., Massachusetts, New York, and Vermont. Fig. 67.

Rarity. None.

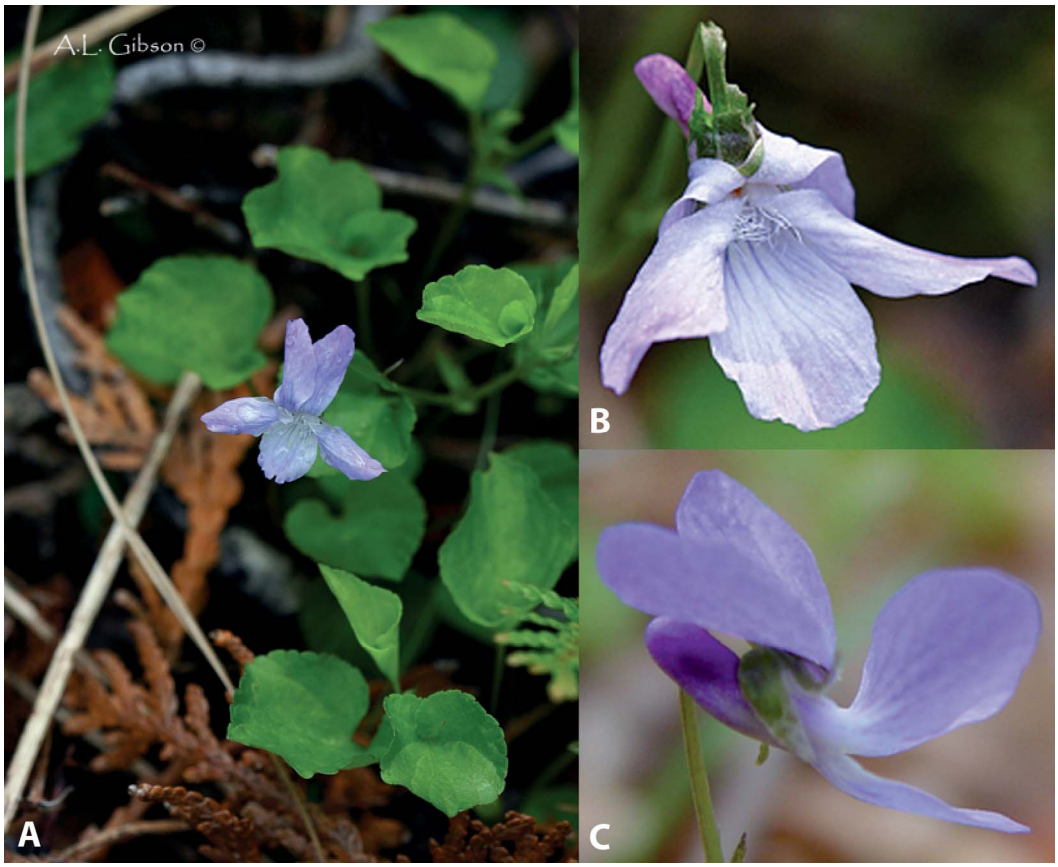

FIG. 68. *Viola labradorica*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous front view (photo: Andrew Lane Gibson). (C) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust).

Phenology. Chasmogamous flower March and October, fruit May–October (in Asia, Chen *et al*. 2007).

Affinities. This species belongs to sect. *Plagiostigma* Godr., subsect. *Patellares* (Boiss.) Rouy & Foucaud.

Hybrids. None.

Comments. Brainerd (1908b) provided the first reports of this species as a spontaneous escape or introduction in The New York Botanical Garden and Harvard Botanical Garden, and an escape following cultivation at his own garden and the residence of a colleague in Brookland (Washington, D.C.), under the name *V. chinensis* G.Don, a synonym of *V. patrinii* Ging. These specimens were incorrectly identified and are all *V. japonica*. Cullina *et al*. (2011) reported this species from Middlesex Co., MA, and a 2018 iNaturalist post confirmed as this was made for plants in the same county. The description was composed from images from the few herbarium specimens available and from Chen *et al*. (2007).

27. ***Viola labradorica*** Schrank, Denkschr. Bot. Ges. Regensb. 1(2): 12. 1818. Type: "New Greenland" [= Labrador] [protologue], [no date], *Kohlmeister s.n*. (holotype: M0112897, internet image). Fig. 68.

Viola debilis Pursh non Michx. (1803), Fl. Amer. sept. 1: 174. 1813; *Viola muhlenbergiana* Ging. var. *minor* Hook., Fl. bor.-amer. 1: 78. 1830; *Viola adunca* Sm. var. *minor* (Hook.) Fernald, Rhodora 51: 57. 1949.

Viola punctata Schwein., Amer. J. Sci. 5: 67. 1822 [illegitimate homonym of *Viola punctata* (Humb. & Bonpl.) Schult. (1819)].

Viola conspersa Rchb., Iconogr. bot. pl. crit. 1: 44. 1823.

Viola muhlenbergii Torr., Fl. northern middle United States 1(2): 256. 1824; *Viola canina* Walter var. *muhlenbergii* (Torr.) A.Gray, Bot. Gaz. 11(11): 292. 1886; *Viola debilis* Michx. f. *muhlenbergii* (Torr.) Farw., Amer. Midl. Naturalist 12: 68, 128. 1930.

Viola leucopetala Greene, Ottawa Naturalist 15: 191. 1901.

Common Names. American dog violet, Labrador violet.

Description. Caulescent perennials from somewhat slender rhizome, stems ascending in flower but commonly reclining in fruit, commonly ≥ 2, $\leq$ 25 cm tall; stems, foliage, and peduncles light to medium yellow-green, glabrous except for scattered short appressed hairs on upper surface of leaf blades; leaves cauline and basal, cauline distributed along stem; stipules free, weakly lacerate; leaves ascending or spreading, leaf blades undivided, largest $\leq 31 \times 29$ mm, broadly ovate or suborbiculate to reniform, base deeply cordate, margins crenate, eciliate, apex broadly rounded to obtuse or apiculate, rarely acutish; chasmogamous flower ≤ 17 mm; calyx glabrous, eciliate; lowest sepals lanceolate to linear-lanceolate, acuminate to narrowly obtuse; auricles short and entire, not elongating in fruit; corolla pale to medium blue, throat white; spur moderately elongate, slender, 4–8 mm, white to pinkish, violet or blue; lateral petals densely bearded with narrowly linear hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 3–6 mm, green drying tan, unspotted or with fine red spots or lines, glabrous; seeds $1.5–2.0 \times 0.8–1.1$ mm, medium-brown, unspotted; $2n = 20$.

Similar Species. This species might be confused with the caulescent habit and white to occasionally pale violet flower of the newly confirmed Asian introduction *V. arcuata* if the deltate-ovate to deltate-reniform leaf blades and entire or minutely toothed stipules of the latter were ignored, but the few fine nectar-guide lines on the spurred petal and the longer spur would differentiate *V. labradorica*. It is similar to *V. appalachiensis* in general foliage and pubescence characters, pale blue corolla with moderately long spur, and weakly lacerate stipules, but it is not mat-forming and the stems are annually deciduous.

Ecology. Moist to wet loamy, peaty, or mucky soils in mesic to wet-mesic forests, alluvial woods and swamps, seepage slopes, marl ravines, and hammocks.

Distribution. Widely distributed in northeastern North America and Appalachian Mountains, extending southward, and in boreal western North America, Greenland and Newfoundland and Labrador to Northwest Territories, south to Maryland, Alabama, and North Dakota, slightly disjunct in southwestern Georgia and the panhandle of Florida. Fig. 69.

Rarity. None.

Phenology. Chasmogamous flower March–July (September), chasmogamous fruit June–August (September), cleistogamous fruit August–September.

Affinities. This species belongs to the Rostrate Violet lineage, sect. *Viola*, subsect. *Rostratae* (Kupffer) W.Becker.

Hybrids. Hybridizes with *V. adunca* (Brainerd 1924; Ballard 1992, 1995; Haines *et al*. 2011), *V. rostrata* (Malte and Macoun 1915; Brainerd 1924; House 1924; Henry 1953a; Scoggan 1978; Ballard 1990a, 1992, 1995; Haines *et al*. 2011), *V. striata* (Gaiser and Moore 1966; Ballard 1990b, 1992, 1995; Haines *et al*. 2011), and *V. walteri* (Ballard 1992, 1993). The first author has observed the hybrids and have found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. Hybrids fail to reproduce by chasmogamous flowers, and cleistogamous capsules fail to produce viable seeds.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), and Gleason and Cronquist (1991) recognized a predominately temperate eastern North American *V. conspersa* Rchb. separate from a boreal taxon with smaller size and "subentire" stipules. Brainerd, Jørgensen et al. (1958), and Russell maintained the boreal violet as *V. labradorica* Schrank, while Fernald, Alexander, Scoggan, and Gleason and Cronquist referred the boreal taxon to *V. adunca* var. *minor* (Hook.) Fernald. Glabrous or glabrate plants of *V. adunca* differ in many vegetative and floral traits from plants of *V. labradorica* from throughout the range of the latter

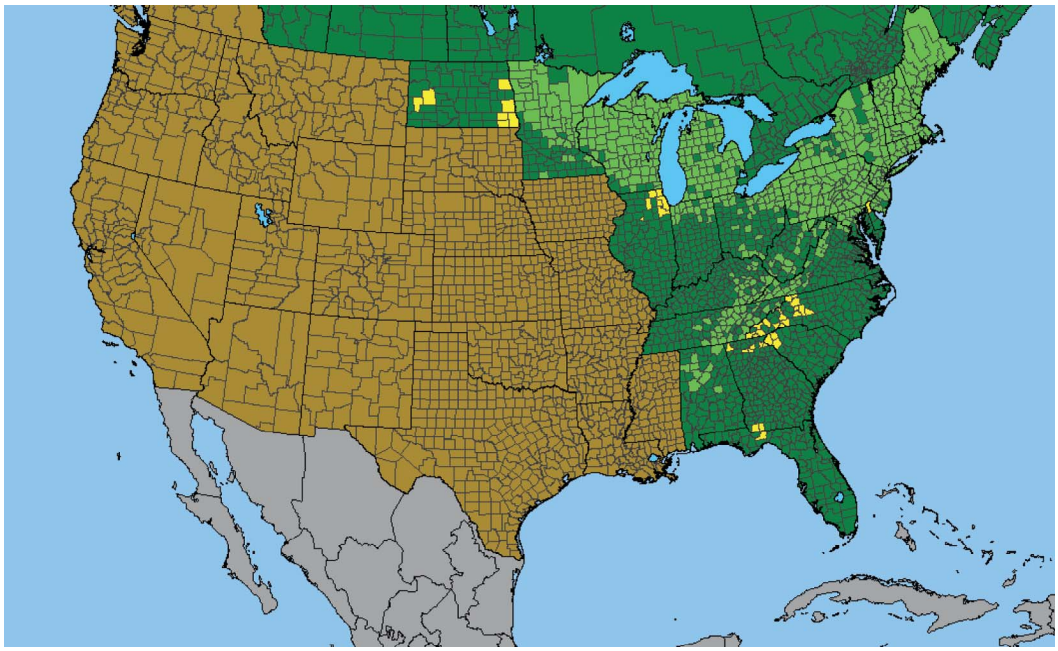

FIG. 69. United States county distribution of *Viola labradorica* (map: Biota of North America Program).

species. Nevertheless, when Fernald (1950) made the combination *V. adunca* var. *minor*, he synonymized under it the names *V. labradorica* Schrank, *V. muhlenbergiana* Ging. var. *minor* Hook., *V. adunca* Sm. var. *glabra* Brainerd, and *V. adunca* f. *glabra* (Brainerd) G.N.Jones, effectively combining all glabrous or glabrate northern rostrate violets under his new combination. Ironically, Hooker cited *V. debilis* Pursh as a synonym under *V. muhlenbergiana* var. *minor*, and Pursh's description clearly refers to the temperate violet previously known as *V. conspersa*. Fernald consequently made the dual error of combining two taxa that were not conspecific and also misapplying the new name, *V. adunca* var. *minor*, to boreal populations attributed by others to *V. labradorica sensu stricto*. Alexander, Scoggan, and Gleason and Cronquist perpetuated this unfortunate compounded mistake. Morphometric studies of floral, stipule, and leaf blade traits, and examination of styles, on numerous herbarium specimens from the ranges of *V. labradorica* and *V. conspersa* (Ballard 1992) revealed a continuum indicating a single taxon. The earliest available name is used here. This merger has been adopted by Ballard (1995, 2000), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney (2015). Little and McKinney reference specimens named this in Colorado and note that some taxonomists have treated it as synonymous with *V. bellidifolia* in that state, the latter apparently perpetuating the unnecessary confusion between the *V. adunca* complex and the present species. The names *V. conspersa* Rchb. var. *masonii* Farw., f. *masonii* (Farw.) House, and *V. adunca* Sm. f. *masonii* B.Boivin are all based on a type that is *V. striata* Aiton (Ballard 1995).

28. ***Viola lanceolata*** L., Sp. pl., ed. 1, 2: 934. 1753. Type: "Habitat in Canada, Sibiria" [Presumably northeastern North America, the Siberian reference an error], [no date], *P. Kalm s.n*. (lectotype (designated by James Reveal in Jarvis (ed.), Order out of Chaos: 924. 2007): LINN-HL1052-6 (*n.v.*), internet image). Fig. 70.

Common Names. Lance-leaved violet, northern water violet.

Description. Acaulescent stoloniferous perennials from slender rhizome, colonial from surficial stolons produced in summer, stolons leafless or leafy and infrequently with 1–few cleistogamous capsules, $\leq$ 30 cm tall; foliage and peduncles green, glabrous (leaf blades very rarely sparsely hirtellous in plants near the southern edge of our region); stipules free, finely glandular-fimbriate;

FIG. 70. *Viola lanceolata*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Seeds from herbarium specimen: Connecticut, Town of Franklin, 22 Sep 1912, *R. W. Woodward s.n.* (CBS18215).

leaves erect, leaf blades undivided, largest ≤ 140(190) × 29 mm, , 3–6(8) × as long as broad, (5)7–29 mm broad, often abruptly tapering to the petiole, narrowly elliptical to lanceolate, base narrowly to broadly cuneate, gland of marginal teeth appressed to incurved, margins appearing subentire, low-serrate or (sub)crenate, eciliate, apex obtuse to acute; chasmogamous peduncle held among or above the leaves; chasmogamous flower ≤ 13 mm; calyx glabrous, eciliate; lowest sepals narrowly triangular to ovate-triangular, acuminate; auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; all petals glabrous (occasionally lateral petals with sparse beard of narrowly linear to slightly clavate hairs); cleistogamous flowers produced after chasmogamous, on erect peduncle nearly or quite as long as petioles; capsule 4–12 mm, green drying light brown, unspotted or with fine red spots, glabrous; seeds 1.1–1.4 × 0.8–1.0 mm, dark olive-brown, unspotted; 2n = 24.

Similar Species. This species is so distinctive that it could only be confused with a few long-leaved species in subsect. *Stolonosae*. It differs from *V. primulifolia* in its leaf blades cuneate at base, and from *V. vittata* in glabrous (rarely sparsely hirtellous) foliage, leafy summer stolons with cleistogamous capsules, proportionally shorter and broader leaf blades with an abruptly tapering leaf blade base, and ascending or incurved leaf teeth (making the margins apparently flush or shallowly crenate).

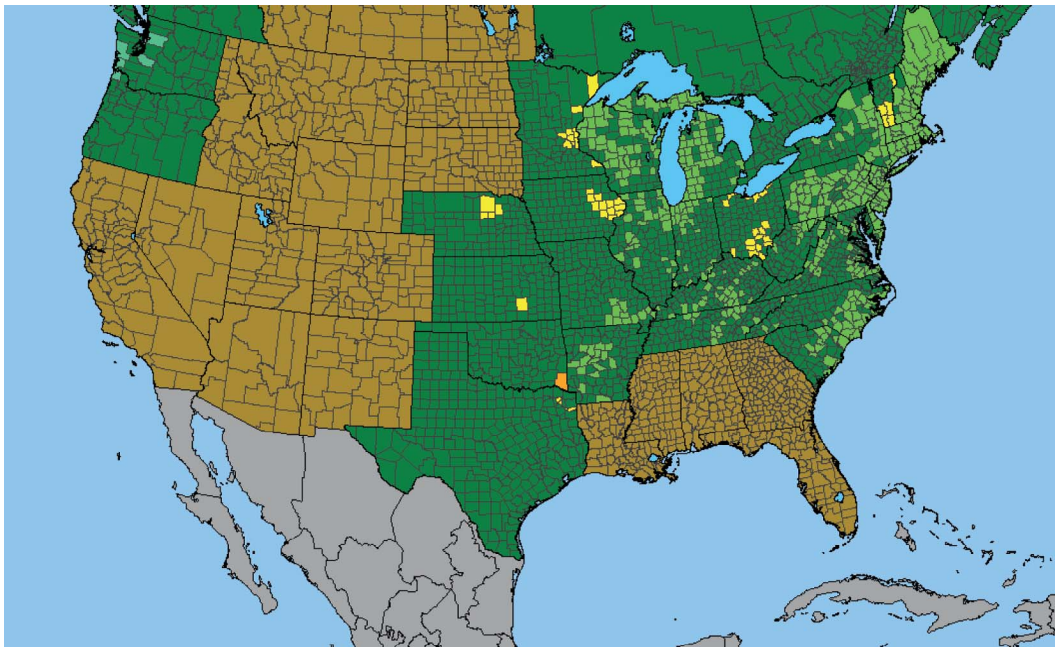

FIG. 71. United States county distribution of *Viola lanceolata* (map: Biota of North America Program).

Ecology. Acid mucky or peaty sand of bogs, pitcher plant seepage bogs, seepage slopes, swamp margins, lakeshores, depression ponds, intermittent wetlands, interdunal swales and ponds, and disturbed sites where topsoil has been scraped to the water table, such as lowland blueberry farms, sand borrowpits, and sandstone quarries.

Distribution. Widely distributed in northeastern North America, Newfoundland and Labrador to eastern Minnesota, south to South Carolina and eastern northeastern Texas, slightly disjunct in northeastern Nebraska and southeastern Kansas; introduced into the Pacific Northwest of British Columbia, Washington, and Oregon. Fig. 71.

Rarity. Listed in Iowa, Minnesota, Ohio, and Vermont (as *V. lanceolata* subsp. *lanceolate*).

Phenology. Chasmogamous flower March–June, chasmogamous fruit June–July, cleistogamous fruit July–November.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. brittoniana* (Forbes 1909; Brainerd 1924; Haines *et al*. 2011), *V. incognita* (Ballard 1995), *V. minuscula* (Brainerd 1924; Russell 1954a, 1955c; Boivin 1966; Cinq-Mars 1966; Ballard 1995), and *V. primulifolia* (Brainerd 1924; Russell 1955c). The first author has observed the hybrids and, in at least those with *V. minuscula* and *V. primulifolia*, has found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. All hybrids will fail to reproduce by chasmogamous flowers. The interploidal hybrid will likely produce abortive cleistogamous capsules, while the latter two hybrids may produce abortive cleistogamous capsules or normal capsules without viable seeds or a substantially reduced proportion of viable seeds. Studies are needed to confirm these predictions.

Comments. The page for *V. lanceolata* in the Linnaean Names Typification Project database incorrectly states that lectotype sheet No. 1052.4 was designated as the lectotype; that sheet number is actually *V. pinnata*, whereas the Kalm specimen of *V. lanceolata* is No. 1052-6 as labeled on the sheet.

Brainerd (1921b), Brainerd Baird (1942), Henry (1953a), Alexander (1963), Scoggan (1978), Strausbaugh and Core (1978), and Swink and Wilhelm (1979) maintained *V. lanceolata* as a species distinct from *V. vittata*. Russell (1955c, 1965), Haines *et al*. (2011), and Ballard (1995, 2013) recognized the two as subspecies under *V.*

lanceolata; while Fernald (1950), Gleason and Cronquist (1991), Ballard (2000), and Weakley *et al*. (2012) treated them as varieties. McKinney and Russell (2002) and Little and McKinney (2015) merged them under *V. lanceolata* without recognition of infraspecific taxa, while Voss and Reznicek (2012) simply recognized the present species and made no comment about *V. vittata* (it was outside the region of concern). Russell's (1956c) generalized maps of regional variation in the two species (which he treated as subspecies), in which he shows an uninterrupted continuum of leaf blade length:breadth ratio and of leaf blade length from north to south, appear to include spring and summer individuals, as summer fruiting plants of the two taxa are sharply distinct in these variables and could not have produced a continuum of variation. Reported sporadic intergradients or "transitional" plants between the two (*e.g*., Russell 1956c, 1965) are quite rare and are represented by plants similar to *V. lanceolata* in the main southeastern range of *V. vittata*. Examinations by the first author of a few specimens identified as transitional plants have yielded misidentifications of chasmogamous flowering plants of *V. vittata* that have not yet produced their extreme summer leaves. The remaining "intermediates" appear to be infrequent hybrids of *V. primulifolia* and *V. vittata*, which resemble *V. lanceolata* but occasionally exhibit hirtellous foliage. Additional evidence suggesting that these are distinct evolutionary species is provided by the fact that the two maintain their multiple diagnostic differences and occupy distinctly different microhabitats in the narrow zone of sympatry in the Carolinas. They are most distinct, and therefore most easily and confidently identified, during summer fruit, when leaves have expanded to their fullest dimensions and plants display their typical difference in presence or absence of surficial stolons (Fernald 1949). Fernald (1950) also indicated a strong tendency toward differential height of the chasmogamous peduncles, which deserves scrutiny. A very limited sampling of seeds suggests that the two may also diverge in seed shape and dimensions, with *V. lanceolata* seeds being larger and obovoid-lanceolate to obovoid and *V. vittata* seeds being smaller and subglobose. Specimens from the southern end of Lake Michigan, previously identified as *V. vittata* Greene or *V. lanceolata* subsp. *vittata* (Greene) N. H. Russell have been examined and proven to be depauperate chasmogamous flowering *V. lanceolata*. *De novo* hybrids between the present species and *V. minuscula* are frequently encountered throughout their broad zone of sympatry. Many reports of *V. primulifolia* from the Great Lakes region have been found to represent *V.* ×*sublanceolata* (*V. lanceolata* × *V. minuscula*), but some are reportedly fertile. See "Comments" under *V. primulifolia* for further discussion.

29. ***Viola latiuscula*** Greene, Pittonia 5: 93. 1902. Type: USA Vermont. Twin Mountains, West Rutland, 24 May, *W. W. Eggleston 2648* (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 223): NDG32742[a]*; isolectotypes: CM1457[a] (*n.v.*)[barcode, accession # is CM107917]*, CM1458[a] (*n.v.*)[barcode, accession # is CM107918]*, GH00067135[a]*, ILL00006622[a]* (*n.v.*), MIN1002774[a]* (*n.v.*), MU000000218[a]* (*n.v.*), NY00097537[a]*, NY00097538[a]*, NY00097539[a]*, PH00029251[a]* (*n.v.*), PH00029252[a]* (*n.v.*), PH00029253[a]* (*n.v.*), RSA0006446[a]* (*n.v.*), S-G-6375[a]* (*n.v.*), UVMVT080304*, UVMVT083115*, and YU069971[a] (*n.v.*); *internet image)). Fig. 72.

Common Name. Broad-leaved wood violet.

Description. Acaulescent rosulate perennials from thick rhizome, ≤ 28 cm tall; foliage and peduncles green, lower surface of leaf blades commonly purple-tinged, glabrous except for papillate or puberulent summit of petioles and scattered small hairs on the upper surface of leaf blades; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest ≤ 99 × 145 mm, leaf blades during chasmogamous flower slightly longer than broad or as broad as long and deltate-triangular, apex acute to short-acuminate, during fruit becoming much broader than long, deltate-reniform, apex abruptly acute or obtuse, base truncate to shallowly cordate, margins crenate, eciliate; chasmogamous peduncle usually held above the leaves; chasmogamous flower ≤ 16 mm; calyx glabrous, eciliate; lowest sepals oblong-lanceolate to ovate-lanceolate, acute or acutish; auricles short and entire, not or scarcely elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with narrowly linear to slightly clavate hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle initially prostrate but arching just before

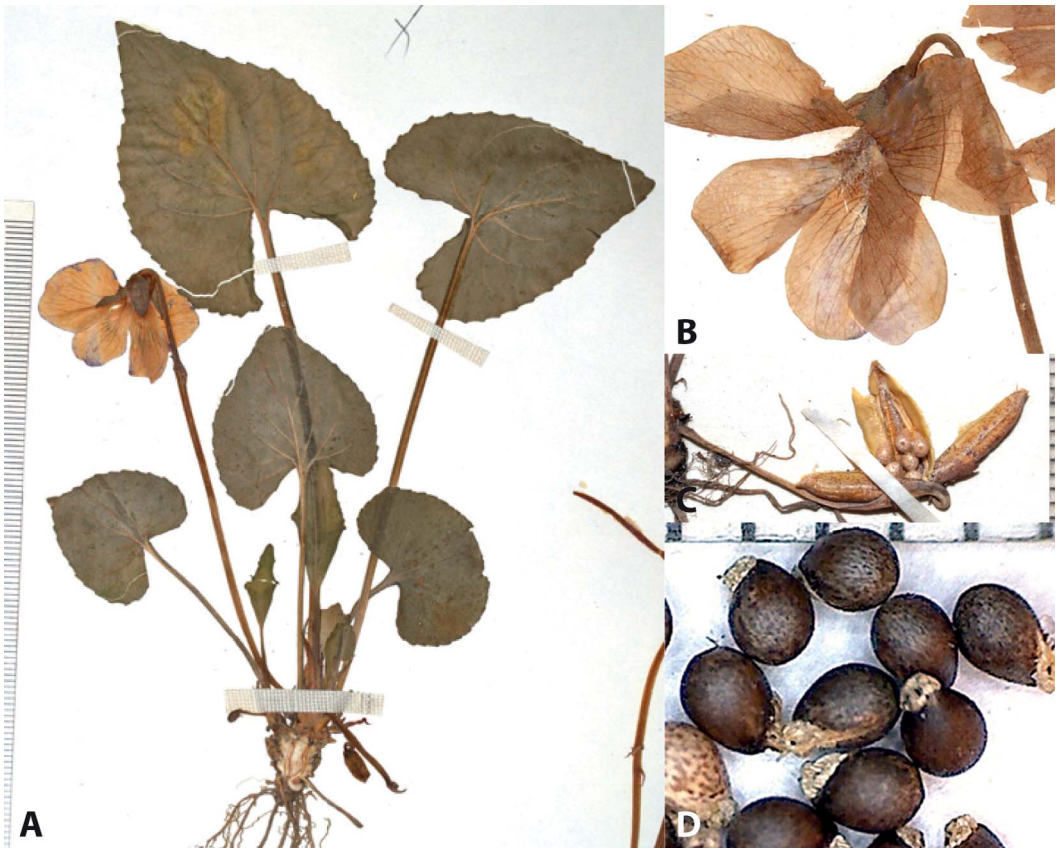

FIG. 72. *Viola latiuscula*. (A) Chasmogamous flowering habit from specimen: Vermont, Twin Mountains, *W. W. Eggleston 2648* (UVMVT083115, isolectotype of *Viola latiuscula*). (B) Chasmogamous flower front view from specimen: Vermont, Twin Mountains, *W. W. Eggleston 2648* (UVMVT083115, isolectotype of *Viola latiuscula*). (C) Cleistogamous fruits from herbarium specimen: Vermont, Fort Ethan Allen, *E. Brainerd 220* (NY). (D) Seeds (pale ones immature) from herbarium specimen: Transplanted from New York, Falconer, *E. Brainerd 76* (NY).

capsule dehiscence, much shorter than petioles; cleistogamous capsule 6–11 mm, yellow-green drying tan with usually weak purple spots or blotches, glabrous; seeds 1.3–2.0 × 1.1–1.3 mm, purplish-black, with very weak darker blotches, spots or streaks; 2n = 54.

Similar Species. This species is similar to a few *Borealiamericanae* taxa with glabrous foliage and leaves nearly as broad as to broader than long. In chasmogamous flower it differs from *V. communis*, *V. domestica*, *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) in its densely bearded spurred petal, from *V. nephrophylla* in its acute sepals, and from *V. pratincola* and *V. retusa* in its short rounded auricles. In cleistogamous fruit it is distinguished from other species by its broadly deltate-reniform leaf blades with truncate to subcordate base and obtuse to abruptly broadly acute apex; from *V. communis*, *V. domestica*, *V. pratincola*, and *V. retusa* in its spotted or blotched cleistogamous capsule on a short prostrate peduncle; from *V. affinis* and *V. missouriensis* by its purplish black seeds and additionally from the latter in its acute eciliate sepals; and from the *V. sororia* variants by its purplish-black weakly marked seeds.

Ecology. Dry sandy or gravelly soils of upland deciduous or mixed forests, and dry ledges.

Distribution. Northeastern endemic, Vermont to southeastern Ontario, south to Connecticut and New York; Henry's (1953a) Pennsylvania reports represent *V. hirsutula* and hybrids, and are excluded. Fig. 73.

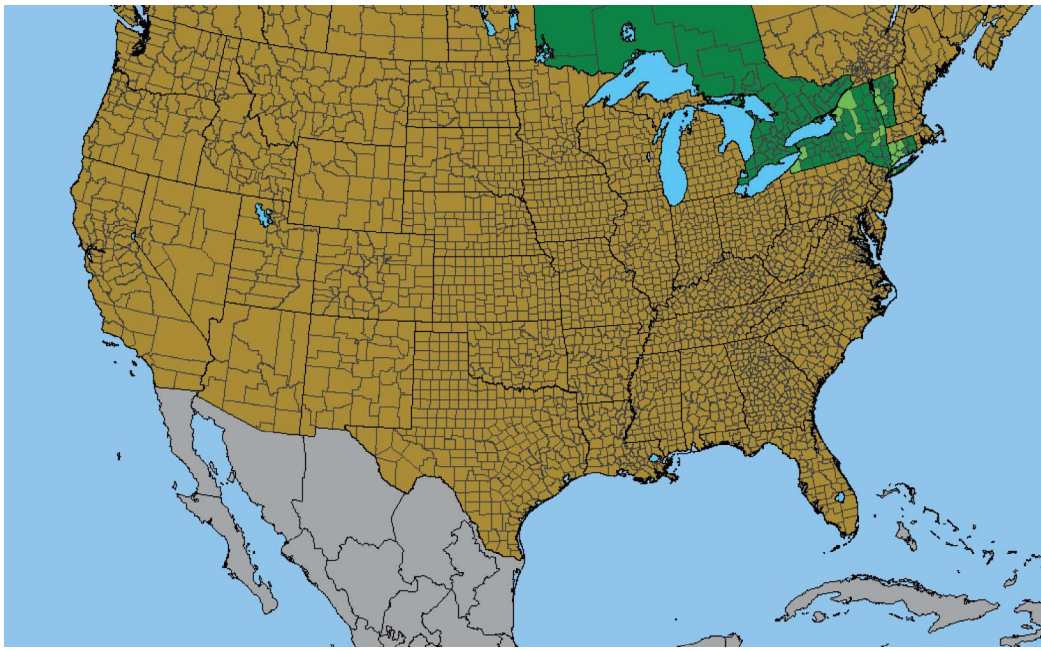

FIG. 73. United States county distribution of *Viola latiuscula* (map: Biota of North America Program).

Rarity. Listed in Vermont.

Phenology. Chasmogamous flower May–June, chasmogamous fruit June–July, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sororia species group.

Hybrids. Hybridizes with *V. fimbriatula* (Brainerd 1924; House 1924), *V. palmata* var. *triloba* (Brainerd 1912, 1924; House 1924), and *V. sororia sensu stricto* (Brainerd 1924, House 1924). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). Both hybrids fail to reproduce by chasmogamous flowers. The first hybrid reportedly produces very few viable cleistogamous seeds.

Comments. Greene provided explicit information in his protologue, stating "This very satisfactory new violet is from Twin Mountains, West Rutland, Vermont, and was collected May 24 and July 15 of 1902, by Mr. W.W. Eggleston, who writes that it grows in open shady well drained soil." Because he cited two separate collections, did not indicate which sheets may be types, and mentioned no herbarium, a lectotype needed to be designated. Several sheets are in the JSTOR Global Plants database, and sheets vary as to collection date and collector number. All specimens except NDG32742 include May 24 1902 and Jul 14 1902 on printed labels, while the NDG32742 sheet includes May 24 and July 15 1902 on its handwritten label. Furthermore, the NDG sheet has "*Viola latiuscula*, Greene, type" written in Greene's hand across the top of the label. McKinney incorrectly designated the May 1902 collection of NY00097537 as holotype. The three flowering plants from the May 24, 1902, collection (Eggleston 2648) on the NDG32742 sheet (denoted by "[a]") were selected by Ballard *et al*. (2020a) as the lectotype. Other May 24 specimens of Eggleston 2648 were treated as isolectotypes. The sterile or fruiting specimens collected on July 15, 1902, (Eggleston 2867) on the NDG32742 sheet (denoted by "[b]" are a syntype, while specimens with the July 14, 1902, collection date are considered original material.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), and Alexander (1963) accepted this species; Fernald included Virginia in its range, but his records from marl pits, rich woods, and brushy clearings in the Coastal Plain

counties of Dinwiddie, Greensville, and Sussex (Fernald 1941) do not match the habitats of the present species and the localities are well out of range for a northern montane species. Fernald's Virginia records are rejected here as probable hybrids of other species. Alexander included New Jersey, and these specimens need examination for confirmation. Scoggan (1978) mentioned specimens from three Ontario counties near Niagara Falls matching this species that need verification; however, one specimen examined from the Ontario side of the "Thousand Islands" region has been confirmed, establishing the species' presence in Canada. A number of specimens have also been confirmed on the New York State side to corroborate its occurrence in Ontario. Henry's (1953a) records from western Pennsylvania have been examined at CM; one specimen was typical *V. hirsutula* and the rest appeared to be hybrids involving that species with *V. cucullata* or *V. sororia* (glabrous variant). Gleason and Cronquist (1991), Ballard (2000), Weakley *et al*. (2012), and Little and McKinney (2015) included it in *V. sororia*; while McKinney (1992) and McKinney and Russell (2002) included it in *V. sororia* var. *sororia*. Haines *et al*. included it partly in *V. affinis* and partly in *V. sororia*. Russell (1965) made a mystifying and inaccurate reference to cut leaf blades and southern geographic distribution, indicating that he confused this with another taxon (perhaps *Viola chalcosperma* Brainerd, an endemic of the Jacksonville, FL, area), but he noted that the granular or pubescent petiole summit mentioned by Brainerd (1921) and Fernald (1950) was also present in occasional Appalachian specimens of *V. affinis*, and he excluded the taxon. Gil-ad (1995, 1997) was unable to study mature seeds but enumerated the features given by others, including Greene, and dismissed the taxon due to the lack of unique "suite of characters" and postulated that it is likely a hybrid involving *V. sororia*, and *V. affinis* or *V. cucullata*. Examination of type material and quite a few other herbarium specimens matching the description has confirmed a consistent suite of diagnostic features: densely bearded spurred petal, essentially glabrous foliage with granular or puberulent petiole summit, frequent small scattered subappressed hairs on the upper surface of the leaf blades, short and very broadly deltate-reniform summer leaf blades with a shallowly cordate to subtruncate base and obtuse or (more commonly) abruptly acute apex, a common purple tinge on the lower surface of the leaf blades, ovate-lanceolate to ovate broadly acute to obtuse lowest sepals, and purple-black seeds with very weak darker blotches, streaks, or spots, often with a relatively long thick caruncle. The first largest leaf blade during chasmogamous flower is often somewhat longer than broad, while all subsequent leaf blades are broadly ovate, broadening in fruit to a distinctive and remarkably short broad deltate-reniform outline with shallowly cordate to truncate base and obtuse to abruptly acute apex. This violet also expresses a preference for dry sandy woodland soils and dry ledges that is quite divergent from other species in the region. It is accepted here as a distinct species which expresses a unique suite of morphological traits and a xeric woodland niche. Russell's specimens of "otherwise *affinis*" in the Appalachian Mountains deserve scrutiny to determine whether he misidentified additional specimens of this species. This narrow regional endemic is rather poorly understood.

30. ***Viola minuscula*** Greene, Leafl. Bot. Observ. 1(4): 247. 1906. Type: unknown. Fig. 74.

Viola pallens (Banks ex Ging.) Brainerd f. *alba* L.R.Perkins, Rhodora 11: 164. 1909.

Viola domingensis Urb., Symb. Ant. 7: 287. 1912.

Viola pallens (Banks ex Ging.) Brainerd var. *subreptans* J.Rousseau, Naturaliste Canad. 65: 306. 1938.

Viola pallens auct.

Common Names. Northern white violet, smooth white violet.

Description. Acaulescent stoloniferous perennials from slender rhizome, colonial from surficial stolons produced in summer, stolons bearing multiple nodes each with a leaf and cleistogamous capsule, $\leq$ 20 cm tall; foliage and peduncles green, lower surface of leaf blade paler than upper (occasionally drying red- or orange-tinged), glabrous or petioles hirsute; stipules free, finely glandular-fimbriate; leaves spreading, leaf blades undivided, largest $\leq$ 73 $\times$ 56 mm, narrowly to broadly ovate, deltate-ovate, suborbiculate or subreniform (very rarely reniform), base shallowly to deeply cordate, lobes roughly parallel to divergent, margins crenate, eciliate, apex abruptly apiculate, obtuse or rounded; chasmogamous peduncle held among or above the leaves;

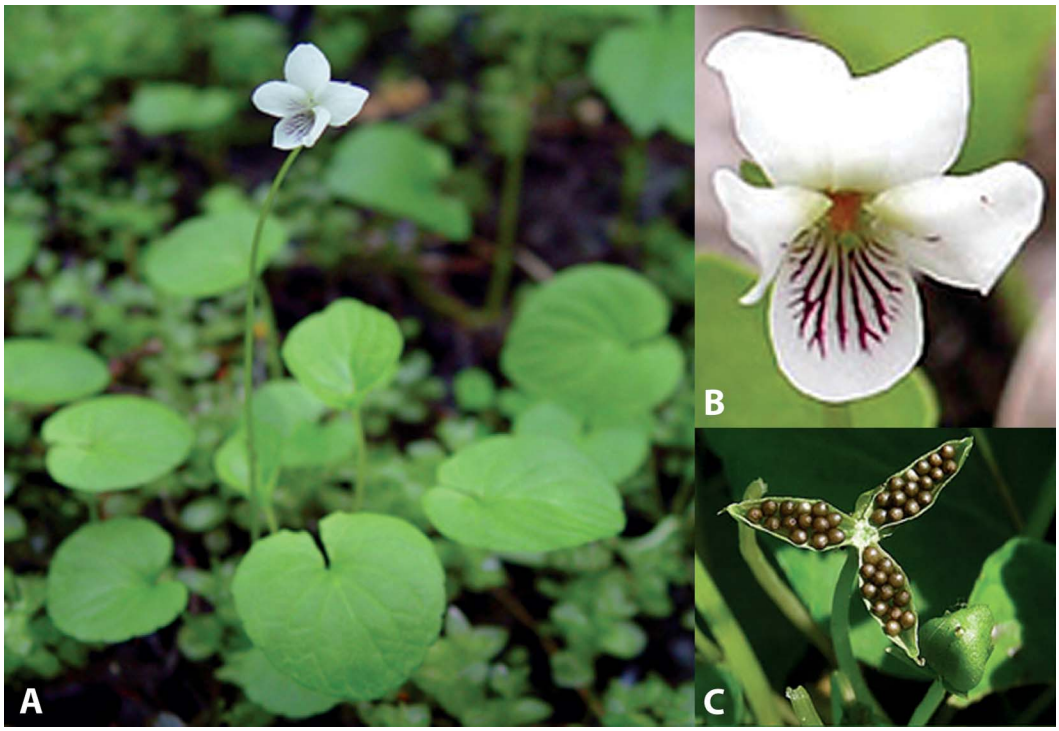

FIG. 74. *Viola minuscula*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower front view (photo: Peter M. Dziuk). (C) Cleistogamous fruit (photo: Peter M. Dziuk).

chasmogamous flower $\leq$ 12 mm; calyx glabrous, eciliate; lowest sepals lanceolate to ovate-lanceolate, obtuse to rounded (rarely acute); auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; all petals glabrous (lateral petals occasionally with sparse beard of narrowly linear hairs); cleistogamous flowers produced after chasmogamous, on ascending or erect peduncle shorter than or surpassing petioles; capsule 6–7.5 mm, green drying tan, unspotted or with fine red spots, glabrous; seeds 0.8–1.4 $\times$ 0.7–0.8 mm, medium to dark olive-brown or brownish-black, with fine black spots; 2n = 24.

Similar Species. This species is most similar to other *Stolonosae* violets with leaf blades nearly as broad as to broader than long. It is distinguishable at any time from *V. renifolia* by its horizontal stoloniform rhizomes and leafy summer stolons and ascending suborbiculate to narrowly ovate glabrous leaf blades, and from *V. palustris* and *V. suecica* in its noncreeping rhizome, the leaves terminating the rhizome in a discrete rosette. Its glabrous leaf blades (occasionally with hirtellous petioles) and subentire to very shallowly crenate margins, unspotted cleistogamous capsule on an erect peduncle, and small dark brown to blackish seeds distinguish it from *V. blanda* and *V. incognita*.

Ecology. Saturated peaty, mucky, or sphagnous substrates in vernal pools, alder swamps, sedge meadows, seepage areas, fens, and bogs (often well out on the bog mat), and marshy edges of streams, rivers, and lakeshores.

Distribution. Transcontinental, Newfoundland and Labrador to Northwest Territories, south to northwestern Georgia, Tennessee, and Iowa, southwestern South Dakota, and Rocky Mountains; Dominican Republic (western North American records require further study to determine whether they represent this taxon). Fig. 75.

Rarity. Listed in Delaware (as *Viola macloskeyi* F.E.Lloyd var. *pallens*), Iowa (as *V. macloskeyi*), and Missouri (as *V. pallens*).

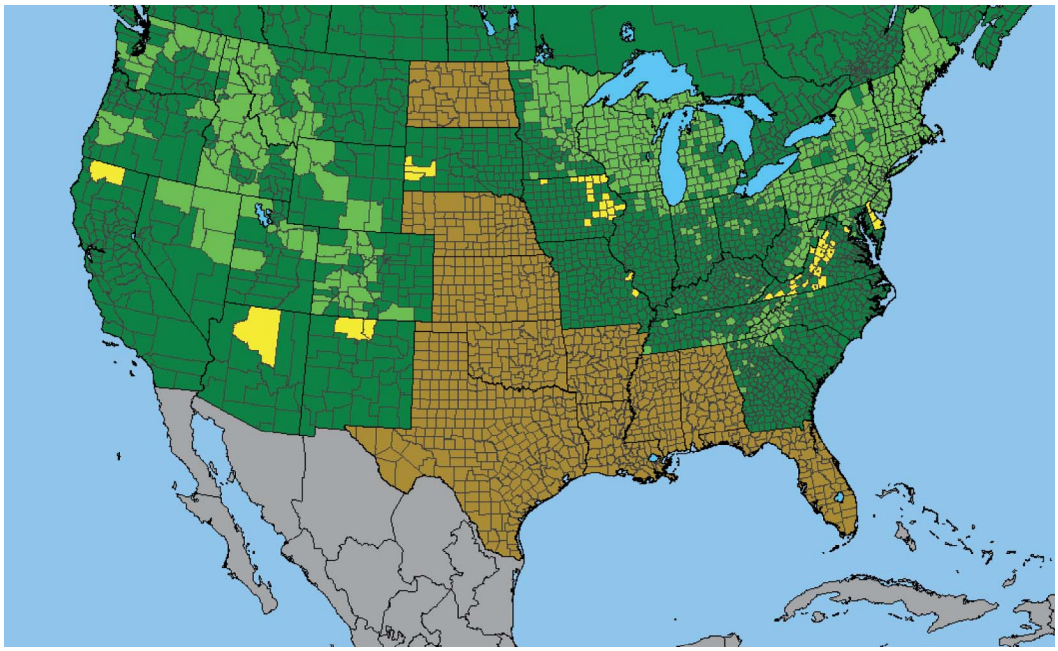

FIG. 75. United States county distribution of *Viola minuscula* (map: Biota of North America Program).

Phenology. Chasmogamous flower April–July, chasmogamous fruit May, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. incognita* (Scoggan 1978; Ballard 1995), *V. lanceolata* (Brainerd 1924; Russell 1954a, 1955c; Boivin 1966; Cinq-Mars 1966; Ballard 1995), *V. macloskeyi* (Russell 1955c), *V. primulifolia* (Dowell 1910; Brainerd 1924; House 1924; Russell 1955c; H.E.B., personal observation), and *V. renifolia* (Brouillet et al. 2022). The first author has observed specimens of the hybrids involving *V. lanceolata* and *V. primulifolia* and found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. All hybrids will fail to reproduce by chasmogamous flowers. The interploidal hybrid will likely produce abortive cleistogamous capsules, while the latter two hybrids may produce abortive cleistogamous capsules or normal capsules without viable seeds or a substantially reduced proportion of viable seeds. Studies are needed to confirm these predictions.

Comments. Greene reported in his protologue that "This interesting violet has been sent me from western New York, Chatauqua County, by Mr. William B. Limberger, with full notes of its habitat, and characteristics as differing from *V. blanda*." The protologue suggests one collection but makes no mention of a herbarium. No specimens have been found thus far in a physical search of NDG by the first author or Barbara Hellenthal, nor have types been located in the JSTOR Global Plants database or in searches of various online regional databases. However, Diane Hurlbut at NYS found a specimen postdating the publication of the name: New York, Randolph, W. B. Limberger, May 1907. (William Limberger lived in Ithaca area of New York and botanized in that region, and some of his collections were deposited at NYS.) The Limberger sheet is *V. minuscula* and could serve as a neotype if no earlier original material can be located.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Haines *et al*. (2011), and Ballard (2013) accepted this as a species, *V. pallens* (Banks ex Ging.) Brainerd, distinct from the far western *V. macloskeyi* Lloyd. Russell (1955c), Russell (1965), and Ballard (1995, 2000) treated it as a subspecies of *V. macloskeyi*, while Scoggan (1978), Gleason and Cronquist (1991), and Weakley *et al*. (2012)

treated it as a variety. Voss and Reznicek (2012) accepted it as *V. macloskeyi* but noted it represented subspecies or variety *pallens*. McKinney and Russell (2002) and Little and McKinney (2015) synonymized it under *V. macloskeyi* without recognition of infraspecific taxa. Phylogenetic investigations by Marcussen *et al*. (2012) placed *V. macloskeyi* into a "western" clade separate from the present taxon, indicating that the two must be treated as separate species. Recent scrutiny of the lectotype of *V. rotundifolia* Michx. var. *pallens* Banks ex Ging. disclosed the creeping rhizomes with separate leaf insertions and broadly reniform leaf blades characteristic of *V. palustris* (an annotation by Wilhelm Becker mistakenly calling it *Viola epipsila* Ledeb. subsp. *repens*), removing the name from consideration. The next available name, *V. minuscula* Greene, with original material and protologue description precisely matching this taxon, is used here. Western North American populations are tentatively included here but are not typical and require reexamination. Ballard *et al*. (2001) demonstrated that Dominican Republic specimens, formerly treated as *V. domingensis* Urban, are morphologically indistinguishable from the present species (then called *V. macloskeyi* subsp. *pallens*) and thus evidently represent an early Antillean dispersal event from eastern North America. Although frequently confused with *V. blanda* and *V. incognita* with which it occasionally grows, it is easily distinguished from those species in chasmogamous flower by its glabrous suborbiculate to ovate leaf blades (although the petioles are often hirtellous) with very shallow marginal crenations and its glabrous or very sparsely bearded lateral petals, and in cleistogamous fruit by its green unspotted cleistogamous capsules on erect peduncles and its smaller olive-brown finely spotted seeds.

31. ***Viola missouriensis*** Greene, Pittonia 4: 141. 1900; *Viola sororia* Willd. var. *missouriensis* (Greene) L.E.McKinney, Sida, Bot. Misc. 7: 42. 1992. Type: USA Missouri. [Jackson Co.], Courtney, Common in sandy bottoms, Flowers white, 30 Apr 1899, *B. F. Bush 70* (lectotype (designated incorrectly as holotype by Landon McKinney, Sida, Bot. Misc. 7: 42. 1992; corrected by Nir Gilad, Boissiera 53: 63. 1997): NY00029621; isolectotypes: NY00029619, NDG33214B (*n.v.*), internet image, MO-1889077). Fig. 76.

Viola illinoensis Greene, Pittonia 4: 293. 1901.

Viola securigera Greene, Pittonia 5: 29. 1902.

Viola candidula Nieuwl., Amer. Midl. Naturalist 3: 85, pl. 2, 3. 1913.

Viola lucidifolia Newbro, Stud. Nat. Hist. Iowa Univ. 17: 56, pl. 4, fig. 3, pl. 8, figs. 24–25. 1936.

Common Name. Missouri violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 40 cm tall; foliage and peduncles green, glabrous throughout; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest $\leq 78 \times 64$ mm, in spring distinctly longer than broad and triangular-acuminate to deltate-ovate or narrowly ovate-triangular, in summer broadening to about as broad as long or broader and deltate- or ovate-triangular, base subcordate to shallowly cordate, margins serrate in basal 2/3, subentire or low-serrate and more remote near apex, eciliate, apex sharply acute to acuminate; chasmogamous peduncle often overtopping leaves; chasmogamous flower $\leq$ 21 mm; calyx glabrous, ciliolate; lowest sepals oblong to ovate-lanceolate, gradually convexly or abruptly tapering to a narrowly obtuse to rounded apex; auricles short and entire, weakly elongating to 2 mm in fruit; corolla violet, area around throat white often with a slightly darker flush surrounding it, throat white; spur short-globose; lateral petals densely bearded with hairs narrowly linear or slightly to distinctly broadened apically, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate or flexuous peduncles arching upward just before capsule dehiscence, shorter than petioles; cleistogamous capsule 7–12 mm, green drying to tan with purple spots or blotches, glabrous; seeds 1.5–2.2 $\times$ 1.0–1.3 mm, medium orange-brown, unspotted or more commonly with small weak darker streaks, blotches, and spots.

Similar Species. Generally, this will be most similar to other *Borealiamericanae* with strictly or essentially glabrous foliage and narrowly ovate-triangular leaf blades in spring that broaden substantially in summer but will differ most obviously in its glabrous leaf blades with the apical portion somewhat attenuate and subentire or with remote very low teeth, and narrowly rounded and usually ciliolate sepals. In chasmogamous flower, this species can be distinguished from *V. affinis* additionally by its glabrous spurred petal; from *V. cucullata* by its short rounded auricles, lack of a conspicuously contrasting dark purple

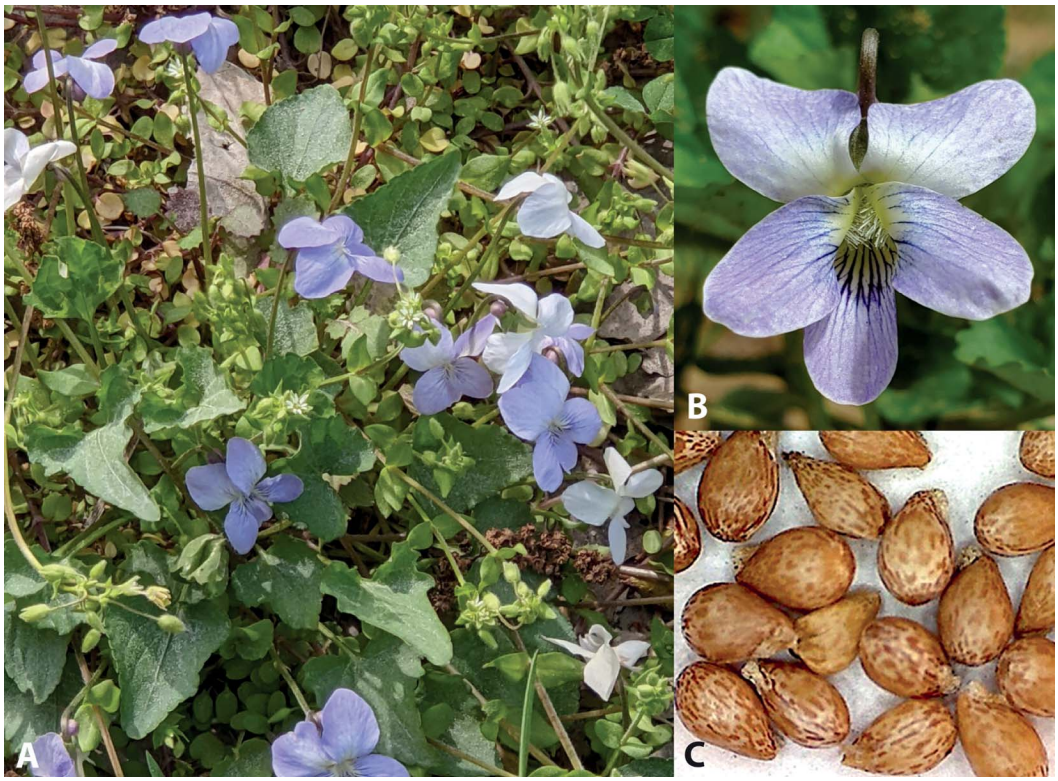

FIG. 76. *Viola missouriensis*. (A) Chasmogamous flowering habit (photo: Alexis Miller). (B) Chasmogamous flower (photo: Angelique McPhail). (C) Seeds from herbarium specimen: Oklahoma, near Fort Gibson, *E. Brainerd 82* (NY).

eyespot around the throat, and lateral petal beards with long narrowly linear to weakly clavate hairs; from *V. langloisii* (just south of our region) by its strongly ascending to erect leaves, and short rounded auricles; and from *V. pratincola* and *V. retusa* by its short rounded auricles. In cleistogamous fruit, it can be separated from *V. communis*, *V. cucullata*, *V. pratincola*, and *V. retusa* by its heavily spotted or blotched cleistogamous capsule on a prostrate peduncle, and orange-brown unspotted or weakly marked seeds; from *V. langloisii* by its prostrate capsule peduncle and rounded ciliolate sepals; and from *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) by its ciliolate sepals and orange-brown unspotted seeds.

Ecology. Sandy soils of bottomland forests along streams, rivers, and lakeshores.

Distribution. Western Midwest, Lower Midwest, and Great Plains, Indiana to Minnesota, south to Louisiana, Texas, and northeastern New Mexico (Gulf Coast records are currently being disentangled from *V. langloisii*). Fig. 77.

Rarity. None.

Phenology. Chasmogamous flower April–June (October–November), chasmogamous fruit May–July, cleistogamous fruit May–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Affinis species group.

Hybrids. Hybridizes with *V. pedatifida* (Ballard 2013), *V. sororia sensu stricto* (Brainerd 1924), and *V. viarum* (Russell 1965; Ballard 2013). Hybrids with other species are possible and should be sought. Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). Brainerd reported that the hybrid with *V. sororia* failed to reproduce by chasmogamous flowers and

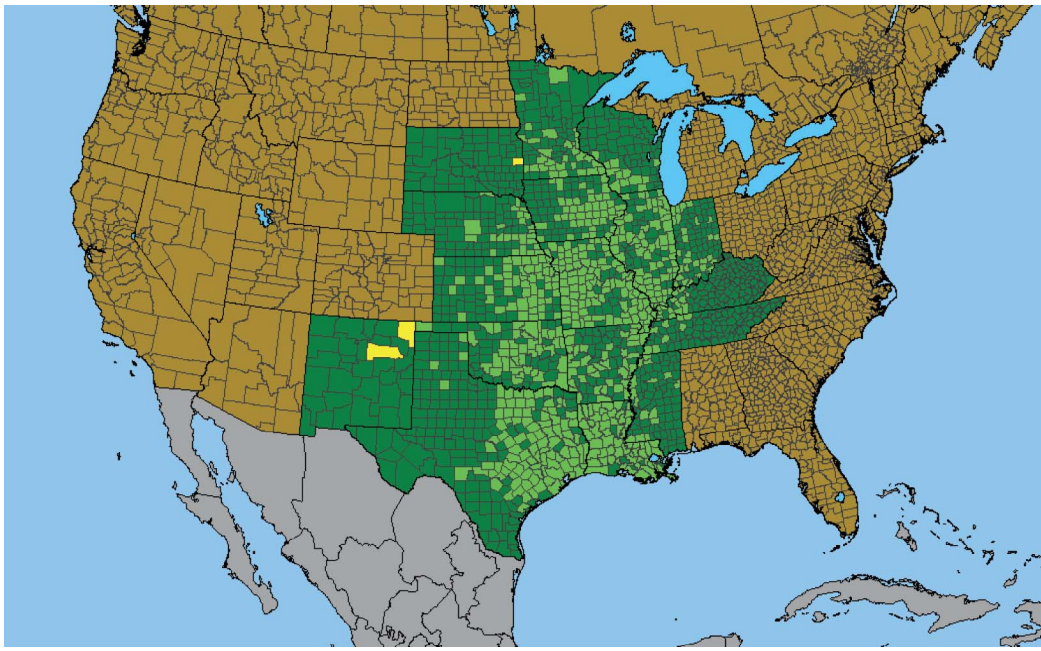

FIG. 77. United States county distribution of *Viola missouriensis* (map: Biota of North America Program).

cleistogamous capsules contained only a few viable seeds. Studies are needed on the reproductive behavior of the other hybrids.

Comments. This species was accepted by Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), Swink and Wilhelm (1979), Gil-ad (1995, 1997, 1998), and Ballard (2013). Gleason and Cronquist (1991) submerged it in *V. sororia*. McKinney (1992) and McKinney and Russell (2002) maintained it as a variety under *V. sororia* while Little and McKinney (2015) reinstated it as a species. Gil-ad and Little and McKinney suggested that southern *V. langloisii* Greene was conspecific with the present species and included it; however, they were evidently unaware of several differences exhibited by *V. langloisii*, including an eciliate calyx, linear-lanceolate acuminate sepals, prominent auricles weakly elongating in fruit, and green unspotted cleistogamous capsules on declined peduncles. Russell (1958a) studied the morphology and ecology of this species. The present species is readily separated from *V. affinis*, with which it is most often confused, by its glabrous foliage, glabrous spurred petal, ciliolate calyx, and obtuse to (narrowly) rounded sepal apices. See *V. affinis* for further comments on distinctions, ecological differences, and morphological integrity in the region of sympatry. Russell (1958a) presented evidence clarifying the taxonomic distinctions of this species. Unfortunately, rampant misidentification of specimens of *V. affinis, V. langloisii*, and *V. langloisii* and other taxa, as well as frequent synonymization of some or all of these taxa, have led to difficulties in interpreting reliable distributions. We are presently separating the three species in the southeastern states, and that portion of the range map should be regarded as very tentative. This and other members of the Affinis species group are currently under study by Remington Burwell at Ohio University.

32. ***Viola monacanora*** J.L.Hastings & H.E.Ballard**, sp. nov.**

Type. **USA**. Virginia. Augusta Co., Immediately WNW of Dripping Rock pull off at Laurel Springs Gap, north of Blue Ridge Parkway, just off BRP land on USFS land, ca. 2.6 air miles SSE of the berg of Sherando; field collected on 4 Aug 2018, cultivated in OU violet garden until 1 Sep 2018, 37.94305°, 78.93967°, Rich mesic forest dominated by red oak, gentle slope, heavy leaf litter, soil rich moist loam with much organic matter, sparse but somewhat diverse understory with Sanguinaria and Stellaria, etc., also several *Viola hirsutula* and apparent hybrids. Scattered plants and small

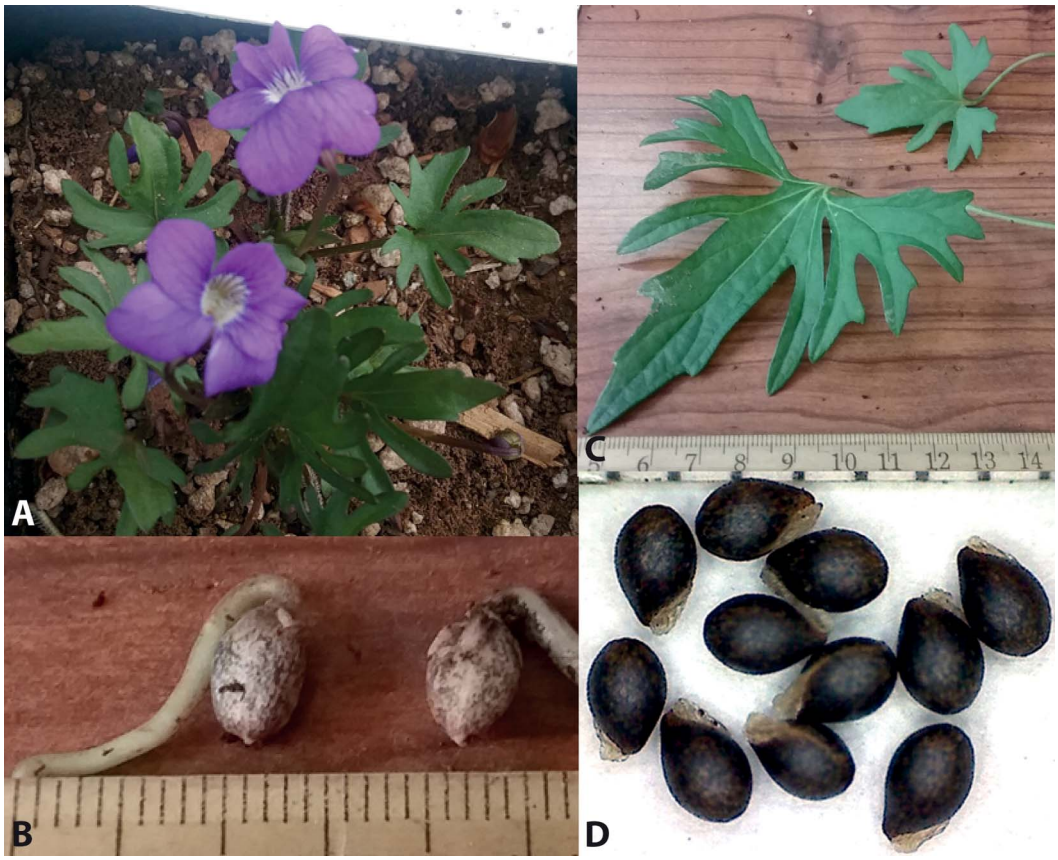

FIG. 78. *Viola monacanora*. (A) Chasmogamous flowering habit (photo: Harvey Ballard). (B) Leaves during cleistogamous fruit (photo: Jennifer Hastings). (C) Cleistogamous fruits (photo: Jennifer Hastings). (D) Seeds from herbarium specimen: Transplanted from Virginia, Blue Ridge Mountains, south of Afton, 13 Aug 2014, *H. Ballard & A. Stuart s.n*. (BHO).

colonies, far less common than hybrids involving locally glabrous *V. sororia*, some with small developing cleistogamous fruits, voucher for DNA 738, 1 Sep 2018, *H. E. Ballard & A. P. Stuart 18-023* (holotype: VPI; isotypes: MO, NCU, NY). Fig. 78.

Diagnosis. This new species of homophyllous cut-leaved violet shares deeply biternately divided leaf blades with *V. baxteri*, *V. brittoniana*, *V. pedatifida*, and *V. subsinuata*. It is most similar to *V. baxteri* and *V. subsinuata*, two other members of the Subsinuata species group in subsect. *Borealia-mericanae*, in its glabrous spurred petal and purple-spotted cleistogamous capsule produced on an initially prostrate peduncle. However, it diverges from both in its glabrous or essentially glabrous foliage, falcate and sharply asymmetrically angulate lobes, eciliate lance- to ovate-triangular acute or acuminate sepals, blackish seeds with minute raised black reticulations, and restriction to rocky woodlands in the Blue Ridge Mountain range.

Common Name. Blue Ridge violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 20 cm tall; foliage and peduncles dark green; petioles, lower surface of leaf blades and peduncles purple-tinged, glabrous (petioles rarely sparsely hirsute, possibly the result of hybridization with ubiquitous *V. sororia*); stipules free, irregularly glandular-fimbriate; homophyllous, leaves ascending, smallest leaf blades palmatifid, largest palmatifid to subbiternate, in fruit becoming deeply biternately divided into 9–11(13) usually falcate linear or linear-lanceolate apically asymmetrically angulate lobes, $\leq 60 \times 55$ mm, outline narrowly ovate-triangular during

chasmogamous flower but broadening to ovate-triangular in fruit, base cordate, margins of ultimate lobes entire or sporadically appressed-crenate, eciliate, apex acute to obtuse; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 22 mm; calyx glabrous, eciliate; lowest sepals lance- to ovate-triangular, acute or acuminate; auricles short and entire, not elongating in fruit or scarcely so to 1 mm; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle prostrate but arching just before dehiscence, shorter than petioles; cleistogamous capsule 5–8 mm, green drying tan or purple-tinged with purple blotches, glabrous; seeds 1.8–2.1 $\times$ 1.2–1.4 mm, blackish with minute raised black reticulations.

Paratypes. **USA**. North Carolina. Wilkes Co., 4 miles east of Moravian Falls, Mixed deciduous forest, 13 May 1956, *A. E. Radford 11231* (NCU). Virginia. Augusta Co., Blue Ridge Parkway, Near ShenandoaFh Valley pulloff on Blue Ridge Parkway, go across street (E) from pulloff and violets are close to road on a slight slope, 38.004472°, –78.887583°, Wooded area, lots of canopy coverage especially *Carya* and *Quercus*, very dense surrounding vegetation, Elev. 727m, Violets very abundant, hybrids with *V. sororia* present, leaves deeply dissected with many lobes, chasmogamous flowers and fruits on the same individuals, 11 May 2017, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-005* (VPI). Blue Ridge Parkway, Near Humpback Rocks Visitor Center and picnic area, approx. 0.25 miles N of Visitor Center, on left (W) side of road, close to road, 37.97575°, –78.901361°, Flat site with some vegetation, wooded area with lots of canopy cover and high litter depth, lots of *Liriodendron*, Elev. 722m, Small population, small range, hybrids with *V. sororia* present, 11 May 2017, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-006* (VPI). Below The Priest Overlook along the Blue Ridge Parkway, between White Rock and Love, 37.89138°, –79.03226°, Dry-mesic forest, in rocky sandy loam, Elev. 808m, Very few, scattered, mostly hybrids with *V. sororia* and *V. palmata* (few pure plants), 13 Oct 2019, *H. E. Ballard & A. P. Stuart 19-009* (VPI). Near Appalachian Trail N of Blue Ridge Parkway and W of Laurel Springs Gap, upslope from the Trail, Rich mesic forest, Scattered in small colonies, 3 Jul 2021, *H. E. Ballard & R. Cook 21-015* (NY, VPI). Bedford Co., Peaks of Otter, E of Peaks of Otter Lake, go 0.75 miles E from Blue Ridge Parkway on Peaks Road, turn left onto road to Fallingwater-Flat Top Trail Head, continue N & NW approx. 0.25mi, population is beyond picnic area on NE side of road, 37.444278°, –79.600083°, Open, vegetated area with some trees, near a river, lots of *Betula*, Elev. 745m, Abundant population, large plants with many leaves, leaves deeply dissected, presence of cleistogamous buds, 25 May 2017, *J. L. Hastings & A. C. Pidock 17-038* (VPI). Peaks of Otter, E of Peaks of Otter Lake, go 0.75 miles E from Blue Ridge Parkway on Peaks Road, turn left onto road to Fallingwater-Flat Top Trail Head, continue N & NW approx. 0.25mi, population is beyond picnic area on NE side of road, 37.444278°, –79.600083°, Open, vegetated area with some trees, near a river, lots of *Betula*, Elev. 745m, collected 25 May 2017 as part of 17-038, cultivated in OU violet garden until 11 Jul 2018, *J. L. Hastings & A. C. Pidock 17-0381G1* (VPI). Peaks of Otter, E of Peaks of Otter Lake, go 0.75 miles E from Blue Ridge Parkway on Peaks Road, turn left onto road to Fallingwater-Flat Top Trail Head, continue N & NW approx. 0.25mi, population is beyond picnic area on NE side of road, 37.444278°, –79.600083°, Open, vegetated area with some trees, near a river, lots of *Betula*, Elev. 745m, collected 25 May 2017 as part of 17-038, cultivated in OU violet garden until 4 Jul 2018, *J. L. Hastings & A. C. Pidock 17-0381G2* (NY). Peaks of Otter, E of Peaks of Otter Lake, go 0.75 miles E from Blue Ridge Parkway on Peaks Road, turn left onto road to Fallingwater-Flat Top Trail Head, continue N & NW approx. 0.25mi, population is beyond picnic area on NE side of road, 37.444278°, –79.600083°, Open, vegetated area with some trees, near a river, lots of *Betula*, Elev. 745m, collected 25 May 2017 as part of 17-038, cultivated in OU violet garden until 25 Jun 2018, *J. L. Hastings & A. C. Pidock 17-0381G2* (NCU). Floyd Co., Buffalo Mountain State Nature Preserve, base of mountain, 36.777769°, –80.481461°, Closed canopy mesic forest, along old logging road, 13 Aug 2014, *H. E. Ballard & A. P. Stuart s.n*. (NY, VPI). Blue Ridge Parkway, In Rocky Knob Recreation Area, approx. 0.5 mile S of Saddle Overlook, approx. 40m W of Blue Ridge Parkway, 36.815611°, –80.345833°, On a gentle slope with lots of leaf litter, seems to grow more

often in grassy patches, Elev. 984m, Abundant population, large leaves deeply dissected, small leaves shallowly lobed, chasmogamous capsules present, light green, 19 May 2017, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-027* (VPI). Blue Ridge Parkway, In Rocky Knob Recreation Area, approx. 0.5 mile S of Saddle Overlook, approx. 40m W of Blue Ridge Parkway, 36.815611°, –80.345833°, On a gentle slope with lots of leaf litter, seems to grow more often in grassy patches, Elev. 984m, collected 19 May 2017 as part of 17-027, cultivated in OU violet garden until 4 Jul 2018, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-027G1* (VPI). Blue Ridge Parkway, In the Rocky Knob Recreation Area, approx. 1mi S of Saddle Overlook, W side of Blue Ridge Parkway across road from Rocky Knob Pulloff, approx. 100m SW of Rocky Knob Visitor Center lot, 36.810583°, –80.351417°, Flat, densely vegetated, forest, individuals found in grassy areas, lots of *Microstegium*, Elev. 996m, Population scattered over a large area, deeply dissected leaves, some individuals have chasmogamous capsules, some plants have cleistogamous capsules, 26 May 2017, *J. L. Hastings & A. C. Pidock 17-039* (VPI). Blue Ridge Parkway, In the Rocky Knob Recreation Area, approx. 1mi S of Saddle Overlook, W side of Blue Ridge Parkway across road from Rocky Knob Pulloff, approx. 100m SW of Rocky Knob Visitor Center lot, 36.810583°, –80.351417°, Flat, densely vegetated, forest, individuals found in grassy areas, lots of *Microstegium*, Elev. 996m, collected 26 May 2017 as part of 17-039, cultivated in OU violet garden until 25 Jun 2018, *J. L. Hastings & A. C. Pidock 17-039G1* (VPI). Blue Ridge Parkway, In the Rocky Knob Recreation Area, approx. 0.5 mile E of Rocky Knob Campground, approx. 30m N of Blue Ridge Parkway, by a fence, 36.831167°, –80.329972°, Gentle slope, grows frequently in clumps of grass, lots of *Acer rubrum*, Elev. 877m, Large population, leaves deeply dissected, many leaves (4-7) per plant, some individuals have chasmogamous capsules, others have cleistogamous capsules, 19 May 2017 *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-028* (NY, VPI). Blue Ridge Parkway, In the Rocky Knob Recreation Area, approx. 0.5 mile E of Rocky Knob Campground, approx. 30m N of Blue Ridge Parkway, by a fence, 36.831167°, –80.329972°, Gentle slope, grows frequently in clumps of grass, lots of *Acer rubrum*, Elev. 877m, collected 19 May 2017 as part of 17-028, cultivated in OU violet garden until 4 Jul 2018, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-028G1* (VPI). Nelson Co., along Blue Ridge Parkway at Alton [sic! –Afton], 2 Jul 1953, *W. E. Buker 15769* (holotype: CM215697). Page Co., Elk Wallow Shelter [=Elkwallow Wayside], along path in somewhat disturbed ground, Mixed deciduous forest, with some pine and hemlock, rare, 7 Jun 1964, *F. R. Fosberg 45478* (US2727672). Stony Man Mountain and vicinity in the Blue Ridge, near Luray, Alt. 3400, 26 Aug 1901, *E. S. Steele 106* (MO3454662). Patrick Co., Blue ridge Mts. At highway #8 near Stuart, [no date], *P. M. Patterson s.n*. (VPI). Rockbridge Co., Blue Ridge Parkway, Approx. 1 mile west of Greenstone Overlook on Blue Ridge Parkway, on N side of road, about 50m away from road, 37.942722°, –78.939861°, Densely vegetated area on a gentle slope, many rocks present, lots of *V. sororia* and *Quercus rubra*, Elev. 915m, Small population, not many individuals, individuals appear to be hybrids with *V. sororia*, 11 May 2017, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-007* (VPI). Blue Ridge Parkway, Approx. 1 mile west of Greenstone Overlook on Blue Ridge Parkway, on N side of road, about 50m away from road, 37.942722°, –78.939861°, Densely vegetated area on a gentle slope, many rocks present, lots of *V. sororia* and *Quercus rubra*, Elev. 915m, Small population, not many individuals, individuals appear to be hybrids with *V. sororia*, collected 11 May 2017 as part of 17-007, cultivated in OU violet garden until 15 Jun 2018, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-007G2* (NY). Blue Ridge Parkway, Approx. 1 mile west of Greenstone Overlook on Blue Ridge Parkway, on N side of road, about 50m away from road, 37.942722°, –78.939861°, Densely vegetated area on a gentle slope, many rocks present, lots of *V. sororia* and *Quercus rubra*, Elev. 915m, Small population, not many individuals, individuals appear to be hybrids with *V. sororia*, collected 11 May 2017 as part of 17-007, cultivated in OU violet garden until 11 July 2018, *J. L. Hastings, H. E. Ballard, B. Sitepu & T. Singh 17-007G1* (VPI). Warren Co., Shenandoah Nat'l Park, Dicky Ridge Trail 4 mi. south of Front Royal Tollgate, 9 Jun 1954, *L. K. Henry s.n*. (CM215698).

Similar Species. This species is most similar to *V. baxteri* and *V. subsinuata* (see "Diagnosis," above, for details).

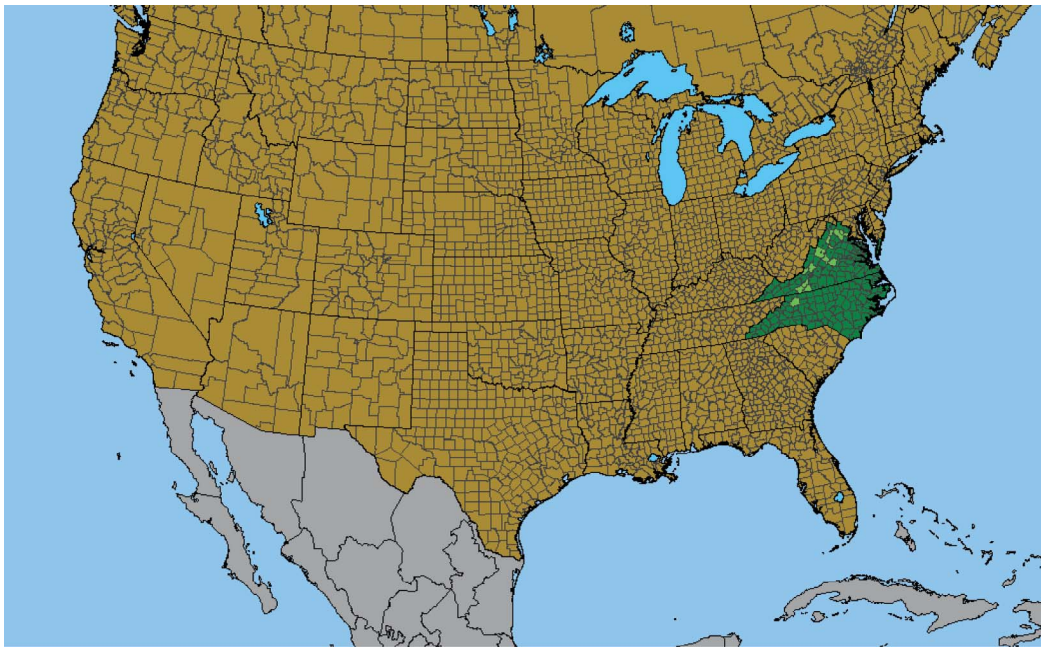

FIG. 79. United States county distribution of *Viola monacanora* (map: Biota of North America Program).

Ecology. Moist rocky loam soils in rich mesic forests at higher elevations of the Appalachian Mountains.

Distribution. Endemic to the Blue Ridge Mountain range, Virginia south to northwestern North Carolina. Fig. 79.

Rarity. None.

Phenology. Chasmogamous flower April–May, chasmogamous fruit May–June, cleistogamous fruit July–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Subsinuata species group.

Hybrids. Hybridizes with *V. sororia sensu stricto* (Hastings 2018; H.E.B., personal observation). No information is available on reproductive behavior of the hybrid.

Comments. The specific epithet of this distinctive violet honors the hardy peoples of the Monacan First Nation, who relatively recently received federal recognition after a decades-long battle, and who have lived for millenia around the northern portion of the Blue Ridge Mountain range where this violet was first determined as a new species. As with *V. baxteri* House, this violet was included in a broadly delimited *V. palmata* by Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), Scoggan (1978), and Strausbaugh (1978); the complex was later called *V. subsinuata* by McKinney (1992), Ballard (2000), Weakley *et al*. (2012), and Little and McKinney (2015). Gil-ad (1995, 1997, 1998) dismissed the assemblage as a series of hybrid derivatives (for more information see "Comments" under *V. baxteri* and *V. subsinuata*). Jennifer Hastings (2018) completed her taxonomic thesis research on this and other cut-leaved violets in the Subsinuata species group (plus *V. palmata*) in Virginia, presenting evidence for the recognition of this newly segregated evolutionary species. It was initially detected from two herbarium specimens, the holotype from Virginia and a specimen from North Carolina (Wilkes Co., 4 miles east of Moravian Falls, 13 May 1956, *A. E. Radford 11231*, NCU). Searches near the collection area of the Virginia specimen and points southward to near the North Carolina border revealed it to be relatively common in moist rocky loam soils of rich mesic forests, especially along the Blue Ridge Parkway. Additional herbarium collections were later found from scattered localities in the Shenandoah National Park. It is distinct from

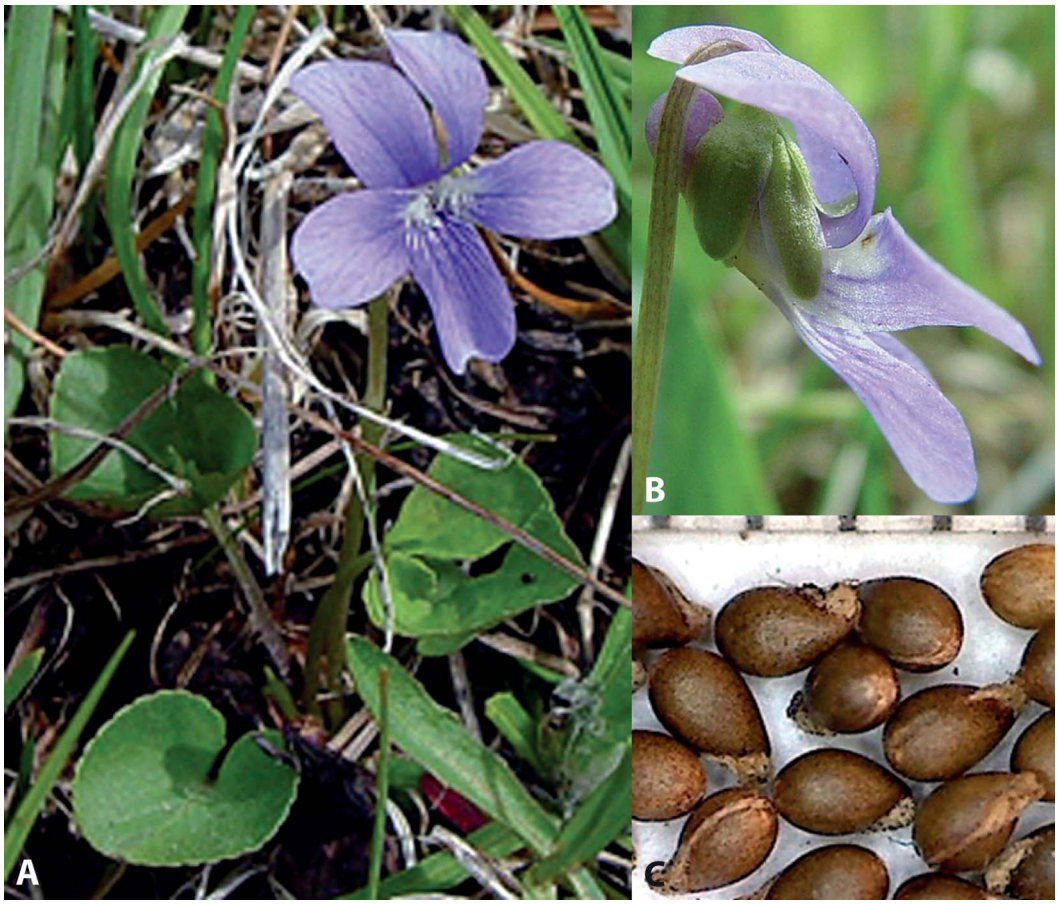

FIG. 80. *Viola nephrophylla*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust). (C) Seeds from herbarium specimen: North Dakota, Butte, 8 Sep 1910, *J. Lunell s.n*. (NY).

other homophyllous cut-leaved violets, especially during cleistogamous fruit, in the characters noted in the diagnosis above. It should be sought farther south in the Blue Ridge Mountain range of the Carolinas. While *V. subsinuata* is widely distributed over the Appalachian Mountains, it is a rare occurrence in the Blue Ridge Mountains (*e.g*., Peaks of Otter). Conversely, *V. monacanora* is quite widespread and relatively common throughout the Blue Ridge mountain range to which it is restricted. Plants with moderately hirsute foliage and commonly more shallowly divided leaf blades represent crosses with *V. sororia* and are common, occasionally outnumbering plants of *V. monacanora*. Such hybrid plants are particularly frequent along and near roadsides and trails and in other areas of localized disturbance.

33. ***Viola nephrophylla*** Greene, Pittonia 3: 144. 1896. Type: USA Colorado. Cimarron River, 29 Aug 1896, *E. L. Greene s.n*. (lectotype (incorrectly designated as holotype by Landon McKinney, Sida, Bot. Misc. 7: 34. 1992; designation to lectotype corrected by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 224): NDG34250 (*n.v.*); isolectotype: NDG34249 (*n.v.*); internet images). Fig. 80.

Viola cucullata Elliott var. *glaberrima* Ging., in DC., Prodr. 1: 292. 1824.

Viola cognata Greene, Pittonia 3: 145. 1896; *Viola nephrophylla* Greene var. *cognata* (Greene) C.L.Hitchc., Vasc. Pl. Pacific NorthW. 3: 445. 1961.

Viola cyclophylla Greene, Pittonia 4: 7. 1899 [illegitimate homonym of *V. cyclophylla* Gandoger (1875)]; *Viola eucycla* Greene [replacement name for *V. cyclophylla* Greene], Pittonia 5: 88. 1902.

Viola vagula Greene, Pittonia 4: 67. 1899.

Viola arizonica Greene, Pittonia 5: 33. 1902; *Viola nephrophylla* Greene var. *arizonica* (Greene) Kearney & Peebles, J. Washington Acad. Sci. 29(11): 487. 1939.

Viola austinae Greene, Pittonia 5: 30. 1902.

Viola galacifolia Greene, Pittonia 5: 30. 1902.

Viola peramoena Greene, Pittonia 5: 94. 1902.

Viola subjuncta Greene, Pittonia 5: 31. 1902.

Viola subrotunda Greene, Pittonia 5: 118. 1903.

Viola lunellii Greene, Leafl. Bot. Observ. 2(2): 95. 1910–1912.

Viola nephrophylla Greene f. *albinea* Farw., Amer. Midl. Naturalist 11: 64. 1928.

Viola mccabeiana M.S.Baker, Madroño 5: 226, pl. 22, fig. 5, pl. 23. 1940.

Viola nephrophylla Greene f. *bicolor* B.Boivin, Naturaliste Canad. 87: 49. 1960.

Common Name. Northern bog violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 16 cm tall; foliage and peduncles green, lower surface of leaf blades commonly purple-tinged, glabrous or upper surface of leaf blades with minute scattered subappressed hairs; stipules free, irregularly glandular-fimbriate; leaves spreading, leaf blades undivided, largest $\leq$ 52 $\times$ 49 mm, ovate to broadly ovate (infrequently narrowly ovate or ovate-triangular), broadening in fruit to deltate-ovate or reniform, base cordate, margins crenate to crenate-serrate, eciliate, apex obtuse to broadly rounded (uncommonly acute); chasmogamous peduncle held above the leaves early in flower, often surpassed by the leaves later; chasmogamous flower $\leq$ 18 mm; calyx glabrous, eciliate; lowest sepals oblong-lanceolate to ovate-lanceolate, obtuse to rounded; auricles short and entire, not elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, on declined or ascending peduncle shorter than petioles; capsule 7–10 mm, green drying to tan, unspotted, glabrous; seeds 1.3–1.9 $\times$ 0.7–1.2 mm, medium brown to dark olive-brown, unspotted or rarely with minute raised darker spots; 2n = 54.

Similar Species. This species has undivided broadly ovate or orbiculate to reniform blades with broadly obtuse (rarely broadly acute) to rounded apex and crenate margins that do not appear to broaden much in fruit, the foliage glabrous except for small scattered subappressed hairs on the upper surface of the blades. As such it could be confused with a diversity of other *Borealiamericanae* taxa with somewhat similar foliage at any time during the growing season, including *V. communis*, *V. latiuscula*, *V. pratincola*, *V. retusa*, *V. sororia* (glabrous variant), and *V. sororia* (*hirsutuloides* variant). In chasmogamous flower it differs from *V. communis*, *V. sororia* (glabrous variant), and *V. sororia* (*hirsutuloides* variant) in its typically densely bearded spurred petal, and additionally from *V. communis* in its obtuse to rounded sepals and short rounded auricles; and from *V. latiuscula*, *V. pratincola*, and *V. retusa* by its rounded sepals, and further from the latter two in its short rounded auricles. In cleistogamous fruit it can be separated from *V. communis*, *V. pratincola*, and *V. retusa* by its short declined or ascending peduncle and brown usually unspotted seeds; and from *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) by its unspotted capsule and brown unspotted seeds.

Ecology. Strongly calciphilic, seasonally or perennially saturated open sites such as bedrock pavement, rocky shores, fens, and wet prairies, occasionally in disturbed sites especially around crushed limestone.

Distribution. Transcontinental, Newfoundland and Labrador and Nunavut to Yukon, south to Connecticut, Arkansas, western Texas, and California. Fig. 81.

Rarity. Listed in Connecticut, New Hampshire, New York, Ohio, Vermont, and West Virginia.

Phenology. Chasmogamous flower April–June (October–November), chasmogamous fruit May–July, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Cucullata species group.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1906c, 1924; House 1924; Haines *et al*. 2011), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Brainerd 1924), *V. cucullata* (Brainerd 1906c, 1924; House 1924; Haines *et al*. 2011), *V. pedatifida* (Brainerd 1913a, 1924), *V. pratincola* (as *V. papilionacea*) (Russell 1952), *V. sagittata* (Gaiser and Moore 1966), and

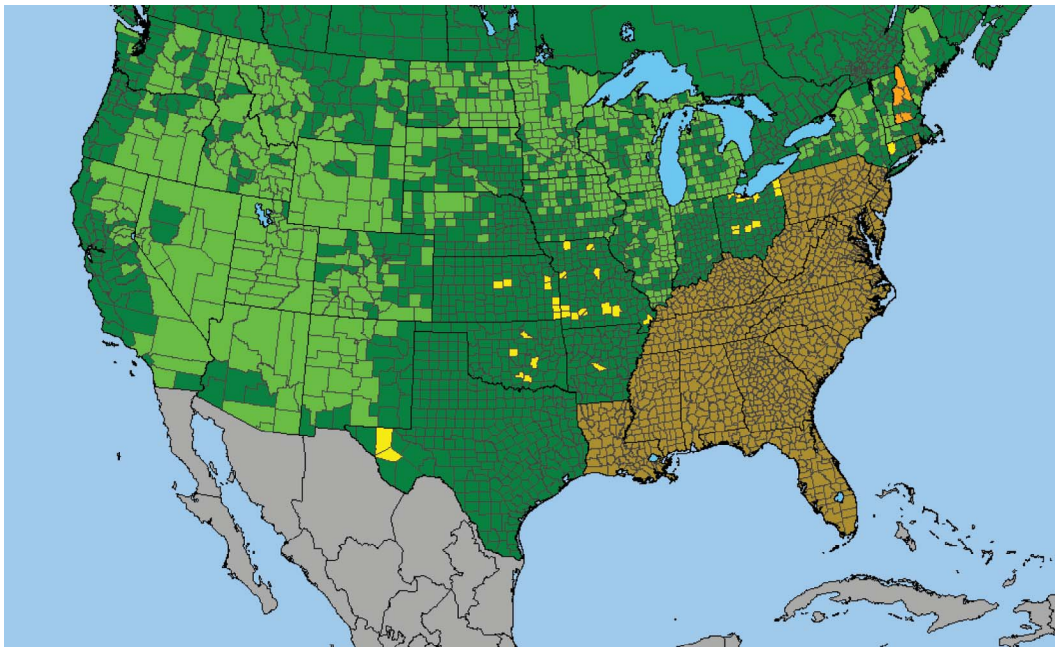

FIG. 81. United States county distribution of *Viola nephrophylla* (map: Biota of North America Program).

V. sororia sensu stricto (Brainerd 1924, Haines *et al*. 2011). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). He noted that hybrids failed to reproduce by chasmogamous flowers and in cleistogamous reproduction were sterile or produced only a few viable seeds.

Comments. Greene cited a single collection in the protologue but made no mention that this constituted a single sheet, and he cited no herbarium. The two sheets cited above at NDG have the same label data and match the protologue, but neither has an indication by Greene as to type status. McKinney (1992) apparently arbitrarily designated NDG34250 as the holotype and NDG34249 as an isotype, and Gil-ad (1995, 1997) later concurred. However, nothing distinguishes the two identical sheets, effectively rendering them syntypes. Ballard *et al*. (2020a) corrected McKinney's initial holotype designation to lectotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1995, 2013), Haines *et al*. (2011), and Voss and Reznicek (2012) recognized this distinctive taxon as a species; Ballard (2013) included *V. pratincola* as a synonym of *V. nephrophylla*, while others referred *V. pratincola* to a broadly delineated glabrous to glabrate *V. papilionacea* Pursh or synonymized it under *V. sororia* Willd. McKinney (1992) and McKinney and Russell (2002) subsumed *V. nephrophylla* under *V. sororia* var. *sororia*, while Little and McKinney later reinstated the present taxon at species rank. Gil-ad (1995, 1997) found evidence of potential hybridization with another unknown species in macromorphological traits and micromorphological features of seeds of certain lectotype plants, but he tentatively accepted the name (and taxon) because other plants on the lectotype sheet expressed no such indications. This transcontinental species is surprisingly uniform in morphology over its broad range, distinct in its broadly ovate to reniform essentially glabrous leaf blades with common purple tinge on the lower surface, crenate blade margins, eciliate calyx, lowest sepals broad and obtuse to rounded, typically densely bearded spurred petal, green unspotted cleistogamous capsule on a declined peduncle, and brown to dark olive-brown seeds. The flowers are typically held above the small leaves during chasmogamous flower. This species

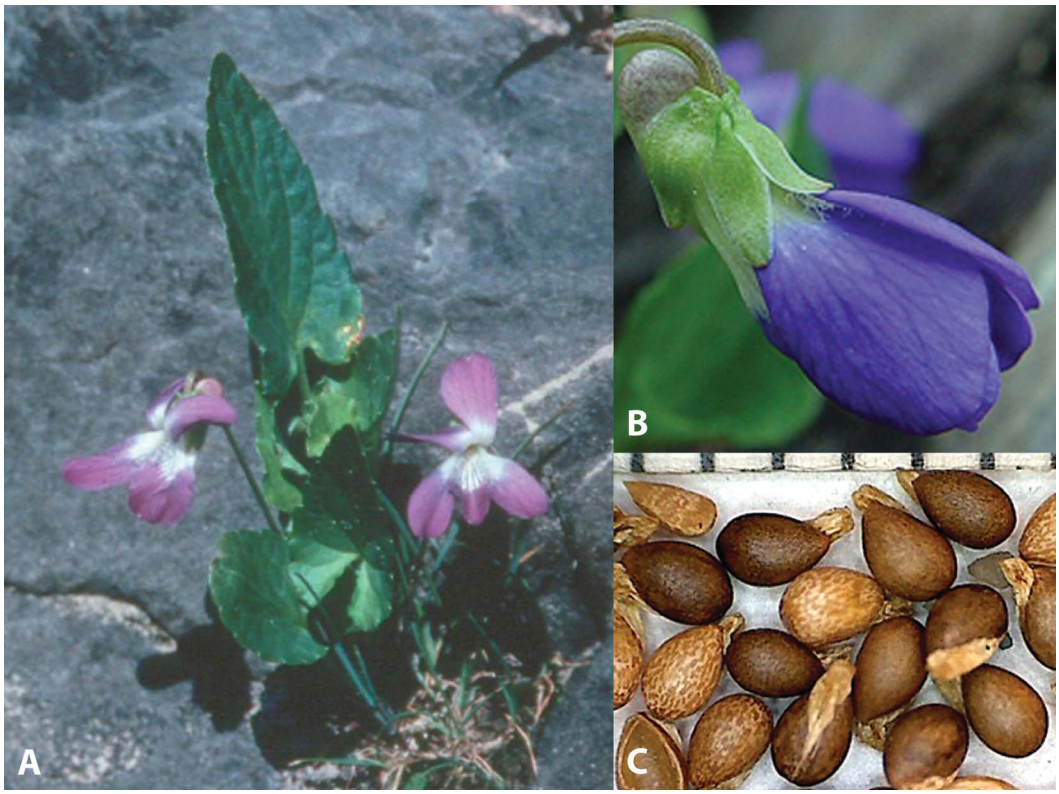

FIG. 82. *Viola novae-angliae*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust). (C) Seeds from herbarium specimen: Maine, Veazie, *M. L. Fernald 243* (NY).

is a very pronounced calciphile. Our current distribution does not include a number of uncertain specimens from montane West Virginia and Virginia that may be this species but require further study; the species also deserves intensive fieldwork in the central Appalachian Mountains to confirm or refute its occurrence there.

The overlooked but widespread Great Plains riverside violet, *V. retusa* Greene, is a near-endemic of the Great Plains recognized in this treatment as a distinct evolutionary species. Similarly, the meadow violet, *V. pratincola* Greene, has been resurrected and is widely distributed in the western portion of the Midwest and easternmost Great Plains. Both have been misidentified as, and often synonymized under, *V. nephrophylla*. Greene described several segregate species (see synonyms) from midwestern and western populations of *V. nephrophylla*, most of which do not appear to differ in any appreciable feature from *V. nephrophylla*. Brainerd Baird (1942) tentatively accepted *V. arizonica* Greene and *V. cognata* Greene but noted that they may be minor "genetic variants." However, other western plants reported with substantially pubescent foliage, often incorrectly referred to *V. arizonica* Greene (which was described as having glabrous foliage, and the type of which is typical *V. nephrophylla*), require closer scrutiny.

34. ***Viola novae-angliae*** House, Rhodora 6: 226. 1904; *Viola sororia* Willd. var. *novae-angliae* (House) L.E.McKinney, Sida, Bot. Misc. 7: 44. 1992. Type: USA Maine. Aroostook Co., Valley of the Saint John River, Fort Kent, sandy shore, 15 Jun 1898, *M. L. Fernald 2245* (holotype: US338658; isotypes: NY00097562, K000327844-image; internet images). Fig. 82.

Common Name. New England violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 27 cm tall; foliage and peduncles green to dark green, upper surface of leaf blades darker, lower surface often purple-

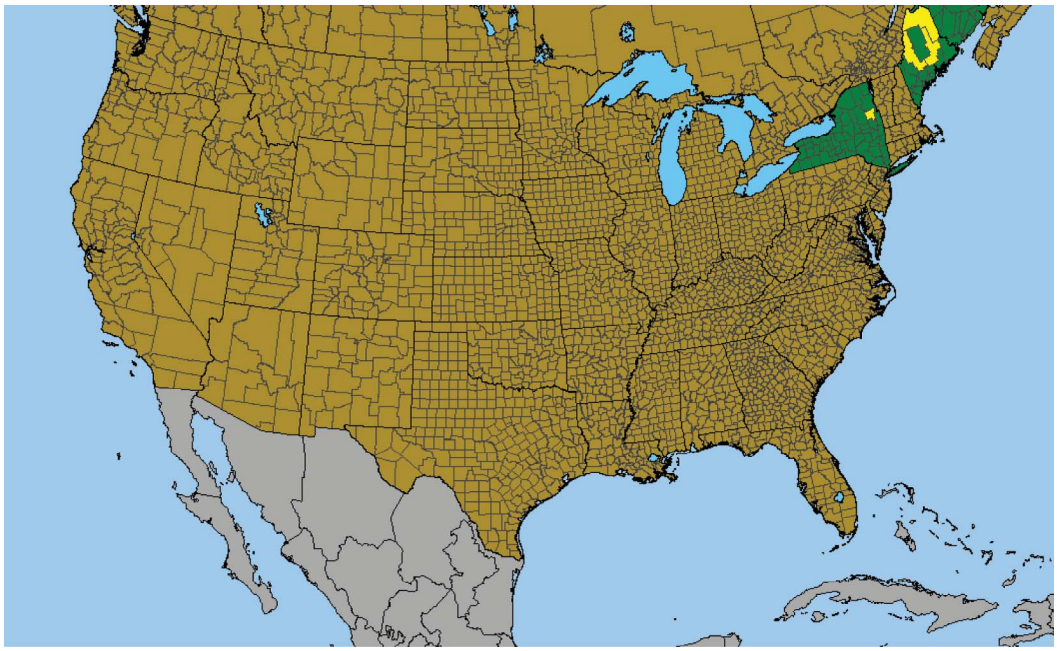

FIG. 83. United States county distribution of *Viola novae-angliae* (map: Biota of North America Program).

tinged, foliage glabrous or petioles sparsely hirsute below middle, peduncles glabrous; stipules free, irregularly glandular-fimbriate; leaves ascending, leaf blades undivided, largest $\leq 52 \times 31$ mm, narrowly triangular-ovate in chasmogamous flower and scarcely broadening in fruit, base subcordate to deeply cordate, margins crenate to serrate, eciliate or sparsely ciliate, apex acuminate to acute; chasmogamous peduncle held among or above the leaves; chasmogamous flower ≤ 25 mm; calyx glabrous, eciliate; lowest sepals oblong, 1.9–2.7 mm wide, length:width ratio > 2.1, narrowly rounded; auricles short to slightly prominent, entire, weakly elongating in fruit to 2 mm; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, the peduncle prostrate but arching upward just before dehiscence, shorter than petioles; cleistogamous capsule 4.5–10 mm, green drying to tan with purple spots or blotches, glabrous; seeds $1.5–1.8 \times 0.9–1.2$, medium yellow-brown to dark brown, unspotted.

Similar Species. Violets likely to be confused with this species are *V. grisea* and *V. septentrionalis*, *Borealiamericanae* violets with pubescent foliage, undivided narrowly ovate or narrowly ovate-triangular leaf blades, the largest of which are longer than broad (at least some of the time), oblong to ovate ciliate obtuse to rounded sepals, prominent auricles, a densely bearded spurred petal, a heavily spotted or blotched cleistogamous capsule on a prostrate peduncle, and unspotted brown seeds. This species differs from *V. grisea* in its glabrous to basally sparsely hirsute petioles, glabrous leaves and peduncle, commonly proportionally narrower leaf blades with fewer marginal teeth, and commonly narrower eciliate sepals; and from *V. septentrionalis* by its consistently narrowly ovate-triangular leaf blades, consistently rounded eciliate sepals, and more broadly ovoid unspotted seeds.

Ecology. Rock crevices in calcareous slate ledges, in sandy loam with gravel in floodplains along ice-scoured rivers, rocky lakeshores.

Distribution. Maine and New Brunswick, disjunct in eastern New York. Fig. 83.

Rarity. Listed in Maine and New York.

Phenology. Chasmogamous flower May–June, chasmogamous fruit June, cleistogamous fruit July–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sororia species group.

Hybrids. Gil-ad (1995, 1997) presented evidence for a hybrid with *V. nephrophylla* from Aroostook Co., ME. This is the first report of hybridization for the species. Hybrids with other species in the region of sympatry should be sought. No information is available on reproduction in the hybrid.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Scoggan (1978), Ballard and Gawler (1994), and Haines *et al*. (2011) recognized this as a distinct species that included the western Upper Great Lakes populations segregated in this treatment as *V. grisea* (see "Comments" under the latter species for nomenclatural and taxonomic details). Gil-ad (1995, 1997, 1998) also recognized this as a distinct species; he included most western Great Lakes populations but segregated specimens from Crawford and Schoolcraft counties in Michigan under his new combination *V. novae-angliae* subsp. *grisea* (Fernald) Gil-ad. Voss and Reznicek (2012) followed this treatment. Gleason and Cronquist (1991) synonymized both taxa under *V. sororia* as a form transitional to *V. sagittata*, while McKinney (1992) demoted them under *V. sororia* in an illegitimate varietal combination, not utilizing the available var. *grisea*. Little and McKinney (2015) reinstated the present taxon as a species but included *V. septentrionalis* var. *grisea* and Gil-ad's combination under *V. novae-angliae* as synonyms. In unpublished studies with much broader sampling (briefly described under *V. grisea*), H.E.B. found no significant differences between material attributed by Gil-ad to *V. novae-angliae* subsp. *grisea* and other western Upper Great Lakes, but he confirmed distinctions between taxa representing the Great Lakes region and Northeast. As narrowly circumscribed here, the name *V. novae-angliae* refers to a locally distributed regional endemic confined to scattered localities in New York, Maine, and New Brunswick. It is rare in the USA, where it has been documented in only three counties of Maine along the Allagash, Penobscot, and St. John rivers, and in one area in New York along the Hudson River. It appears to be more frequent (based on herbarium collections) in New Brunswick, where it has been collected along the Miramichi River and also on the rocky shore of Lake Utopia. Literature reports from New Hampshire and Vermont lack confirming vouchers (Haines *et al*. 2011).

35. ***Viola nuttallii*** Pursh, Fl. Amer. sept. 1: 174. 1813; *Crocion nuttallii* (Pursh) Nieuwl. & Lunell, Amer. Midl. Naturalist 4: 478. 1916. Type: USA Missouri, [no date], *Herb. Nuttall s.n*. (holotype: PH00029269; possible isotype: BM000617588 (*n.v.*); internet images). Fig. 84.

Common Names. Nuttall's violet, yellow prairie violet.

Description. Caulescent perennials from thick rhizome, stems often declining at base, unbranched, solitary or multiple, $\leq$ 19 cm tall; stems, foliage, and peduncles gray-green, puberulent; leaves cauline and basal, basal usually $\geq$ 2, cauline leaves well distributed along the stem; stipules free or weakly adnate, entire or weakly erose; leaves erect to ascending, leaf blades undivided, largest $\leq 53 \times 12$ mm, linear-lanceolate to lanceolate, base cuneate, margins subentire or with 1–3 shallow remote teeth, ciliolate, apex acute to obtuse; chasmogamous flower $\leq$ 15 mm; calyx glabrous or papillate-puberulent, eciliate or ciliolate; lowest sepals linear-lanceolate, acute; auricles prominent and entire or weakly erose, not elongating in fruit; corolla wholly yellow, upper petals purple or purple-brown on back; spur short-globose; lateral petals sparsely to densely bearded with clavate to reniform hairs, spurred petal glabrous; cleistogamous flowers lacking; capsule 6–9 mm, green drying tan, unspotted, glabrous or sparsely puberulent; seeds ca. 3×1 mm, medium brown, unspotted; $2n = 24$.

Similar Species. This species is distinctive in our region in its caulescent habit, gray-green puberulent foliage, narrow long linear-lanceolate to lanceolate leaf blades, and yellow corolla. Only *V. vallicola* var. *vallicola*, a species occurring within a few counties to the west of our region, could be confused with it. It differs from *V. vallicola* in its consistently puberulent foliage, longer narrower leaf blades with narrowly cuneate base, and larger medium brown seeds.

Ecology. Grasslands in our region, sagebrush and chaparral in the West.

Distribution. Southwestern Minnesota to Alberta, south to Kansas and northeastern New Mexico. Fig. 85.

FIG. 84. *Viola nuttallii*. (A) Chasmogamous flowering habit (photo: Katy Chayka, Minnesota Wildflowers website). (B) Chasmogamous flower front view (photo: Peter M. Dziuk, Minnesota Wildflowers website). (C) Chasmogamous flower back/top view (photo: Katy Chayka, Minnesota Wildflowers website).

Rarity. Listed in Minnesota.

Phenology. Chasmogamous flower May–June, chasmogamous fruit May–June.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Nuttallianae species group.

Hybrids. None.

Comments. Brainerd (1921b) and Alexander (1963) included *V. vallicola* in a broadly delimited *V. nuttallii* but recognized *Viola praemorsa* Douglas ex Lindl., a violet of the western Great Plains, as a distinct species. Russell (1965) submerged all three species under *V. nuttallii*, and he used *V. vallicola* as the source of the figure for his very broadly delineated *V. nuttallii*. Scoggan (1978) and Gleason and Cronquist (1991) treated all three as varieties under *V. nuttallii*, while Little and McKinney (2015) maintained all three at species rank. Brainerd Baird (1942) maintained *V. nuttallii* and *V. praemorsa* and provided separate accounts of these but confusingly referred to *V. vallicola* as a "well recognized varying form" under *V. nuttallii*. Fabijan *et al.* (1988) conducted a comprehensive and illuminating taxonomic revision of the Nuttallianae group, presenting abundant macromorphological, morphometric, cytogenetic, and biochemical evidence for maintaining all three as distinct and distinctive species in our region, with other taxa represented in areas farther west. All three are accepted here as distinct and readily identifiable evolutionary species with different ploidy levels (the present species being tetraploid, *V. vallicola* diploid, and *V. praemorsa* hexaploid). Limited field studies and examinations of several representative herbarium collections have revealed no evidence of "intergradation" (with the several diagnostic characteristics in mind); any interploidal hybrids would be expected to be wholly sterile at any rate. The present species and *V. vallicola* range extensively across the Great Plains. All three species in the Nuttallianae group in our region are immediately recognizable by their yellow corollas, multiple stems, and leaves distinctly to much longer than broad (*V. nuttallii* and *V. praemorsa* with leaf blades cuneate at the base). The leaf blades of *V. nuttallii* alone distinguish it from the other two, being much longer and narrower and with more narrowly cuneate leaf base.

36. *Viola odorata* L., Sp. pl., ed. 1, 2: 934. 1753; *Viola martii* Wiesb. subsp. *odorata* (L.) Schimp. & Spenn., Fl. Friburg. 3: 1036. 1829 [nomen illegitimum]. Fig. 86.

Viola thomsonae Chapm., Fl. South. U.S., ed. 3: 34. 1897 ["1896"].

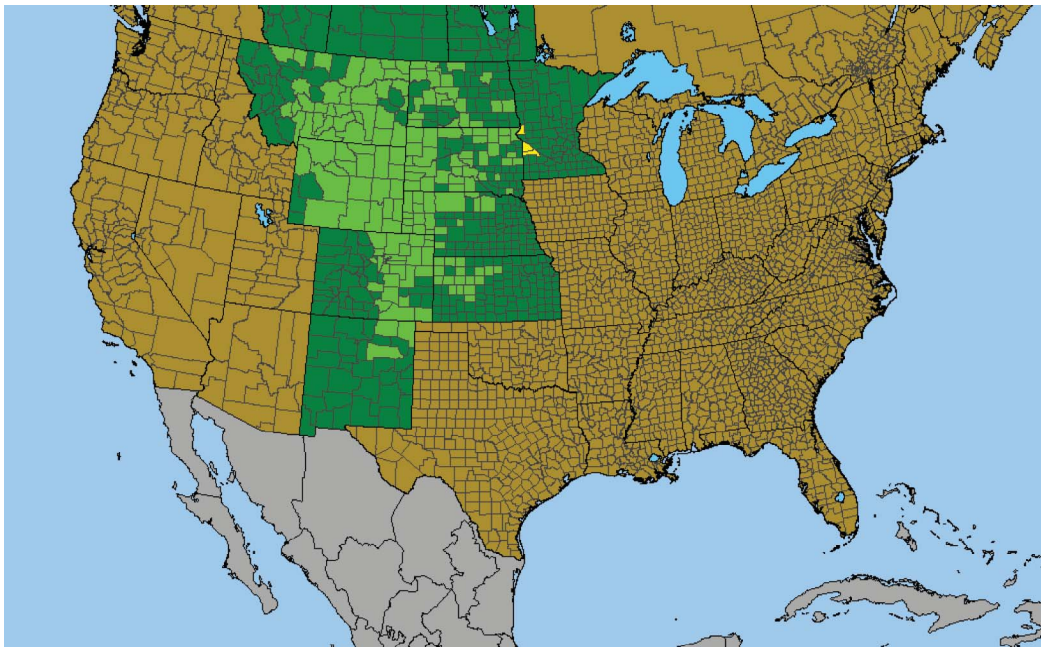

FIG. 85. United States county distribution of *Viola nuttallii* (map: Biota of North America Program).

Viola hirta L. var. *odorata* (L.) Fiori, A.Fiori & al., Fl. Anal. Italia 1: 405. 1898.

Viola hirta L. subsp. *odorata* (L.) Fiori, A.Fiori & al., Fl. Anal. Italia 1: 404. 1898.

Viola odorata L. proles *barcinonensis* Sennen, Bol. Soc. Ibér. Ci. Nat. 25: 136. 1926.

Viola gonzaloi Sennen var. *semiglabra* Sennen, Exsicc. (Pl. Esp.) 1929: no. 7283. 1930 [*nomen nudum*].

Viola odorata L. subsp. *texidoris* Sennen, Butl., st. Catalana Hist. Nat. 32: 112. 1932.

Viola taynensis Elisafenko, Rast. Mir Aziatsk. Rossii 1(17): 24. 2015.

FIG. 86. *Viola odorata*. (A) Chasmogamous flowering habit (photo: Paul Busselen). (B) Chasmogamous flower profile view (photo: Tony Frates). (C) Seeds from herbarium specimen: Ohio, 6 Jul 1936, *F. O. Grover s.n.* (OS367834).

Common Names. English violet, sweet violet.

Description. Acaulescent stoloniferous mat-forming perennials from somewhat slender to thick brown horizontal rhizome, stolons surficial, produced year-round, greenish, leafless, nonreproductive, terminating in a plantlet, $\leq$ 15 cm tall; foliage and peduncles green, foliage puberulent to hirtellous, peduncles glabrous or hirtellous; stipules free, glandular-fimbriate; leaves spreading, leaf blades undivided, largest $\leq$ 45 $\times$ 44 mm, orbiculate to broadly ovate-deltate (rarely narrowly ovate or reniform), base deeply cordate at base, margins regularly crenate, ciliate, apex broadly rounded or obtuse; chasmogamous peduncle among or above the leaves; chasmogamous flower $\leq$ 19 mm; calyx glabrous, commonly ciliate; lowest sepals broadly oblong or ovate-lanceolate to narrowly ovate, obtuse with a small callus at tip; auricles short and entire, not elongating in fruit; corolla white or blue (rarely pink or rose), throat white, rarely "double-flowered"; spur weakly to moderately developed, slender or thick, 5–7 mm, white or blue; lateral petals glabrous or bearded with narrowly linear or slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles and arching upward just before capsule dehiscence; cleistogamous capsule 4.5–6.5 mm, green drying tan with purple spots or blotches, puberulent or hirtellous; seeds (2.7)3.0–4.0 $\times$ 1.7–2.0 mm, ivory or tan to light orange-brown, unspotted; 2n = 20.

Similar Species. Although this introduced and occasionally cultivated species has often been misidentified as several different species due to lax observation, its mat-forming habit with rosettes connected by green cordlike stolons, densely puberulent to hirtellous foliage, and orbiculate to ovate-deltate leaf blades with closely and regularly crenate margins and broadly obtuse to broadly rounded apex should distinguish it at any time of the growing season. Vaguely similar acaulescent nonstoloniferous violets include *V. communis*, *V. domestica*, *V. latiuscula*, *V. sororia sensu stricto*, *V. sororia* (glabrous variant), and *V. sororia* (*hirsutuloides* variant). In chasmogamous flower it differs from all of the above in its somewhat elongate spur, and the style terminating in a prolonged downward-pointing "hook" and it also can be distinguished from the mat-forming *V. appalachiensis* and *V. walteri* by its membranous or semiherbaceous glandular-fimbriate stipules, and long hooked style. In cleistogamous fruit it is immediately different from all of the above species in its puberulent or hirtellous capsule and rather large unspotted ivory to light orange-brown seeds.

Ecology. Lawns, cemeteries, urban woodlots, and roadsides.

Distribution. European, frequently escaped from cultivation in the Northeast and Great Lakes regions, northern Rockies, and western coastal states but rare elsewhere. Fig. 87.

Rarity. None.

Phenology. Chasmogamous flower March–May, chasmogamous fruit May–June, cleistogamous fruit May–July.

Affinities. This species belongs to sect. *Viola*, subsect. *Viola*.

Hybrids. None.

Comments. Brainerd (1921b) and Brainerd Baird (1942) did not mention it because they excluded all nonnative species, and Strausbaugh and Core (1978) did not mention it, presumably because it did not occur in West Virginia at that time. Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Haines *et al*. (1991), Ballard (1995, 2000), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney (2015) included it. The puberulent foliage, stout green cordlike vegetative stolons, somewhat exserted orange stamens, downward-hooked style, hirtellous spotted or blotched cleistogamous capsule, and large pale seeds easily distinguish this from native species. It is often misidentified as *V. sororia*, and it is surely more widely distributed than range maps indicate. Populations often have both purple and white floral morphs; the purple form tends to have lateral petals densely bearded within, while the white form typically lacks beards.

37. *Viola palmata* species complex

Infraspecific taxa belonging to this species include the following:

37a. *Viola palmata* L. var. *palmata*

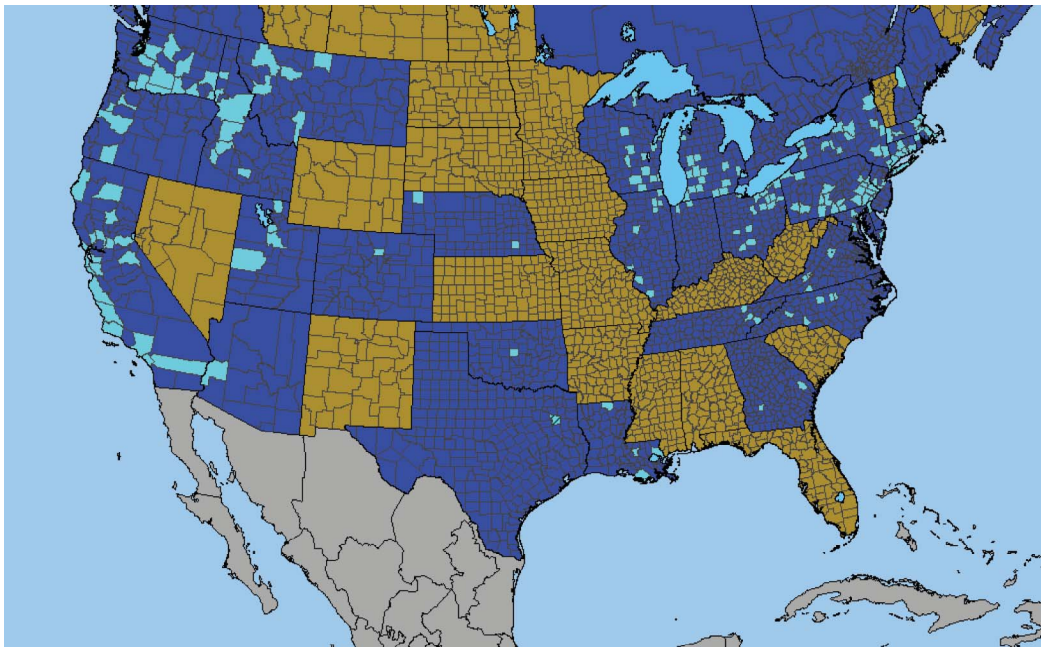

FIG. 87. United States county distribution of *Viola odorata* (map: Biota of North America Program).

37b. *Viola palmata* L. var. *triloba* (Schwein.) Ging.

37c. *Viola palmata* (*avipes* variant)

37d. *Viola palmata* (*pseudostoneana* variant)

Common Names. Northern three-lobed violet, southern three-lobed violet, Appalachian bird's-foot violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 36 cm tall; foliage and peduncles green to gray- or blue-green, lower surface of leaf blades occasionally paler than upper surface, often purple-tinged; petioles, peduncles, and calyx often red-purple– to purple-spotted, foliage and peduncles moderately to densely hirtellous or hirsute (glabrous or sparsely hirsute in var. *triloba* and the southeastern *V. palmata* [glabrate variant]); stipules free, glandular-fimbriate; heterophyllous, leaves ascending to spreading, earliest and latest leaf blades undivided (these occasionally lost or withered), largest in chasmogamous flower through midcleistogamous fruit shallowly to moderately lobed in var. *triloba*, or divided nearly or fully to summit of petiole, deeply pedately divided in var. *palmata*, *V. palmata* (*avipes* variant), and *V. palmata* (glabrate variant) into 3, 5, or 7(9) lobes or biternately divided in the southeastern *V. palmata* (Red Hills variant) and *V. palmata* (*pseudostoneana* variant)into 5 or 7(9) lobes, the largest $\leq$ 113 $\times$ 110 mm, outline ovate to broadly ovate, deltate or reniform, in summer broadening to deltate or reniform, base deeply cordate, margins irregularly or remotely serrate, ciliolate or ciliate, apex acute to broadly obtuse; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 28 mm; calyx glabrous, ciliate (auricles ciliate, sepals eciliate in var. *triloba* and *V. palmata* [glabrate variant]); lowest sepals oblong-lanceolate to ovate and obtuse to rounded (in var. *palmata*, var. *triloba*, *V. palmata* [*avipes* variant], and *V. palmata* [*pseudostoneana* variant]) or linear-lanceolate to lance-triangular and acuminate (in *V. palmata* [glabrate variant] and *V. palmata* [Red Hills variant]); auricles short and entire, not elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with narrowly linear or slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncles initially prostrate but arching upward just before capsule dehiscence, shorter than petioles, capsule 7–14 mm, green drying tan with purple spots or blotches, glabrous; seeds (1.7)2.0–2.5 $\times$ 1.2–1.5

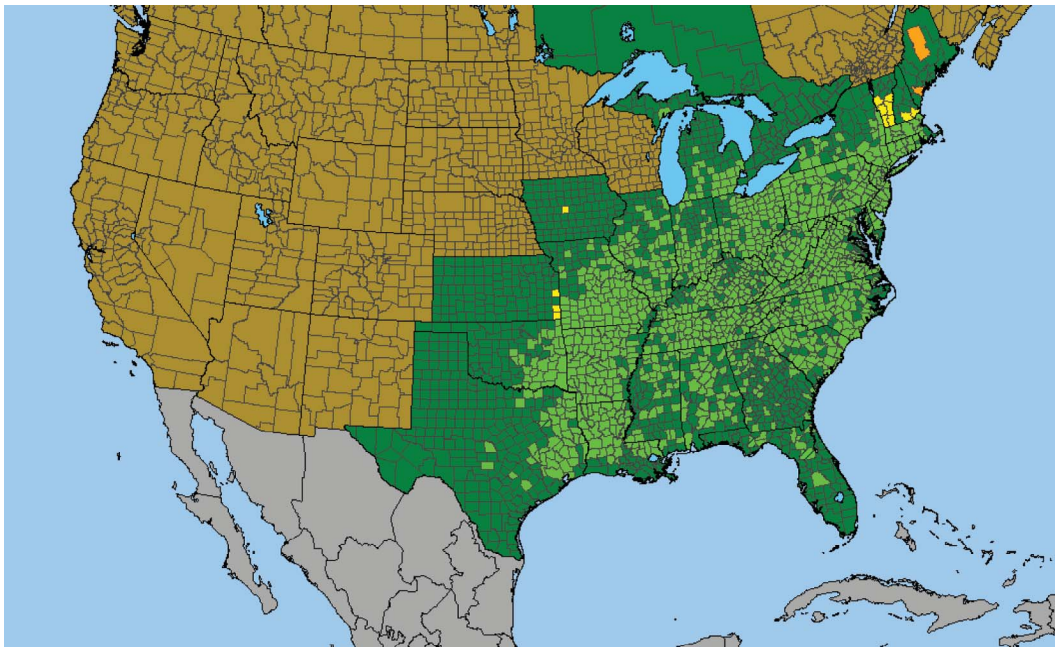

FIG. 88. United States county distribution of *Viola palmata* species complex (map: Biota of North America Program).

mm, light brown to brown with small darker brown streaks or blotches; 2n = 54.

Similar Species. This species is most similar to the other heterophyllous violet with pubescent foliage in our region, *V. stoneana*. It differs from that species in its densely hirsute foliage, primary divisions of the pedately divided leaf blades (or biternately divided blades in *V. palmata* [*pseudostoneana* variant]) not usually abruptly contracted into long slender "petiolules" (lobes of deeply pedately divided leaf blades in Lower Midwest populations with short slender "petiolules"), hirsute peduncle, ciliate calyx, oblong-ovate to ovate obtuse to rounded sepals, densely spotted or blotched cleistogamous capsule on a prostrate peduncle, and light brown to brown seeds with small darker streaks or blotches.

Ecology. Dry sandy, sandy loam, or clayey soils in dry to dry-mesic woods, often on slopes or bluffs, and on margins of wetter forests, swamps, or floodplains.

Distribution. Widespread in eastern North America, Maine to southern Ontario, and Iowa south to Florida and Texas. Fig. 88.

Rarity. See infrageneric taxa.

Phenology. Chasmogamous flower March–June, chasmogamous fruit April–July, cleistogamous fruit May–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Palmata species group.

Hybrids. See infraspecific taxa.

Comments. Elliott (1817) and other botanists following Linnaeus (1753) routinely described a heterophyllous violet when referencing the name *V. palmata* L. More than 150 yr later, Brainerd (1910c) took up the opposing viewpoint, arguing vehemently that the name should be attributed to the homophyllous cut-leaved violet predominately distributed in the Appalachian Mountains and associated uplands. He proposed taking up the name *Viola triloba* Schwein. for the widely distributed heterophyllous violet. For the southern heterophyllous violet with midseason leaf blades deeply 3- to 5-lobed, he created the new combination *V. triloba* var. *dilatata* (Elliott) Brainerd. For the northern heterophyllous violet with shallowly to moderately lobed leaf blades, he applied the name *V. triloba* var. *triloba*. This taxonomic interpretation was adopted by Brainerd

(1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), and Swink and Wilhelm (1979). McKinney (1992) examined the protologue and original material of Linnaeus's *V. palmata* and reinterpreted the name to refer to the heterophyllous violet known since Brainerd's time as *V. triloba* (including its var. *dilatata*), and he argued that the earliest available name for the Appalachian region's homophyllous cut-leaved violet was *V. subsinuata* (Greene) Greene. Gil-ad (1995, 1997) rejected McKinney's argument in favor of Brainerd's interpretation, retaining *V. triloba* Schwein. as the correct name for the heterophyllous violet and suggested that macromorphological features of Linnaeus's original material of *V. palmata* suggested hybridization between a homophyllous cut-leaved violet and a heterophyllous violet such as *V. triloba*. Gil-ad examined macromorphological features and micromorphology of lateral petal trichomes and seed coats of several specimens identified as *V. triloba* var. *triloba* and a few specimens from the Lower Midwest portion of the range of var. *dilatata*. He reported considerable variation in seed macromorphology and micromorphological features within and among the populations and specimens of var. *triloba*, as well as micromorphological features on seed coats similar to those found in *V. affinis* and *V. sororia*, suggesting introgression. Gil-ad's field observations of var. *dilatata* at three oak woodlands on limestone in Missouri supported Russell's statement that var. *triloba* and var. *dilatata* do not occur together. Gil-ad noted a number of macromorphological differences between the two varieties he studied, including density of foliage indument, features of the leaf blade, corolla color, density of calyx ciliation, shape of lateral petal trichomes, capsule shape, and seed dimensions. He was only able to examine partially mature seeds for micromorphological features but noted features similar to those on seeds of var. *triloba* as well as features similar to those of *V. affinis*, *V. missouriensis*, and *V. nephrophylla*. His data could not rule out the possibility of a hybrid origin for var. *dilatata*. Gil-ad accepted *V. triloba sensu stricto* as a distinct taxon but rejected var. *dilatata* as a probable hybrid derivative, mainly due to lack of unique seed micromorphological features. Ballard (2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015) adopted McKinney's interpretation of the names *V. palmata* L. and *V. subsinuata* (Greene) Greene, in most instances applying the former name to a broadly delimited assemblage of several species accepted here as distinct. Ballard (1995) and Voss and Reznicek (2012) merged the homophyllous cut-leaved violets (excluding *V. pedatifida*) and heterophyllous violets of Michigan into *V.* ×*palmata* and *V. palmata*, respectively, whereas Gleason and Cronquist (1991) conducted wholesale lumping of many formerly recognized heterophyllous and homophyllous cut-leaved taxa into a highly heterogenous *V. palmata*.

The first author has made independent examinations of protologues and original material of Linnaeus's name and of the pre-Linnaean names he synonymized under it, and has arrived at the same conclusion as McKinney. The name *V. palmata* L. unambiguously refers to the widely distributed heterophyllous violet previously attributed to *V. triloba*. Linnaeus's own description of *V. palmata*, "*Viola* acaulis, foliis palmatis quinquelobis dentatis indivisisque," indicates that some leaves are palmately 5-lobed and others are undivided. Linnaeus next presents Gronovius's "Flora Virginica" description, followed by Plukenet's "Mantissa" description, and finally Plukenet's ''Amaltheum'' description. Gronovius's publication also cites Plukenet's "Mantissa" description and Plukenet's "Amaltheum" description but ends with the statement "*Viola* Martia coerulea inodora, radice tuberosa: foliis variis, aliis integris, aliis incisis. *Clayt. n*. 793". Once again, Gronovius specifically references a specimen that bears some undivided leaf blades and some divided leaf blades. In addition, the illustration in Plukenet's "Amaltheum" clearly depicts a heterophyllous violet, and the herbarium specimen on which it is based (LINN, image!) is a heterophyllous violet. As further evidence, the lectotype sheet (no. 486, *Herb. Jacquin, LINN-HL1052-1*, image!) and a syntype sheet (*J. Clayton 468 & 793*, ex *Herb. Gronovius*, BM000042617, image!) both display the deeply pedately divided leaf blade with 5 slender lobes characteristic of many southeastern plants which Brainerd and others have identified as *V. triloba* var. *dilatata*. One of Brainerd's lines of evidence arguing for a homophyllous violet as Linnaeus's *V. palmata* was the reference to Florida by Plukenet's ''Amaltheum'' description, and Brainerd asserted that the only pubescent cut-leaved violet he knew in Florida was *V. palmata*

(*sensu* Brainerd and others). He was referring particularly to living plants and specimens sent to him by "Mrs. Chase" from a single unspecified locality in Lake Co., FL. He maintained the living plants and made at least two more sheets. The specimens are anomalous, with two of three specimens producing deeply palmately divided leaf blades (one specimen has a leaf scarcely pedately lobed) but with the lobing pattern on some leaf blades distinctly pedate and the venation on most leaf blades clearly pedate, suggesting a hybrid involving *V. palmata* var. *palmata* or *V. septemloba* with another species (or each other). Plants of a number of heterophyllous violet taxa lacking an undivided leaf are not rare. Contrary to Brainerd's statement that there are no pubescent heterophyllous violets in Florida, Russell (1965) maps his *V. triloba* var. *dilatata* throughout much of Florida and adjacent areas, and we have examined a substantial number of such herbarium specimens and a few living populations from northern Florida and adjacent southeastern states. The cumulative evidence is overwhelmingly in favor of the name *V. palmata* L. representing a heterophyllous violet, specifically that which has been regarded since Brainerd's time as *V. triloba* Schwein. Given that Linnaeus's type material of *V. palmata* represents the more deeply divided-leaved southern taxon, *V. palmata* var. *palmata*, *V. palmata* var. *dilatata* Elliott becomes a synonym of var. *palmata*. The shallowly lobed northern taxon, retained here as a variety until further studies clarify its evolutionary and taxonomic status, requires a different name, and the earliest available name unambiguously applied to it is *V. palmata* L. var. *triloba* (Schwein.) Ging.

Populations from the Lower Midwest were segregated by Greene as *V. falcata* early on but are tentatively included in eastern Piedmont and Coastal Plain *V. palmata* var. *palmata*, as reinterpreted here pending further investigation. The two sets of populations appear to diverge somewhat in features of blade dissection and seed traits, and they may occupy somewhat different microhabitats, but the extensive degree of leaf blade variation observed within populations in the two regions makes assessment difficult. Elliott (1817), in describing *V. palmata* L. followed by four new varieties, stated that the three upper petals were bearded and the two lower were naked. Assuming he was cognizant of the resupinate nature of violet flowers, this would imply that the spurred as well as lateral petals were bearded. Henry (1953a) claimed that the spurred petal in western Pennsylvania plants was also bearded, but many other botanists and the first author have confirmed the spurred petal to be glabrous in countless herbarium specimens and living populations. The basis of this discrepancy is elusive. Vitek *et al*. (2012) and Cheon *et al*. (2019) reported *V. palmata* naturalized in Austria and Korea, respectively. Although no images of the plants were included in the first communication, the second report had photographs of the violet, and the descriptions are not *V. palmata*; these reports match the mysterious *V. egglestonii* (Canada variant).

The *V. palmata* species complex encompasses a large degree of potentially taxonomically important variation and probably includes multiple undescribed taxa, particularly in the southeastern USA In our region, the complex includes the deeply cut-leaved several-lobed *V. palmata* var. *palmata* predominately in the southeastern Piedmont, Coastal Plain, and Lower Midwest; the shallowly cut-leaved few-lobed *V. palmata* var. *triloba* predominately in the Northeast and the Appalachian Mountains; the deeply pedately divided *V. palmata* (*avipes* variant) and the biternately divided *V. palmata* (*pseudostoneana* variant) in the Appalachian Mountains. For distinctions among these taxa, see the key. In the Southeast, a number of other variants have been identified, including *V. palmata* (glabrate variant) and *V. palmata* (Red Hills variant). Jonathon Osborne at the University of Southern Mississippi is conducting Masters thesis research on the *V. palmata* complex in Mississippi and Alabama, under the mentorship of Dr. Mac Alford.

37a. *Viola palmata* L. var. ***palmata***, Sp. pl., ed. 1, 2: 933. 1753. Type: USA, Virginia, [no date], *J. Clayton 468* in Herb. Jacquin (lectotype (incorrectly designated as holotype by Landon McKinney, Sida, Bot. Misc. 7: 12. 1992; corrected to lectotype by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 224): LINN1052.1 (*n.v.*), internet image); isolectotype: BM000042617 (*n.v.*), internet image). Fig. 89.

Viola palmata L. var. *dilatata* Elliott, Sketch bot. S. Carolina 1(3): 300. 1817; *Viola triloba* Schwein. var. *dilatata* (Elliott) Brainerd, Bull. Torrey Bot. Club 37: 587. 1911; *Viola triloba* Schwein. f. *dilatata* (Elliott) E.J.Palmer &

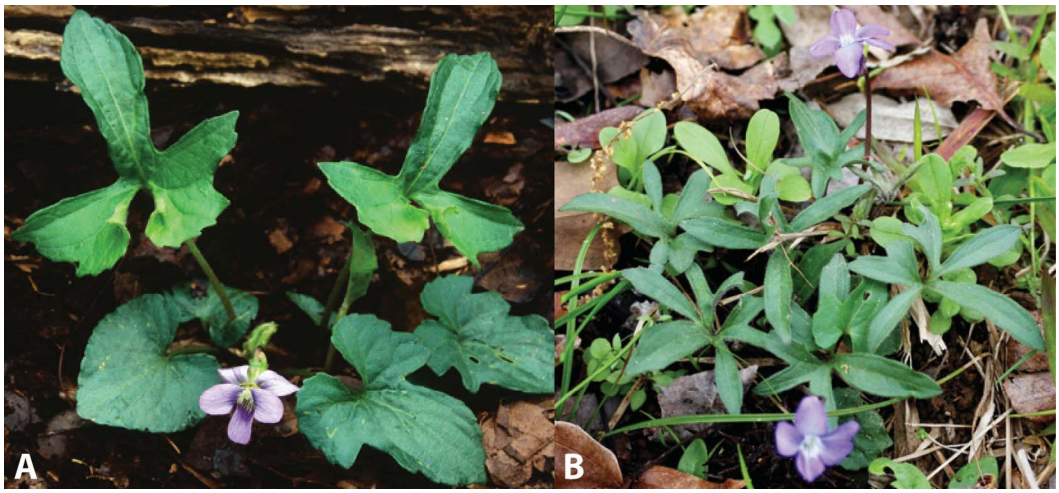

FIG. 89. *Viola palmata* var. *palmata*. (A) Chasmogamous flowering habit (3-lobed leaf blades) (photo: Kim Blaxland). (B) Chasmogamous flowering habit (5-lobed leaf blades) (photo: Kim Blaxland).

Steyerm., Brittonia 10: 115. 1958. Type: CHARL [not located there].

Viola falcata Greene, Pittonia 4: 3. 1899. Type: USA, Illinois, Cobden, 15 Jun 1898, *E. L. Greene s.n.* (lectotype (**designated here**): NDG33531 (*n.v.*); isolectotypes: NDG33528 (*n.v.*), NDG33529 (*n.v.*), NDG33530 (*n.v.*), NDG33532 (*n.v.*); all internet images).

Common Name. Southern three-lobed violet.

Description. Foliage and chasmogamous and cleistogamous peduncles moderately to densely hirsute, green, margins of leaf blades ciliate, peduncles moderately hirsute; larger leaf blades deeply pedately divided into 3, 5, or 7(9) linear to rhombic-lanceolate or ovate-lanceolate lobes, the lateral primary divisions occasionally scarcely divided and appearing "dilated," sinuses between primary divisions reaching nearly or quite to the petiole summit, the longest axis of the lateral primary division or the lobe of the lateral primary division nearest the terminal primary division $>$ 1/2 the length of the midrib; calyx strongly ciliate; lowest sepals oblong-ovate to ovate, obtuse to rounded at apex; cleistogamous capsule heavily purple-spotted or -blotched, on an initially prostrate peduncle arching upward abruptly just prior to dehiscence. Other features as in *V. palmata sensu lato*.

Similar Species. See the species complex.

Ecology. Drier to dry somewhat acidic or somewhat alkaline sandy or sandy loam soils in dry oak and oak-pine woodlands, oak savannas, or open forests on slopes and bluffs.

Distribution. Atlantic and Gulf Coastal Plains and lower to middle Piedmont in the Southeast, and in the Lower Midwest, Virginia to Tennesse, western Indiana, southern Illinois and eastern Kansas, south to Florida and eastern Texas (includes. *palmata* var. *triloba*, currently being disentangled from var. *palmata*; see Russell [1965] for an older taxon-specific map). Fig. 90.

Rarity. None.

Phenology. Phenology presumably same as the species complex.

Affinities. Same as the species complex.

Hybrids. Hybridizes with *V. emarginata sensu stricto* (Brainerd 1924). Brainerd reported that this exhibits intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). The hybrid fails to reproduce by chasmogamous flowers and produces either abortive cleistogamous capsules or very few viable seeds.

Comments. In describing *V. palmata*, Linnaeus (1753) specified no types, although he did state "Habitat in Virginia." McKinney (1992) incorrectly designated the LINN1052.1 sheet in the Linnaean Herbarium as the holotype. Ballard *et al*. (2020a) corrected his designation to lectotype. Stephen Elliott's (1817) protologue for *V. palmata* var. *dilatata* notes that "This is the common

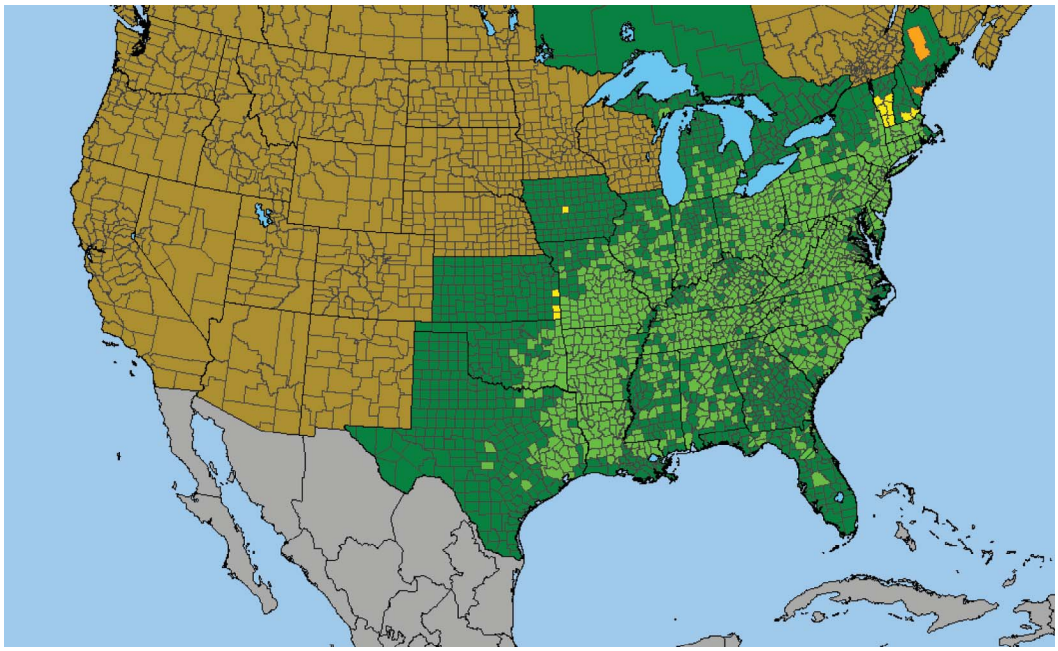

FIG. 90. United States county distribution of *Viola palmata* var. *palmata* and var. *triloba* combined (map: Biota of North America Program).

variety in the upper districts of Georgia and Carolina." He cited no specific collection, but Stafleu and Cowan (1976) state that Elliott's herbarium is deposited at CHARL, with a few types at NY and some original material also at PH. Unfortunately, a thorough examination of his herbarium at CHARL by the first author revealed that at some time subsequent to Elliott's publication, specimens and labels were removed from most of the sheets and later reattached with no attempt to correctly place labels in association with their original specimens. As a result, none of the published varieties of *V. palmata* except for var. *heterophylla* are currently represented in his herbarium with intact labels or recognizable specimens. Nevertheless, Elliott's description of the present taxon still allows for relatively clear interpretation of which taxon he had in mind. A neotype for var. *dilatata* must eventually be designated. In Greene's protologue for *V. falcata*, he specified a single apparent collection, "In oak woods near Cobden, Illinois, 15 June 1898," but he designated no type, referenced no single sheet, and made no mention of a herbarium. None of the sheets listed above has any indication of type status on the sheets. The most representative sheet, NDG33531, bears three cleistogamous fruiting plants showing some of the population's variation and is designated here as lectotype, making the remaining duplicates isolectotypes.

The present taxon, as circumscribed here, is confined to the middle and lower Piedmont and Coastal Plain regions in the southeastern USA and in the Lower Midwest. Russell (1965) maps these two regions as separate areas, and further research is needed to determine whether confirmed records bridge this reportedly bimodal distribution. Plants with biternately divided leaf blades from the Appalachian Mountains and Western Allegheny Plateau have previously been included here but these belong to *V. palmata* (*pseudostoneana* variant), while plants with biternately divided leaf blades from the Gulf Coastal Plain region west to Arkansas and Oklahoma belong to *V. palmata* (Red Hills variant). Even extracting multiple apparently distinct taxa from this melange of variants leaves substantial morphological polymorphism especially in dissection of leaf blades during chasmogamous flower through midcleistogamous fruit in var. *palmata*. Von Schweinitz (1822) remarked on this nearly 200 yr ago, noting that he had observed nearly every possible variation in this taxon (he may have included several other heterophyllous taxa which were subsequently

FIG. 91. *Viola palmata* var. *triloba*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: Andrew Lane Gibson). (C) Seeds from herbarium specimen: Transplanted from Ohio, Athens Co., *H. Ballard 15-055Z* (BHO).

treated as distinct species). He also stated that Elliott's *V. palmata* var. *dilatata* could serve as the type of *V. palmata*. For more information, see "Comments" under the *V. palmata* species complex. Populations in the southeastern region (now var. *palmata*) grow in somewhat acidic soils, while those in the Lower Midwest (formerly *V. falcata*) are commonly on circumneutral or possibly somewhat alkaline often cherty soils overlying limestone. A rangewide study of these and other members of the species complex is sorely needed.

Given the various interpretations of the varieties of *V. palmata* and the challenge of reidentifying and remapping numerous specimens in a finite period of time, we have presented a composite distribution map of var. *palmata* and var. *triloba* for the two taxa.

37b. *Viola palmata* L. var. ***triloba*** (Schwein.) Ging., in DC., Prodr. 1: 291–292. 1824; *Viola triloba* Schwein., Amer. J. Sci. 5: 57. 1822. Type: USA [North] Carol.[ina], Salem, "rich woodland and meadows" [protologue] [no date], [*L. D. von Schweinitz s.n.*] (lectotype (incorrectly designated as holotype by Landon McKinney, Sida, Bot. Misc. 7: 12. 1992; **corrected to lectotype here**): PH00029298, internet image). Fig. 91.

Viola congener Leconte, Ann. Lyceum Nat. Hist. New York 2: 140. 1828 ["1826"].

Viola palmata L. f. *striata* O.R.Willis, Bull. Torrey Bot. Club 16: 278. 1889.

Viola ornithodes Greene, Leafl. Bot. Observ. 1(4): 218. 1903–1906.

Viola vespertilionis Greene, Leafl. Bot. Observ. 1(4): 217. 1903–1906.

Viola triloba Schwein. f. *albida* Steyerm., Rhodora 54: 256. 1952.

Viola triloba Schwein. f. *annjoae* Creutz, Wild Fl. 35: 9, fig. 1, 4–7. 1959.

Common Name. Northern three-lobed violet.

Description. Foliage and peduncles moderately to densely hirsute, green, margins of leaf blades ciliate, peduncles nearly glabrous or sparsely hirsute; larger leaf blades shallowly to moderately pedately divided into 3 or 5 lobes, central lobe of terminal primary division elliptical to ovate or broadly triangular, lateral divisions undivided or shallowly cleft, sinuses between primary divisions not reaching more than 1/2 (2/3) the distance to the petiole summit, the longest axis of the lateral primary divisions or the intermediary lobe nearest the terminal primary division $<$ 1/2 the length of the midrib; calyx ciliate; lowest sepals oblong-ovate to ovate, obtuse to rounded at apex; cleistogamous capsule heavily purple-spotted or -blotched, on an initially prostrate peduncle arching upward abruptly just prior to dehiscence. Other features as in the species complex.

Similar Species. Same as the species complex.

Ecology. Dry to dry-mesic somewhat acidic sandy or clayey loam soils in dry to dry-mesic oak woodlands, often on slopes or drier terraces above streams, rivers, and lakes.

Distribution. Atlantic and Gulf Coastal Plains and lower to middle Piedmont in the Southeast, and in the Lower Midwest, Virginia to Tennessee, western Indiana, southern Illinois and eastern Kansas, south to Florida and eastern Texas (includes. *palmata* var. *triloba*, currently being disentangled from var. *palmata*; see Russell [1965] for an older taxon-specific map). See Fig. 90.

Rarity. Listed in Ontario and Vermont; Maine and Rhode Island (as *V. palmata*); and New Hampshire (as *V. palmata* var. *palmata*, but incorrect application).

Phenology. Phenology presumably same as the species complex.

Affinities. Same as the species complex.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1924), *V. brittoniana* (Brainerd 1906c, 1924), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Brainerd 1912, 1924), *V. cucullata* (Brainerd 1906c, 1913c, 1924; House 1924; Haines *et al*. 2011), *V. fimbriatula* (Brainerd 1906c, 1924; Haines *et al*. 2011), *V. hirsutula* (Brainerd 1906c, 1912, 1924; House 1924), *V. latiuscula* (Brainerd 1912, 1924; House 1924), *V. sagittata* (Brainerd 1906c, 1913c, 1924; House 1924), *V. sororia sensu stricto* (Greene 1989c; Brainerd 1912, 1924; House 1924; Scoggan 1978; Haines *et al*. 2011; Ballard 2013), *V. stoneana* (Brainerd 1910b, 1912, 1924), and *V. subsinuata* (Pollard 1902a; Brainerd 1912, 1924; Haines *et al*. 2011). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All the hybrids fail to reproduce by chasmogamous means. Some hybrids produce abortive cleistogamous flowers or capsules, while others produce very few viable seeds. The hybrid with *V. sororia* is subfertile, with up to 1/3 of its ovules fertilized.

Comments. In his protologue for *V. triloba*, von Schweinitz prefaced his description, "With diffidence, I venture to propose this new species, notwithstanding its striking characters, because I have found it but rarely. I have however met with it twice or thrice in different years, and in different places—videlicet rich woodland and meadows—constantly under the form here described. At all events it deserves to be pointed out for further observation." He cited no type specimen and referenced no specific collections. Stafleu and Cowan (1985) remark that von Schweinitz's types and herbarium reside at PH but additional material in several other herbaria. The sole von Schweinitz specimen of *V. triloba* at PH bears von Schweinitz's label but no indication by the author that the specimen is a type. Both McKinney and Gil-ad identified this sheet as holotype and published it as such, but the possibility still exists that von Schweinitz also used specimens dispersed to other herbaria in describing the species. The designation of the PH00029298 sheet to lectotype is corrected here.

Specimens presently identified as var. *triloba* in the main range of var. *palmata* may, at least in part, represent *de novo* hybrids of var. *palmata* and *V. sororia*, as the latter commonly grow near one another. For more information, see "Comments" under the species complex.

37c. *Viola palmata* (*avipes* variant). Fig. 92.

Common Name. Appalachian bird's-foot violet.

Description. Foliage and peduncles moderately to densely hirtellous or hirsute, blue- or gray-green, lower surface of leaf blades strongly purple-tinged, peduncles and calyx strongly purple-spotted, margins of leaf blades ciliate, peduncles sparsely to moderately hirtellous or hirsute; larger

FIG. 92. *Viola palmata* (*avipes* variant). Chasmogamous flowering habit (photo: Harvey Ballard).

leaf blades deeply pedately divided into 5 main lobes, the terminal primary linear-lanceolate division unlobed, lateral primary divisions widely divergent and each bilobate with the upper lobe linear-lanceolate and lower lobe bent downward and asymmetrically cleft with a smaller bottom lobe, these overlapping at the inner edges in living material, sinuses between primary divisions reaching nearly to the petiole summit; calyx ciliate; lowest sepals ovate, broadly rounded at apex; cleistogamous capsule heavily purple-spotted or blotched, on an initially prostrate peduncle arching upward abruptly just prior to dehiscence; seeds not yet known. Other features as in *V. palmata sensu lato*.

Similar Species. See the species complex.

Ecology. Moist sandy loam on shallow to steep slopes of open dry-mesic forests. The few plants on the Allegheny/Bath county line grew among heavy leaf litter in a very small area near the base of the steep slope below a large shale barrens complex, while the larger number of plants at the Floyd Co. site grew scattered in rocky soils in open rich dry-mesic forest.

Distribution. Two small populations known in Virginia's Appalachian Mountains, one in Douthat State Park on the Allegheny/Bath county line, and the other in Buffalo Mountain State Nature Preserve in Floyd Co. Fig. 93.

Rarity. None.

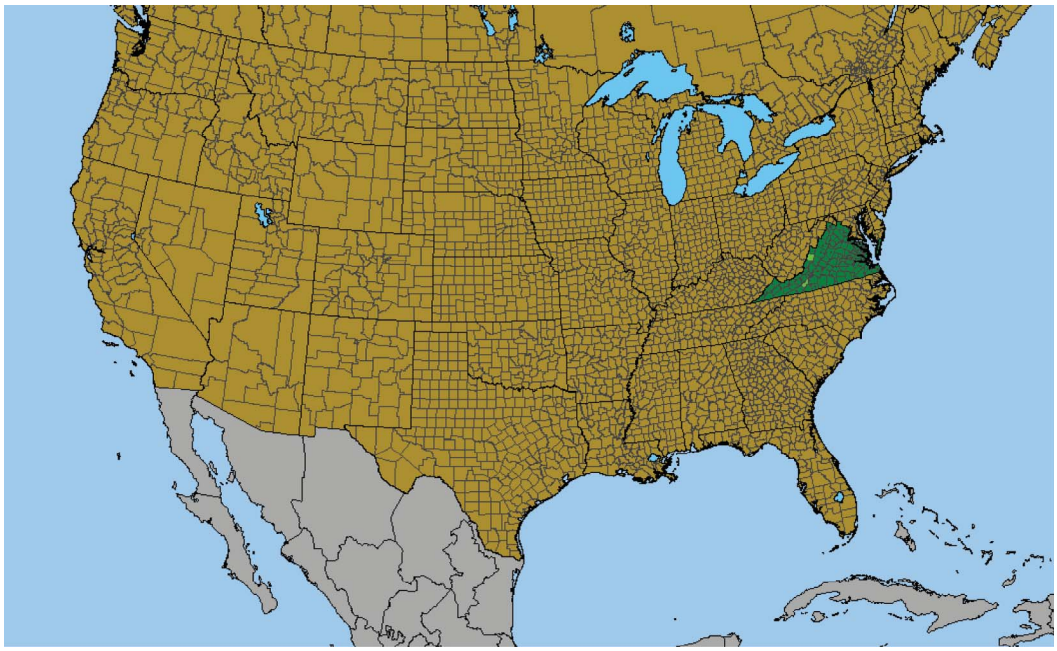

FIG. 93. United States county distribution of *Viola palmata* (*avipes* variant) (map: Biota of North America Program).

Phenology. Phenology presumably the same as the species complex.

Affinities. Same as the species complex.

Hybrids. None.

Comments. This is a very distinctive and rather local endemic in the Virginia mountains, occurring as scattered plants in two very small populations. Both populations are the result of intensive fieldwork with recurrent trips to the two sites; no herbarium specimens yet exist. The Allegheny/Bath Co. population has not been relocated in recent years. It should be vigorously sought in the Ridge and Valley province of western Virginia. The common name "Appalachian bird's-foot violet" well represents the distinctively divided leaf blades of this very rare variant.

37d. *Viola palmata* (*pseudostoneana* variant). Fig. 94.

Common Name. None.

Description. Foliage and peduncles moderately to densely hirsute, green, margins of leaf blades ciliate; larger leaf blades deeply biternately divided into (5)7 or 9 linear-lanceolate lobes, the terminal primary division divided just above the base into 2 linear-lanceolate suberect or strongly ascending to spreading (one on each side), the lateral primary divisions each deeply divided into 2–3 linear-lanceolate lobes or lunate to angulate, uncleft and merely toothed, sinuses between primary and lateral divisions reaching nearly to the petiole summit; calyx ciliate; lowest sepals in chasmogamous flower oblong-ovate to ovate and obtuse to rounded, in cleistogamous fruit broadly lanceolate and acuminate; cleistogamous capsule finely to heavily purple-spotted or -blotched, on an initially prostrate peduncle arching upward abruptly just prior to dehiscence; seeds pale golden- or honey-yellow with small scarcely visible to weak yellow-brown streaks and blotches. Other features as in *V. palmata*.

Similar Species. See the species complex.

Ecology. Drier sandy or sandy loam soils in open dry to dry-mesic woodlands, often on steeper slopes.

Distribution. Higher elevations of the Appalachian Mountains in the Ridge and Valley province, southern Pennsylvania south to North Carolina and eastern Tennessee. Fig. 95.

Rarity. None.

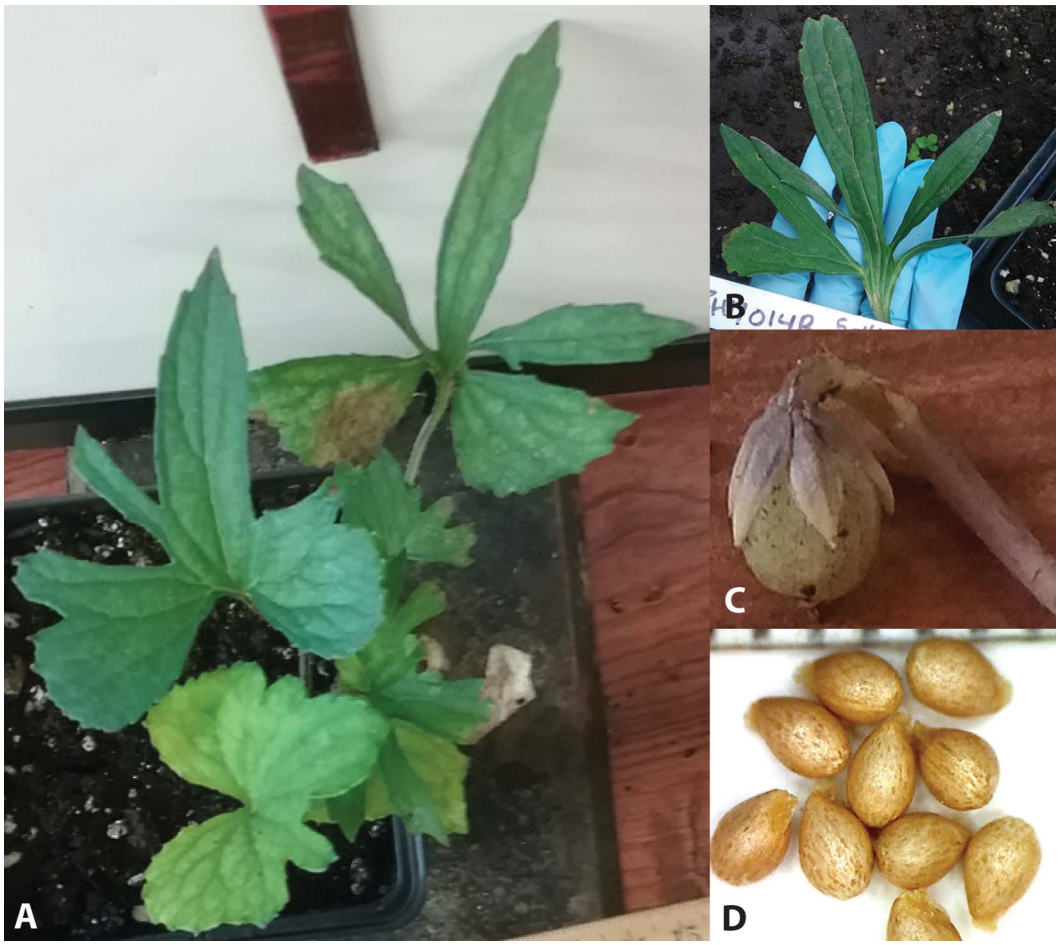

FIG. 94. *Viola palmata* (*pseudostoneana* variant). (A) Cleistogamous fruiting habit (photo: Jennifer Hastings). (B) Cleistogamous fruiting habit (photo: Jennifer Hastings). (C) Cleistogamous fruit (photo: Jennifer Hastings). (D) Seeds (photo: Jennifer Hastings).

Phenology. Phenology presumably same as species complex.

Affinities. Same as the species complex.

Hybrids. Hybridizes with *V. affinis* (Hastings 2018; H.E.B., personal observation) and *V. sororia sensu stricto* (Hastings 2018; H.E.B., personal observation). We have observed that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). Studies of reproductive behavior are needed.

Comments. This taxon is morphologically distinctive. It occurs sporadically along the central and southern Appalachian Mountains, based on herbarium specimens and on limited field studies in Pennsylvania and Virginia. The deeply biternate leaf blades vaguely recall those of *V. stoneana* but the insertion of the lateral lobes on the terminal primary division is subbasal rather than medial, and the present taxon has rather densely hirsute foliage (at least during chasmogamous flower) and other features similar to the accepted varieties of *V. palmata*. It shares biternate leaf blades with *V. palmata* (Red Hills variant) to the south of our region as well but mainly differs from that in the suberect to somewhat spreading lateral lobes on the terminal primary division of the leaf blade, chasmogamous flowers with shorter ovate-lanceolate to ovate obtuse sepals, cleistogamous fruits with broadly lanceolate acuminate sepals, and distribution at higher elevations in the central Appalachian Mountains; some reports of *V. triloba*

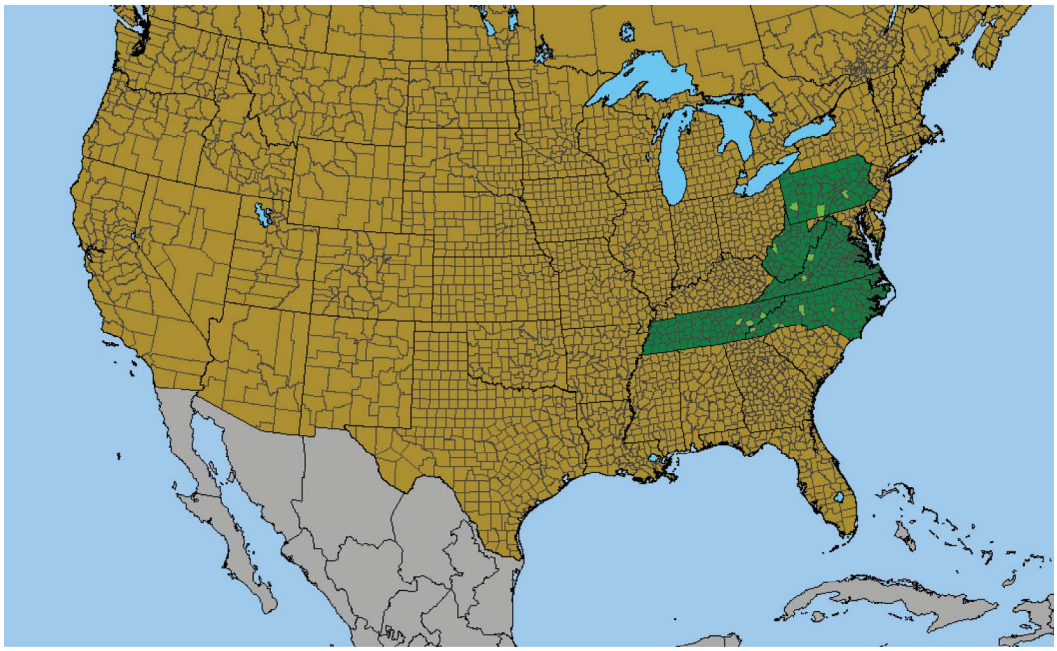

FIG. 95. United States county distribution of *Viola palmata* (*pseudostoneana* variant) (map: Biota of North America Program).

var. *dilatata* from the southern Appalachians in North Carolina and Tennessee are very likely this taxon. Henry's (1953a) report of *V. triloba* var. *dilatata* from Allegheny Co., PA, probably represents this taxon; a number of other herbarium specimens of the present taxon from west-central and montane areas of that state have been confirmed. Field studies by Jennifer Hastings (2018) have located a number of sites scattered along the Ridge and Valley province of western montane Virginia for this taxon. It is often found at sites with *V. palmata* var. *triloba* and *V. subsinuata*, and occasionally with *V. monacanora*; such mixed-species communities of diverse taxa with variously lobed leaf blades, plus their frequent hybrids with *V. sororia* and other entire-leaved species, has reasonably led some taxonomists to treat all plants as one extensively polymorphic violet species (*e.g.*, a heterogeneous and very broadly delimited *V. palmata*). Although surely more widely distributed than its sporadic Appalachian montane records suggest, the present taxon is poorly understood, since all specimens have been dismissed as *V. palmata* var. *dilatata*. It has only recently been narrowly delineated and recognized as a potentially distinct taxon and needs further study. Studies of population samples from several Virginia localities demonstrate that hybridization with *V. sororia* is common, producing plants with leaf blades less deeply dissected and often less pronouncedly biternate, and seeds with a darker, yellow-brown or brown ground color and more prominent brown streaks.

38. *Viola palustris* L., Sp. pl., ed. 1, 2: 934. 1753. Type: "Habitat in Europae frigidioris paludibus" [protologue] (lectotype (designated by Jonsell & Jarvis, Nordic J. Bot. 22 : 82. 2002): Herb. Linn. No. 278 (LAPP) (*n.v.*)). Fig. 96.

Viola palustris L. var. *pensylvanica* Ging., in DC., Prodr. 1: 294. 1824.

Viola rotundifolia Michx. var. *pallens* Banks ex Ging., in DC., Prodr. 1: 295. 1824; *Viola pallens* (Banks ex Ging.) Brainerd, Rhodora 7: 247. 1905; *Viola macloskeyi* F.E.Lloyd subsp. *pallens* (Banks ex Ging.) M.S.Baker, Madroño 12: 60. 1953; *Viola macloskeyi* F.E.Lloyd var. *pallens* (Banks ex Ging.) C.L.Hitchc., Vasc. Pl. Pacific NorthW. 3: 445. 1961. Type: Canada, Newfoundland and Labrador, 1766, *J. Banks s.n.* (lectotype (designated by Ballard Jr., H. E., D. A. Casamatta, M. M. Hall, R. A. McCauley, M. C. Segovia-Salcedo, and R. G. Verb, Brittonia 53(1): 131. 2001): BM000617600 (*n.v.*), internet image).

FIG. 96. *Viola palustris*. (A) Chasmogamous flowering habit (photo: Kim Blaxland). (B) Chasmogamous flower front view (photo: Kim Blaxland). (C) Chasmogamous fruit (photo: James Lindsey).

Viola palustris L. var. *leimonia* J.K.Henry, Fl. s. Brit. Columbia: 207. 1915.

Viola palustris L. subsp. *typica* M.S.Baker, Madroño 3: 235. 1936 [*nomen invalidum*].

Common Name. Northern marsh violet.

Description. Acaulescent stoloniferous perennials, colonial from slender creeping rhizome and lateral stolons, leaves, flowers, and fruits inserted separately along rhizome near apex, stolons surficial, produced in summer with leaves and cleistogamous flowers and fruits, $\leq$ 15 cm tall; foliage and peduncles gray-green, glabrous; leaves 2–5 during chasmogamous flower, spreading; stipules free, brownish, irregularly glandular-fimbriate; leaf blades undivided, largest $\leq 70 \times 41$ mm during fruit, round-reniform to reniform, base cordate, margins subentire to pronouncedly crenate, eciliate, apex subobtuse to rounded; chasmogamous peduncle held among or above the leaves; bracts positioned at or below the middle of the peduncle; chasmogamous flower $\leq$ 16 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate, rounded; auricles short and rounded, not elongating in fruit; corolla whitish or pink-mauve, throat greenish-white; spur short-globose, *ca*. 2.0 mm long, 1.5 $\times$ as long as auricles; all petals glabrous within; style and stamen appendages weakly exserted and scarcely visible in living material; cleistogamous flowers produced after chasmogamous, on ascending or erect peduncle shorter than or surpassing petioles; capsule 5–8 mm, green drying tan, unspotted or with fine red spots, glabrous; seeds *ca*. 1.7×1.0 mm, very dark brown to black, unspotted; $2n = 48$.

Similar Species. This species and *V. suecica* belong to the Palustres species group, sharing a creeping node-rooting rhizome with lateral stolons, leaves not forming a rosette but inserted individually along the length of the rhizome nearer the apex, broad stipules, reniform leaf blades, and violet corollas. It differs most conspicuously from *V. suecica* in its glabrous foliage, more numerous and larger leaves (at least during chasmogamous flower), bracts positioned at or below the middle of the peduncle, glabrous lateral petals, and darker unspotted seeds. In cleistogamous fruit, if the creeping rhizome with leaves inserted separately along its length are ignored, it can be distinguished from from *V. incognita* and *V. renifolia* by its subentire to crenate leaf blade margins, unspotted cleistogamous capsule, and dark unspotted seeds; and from *V. minuscula* by the proportionally broader glabrous leaves, and larger unspotted seeds.

Ecology. Alpine meadows, marshes, bogs, and lakeshores.

Distribution. Circumboreal; transcontinental Greenland, Newfoundland and Labrador to Alaska, south to New England (Maine and New Hampshire), South Dakota, Rocky Mountains (Colorado, Utah, and Idaho) and northern Cal-

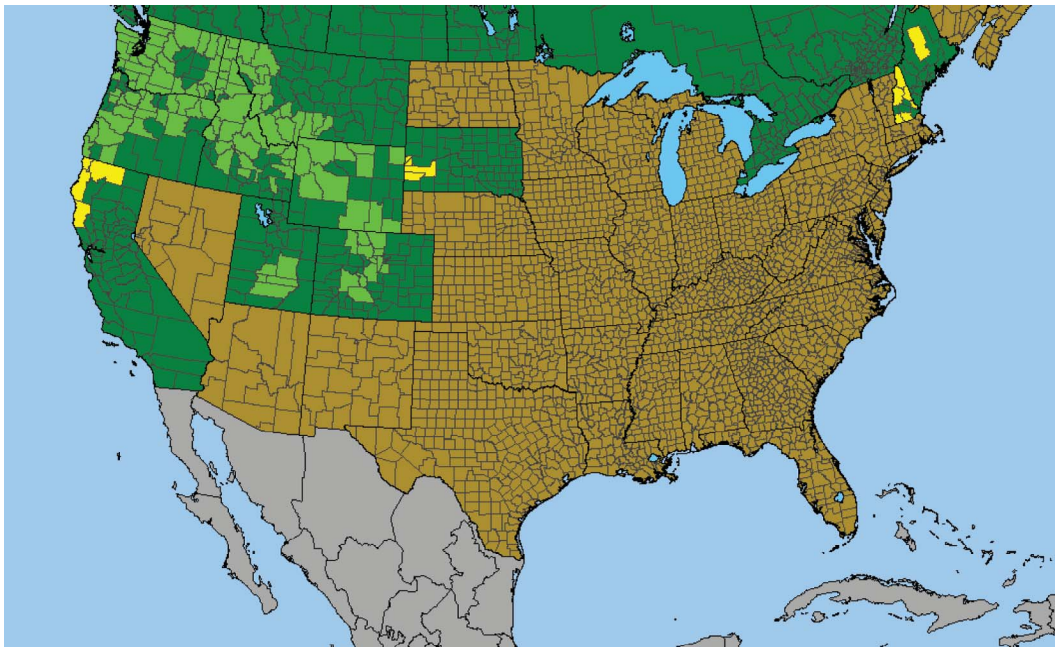

FIG. 97. United States county distribution of *Viola palustris*, including subsp. *palustris* and western *V. suecica* (map: Biota of North America Program).

ifornia (including *V. palustris* subsp. *brevipes* and western *V. suecica*, pending further studies to disentangle these taxa from *V. palustris sensu stricto*); Eurasia. Fig. 97.

Rarity. Listed in New Hampshire.

Phenology. Chasmogamous flower June–August, chasmogamous fruit July–August, cleistogamous fruit July–September.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer, in the Palustres species group.

Hybrids. Hybridizes with *V. suecica* (as *epipsila* subsp. *repens*) (Blaxland 2022), and probably with *V. minuscula* based on herbarium specimens and indications by Haines *et al*. (2011). The latter hybrid should be sought and examined, as the two species grow intermingled in the zone of overlap, according to northeastern herbarium specimens and floras. Both hybrids would be roughly intermediate in characteristics of foliage and chasmogamous floral traits (or more similar to *V. palustris* but would presumably be utterly sterile as triploids, failing to reproduce by chasmogamous flowers and producing abortive cleistogamous capsules or normal capsules without viable seeds. Studies are needed to assess these predictions.

Comments. Brainerd (1921b), Fernald (1950), Alexander (1963), Russell (1965), and Gleason and Cronquist (1991) recognized a broadly delimited *V. palustris* that explicitly or implicitly included *V. epipsila* (here treated as *V. suecica*). Brainerd Baird (1942), Scoggan (1978), Ballard (1985, 1995), Haines *et al*. (2011), and Little and McKinney (2015) maintained both as distinct species. White-flowered plants or populations found throughout the Rocky Mountain region of the West (particularly in the northern USA and adjacent Canada) were initially named *V. palustris* subsp. *brevipes* M.S.Baker. Clausen (1964) and Sorsa (1968) reported meiotic irregularities in plants matching Baker's description from the type locality in Colorado that indicated hybridization with another species or hybrid derivation, but morphologically the taxon was relatively stable and fertile. Scoggan and Haines treated the western white-flowered taxon as subsp. *brevipes*. Sorsa highlighted the taxonomic difficulties posed by an additional taxon in the Pacific Northwest coastal areas with an octoploid chromosome number like

that of *V. palustris* but with certain morphological features similar to those of *V. epipsila* (= *V. suecica*). Marcussen *et al*. (2012) and Blaxland *et al*. (2018) demonstrated different evolutionary origins and morphological distinctions between the Pacific Northwest violet and *V. palustris*, and Blaxland *et al*. described *V. pluviae* for the Pacific Northwest species.

During recent preparation of a worldwide classification of the genus *Viola* (Marcussen *et al*. 2022), Thomas Marcussen, Alexander Sennikov, and Jiří Danihelka reexamined morphology, cytology, and nuclear DNA content for the Palustres taxa worldwide. They recognized five distinct species, consisting of *V. epipsila sensu stricto* in western Eurasia; *V. palustris* in Europe and eastern North America; *V. suecica* (including the names *V. achyrophora*, *V. epipsiloides*, and *V. epipsila* subsp. *repens*) in Iceland and Siberia eastward through Beringia to central North America; *V. pluviae* in western coastal North America; and *V. palustris* var. *brevipes* (to be raised to species rank) in the Rocky Mountains of western North America. They indicated that *V. suecica* is composed of two morphologically distinct subspecies, subsp. *suecica* in Europe and *V. epipsila* subsp. *repens* (to be transferred to *V. suecica*) in North America. They are presently preparing a manuscript to elucidate the new taxonomic delimitations in the Palustres violets (T. Marcussen, personal communication).

At present we are delimiting *V. palustris* to include subsp. *brevipes* and map it as such, until further taxonomic studies disentangle the distinctions and ranges of the taxa. *Viola palustris sensu lato* ranges across North America, reaching south into our region only in the White Mountains of New Hampshire and in northern Maine. Previous reports of the present species in Maine were tentative, given the relative abundance of *V. minuscula* and difficulties with distinguishing the two species or possible hybrids between them. Nevertheless, we have confirmed the identity of some herbarium specimens from northern Maine to substantiate the occurrence of *V. palustris* there. As with *V. suecica*, the first author has relied heavily on the observations and images by Kim Blaxland ("Botanikim" website; Blaxford 2022), and on online images from far eastern North America, to characterize this species.

39. *Viola patrinii* DC., Prodr. 1: 293. 1824; *Viola mandshurica* W.Becker var. *patrinii* (Ging.) Y.N.Lee, Fl. Korea: 1159. 1996. Fig. 98.

Viola primulifolia Lour., Fl. Cochinch.: 513. 1790, *sensu auct*.

Viola nepaulensis DC. ex D.Don, Prodr. Fl. Nepal.: 205. 1825.

Viola grandifolia Wall., Numer. List: no. 1447. 1829 [not validly published].

Viola mysurensis B.Heyne ex Wall., Numer. List: no. 1446. 1829 [not validly published].

Viola chinensis G.Don, Gen. Hist. 1: 322. 1831.

Viola roxburghiana Voigt, Hort. Suburb. Calcutt.: 76. 1845.

Viola patrinii Ging. var. *subsagittata* Maxim., Mém. Acad. Imp. Sci. St.-Pétersbourg Divers Savans 9: 49. 1859; *Viola patrinii* Ging. f. *subsagittata* (Maxim.) Regel, Mém. Acad. Imp. Sci. Saint Pétersbourg, Sér. 7, 4(4): 24. 1861.

Viola patrinii Ging. var. *angustifolia* Regel, Bull. Soc. Imp. Naturalistes Moscou 34(II): 476. 1862; *Viola primulifolia* Lour.var. *angustifolia* (Regel) Nakai, Bull. Soc. Bot. France 72: 191. 1925; *Viola patrinii* Ging. f. *angustifolia* (Regel) F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 212. 1954.

Viola betonicifolia Bojer ex Baker, Fl. Mauritius: 10. 1877 [not validly published].

Viola averyi Kellogg, Pacific Rural Press 1879: 354. 1879.

Viola patrinii Ging. f. *hispida* W.Becker, Beih. Bot. Centralbl. 34(2): 245. 1916.

Viola phalacrocarpa Maxim. var. *glaberrima* W.Becker, Beih. Bot. Centralbl. 34(2): 246. 1916; *Viola phalacrocarpa* Maxim. f. *glaberrima* (W.Becker) F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 213. 1954.

Viola primulifolia var. *glabra* Nakai, Bull. Soc. Bot. France 72: 190. 1925; *Viola patrinii* Ging. f. *glabra* (Nakai) F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 212. 1954.

Viola primulifolia var. *prunellifolia* Nakai, Bull. Soc. Bot. France 72: 189. 1925.

Viola patrinii Ging. f. *prunellifolia* (Nakai) F.Maek., H.Hara, Enum. Spermatophytarum Japon. 3: 212. 1954.

Viola patrinii Ging. f. *toyokoroensis* Koji Ito, J. Jap. Bot. 71: 301. 1996.

Common Name. None in English.

Description. Acaulescent rosulate perennials from somewhat thick rhizome, $\leq$ 20 cm tall; foliage glabrous or puberulent, peduncles and

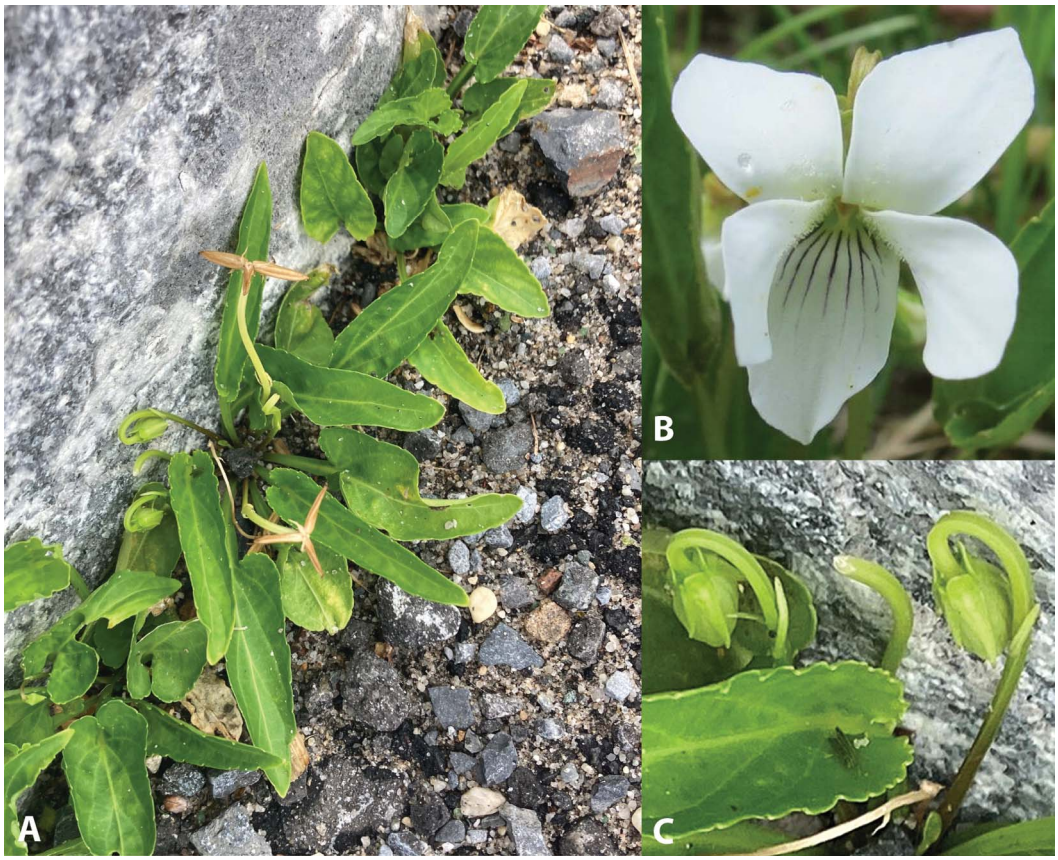

FIG. 98. *Viola patrinii*. (A) Cleistogamous fruiting habit (photo: "er-birds" [iNaturalist post 128326824]). B. Chasmogamous flower (photo: Vladimir Arkhipov). (C) Cleistogamous fruit (photo: "er-birds"; see Fig. 95A).

calyces green, plant glabrous throughout; stipules adnate to petiole for up to 2/3 their length, entire to remotely denticulate; petioles long and prominently winged; leaves erect, leaf blades undivided, largest $\leq 60 \times 20$ mm, narrowly lance-triangular to narrowly elliptical, base broadly cuneate or truncate to shallowly cordate with short divergent basal lobes, margins subentire to shallowly crenate, eciliate, apex acuminate to a narrowly rounded tip; chasmogamous peduncle held among leaves; chasmogamous flower *ca*. 10 mm; calyx glabrous, eciliate; lowest sepals lanceolate to ovate-lanceolate, acute to slightly obtuse; auricles short and rounded, not elongating in fruit; corolla white, throat white; spur cylindrical, *ca*. 3 mm, white; lateral petals densely bearded; chasmogamous and cleistogamous capsule not reported; seeds yellow-brown to dark brown; 2n = 12, 24, 36.

Similar Species. This species and others most similar to it are members of the predominately Asian subsect. *Patellares*, which consists of acaulescent nonstoloniferous violets with stipules at least half-adnate to their petioles, somewhat to very elongate spurs, and usually violet to purple corollas (this species produces white flowers). Three species in the subsection that are introduced in our region, including this one, have leaf blades longer than broad. This species differs from *V. japonica* in its glabrous or puberulent foliage, prominent wings on the petioles, white corolla with much shorter spur, and densely bearded lateral petals. It is distinct from *V. inconspicua* in the prominent wings on the petioles, entire to denticulate stipules, white corolla with slightly shorter spur, and yellow to brown seeds.

Ecology. Marshy to moist open places, and shaded forest edges in its native range (Chen *et al*.

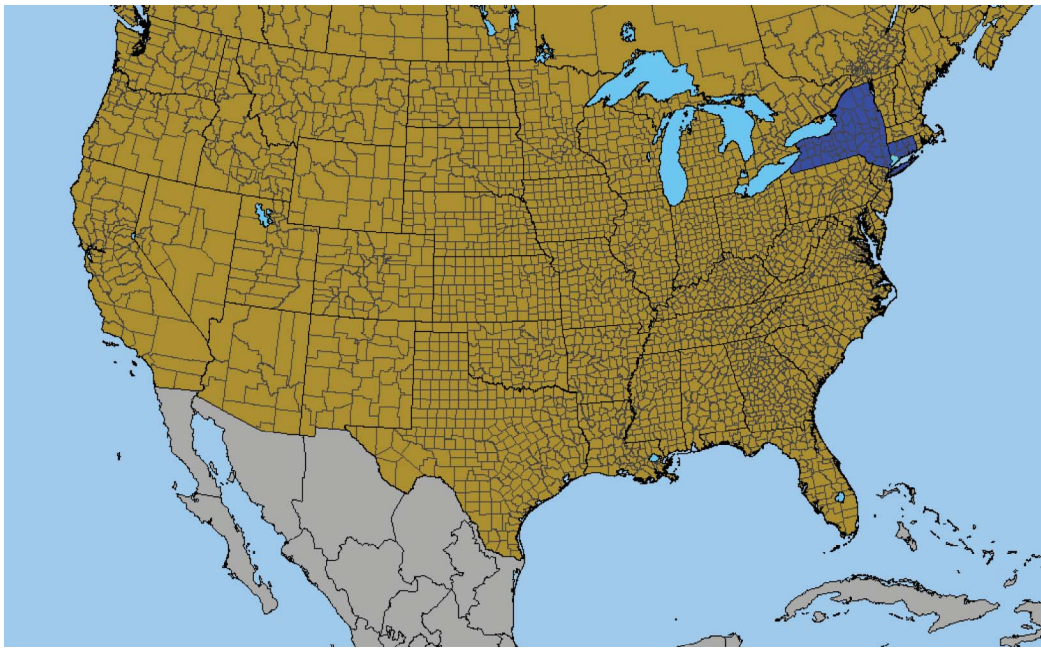

FIG. 99. United States county distribution of *Viola patrinii* (map: Biota of North America Program).

2007); recently introduced into suburban plantings and pavement cracks in our region.

Distribution. Widespread as a native in boreal and temperate eastern Asia; introduced to Costa Rica, Jamaica, Connecticut, and New York. Fig. 99.

Rarity. None.

Phenology. Chasmogamous flower May–June, fruit June–September in its native range (Chen *et al*. 2007).

Affinities. This species belongs to sect. *Plagiostigma* Godr., subsect. *Patellares* (Boiss.) Rouy & Foucaud.

Hybrids. None.

Comments. Despite previous reports using the name *V. patrinii*, the localities reported here are the first confirmed in North America; other records belong to different introduced Asian species. The description was composed mostly from Chen *et al*. (2007), and a few iNaturalist images.

40. ***Viola pectinata*** E.P.Bicknell, Torreya 4: 129. 1904; *Viola brittoniana* Pollard var. *pectinata* (E.P.Bicknell) Alexander, in Gleason, New Ill. Fl. Northeastern U.S. 2: 558. 1952; *Viola brittoniana* Pollard f. *pectinata* (E.P.Bicknell) Gil-ad, Boissiera 53: 54. 1997. Type: USA, New York. [Nassau Co.], L.[ong] I.[sland], Woodmere, border of salt marsh with *V. brittoniana*, 21 May 1904, *E. P. Bicknell s.n*. (holotype: NY00018233; isotype: GH00067144). Fig. 100.

Common Name. Pectinate violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm tall; foliage and peduncles green, lower surface of leaf blades commonly tinged with purple, surfaces glabrous or sparsely appressed-hirtellous along veins; stipules free, glandular-fimbriate; leaves ascending; leaf blades undivided, largest $\leq$ 65 $\times$ 87 mm, in chasmogamous flower longer than broad, narrowly ovate-triangular (rarely lance-triangular) with acute or acuminate (occasionally narrowly rounded) apex, in fruit as broad as to much broader than long, broadly ovate to deltate-reniform with abruptly acute apex, base subtruncate to cordate, margins prominently serrate and becoming pectinate near widest point of leaf, eciliate or ciliolate, apex sharply acute to subacuminate; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 22 mm; calyx glabrous, eciliate; lowest sepals linear-lanceolate to lanceolate, acuminate; auricles short or prominent, entire or erose,

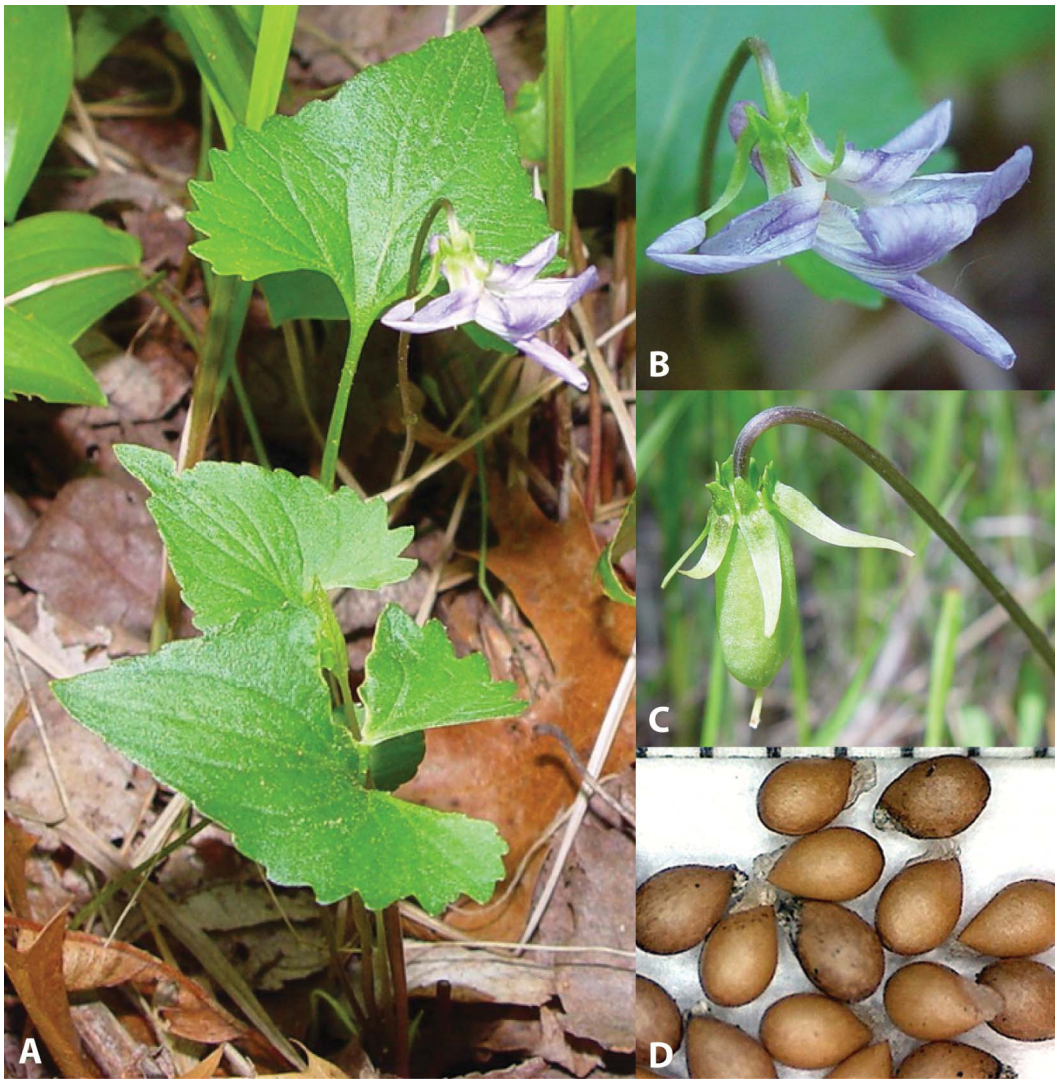

FIG. 100. *Viola pectinata*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust). (C) Chasmogamous fruit (photo: Arthur Haines, Native Plant Trust). (D) Seeds from herbarium specimen: Transplanted from North Carolina, Gates Co., *H. Ballard et al. 15-016W* (BHO).

elongating to 3 mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, on erect peduncles much shorter than to slightly surpassing the petioles; capsule 9–14(18) mm, yellow-green drying tan, unspotted, glabrous; seeds 1.3–1.9 × 0.8–1.3 mm, light to medium-dark brown, unspotted.

Similar Species. This species is unique among the *Borealiamericanae* in its undivided leaf blades with prominently pectinate margins, and it is similar to other species with strictly or nearly glabrous foliage and leaf blades longer than broad in chasmogamous flower that broaden substantially in fruit. In chasmogamous flower, besides the leaf blade features this species can be distinguished from *V. affinis* by its prominent quadrate auricles; from *V. cucullata* by its lack of a conspicuously contrasting dark purple eyespot around the throat,

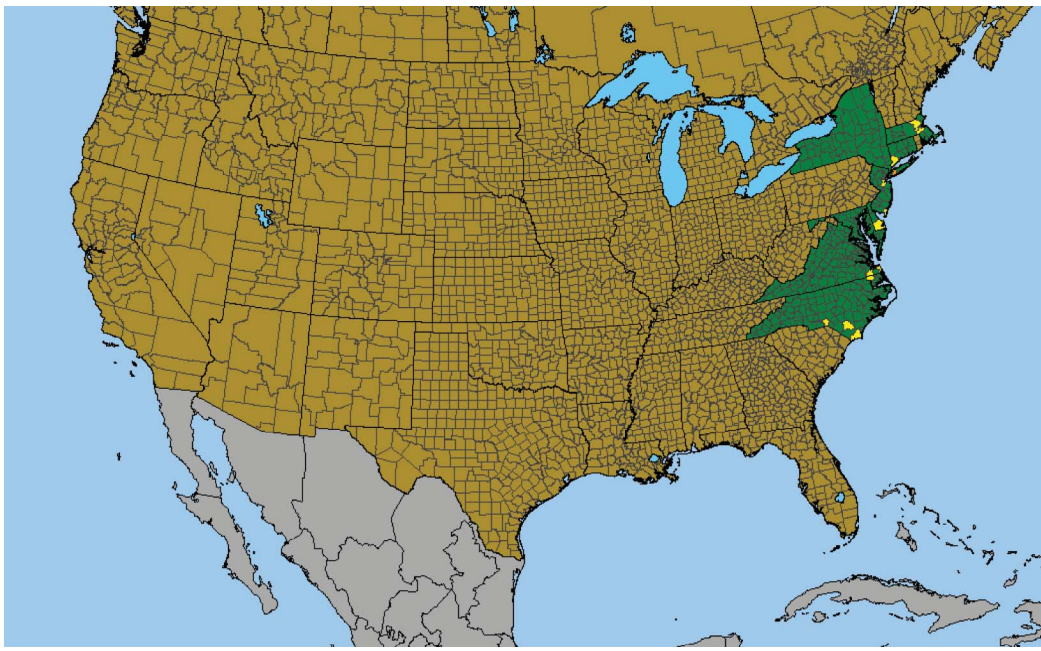

FIG. 101. United States county distribution of *Viola pectinata* (map: Biota of North America Program).

long filiform to narrowly linear hairs in the lateral petal beards, and densely bearded spurred petal; from *V. langloisii* south of our region by its strongly ascending to erect leaves, and densely bearded spurred petal; from *V. missouriensis* by its linear-lanceolate to lanceolate acuminate eciliate sepals, and densely bearded spurred petal; and from *V. pratincola* and *V. retusa* by its occasionally sparsely appressed-hirtellous leaf laminas. In cleistogamous fruit, its distinctive leaves and unspotted light to medium-dark brown seeds separate it from *V. communis*, *V. cucullata*, *V. langloisii*, *V. pratincola*, and *V. retusa*; and additionally its unspotted cleistogamous capsule on an erect peduncle set it apart from *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant).

Ecology. Moist sandy or peaty soils, sphagnous ground and seeps of coastal (occasionally brackish) marshes and riverbanks, and fields, meadows, trail edges, and forest clearings in formerly natural habitats.

Distribution. Atlantic Coastal Plain, closely following the distribution of *V. brittoniana*, Massachusetts south to North Carolina. Fig. 101.

Rarity. Listed in New Jersey (as *V. brittoniana* var. *pectinata*).

Phenology. Chasmogamous flower April–June, chasmogamous fruit May–July, cleistogamous fruit July–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Pedatifida species group.

Hybrids. Hybridizes with *V. brittoniana* (Brainerd 1906c, 1924; Haines *et al*. 2011; H.E.B., personal observation) and *V. cucullata* (Brainerd 1924). The first author has observed several specimens and a few living plants of the hybrid and found them to exhibit more or less precisely intermediate characteristics of chasmogamous flowers, foliage, and cleistogamous capsule traits. No information on chasmogamous reproduction is available, but cleistogamous capsules in hybrid individuals transplanted from multiple sites in New Jersey and North Carolina were fully formed and mostly or entirely full of viable seeds.

Comments. Brainerd (1921b), Russell (1965), Ballard (2000), Weakley *et al*. (2000), and Little and McKinney (2015) included the present species in *V. brittoniana*, and McKinney (1992) and McKinney and Russell (2002) included it in *V. pedatifida* subsp. *brittoniana*, without formal recognition. Brainerd Baird (1942) and Alexander

(1963) treated it as a variety, while Gil-ad (1995, 1997) made a new combination for it as a form, under *V. brittoniana*. Haines *et al*. (2011), however, maintained it as a distinct species. All authors prior to Haines *et al*. who explicitly mentioned this taxon by name asserted that it was identical to *V. brittoniana sensu stricto* in all features except for an undivided leaf blade. Gil-ad described some micromorphological differences in seed coat sculpturing. Haines *et al*. pointed out that the present taxon differed substantially from *V. brittoniana* in outline and marginal dentition and that crosses between the two taxa expressed intermediacy, indicating multi-genic differences in leaf blade morphology and not a simple allelic phenotype difference. More thorough examination of many specimens and a number of populations in the field, comparing this and *V. brittoniana sensu stricto*, have supported the argument of Haines *et al*., revealing a number of additional differences besides leaf cutting. These include a strongly triangular to deltate-triangular leaf blade outline, subcordate to truncate base, narrowly acute apex, numerous and pronounced marginal teeth, and additional micromorphological differences observed in lateral petal trichomes and seed surfaces. Although the present taxon grows as scattered plants or very small populations in the immediate vicinity of *V. brittoniana* in the northern states, it commonly forms substantial to large uniform populations well removed from the latter species in Virginia and the Carolinas. Furthermore, harvested mature cleistogamous seeds from living plants from New Jersey are statistically indistinguishable in dimensions from *V. brittoniana* in the area, whereas seeds from plants in the mid-Atlantic Coastal Plain are statistically larger than seeds of *V. brittoniana* taken from the same area. The current evidence indicates that the present taxon is divergent from *V. brittoniana* in a number of vegetative and reproductive traits, and in the southern half of its range the taxon maintains itself separately from *V. brittoniana*. Herbarium specimens and living plants of presumed F_1 hybrids between the two taxa have been confirmed from throughout the range of the present species. Under the unified species concept, the present taxon is justifiably maintained at species rank.

41. ***Viola pedata* L.**

Infraspecific taxa belonging to this species include the following:

41a. *Viola pedata* L. subsp. *pedata*

41b. *Viola pedata* L. subsp. *cuneatiloba* (Brainerd ex Fernald) H.E.Ballard

Common Names. Bird's-foot violet, crow's-foot violet, squirrel corn bird's-foot violet.

Description. Acaulescent rosulate perennials from thick barrel-like rhizome, $\leq$ 23 cm; foliage and peduncles gray-green, often finely red-spotted, glabrous or sparsely hispidulous; stipules adnate to petiole for most of their length, glandular-fimbriate; homophyllous, leaves erect to ascending, smaller leaf blades shallowly to moderately pedately divided, larger blades deeply pedately divided into usually 7–11 linear-oblanceolate lobes, 1 lobe in the terminal primary division and 3–5 in each lateral primary division, outline broadly ovate to reniform, base typically truncate to cordate, margins entire or with 1–2 subapical crenations or teeth on either side, apex broadly rounded, or rarely leaf blades broadly obrhombic to broadly obovate in outline and with a few shallow apical lobes due to partial fusion of leaf segments (subsp. *pedata*), or at least some leaf blades deeply "triternate" with the terminal primary division and lateral secondary divisions deeply divided into a number of crowded narrowly linear ultimate segments (subsp. *cuneatiloba*), largest $\leq 52 \times 70$ mm, margins ciliate; chasmogamous peduncle held above leaves; chasmogamous flower $\leq$ 30 mm; calyx glabrous, ciliate; lowest sepals linear-lanceolate, acuminate; auricles prominent, entire, not elongating in fruit; corolla pale to medium blue or upper petals purple-black, white throat color extending onto visible proximal portions of lateral and spurred petal, throat white; spur inconspicuous, slender; all petals glabrous; cleistogamous flowers lacking; capsule 5–10 mm, green drying brown, unspotted or commonly with dense fine red spots, glabrous; seeds $1.7–1.8 \times 0.9–1.1$ mm, medium orange-brown, unspotted; $2n = 54$.

Similar Species. This species is unique in its short erect barrel-like rhizome, long-adnate stipules, blue corolla (occasionally with upper petals purple-black) with all petals glabrous within, and a short slender cylindrical spur. The leaf blades of *V. pedata* subsp. *pedata* are superficially similar to those of *V. pedatifida,* with which it is commonly confused, but it differs most obviously in the undivided terminal primary division of the leaf blade, and by its glabrous petals (and the

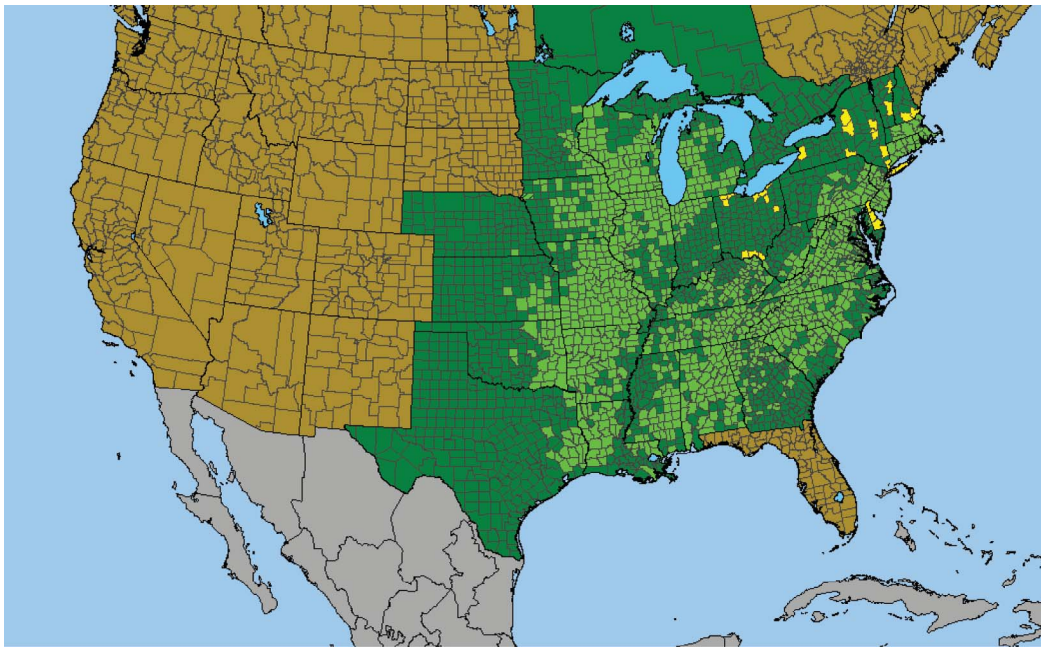

FIG. 102. United States county distribution of *Viola pedata* (map: Biota of North America Program).

bicolorous corolla pattern). The other infraspecific taxa have more conspicuously unusual leaf blade division patterns and are even more divergent from other species in our region.

Ecology. Dry sandy or gravelly soils in prairies, openings in oak savannas and xeric slopes in oak woods, often also on well-drained roadbanks below forests.

Distribution. Widely distributed in eastern North America, New Hampshire to North Dakota, south to southern Georgia and eastern Texas. Fig. 102.

Rarity. Listed in New York, Ohio, and Ontario; in Delaware and New Hampshire (as *V. pedata* var. *pedata*).

Phenology. Chasmogamous flower March–July (Sepember–November), chasmogamous fruit May–July.

Affinities. This species belongs to the monotypic Birds-foot Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Pedatae* (Pollard) Brizicky.

Hybrids. Russell and Bowen (1960) reported hybridization with *V. primulifolia* to account for the leaf morphology of *V. pedata* var. *flabellata* D.Don, another taxon south of our region; this hypothesis was not supported in unpublished studies with additional specimens by the first author.

Comments. Brainerd (1921b), Russell (1965), Gleason and Cronquist (1991), McKinney (1992), Ballard (2000, 2013), Haines *et al*. (2011), and Voss and Reznicek (2012) recognized *V. pedata* without infraspecific taxa. Brainerd Baird (1942), Henry (1953a), Alexander (1963), Scoggan (1978), Strausbaugh and Core (1978), and Swink and Wilhelm (1979) distinguished plants with bicolorous corollas as var. *pedata* and those with concolorous corollas as var. *lineariloba* DC. (Brainerd Baird inadvertently misspelling the epithet as "*liniarifolia*"), while Ballard (1995) treated the concolorous-flowered taxon as f. *rosea* Sanders, the earliest name at the rank of forma that was appropriate for a widespread population-level polymorphism. Fernald (1949) recognized distinctive plants with triternately divided leaf blades in the east-central Appalachian Mountains and adjacent Piedmont as f. *cuneatiloba* under var. *lineariloba* (Fernald 1950).

Until now, Fernald's form has been ignored in the taxonomic literature. Weakley *et al*. (2012) synonymized all names associated with corolla color but recognized var. *pedata* for plants with deeply pedately divided leaf blades and var.

flabellata for plants endemic to the Sandhills region with obcuneate apically incised or toothed leaf blades. Although some authors have mentioned that var. *linearilobа* DC., with concolorous flowers, produces leaf blades divided into linear lobes, this supposed distinction actually confuses the different morphologies of leaves produced during early chasmogamous flower *versus* those during late chasmogamous flower and fruit on the same plants. The two corolla color morphs (excluding albinos) behave as classic population-level allelic polymorphisms without coordinate differences in leaf morphology or other features and expressed with a slight geographic north-south trend. While northern populations are largely or exclusively composed of concolorous-flowered individuals, the proportion of bicolorous-flowered plants generally increases moving southward. Although the bicolorous form in particular is striking, the two floral forms are not regarded here as worthy of formal taxonomic recognition. Albinos are found in both color forms, and rose-colored petals have been documented rarely in the concolorous-flowered form. The leaf variants, on the other hand, are unusual and geographically restricted, and may produce either corolla color morph. Most specimens of subsp. *cuneatiloba* with label data specifying corolla color or with plants exhibiting it bear bicolorous corollas (in opposition to Fernald's inclusion of it under concolorous-flowered var. *linearilobа*). Neither the early nor late sets of leaves in subsp. *pedata* are identical to those of the other infraspecific taxa. The production of either corolla color morph in the taxa recognized here, and the morphological differences in leaf dissection across the growing season among the taxa, indicate that the three taxa constitute distinct gene pools with different developmental genetic programs. Because the *cuneatiloba* taxon is ecologically and geographically restricted to a region with a geologic basis, a new combination at subspecies rank is made here; the same action will be taken later for var. *flabellata*. The rank of subspecies is adopted, following the recommendation of Ellison *et al*. (2014) to utilize subspecies as the appropriate rank to formally recognize a taxon between the ranks of species and forma. Since var. *ranunculifolia* as a leaf phenotype appears sporadically over the range of the species and shows no particular ecological, geologic restriction, or geographic restriction, it appears to represent arrested random leaf development mostly in subsp. *pedata*, and it is included as a synonym under that name.

41a. *Viola pedata* L. subsp. ***pedata***, Sp. pl., ed. 1, 2: 933. 1753. Type: USA "Habitat in Virginia" [protologue], [no date], [Kalm s.n.] (lectotype designated by Reveal & al., Huntia 7: 238. 1987: Herb. Linn. No. 1052.2 (LINN-HL1052-2), Global Plants Database image!). Fig. 103.

Viola multifida Mill., Gard. Dict., ed. 8: n. 5. 1768.

Viola ranunculifolia Juss. ex Poir., Encycl. [J. Lamarck *et al*.] 8: 626. 1808; *Viola pedata* L. var. *ranunculifolia* (Juss. ex Poir.) Ging. ex DC., Prodr. 1: 291. 1824; *Viola pedata* L. f. *ranunculifolia* (Juss. ex Poir.) Fernald, Rhodora 51: 56. 1949.

Viola digitata Pursh, Fl. Amer. sept. 1: 171. 1813.

Viola pedata L. var. *velutina* Schwein., Amer. J. Sci. 5: 51. 1822.

Viola pedata L. var. *atropurpurea* DC., Prodr. 1: 291. 1824.

Viola pedata L. var. *linearilobа* DC., Prodr. 1: 291. 1824; *Viola pedata* L. f. *linearilobа* (Ging.) F.Seym., Fl. New England, ed. 2: 602. 1982.

Viola pedata L. var. *alba* Thurb., Bull. Torrey Bot. Club 1(5): 20. 1870; *Viola pedata* L. f. *alba* (Thurb.) Britton, Bull. Torrey Bot. Club 17: 124. 1890; *Viola pedata* L. var. *linearilobа* DC. f. *alba* (Thurb.) House, Bull. New York State Mus. Nat. Hist. 243-244: 46. 1923 ["1921"].

Viola pedata L. f. *bicolor* Pursh ex Britton, Bull. Torrey Bot. Club 17: 123. 1890.

Viola ampliata Greene, Leafl. Bot. Observ. 1(1): 3. 1903–1906.

Viola pedata L. var. *inornata* Greene, Pittonia 3: 35. 1896; *Viola inornata* (Greene) Greene, Leafl. Bot. Observ. 1(1): 2. 1903–1906.

Viola pedata L. f. *rosea* A. L. Sanders, Rhodora 13: 172. 1911; *Viola pedata* L. var. *linearilobа* DC. f. *rosea* (A. L. Sanders) House, Bull. New York State Mus. Nat. Hist. 243–244: 56. 1923 ["1921"].

Common Names. Bird's-foot violet, crow's-foot violet.

Description. Largest leaf blades deeply pedately divided into usually 7–11 linear-oblanceolate lobes, 1 lobe in the terminal primary division and 3–5 in each lateral primary division, outline broadly ovate to reniform, base typically truncate to cordate, margins entire or with 1–2 subapical crenations or teeth on either side, apex broadly

FIG. 103. *Viola pedata* subsp. *pedata*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (bicolorous floral morph) (photo: Arthur Haines, Native Plant Trust). (C) Chasmogamous flower front view (concolorous floral morph) (photo: Arthur Haines, Native Plant Trust).

rounded, or rarely leaf blades obrhombic or obovate in outline and shallowly to moderately lobed due to partial fusion of leaf segments (see "Comments" regarding the "*ranunculifolia*" phenotype under *V. pedata*). Other features are identical to the species.

Similar Species. Same as the species.

Ecology. Same as the species.

Distribution. Same as the species. See Fig. 102.

Rarity. Same as the species.

Phenology. Same as the species.

Affinities. Same as the species.

Hybrids. None.

Comments. The bicolorous floral morph of subsp. *pedata* in particular has been lauded as "the queen of violets," and it is certainly one of the more stunning violets of our region. Even extracting the two subspecies expressing the most extreme examples of leaf blade dissection (subsp. *cuneatiloba*, and var. *flabellata* south of our region, the remaining "typical" variety still embraces considerable leaf blade variation, including both developmental variation within individuals through the growing season and among individuals within populations. The present taxon is easily distinguished in chasmogamous flower from *V. pedatifida*, but fruiting specimens are often confused in their broad zone of overlap in the Midwest. The strictly pedately divided leaf blades of subsp. *pedata* are diagnostic, and the short vertical barrel-like rhizome, long-adnate stipules, and lack of cleistogamous reproduction further separate it. *Viola pedata* as a whole inhabits far more xeric, sandy, or gravelly acidic soils than are

FIG. 104. *Viola pedata* subsp. *cuneatiloba*. Chasmogamous flowering habit from herbarium specimen: West Virginia, Greenbrier Co., Kate's Mountain, *J. K. Small s.n*. (part of holotype of *V. pedata* f. *cuneatiloba* Brainerd ex Fernald).

typical for *V. pedatifida*. Robarts (2013) conducted population genetic studies on the subspecies and found significant diversity.

41b. *Viola pedata* L. subsp. ***cuneatiloba*** (Brainerd ex Fernald) H.E.Ballard, **comb. nov.** *Viola pedata* L. f. *cuneatiloba* Brainerd ex Fernald, Rhodora 51: 56, pl. 1136, fig. 3. 1949. Type: USA West Virginia. Greenbrier Co., Kate's Mountain, near White Sulphur Springs, 3300 feet, *J. K. Small s.n*. (holotype: GH00067145, internet image). Fig. 104.

Common Name. Squirrel corn bird's-foot violet.

Description. Smaller leaf blades pedate-pinnatifid or "biternately" divided, largest leaf blades deeply "triternately" dissected, with the terminal primary division and lateral secondary divisions deeply divided into a number of crowded narrowly linear ultimate segments. Other features are identical to the species.

Similar Species. Same as the species.

Ecology. Same as the species.

Distribution. Regional endemic of the central Appalachian Shale Barrens region, southwestern New Jersey and Pennsylvania to Virginia and eastern West Virginia. Fig. 105.

Rarity. None.

Phenology. Presumably same as the species.

Affinities. Same as the species.

Hybrids. None.

Comments. This regional endemic has been synonymized under *V. pedata* without recognition following Fernald's description as a form. It appears to be restricted to shale barrens slopes. Specimens are common throughout the narrow regional distribution noted, suggesting that an ecological or physiological component may have been involved in the evolution of the taxon, or perhaps the ancestral population originated in a small geographic area or "refugium" before dispersing. With the distinctive morphology of the leaf blades and confinement to the Shale Barrens region, subspecies status seems appropri-

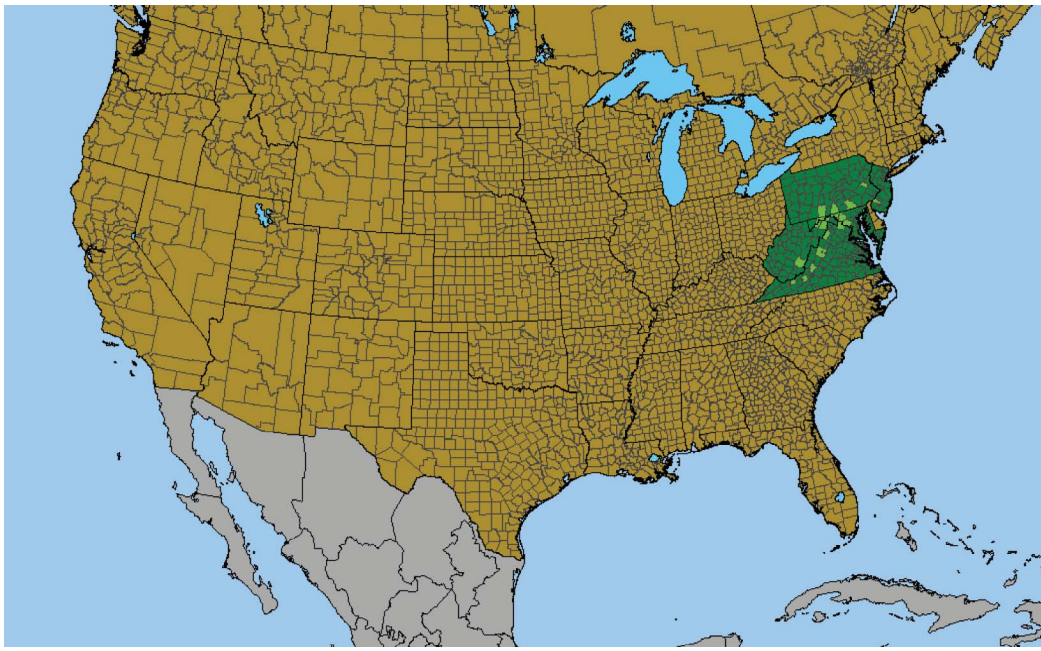

FIG. 105. United States county distribution of *Viola pedata* subsp. *cuneatiloba* (map: Biota of North America Program).

ate. Adopting the recommendation of Ellison *et al*. (2014) to utilize subspecies as the appropriate rank to formally recognize a taxon between the ranks of species and forma, f. *cuneatiloba* is raised to subspecies here. The "triternately" dissected leaf blades superficially resemble squirrel corn (*Dicentra canadensis* (L.) Bernh.), prompting the common name proposed here. See *V. pedata* for comments regarding the nomenclatural origin of this taxon. Although a substantial number of collections have been confirmed, this taxon is poorly known, and photographs are unavailable; it should be sought and studied in its narrow geographic distribution.

42. ***Viola pedatifida*** G.Don, Gen. hist. 1: 320. 1831; *Viola palmata* L. var. *pedatifida* (G.Don) Cronquist, Man. Vasc. Pl. NorthE. U.S. Canad., ed. 2: 864. 1991 Type: unknown. Fig. 106.

Viola delphinifolia Nutt. ex Torr. & A.Gray, Fl. N. Amer. 1(1): 136. 1838.

Common Names. Larkspur violet, prairie violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 27 cm tall; foliage and peduncles green with lower surface of leaf blades often tinged purple, petioles and peduncles glabrous or occasionally sparsely hirtellous (possibly resulting from hybridization with *V. sororia*), leaf blades finely appressed-hirtellous along veins and ciliolate; stipules free, irregularly glandular-fimbriate; homophyllous, leaves erect to ascending, smallest leaf blades palmatifid, largest deeply (sub)triternately divided into (13)17–25 narrowly linear ultimate lobes, central lobe of terminal primary division not distinctly broader than its lateral lobes, largest $\leq$ 55 $\times$ 87 mm, outline deltate-reniform or less often broadly ovate, base broadly cuneate to subcordate, margins entire, appressed-ciliolate, apex obtuse to truncate; chasmogamous peduncle held among or above the leaves; chasmogamous flower $<$ 25 mm; calyx glabrous, ciliate; lowest sepals lanceolate, acuminate; auricles short to somewhat prominent and entire, elongating to 3 mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, peduncle erect and commonly shorter than the petioles; capsule 9–12 mm, green drying tan, unspotted, glabrous; seeds 1.7–2.2(2.5) $\times$ 1.1–1.3 mm, medium brown, unspotted; $2n = 54$.

FIG. 106. *Viola pedatifida*. (A) Chasmogamous flowering habit (photo: Peter M. Dziuk). (B) Leaf (photo: Peter M. Dziuk). (C) Chasmogamous flower front view (photo: Katy Chayka). (D) Seeds from herbarium specimen: Minnesota, plant X, *O. Gockman s.n.* (BHO).

Similar Species. The broadly ovate to deltate-reniform triternately divided leaf blades with slender linear ultimate segments are distinctive in this species and few others can be confused with it. It occasionally grows with *V. pedata* in drier prairies and the two are commonly mistaken for each other, but this species can immediately be distinguished by its ascending elongate rhizome, 2- to 3-times-divided terminal primary division on the largest leaf blades, free stipules, and densely bearded lateral and spurred petals. Like all other native *Viola* species in our region except for *V. pedata*, it expresses a mixed breeding system that shifts to cleistogamy in the summer, in which the capsules can easily be identified as cleistogamous by the tiny tightly curled style at the apex; *V. pedata* is strictly chasmogamous and, as such, does not produce such capsules after chasmogamous flower. This species can be distinguished from *V. brittoniana*, the other cut-leaved species in the Pedatifida group, by its more extensively divided leaf blades with equally slender ultimate segments, usually ciliate sepals, and larger seeds. It was previously confused with but is different from *V. tenuisecta* in its triternate leaf blades appressed-hirtellous along veins, lanceolate sharply acuminate ciliate sepals, prominent auricles, densely bearded spurred petal, unspotted cleistogamous capsule on an erect peduncle, and unspotted brown seeds. It can be distinguished from *V. baxteri* and *V. subsinuata* by its glabrous or sparsely hirtellous foliage, the indument (when present) composed of shorter hairs, lanceolate sharply acuminate ciliate sepals, prominent auricles, densely bearded spurred petal, unspotted cleistogamous capsule on an erect peduncle, and unspotted brown seeds.

Ecology. Rich organic often alkaline loam of dry-mesic and mesic prairies, openings in savannas.

Distribution. Great Plains and Prairie provinces, southwestern and northern Michigan to Alberta, south to northwestern Arkansas, eastern Oklahoma, and northeastern Wyoming; slightly disjunct in

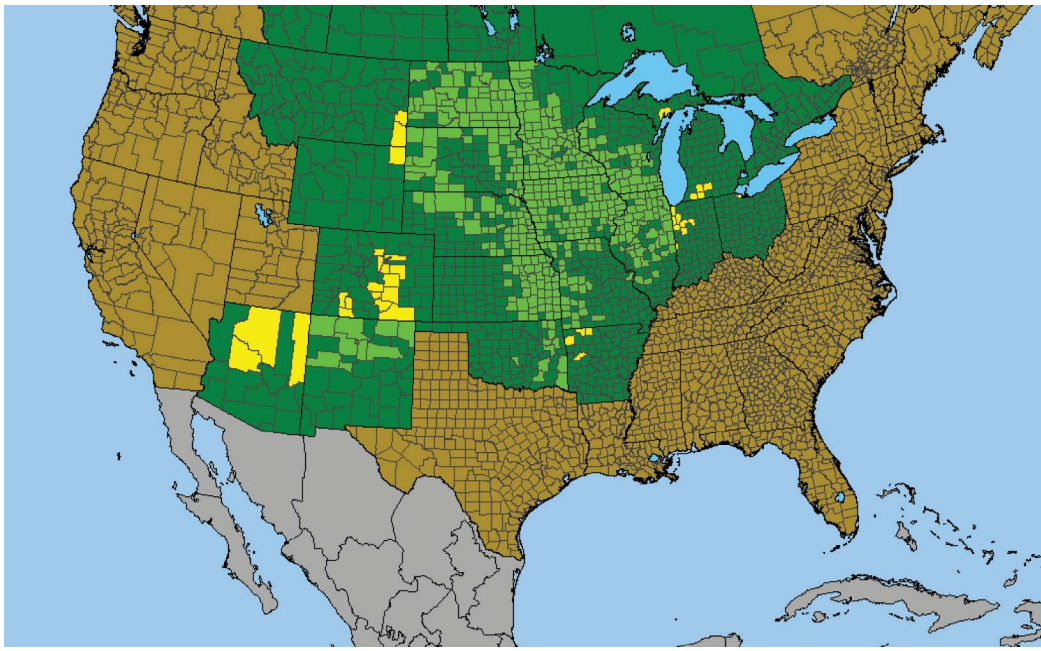

FIG. 107. United States county distribution of *Viola pedatifida* (map: Biota of North America Program).

the Southwest in Colorado, northern New Mexico, and Arizona; and in the eastern Great Lakes region in south-central Ontario near Brantford, and northern Ohio. Fig. 107.

Rarity. Listed in Indiana, Michigan, Ohio, and Ontario.

Phenology. Chasmogamous flower April–May, chasmogamous fruit May–June, cleistogamous fruit May–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Pedatifida species group.

Hybrids. Hybridizes with *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Greene 1903a; Brainerd 1913a, 1924), *V. missouriensis* (Ballard 2013), *V. nephrophylla* (Brainerd 1913a, 1924), *V. pratincola* (as *V. papilionacea*) (Russell 1956a), *V. sagittata* (Brainerd 1913a, 1924; Ballard 2013), *V. sororia sensu stricto* (Greene 1898a, 1903a, 1906b; Brainerd 1913a, 1924; Russell 1956a; Ballard 1995, 2013), and *V. sororia* (glabrous variant) (Brainerd 1913a, 1924). Brainerd reported that hybrids express intermediate or recombinant traits in foliage, chasmogamous flowers, cleistogamous capsules, and seeds (when these do not abort). None of the hybrids reproduce by chasmogamous flowers. Brainerd reports dramatic reductions of viable seeds in the cleistogamous capsules of all hybrids studied. We have observed many herbarium specimens, and living plants at many sites of hybridization in the eastern portion of the range of *V. pedatifida*, and we confirm Brainerd's observations.

Comments. Following Don's brief description, his protologue states merely that the new species is "Native of North America." He mentioned no collections, cited no types or indicated no herbarium. No types have been found to date. The species needs neotypification.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), Scoggan (1978), Swink and Wilhelm (1979), Ballard (1995, 2013), Gil-ad (1995, 1997, 1998), and Voss and Reznicek (2012) recognized this as a distinct species. Russell stated that it intergraded with *V. palmata* (*V. baxteri* as treated here) at the eastern end of its range, but he collectively interpreted hybrids of *V. pedatifida* and *V. sororia* in southwestern Michigan and specimens referred to here as *V. baxteri* (and hybrids with *V. sororia*)

as a continuum of "intergradation" between midwestern *V. pedatifida* and Appalachian *V. subsinuata* (which Russell called *V. palmata*). Gleason and Cronquist (1991) similarly viewed the two taxa as intergrading, merging them as varieties under *V. palmata*. McKinney (1992) and McKinney and Russell (2002) recognized the similarity of *V. brittoniana* and the present species and reduced the former to a subspecies under *V. pedatifida*. Little and McKinney (2015) later reinstated *V. brittoniana* to species rank. This very morphologically uniform species is almost entirely confined to mesic blacksoil prairies and other prairie-like sites, with its midwestern range tightly adhering to Transeau's (1935) Prairie Peninsula. Many populations in the southwestern Great Lakes region have been extirpated by habitat conversion of roadside and railroad rights-of-way in the last two decades, heavily fragmenting the eastern portion of its geographic distribution and nearly eliminating its Prairie Peninsula distribution. It commonly hybridizes with *V. sororia* very commonly, wherever its grassland habitat contacts the woodland habitat of the latter species. The taxon represented by disjunct populations in the Shale Barrens region of montane western Virginia, where it was originally reported as *V. pedatifida* by Platt (1950) and characterized further by Weakley *et al*. (2012), were more recently revealed by Bethany Zumwalde (2015) to be a highly distinctive county-level endemic, *V. tenuisecta*, described as a new species in this treatment.

43. ***Viola pratincola*** Greene, Pittonia 4: 64. 1899. Type: USA Minnesota. Windom, 1 Jul 1898, *E. L. Greene s.n*. (incorrectly designated as holotype by Landon McKinney, Sida, Bot. Misc. 7: 36. 1992; corrected to lectotype by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 225): NDG32745 (*n.v.*); isolectotype: NDG32746 (*n.v.*); both internet images). Fig. 108.

Common Name. Meadow violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 15 cm tall; foliage, peduncles, and calyces green, glabrous; stipules free, irregularly glandular-fimbriate; largest leaves spreading to ascending, leaf blades undivided, largest $\leq 61 \times 79$ mm, in chasmogamous flower slightly longer than to as broad as long, narrowly ovate to ovate-deltate, base cordate, apex acute or subacuminate, broadening in fruit to broadly ovate-deltate to reniform, base shallowly cordate to cordate, apex commonly abruptly acute, margins uniformly crenate-serrate to the apex, eciliate; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 15 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate, apex acute to sharply acute from near the base; auricles short and truncate, weakly elongating in fruit to 1.5–2 mm; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform hairs, spurred petal sparsely bearded; all petals broadly rounded at apex; cleistogamous flowers produced after chasmogamous, on ascending to erect peduncle; capsule 10–12 mm, green drying to tan, unspotted, glabrous; seeds $1.4–2.1 \times 0.8–1.3$ mm, medium brown with dense minute raised black spots.

Similar Species. This species would most likely be confused with other species having the glabrous foliage, leaf blades nearly as broad as to broader than long with acute apex, and unspotted cleistogamous capsules on ascending peduncles. In chasmogamous flower it differs from *V. communis*, *V. domestica*, *V. cucullata*, *V. missouriensis*, *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) in its sparsely bearded spurred petal; additionally from *V. communis* in its dull narrowly ovate to ovate-deltate leaf blades with acute apex and more prominently serrate margins, and ovate-lanceolate sepals, which are acuminate from near the base; from *V. cucullata* in its uniformly violet to purple corolla lacking a contrasting eyespot, short truncate auricles, and long lateral petal beards; from *V. domestica* in its smaller stature, ovate-lanceolate acuminate sepals, and common occupation of wild habitats; from *V. missouriensis* in its leaf blades with uniformly serrate margins to the apex, and eciliate ovate-lanceolate acuminate sepals; and from *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) in its ovate-lanceolate acuminate sepals. In chasmogamous flower it also differs from *V. nephrophylla* in its narrowly ovate to ovate-deltate leaf blades with acute apex, ovate-lanceolate acuminate sepals, and sparsely bearded spurred petal; and from *V. retusa* in its broader less sharply acute leaf blades, and broader sepals. In cleistogamous fruit it can be distinguished from *V. missouriensis*, *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) by its unspotted cleistogamous capsule on an ascending to erect peduncle, and spotted seeds; from *V. communis* by its more prominently acute and serrate leaf blades,

FIG. 108. *Viola pratincola*. (A) Chasmogamous flowering habit (photo: Harvey Ballard). (B) Cleistogamous fruiting habit from herbarium specimen: MO, Courtney, *B. F. Bush 7993A* (NY05376172). (C) Chasmogamous flower profile view (photo: Harvey Ballard). (D) Cleistogamous fruit from herbarium specimen: Missouri, Courtney, *B. F. Bush 7993A* (NY05376172). (E) Seeds from herbarium specimen: Minnesota, Lincoln Co., *Moore & Ownbey 22260* (MIN550193).

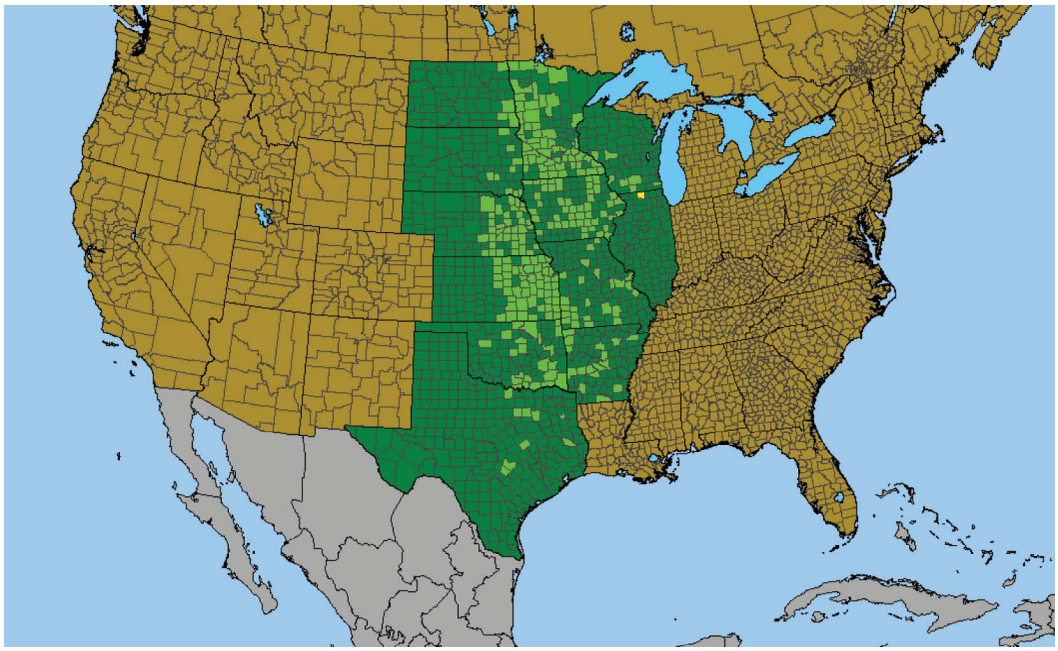

FIG. 109. United States county distribution of *Viola pratincola* (map: Biota of North America Program).

and ovate-lanceolate acuminate sepals; from *V. cucullata* by its shorter cleistogamous peduncle, broader sepals less than 1/2 the length of the capsule, auricles weakly elongating, and spotted seeds; from *V. domestica* by its taller cleistogamous peduncle, ovate-lanceolate acuminate sepals, and more densely spotted seeds; from *V. nephrophylla* by the ascending to erect cleistogamous peduncle, ovate-lanceolate acuminate sepals, and spotted seeds; and from *V. retusa* by its broader sepals and smaller seeds.

Ecology. Wet prairies bordering streams and rivers, less often streambanks and swampy woodlands, often invading anthropogenic sites such as low-lying lawns and railroad rights-of-way.

Distribution. Eastern Great Plains and western Midwest and Lower Midwest, southern Wisconsin to eastern North Dakota, south to Arkansas and eastern Texas. Fig. 109.

Rarity. None.

Phenology. Chasmogamous flower April–May, chasmogamous fruit April–July, cleistogamous fruit May–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Cucullata species group.

Hybrids. Hybridizes with *V. nephrophylla* (*V. pratincola* called *V. papilionacea*) (Russell 1952), *V. pedatifida* (*V. pratincola* called *V. papilionacea*) (Russell 1956a).

Comments. Greene wrote in his protologue, "I collected this plant in its summer condition, on the first of July, 1898, in a low meadow of natural vegetation (the land never having been ploughed) near the banks of the Des Moines River, at Windom, Minnesota. It was growing in great abundance in the rich black prairie soil among grasses and lilies (*Lilium umbellatum*). Copious living specimens of the plant in full vernal flower were sent me this season, from the same spot, by my niece, Miss Nellie C. Greene, so that I have now all needful data from which to determine its rank." The protologue describes one quite specific collection, but it makes no reference to a single sheet and does not mention a herbarium. The JSTOR Global Plants database has three NDG sheets, all with identical label information and no indication by Greene on any as to type status. Sheet NDG32749 is morphologically different from the other sheets in multiple traits that do not fully match the description, and this sheet

should be excluded from consideration. There is no justification for McKinney or Gil-ad arbitrarily choose NDG32745 to be the holotype. McKinney was first to designate sheet NDG32745, and his designation was corrected to lectotype by Ballard *et al*. (2020a).

This species was noted only in passing as a name by Brainerd (1921) under his broadly defined and heterogeneous *V. papilionacea*. He didn't consider it worth formal distinction. Based on his annotated collections at VT and elsewhere and his literature, however, he saw very few specimens and evidently did not cultivate it in his garden. Other taxonomists have batted Greene's name between *V. nephrophylla* and *V. sororia* as a synonym. Russell initially called plants in Iowa and Minnesota *V. papilionacea* (Russell 1953, 1959) and studied it under that name (Russell and Graham 1958), but he later applied the name *V. pratincola* to those and other violets in the eastern Great Plains and western Midwest (Russell 1965). It was recently successfully delimited from other members of the Cucullata and Sororia species groups and placed in the former, due to its glabrous foliage, eciliate sepals, and unspotted cleiostogamous capsule on ascending peduncle. Numerous herbarium specimens and images express very uniform morphology, with many populations represented over several states; a living population in southern Wisconsin was also inspected. This species, primarily of wet prairies and other open moist sites, especially near streams and rivers, often also invades anthropogenically disturbed sites such as low-lying lawns and railroad rights-of-way (like many other species of floodplains). It appears (based on occasional mixed collections) to occasionally grow in local sympatry with *V. nephrophylla* but less often with *V. retusa*. *Viola communis*, this species, and *V. retusa* form a crude "transitional" series in which the shape of leaf blades and sepals change from orbiculate to reniform-deltate obtuse to rounded leaf blades, and ovate-triangular sepals acuminate from the middle in *V. communis*; to narrowly ovate to ovate-deltate leaf blades, and lanceolate sepals acuminate or slightly convexly tapering from the base in *V. pratincola*; to narrowly ovate-triangular to triangular-deltate leaf blades, and linear-lanceolate sepals acuminate from the base. Distributions and habitats also show an apparent transition, with *V. communis* in floodplain-related niches of the eastern Midwest, *V. pratincola* in wet prairies beside streams and rivers and in other moist to wet open sites of the western Midwest and Great Plains, and finally *V. retusa* in sand and gravel alluvium along streams and rivers almost exclusively in the Great Plains. Russell and Graham (1958) examined the morphological variation and taxonomic distinctions of this species (called *V. papilionacea*).

44. ***Viola primulifolia*** L., Sp. pl., ed. 1, 2: 934. 1753. Type: "Habitat in Sibiria, Virginia" [protologue], [no date], *J. Clayton 470* (lectotype (designated by James Reveal in Jarvis (ed.), Order out of Chaos: 924. 2007): BM000042606 (*n.v.*), internet image). Fig. 110.

Viola acuta Bigelow, Fl. Boston., ed. 2: 95. 1824; *Viola primulifolia* L. var. *acuta* (Bigelow) Torr. & A.Gray, Fl. N. Amer. 1(1): 139. 1838.

Viola primulifolia L. var. *boscii* Ging., in DC., Prodr. 1: 293. 1824.

Viola primulifolia L. var. *nuttallii* Ging. in DC., Prodr. 1: 293. 1824.

Viola primulifolia L. var. *ovata* Raf. ex Ging., in DC., Prodr. 1: 293. 1824.

Viola radicans DC. ex Ging., in DC., Prod. 1: 297. 1824.

Viola primulifolia L. var. *villosa* Eaton, Man. bot., ed. 5: 443. 1829; *Viola primulifolia* L. subsp. *villosa* (Eaton) N.H.Russell, Amer. Midl. Naturalist 54: 487. 1955.

Viola primulifolia L. var. *australis* Pollard, Bot. Gaz. 26: 342. 1898.

Viola reptabunda Greene, Leafl. Bot. Observ. 2(2): 94. 1910–1912.

Viola senecionis Greene, Leafl. Bot. Observ. 2(2): 94. 1910–1912.

Viola rugosa Small, Man. S. E. Fl.: 891. 1933.

Viola primulifolia L. f. *subcordata* Griscom, Rhodora 38: 50. 1936.

Common Name. Primrose-leaved violet.

Description. Acaulescent stoloniferous perennials from slender rhizome, colonial from surficial stolons produced in summer, stolons bearing multiple nodes each with a leaf and cleistogamous capsule, $\leq$ 31 cm tall; foliage and peduncles green, or petioles and peduncles red-tinged, glabrous, or occasionally hirsute; stipules free, finely glandular-fimbriate; leaves erect, leaf blades undivided, largest $\leq$ 62(85) $\times$ 35(50) mm, elliptic or ovate-lanceolate to ovate-triangular (rarely ovate), base broadly cuneate to shallowly cordate, margins

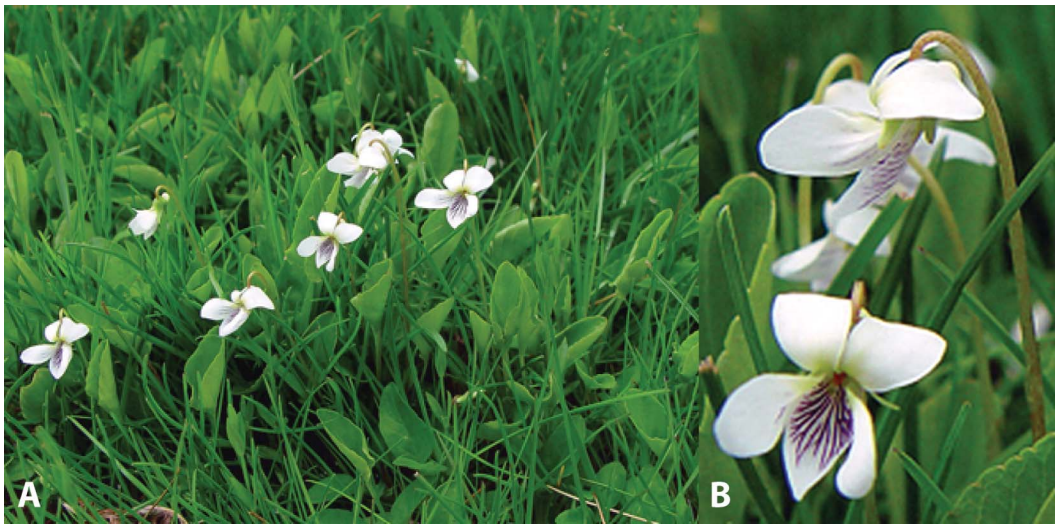

FIG. 110. *Viola primulifolia*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower front and profile views (photo: Arthur Haines, Native Plant Trust).

crenate, eciliate, apex acute to narrowly rounded; chasmogamous peduncle held among or above the leaves; chasmogamous flower $\leq$ 10 mm; calyx glabrous, eciliate; lowest sepals lanceolate, acute; auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; all petals glabrous or lateral petals bearded with sparse to dense slightly clavate hairs; cleistogamous flowers produced after chasmogamous, peduncle erect and nearly to quite as long as petioles; capsule 5–11 mm, green drying light brown, unspotted or with fine red dots, glabrous; seeds (1.3)1.5–1.7 $\times$ 0.9–1.0 mm, dark brown, unspotted; $2n = 24$.

Similar Species. This species is sufficiently distinct in leaf morphology that it is likely to be confused only with two other long-leaved species in subsect. *Stolonosae*. It differs most obviously from *V. lanceolata* and *V. vittata*, with which it occasionally grows and hybridizes, in its proportionally and physically broader leaf blades with broadly cuneate to shallowly cordate base. Its foliage is occasionally hirtellous, especially in populations in the middle and southern portions of its range, providing an additional difference from *V. lanceolata*, and produces leafy summer stolons with cleistogamous capsules, differing further from *V. vittata*. It might be mistaken for *V. blanda*, but its leaves are erect, the basal lobes on plants with subcordate or shallowly cordate leaf blades are extremely short and divergent, pubescence (if present) is not confined to the upper surface of the leaf blades, and the unspotted cleistogamous capsule sits on a tall erect peduncle.

Ecology. Moist somewhat acidic sandy, mucky, or peaty soils of bogs, pocosins, wet savannas, meadows; edges of ponds, streams, and marshes; and in and along borders of swamps.

Distribution. Primarily Atlantic and Gulf Coastal Plains, inland into the Appalachian Mountains and Western Allegheny Plateau, Maine to southeastern Oklahoma, south to Florida and Texas (reports from the Great Lakes region are tentatively assigned to *V.* $\times$*sublanceolata* pending further investigation). Fig. 111.

Rarity. Listed in Illinois, Indiana, New York, and Ohio.

Phenology. Chasmogamous flower December–June, chasmogamous fruit January–June, cleistogamous fruit March–October.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. cucullata* (Bicknell 1904; Brainerd 1906c,1909, 1924; House 1924), *V. lanceolata* (Brainerd 1924; Russell 1955c), *V. minuscula* (Dowell 1910; Brainerd 1924; House 1924; Russell 1955c; H.E.B., personal observation), and *V. vittata* (Brainerd 1924; Russell 1955c;

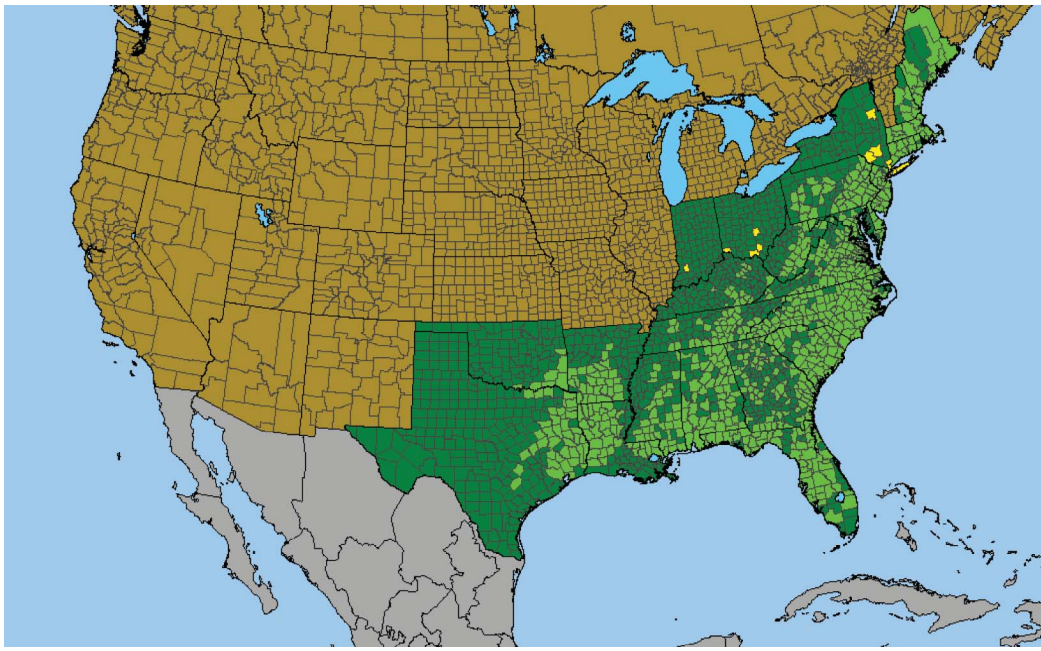

FIG. 111. United States county distribution of *Viola primulifolia* (map: Biota of North America Program).

H.E.B., personal observation). The first author has observed the hybrids between acaulescent white species and have found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. All hybrids fail to reproduce by chasmogamous flowers and produce abortive cleistogamous capsules or normal capsules with a substantially reduced proportion of viable seeds. Russell and Bowen's (1960) and Russell's (1965) reports of hybridization with *V. pedata* were based on nonreproductive individuals of *V. pedata* var. *flabellata*; in unpublished studies of broader sampling the first author rejected the hypothesis (see "Comments" under *V. pedata*). Although fantastically rare, two different hybrids involving acaulescent blue and white violets have been reported; for information concerning evidence supporting the interpretation of parentage for *V. cucullata* × *V. primulifolia*, see the first-named species.

Comments. Brainerd (1921b), Brainerd Baird (1942), Russell (1965), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (2000), McKinney and Russell (2002), Haines *et al*. (2011), and Weakley *et al*. (2012) recognized this as a distinct species without infraspecific taxa. Fernald (1950) distinguished var. *acuta* (Bigelow) Torr. & A.Gray and var. *villosa* Eaton as well as the typical variety, Henry (1953a) reported *V. primulifolia* var. *acuta*, Russell (1955c) separated out subsp. *villosa* (Eaton) N.H.Russell and subsp. *primulifolia*, and Alexander distinguished var. *villosa* Eaton and f. *subcordata* Griscom from typical *V. primulifolia*. Ballard (1995) assigned all material intermediate between *V. lanceolata* and *V. minuscula* (then referred to *V. macloskeyi*) to *V.* ×*primulifolia*, confounding the predominately eastern and southeastern *V. primulifolia* with apparently sterile ×*sublanceolata* House (*V. lanceolata* × *V. macloskeyi* [= *V. minuscula*]) , as well as reportedly fertile populations in the western Upper Great Lakes region. Voss and Reznicek (2012) tentatively included *V. primulifolia* in Michigan, noting that this included many records representing the sterile hybrid *V.* ×*sublanceolata* and a few collections of apparently fertile plants in the Upper Peninsula. The species, as represented by populations in the Appalachian Mountains and adjacent uplands, and on the Atlantic and Gulf Coastal Plains, displays complex and incongruent variation patterns in leaf blade shape and foliage and peduncle indument. Generally, populations in the central Appalachians and on the Piedmont and the northern Atlantic Coastal Plain southward often (but not always) possess hirtellous foliage and peduncles, whereas

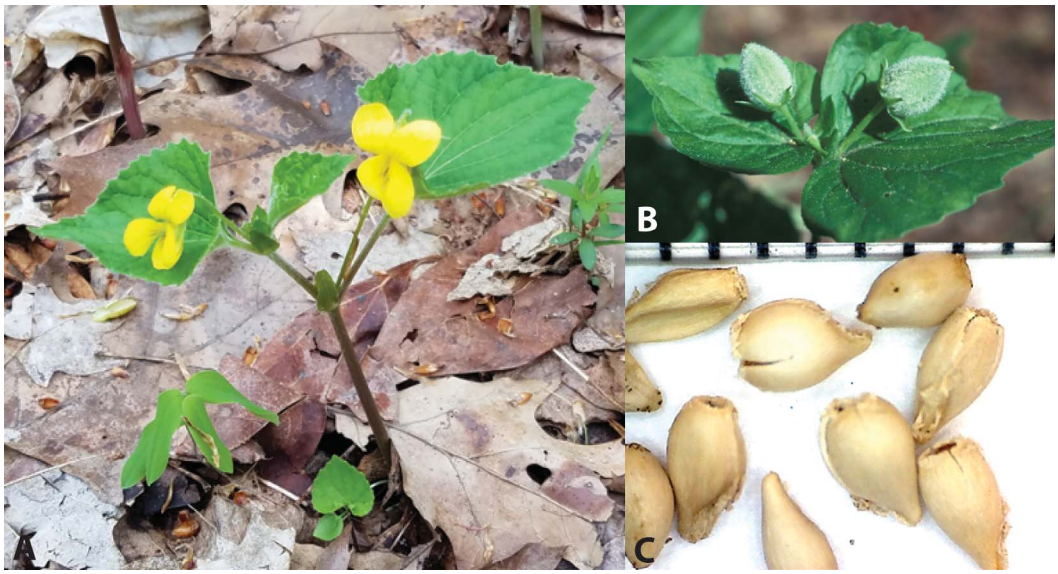

FIG. 112. *Viola pubescens*. (A) Chasmogamous flowering habit (photo: Harvey Ballard). (B) Cleistogamous fruit (photo: John Lynch). (C) Seeds from herbarium specimen: Ohio, 10 Jul 1961, *A.W. Cusick s.n*. (OS66616).

populations to the north virtually always have glabrous foliage and peduncles. Over the last half-century, infraspecific categories have been abandoned, since assigning names of the various infraspecific taxa to specimens would become a fruitless and occasionally frustrating exercise. Plants resembling *V. primulifolia* have commonly been reported as such in the western Great Lakes region, but most have been found to represent the frequent occurring sterile hybrid *V. lanceolata* × *V. minuscula* (*V.* ×*sublanceolata* House). However, some populations in northern Michigan and also in the Anoka Sand Plains of eastern Minnesota reportedly reproduce at least by cleistogamous fruits. These are tentatively included in *V.* ×*sublanceolata* pending further study on their evolutionary and taxonomic status.

45. ***Viola pubescens*** Aiton, Hort. Kew., ed. 1, 3: 290. 1789; *Viola uniflora* L. var. *pubescens* (Aiton) Regel, Bull. Soc. Imp. Naturalistes Moscou 34(2): 500. 1861; *Crocion pubescens* (Aiton) Nieuwl. & Kaczm., Amer. Midl. Naturalist 3: 215. 1914. Type: Hort. Kew., 1775, [*W. Young s.n*.] (holotype: BM000617590 (*n.v.*), internet image). Fig. 112.

Viola pubescens Aiton var. *eriocarpa* [epithet originally incorrectly spelled *eriocarpon*] Nutt., Gen. N. Amer. Pl.: 150. 1818; *Viola pubescens* Aiton f. *eriocarpa* (Nutt.) Farw., Pap. Michigan Acad. Sci. 2: 33. 1923 [“1922”].

Viola pensylvanica Michx., Fl. bor.-amer., ed. 1, 2: 149. 1803.

Viola pubescens Aiton var. *peckii* House, Bull. New York State Mus. Nat. Hist. 243-244: 50. 1923; *Viola pubescens* Aiton f. *peckii* (House) Levesque, Naturaliste Canad. 93: 515. 1966.

Viola pubescens Aiton var. *typica* Grover, Ohio J. Sci. 39: 146. 1939 [*nomen invalidum*].

Common Names. Downy yellow violet, hairy yellow violet.

Description. Caulescent perennials from thick rhizome, stems erect, commonly solitary, ≤ 37 cm tall; stems, foliage, and peduncles gray-green, spreading-hirsute, lower surface of leaf blades often paler; leaves cauline (very rarely with 1 basal leaf per stem), 2–3, clustered in upper 1/3–1/5 of stem; stipules free, broadly ovate (rarely ovate-lanceolate), broadly cuneate at base, entire or weakly erose; leaves spreading, leaf blades undivided, largest ≤ 75 × 80 mm, upper broadly ovate to reniform, lower broadly reniform, base broadly cuneate to truncate, margins serrate, ciliate, apex broadly obtuse to rounded, uppermost fully expanded leaf blade (at second node) with 13–26 marginal teeth per side, 16 or more in northern populations; chasmogamous flower ≤ 13

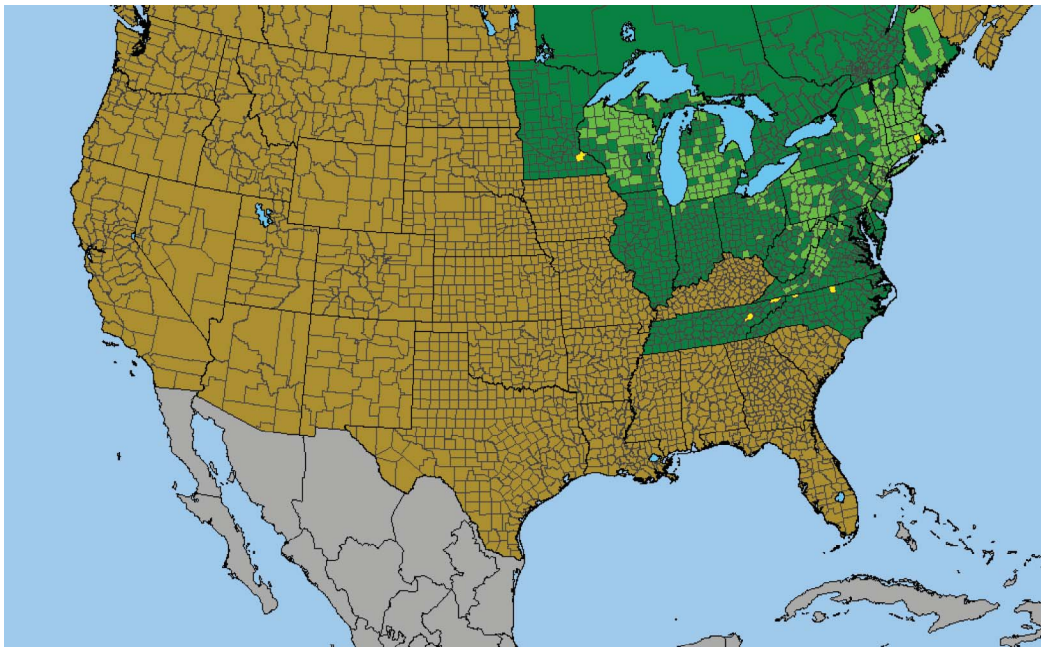

FIG. 113. United States county distribution of *Viola pubescens* (map: Biota of North America Program).

mm; calyx hirtellous, ciliate; lowest sepals linear-lanceolate to lanceolate (rarely ovate-lanceolate), acute to obtuse; auricles short and entire, not elongating in fruit; corolla wholly yellow with purple-black lines at base of petals and purple-tinged on back of petals; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 7–14 mm, green drying tan or brown, unspotted, glabrous or densely tomentose; seeds 2.3–3.0 × 1.3–1.9 mm, medium orange-brown, unspotted; 2n = 12.

Similar Species. As narrowly circumscribed here, this species is very uniform in morphology, as compared to the much more variable *V. eriocarpa* with which it is often confused. Confusion has been historically due largely to quite extensive recognized local and regional trait variation in *V. eriocarpa*, resulting in large-scale misidentification of *V. eriocarpa* specimens with some but not all of the traits of *V. pubescens*, particularly widespread moderately to heavily hirtellous few-stemmed individuals (or populations) of *V. eriocarpa*. This species can easily be separated from *V. eriocarpa* by typically solitary stems, virtual absence of basal leaves, densely spreading-hirsute foliage and peduncles, 2–3 cauline leaves clustered in the upper 1/5–1/3 of the stem, typically ovate stipules with cuneate base, broader cauline leaf blades with broadly cuneate to truncate base and obtuse to short abruptly acute apex, and first fully expanded leaf (at the second node) with 13–26 marginal teeth per side (northern populations having 16 or more. thus expressing no overlap with *V. eriocarpa*).

Ecology. Sandy or gravelly soils of dry to dry-mesic forests, drier forested borders of swamps, and well drained (occasionally "wet") slopes in woodlands with northern aspect.

Distribution. Appalachian Mountains, Northeast, and Great Lakes regions, Maine and Quebec to southeastern Minnesota, south to northern North Carolina, eastern Tennessee, and Ohio. Fig. 113.

Rarity. Listed in Rhode Island.

Phenology. Chasmogamous flower March–June, chasmogamous fruit April–August, cleistogamous fruit June–August.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Nudicaules species group.

Hybrids. There are many reports of "extensive" hybridization with *V. eriocarpa*, such erroneously

inferred "intergradation" often being used as ammunition to merge the two taxa (Russell 1965; Scoggan 1978). Such plants have been unambiguously identified as belonging to the highly variable *V. eriocarpa*. In fact, confirmed hybrids in the broader lineage, sect. *Chamaemelanium*, which contains this and other caulescent yellow-flowered violets, are exceedingly rare, and aside from a couple of widely scattered reports of the hybrid of *V. canadensis* and *V. eriocarpa*, *bona fide* hybrids are confined to western North America.

Comments. Aiton's protologue states "Nat. of North America. Introd. 1772, by Mr. William Young." No type was cited but the protologue suggests a single collection. Stafleu and Cowan (1988) note that Young's herbarium was deposited at BM. Thus far only one sheet has been identified as matching the protologue and other relevant information. There is sufficient evidence to indicate that the BM000617590 sheet is the holotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), and Weakley *et al*. (2012) recognized this as a distinct species separate from *V. eriocarpa* Schwein. (which is occasionally referred to by the misapplied name *V. pensylvanica* Michx., noted by Jones [1959] as a synonym of the present species). Fernald, Henry, Alexander, and Scoggan additionally recognized var. *peckii* House for plants with darker foliage and glabrous capsules, but such plants were later found to be distributed throughout the range of the species and are treated here as a population-level polymorphism of fruit indument, thus unworthy of formal taxonomic recognition. Russell (1965), Ballard (1995, 2000), McKinney and Russell (2002), Haines *et al*. (2011), and Little and McKinney (2015) merged *V. eriocarpa* and the present species, treating them as varieties under *V. pubescens*, while Gleason and Cronquist (1991), Voss and Reznicek (2012), and Ballard (2013) synonymized all under *V. pubescens* without formal recognition of infraspecific taxa. Lévesque and Dansereau (1966) conducted thorough studies of the caulescent yellow-flowered violets of the Nudicaules group and provided a compelling case for distinguishing the two taxa at species rank. Recent reevaluation of Missouri populations previously treated by Ballard (2013) as *V. pubescens* in the broad sense have revealed that they are all *V. eriocarpa sensu stricto*. Conversely, Russell (1965) attributed virtually all Missouri specimens to his *V. pubescens* var. *pubescens*.

Recent studies have revealed more extensive local and regional variation in *V. eriocarpa* than has previously been appreciated, and has conversely demonstrated a larger number of non-overlapping or scarcely overlapping traits distinguish *V. pubescens* from *V. eriocarpa*. See *V. eriocarpa* for fuller discussion of the variation in that species.

The ranges of *V. eriocarpa* and *V. pubescens* overlap completely, with the latter's range nested within the former but restricted almost completely to northeastern North America. This species is among the rarer members of our Nudicaules group, surpassed in rarity only by *V. glaberrima* and *V. tripartita* in our region. We have only encountered populations of *V. pubescens* a few times in many years of botanizing, whereas we have encountered *V. eriocarpa* in nearly every mesic and bottomland forest. In these situations, *V. eriocarpa* usually forms large colonies, whereas *V. pubescens* grows as a few or a few dozen individuals in a highly localized area.

46. ***Viola rafinesquei*** Greene, Pittonia 4: 9. 1899 [replacement name for *V. bicolor* Pursh] ; *Viola bicolor* Pursh, Fl. Amer. sept. 1: 175. 1813 [illegimate homonym of *Viola bicolor* Hoffm. (1804)] ; *Mnemion rafinesquii* (Greene) Nieuwl., Amer. Midl. Naturalist 3: 217. 1914; *Viola kitaibeliana* Schult. var. *rafinesquii* (Greene) Fernald, Rhodora 40: 443. 1938. Type: USA [Pennsylvania. Cumberland Co., Carlisle], Connedagwinit Cave [now Conodoguinet Cave, at Cave Hill Park and Nature Center], [no date], [*F. Pursh s.n.*] (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 225): K000651424 (*n.v.*), internet image). Fig. 114.

Viola rafinesquii Greene f. *caerulea* Moldenke, Phytologia 26(4): 225. 1973.

Viola rafinesquii Greene f. *minor* Moldenke, Phytologia 26(4): 226. 1973.

Common Names. Field pansy, wild pansy.

Description. Caulescent annuals from slender taproot, stems erect, solitary, $\leq$ 27 cm tall; stems, foliage, and peduncles green, quadrate stems recurved-puberulent or -hispidulous on face directly above a leaf node but essentially glabrous on the other faces, leaves glabrous or occasionally

FIG. 114. *Viola rafinesquei*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: D. Busemeyer). (C) Seeds from herbarium specimen: Ohio, 28 Apr 1984, *P. Lewis 1836* (OS422620).

sparsely hirtellous along veins, peduncles glabrous; leaves cauline, distributed along stem; stipules free, deeply palmately to subpinnately lobed, terminal lobe oblanceolate, slightly larger than lateral lobes, similar in shape, with 0–3 crenations per margin; leaves ascending, leaf blades undivided, upper $\leq 24 \times 6$ mm (including indistinguishable petiole), oblanceolate or obspatulate to obovate, base narrowly cuneate and decurrent onto indistinct petiole, lower $\leq 14 \times 11$ mm, broadly oblong-ovate to orbiculate or subreniform, subcordate and distinct from petiole, margins entire or inconspicuously crenate or serrate on each side, appressed-ciliate to eciliate, apex obtuse to broadly rounded; chasmogamous flower ≤ 14 mm, petals much longer than sepals; calyx glabrous, densely ciliate; lowest sepals broadly lanceolate to ovate-lanceolate, sharply acute; auricles prominent, entire or erose, not elongating in fruit; corolla commonly pale blue, infrequently white, throat yellow; spur short, thick, slightly extending beyond auricles; lateral petals densely bearded with narrowly linear to slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 3.5–6 mm, green drying tan, unspotted, glabrous; seeds 1.2–1.5 $\times$ 0.6–0.9 mm, tan to golden orange or lighter red-brown, unspotted; 2n $= 34$.

Similar Species. This species is quite easily distinguished from the two widely distributed, introduced pansy species, *V. arvensis* and *V. tricolor*, in the absence of basal leaves, its commonly uniformly pale blue corolla and yellow throat, stipules with the terminal lobe slightly larger than but similar in shape to the lateral lobes

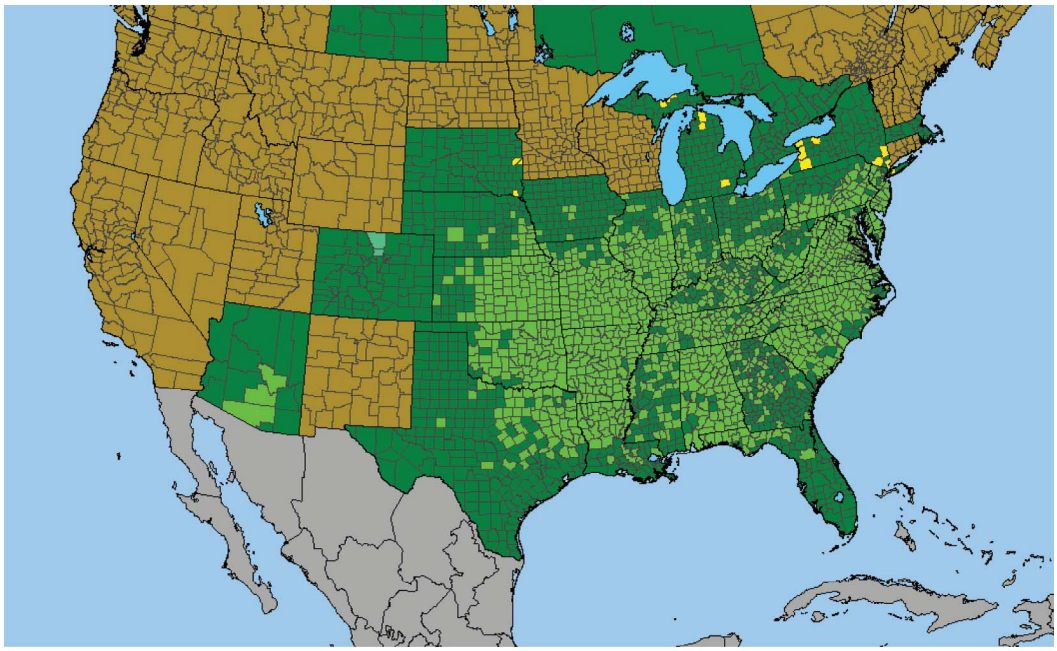

FIG. 115. United States county distribution of *Viola rafinesquei* (map: Biota of North America Program).

and with margins entire or with up to 3 crenations per side, and leaf blade short and rather quadrate with margins entire or with up to 2 shallow crenations per side. It differs further from *V. arvensis* in the petals well surpassing the sepals, a trait it shares with *V. tricolor*.

Ecology. Noticeably calciphilic, floodplains, alvars, and other open natural sites, also dry rocky woods and barrens; somewhat weedy (like other pansies) and extending along trails, roadsides, pastures, and lawns.

Distribution. Widespread in eastern North America and sporadic in the Southwest, Massachusetts, and southwestern Ontario to eastern South Dakota, south to Florida and Texas; disjunct in Arizona and Saskatchewan, adentive in northern Colorado. Fig. 115.

Rarity. Listed in New York and Ontario (as *V. bicolor*).

Phenology. Chasmogamous flower February–May, chasmogamous fruit March–May, cleistogamous fruit May–June.

Affinities. This species belongs to the Pansy lineage, sect. *Melanium* Ging., subsect. *Cleistogamae* Marcussen & Danihelka.

Hybrids. None.

Comments. Pursh provided the brief and generalized statement, "In fields of Pensylvania and Virginia," in his protologue, but he cited no specific collections or types. According to Stafleu and Cowan (1983), Pursh's herbarium was distributed to a number of institutions including BM, K, OXF, and PH. Besides the Pennsylvania specimen designated as the lectotype by Ballard *et al*. (2020a), two Maryland specimens are likely duplicates and probably constitute original material: USA [Maryland]. Antietam, Wet ground, similar to the one from Carlisle Cave, 1806, [F.] P.[ursh s. n.] (PH00039358, internet image!); and USA [Maryland]. Antietam, [no date], [F. Pursh s. n.] (K00032789, internet image!). Early in the last century, the name *V. bicolor* Gilib. (Fl. Lit. Inch. 2: 123. 1782) was believed to invalidate the later use of the name by Pursh (Fl. Amer. Sept. 1: 175. 1813), and the use of Greene's replacement name *V. rafinesquii* came into vogue. Later, the International Botanical Congress placed Gilibert's publication on the list of sanctioned works, leading to rejection of the name *V. bicolor* Gilib. and allowing for application of the name *V. bicolor* Pursh for the present species. An earlier validly published use of the name *V. bicolor* by Hoffman in 1804, predating *V. bicolor* Pursh, was recently

brought to light by violet specialist Thomas Marcussen (personal communication) for a European violet, forcing us to return to the next available name, *V. rafinesquei* Greene for our wild pansy. Alan Weakley (personal communication) pointed out the correct spelling of the specific epithet.

Brainerd (1921b), Brainerd Baird (1942), Alexander (1963), Russell (1965), Strausbaugh and Core (1978), and Gleason and Cronquist (1991) recognized the present taxon as a distinct species under the name *V. rafinesquii* Greene, while Ballard (2000, 2013), McKinney and Russell (2002), Weakey *et al*. (2012), and Little and McKinney (2015) did so under the name *V. bicolor* Pursh. Fernald (1950), Henry (1953a), and Swink and Wilhelm (1979) treated it as *V. kitaibeliana* Shult. var. *rafinesquii* (Greene) Fernald, and Scoggan simply synonymized it under *V. kitaibeliana* Shult. without recognition.

The nativity of this species has been the subject of debate. Fernald (1938) made an empassioned argument for the present species as an introduction from Europe and as conspecific with Old World *V. kitaibeliana* Schult. He based his arguments on ubiquity of the present taxon in disturbed sites and virtual (to him) morphological identity with *V. kitaibeliana* (he compared photographs of North American wild pansy with Old World specimens). In rebuttal, Clausen *et al*. (1964) provided an equally compelling set of arguments for native status in North America. While seemingly compelling, Fernald's arguments are all countered by equally convincing and more modern evidence supporting native status. This is the only species in Sect. *Melanium* to evolve cleistogamous reproduction, it differs morphologically from *V. kitaibeliana* in a number of traits in the leaves and chasmogamous flowers (none of Fernald's material from Europe matches the type and other confirmed specimens of *V. kitaibeliana*), it possesses a different chromosome number, and in unpublished molecular phylogenies it falls out in a basal position to the rest of the section. Moreover, it favors native habitats such as alkaline floodplains in which the natural disturbance regime promotes weediness, just like other fully accepted natives such as *Acer negundo* L., *Packera aurea* (L.) Á.Löve & D.Löve, *Pilea pumila* A.Gray, and *V. striata* Aiton. The overwhelming preponderance of evidence is in favor of native status. This is the only indigenous (although occasionally weedy) New World pansy in an otherwise Eurasian lineage, Sect. *Melanium*. Given its several divergent features from other members of the section, it was recently placed in subsect. *Cleistogamae* as the sole member (Marcussen *et al*. 2022).

47. ***Viola renifolia*** A.Gray, Proc. Amer. Acad. Arts 8: 288. 1873; *Viola blanda* Willd. var. *renifolia* (A.Gray) A.Gray, Bot. Gaz. 11: 255. 1886. Type: USA New Hampshire. Hanover, *F. A. Sherman s.n*. (lectotype (**designated here**): GH00067153; isolectotypes: K000370203, MO3723936; all internet images). Fig. 116.

Viola mistassinica Greene, Pittonia 4: 5. 1899. *Viola brainerdii* Greene, Pittonia 5: 89. 1902; *Viola renifolia* A.Gray var. *brainerdii* (Greene) Fernald, Rhodora 14: 88. 1912.

Common Name. Kidney-leaved violet.

Description. Acaulescent rosulate perennials from slender rhizome, $\leq$ 10 cm tall; foliage and peduncles gray-green, petioles and peduncles often red-tinged, upper surface of leaf blade darker than lower and shiny, all glabrous, or peduncles and/or petioles densely hirsute and/or one or both surfaces of leaf blades appressed-tomentose; stipules free, glandular-fimbriate; leaves widely spreading or more often prostrate on the substrate, especially during fruit, leaf blades undivided, largest $\leq 62 \times 77$ mm, rarely broadly ovate but commonly (sub)orbiculate to broadly reniform, base deeply cordate, margins low-serrate, eciliate or ciliate, apex broadly obtuse to truncate, occasionally apiculate; chasmogamous peduncle held above the leaves, glabrous or hirsute if foliage is hirsute; chasmogamous flower $\leq$ 12 mm; calyx glabrous, eciliate or long-ciliate; lowest sepals lanceolate to ovate-lanceolate, obtuse; auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; all petals glabrous or lateral petals occasionally with sparse beard of slightly clavate hairs; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle initially prostrate but arching upward just before capsule dehiscence, much shorter than petioles; cleistogamous capsule 5–10 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.7–2.4 $\times$ 1.2–1.4 mm, lighter medium to medium orange-brown to brown, unspotted; $2n = 24$.

Similar Species. This species is most similar to other *Stolonosae* violets with leaf blades nearly as broad as to broader than long. It differs from all

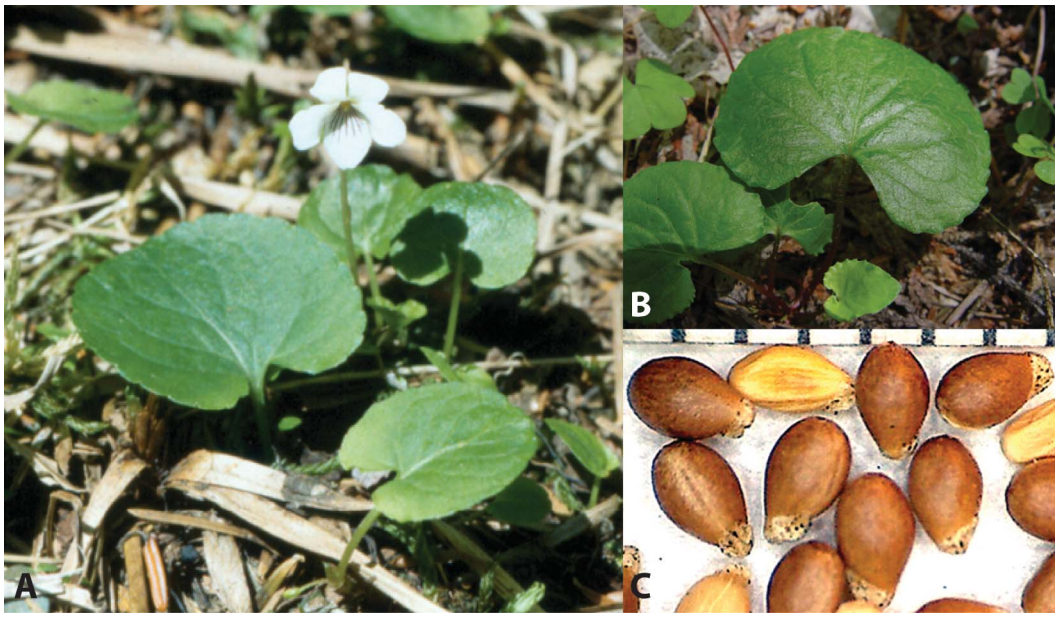

FIG. 116. *Viola renifolia*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Leaves (photo: Donald Cameron, Native Plant Trust). (C) Seeds from herbarium specimen: Connecticut, Litchfield, 2 Jul 1929, *E. H. Eames 10938* (CBS028123).

Stolonosae in our region in the total absence of stolons, and from most species except *V. blanda* in its widely spreading to prostrate leaves. In chasmogamous flower it is obviously different from *V. palustris* and *V. suecica* in its white corolla. It can be distinguished from *V. minuscula* in its petioles and leaf laminas being glabrous, densely hirsute, or one or both laminas hirsute, its proportionally broader leaf blades with noticeably serrate margins, heavily purple-spotted or -blotched cleistogamous capsule on a short prostrate peduncle, and orange-brown to brown seeds. It is most similar to and often confused with *V. incognita*; if its lack of a horizontal stoloniform rhizome and stolons, and widely spreading to prostrate leaves are ignored, it can be separated by the glabrous or wholly densely hirsute foliage or one or both leaf blade surfaces densely hirsute, its orbiculate to reniform leaf blades, glabrous or occasionally sparsely bearded lateral petals, and slightly larger seeds.

Ecology. Dry organic-rich often sandy or rocky soil, or ledges in dry or dry-mesic forests, somewhat of a calciphile and often on limestone.

Distribution. Predominately boreal and alpine, Newfoundland and Labrador and Nunavut to Alaska, south to Pennsylvania, Michigan, northeastern Iowa, and the northwestern Rocky Mountains (south to northwestern Wyoming, Idaho, and Washington); slightly disjunct in Colorado and Badlands of southwestern South Dakota and northeastern Wyoming. Fig. 117.

Rarity. Listed in Connecticut, Iowa, and Pennsylvania.

Phenology. Chasmogamous flower April–July, chasmogamous fruit June–August, cleistogamous fruit June–September.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. incognita* (Russell 1954a; Ballard 1995). Hybrids with *V. blanda* and *V. minuscula* are possible and should be sought in the zone of sympatry. The reproductive behavior of the hybrids is not reported, but the interploidal hybrids with *V. blanda* or *V. incognita* would presumably be sterile, failing to reproduce by chasmogamy or cleistogamy. Studies are needed to evaluate these predictions.

Comments. Gray's protologue states "This Violet was first brought to my notice by Miss Shattuck of Mount Holyoke Seminary, who

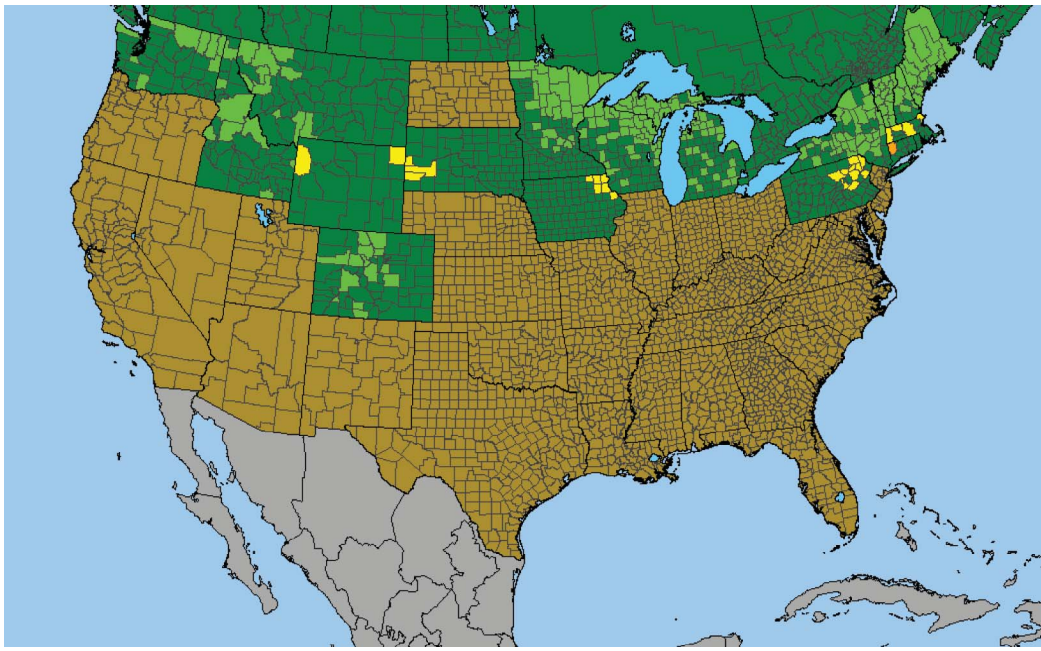

FIG. 117. United States county distribution of *Viola renifolia* (map: Biota of North America Program).

collected it at, or received it from, 'East Elba, New York.' Later Mr. Henry Gillman sent it from Ontonagon, Lake Superior; and now I have fresh specimens and the living plant from Mr. Frank A. Sherman, of Hanover, New Hampshire. Also specimens from the colder parts of Oneida Co., New York, from Professor Paine." Gray cited four collections but did not specify one as the type; Stafleu and Cowan (1976) confirmed that Gray's herbarium and types are at GH, but that material was distributed by Gray to other herbaria. The following syntypes were found through in-person searches and examination of the JSTOR Global Plants database: (1) USA New York. East Elba, Miss Shattuck s.n. (GH00067151); (2) USA Michigan. Ontonagon, Lake Superior, H. Gillman s.n. (GH00067152; isosyntype: NY00097582); (3) USA New Hampshire. Hanover, 1870, F. A. Sherman s.n. (GH00067153; isosyntypes: K000370203, MO279856); (4) USA New York. Oneida County, Professor [J. A.] Paine s.n. (GH00067154); all internet images. At GH, collections 1, 2, and 3 were on one sheet and 4 was on a separate sheet. Sherman's collection is representative of the species, and the GH00067153 is designated here as the lectotype, with K000370203 and MO279856 becoming isolectotypes.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Russell (1955c), Alexander (1963), Russell (1965), Scoggan (1978), Gleason and Cronquist (1991), Ballard (1995, 2000), Haines *et al*. (2011), Voss and Reznicek (2012), and Little and McKinney (2015) accepted this distinctive species. Brainerd, Brainerd Baird, Fernald, Alexander, and Scoggan also recognized var. *brainerdii* for plants with both surfaces of leaf blades glabrate to wholly glabrous. Later taxonomists realized that variation in foliage indument occurred within populations and did not correlate with any other morphological feature. Recognition of infraspecific taxa on the basis of indument was trivial and fruitless, and infraspecific taxa in the present species were abandoned. This species is distinctive in being the only one of the *Stolonosae* that never produces surficial stolons or stoloniform rhizomes. It is easy to identify in chasmogamous flower by its strongly reniform or occasionally orbiculate leaf blades, upper leaf blade surface commonly glabrous and shiny or one or both surfaces densely tomentose, margins distinctly low-serrate, purple-spotted or -blotched cleistogamous capsule on prostrate peduncle, and brown seeds. The leaves, especially in summer fruit, commonly lie flat on the substrate. The drier forest microhabitat, especially on calcareous soils

or in rock crevices, is also distinctive. Specimens in boreal or alpine regions bearing stolons invariably show other signs of hybridization, usually with *V. incognita*, such as variably pubescent foliage, well-bearded lateral petals, or infertile cleistogamous capsules. In a molecular phylogenetic study of North American and Hawaiian *Viola* taxa and lineages, Marcussen *et al*. (2012) demonstrated that *V. renifolia* and *V. minuscula* (as *V. pallens*) were tetraploid parents of the allo-octoploid *V. blanda* and *V. incognita*. Given several shared morphological similarities in foliage, flowers, and seeds between the present species and its allopolyploid derivative *V. incognita*, it is not surprising that the two species have frequently been confused. Russell (1954b) conducted analyses of variation in leaf pubescence over the ranges of this species and *V. incognita*; in *V. renifolia* Russell discovered a third unreported pubescence type but found the three randomly distributed over the species range. He concluded there was no basis for formal recognition of infraspecific taxa related to pubescence type.

48. ***Viola retusa*** Greene, Pittonia 4: 6. 1899. Type: USA, Colorado, Fort Collins, 5,000 feet, 2 May 1896, *C. F. Baker s.n*. (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 225): NDG033232 (*n.v.*); isolectotypes: NY00097585 (*n.v.*), NY00097586 (*n.v.*); all internet images). Fig. 118.

Common Name. Great Plains riverside violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 15 cm tall; foliage and calyces green, peduncles tinged or finely spotted with reddish-purple, foliage and peduncles glabrous; stipules free, irregularly glandular-fimbriate; leaves spreading, leaf blades undivided, largest $\leq$ 55 $\times$ 40 mm, ovate- to deltate-triangular, as broad as long (rarely with the largest leaf longer than broad), base cordate, apex acuminate to acute, broadening in fruit to broadly deltate-triangular or deltate-reniform, base subtruncate to shallowly cordate, apex abruptly acute, margins crenate to crenate-serrate, eciliate; chasmogamous peduncle held mostly among the leaves or occasionally above them in early flower; chasmogamous flower $\leq$ 28 mm; calyx glabrous, eciliate; lowest sepals linear-lanceolate to lance-triangular, acuminate; auricles promiment and erose (rarely short and entire), weakly elongating in fruit to 1.5(–2) mm; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform hairs, spurred petal densely bearded; upper petals commonly retuse; cleistogamous flowers produced after chasmogamous, on declined or ascending peduncle that soon becomes erect and are slightly shorter than or equalling the petioles; capsule 5–10 mm, green drying to tan, unspotted, glabrous; seeds 1.7–2.2 $\times$ 1.0–1.3 mm, medium brown with minute raised black spots.

Similar Species. This species is most similar to other *Borealiamericanae* violets with leaves longer than broad in chasmogamous flower that broaden to as broad as long in fruit, namely *V. affinis*, *V. cucullata*, *V.* "*impostor*" (see the "Potential Taxa" section), *V. langloisii*, *V. missouriensis*, and *V. pratincola*; it has also been confused with *V. nephrophylla*, which is regionally sympatric with this species and occasionally grows near it. In chasmogamous flower it differs from all of the above in the slender commonly retuse upper petals, from *V. cucullata*, *V.* "*impostor*," *V. langloisii* to the south of our region, and *V. missouriensis* in its densely bearded spurred petal, additionally from *V. cucullata* by its lateral petal beards with long filiform hairs and from *V. missouriensis* in its narrower long-acuminate eciliate sepals; from *V. affinis* in its glabrous foliage and peduncle, and prominent auricles; and from *V. pratincola* in its more slender long-acuminate sepals and more densely spurred petal. In cleistogamous fruit it can be distinguished from *V. affinis* and *V. missouriensis* by its unspotted cleistogamous capsule on an eventually erect peduncle, and medium brown spotted seeds; from *V. cucullata* and *V.* "*impostor*" by its shorter auricles and spotted seeds; from *V. langloisii* by its erect leaves, erect cleistogamous peduncle, and medium brown spotted seeds; from *V. nephrophylla* but its glabrous foliage, leaf blades with abruptly acute to acuminate apex, slender long-acuminate sepals, prominent auricles, and larger spotted seeds; and from *V. pratincola* from leaf blades with more prolonged apex, and more slender long-acuminate sepals.

Ecology. Gravel alluvium and riparian zones, occasionally under open woods bordering riverbanks.

Distribution. Nearly endemic to the Great Plains, North Dakota and southern Wyoming south

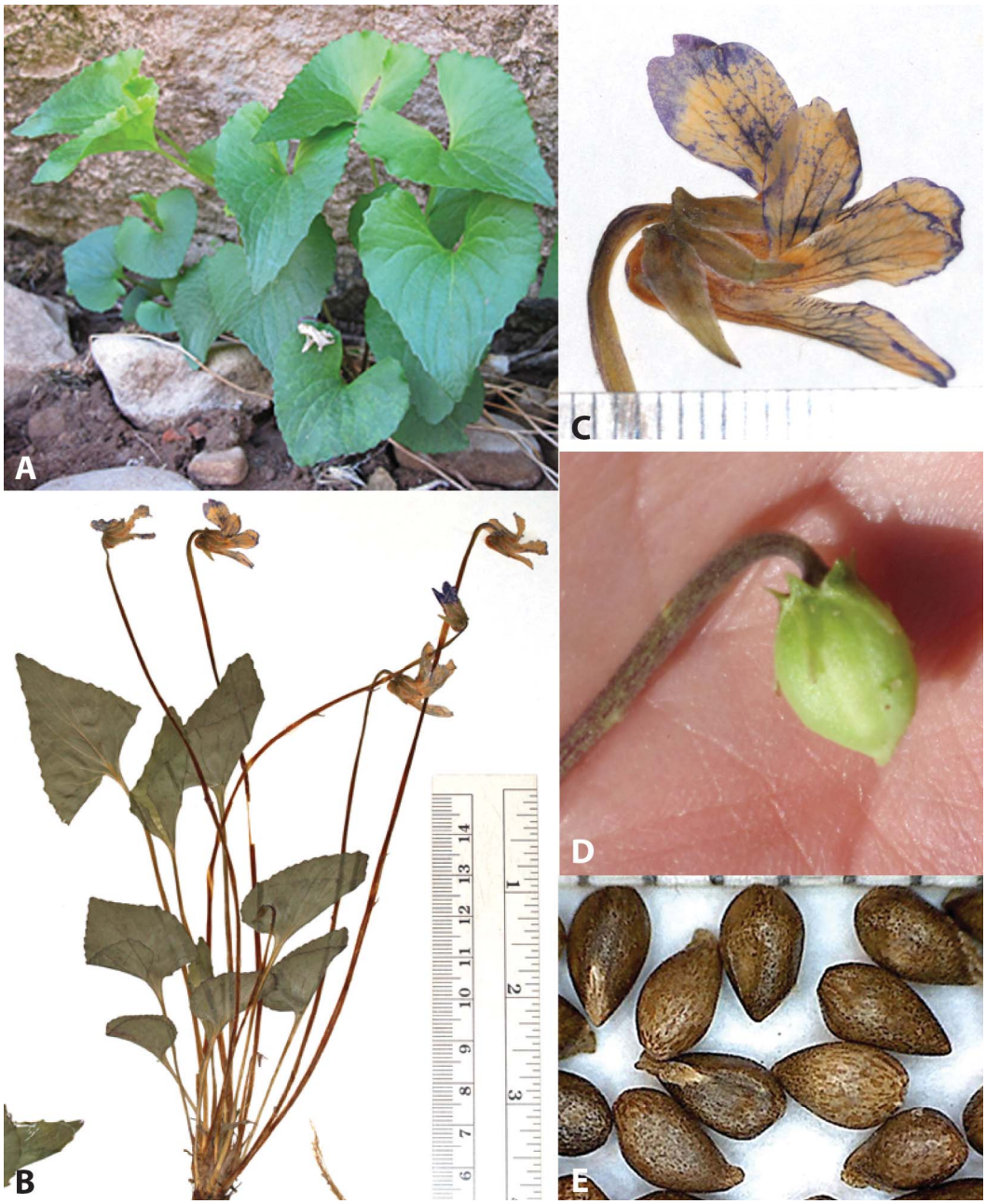

FIG. 118. *Viola retusa*. (A) Late chasmogamous flowering habit (photo: Ross McCauley). (B) Chasmogamous flowering habit from herbarium specimen: Kansas, Wilson Co., *S. Stephens 30040* (NY). (C) Chasmogamous flower profile view from herbarium specimen: Kansas, Wilson Co., *S. Stephens 30040* (NY). (D) Cleistogamous fruit (photo: Ross McCauley). (E) Seeds from herbarium specimen: Colorado, New Windsor, [donor] G. E. Osterhout, *W. W. Eggleston and R. L. Schneider 22927* (NY).

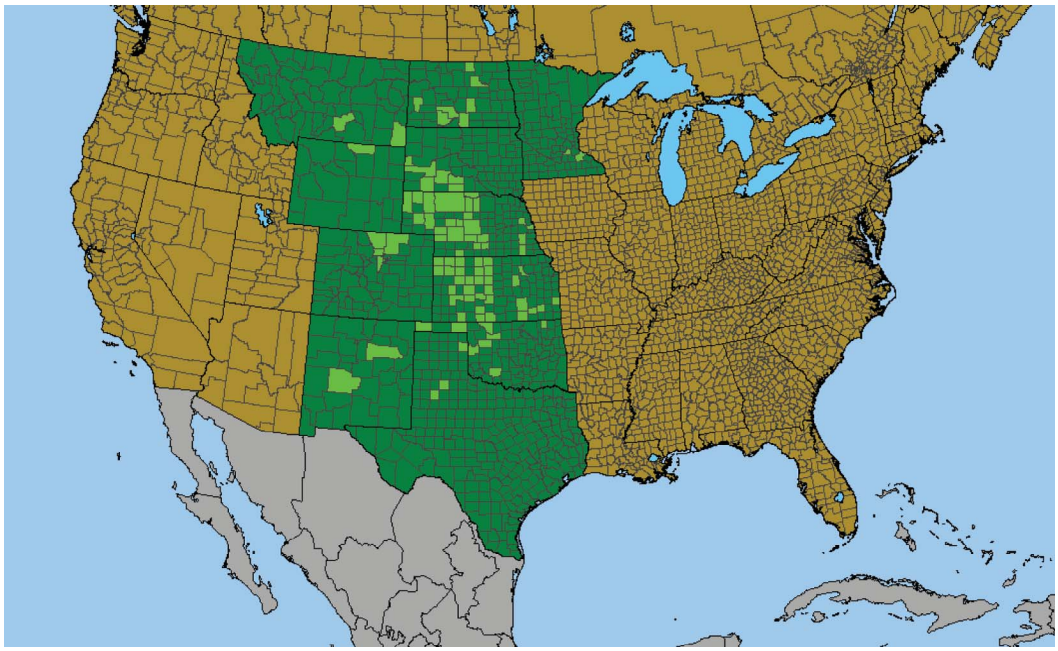

FIG. 119. United States county distribution of *Viola retusa* (map: Biota of North America Program).

to Oklahoma and New Mexico; slightly disjunct in southeastern Minnesota. Fig. 119.

Rarity. None.

Phenology. Chasmogamous flower April–May, chasmogamous fruit April–July, cleistogamous fruit May–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Cucullata species group.

Hybrids. None.

Comments. Greene wrote "Plains of northern Colorado, toward the foothills; the best specimens from Carl F. Baker, collected at Fort Collins, 2 May, 1896, and named by me *V. cognata* at the time...." He cited one collection but did not identify one sheet or designate it as a type, and mentioned no particular herbarium. The JSTOR Global Plants database has images of three sheets matching the protologue, with mostly the same information. The NDG033232 sheet has the original identification of "*Viola cucullata* Gray" and the subsequent identification of "*Viola cognata*" above it both struck out and replaced by "*retusa*," possibly in Greene's hand, while the two NY sheets still retain the original identification of "*Viola cucullata* Gray." The NDG sheet has the most luxuriant chasmogamous flowering specimens that best represent the taxon. It was selected as lectotype by Ballard *et al*. (2020a), rendering the NY00097585 and NY00097586 sheets as isolectotypes.

This violet of gravel and sand alluvium along streams and rivers in the Great Plains was described by Greene in 1899 but immediately passed into obscurity. It was momentarily resurrected by Brainerd (1913d) in his Violaceae treatment in Britton and Brown's *Illustrated Flora*, then again inexplicably dropped from Brainerd's own violet opus (Brainerd 1921b)—to the present time. The lack of mention of the name, considering its publicity in the 1913 treatment, is bizarre. Nevertheless, Ross McCauley and the first author have confirmed it as a morphologically distinct and very uniform species well represented by a substantial number of chasmogamous flowering and cleistogamous fruiting herbarium specimens, inhabiting an ecologically distinctive riparian border niche across the Great Plains region and eastward sporadically into Iowa and Minnesota. Specimens with well-formed chasmogamous and cleistogamous capsules full of apparently viable seeds provide further evidence that it is not a *de novo* hybrid. It is accepted here as a distinct but

wholly overlooked species. Russell's (1965) distribution maps and annotations on herbarium specimens indicate that he included most specimens in *V. pratincola* and a small remainder in *V. missouriensis* or *V. nephrophylla*. This violet is surely more common in the Great Plains than the scattered herbarium collections suggest; searches should concentrate on the characteristic sand and gravel riparian border habitat. Ross McCauley (personal communication) recently found it in northeastern New Mexico and included it in the forthcoming Violaceae treatment for the new flora of that state.

49. ***Viola rostrata*** Pursh, Fl. Amer. sept. 1: 174. 1813; *Lophion rostratum* (Pursh) Nieuwl. & Kaczm., Amer. Midl. Naturalist 3: 216. 1914. Type: [USA Pennsylvania], Easton, [no date], [*F. Pursh s.n.*] (neotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 226): K000327818, internet image). Fig. 120.

Viola rostrata Pursh f. *phelpsiae* Fernald, Rhodora 17: 180. 1915; *Viola rostrata* Pursh var. *phelpsiae* (Fernald) Farw., Rep. (Annual) Michigan Acad. Sci. 19: 259. 1917; *Viola rostrata* Pursh f. *phelpsiae* House, Bull. N.Y. State Mus. 243-244: 51. 1923 [illegitimate homonym of *Viola rostrata* f. *phelpsiae* Fernald (1915); House was unaware of Fernald's earlier publication of the same name and rank].

Viola rostrata Pursh var. *elongata* Farw., Rep. (Annual) Michigan Acad. Sci. 19: 249. 1917.

Viola rostrata Pursh f. *trirostrata* Grover, Ohio J. Sci. 39: 147. 1939.

Common Name. Long-spurred violet.

Description. Caulescent perennials from somewhat slender rhizome, stems ascending in flower but often reclining in fruit, commonly ≥ 2, ≤ 20 cm tall; stems, foliage, and peduncles dark green, glabrous or upper surface of leaf blades with sparse short appressed hairs; leaves cauline and basal, cauline distributed along stem; stipules free, weakly lacerate; leaves ascending to spreading, leaf blades undivided, largest $\leq 43 \times 31$ mm, narrowly to broadly ovate, base deeply cordate, margins remotely serrate-crenate, eciliate, apex acute to acuminate; chasmogamous flower ≤ 23 mm; calyx glabrous, eciliate; lowest sepals linear-lanceolate, sharply acute; auricles short to somewhat developed and entire, not elongating in fruit; corolla pale violet with pronounced purple-black eyespot, throat white; spur very long, slender, 10–20 mm, pale violet; all petals glabrous; cleistogamous flowers produced after chasmogamous, capsule 4.5–8 mm, green drying tan, unspotted or with fine red spots or lines, glabrous; seeds 1.8–2.0 $\times$ 1.1–1.2 mm, medium brown, unspotted; 2n = 20.

Similar Species. In chasmogamous flower this caulescent species is unmistakable in its very elongate spur, glabrous petals, and pale violet corolla with dense coalescing nectar-guide lines forming a conspicuously contrasting dark eyespot around the throat. In cleistogamous fruit it is most often confused with species commonly growing with it: *V. canadensis*, *V. eriocarpa*, *V. labradorica*, and *V. striata*. It differs from *V. canadensis* in its wholly herbaceous weakly lacerate stipules, and leaf blades with remotely serrate-crenate margins; from *V. eriocarpa* in its glabrous foliage or leaf blades with sparse small hairs, and wholly herbaceous weakly lacerate stipules; and from *V. labradorica* and *V. striata* in its proportionally longer leaf blades with a more prolonged abruptly acute to acuminate apex and remote serrate-crenate margins, and proportionally longer stipules.

Ecology. Well-drained sandy soils in dry-mesic forests, acidic cove forests, and on drier slopes and terraces in mesic and wet-mesic forests, often under *Tsuga canadensis* (L.) Carriére to the south.

Distribution. Widespread in the Appalachian Mountains and associated uplands, Northeast and Great Lakes, Quebec and Connecticut to eastern Wisconsin, south to northern Georgia and northern Alabama. Fig. 121.

Rarity. Listed in Maryland, New Hampshire, New Jersey, Quebec, and Wisconsin.

Phenology. Chasmogamous flower April–June (July), chasmogamous fruit April–June, cleistogamous fruit July–August.

Affinities. This species belongs to the Rostrate Violet lineage, sect. *Viola*, subsect. *Rostratae* (Kupffer) W.Becker.

Hybrids. Hybridizes with *V. labradorica* (Brainerd 1924; Henry 1953a; Scoggan 1978; Ballard 1990a, 1992, 1995; Haines *et al*. 2011) and *V. striata* (Brainerd 1924; Henry 1953a; Boivin 1966; Cooperrider 1986; Ballard 1990a, 1992, 1995). The first author has observed the hybrids and

FIG. 120. *Viola rostrata*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust). (C) Cleistogamous fruit (photo: Bruce Patterson, Native Plant Trust). (D) Seeds from herbarium specimen: Ohio, Hocking Co., Neotoma Ecology Lab, 7 Sep 1970, *[no collector]* (OS394000).

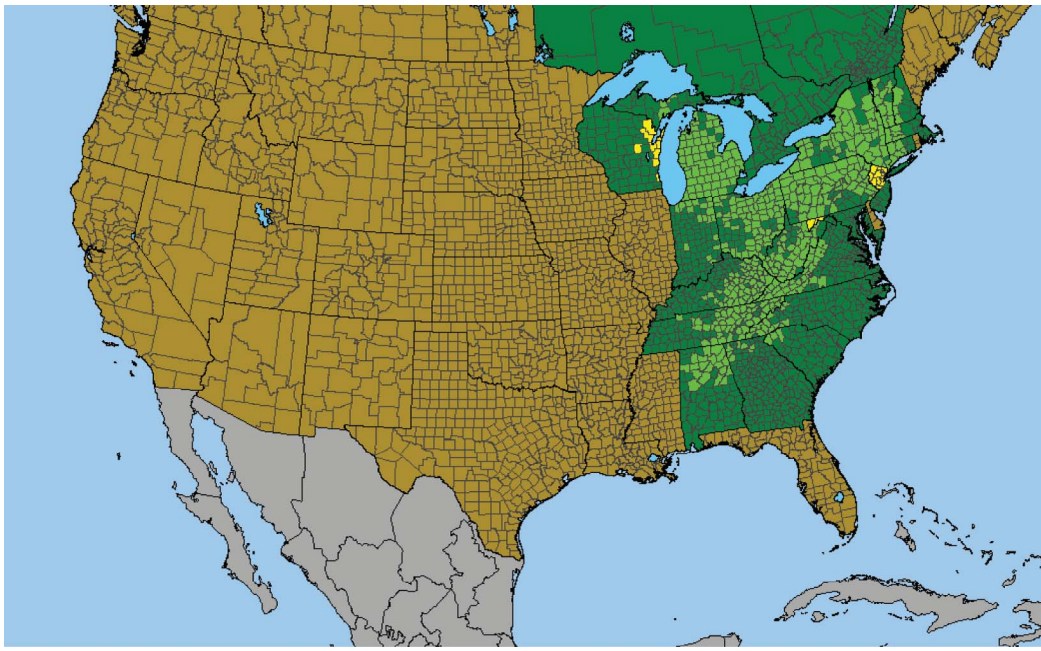

FIG. 121. United States county distribution of *Viola rostrata* (map: Biota of North America Program).

found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. Hybrids fail to reproduce by chasmogamous flowers, and cleistogamous capsules commonly abort before maturity.

Comments. Pursh noted in his protologue that this species was found "On shady rocks: near Eastown [= Easton], Pensylvania." According to Stafleu and Cowan (1983), Pursh's herbarium was dispersed to several herbaria, including BM, K, OXF, and PH. Pursh cited no types and did not mention a herbarium, but he stated a single area, suggestive of one collection. One sheet at K matches the protologue, with the handwritten statement "Herb. Pursh propr." at the bottom, but lacks a date. Harvey Ballard incorrectly annotated this sheet as holotype in 1995. Because it is not certain that the sheet was actually used by Pursh in formulating the description, Ballard *et al*. (2020a) conservatively designated K000327818 as a neotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1995, 2000), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney 2015) have all recognized this distinctive taxon at species rank. The species is unmistakable in chasmogamous flower, with its very long spur and pale violet corolla with striking dark purple eyespot, and beardless lateral petals. Hybrids with other *Rostratae* species are immediately obvious in chasmogamous flower, inheriting the longer spur and dark eyespot from the present species but exhibiting the lateral petal beards from other species.

50. ***Viola rotundifolia*** Michx., Fl. bor.-amer., ed. 1, 2: 150. 1803. Type: "*Viola rotundifolia* Mich.-Poir. Encycl. no. 9," [protologue] Amériq: Sept:, [no date], [*A*.] *Michaux* [*s. n*.] (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 226): MNHN-P-P04641469 (*n.v.*), internet image). Fig. 122.

Viola clandestina Pursh, Fl. Amer. sept. 1: 173. 1813.

Common Names. Early yellow violet, round-leaved violet.

Description. Apparently acaulescent rosulate perennials from somewhat thick rhizome, producing a prostrate nonrooting stem ("stolon") in summer terminating in a raceme of 1–3 cleistogamous fruits, $\leq$ 11 cm tall; foliage and peduncles

FIG. 122. *Viola rotundifolia*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Leaves during chasmogamous fruit (photo: Harvey Ballard). (C) Chasmogamous flower front view (photo: Andrew Lane Gibson). (D) Seeds from herbarium specimen: Connecticut, Litchfield, 20 Jul 1919, *Evans s.n.* (YU053115).

mostly gray-green, upper surface of leaf blades dark green, with petioles, chasmogamous peduncles, and summer stem usually red-spotted, glabrous or petioles hirsute and/or upper surface of leaf blades sparsely appressed-pubescent; stipules free, entire; leaves spreading or more often prostrate on the substrate in living material, especially during fruit, petioles fleshy, leaf blades undivided, largest $\leq$ 140 $\times$ 108 mm, narrowly ovate or elliptical to suborbiculate, base narrowly cordate, inner edge of lobes often meeting, margins rounded-crenate, eciliate, apex obtuse to rounded; chasmogamous flower $\leq$ 14 mm; calyx glabrous, eciliate or ciliate; lowest sepals narrowly oblong to ovate-lanceolate, obtuse to truncate; auricles prominent, entire or slightly emarginate, not elongating in fruit; corolla wholly yellow; spur short-globose; lateral petals densely bearded with

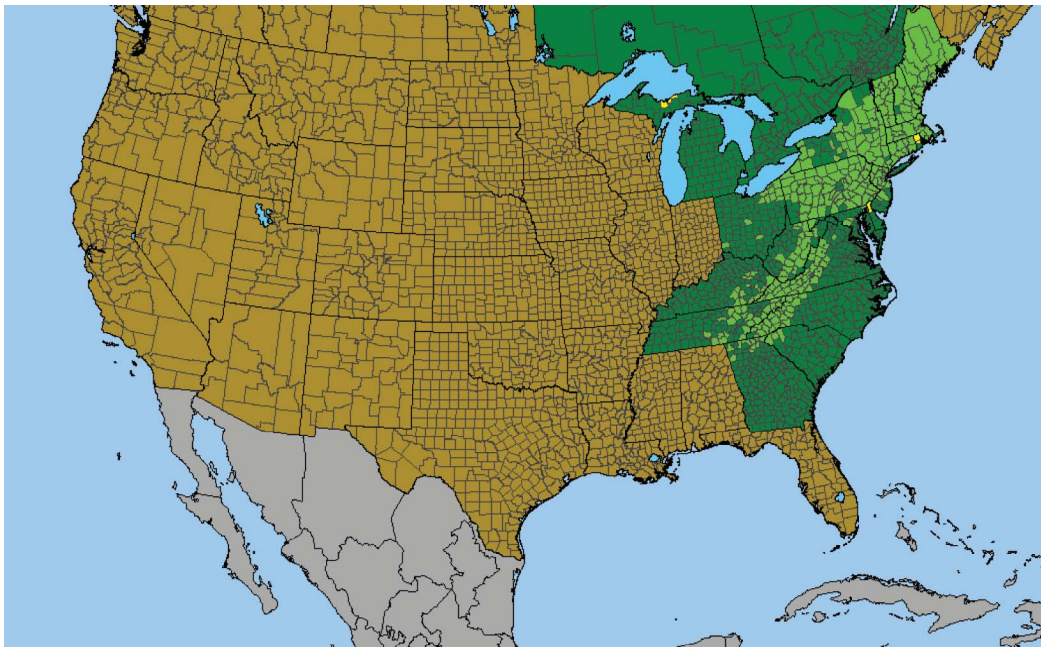

FIG. 123. United States county distribution of *Viola rotundifolia* (map: Biota of North America Program).

narrowly linear hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, often borne on prostrate summer stem; cleistogamous capsule 5–8 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.8–2.0 × 1.0–1.3 mm, ivory to light orange-brown, unspotted; 2n = 12.

Similar Species. None.

Ecology. Rich mesic and cove forests, often in somewhat acidic rocky soils or heavily organic substrates.

Distribution. Appalachian Mountains and associated uplands, extending northeastward, Quebec and Connecticut to Ohio, south to western South Carolina, northern Georgia, and eastern Tennessee; recently discovered as disjunct in central Upper Peninsula of Michigan. Fig. 123.

Rarity. Listed in Delaware and Rhode Island.

Phenology. Chasmogamous flower March–May, chasmogamous fruit April–June, cleistogamous fruit July–September.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., Orbiculates species group. Although it resembles *V. orbiculata* Geyer ex A.Gray and *V. sempervirens* Greene in certain morphological features, it does not consistently form a clade with those species in phylogenetic studies, and differs in style features and in producing a prostrate nonrooting stem only during cleistogamous fruit. Future studies may show that it should be placed into its own species group.

Hybrids. None.

Comments. In his brief protologue Michaux mentions "Hab. in excelsis montibus Carolinae." He cited no specimens or types. According to Stafleu and Cowan (1981), Michaux's North American herbarium is at P as a separate historical collection, with some duplicates in Herb. Richard. The herbarium database at P has images and data for three sheets presumed to be original material, all matching the protologue information. Sheet P04641469 bears a representative plant with the prostrate summer stem and a three-fruited cyme; Ballard *et al*. (2020a) selected this as the lectotype. Two other syntype sheets are "*Viola rotundifolia*," Amériq: Sept: (Mr LeConte [s. n.]) ["Herbarium Richard" written in different hand and ink] (MNHN-P-P04641484 (*n.v.*), internet image); and "*Viola rotundifolia* Michaux," fl. luteus, in altis montib. Carol., [A. Michaux s. n.?] ["Herbarium Richard" written in different hand and ink]

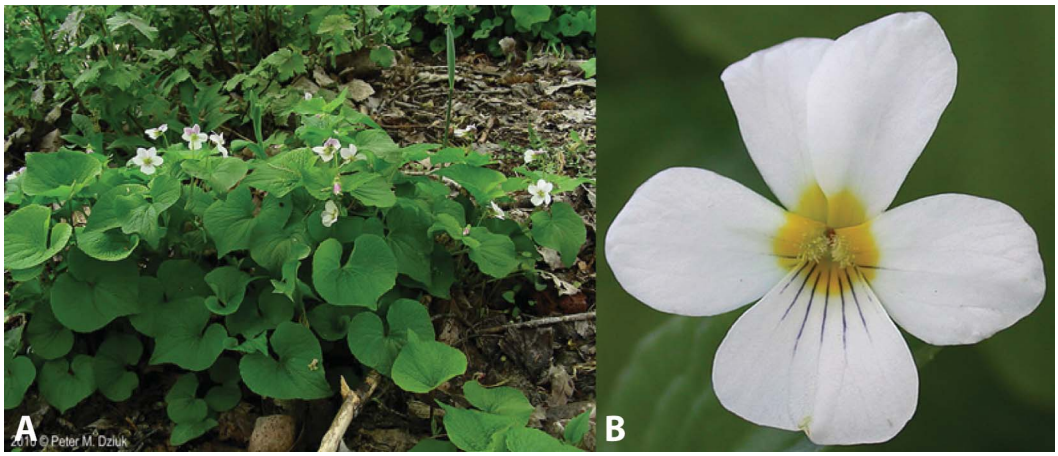

FIG. 124. *Viola rugulosa*. (A) Chasmogamous flowering habit by Peter M. Dziuk). (B) Chasmogamous flower front view (photo: Peter M. Dziuk).

(MNHN-P-P04641488 (*n.v.*), internet image). The latter sheet has three species, with the upper right plant representing *V. rotundifolia*.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Gleason and Cronquist (1991), Ballard (2000), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015) have recognized this distinctive taxon at species rank. The species is unmistakable especially in chasmogamous flower by its acaulescent habit and yellow corolla, and is distinctive in vegetative or fruiting condition in its widely spreading or prostrate undivided elliptical to suborbiculate crenately margined leaf blades and fleshy petioles. It was first documented by W. A. MacKinnon in 2019 from Alger County in Michigan's Upper Peninsula—a significant disjunction for this primarily Appalachian Mountain violet (Reznicek *et al*. 2022). It should be sought in intervening areas. Russell (1955b) examined variation in this species and found it among the least variable violets in our North America.

51. ***Viola rugulosa*** Greene, Pittonia 5: 26. 1902; *Viola canadensis* L. var. *rugulosa* (Greene) C.L.Hitchc., Vasc. Pl. Pacific NorthW. 3: 442. 1961; *Lophion rugulosum* (Greene) Lunell, Amer. Midl. Naturalist 5: 238. 1918. Type: USA Minnesota. Hennepin Co., Rich woods, Jun 1891, *J. H. Sandberg s.n*. (holotype: NDG32494, internet image). Fig. 124.

Viola rydbergii Greene, Pittonia 5: 27. 1902.

Viola neomexicana Greene, Pittonia 5: 28. 1902.
Viola muriculata Greene, Pittonia 5: 28. 1902.
Viola geminiflora Greene, Pittonia 5: 29. 1902.

Common Name. Western tall white violet.

Description. Caulescent perennials, commonly densely colonial from thick stoloniform elongate rhizome often terminating in a plant, stems erect, solitary or multiple, $\leq$ 40 cm tall; stems, foliage, and peduncle gray-green, densely hirtellous or hirsute; leaves cauline and basal, cauline distributed along stem; stipules membranous and commonly deciduous in fruit, free, lanceolate, entire; leaves ascending or spreading, leaf blades undivided, largest $\leq 90 \times 101$ mm, upper ovate with acute or subacuminate apex, middle and lower broadly ovate to reniform with acute or obtuse apex, base cordate, margins crenate-serrate, ciliate; chasmogamous flower $\leq$ 16 mm; calyx glabrous or hirtellous, ciliate; lowest sepals lanceolate to commonly linear-lanceolate, acute; auricles short and entire, not elongating in fruit; corolla white gradually fading to pink or pale purple on dorsal surface of petals, ventral surface of petals pink- or violet-tinged, throat yellow; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 7.5–12 mm long, green drying tan, unspotted, papillate-puberulent or hirtellous to sparsely hirsute (infrequently glabrous); seeds 2.0–2.2 $\times$ 1.2–1.3 mm, light brown, unspotted, caruncle obsolete; $2n = 24$.

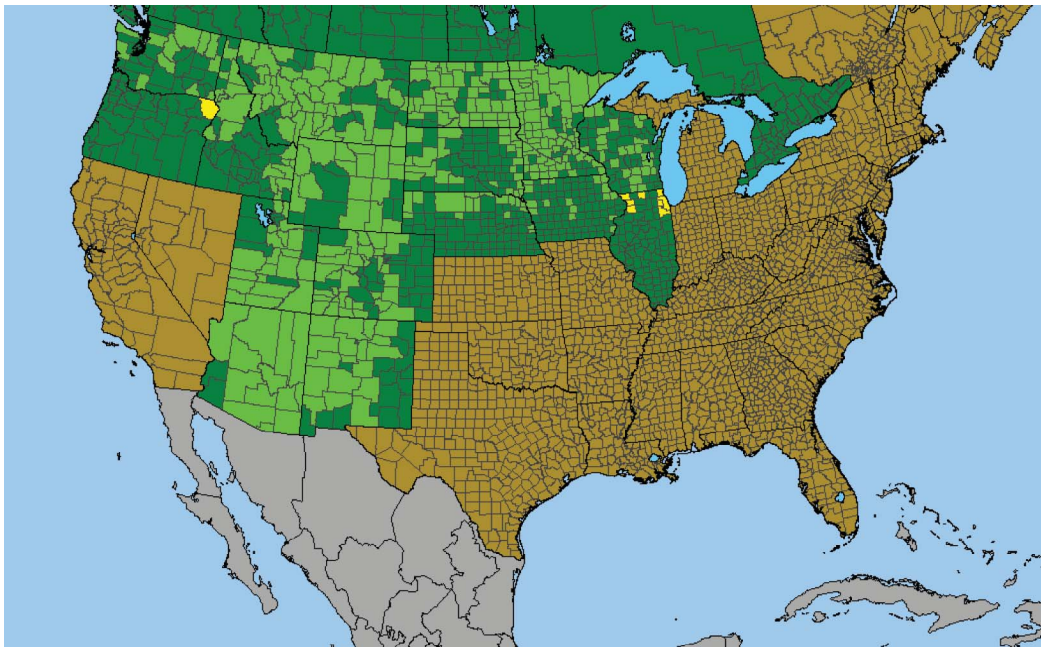

FIG. 125. United States county distribution of *Viola rugulosa* (map: Biota of North America Program).

Similar Species. This species and *V. canadensis* share a white corolla with yellow throat, and an obsolete seed caruncle. This predominately Great Plains and western species is most often be confused with *V. canadensis*, which appears not to grow at the same sites where their ranges slightly overlap in the western Midwest, and with *V. eriocarpa* (which does overlap in range and often grows with this) and *V. striata* (which does not overlap in range). It differs from *V. canadensis* in its colonial or mat-forming habit due to long-creeping stoloniform rhizomes, densely hirtellous or hirsute foliage and peduncle, acute to subacuminate upper leaf blades with margins more remotely and less prominently crenate-serrate, deeply cordate basal leaf blades, and commonly linear-lanceolate usually glabrous or hirtellous ciliate sepals. It can be distinguished in chasmogamous flower from *V. eriocarpa* and *V. striata* by its membranous lanceolate entire stipules that are commonly deciduous in summer, and white corolla with yellow throat. In cleistogamous fruit, besides the stipule features and obsolete seed caruncle, it can be separated from *V. eriocarpa* by sharply acute apex and more numerous marginal teeth on the leaf blades; and from *V. striata* by the low crenate-serrate leaf blade margins, very short rounded auricles, and often papillate-puerulent to hirtellous capsule.

Ecology. Moist loamy or sandy soils in mesic and dry-mesic forests along rivers and streams, occasionally in grasslands near forests.

Distribution. Western Great Lakes region, northern Great Plains and Rocky Mountains, northwestern Ontario and northern Illinois to British Columbia, south to Nebraska, New Mexico, Arizona, and northeastern Oregon. Fig. 125.

Rarity. None.

Phenology. Chasmogamous flower April–June, chasmogamous fruit May–July, cleistogamous fruit July–August.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Canadenses species group.

Hybrids. Although Russell (1965) and others have reported "intergradation" with *V. canadensis*, no compelling evidence to support hybridization has yet been presented.

Comments. Greene stated in his protologue that this species was "...known to me only in specimens distributed by Mr. Sandberg, from 'rich woods' in Hennepin Co., Minnesota, June, 1891."

Greene cited only one collection in the protologue, but he gave no indication that this was represented by only one specimen, and he mentioned no herbarium. However, only one specimen was found in a search at NDG (NDG32494) and other herbaria known to harbor Greene's specimens. Greene identified that sheet as "*Viola rugulosa*, Greene, type!" in his own hand. There is sufficient evidence to justify accepting the NDG specimen as the holotype.

Brainerd (1921b), Brainerd Baird (1942), and Alexander (1963) recognize the present taxon as a species distinct from *V. canadensis*. Russell (1965), Scoggan (1978), Gleason and Cronquist (1991), Weakley *et al*. (2012), and Little and McKinney (2015) treated it as *V. canadensis* var. *rugulosa* (Greene) C.L.Hitchc. Some populations of otherwise typical *V. canadensis* in the southern Appalachian Mountains produce stoloniform rhizomes. Alexander and Gleason and Cronquist mistakenly included these in their circumscription of the present taxon. Russell's statement that this and *V. canadensis* "intergrade" in the zone of overlap has not been supported by examinations of many herbarium collections and limited field observations; the two taxa maintain their morphological distinctions in Illinois and Wisconsin, where their ranges overlap. We have seen no collections of the two from the same sites, indicating that there may be some degree of ecological isolation as well. While *V. canadensis* is confined to rich mesic woodlands, the present species often occurs in drier woodlands and extends beyond woodland borders into adjacent grassland areas. No instances of hybridization have been reported. *Viola rugulosa* is widespread and relatively common in the northern Great Plains, but the western limits of the taxon are still unclear. This taxon and the rest of the *V. canadensis* complex in the West are still relatively poorly known and deserve further study. Given indications in some type material (most specimens unfortunately lacking rhizomes) and other specimens, Greene's western names in this complex more closely match *V. rugulosa* than *V. canadensis*, and they are consequently included here. The distribution map reflects this tentatively expanded range for *V. rugulosa* until further research clarify the situation definitively. A rather cumbersome common name has been proposed that distinguishes this from *V. canadensis*.

52. ***Viola sagittata*** Aiton, Hort. Kew., ed. 1, 3: 287. 1789. Type: England. Hort. Fothergill (ex America Pensylvania), [no date], [*J. Fothergill s.n.*] (lectotype (designated incorrectly as holotype by Nir Gil-ad, Boissiera 53: 75. 1997; corrected to lectotype by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 227.): BM001122805, internet image, MICH-photo (*n.v.*)). Fig. 126.

Viola dentata Pursh, Fl. Amer. sept. 1: 172. 1813.

Viola subsagittata Greene, Pittonia 3: 315. 1898; *Viola sagittata* Aiton var. *subsagitata* (Greene) Pollard, Bot. Gaz. 26: 340. 1898.

Viola sagittata Aiton var. *glabra* Pennell, Bartonia 12: 19. 1931.

Viola sagittata Aiton f. *carlii* Creutz, Wild Fl. 35: 9, fig. 2. 1959.

Common Names. Arrow-leaved violet, arrowhead violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm tall; foliage and peduncles green (lower surface of leaf blades commonly purple-tinged in serpentine populations), leaves glabrous or hirtellous, peduncles glabrous; mostly heterophyllous, leaves erect, leaf blades during chasmogamous flower undivided or with small basal teeth or slender lobes, in fruit commonly pedately divided into 5(7) segments, with lateral primary divisions each divided into 2(3) slender teeth or lobes, these $\leq$ 1/4 length of the midrib; stipules free, irregularly glandular-fimbriate; largest leaf blades $\leq$ 83 $\times$ 33 mm, during chasmogamous flower narrowly elliptical or ovate-lanceolate, during fruit becoming sagittate to lance-triangular, base subtruncate to hastate, margins serrate proximally but subentire distally, eciliate or ciliate, apex acute to acuminate; chasmogamous peduncle held above the leaves; chasmogamous flower $\leq$ 26 mm; calyx glabrous, eciliate; lowest sepals linear-lanceolate to lance-triangular, acuminate; auricles mostly prominent and entire, elongating to 3 mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, the peduncle erect and nearly to quite as long as the petioles; capsule (6)8–14 mm, green drying tan or green-brown, unspotted, glabrous; seeds 1.2–1.8 $\times$ 0.8–1.3 mm, medium pinkish-brown or medium to dark red-

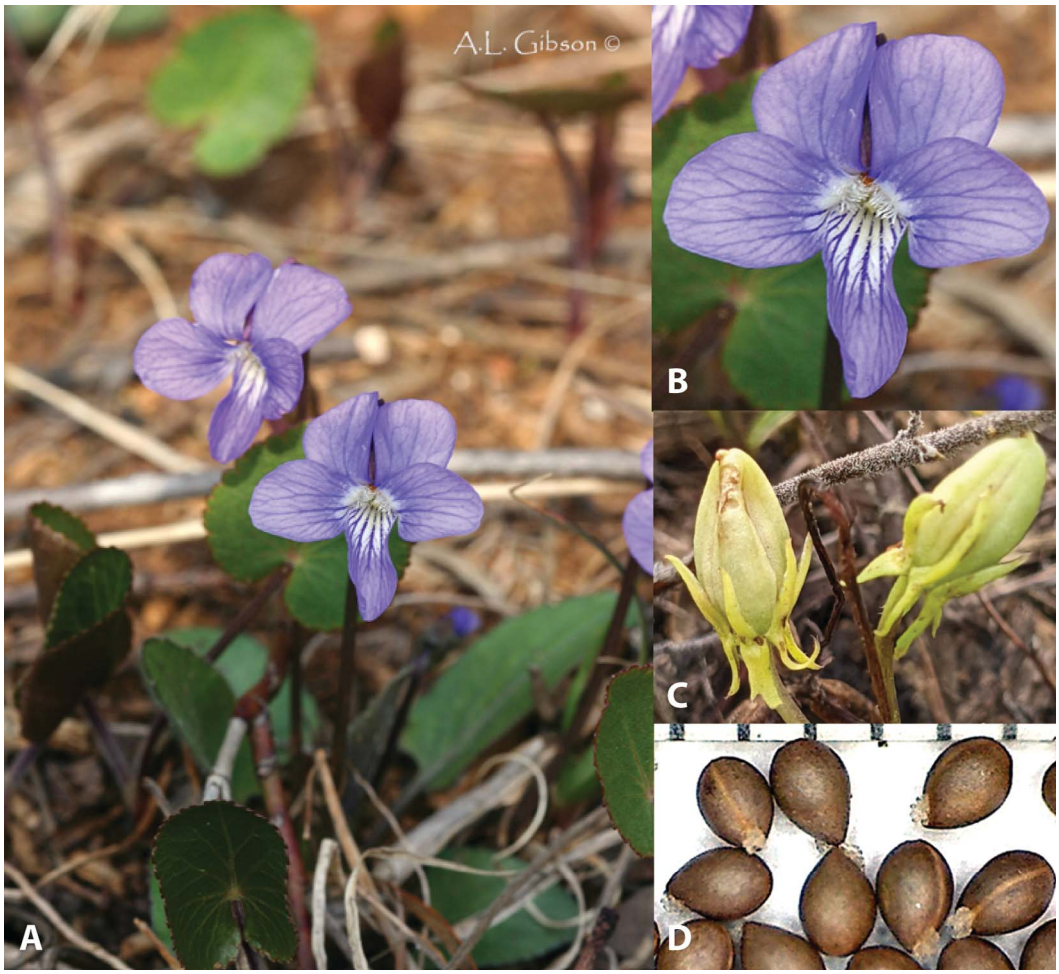

FIG. 126. *Viola sagittata*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: Andrew Lane Gibson). (C) Cleistogamous fruit (photo: Anna Mindel). (D) Seeds from herbarium specimen: Transplanted from Ohio, Scioto Co., *H. Ballard et al. 15-044X* (BHO).

brown, unspotted or with weak small blotches; 2n = 54.

Similar Species. This species could be mistaken for a few heterophyllous violets in the Sagittata species group, namely *V. emarginata*, *V. fimbriatula*, and *V. septemloba*. It differs from *V. emarginata* in foliage indument ranging from glabrous to uniformly moderately spreading-hirtellous, petioles lacking wings, typically uniformly green leaves lacking a purple tinge on the lower leaf blade surface, and blades in summer fruit becoming sagittate to lance-triangular with 2(3) slender teeth or lobes at base on each side. It can be distinguished from *V. fimbriatula* by its glabrous to uniformly moderately spreading-hirtellous foliage and typically glabrous peduncle, erect leaves, unwinged petioles, eciliate sepals, and erect cleistogamous peduncle; and from its light to medium green nonsucculent foliage, short basal lateral teeth or lobes, smaller flowers, and smaller brown seeds. It differs from *V. septemloba* in its often spreading-hirtellous and nonsucculent foliage, short basal lateral teeth or lobes, smaller flowers, and smaller brown seeds.

Ecology. Seasonally moist to wet sandy acidic soils in meadows, lakeshores, swamp margins, prairies, interdunal swales, quarries and borrow pits, and forest clearings, occasionally in closed-canopy oak or oak-pine woodlands and pine plantations.

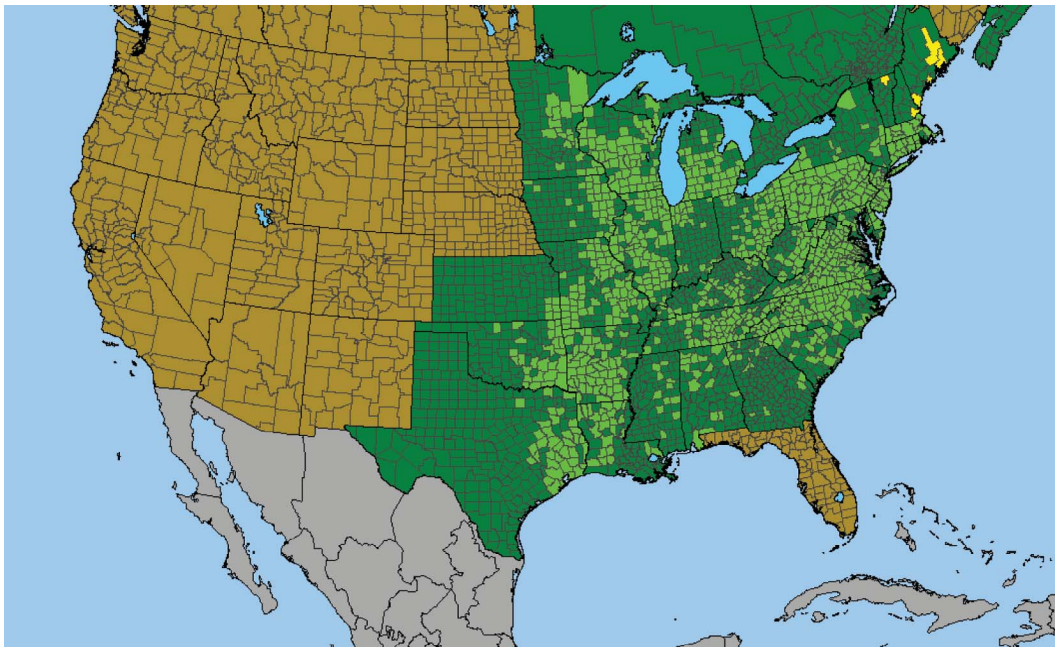

FIG. 127. United States county distribution of *Viola sagittata* (map: Biota of North America Program).

Distribution. Widespread in eastern North America, Nova Scotia, southwestern Quebec to Minnesota, south to Georgia and eastern Texas. Fig. 127.

Rarity. Listed in Quebec (as *V. sagittata* var. *sagittata*) and Vermont.

Phenology. Chasmogamous flower May–July, chasmogamous fruit May–June (August), cleistogamous fruit July–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sagittata species group.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1906c, 1910b, 1924; House 1924; Russell and Risser 1960; Russell 1965), *V. baxteri* (H.E.B., personal observation), *V. brittoniana* (Brainerd 1906c, 1924; House 1906b, 1924), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Brainerd 1906c, 1924; House 1924), *V. cucullata* (Brainerd 1906c, 1924), *V. emarginata sensu stricto* (Brainerd 1906c, 1924), *V. fimbriatula* (Brainerd 1906c, 1907b, 1924; House 1924; Cinq-Mars 1966; Haines *et al*. 2011), *V. rosacea* south of our region (Brainerd 1924), *V. hirsutula* (Henry 1953a), *V. nephrophylla* (Gaiser and Moore 1966), *V. palmata* var. *triloba* (Brainerd 1906c, 1913c, 1924; House 1924), *V. pedatifida* (Brainerd 1913a, 1924; Ballard 2013), *V. sororia sensu stricto* (Brainerd 1924; Russell and Cooperrider 1955), and *V. subsinuata* (Brainerd 1906c, 1913c, 1924; Dowell 1910; House 1924). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All hybrids fail to reproduce by chasmogamous flowers. Most hybrids express a substantial or severe reduction in proportion of viable seeds. The hybrid with *V. emarginata sensu stricto* is widely variable, some plants almost fully fertile and others producing few viable seeds; the hybrid with *V. fimbriatula* is largely or fully fertile in producing a large proportion of viable seeds.

Comments. The brief protologue described in Hortus Kewensis stated that the plant was "Nat. of Pensylvania. Introd. 1775, by John Fothergill, M.D." The protologue suggests a single collection from the Royal Botanic Garden at Kew. However, Stafleu and Cowan (1976) observed that Fothergill's garden collections were deposited at both BM and LINN. The sheet at BM has two collections on it; BM001122805 matches "1" of the handwritten note on the back with the statement "Hort. Fothergill (ex America Pensylva-

nia)"; BM000617472 matches "2" of the note, "Hort. Kew 1778." Both are presumably original material. Harvey Ballard previously incorrectly annotated the sheet as holotype. Gil-ad also annotated the sheet as the holotype but later restricted his designation to the three leaves and cleistogamous material of BM001122805 (Gil-ad 1995, 1997). Gil-ad's designation was corrected to lectotype by Ballard *et al*. (2020a). The other Fothergill collection, BM000617472, remains a syntype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Strausbaugh and Core (1978), Swink and Wilhelm (1979), and Gil-ad (1995, 1997, 1998) adopted a narrowly defined *V. sagittata* that was distinct from *V. fimbriatula* Scoggan (1978), McKinney (1992), Ballard (1995, 2000, 2013), McKinney and Russell (2002), Voss and Reznicek (2012), and Weakley *et al*. (2012), and Little and McKinney (2015) reduced *V. fimbriatula* to *V. sagittata* Aiton var. *ovata* (Nutt.) Torr. & A. Gray, while Gleason and Cronquist synonymized *V. fimbriatula* under *V. sagittata* with no recognition of infraspecific taxa. Brainerd, Brainerd Baird, Fernald, Alexander, and Strausbaugh and Core also distinguished *V. sagittata* from *V. emarginata* (Nutt.) Leconte. Russell and Risser (1960) and Russell (1965) misapplied the name *V. emarginata* to refer to hybrid plants of *V. affinis* × *V. sagittata*, but he unwittingly included *bona fide V. emarginata* (based on his annotations) in a more broadly delimited *V. sagittata*. McKinney (1992), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015) explicitly included *V. emarginata* in their synonymy of *V. sagittata*. Given the several consistent morphological differences in leaves, chasmogamous flowers, cleistogamous capsules, and seeds, as well as divergent ecological niches inhabited by the three taxa, the narrowest delimitation of *V. sagittata* as a species distinct from *V. fimbriatula* and the *V. emarginata* species complex is followed here.

The present species is somewhat variable in foliage indument and degree of leaf blade dissection, with the extremes most obvious in fruiting plants. The wholly glabrous sagittate extreme bears summer leaf blades with 2–3 linear-falcate basal lobes on each side, and it appears to be more common near the southern shores of the Great Lakes and along the Atlantic and Gulf Coastal Plains, where it is most characteristic of seasonally to permanently wetter microsites such as ditches, edges of sandy lakeshores, and lakeplain wet prairies. The other extreme constitutes the majority of midwestern plants, with moderately hirtellous foliage and occasionally sparsely hirtellous peduncles and sparsely ciliate sepals, the leaf blades with somewhat less pronounced basal lobes or with merely slightly larger basal teeth or shallow basal incisions; these plants are common in drier microsites such as sand barrens and drier sandy old fields. This latter extreme represents the older names *V. sagittata* var. *subsagittata* (Greene) Pollard or *V. subsagittata* Greene, and it has frequently been the cause of confusion with *V. fimbriatula*. "Intermediate" plants with all manner of expressions of leaf blade lobing and indument are found throughout the zone of overlap, with these features occasionally varying somewhat within populations and among populations in the Great Lakes region. Both are included under *V. sagittata* without formal recognition. As Brainerd and others have suggested, this local and regional polymorphism might be the product of past hybridization between *V. fimbriatula* and *V. sagittata*, but the two are now quite consistently divergent in several vegetative and reproductive features, and they are maintained here as distinct species (as is *V. emarginata*).

53. *Viola selkirkii* Pursh ex Goldie, Edinburgh Philos. J. 6: 324. 1822. Type: [Canada] Montreal, [no date], [*J*.] *Goldie* [*s.n*.] (lectotype (**designated here**): K000370205, internet image!). Fig. 128.

Viola kamtschatica Ging., Linnaea 1(3): 406. 1826.

Viola umbrosa Fr., Novit., edit altera: 271. 1828.

Common Names. Great-spurred violet, Selkirk's violet.

Description. Acaulescent rosulate perennials from somewhat thick rhizome, ≤ 10 cm tall; foliage and peduncles green, upper surface of leaf blades dark green, glabrous except for scattered appressed hairs on upper surface of leaf blades; stipules adnate to petiole for up to 1/2 their length, glandular-dentate; leaves widely spreading to prostrate, leaf blades undivided, largest ≤ 50 × 40 mm, ovate to subreniform, base deeply and narrowly cordate, inner edges of basal lobes commonly attingent or overlapping in living

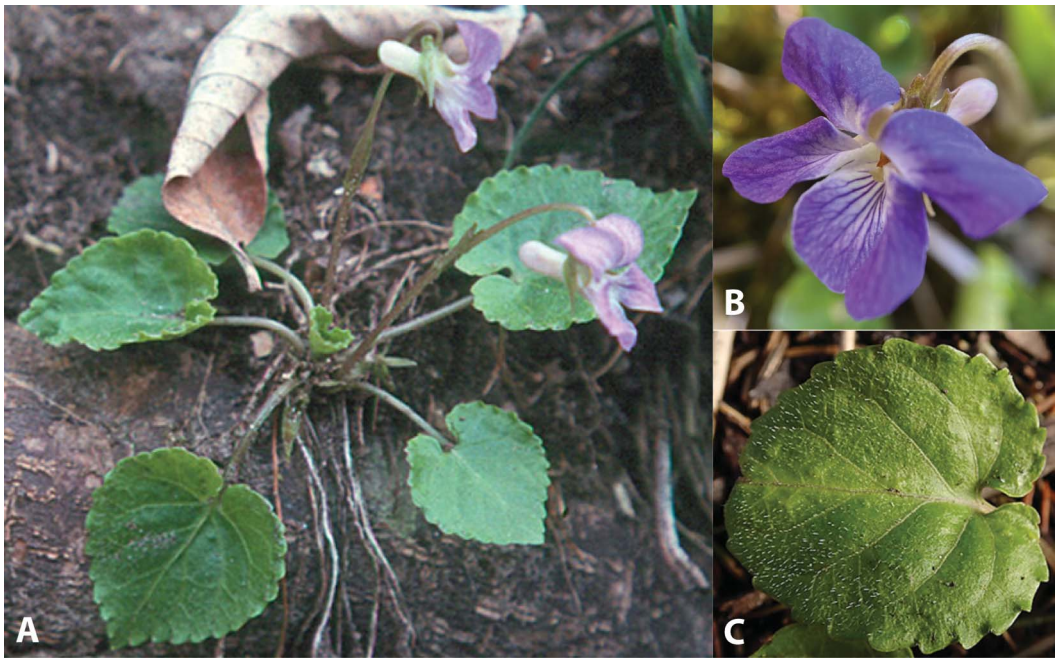

FIG. 128. *Viola selkirkii*. (A) Chasmogamous flowering habit (photo: Arthur Haines, Native Plant Trust). (B) Chasmogamous flower (photo: Adam Heikkela). (C) Leaf (photo: Peter M. Dziuk).

material , margins crenate (rarely crenate-serrate), eciliate, apex sharply obtuse or apiculate; chasmogamous peduncle held above leaves; chasmogamous flower $\leq$ 15 mm; calyx glabrous, eciliate; lowest sepals lanceolate to ovate-lanceolate, sharply acute to obtuse; auricles prominent and entire to erose, not elongating in fruit; corolla pale blue to purple, throat white (exposed around throat); spur thick and club-shaped, 4–7 mm, pale blue to purple; all petals glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle initially prostrate but arching just before capsule dehiscence, much shorter than petioles; cleistogamous capsule 4–8 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.5–2.0 $\times$ 1.0–1.1 mm, light orange-brown, unspotted; $2n = 24$.

Similar Species. This species is distinctive in its pale blue to purple corolla with glabrous petals and a somewhat elongate thick club-shaped spur, and strongly adnate stipules characteristic of members of subsect. *Patellares*, to which it belongs. Vegetatively or in cleistogamous fruit is is most often mistaken for other acaulescent uncut-leaved species with leaf blades nearly as broad as to broader than long, such as *V. blanda*, *V. hirsutula*, *V. incognita*, *V. septentrionalis*, and *V. sororia sensu stricto*, all of which might or do grow near or with it and which share the spotted or blotched cleistogamous capsule on a prostrate peduncle. When the adnate stipules are ignored, this species differs from *V. blanda* in lacking stoloniform rhizomes and stolons, its prominent auricles, and larger lighter seeds; from *V. incognita* in the absence of stoloniform rhizomes and stolons, foliage glabrous except for scattered appressed hairs on the upper surface of the leaf blades, leaf blades widely spreading or prostrate with inner edges of the basal lobes commonly attingent or overlapping in living material and margins shallowly crenate, prominent auricles, and smaller seeds; from *V. hirsutula* in the leaf blades with inner edges of the basal lobes commonly attingent or overlapping in living material and margins shallowly crenate, their upper surface uniformly dark green, and its prominent auricles; and from *V. septentrionalis* and *V. sororia sensu stricto* in its glabrous foliage and peduncle with hairs otherwise restricted to the upper surface of the leaf blades, glabrous eciliate sepals, prominent auricles, and lighter unspotted seeds.

Ecology. Organic-rich soils in rich dedicuous or mixed forests, often on boulders or ledges, pronouncedly calciphilic.

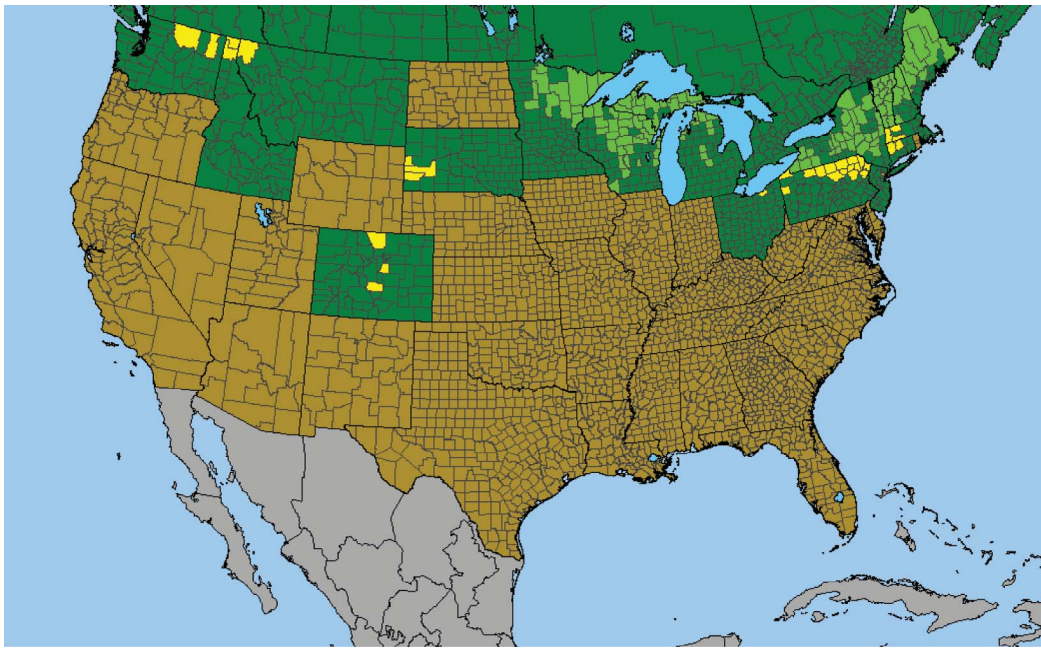

FIG. 129. United States county distribution of *Viola selkirkii* (map: Biota of North America Program).

Distribution. Circumboreal, Greenland and Newfoundland and Labrador to Alaska, south to Rhode Island, Pennsylvania, Wisconsin, northern Minnesota, and northwestern Rocky Mountains; disjunct in South Dakota and Colorado; Eurasia. Fig. 129.

Rarity. Listed in Connecticut.

Phenology. Chasmogamous flower April–May (September), chasmogamous fruit May–June (September), cleistogamous fruit July–August.

Affinities. This species belongs to sect. *Plagiostigma* Godr., subsect. *Patellares* (Boiss.) Rouy & Foucaud.

Hybrids. None.

Comments. Goldie's protologue stated "Mountains about Montreal, nowhere else." While the collection data are reasonably specific, he gave no indication of a single collection and did not designate a type. Stafleu and Cowan (1976) note that Goldie's collections are found at K and several other herbaria. A sheet at K contains two separate collections: K000370205, with the handwritten data "fl. caeruleo, Goldie, Montreal, prope *V. cucullatam*" and K000370204, with an 1888 collection from Greenland. Only the K000370205 sheet appears to be original material and is designated here as the lectotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), Scoggan (1978), Gleason and Cronquist (1991), Ballard (1995, 2000), and Little and McKinney (2015) have accepted this distinctive species. This circumboreal violet is the sole native New World representative of the diverse and otherwise Eurasian subsect. *Patellares* (Boiss.) Rouy & Foucaud, which also is represented by three other spontaneous Asian violet introductions to our region. It is immediately recognizable in chasmogamous flower by its elongate club-shaped spur and beardless petals. In cleistogamous fruit it is distinct from other acaulescent species with undivided leaf blades by the ovate to subreniform blade outline, the basal lobes commonly attingent or overlapping in living material, glabrous foliage except for scattered appressed hairs on the upper surface of the leaf blades, short conspicuously adnate stipules, purple-spotted or -blotched cleistogamous capsule on a prostrate peduncle, and light orange-brown seeds. Russell (1956b) studied morphological variation across its North Amer-

FIG. 130. *Viola septemloba*. (A) Chasmogamous flowering habit (photo: M. C. Willy). (B) Leaves during chasmogamous flower (3-lobed leaf blades) (photo: Old Bean Adams). (C) Leaf during chasmogamous flower (rare biternate morph) (photo: Jessica McAlpine). (D) Chasmogamous flower front view (photo: Old Bean Adams). (E) Chasmogamous flower profile view (photo: M. C. Willy). (F) Seeds from herbarium specimen: Transplanted from North Carolina, Brunswick Co., *H. Ballard 15-002Y and A. Stuart* (BHO).

ican range and found it to be among the least variable species on the continent.

54. ***Viola septemloba*** Leconte, Ann. Lyceum Nat. Hist. New York 2: 141. 1828 ["1826"]. Type: "Habitat in Carolina et Georgia in pinetis solum, per tractum quae regio inferior vocatur" [protologue]; J. E. Leconte, Plate number 5 of Leconte's unpublished watercolors, Call number QK 495 V811 L496f, University of Notre Dame Libraries, Department of Special Collections, Section of Rare Books (lectotype (designated by Nir Gil-ad. 1997. Boissiera 53: 76): ND, isolectotype: K). *Viola vicinalis* Greene, Pittonia 4: 9. 1899 [replacement name for *V. insignis* Pollard]; *Viola insignis* Pollard, Bot. Gaz. 26: 334. 1898 [illegitimate homonym of *V.* ×*insignis* K.Richt. (1888)]. Fig. 130.

Common Name. Southern coast violet.

Description. Acaulescent rosulate perennials from thick rhizome, ≤ 25 cm tall; foliage commonly somewhat succulent, foliage and peduncles green, lower surface of leaf blades occasionally tinged with purple, glabrous throughout; stipules free, irregularly glandular-fimbriate; heterophyllous, juvenile plants not producing divided leaf blades, reproductive plants with smallest leaf blades undivided, larger blades moderately to deeply pedately or occasionally biternately divided into (3)5 or 7(9) lanceolate or

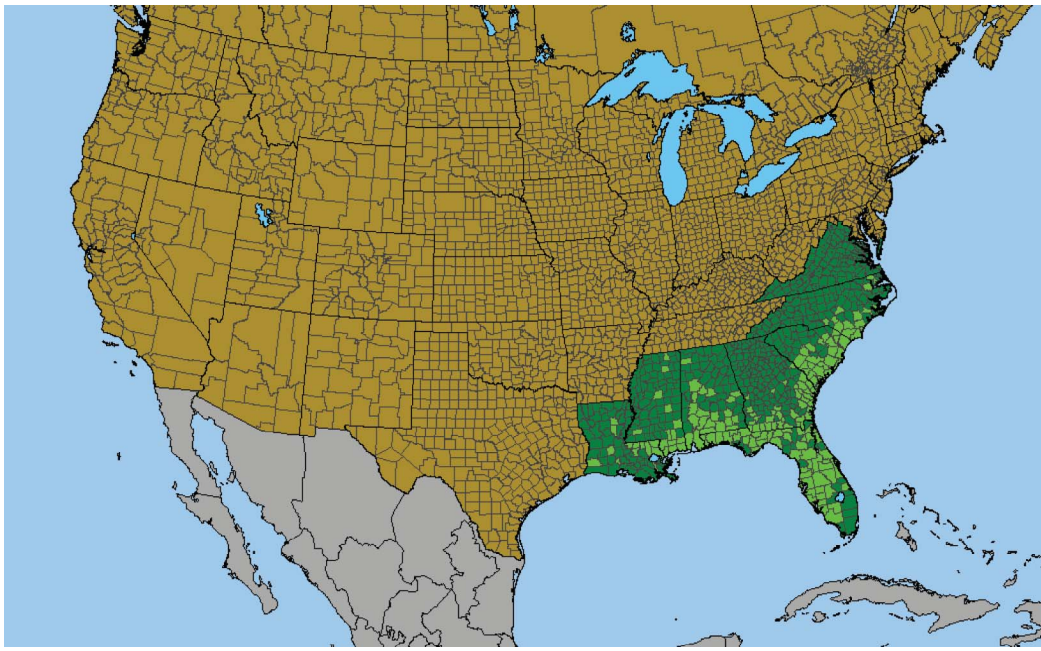

FIG. 131. United States county distribution of *Viola septemloba* (map: Biota of North America Program).

elliptical lobes with rounded apices, the terminal lobe usually distinctly broader than others, the lowest lobe of the lateral primary divisions oriented downward, largest $\leq 45 \times 58$ mm, outline ovate to broadly ovate, base cordate, margins entire (rarely remotely crenate-serrate), eciliate, apex obtuse; chasmogamous peduncle held above the leaves; chasmogamous flower ≤ 30 mm; calyx glabrous, eciliate; lowest sepals lanceolate, acuminate; auricles short to prominent and entire, elongating to 2.5 mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; cleistogamous flowers produced after chasmogamous, peduncle erect and nearly or quite equaling petioles; capsule 13–18 mm, green drying tan, unspotted, glabrous; seeds (1.5)1.9–2.5 $\times$ 1.4–1.6 mm, brownish-black, unspotted; $2n = 54$.

Similar Species. This heterophyllous species is occasionally confused with *V. sagittata* (another member of the Sagittata group) and homophyllous cut-leaved *V. brittoniana*; the ranges of these three converge on the Coastal Plain, but the local and regional distributions of *V. brittoniana* and *V. septemloba* are virtually non-overlapping. This differs from *V. brittoniana* in having subsucculent glabrous gray-green foliage, the earliest and latest leaf blades undivided, cut leaf blades mostly pedately divided with the terminal lobe commonly undivided and broader and longer than the other lobes, the chasmogamous peduncle held above the leaves, often larger flower, and larger brownish-black seeds; and from *V. sagittata* in its subsucculent gray-green foliage, commonly more elongate and more numerous lateral lobes, typically larger flowers, and larger brownish-black seeds.

Ecology. Sandy soils of pine woodlands, especially frequently burned longleaf pine savannas.

Distribution. Southeastern Atlantic and Gulf Coastal Plains, southeastern Virginia south to Florida, west to Louisiana. Fig. 131.

Rarity. None.

Phenology. Chasmogamous flower February–May, chasmogamous fruit April–June, cleistogamous fruit July–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sagittata species group.

Hybrids. Hybridizes with *V. emarginata sensu stricto* (House 1914; Brainerd 1924). Brainerd reported that this exhibits intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). The species occasionally grows in local sympatry with others (*e.g.*, *V. sagittata*), and such hybrids should be sought.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Russell (1965), and Gil-ad (1995, 1997, 1998) accepted the present taxon as a distinct species. Gleason and Cronquist (1991) subsumed it into a very broadly defined *V. palmata*. McKinney (1992) and McKinney and Russell (2002) merged this and *V. egglestonii*, recognizing them as varieties of *V. septemloba* on the basis of similar leaf blade dissection pattern, but Little and McKinney (2015) reinstated the present taxon to species rank. Early on, Brainerd and his contemporaries did not distinguish the present species from *V. brittoniana*, referring to both as *V. septemloba*. Additionally, the present species has been frequently confused with *V. brittoniana* or hybrids of *V. brittoniana* (especially the hybrid with *V. sagittata*). These factors have led to a number of erroneous reports of *V. septemloba* from the northern Atlantic Coastal Plain.

This and another heterophyllous species, *V. edulis*, exhibit what the first author has called "delayed heterophylly," in which juvenile and early chasmogamous-flowering individuals often do not produce the divided leaf blades of later reproductive individuals. Populations of this species in particular commonly include reproductive individuals with the largest leaf blades deeply lobed in chasmogamous flower and cleistogamous fruit as well as fully intermixed juvenile plants completely lacking cut leaf blades. Inspection shows that these are typical *V. septemloba*, but juveniles are occasionally unknowingly segregated as an uncut-leaved species. One of the syntype sheets for the name *V. langloisii*, a southeastern species just south of our region, includes a specimen of *V. septemloba* with only uncut leaf blades. The extent of leaf dissection in this is quite variable, with individual plants not infrequently producing some 3-lobed blades and others with 5-, 7-, or 9-lobed blades. Brainerd (1911a) discussed this intraplant and population-level variability in relation to the synonym *V. insignis* Pollard, distinguished from the present species originally for having merely 3-lobed leaves. Russell's (1965) illustration for *V. edulis* (which he called *V. esculenta*) is not the latter but a plant of *V. septemloba* with 3-lobed leaf blades.

In Brainerd Baird's time the geographic distributions of *V. brittoniana* and *V. septemloba* were thought not to overlap at the state level; however, increased botanical surveys and collections have found regional co-occurrence in the Carolinas, where the local range of *V. brittoniana* shifts up onto the Upper Coastal Plain and adjacent Lower Piedmont into moister organic soils near streams closer to the "Fall Line," while *V. septemloba* remains on the Lower and Middle Coastal Plain in its preferred habitat of sandy soils in frequently burned longleaf pine savanna. No hybrids between the two have been reported, but they may be expected in North Carolina. The northern range limit for *V. septemloba* based on confirmed records has usually been noted as North Carolina, but House (1924) and Brainerd (1924) report a hybrid with *V. emarginata* from Gilmerton in Norfolk Co., VA. We have also confirmed an old misidentified herbarium specimen of this species at VPI from that area of Virginia. The species was not mentioned by Weakley *et al*. (2012) but was noted from southeastern Virginia by Ballard *et al*. (2020a). Extant populations of the species should be sought in that area. Winn and Moriuchi (2009) investigated the evolutionary benefits of the chasmogamous-cleistogamous mixed mating system in this species.

55. ***Viola septentrionalis*** Greene **species complex**

Infraspecific taxa belonging to this species include the following:

55a. *Viola septentrionalis* Greene *sensu stricto*

55b. *Viola septentrionalis* (Upper Midwest variant)

Common Name. Northern blue violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm tall; foliage and peduncles gray-green, upper surface of leaf blades darker green than lower, lower commonly tinged with purple, sparsely to densely hirsute; stipules free, irregularly glandular-fimbriate; leaves ascending to spreading, leaf blades undivided, largest $\leq$ 98 $\times$ 89 mm, narrowly or broadly ovate in chasmogamous flower, broadening to deltate-reniform in fruit, margins serrate (occasionally weakly so), densely ciliate with spreading hairs

(these often long), apex acute to obtuse or rounded; chasmogamous peduncle held above the leaves early in flower, among the leaves later; chasmogamous flower $\leq$ 22 mm; calyx glabrous or pubescent, sparsely to densely ciliate nearly or fully to apex (hairs often long); lowest sepals broadly ovate-lanceolate to ovate and obtuse to rounded, or occasionally ovate-triangular and sharply acute; auricles prominent and entire to erose, elongating to 3 mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles and arching just before capsule dehiscence; cleistogamous capsule 5–8 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.2–2.3 $\times$ 0.8–1.2 mm, narrowly obovoid, light-medium brown to dark brown, unspotted (eastern and northern populations) or 1.9–2.1 $\times$ 1.2–1.3, broadly obovoid, red-brown with small weak darker streaks or raised darker spots (Upper Midwest populations); 2n = 54.

Similar Species. The most similar species likely to be confused with this violet are *V. grisea* and *V. novae-angliae* with narrowly ovate-triangular leaf blades even in fruit, and a densely bearded spurred petal; and *V. sororia sensu stricto* with leaf blades about as broad as to broader than long; all these have pubescent foliage, obtuse to rounded sepals and a heavily spotted or blotched cleistogamous capsule on a prostrate peduncle. This species differs from *V. grisea* and *V. novae-angliae* in its narrowly to broadly ovate leaf blades and more narrowly obovoid seeds, and from *V. sororia sensu stricto* by the spreading and often longer hairs on the leaf blade margins, sepals ciliate (often with longer hairs) to the apex, prominent auricles elongating weakly in fruit, and brown seeds lacking spots or with small weak darker spots or streaks.

Ecology. Thin sandy or gravelly loam soils in dry-mesic forests, on cliffs and ledges, commonly in limestone rubble or over dolomite or limestone bedrock, frequently growing under *Thuja* or *Juniperus* in the northern portion of its range.

Distribution. Interruptedly transcontinental, primarily boreal, Appalachian, Northeast, Upper Midwest and northern Rocky Mountains, Newfoundland and Labrador to Saskatchewan and British Columbia, south to western North Carolina and eastern Tennessee, eastern Iowa, western Montana, and eastern Washington. Fig. 132.

Rarity. Listed in New Jersey and West Virginia.

Phenology. Chasmogamous flower May–June, chasmogamous fruit June, cleistogamous fruit May–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sororia species group.

Hybrids. See infraspecific taxa.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Gil-ad (1995, 1997, 1998), and Weakley *et al*. (2012) recognized this as a distinct species. Gil-ad presented a long list of macromorphological distinctions in leaves, chasmogamous flowers, cleistogamous capsules, and seeds, as well as unique micromorphological features of lateral petal trichomes and seed coats, to support its maintenance as a species. Weakley *et al*. mentioned that its status and distribution in the central and southern Appalachians is obscure. Gleason and Cronquist (1991), Ballard (1995, 2000), Haines *et al*. (2011), and Little and McKinney (2015) synonymized it under *V. sororia*, while McKinney (1992) and McKinney and Russell (2002) subsumed it under *V. sororia* var. *sororia*. The present species has regularly been confused with and often synonymized with *V. sororia sensu stricto*, but it is consistently different in several features of foliage, chasmogamous flowers, cleistogamous capsules, and seeds. The species is still somewhat poorly understood, especially outside of New England and maritime Canada where it is most common in our region.

This predominately boreal species ranges southward into high elevations of the central and southern Appalachian Mountains and westward across Canada. Very recent scrutiny of specimens from the Thunder Bay District of Ontario, eastern Minnesota, and easternmost Iowa have revealed a subtly different taxon, the Upper Midwest variant, that appears to exhibit consistently densely hirsute foliage and peduncle, consistently densely ciliate sepals with the apex commonly broadly rounded, and seeds with small weak darker spots or streaks.

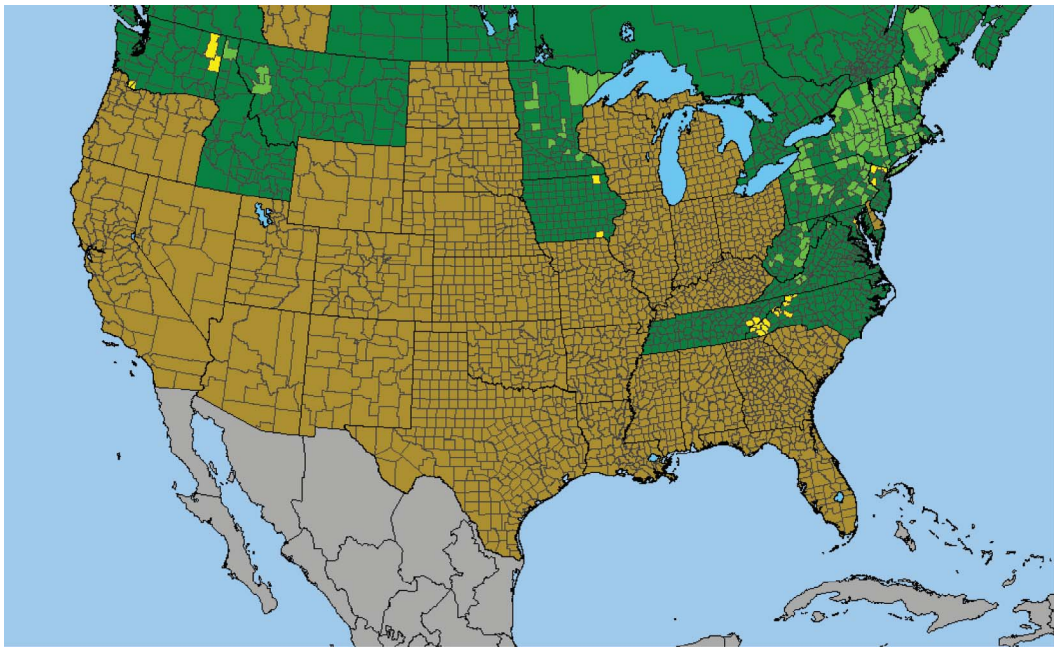

FIG. 132. United States county distribution of *Viola septentrionalis* species complex (map: Biota of North America Program).

Populations of *V. septentrionalis sensu stricto* elsewhere in the Northeast (ranging to the north and east of the Thunder Bay District in Ontario) vary considerably in foliage and peduncle indument and sepal ciliation, with some plants nearly glabrate, sepals virtually eciliate and often acuminate from the middle, and unspotted seeds. The Upper Midwest variant and its distribution require further study.

55a. ***Viola septentrionalis*** Greene ***sensu stricto***, Pittonia 3: 334. 1898. Type: Canada. [Ontario] near Ottawa, 30 May 1898, *J. M. Macoun 18761* (designated incorrectly as holotype by Landon McKinney, Sida, Bot. Misc. 7: 36. 1992; corrected to lectotype by Nir Gil-ad, Boissiera 53: 78. 1997): NDG33738 (*n.v.*), internet image; isolectotype: CAN119225 (*n.v.*)). Fig. 133.

Viola macounii Greene, Pittonia 3: 335. 1898.
Viola fletcheri Greene, Pittonia 4: 296. 1901.
Viola subviscosa Greene, Pittonia 4: 293. 1901.
Viola nesiotica Greene, Pittonia 5: 102. 1902.
Viola septentrionalis Greene f. *alba* Vict. & J.Rousseau, Contr. Inst. Bot. Univ. Montreal 36: 20. 1940.

Common Name. Northern blue violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 29 cm tall; foliage and peduncles gray-green, upper surface of leaf blades darker green than lower, lower commonly tinged with purple, sparsely to densely hirsute; stipules free, irregularly glandular-fimbriate; leaves ascending to spreading, leaf blades undivided, largest $\leq$ 98 $\times$ 89 mm, narrowly or broadly ovate in chasmogamous flower, broadening to deltate-reniform in fruit, margins serrate (occasionally weakly so), densely ciliate with spreading hairs (these often long), apex acute to obtuse or rounded; chasmogamous peduncle held above the leaves early in flower, among the leaves later; chasmogamous flower $\leq$ 22 mm; calyx glabrous or pubescent, sparsely to densely ciliate nearly or fully to apex (hairs often long); lowest sepals broadly ovate-lanceolate to ovate or ovate-triangular, sharply acute or obtuse to rounded; auricles prominent and entire to erose, elongating to 3 mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal densely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles and arching just before capsule dehis-

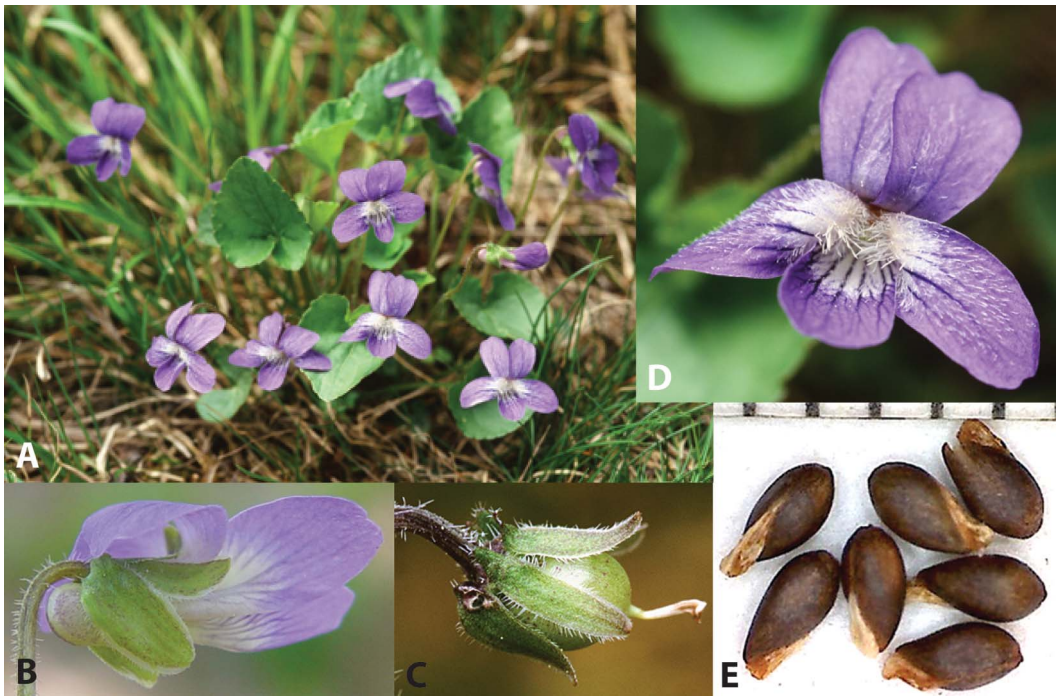

FIG. 133. *Viola septentrionalis* sensu stricto. (A) Chasmogamous flowering habit (photo: Kim Blaxland). (B) Chasmogamous flower front view (photo: Kim Blaxland). (C) Chasmogamous flower profile view (photo: Arthur Haines, Native Plant Trust). (D) Chasmogamous fruit (photo: Kim Blaxland). (E) Seeds from herbarium specimen: Nova Scotia, North Sydney, *H. Robinson 611* (NY).

cence; cleistogamous capsule 5–8 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.2–2.3 × 0.8–1.2 mm, light-medium brown to dark brown, unspotted; 2n = 54.

Similar Species. The most similar violets likely to be confused with this species are *V. novae-angliae* and *V. sororia sensu stricto*, *Borealiamericanae* violets with densely pubescent foliage, undivided leaf blades, oblong to ovate ciliate obtuse to rounded sepals, and a heavily spotted or blotched cleistogamous capsule on a prostrate peduncle. This species differs from *V. grisea* in its narrowly ovate to ovate leaf blades with acute to rounded apex that broaden to deltate-reniform in fruit and have more uniformly serrate margins; and from *V. sororia sensu stricto* by its spreading-hirsute leaf blade margins, sepals ciliate to the apex and often hirtellous on the lamina, auricles prominent and elongating in fruit, densely bearded spurred petal, and seeds narrowly obovoid, light to dark brown and unspotted.

Ecology. Thin sandy or gravelly loam soils in dry-mesic forests, on cliffs and ledges, commonly in limestone rubble or over dolomite or limestone bedrock, frequently growing under *Thuja* or *Juniperus* in the northern portion of its range.

Distribution. Interruptedly transcontinental, primarily boreal, Appalachian, Northeast, and northern Rocky Mountains, Newfoundland and Labrador to Saskatchewan and British Columbia, south to western North Carolina and eastern Tennessee; western Montana and eastern Washington; reports from Michigan and Wisconsin are misidentifications of *V. communis* or *V. sororia*, reports from eastern Iowa, Minnesota, and northwestern Ontario are referred to *V. septentrionalis* (Upper Midwest variant). Fig. 134.

Rarity. Same as the species complex.

Phenology. Presumably same as the species complex.

Affinities. Same as the species complex.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1904b, 1907b, 1924; House 1924), *V. cucullata* (Brainerd 1904b, 1924; House 1924; Russell 1955a), *V. fimbriatula* (Brainerd 1904b, 1905,

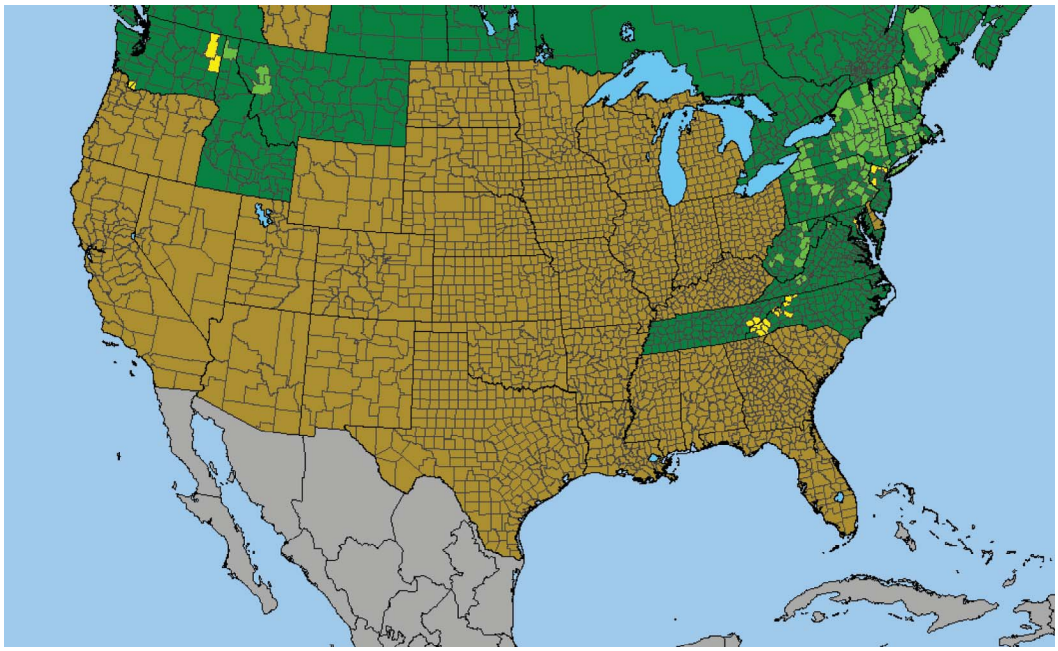

FIG. 134. United States county distribution of *Viola septentrionalis* sensu stricto (map: Biota of North America Program).

1924; House 1924), and *V. sororia sensu stricto* (Brainerd 1904b, 1924,;House 1924). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All hybrids fail to reproduce by chasmogamous flowers, and all either produce abortive cleistogamous capsules or capsules with very few viable seeds (up to 1/8 of ovules fertilized in the most fertile hybrid, with *V. fimbriatula*.

Comments. Greene's protologue states that plants were collected from "Rich soil along the borders of thickets, near Ottawa, Ontario, in full petaliferous flower 10 May, 1898, and in fruit from the apetalous flowers a month later, J. M. Macoun; Canadian Survey n. 18,561." The protologue describes two different collections, does not refer to either as types, does not indicate that either collection is represented by a single sheet, and does not mention a herbarium. Only one sheet at NDG matches the protologue information precisely. McKinney first designated the NDG sheet incorrectly as the holotype; Gil-ad corrected this error to lectotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Gil-ad (1995, 1997, 1998), and Weakley *et al*. (2012) recognized this as a distinct species. Gil-ad presented a long list of macromorphological distinctions in leaves, chasmogamous flowers, cleistogamous capsules, and seeds, as well as unique micromorphological features of lateral petal trichomes and seed coats, to support its maintenance as a species. Weakley *et al*. (2012) mentioned that its status and distribution in the central and southern Appalachians is obscure. Gleason and Cronquist (1991), Ballard (1995, 2000), Haines *et al*. (2011), and Little and McKinney (2015) synonymized it under *V. sororia*, while McKinney (1992) and McKinney and Russell (2002) subsumed it under *V. sororia* var. *sororia*.

Viola septentrionalis (Upper Midwest variant) is newly detected, and not much is yet known about it. Thus far it can only be reliably distinguished from *V. septentrionalis sensu stricto* from the seeds. Field studies and more intensive sampling in the western Great Lakes region would provide a greater understanding of the two taxa.

55b. *Viola septentrionalis* Greene **(Upper Midwest variant).** Fig. 135.

Common Names. None.

FIG. 135. *Viola septentrionalis* (Upper Midwest variant). Seeds from herbarium specimen: Minnesota, Clearwater Co., *Ownbey 5975* (MIN700496).

Description. Acaulescent rosulate perennials from thick rhizome, ≤ 29 cm tall; most features same as *V. septentrionalis sensu stricto*, but foliage uniformly densely hirsute; calyx commonly pubescent, densely ciliate nearly or fully to apex (hairs often long); lowest sepals consistently broadly ovate-lanceolate to ovate, obtuse to rounded; seeds 1.9–2.1 × 1.2–1.3 mm, broadly obovoid, red-brown, with small weak darker streaks or darker raised spots; 2n = 54.

Ecology. Broad habitat type is somewhat similar to *V. septentrionalis sensu stricto* in terms of sandy or gravelly or rocky soils in open dry-mesic or mesic northern forests, but consistently on or around outcropping basaltic (presumably somewhat acidic) exposures.

Distribution. Upper Midwest and adjacent northwestern Ontario, Thunder Bay District southward into Minnesota, then sporadically southward to southeastern Iowa. Fig. 136.

Rarity. None.

Phenology. Presumably same as the species complex.

Affinities. Same as the species complex.

Hybrids. None.

Comments. Fernald (1950), Alexander (1963), and Scoggan (1978) reported *V. septentrionalis* from Michigan and westward in the Midwest. Specimens from Minnesota could certainly be the basis for reports, which would probably represent this variant; however, the first author has examined all major herbarium collections in Wisconsin and has not yet confirmed the presence of *V. septentrionalis* in that state. The collections in Michigan must be reexamined, as Ballard's early studies (Ballard 1995) included *V. septentrionalis* in a broadly defined *V. sororia*. Russell (1965) mapped *V. septentrionalis* in the western Great Lakes region but inexplicably placed records in southern Michigan and southern Wisconsin, not at all biogeographically sensible for this generally boreal or high-elevation montane species. These have been dismissed as *V. sororia*. This variant is not dramatically divergent from *V. septentrionalis sensu stricto* elsewhere across its range, but specimens are quite uniform in foliage and peduncle indument, a broader ciliate sepals with obtuse to rounded apex, and are distinctive in seeds with weak but noticeable small dark streaks and spots. Plants and populations elsewhere in the eastern range of the species are quite variable in the same features, and seeds are uniformly unspotted. Since the specimens represent a southward extension of an otherwise boreal Canadian range for the species in the Great Lakes region and central Canada, the plants deserve further scrutiny. The variant should be sought elsewhere in the Driftless Area and southward along the river valley bordering Iowa and Illinois.

56. ***Viola sororia*** **species complex**

Infraspecific taxa belonging to this species include the following:

56a. *Viola sororia* Willd. *sensu stricto*
56b. *Viola sororia* (glabrous variant)
56c. *Viola sororia* (*hirsutuloides* variant)

Common Names. Common wood violet, woolly blue violet.

Description. Acaulescent rosulate perennials from thick commonly branching rhizome, ≤ 34 cm tall; foliage and peduncles green with leaves often turning yellow-green in fruit, sparsely to densely hirsute, and calyx ciliate in basal half (*V. sororia sensu stricto*), or foliage and peduncles green and glabrous and calyx eciliate (*V. sororia* [glabrous variant]), or foliage and peduncles darker blue-green with midrib, lower surface of leaf blades, petioles, and calyx purple-tinged, foliage and peduncles glabrous or with petioles occasionally sparsely hirtellous, and calyx eciliate (*V. sororia* [*hirsutuloides* variant]); stipules free, irregularly glandular-fimbriate; leaves ascending to spreading, leaf blades undivided, largest ≤ 121

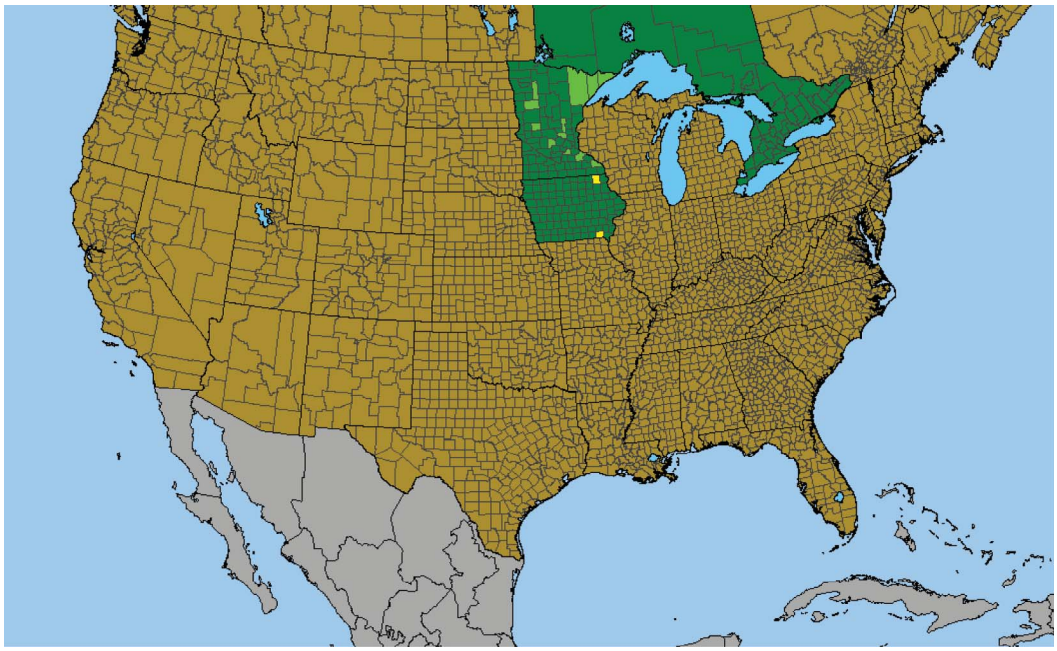

FIG. 136. United States county distribution of *Viola septentrionalis* (Upper Midwest variant) (map: Biota of North America Program).

× 126 mm, in flower ovate to reniform with base cordate and apex acute to broadly rounded, in fruit broadening to ovate-deltate or reniform-deltate, base deeply cordate to nearly truncate, apex abruptly acute or obtuse-angulate, and margins appressed-ciliate and prominently incurved-serrate with teeth lower and more remote near apex (*V. sororia sensu stricto* and *V. sororia* [glabrous variant]), or leaf blades broadly rounded at apex, margins eciliate and shallowly and closely crenate or crenulate-serrulate (*V. sororia* [*hirsutuloides* variant]); chasmogamous peduncle held among the leaves (occasionally above the leaves earlier in flower, especially in lawns and other disturbed sites); chasmogamous flower ≤ 21 mm; calyx glabrous; lowest sepals narrowly oblong-ovate to ovate, or occasionally ovate-triangular with distal half subattenuate, obtuse to rounded; auricles short and entire, not elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with filiform to slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on prostrate peduncle much shorter than petioles and arching upward just before capsule dehiscence; cleistogamous capsule 6–11 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.5–2.6 × 0.9–1.6 mm, light to dark gray or grayish-brown with weak brown streaks or blotches; 2n = 54.

Similar Species. The glabrous or densely hirsute foliage and ovate to reniform leaf blades with shallowly to deeply cordate base in this species are traits shared with most homophyllous uncut-leaved *Borealiamericanae* violets, and this has consequently led to great confusion and synonymization of many taxa into a hugely heterogeneous *V. sororia sensu lato*. With its sparsely to densely hirsute foliage and ciliate sepals, *V. sororia sensu stricto* differs from *V. septentrionalis* in the appressed-ciliate leaf blade margins, glabrous spurred petal, sepals glabrous on the lamina and short-ciliate only in the basal half, short rounded auricles, and seeds medium gray to gray-brown with small weak streaks or blotches; and from *V. hirsutula* in sparsely to densely hirsute foliage with pubescence not confined to the upper surface of leaf blades, spreading to ascending uniformly green leaves, ciliate sepals, glabrous spurred petal, and gray to gray-brown seeds with small weak streaks or blotches. With glabrous foliage and eciliate sepals, *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) differ from *V. hirsutula* in spreading to ascending glabrous

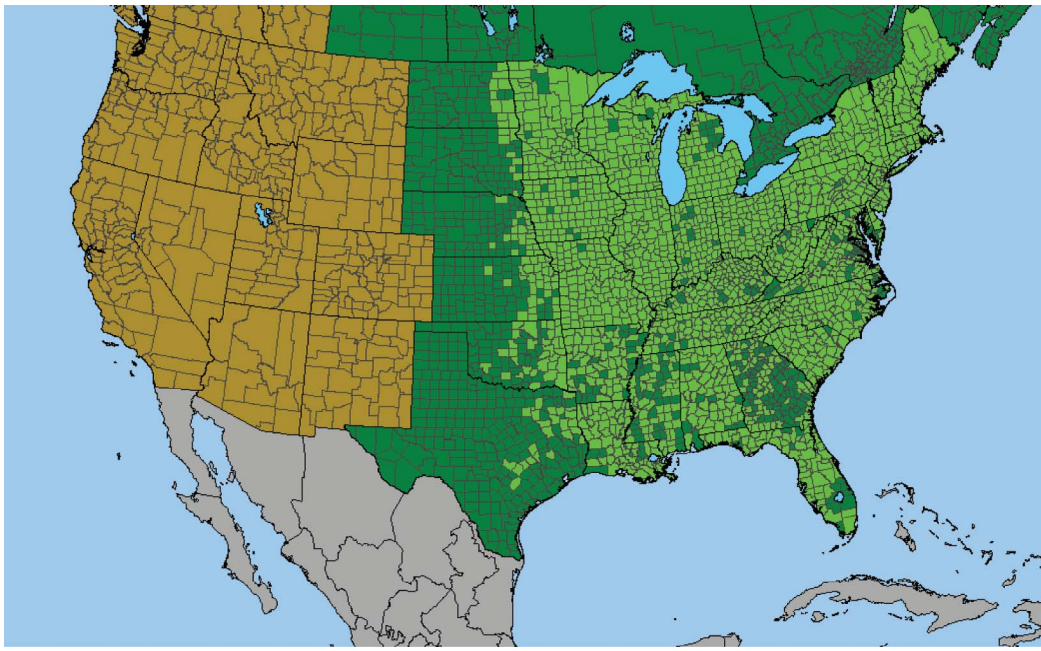

FIG. 137. United States county distribution of *Viola sororia* species complex (map: Biota of North America Program).

uniformly green leaves, glabrous spurred petal, and gray to gray-brown seeds with small weak streaks or blotches. The two variants can be separated in chasmogamous flower from *V. communis* and *V. domestica* by their oblong-ovate to ovate sepals with obtuse to rounded apex, and short rounded auricles, and further from *V. communis* by their dull leaf surfaces; from *V. cucullata* in flowers held among the leaves, oblong-ovate to ovate obtuse to rounded sepals, short rounded auricles, corolla blue to purple without a contrasting eyespot around the throat, and lateral petal beards with long filiform to slightly clavate hairs; from *V. nephrophylla* by their glabrous spurred petal, and from *V. pratincola* by their oblong-ovate to ovate obtuse to rounded sepals, short rounded auricles, and glabrous spurred petal. In cleistogamous fruit *V. sororia* (glabrous variant) and *V. sororia* (*hirsutuloides* variant) differ from *V. communis*, *V. cucullata*, *V. domestica*, *V. langloisii* just south of our range, *V. nephrophylla*, and *V. pratincola* in their densely spotted or blotched cleistogamous capsules on prostrate peduncles; and from *V. affinis*, *V. hirsutula, V. latiuscula*, and *V. missouriensis* in their oblong-ovate to ovate obtuse to rounded speals, short rounded auricles, and gray to gray-brown seeds with small weak streaks or blotches.

Ecology. Moist loamy, clayey, or silty loam soils in dry-mesic, mesic and wet-mesic forests, on slopes, coves, or terraces along streams and rivers, and along prairie-forest borders; also in lawns, meadows, and roadsides.

Distribution. Widely distributed in eastern North America, southern Newfoundland and Labrador to southeastern Saskatchewan, south to Florida and eastern Texas. Fig. 137.

Rarity. None.

Phenology. Chasmogamous flower February–May (September–October), chasmogamous fruit February–June, cleistogamous fruit June–October.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Sororia species group.

Hybrids. See infraspecific taxa.

Comments. Even after segregating several distinct species out of *V. sororia* in the broadest sense, the complex is still a small and somewhat heterogeneous assemblage of three incompletely

understood taxa that share undivided ovate to reniform leaf blades, a glabrous spurred petal, obtuse to rounded sepals, short rounded auricles not elongating in fruit, and purple-spotted or -blotched cleistogamous capsules on short prostrate to arching peduncles. Widely distributed *V. sororia sensu stricto* typically has sparsely to densely hirsute foliage and peduncles, leaf blades ovate to reniform with apex often abruptly obtuse or acute and marginal serrations prominently incurved and more remote near apex, chasmogamous flowers held among the leaves, sepals ciliate in the basal half, seeds medium gray with prominent dark gray streaks or blotches, and foliage occasionally turning yellow-green in midsummer. Populations commonly show some variability in foliage pubescence, and it is not uncommon to find individuals with nearly glabrous foliage; in fact, on any given plant, one or more leaves may be nearly glabrous while others may be densely hirsute or express localized pubescence. The other two taxa in the complex have glabrous foliage (except possibly for scattered minute appressed hairs on the upper leaf surface that require magnification) and eciliate sepals, foliage that does not usually turn yellow-green later, and (based on very limited sampling) different seed color patterns. *Viola sororia* (glabrous variant) is, on the basis of only very few and scattered specimens, distributed at higher elevations in the Appalachian Mountains and adjacent uplands as well as the eastern Piedmont, and it is morphologically similar to *V. sororia sensu stricto* except for glabrous foliage and eciliate sepals, leaf blades with slightly more uniformly crenate-serrate margins, and seeds pale gray to gray-brown with prominent indistinct darker streaks or blotches. *Viola sororia* (*hirsutuloides* variant) has been found very sporadically throughout the Appalachian Mountains and associated uplands, from New York to northern Georgia, and is more divergent from the two taxa above in its darker blue-green foliage and peduncles, the lower surface of leaf blades distinctly paler than the upper, with the midrib on the upper surface, lower surface of the leaf blades, petioles, peduncles and calyces purple-tinged, and leaf blades ovate or orbiculate to reniform with apex broadly rounded, margins uniformly low-crenate, and chasmogamous flowers often held above the leaves. These three taxa occupy mesic forests and terraces bordering floodplains and swamps, but they may be ecologically separated somehow. These taxa require much additional study to determine their morphological distinctions, geographic distributions, ecology, and taxonomic status. The entire complex is mapped together, due to our very fragmentary understanding of distributions for the two variants separate from *V. sororia sensu stricto*. For information on other species that have historically been included within the broader *V. sororia* assemblage, see "Comments" under *V. communis*, *V. domestica*, *V. pratincola*, and *V. septentrionalis*.

56a. *Viola sororia* Willd. ***sensu stricto***, Hort. Berol. [Willdenow] 1(6): pl. 72. Apr 1806; *Viola cucullata* Aiton var. *sororia* (Willd.) Torr. & A.Gray, Fl. N. Amer. 1(1): 137. 1838; *Viola palmata* L. var. *sororia* (Willd.) Pollard, Bot. Gaz. 26: 332. 1898. Type: "Habitat in America boreali" [protologue], [USA], Pennsylvania, [no date], [no collector], (lectotype (designated by Nir Gil-ad, Boissiera 53: 81. 1997): sheet No. 3, B-W4898, photo: MICH (*n.v.*)). Fig. 138.

Viola asarifolia Pursh, Fl. Amer. sept. 2: 732 [supplement]. 1813; *Viola palmata* L. var. *asarifolia* (Pursh) House, Torreya 2: 68. 1902.

Viola barbata Muhl.,Cat. pl. Amer. sept., ed. 1: 25. 1813 [nomen nudum]; *Viola barbata* Willd. ex Schult., in Roemer & Schultes, in Roemer & Schultes, Syst. veg. 5: 362. 1819. Type: "Pensylvania", [no date], *W. Muhlenberg s.n.* (Type: B-W04897-010 (*n.v.*), internet image).

Viola palmata L. var. *variegata* Stowell, J. Trenton Nat. Hist. Soc. 1: 26. 1887.

Viola cuspidata Greene, Pittonia 3: 314. 1898.

Viola dicksonii Greene, Pittonia 4: 65. 1899.

Viola nodosa Greene, Pittonia 4: 296. 1901.

Viola sororia Willd. f. *beckwithae* House, New York State Mus. Bull. 243–244: 40. 1923.

Viola sororia Willd. var. *incognita* J.Lacey, Sida 3: 312. 1969.

Viola sororia Willd. f. *pallida* Seymour, Fl. Vermont, ed. 4: 382. 1969.

Common Names. Common wood violet, woolly blue violet.

Description. Foliage, peduncles, and calyces green, leaves often turning yellow-green in fruit, foliage and peduncles moderately to densely hirsute, calyces ciliate in basal 1/2(2/3); leaf blade outline ovate, apex acute to obtuse, margins prominently incurved-serrate with teeth lower and more remote near apex, appressed-ciliate;

FIG. 138. *Viola sororia* Willd. *sensu stricto*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flowers front view (photo: Andrew Lane Gibson). (C) Cleistogamous fruit (photo: Harvey Ballard). (D) Seeds from herbarium specimen: Vermont, Middlebury, *E. Brainerd 159* (NY).

seeds 1.5–2.6 × 0.9–1.6 mm, dark gray to dark grayish-brown or blackish, appearing unspotted or with small usually weak blackish streaks. Other features same as the species complex.

Similar Species. See the species complex.

Ecology. Same as the species complex.

Distribution. Same as the species complex. See Fig. 137.

Rarity. None.

Phenology. Same as the species complex.

Affinities. Same as the species complex.

Hybrids. Hybridizes with *V. affinis* (Brainerd 1904b, 1924; Gaiser and Moore 1966; Haines *et al*. 2011), *V. baxteri* (Brainerd 1924; H.E.B., personal observation), *V. brittoniana* (Brainerd 1924; Haines *et al*. 2011), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Dowell 1910; Greene 1914; Brainerd 1924; House 1924; Henry 1953a), *V. cucullata* (Brainerd 1904b, 1924; House 1924; Henry 1953a; Haines *et al*. 2011), *V. emarginata* (Brainerd 1924), *V. fimbriatula* (Brainerd 1904b, 1924; House 1924; Henry 1953a; Haines *et al*. 2011), *V. hirsutula* (Brainerd 1924; Henry 1953a), *V. latiuscula* (Brainerd 1924; House 1924), *V. missouriensis* (Brainerd 1924), *V. monacanora* (Hastings 2018; H.E.B., personal observation), *V. nephrophylla* (Brainerd 1924; Haines *et al*. 2011), *V. palmata* var. *palmata* (Ballard 2013), *V. palmata* var. *triloba* (Brainerd 1912, 1924; Scoggan 1978; Haines *et al*. 2011; H.E.B., personal observation), *V. palmata* (*pseudostoneana* variant) (Hastings 2018; H.E.B., personal observation), *V. pedatifida* (Greene 1898a, 1903a, 1906b; Brainerd 1913a,

1924; Russell 1956a; Ballard 1995, 2013), *V. sagittata* (Brainerd 1924; Russell and Cooperrider 1955), *V. septentrionalis* (Brainerd 1904b, 1924), *V. stoneana* (H.E.B., personal observation), *V. subsinuata* (House 1923, 1924; Brainerd 1924; Haines *et al*. 2011; Hastings 2018; H.E.B., personal observation), and *V. viarum* (H.E.B., personal observation). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). He noted that all hybrids fail to reproduce by chasmogamous flowers, and all produce abortive cleistogamous capsules or capsules with a substantially reduced proportion of viable seeds or very few seeds at all.

Comments. Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Gil-ad (1995, 1997, 1998), and Weakley *et al*. (2012) distinguished the present species from *V. septentrionalis* Greene. Gil-ad provided a host of macromorphological characteristics and supporting micromorphological traits to uphold their recognition as distinct species. Gleason and Cronquist (1991), Ballard (1995, 2000), Haines *et al*. (2011), Voss and Reznicek (2012), and Little and McKinney (2015) synonymized the latter under *V. sororia*, while McKinney (1992) placed the latter under *V. sororia* var. *sororia*. Brainerd, Brainerd Baird, Fernald, Henry, Alexander, and Strausbaugh and Core segregated all strictly to essentially glabrous populations as *V. papilionacea* Pursh, including *V. pratincola* Greene described from southern Minnesota without formal recognition. Russell (1965) took a different approach and upheld *V. pratincola* as a distinct species, mapping it broadly from the eastern Great Plains and western Midwest, distinguishing it from a broadly delimited and more eastern *V. sororia* into which he included all other glabrous or glabrate variants. He argued that *V. pratincola* was morphologically different from *V. sororia* and related variants and inhabited open, prairie-like habitats and prairie-forest borders, often becoming quite weedy and common along roadsides, railroad rights-of-way, and lawns. He regarded other plants previously called *V. papilionacea* as nothing more than glabrate to glabrous *V. sororia*. Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1995, 2000), Weakley *et al*. (2012), and Little and McKinney (2015) recognized an even more broadly delimited *V. sororia* that included *V. pratincola* and all other glabrous or glabrate variants; while McKinney (1992) and McKinney and Russell (2002) placed everything under *V. sororia* var. *sororia*. Gil-ad (1997) studied specimens referred to *V. papilionacea* by Brainerd and found a diverse range of traits and a mixture of micromorphological traits suggestive of hybridization, with no unique traits. He excluded it as a series of hybrid derivatives. Similarly, he examined seeds from type material and found micromorphological features resembling those of *V. nephrophylla* and *V. affinis*; seeds of another specimen from Iowa possessed features suggestive of *V. nephrophylla* and *V. sororia*. Finding no unique macromorphological features and micromorphological features apparently blending those of other species, he concluded that *V. pratincola* represented a hybrid derivative. Recent field and herbarium studies of the Sororia species group have supported Gil-ad's taxonomic approach to delineate *V. sororia* very narrowly and to distinguish it from *V. septentrionalis* and from plants with strictly or essentially glabrous foliage and eciliate calyces. However, more extensive field and herbarium studies and substantially broader sampling of macromorphological and micromorphological characters have demonstrated the existence of multiple taxa from the heterogeneous "*papilionacea*" assemblage previously stuck for the most part under *V. sororia*, all of which are fertile and fully distinct on their own merit. These are recognized in this treatment as *V. communis* Pollard, *V. domestica* E.P.Bicknell, and *V. pratincola* Greene, all of which are placed in the Cucullata species group. Two additional taxa of *V. sororia* are currently under study, the glabrous variant and the *hirsutuloides* variant.

Its broadly mesic (dry-mesic to wet-mesic) forested microhabitats and broad eastern North American range bring *V. sororia sensu stricto* into contact with the majority of other *Borealiamericanae* violets, with which it very readily hybridizes. The hybrids range from subfertile to nearly sterile. See the "Hybrids" section for a comprehensive list. This taxon is mapped with the two variants for the *V. sororia* species complex, due to very fragmentary knowledge of the distributions of the individual taxa under study.

56b. *Viola sororia* (glabrous variant). Fig. 139.

Viola cucullata Aiton var. *glaberrima* Ging., in

FIG. 139. *Viola sororia* (glabrous variant). (A) Chasmogamous flowering habit (photo: Alan Weakley). (B) Chasmogamous flower front view (photo: Alan Weakley). (C) Seeds from a herbarium specimen: Transplanted from Virginia, Giles Co., Mountain Lake Road crossing with Appalachian Trail, *H. Ballard s.n*. (BHO).

DC., Prodr. 1: 292. 1824. Type: "in hortis Europaeis culta" [protologue], 1809, *M. Balbis s.n*. (Type: G-DC G00208904 (*n.v.*), internet image).

Common Names. None.

Description. Plant glabrous, calyx eciliate; leaf blade outline ovate, apex mostly obtuse to rounded, eciliate; seeds 1.5–2.0 × 1.0–1.3 mm, light to medium gray or gray-brown with small prominent gray or gray-brown streaks. Other features same as the species complex.

Ecology. Apparently similar to the species complex but needs study.

Similar Species. See the species complex.

Distribution. Specimens and scattered uniform populations in New York, Pennsylvania, Virginia, and North Carolina suggest a distribution in the Appalachian Mountains, adjacent uplands, and Piedmont; specimens outside this distribution may represent uniform populations or possibly single individuals in polymorphic *V. sororia* populations. No map is presented.

Rarity. None.

Phenology. Presumably the same as the species complex.

Affinities. Same as the species complex.

Hybrids. Reports of hybrids involving "*V. papilionacea*" probably refer to this, *V. communis*, or the *hirsutuloides* variant of *V. sororia*. They include *V. affinis* (Brainerd 1904b, 1924), *V. brittoniana* (Brainerd 1924), *V. cucullata* (Brainerd 1906c), *V. emarginata* (Brainerd 1924), *V. fimbriatula* (Brainerd 1904b, 1906c, 1924), *V. hirsutula* (Brainerd 1907b, 1924; Henry 1953a), possibly *V. nephrophylla* (Brainerd 1924), *V. palmata* var. *triloba* (Brainerd 1912, 1924), *V. pedatifida* (Greene 1903a; Brainerd 1913a, 1924), *V. sagittata* (Brainerd 1906c, 1924), *V. sororia sensu stricto* (Brainerd 1924; Henry 1953a), *V. stoneana* (Brainerd 1912, 1924), and *V. subsinuata* (Dowell 1910; Brainerd 1912; Brainerd 1924). The actual parentage of these hybrids (with respect to which glabrous phenotype was actually involved) needs to be established beyond doubt. Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All hybrids fail to reproduce

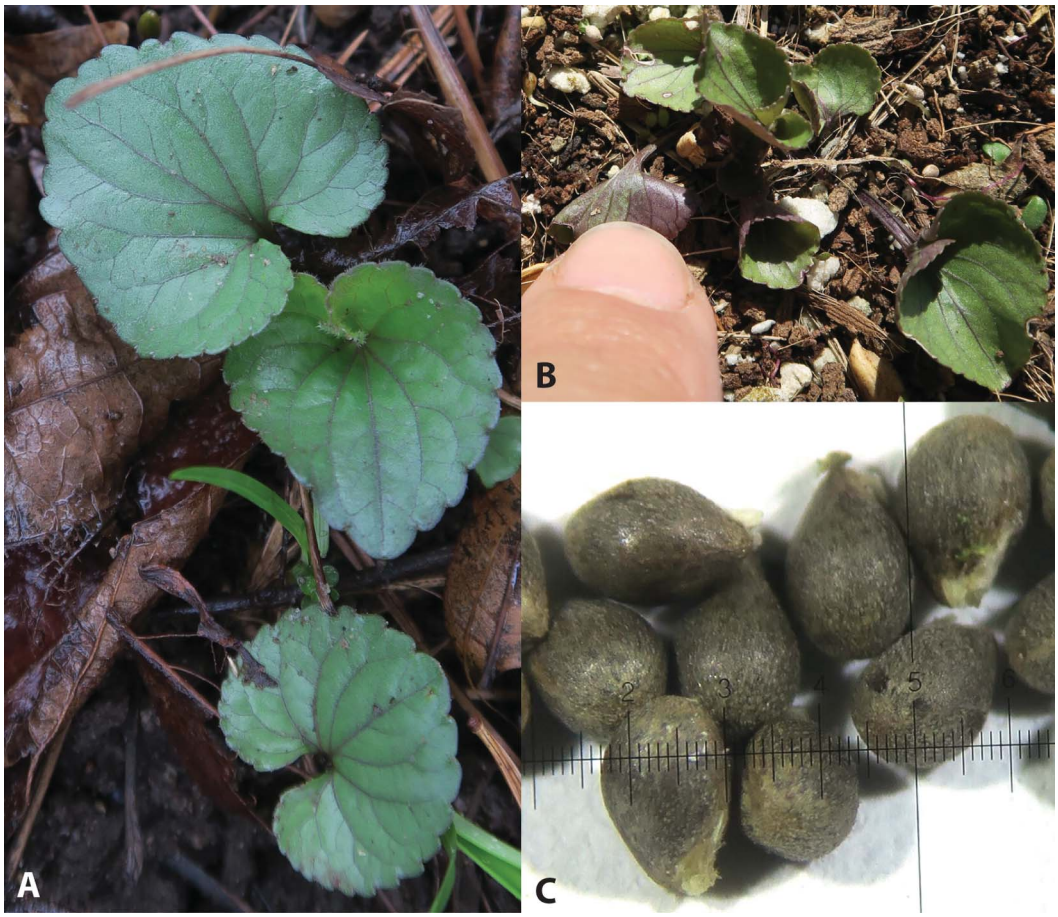

FIG. 140. *Viola sororia* (*hirsutuloides* variant). (A) Early spring habit (photo: David Werier). B. Underside of leaf blade (photo: David Werier). (B) Seeds from potted plant (photo: David Werier).

by chasmogamous flowers, and the cleistogamous capsules are abortive or produce a drastically diminished proportion of viable seeds.

Comments. The brief protologue and type material of *V. cucullata* Aiton var. *glaberrima* Ging. at the de Candolle Herbarium in Geneva appear to match this variant of *V. sororia*.

The present taxon is most similar to *V. sororia sensu stricto* but the foliage is glabrous and does not usually turn yellow-green in later summer or fall, the leaf blades are typically more obtuse to rounded at apex and margins are more evenly crenate-serrate, and the seeds are paler overall. As uniform populations, this taxon appears to be more geographically restricted than *V. sororia sensu stricto*, in the Appalachian Mountains, uplands, and Piedmont. The glabrous foliage and eciliate sepals, and the paler seed pigmentation seen in some specimens, may represent a joint pleiotropic genetic effect.

56c. *Viola sororia* (*hirsutuloides* variant). Fig. 140.

Common Names. None.

Description. Foliage, peduncles, and calyx darker blue-green, with midrib, lower surface of leaf blades, petioles, and calyx purple-tinged and glabrous throughout except for occasionally sparsely hirtellous petioles and scattered minute appressed hairs on the upper leaf blade surfaces that may require magnification to see; leaf blades ovate to suborbiculate or reniform with base cordate and apex broadly rounded, margins uniformly shallowly crenate, eciliate; seeds unknown. Other features same as the species complex.

Similar Species. See the species complex.

Ecology. Apparently similar to the species complex but needs study.

Distribution. Very scattered observations from New York, eastern Ohio, and northern Georgia suggest possible distribution in the Appalachian Mountains and adjacent uplands, perhaps roughly approximating the range of *V. hirsutula*; needs further study. No map is presented.

Rarity. None.

Phenology. Presumably same as the species complex.

Affinities. Same as the species complex.

Hybrids. Reports of hybrids involving "*V. papilionacea*" might refer to this, *V. communis*, or the glabrous variant of *V. sororia*, but most likely the latter two. They include *V. affinis* (Brainerd 1904b, 1924), *V. brittoniana* (Brainerd 1924), *V. cucullata* (Brainerd 1906c), *V. emarginata* (Brainerd 1924), *V. fimbriatula* (Brainerd 1904b, 1906c, 1924), *V. hirsutula* (Brainerd 1907b, 1924, Henry 1953a), possibly *V. nephrophylla* (Brainerd 1924), *V. palmata* var. *triloba* (Brainerd 1912, 1924), *V. sagittata* (Brainerd 1906c, 1924), *V. sororia sensu stricto* (Brainerd 1924, Henry 1953a), *V. stoneana* (Brainerd 1912, 1924), and *V. subsinuata* (Dowell 1910, Brainerd 1912, 1924). The actual parentage of these hybrids (with respect to which glabrous taxon was actually involved) needs to be established beyond doubt. Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). All hybrids fail to reproduce by chasmogamous flowers, and the cleistogamous capsules are abortive or produce a drastically diminished proportion of viable seeds.

Comments. Although this is a distinctive extreme in the *V. sororia* complex when examined together with the other taxa, it is extremely elusive to find (such that we have no good images) and remains poorly known. Moreso than the glabrous variant, it is not well represented in herbarium collections (presumably because it looks similar to *V. sororia* and is passed over as too common to collect). Cleistogamous capsules and seeds have yet to be characterized. As with other variants, this needs further study. All three taxa in the species complex are mapped together, due to fragmentary knowledge of their individual distributions.

57. *Viola stoneana* House, Bull. Torrey Bot. Club 32: 253, pl. 16. 1905. Type: USA Pennsylvania. Chester Co., Kennett Square, Colony No. 6, 4 Jul 1903, *W. Stone 5113* (holotype: US490405 [barcode 00114618]; isotypes: F676547, NY01911884; all internet images). Fig. 141.

Common Name. Stone's violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 34 cm tall; foliage and peduncles green, lower surface of leaf blades occasionally paler than upper, foliage and peduncles glabrous or petioles and lower surface of leaf blades sparsely hirsute; stipules free, glandular-fimbriate; heterophyllous, leaves ascending to spreading, earliest and latest leaf blades undivided, blades in chasmogamous flower through summer cleistogamous fruit deeply biternately divided into 7 or 9 lobes with central and lateral lobes of the terminal primary division rhombic-lanceolate and lateral primary divisions deeply 2–3-cleft, sinuses of terminal and lateral primary divisions reaching nearly to petiole summit, base of divisions usually constricted to a slender elongate "petiolule," largest $\leq 110 \times 148$ mm, outline ovate to broadly ovate, in summer broadening to reniform, base deeply cordate, margins irregularly or remotely serrate, ciliolate, apex obtuse; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 22 mm; calyx glabrous, eciliate; lowest sepals lance- to ovate-triangular, acuminate; auricles short and entire, not elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with narrowly linear or slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, on ascending to erect peduncles nearly equaling (rarely much shorter than) petioles, capsule 7–14 mm, green drying tan with weak (rarely strong) purple spots or blotches, glabrous; seeds $1.8–2.3 \times 1.1–1.6$ mm, seeds ivory to tan or light gray-brown, unspotted or with small weak brown spots or rectangular blotches.

Similar Species. This species is most similar to the other widespread heterophyllous violet with pubescent foliage in our region, *V. palmata*. It differs from that species in its nearly glabrous to glabrate foliage, primary divisions of the divided

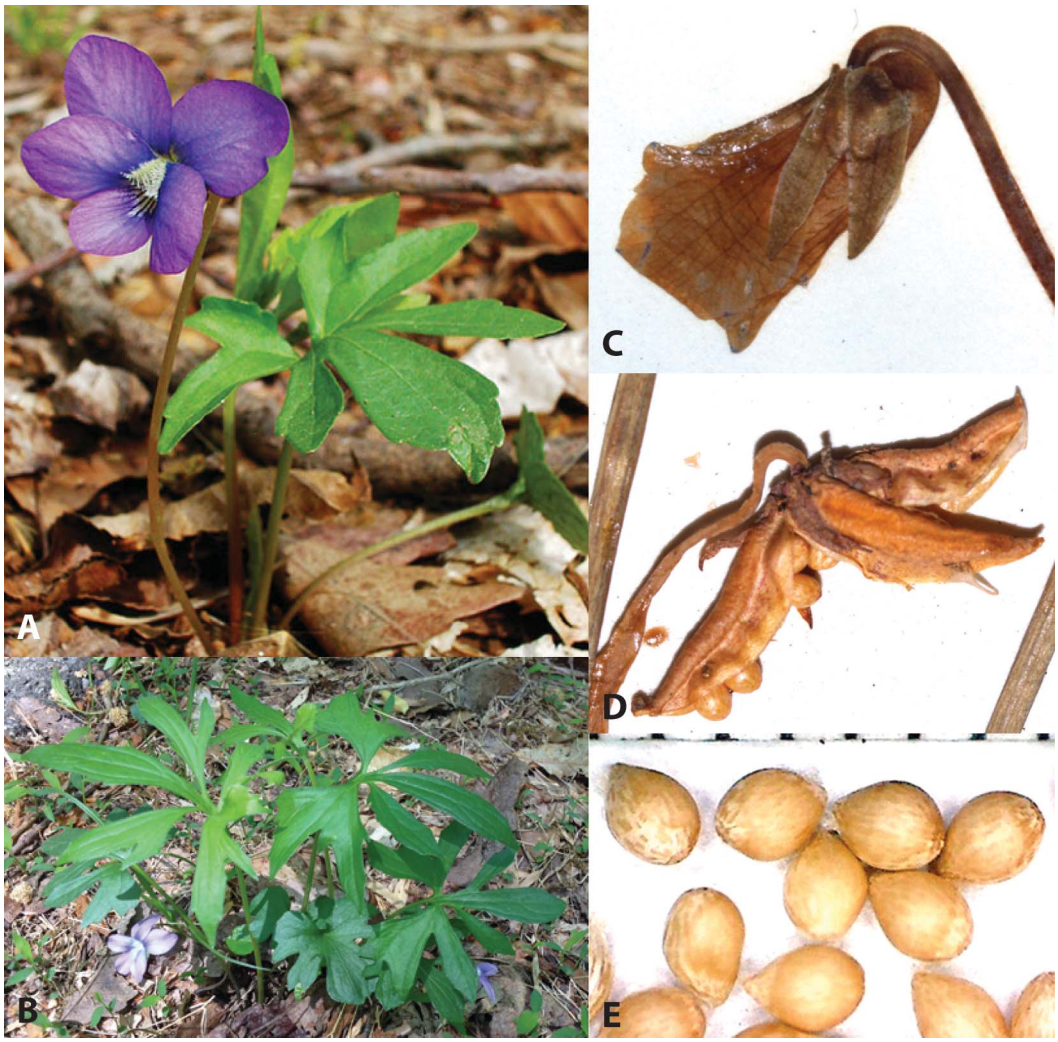

FIG. 141. *Viola stoneana*. (A) Chasmogamous flowering habit (photo: David Smith). (B) Chasmogamous flowering habit (photo: Harvey Ballard). (C) Chasmogamous flower profile view from herbarium specimen: Washington, DC, In viciniius Washington, 12 May 1873, *J. W. Chickering Jr. s.n*. (NY). (D) Cleistogamous fruit from herbarium specimen: New Jersey, Iselin, *W. D. Miller 1506* (NY). (E) Seeds from herbarium specimen: Transplanted from Delaware, First State National Monument adjoining Brandywine Creek State Park, *H. Ballard et al. 15-027Y* (BHO).

leaf blades typically abruptly contracted into slender "petiolules," glabrous peduncle, eciliate calyx, lance-triangular to ovate-triangular acuminate sepals, finely spotted cleistogamous capsule on a suberect peduncle, and ivory to light gray-brown unspotted or weakly spotted seeds.

Ecology. Moist loamy soils of rich mesic forest slopes and bases of slopes.

Distribution. Distributed along and near the "fall line" between the upper Atlantic Coastal Plain and the lower Piedmont, southeastern New York to eastern Pennsylvania, south to northern Virginia, disjunct in east-central North Carolina. Fig. 142.

Rarity. None.

Phenology. Chasmogamous flower April–July, chasmogamous fruit May–August, cleistogamous fruit May–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium*

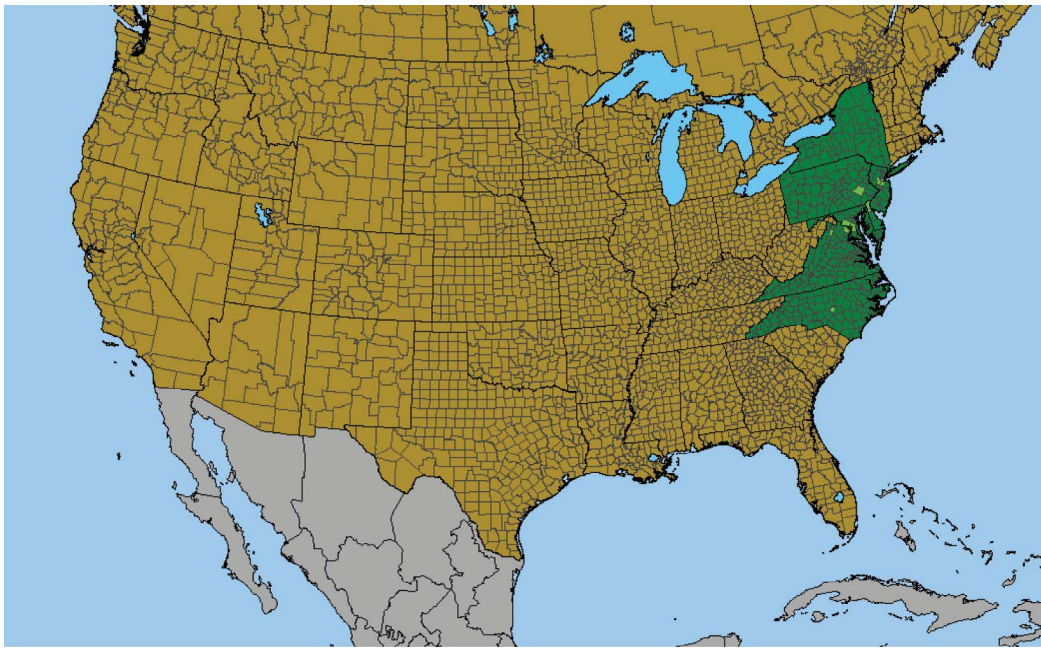

FIG. 142. United States county distribution of *Viola stoneana* (map: Biota of North America Program).

W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Palmata species group.

Hybrids. Hybridizes with *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Brainerd 1912, 1924), *V. emarginata* (Brainerd 1924), *V. hirsutula* (Brainerd 1912, 1924), *V. palmata* var. *triloba* (Brainerd 1910b, 1912, 1924), and *V. sororia sensu stricto* (H.E.B., personal observation). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). He noted no reproduction by chasmogamous flowers, and substantially to dramatically reduced viable seed production in cleistogamous capsules.

Comments. House stated in his protologue that "The type of *Viola Stoneana* is Witmer Stone's no. 5113, collected near Kennett Square, Pa., May 7, 1903. No. 5112, a flowering specimen, is identical (National Herbarium numbers, 490405 and 490404.) Material in the National Herbarium shows the range of this species to extend as far south as Virginia." Since the protologue specifies Stone 5113 at US, with an accession number, as the "type," the US sheet is unambiguously the holotype. On the holotype sheet the date given is "July 4/03", and at the bottom is written, in the same hand as the label data, "(printed date is an error)." A VT sheet is ambiguous, with most of the same collection data as the holotype but with "May 25/03" clearly written on the label, discounting it as an isotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950) (who erroneously reported it from Kentucky), and Alexander (1963) accepted the present species as distinct. Russell (1965) misapplied the name to a putative hybrid assemblage in the southern Appalachians. Gleason and Cronquist (1991), McKinney (1992), Ballard (2000), McKinney and Russell (2002), Weakley *et al*. (2012), and Little and McKinney (2015) included it in a broadly defined *V. palmata*. Gil-ad (1995, 1997, 1998) examined specimens identified as this by Brainerd and a collection made by himself from northeastern North Carolina. He noted similarities with *V. triloba* as well as differences in leaf blade shape, color pattern of the capsules, and shorter seed caruncle. Micromorphological characters of the seeds were not unique, appearing to share features with *V. affinis*, *V. sororia*, and *V. triloba*. Correlations of macromorphological and micromorphological features led him to conclude that *V. stoneana* was likely a hybrid derivative involving *V. triloba* and *V. affinis*, *V. missouriensis*, or *V. sororia*. Gil-ad stated that *V. stoneana* should

"perhaps be recognized on the basis of micromorphology and distribution alone," but he continued that it should be dismissed due to evidence of hybrid origin. We have examined a substantial number of specimens from the range confirmed by Brainerd, and the first author has visited and studied materials from several northeastern populations as well as a newly discovered North Carolina population that was based on a misidentified specimen. This species diverges consistently in a substantial suite of features of foliage, chasmogamous flowers, cleistogamous capsules, and seeds from *V. palmata* and other similar heterophyllous taxa that cannot be constructed as the product of hybridization involving any known taxa. Moreover, correctly identified specimens and confirmed living populations are highly uniform in morphology, fully fertile and reproduce by both chasmogamous and cleistogamous flowers, have a definably discrete range along the "fall line" of the northeastern and east-central Piedmont, and inhabit richer mesic forests and forest slopes than the the dry-mesic forests preferred by *V. palmata* and other taxa in the Palmata species group. It rarely makes contact with *V. palmata* or other presumably related species. Under the unified species concept, available evidence supports recognition of the present taxon as a distinctive regionally endemic species. Most collections have been taken in the northeastern states, from southeastern Pennsylvania south to Fairfax, VA; however, a collection from Nash Co. by Gil-ad (1995, 1997) and a collection from Chatham Co. by the first author document a range extension southward into east-central North Carolina. Additional fieldwork is urged to seek this interesting species in southern Virginia and elsewhere in North Carolina. Plants with less deeply divided leaf blades and more heavy foliage pubescence are frequent hybrids with *V. sororia*; some of these have inaccurately been identified or annotated as *V. stoneana*, adding to unnecessary confusion and misinterpretation of close similarity to *V. palmata*.

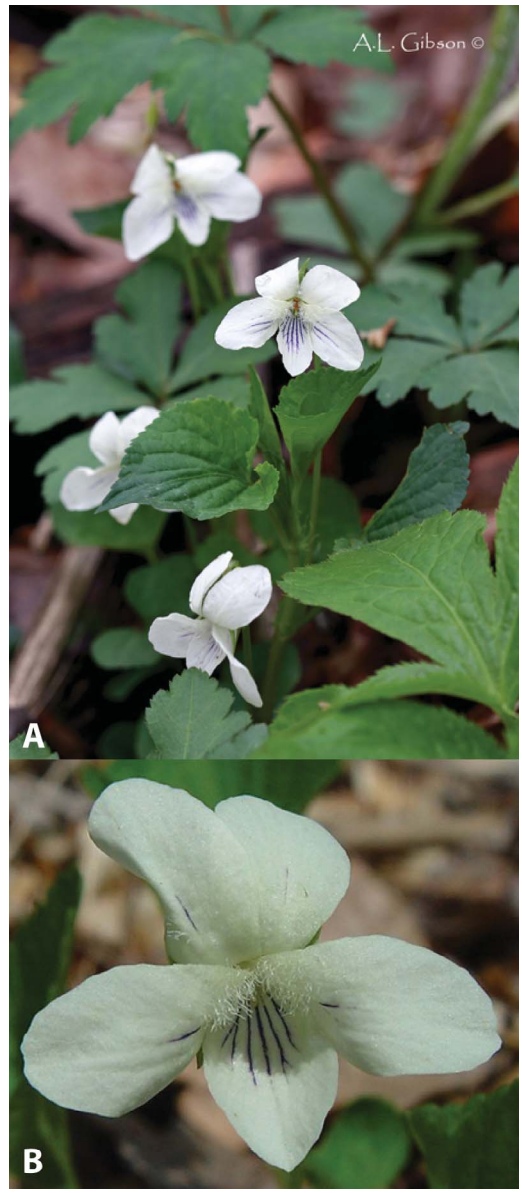

FIG. 143. *Viola striata*. (A) Chasmogamous flowering habit (photo: Andrew Lane Gibson). (B) Chasmogamous flower front view (photo: Arthur Haines, Native Plant Trust).

58. ***Viola striata*** Aiton, Hort. Kew., ed. 1, 3: 290. 1789; *Lophion striatum* (Aiton) Nieuwl. & Kaczm., Amer. Midl. Naturalist 3: 216. 1914. Type: England. Kew Garden, [*W. Young s.n.*?] 178 (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 227.): LINN-HS1380-31-2 (*n.v.*), internet image). Fig. 143.

Viola debilis Michx., Fl. bor.-amer., ed. 1, 2: 150. 1803.

Viola repens Schwein., Amer. J. Sci. 5: 70. 1822.

Viola lewisiana Ging., in DC., Prodr. 1: 298. 1824.

Viola striata Aiton var. *lutescens* Alph.Wood ex N.Coleman, Kent. Sci. Inst., Misc. Publ 2 [Cat. Fl. Pl. S. Peninsula Michigan]: 8. 1874.

Viola conspersa Rchb. var. *masonii* Farw., Rep. (Annual) Michigan Acad. Sci. 19: 248. 1918; *Viola adunca* Sm. f. *masonii* (Farw.) B.Boivin, Naturaliste Canad. 93: 437. 1966; *Viola* conspersa Rchb. f. *masonii* (Farw.) House [no publication information].

Viola striata Aiton f. *albiflora* Farw., Amer. Midl. Naturalist 11: 67. 1928.

Common Names. Cream violet, pale violet, striped violet.

Description. Caulescent perennials from somewhat slender rhizome, stems ascending in flower but often reclining in fruit, older dead stems often persistent, commonly $\geq$ 2, $\leq$ 54 cm tall; stems, foliage, and peduncles green, glabrous or glabrate to hirtellous; leaves cauline and basal, cauline distributed along stem; stipules free, strongly lacerate; leaves ascending to spreading, leaf blades undivided, largest $\leq$ 72 $\times$ 51 mm, ovate to suborbiculate or reniform, base subcordate to cordate, margins closely crenulate, eciliate or appressed-ciliolate, apex obtuse to short-acuminate; chasmogamous flower $\leq$ 20 mm; calyx glabrous, ciliolate; lowest sepals linear-lanceolate, acuminate; auricles prominent, quadrate, entire or erose, not elongating in fruit; corolla cream-white, throat white; spur moderately short, slender or thickish, 3–6 mm, cream-white; lateral petals densely bearded with filiform hairs, spurred petal glabrous; cleistogamous flowers after chasmogamous; capsule 3.5–7 mm, green drying to tan, unspotted or with fine red spots or lines, glabrous; seeds (1.4)2.0–2.6 $\times$ 1.1–1.6 mm, medium brown, unspotted; $2n = 20$.

Similar Species. The species is distinct in many features of foliage and chasmogamous flowers from other members of subsect. *Rostratae* in our region. It is most similar in its cream-white corolla to *V. arcuata*, *V. canadensis*, and *V. rugulosa* but has occasionally been misidentified as *V. eriocarpa* in vegetative or fruiting state. It differs from *V. arcuata* in its ovate or suborbiculate to reniform closely crenulate leaf blades, broader and proportionally shorter lacerate to fimbriate stipules, and longer spur; from *V. canadensis* and *V. rugulosa* in its closely crenulate leaf blade margins, herbaceous lacerate to fimbriate stipules, uniformly cream-white corolla and prominent quadrate auricles; and from *V. eriocarpa* vegetatively or in fruit in its closely crenulate leaf blade margins, lacerate to fimbriate stipules, and smaller glabrous capsule.

Ecology. Apparently calciphilic, inhabiting mesic to wet-mesic alkaline clayey and silty soils along streams and floodplains, somewhat weedy and often expanding along trails and into adjacent anthropogenic areas such as abandoned pastures, lawns, and roadsides.

Distribution. Widely distributed in eastern North America, native in New York and southern Ontario to Wisconsin, south to northern South Carolina, northern Alabama, and eastern Oklahoma; adventive or escaped from plantings in Quebec, New England, and eastern Nebraska. Fig. 144.

Rarity. Listed in Iowa and Wisconsin.

Phenology. Chasmogamous flower March–June (September), chasmogamous fruit June, cleistogamous fruit August–October.

Affinities. This species belongs to the Rostrate Violet lineage, sect. *Viola*, subsect. *Rostratae* (Kupffer) W.Becker.

Hybrids. Hybridizes with *V. appalachiensis* (Ballard 1992, 1993), *V. labradorica* (Gaiser and Moore 1966; Ballard 1990b, 1992, 1995; Haines *et al*. 2011), *V. rostrata* (Brainerd 1924; Henry 1953a; Boivin 1966; Cooperrider 1986; Ballard 1990a, 1992, 1995), and *V. walteri* (Ballard 1992, 1993). The first author has observed the hybrids and have found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. Brainerd reported that *V. rostrata* $\times$ *V. striata* produced an abundance of cleistogamous flowers that failed to develop into mature capsules with viable seeds. Observations (H.E.B.) of field and herbarium specimens of all rostrate violet hybrids confirm the author's findings that hybrids are sterile.

Comments. Aiton's protologue stated that the present species was "Nat. of North America. Introd. 1772, by Mr. William Young. Fl. June and July." He cited no types, but Stafleu and Cowan (1976) pointed out that virtually all types for Hortus Kewensis are at BM. A sheet found in the JSTOR Global Plants database is likely original material, in Herb. Sloane (cited above), from Kew Garden in 1783, some years after Young's introduction of the plant into the Royal Botanic

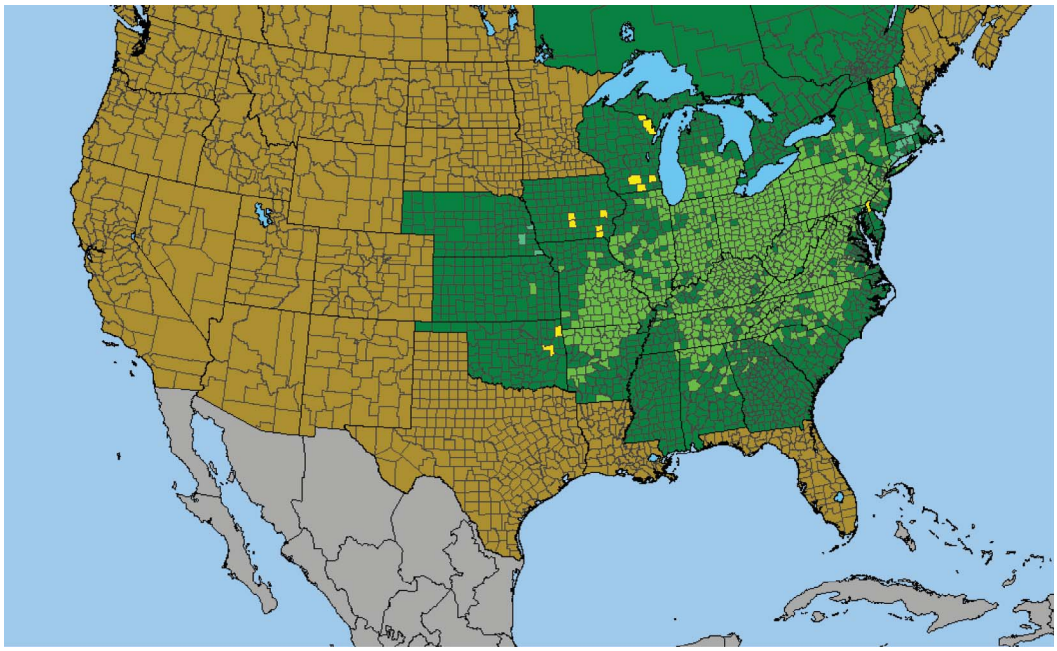

FIG. 144. United States county distribution of *Viola striata* (map: Biota of North America Program).

Garden at Kew. A second specimen in the database is rejected as original material, with label data as "USA America sept. prope Ohio, 1764, J. Bartram [s. n.] (BM000617517!)," although Harvey Ballard incorrectly annotated it in 1995 as holotype. The LINN sheet was designated by Ballard *et al*. (2020a) as the lectotype.

All authors have accepted this distinctive species as such, including Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1992, 1995, 2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), Weakley *et al*. (2012), and Little and McKinney (2015). This species has weedy tendencies and commonly grows in quite dense populations, following trails and extending into adjacent disturbed sites from natural areas. Hybrids have been documented with every other eastern rostrate violet except *V. adunca* (with which it does not overlap in geographic distribution), and those involving *V. labradorica* and *V. rostrata* are commonly encountered. Hybrids inherit partial characteristics of the closely crenulate leaf blade margins, fimbriate stipules, ciliate calyx, prominent auricles, cream-white corolla, and shorter spur of *V. striata*, and are thus easily identified as such.

59. ***Viola subsinuata*** (Greene) Greene, Pittonia 4: 4. 1899; *Viola emarginata* (Nutt.) Leconte var. *subsinuata* Greene, Pittonia 3: 313. 1898. Type: USA Tennessee. Cocke Co., Collected within 3 mi. of Wolf Creek Station, 11 Sep 1897, *Kearney 615* (incorrectly designated as holotype by Landon McKinney, Sida, Bot. Misc. 7: 45. 1992; corrected to lectotype by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 227): NDG33272, internet image). Fig. 145.

Viola palmata auct.

Common Names. Early blue violet, hand-leaved violet, wavy-leaved violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 28 cm tall; foliage and peduncles green, lower surface of leaf blades, petioles, and peduncles often tinged with purple, mostly moderately to densely hirsute; stipules free, irregularly glandular-fimbriate; homophyllous, leaves ascending, smallest leaf blades palmatifid, largest leaf blades deeply biternately divided into 7 or 9 narrowly linear or linear-lanceolate lobes, the lateral second-order lobes of the terminal primary division attached medially and suberect or ascend-

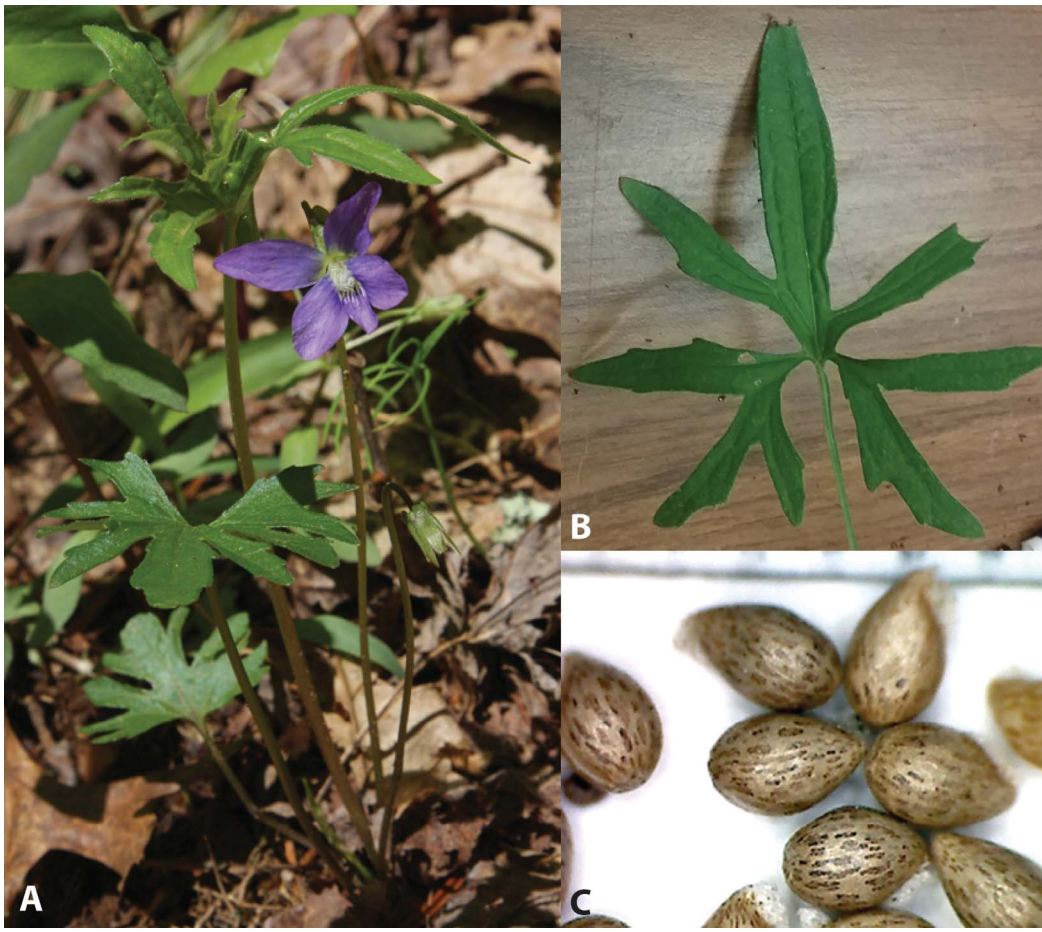

FIG. 145. *Viola subsinuata*. (A) Chasmogamous flowering habit (photo: Bruce Sorrie). (B) Leaf during cleistogamous fruit (photo: Jennifer Hastings). (C) Seeds of *Viola subsinuata* (photo: Jennifer Hastings).

ing to spreading, outline narrowly ovate to ovate during chasmogamous flower, broadening to broadly ovate or reniform in fruit, base cordate, margins of the ultimate segments in fruit entire or with 1–2 inconspicuous short appressed or incurved teeth on either side, margins ciliate, apex acute to obtuse; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 25 mm; calyx glabrous, ciliate; lowest sepals oblong to ovate, obtuse to rounded; auricles short and entire, not elongating in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle prostrate but arching upward just before dehiscence, shorter than petioles; cleistogamous capsule 6–8 mm, green drying tan with purple spots or blotches, glabrous; seeds 1.8–2.1 $\times$ 1.1–1.3 mm, white or ivory to light reddish-brown with small prominent yellow-brown to dark brown streaks; 2n = 54.

Similar Species. This species is most similar to other homophyllous cut-leaved taxa in the Pedatifida and Subsinuata species groups. It differs from *V. brittoniana* and *V. pedatifida* by its densely hirsute foliage, short rounded auricles, oblong to ovate ciliate obtuse to rounded sepals, glabrous spurred petal, heavily spotted cleistogamous capsule on short prostrate peduncle, and pale to light reddish-brown seeds with small streaks. It can be distinguished from *V. monacanora* in its densely hirsute foliage, oblong or narrowly ovate ciliate obtuse to rounded sepals, and pale to light reddish-brown seeds with small streaks. It can be distinguished from *V. baxteri* by the several

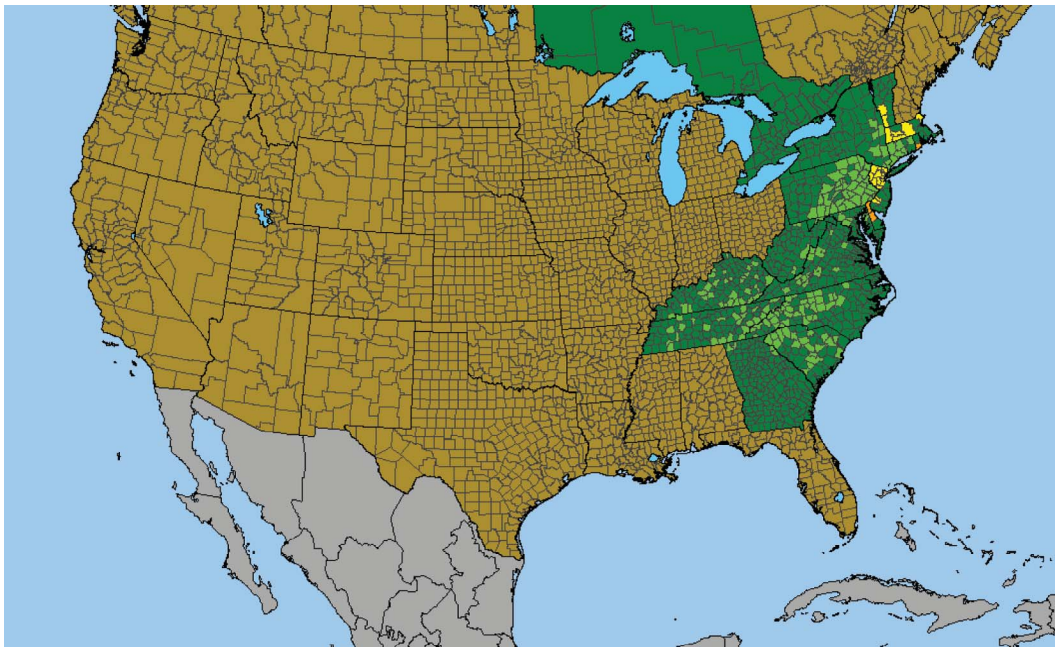

FIG. 146. United States county distribution of *Viola subsinuata* (map: Biota of North America Program).

features of leaf dissection noted in the key, as well as its prominently streaked seeds. It is easily separated from *V. tenuisecta* in its densely hirsute foliage, biternately divided leaf blades with proportionally broader ultimate segments, and oblong or narrowly ovate ciliate obtuse to rounded sepals.

Ecology. Sandy or loamy soils in rich dry and dry-mesic forests, probably associated with mafic rocks in some areas.

Distribution. Mainly at higher elevations in the Appalachian Mountains, extending onto the Piedmont northward and the Interior Lowland Plateau southward, Massachusetts and Vermont to New York, south to northern Georgia and western Tennessee (records for western Kentucky and western Tennessee require further study). Fig. 146.

Rarity. Listed in Delaware, Rhode Island, and Vermont.

Phenology. Chasmogamous flower April–May, chasmogamous fruit April–June, cleistogamous fruit May–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Subsinuata species group.

Hybrids. Hybridizes with *V. affinis* (Dowell 1910; Brainerd 1924; House 1924), *V. brittoniana* (Brainerd 1906c; House 1924), *V. communis* (or possibly the glabrous or *hirsutuloides* variants of *V. sororia*) (Dowell 1910; Brainerd 1912, 1924), *V. cucullata* (Brainerd 1913c, 1924; House 1924; Haines *et al*. 2011), *V. fimbriatula* (Brainerd 1913c, 1924; House 1924; Haines *et al*. 2011), *V. hirsutula* (Brainerd 1906c, 1912, 1924), *V. palmata* var. *triloba* (Pollard 1902a; Brainerd 1912, 1924; Haines *et al*. 2011), *V. sagittata* (Brainerd 1906c, 1913c, 1924; Dowell 1910; House 1924), *V. sororia sensu stricto* (House 1923, 1924; Brainerd 1924; Haines *et al*. 2011; Hastings 2018; H.E.B., personal observation). Brainerd reported that these exhibit intermediate or recombinant characteristics of foliage, chasmogamous flowers, cleistogamous capsules, and seeds (where these did not abort). Brainerd reported no chasmogamous reproduction and nearly complete sterility or highly impaired fertility in cleistogamous capsules, with comparatively few viable seeds produced in all hybrids.

Comments. Greene's protologue notes that "The only specimens seen are in the herbarium of my friend T. H. Kearney, Jr. The autumnal specimens were collected by himself in September, 1897." His statement suggests two collections but he did not specify either as the type or indicate a single

specimen in either case. The JSTOR Global Plants database has an image of one specimen, with one chasmogamous flowering plant (referred to by the handwritten addition "fls. Apr. 2" to the label) and two cleistogamous fruiting specimens presumably collected on the autumn date. The sheet has a note in Greene's hand at the bottom, "*V. subsinuata* Greene Type!." McKinney incorrectly declared the sheet as a holotype, but he serendipitously did not include the handwritten portion specifying the flowering plants, so his selection of type material refers only to the cleistogamous fruiting plants. His error in identifying the sheet as the holotype was corrected to lectotype by Ballard *et al*. (2020a).

Elliott (1817) and other botanists followed Linnaeus (1753) in applying the name *V. palmata* to a heterophyllous violet. Brainerd (1910c) opposed this interpretation, arguing that Linnaeus's name should be attributed to the homophyllous cut-leaved violet predominately distributed in the Appalachian Mountains and associated uplands, and he asserted that the widespread eastern heterophyllous violet should be treated as *V. triloba*. Brainerd's proposals were followed by Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965), Scoggan (1978), Strausbaugh and Core (1978), and Swink and Wilhelm (1979). McKinney (1992) reexamined original material of the name *V. palmata* L. and Linnaeus's protologue and came to the opposite conclusion, that there was abundant evidence to indicate that Linnaeus intended the name for a heterophyllous violet long-treated as *V. triloba*. Gil-ad (1995, 1997, 1998) rejected McKinney's interpretation, hypothesizing that the lectotype of *V. palmata* had macromorphological features suggestive of hybridization. Gil-ad studied a modest number of samples from disparate parts of the range of the Subsinuata species group as a whole and, unsurprisingly, found substantial divergence in macromorphological features of the specimens and a lack of unique traits defining them as a single taxon; he also found confusing patterns of micromorphological traits in the seeds suggestive of various hybrids involving *V. pedatifida* and other undivided-leaved species. He dismissed the assemblage as a series of hybrid derivatives. Ballard (2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Weakley *et al*. (2012), and Little and McKinney (2015) adopted McKinney's interpretation of the names *V. palmata* L. and *V. subsinuata*, in most instances applying the former name to a broadly delimited assemblage of several species accepted here as distinct. Ballard (1995) and Voss and Reznicek (2012) merged the homophyllous cut-leaved violets (excluding *V. pedatifida*) and heterophyllous violets of Michigan into *V.* ×*palmata* and *V. palmata*, respectively, whereas Gleason and Cronquist (1991) merged several distinct heterophyllous and homophyllous cut-leaved taxa under *V. palmata* var. *palmata*. For obvious reasons, the nomenclatural confusion involving *V. subsinuata* and the *V. palmata* species complex, and misidentifications of *de novo* hybrids as species, have rendered recent distributional maps for "*V. palmata*" highly inaccurate and suspect.

For clarification on the disastrous nomenclatural confusion precipitated by Brainerd's misinterpretation of Linnaeus's *V. palmata*, see comments under the *V. palmata* species complex. The first author's independent analysis of Linnaeus's protologue and the pre-Linnaean documents he cited in synonymy of his name has led to the same conclusion as McKinney. McKinney resurrected the name *V. subsinuata* (Greene) Greene as the earliest available name for the homophyllous cut-leaved Appalachian taxon, and that is correct. The type material of that name is in chasmogamous flower, so it doesn't portray the fully expanded leaf blades of summer cleistogamous fruit that develops the characteristics especially useful for discerning individual taxa within the species complex. Brainerd recognized three ecotypes he believed were weakly defined on the basis of leaf morphology but intergraded too extensively to recognize formally (see "Comments" under *V. baxteri*). Most specialists have similarly treated *V. subsinuata* (named *V. palmata* prior to McKinney's work) as a highly polymorphic species. Nevertheless, our ongoing studies including extensive field and laboratory sampling of populations and herbarium specimens in the eastern Great Lakes, Western Allegheny Plateau, and central Appalachian Mountains have revealed several fully fertile, locally or regionally endemic evolutionary species differing uniformly in traits of foliage, flowers and seeds, micromorphological features of petal hairs and seed surface, soil preferences, and (with limited applications) microsatellite markers. *Viola tenuisecta* has been distinguished from *V. pedatifida* and shown to belong to the Subsinuata species group, while *V. baxteri* House and *V. monacanora* have been segregated from the Sub-

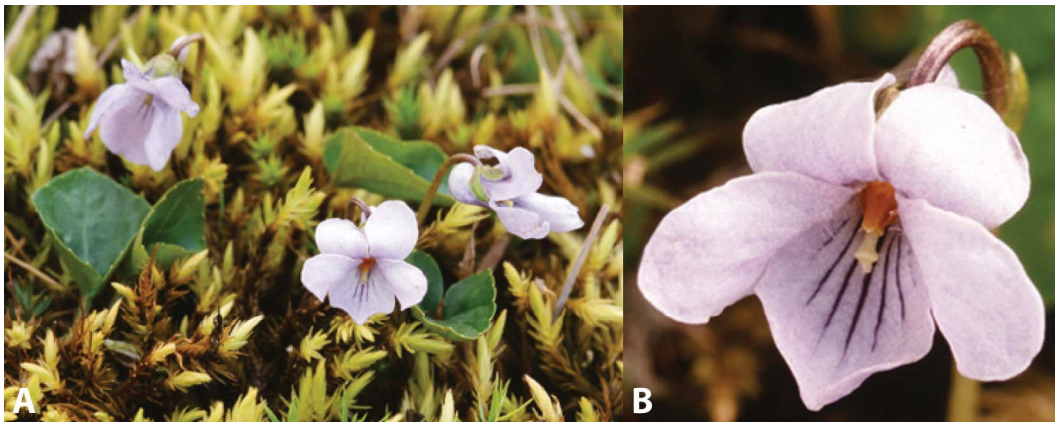

FIG. 147. *Viola suecica*. (A) Chasmogamous flowering habit (photo: Kim Blaxland). (B) Chasmogamous flower front view (photo: Kim Blaxland).

sinuata species group, leaving a much more narrowly circumscribed and much better understood *V. subsinuata*. In North Carolina, an additional taxon, *V. subsinuata* (Chapel Hill variant) is represented by several herbarium specimens. Brainerd mentioned this species (as *V. palmata*) as occurring as far south as Florida on the basis of a transplanted living collection sent to him by Agnes Chase from Lake Co. (locality undisclosed) in 1907, and which he maintained and made at least three collections of. Although three specimens lack undivided leaves—which can happen occasionally with all heterophyllous taxa—most leaves on each specimen show a very clear pedate pattern of branching in the venation and often also in the lobes themselves. The seeds are also more prominently blotched and darker, a color pattern in line with some members of the Palmata group more than with the *V. subsinuata* species complex. The Florida plants are not included here. For more information on the *V. subsinuata* species complex and its long-term nomenclatural confusion with the *V. palmata* species complex, see "Comments" under the latter. Hybrids of taxa in the *V. subsinuata* species complex with *V. sororia* or other undivided-leaved species are common, often commingled with typical individuals of taxa in this complex where frequent disturbance or intermediate microsites are maintained, and occasionally more abundant locally than the rarer parental species (usually the divided-leaved taxon). Hybrids are frequently included on herbarium sheets with typical individuals of this species, or in place of typical representatives. Such hybrids produce shallowly palmatifid to moderately subbiternately divided leaf blades and intermediate or recombinant floral, cleistogamous capsule, and seed traits; they are generally infertile or subfertile with respect to cleistogamous reproduction. If viable seeds are produced, these are commonly heterogeneous in dimensions and color pattern, and some seeds usually reflect the traits of the parental species.

60. ***Viola suecica*** Fr., Summa Veg. Scand.: 556. 1849. Type: Norway, Finnmark: Tana, Finnmarken vid Polmach [= Polmak], 19 Jul 1802, *G. Wahlenberg s.n.* (Type: UPS-V-1041820 (*n.v.*), internet image). Fig. 147.

Viola achyrophora Greene, Pittonia 5: 33. 1902. Type: USA [Alaska] British Behring Sea Commission Collection, St. Paul Island, Jul 1897, *J. M. Macoun s.n.* (lectotype (**designated here**): NDG32053 (*n.v.*), internet image).

Viola epipsila Ledeb. subsp. *repens* W.Becker, Beih. Bot. Centralbl. 34(Abt. 2): 406. 1917; *Viola repens* Turcz., Bull. Soc. Nat. Mosc. 11: 88. 1838 [illegitimate homonym of *V. repens* Schwein. (1822)]; *Viola repens* Turcz. ex Trautv. & C.A.Mey., Fl. Ochot. [Middend. Reise N. & O. Sibir. 1: 11]: 18. 1856 [nomen superfluum]; *Viola epipsila* Ledeb. var. *repens* (W.Becker) R.J.Little, J. Bot. Res. Inst. Texas 4(1): 225. 2010. Type: "Originale Turcz. in Herb. Acad. Sci. Petrop.: in saxis humidis ad fl. Schilka a 1833, in humidis pr. Krugloie a. 1834.–Tiling Fl. ajan. nr. 50."

Common Name. Dwarf marsh violet.

Description. Acaulescent stoloniferous perennials, colonial from slender creeping rhizome and lateral stolons, leaves, flowers, and fruits inserted

separately along rhizome near apex, stolons surficial, produced in summer with leaves and cleistogamous flowers and fruits, ≤ 12 cm tall; foliage and peduncles gray-green, glabrous, or lower surface of blades with fine hairs along proximal veins; leaves 1–2 and 8–25 mm during chasmogamous flower, spreading; stipules free, green or pink, irregularly glandular-fimbriate; leaf blades undivided, largest ≤ 55 × 41 mm during fruit, round-reniform to reniform, base cordate, margins shallowly crenate, eciliate, apex subobtuse to rounded; chasmogamous peduncle held among or above the leaves; bracts positioned above the middle, often near the apex of the peduncle; chasmogamous flower ≤ 16 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate, rounded; auricles short and rounded, not elongating in fruit; corolla pink-purple (rarely whitish), throat greenish-white; spur short-globose, ca. 1.5 mm long, 2–3 × as long as auricles; lateral petals sparsely bearded within with narrowly linear hairs; style and stamen appendages prominently exserted and fully visible in living material; cleistogamous flowers produced after chasmogamous, on ascending or erect peduncle shorter than or surpassing petioles; capsule 6–9 mm, green drying tan, unspotted or with fine red spots, glabrous; seeds 1.8–2.0 × 1.0 mm, dark gray to olive-green, blotched; 2n = 24.

Similar Species. As members of the Palustres species group, this species and *V. palustris* share a creeping node-rooting rhizome with lateral stolons, the leaves not forming a discrete rosette but instead inserted individually along the length of the rhizome nearer the apex with flowers and fruits in the leaf axils, broad stipules, reniform leaf blades, and violet corollas. It differs most conspicuously from *V. palustris* in its fewer and smaller leaves with the lower surface of leaf blades occasionally appressed-hirtellous, bracts positioned above the middle of the peduncle, lateral petals sparsely bearded, and dark gray to olive-green blotched seeds. In cleistogamous fruit, if the rhizome and lateral stolons with leaves inserted separately are disregarded, it may be confused with other *Stolonosae*. It can be distinguished from *V. incognita* and *V. renifolia* by its subentire to crenate leaf blade margins, unspotted cleistogamous capsule, and gray to greenish blotched seeds; and from *V. minuscula* by the proportionally broader leaf blades often with the lower surface appressed-hirtellous along veins, and dark gray to greenish blotched seeds.

Ecology. Alpine meadows, marshes, bogs, and shores of lakes and streams.

Distribution. Interruptedly circumboreal, Nunavut and western Ontario to Alaska, south to northern Michigan and northern Minnesota (western USA records tentatively left in *V. palustris* pending further study); boreal East Asia. Fig. 148.

Rarity. Listed in Michigan (as *Viola epipsila*).

Phenology. Chasmogamous flower June–August, chasmogamous fruit July–August, cleistogamous fruit July–September.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer, in the Palustres species group.

Hybrids. Hybridizes with *V. palustris* (Blaxland 2022). Hybrids with *V. minuscula* and other species are possible in the zone of sympatry and should be sought. Due to the difference in ploidy level, hybrids with *V. palustris* would probably fail to reproduce by chasmogamous flowers, which would have sterile pollen, and cleistogamous capsules would likely be abortive or contain no viable seeds. Studies are needed to confirm these predictions.

Comments. Type material was recently identified by Thomas Marcussen and others for this species (T. Marcussen, University of Oslo, personal communication). Regarding type material for *V. achyrophora*, Greene wrote in the protologue that the specimens were taken from "St. Paul Island, Bering Sea, July 18, 1897, James M. Macoun, the specimens distributed under the name of *V. palustris*...." The protologue provides reasonably specific information to indicate one collection, but does not note a single sheet, cites no type, and mentions no single herbarium. Greene's reference to "specimens distributed" clearly suggests that duplicate sheets were distributed to other herbaria. Only one image is in the JSTOR Global Plants database, of the Macoun sheet at NDG. That sheet has the original identification "*Viola palustris* L.," presumably in Macoun's hand, on the label; at the top of the label is written "*Viola achyrophora*, Greene, type!" in Greene's hand. The protologue states the collection date as "July 18," but the label on the NDG sheet mentions no

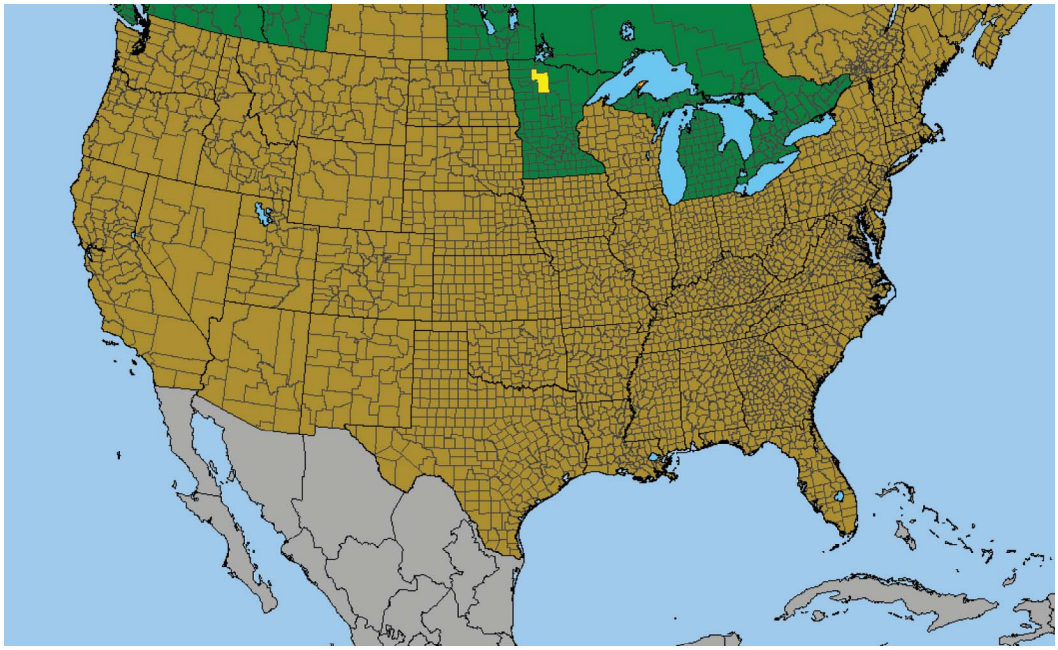

FIG. 148. United States county distribution of *Viola suecica* [western distribution included in *V. palustris* while disentangling specimens of the taxa] (map: Biota of North America Program).

day. If the day specified in the protologue is in error (which is fairly common with Greene's collections), then a probable isolectotype is this: "St. Paul Island, Damp banks, 10 Jul 1897, J. M. Macoun s.n. (CAN 81114)," in the CAN database. Regardless, the NDG sheet is designated here as the lectotype.

Brainerd (1921b), Fernald (1950), Alexander (1963), Russell (1965), and Gleason and Cronquist (1991) included this in *V. palustris*. Brainerd Baird (1942), Scoggan (1978), Ballard (1995), Voss and Reznicek (2012), and Little and McKinney (2015) maintained it as *V. epipsila* Ledeb. subsp. *repens* W.Becker. Brainerd Baird noted that the present taxon only extended into western North America, but subsequent decades have provided many additional records in the central portion of Canada, as far east as the Thunder Bay District and northward in western Ontario. The first report of this species in the eastern United States was made by Ballard (1985) under the name *V. epipsila* subsp. *repens*. The first author recently confirmed a second report, based on a specimen from northern Minnesota at MIN that had been misidentified (Ballard 2022). Little and McKinney (2015) refuted reports of the species from California due to lack of confirmed specimens (M. Sorsa, personal communication to Little), and from Nevada and Utah due to its absence in floras by Welsh *et al*. (1987) and Holmgren (2005), respectively. We are tentatively excluding those states in the distribution given here, awaiting evidence supporting its occurrence south and west of Colorado and Washington. Specimens of this tetraploid species have commonly been misidentified as octoploid *V. palustris*. Plants of Palustres violets along the Pacific Northwest coast and nearby areas with 2 leaves during chasmogamous flower and bracts above the middle of the peduncle but glabrous leaves have been a major source of confusion. In studies of North American Palustres violets, Sorsa (1968) documented an octoploid ploidy level similar to *V. palustris* in the problematic Pacific Northwest violet. Marcussen *et al*. (2012) demonstrated through molecular phylogenetic studies that the Pacific Northwest violet had a different allopolyploid origin than *V. palustris*. Blaxland *et al*. (2018) recently described the violet as *V. pluviae*, diagnostic characters to separate it from related or similar violets, and additional information, clearing up much of the taxonomic confusion in the West. We have not made special studies of *V. suecica* (the newest correct name for our tetraploid Palustres violet) or *V. palustris* in our region and have relied heavily on the research notes, descriptions, illustrations

and images of the late Kim Blaxland (2022), an accomplished violet taxonomist who investigated the Palustres violets and numerous other *Viola* taxa in North America and provided a wealth of features, photographs, and illustrations, as well as further information in Blaxland *et al*. (2018), to distinguish the species. For further comments on species-level and infrageneric taxonomic diversity in the Palustres violets in North America and worldwide, see "Comments" under *V. palustris*. Given the taxonomic diversity of Palustres violets in western North America, long-standing historical submergence of this species under *V. palustris*, and challenges of identifying many specimens without ploidy information, western USA records are left in *V. palustris* until further studies can sort out the taxa in that region.

61. ***Viola tenuisecta*** Zumwalde & H.E.Ballard, **sp. nov.**

Type. **USA**. Virginia. Bath Co., Douthat State Park, E of Administration Bldg/Visitor Center, N of Beard's Gap Trail on lower slopes from NE of garage buildings (37.896132°, –79.799904°) for 0.38km (37.896221°, –79.79558°), probably continuing eastward in appropriate habitat, Steep S-facing slopes of shale barren area, in small forest patches scattered through barren openings and forest below openings, in sparsely vegetated light dry sand and small gravel among calciphilous plants, Intermittent, several 100 to perhaps 1000 individuals, just beginning cleistogamous reproduction, 16 Jul 2022, *H. E. Ballard, Jr. 22-001* (holotype: VPI; isotype: NY). Fig. 149.

Diagnosis. This new species of dimorphic homophyllous cut-leaved violet belongs to the Subsinuata species group of subsect. *Borealiamericanae* and is unique in its extensively tri- to tetraternately dissected summer leaf blades with primary divisions commonly conspicuously narrowed at base into "petiolules." It was previously confused with, and is superficially most similar to, *V. pedatifida* in its slender ultimate leaf segments and "prairie-like" shale woodland habitat. Besides its leaf dimorphism and more extensively dissected summer leaf blades, the new species differs from *V. pedatifida* in its consistently glabrous foliage, eciliate sepals, short auricles in chasmogamous flower only slightly elongating in cleistogamous fruit, glabrous spurred petal, purple-spotted (very rarely unspotted) cleistogamous capsule on a very short declined peduncle, gray to reddish-brown seeds typically with minute raised black spots, and restriction to less acidic soils of open woodland "glades" bordering shale barrens and of closed-canopy woodlands in western montane Virginia.

Common Name. Virginia shale woodland violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 15 cm tall; foliage and peduncles blue-green, upper surface of leaf blades darker than lower, petioles, lower surface of blades, peduncles, calyx, and often blade margins purple-tinged, glabrous throughout; stipules free, irregularly glandular-fimbriate; homophyllous, leaves spreading, smallest leaf blades palmatifid or biternately divided, largest during chasmogamous flower biternately to subtriternately divided into somewhat broad ultimate lobes, during fruit becoming tri- to tetraternately dissected into 17–27 narrowly linear narrowly rounded ultimate lobes, primary divisions in fruit often constricted at base into a very slender elongate "petiolule," largest $\leq$ 110 $\times$ 150 mm, outline ovate in flower, orbiculate to reniform in fruit, base subcordate to cordate, margins entire or with a minute subapical tooth on either margin, eciliate, apex broadly rounded; chasmogamous peduncle held above the leaves in early flower, often among or below leaves later; chasmogamous flower $\leq$ 21 mm; calyx glabrous, eciliate; lowest sepals ovate-lanceolate to narrowly ovate, broadly acute to obtuse; auricles short and entire, becoming quadrate and weakly elongating to 1.5 mm in fruit; corolla blue to purple, exposed proximal portion of bottom petal white, throat white; spur short-globose; lateral petals bearded with filiform to narrowly linear hairs, spurred petal glabrous; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, the peduncle declined, arching just before dehiscence, very short (often scarcely more than 2 $\times$ as long as the capsule); cleistogamous capsule 6–9 mm, green drying tan and purple-tinged with fine purple spots (very rarely unspotted), glabrous; seeds 1.7–2.4 $\times$ 1.1–1.5 mm, gray, gray-brown, or light to medium (reddish-)brown, with sparse to dense minute raised black spots (rarely unspotted).

Paratypes. **USA** Virginia. Alleghany Co., 2.5 miles N of Hwy 60 on Hwy 629, above Wilson Creek, 1946, *R. B. Platt s.n*. (PENN). Bath Co., Northwest-trending spur ridge on west side of Beards Mountain, approx. 5.4km southwest of Nimrod Hall, west of Cowpasture River, Forested ridgecrest and north-facing slope atop shale barrens,

Associates at ridgecrest include *Schizachyrium scoparium*, *Carex pensylvanica*, *Trifolium virginicum*, *Danthonia spicata*, *Asclepias verticillata*, *Scutellaria ovata* var. *rugosa* with species typical of forested habitats downslope within in *Carya glabra-Quercus rubra-Q. montana* matrix, Elevation 610m., 27 Jun 2013, *J. F. Townsend, H. Ballard, & T. Wieboldt 4484* (VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, at crest follow trail S for a couple miles, population will be on other (W) side of mountain, 37.951111°, –79.735167°, Shale woodlands, canopy has not leafed out yet, lots of leaf litter, very steep slope, unable to sample entire population, lots of Carya, Elev. 624m, Many individuals, densely populated, many leaves per plant (3-6), leaves finely dissected, presence of chasmogamous capsules and cleistogamous buds and capsules, 10 May 2017, *J. L. Hastings, H. E. Ballard, B. S. Sitepu, B.S., & T. Singh 17-002* (MO, NY, VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, at crest follow trail S for a couple miles, population will be on other (W) side of mountain, collected 10 May 2017 as part of 17-002, cultivated in OU violet garden until 12 June 2018, *J. L. Hastings 17-002G1* (VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, at crest follow trail S for a couple miles, population will be on other (W) side of mountain, collected 10 May 2017 as part of 17-002, cultivated in OU violet garden until 18 July 2018, *J. L. Hastings 17-002G2* (NY). Ridgecrest along Beards Mountain Trail, 9.1km NNE of Clifton Forge, 1.5km E of Douthat Lake, *Carya glabra-Quercus rubra-Q. montana* woodland w/*Draba ramossisima*, *Scutellaria ovata* var. *rugosa*, *Carex pensylvanica*, *Antennaria virginica*, *Allium cernuum*, *Hedeoma pulegioides*, Elevation 1,091m., 21 Aug 2013, *J. F. Townsend 4543* (VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, at crest follow trail S for approx. 1 mile, population is scattered on either side of trail, 37.954778°, –79.727917°, Shale woodlands, gentle slope, on the top of the hill, very shaded, many Carya and Quercus alba, sparse vegetation, few additional herbs, Elev. 642m, Many individuals present, plants tall, larger leaves more dissected than smaller leaves, short chasmogamous fruits, 10 May 2017, *J. L. Hastings, H. E. Ballard, B. S. Sitepu, B.S., & T. Singh 17-003* (VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, at crest follow trail S for approx. 1 mile, population is scattered on either side of trail, collected 10 May 2017 as part of 17-003, cultivated in OU violet garden until 12 June 2018, *J. L. Hastings 17-003G1* (VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, at crest follow trail S for approx. 1 mile, population is scattered on either side of trail, collected 10 May 2017 as part of 17-003, cultivated in OU violet garden until 18 July 2018, *J. L. Hastings 17-003G2* (NY). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, go S and population is on top of ridge, 37.963166°, –79.715722°, Shale woodlands, very steep slope, right below a big rock formation, opening in the canopy where many of the plants are located, sparsely vegetated understory, Elev. 525m, Very small population, only approx. a dozen plants, leaves finely dissected, 11 May 2017, J. L. Hastings, H. E. Ballard, B. S. Sitepu, B.S., & T. Singh 17-004 (VPI). Beards Mountain, on trail off Wallawhatoola Road, cross bridge, follow switchback trail up Beards Mountain, go S and population is on top of ridge, Collected 10 May 2017 as part of 17-003, cultivated in OU violet garden until 18 July 2018, 18 July 2018, J. L. Hastings 17-004G1 (VPI). Beards Mountain, 21 Aug 2014, B. A. Zumwalde s.n. (VPI). Located on U.S. Forest Service property 0.9km northeast of Copeland and 12.6km south-southwest of Millboro Springs, just west of railroad tracks, Shale barren, Southeast-facing with Heuchera *pubescens*, *Penstemon canescens*, *Eriogonum allenii*, *Calystegia spithamea* ssp. *purshiana*, *Clematis albicoma*, *Antennaria parlinii* ssp. *parlinii*, *Silene caroliniana* var *pensylvanica*, etc., base of barren, Common, 5 May 2008, *J. F. Townsend 3932* (VPI105151). George Washington & Jefferson National Forest, east of Copeland, Shaded wooded borders surrounding shale barrens openings, Apr 2014, *B. A. Zumwalde s.n*. (VPI). Near (E of) Copeland, off Pads Creek Road, approx. 5.2 miles past intersection of 633, continue walking down Pad's Creek Road for 0.9mi where intersection occurs, site is approx. 20m N of road, 37.886194°, –79.690361°, Steep slope, Viola present on the lower slope, shale woodland, densely vegetated, Elev. 378m, Small population over small area, plants mostly small, with a couple large ones scattered around, past chasmogamous flowering/

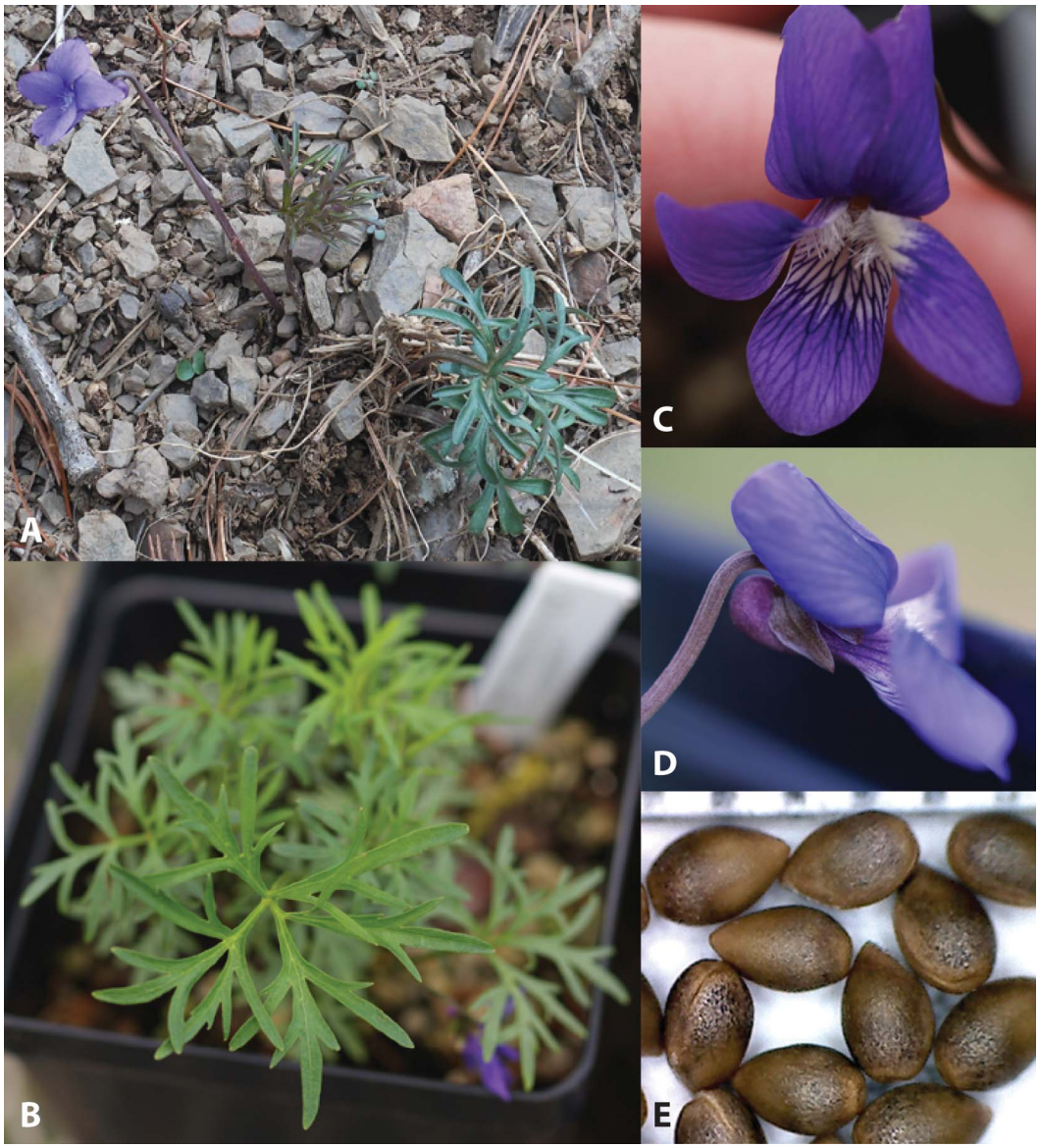

FIG. 149. *Viola tenuisecta*. (A) Chasmogamous flowering habit (photo: Harvey Ballard). (B) Leaves during late chasmogamous flower (photo: Bethany Zumwalde). (C) Chasmogamous flower front view (photo: Bethany Zumwalde). (D) Chasmogamous flower profile view (photo: Bethany Zumwalde). (E) Seeds from herbarium specimen: Transplanted from Virginia, Bath Co., Beards Mountain, *J. Hastings JH17004D* (BHO).

fruit, cleistogamous buds present , 24 May 2017, *J. L. Hastings & A. C. Pidock 17-034* (VPI). George Washington & Jefferson National Forest, just E of Copeland, NE of and upslope from the 'Y' intersection of Pads Creek Road and a smaller unnamed road, collected 4 Jul 2021, cultivated in OU violet garden until 2 May 20, 37.886609°, –79.690402°, Shaded presumably alkaline glades surrounding shale barrens openings, Frequent, many immatures, some adults, a small percentage with cleistogamous fruits, 2 May 2022, *H. E. Ballard Jr. 21-017* (VPI). E of Copeland, population intermittent from 37.886417°, –79.69015° to 37.886917°, –79.689483°, Steep south-facing slope, shaded gladey edges of more open shale barrens areas, plants growing in sparsely vegetated soil with shale gravel, 28 Jun 2013, *H. E. Ballard Jr. & J. Zink 13-035* (NY, VPI). In Brushy Hollow, About

0.4 mi E of Wilson Creek, southern portion of Douthat State Park, about 4 mi N of Clifton Forge, Small, SSE'ly- facing shale barren woodland about midslope, Elevation: 1500 ft., 2 May 2006, *T. F. Wieboldt 11784* (VPI104760). Douthat State Park - shale barrens next to Alleghany County line, 0.75km east of Va 629, ca. 6km north of Clifton Forge, in open woodland habitat, Associates include *Houstonia longifolia*, *Trifolium virginicum*, *Antennaria virginica*, *Symphyotrichum cordifolium*, *Dichanthelium boscii*, *Allium cernuum*, *Viola subsinuata*, Elevation 445m., Sparsely distributed, 16 May 2013, *J. F. Townsend & H. Ballard, 4340* (Virginia Division of Natural Heritage, VPI). Douthat State Park, park at Brushy Hollow Trail Head off Douthat State Park Road (629), follow Trail E for approx. 0.5 mile, cross stream and climb up the mountain approx. 50m, 37.881889°, –79.798639°, Steep slope with dense vegetation at the bottom and sparse vegetation higher up, lots of Pinus, Elev. 466m, Leaves deeply dissected, plants past chasmogamous flowering stage but have well developed chasmogamous capsules, plants abundant, variety of sizes, 23 May 2017, *J. L. Hastings & A. C. Pidock 17-029* (NY, VPI). Douthat State Park, park at Brushy Hollow Trail Head off Douthat State Park Road (629), follow Trail E for approx. 0.5 mile, cross stream and climb up the mountain approx. 50m, collected 23 May 2017 as part of 17-029, cultivated in OU violet garden until 4 July 2018, *J. L. Hastings 17-029G1* (VPI). Directly behind state park headquarters, East of Wilson Creek and St. Rt. 629 about 5 miles N of Clifton Forge, in open shale barren woodland, Steep S- to SW facing slope at end of spur ridge, Elevation 1450-1500 ft., Numerous plants, mostly finished flowering, 2 May 2006, *T. F. Wieboldt 11768* (VPI104766). Douthat State Park, E of Administration Bldg, N side of Brushy Gap Trail, Shaded S-facing presumably alkaline glades surrounding shale barrens openings, Many sterile plants, a few plants with dried dehisced chasmogamous capsules, others with developing heavily purple-spotted cleistogamous capsules on very short declined peduncles, 27 Jun 2013, *H. E. Ballard Jr, & Zink 13-033* (NY, VPI). E of (behind) Admin Bldg, N side of Brushy Gap Trail, Rather steep S-facing slope, shaded wooded borders around shale barrens openings, Many scattered plants w/1-2 leaves but no reproduction, 1 plant w/dehisced CH capsule, a few with mature CL capsules, mostly heavily purple-spotted but one plant with unspotted capsule, all on very short declined peduncles, 16 Aug 2013, *H. E. Ballard Jr. & A. P. Stuart 13-048* (NCU). Douthat State Park, near (E of) the Admin building, about 0.25mi on trail, on slope to north of trail, 37.89597°, –79.79984°, About halfway up the mountain on a steep slope, the substrate is loose rock in a shale woodland area, lots of Carya and Quercus, Elev. 430m, Large population, leaves large, finely dissected, 9 May 2017, *J. L. Hastings, H. E. Ballard, B. S. Sitepu, and T Singh 17-001* (VPI). Douthat State Park, slope east of Admin building, north side of and above Beard's Gap trail, 37.89577°, –79.79894°, Lowest 1/3 of steep shale barren slope with sparsely vegetated gravelly sandy soils, mostly under tree cover, Hundreds of plants over least vegetated areas lacking acidopholous plants, some in cleistogamous fruit, voucher for DNA 742, 17 Aug 2018, *H. E. Ballard Jr. & S. Dailey 18-030* (NY, VPI). On SW end of Rough Mountain, ca 5.5 mi NE of Clifton Forge, Station first reported by R.B. Platt in Castanea 15:128-129 (1950), Scattered frequently over shaly slopes, woods, and barrens, Elevation 1185 ft., 24 Apr 2007, *T. F. Wieboldt & F. Huber 11873* (VPI105964).

Similar Species. This species is most similar overall to other homophyllous cut-leaved taxa in the Pedatifida and Subsinuata species groups, and especially similar to *V. pedatifida* as noted in the diagnosis above. Besides its glabrous foliage, leaf dimorphism, and more extensively dissected summer leaf blades, this species differs from *V. brittoniana* and *V. pedatifida* in its broader acute to obtuse eciliate sepals, short entire auricles, glabrous spurred petal, finely spotted cleistogamous capsule on a very short declined peduncle, and gray to brown unspotted or minutely spotted seeds; and can be distinguished from *V. baxteri* and *V. subsinuata* by its eciliate sepals, finely spotted cleistogamous capsule on a very short declined peduncle, and gray to brown unspotted or minutely spotted seeds.

Ecology. Dry to seasonally moist less acidic sandy soils and rock outcrops in shaded microsites in and around shale barrens openings.

Distribution. County-level endemic of northern Alleghany and southern Bath counties, Virginia. Fig. 150.

Rarity. Listed in Virginia (as *Viola* species 1).

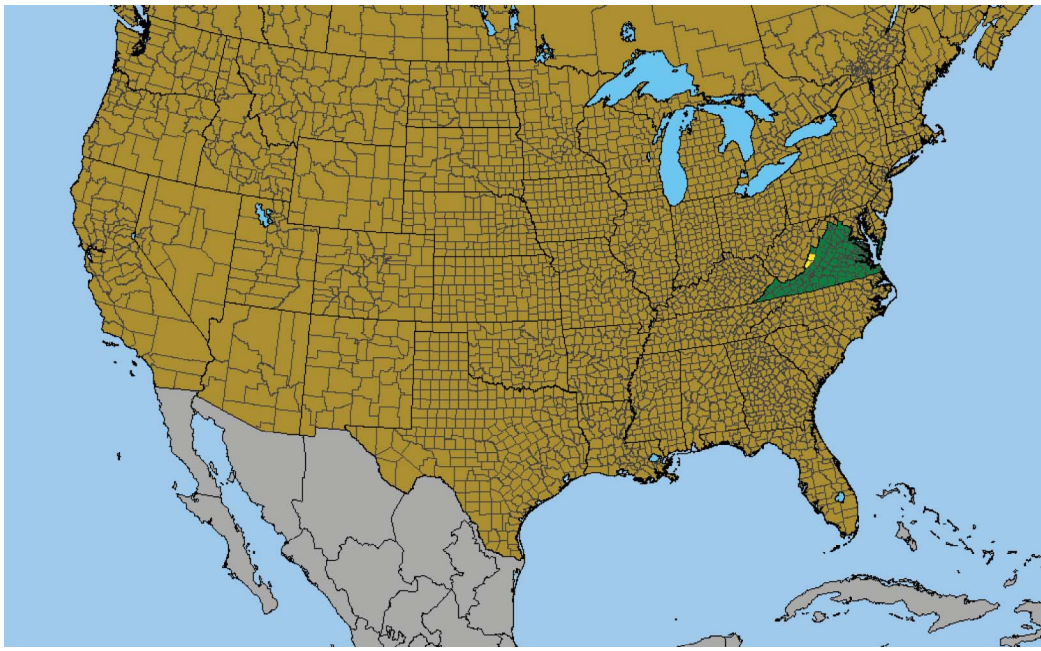

FIG. 150. United States county distribution of *Viola tenuisecta* (map: Biota of North America Program).

Phenology. Chasmogamous flower March–April, chasmogamous fruit April–May, cleistogamous fruit May–August.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Subsinuata species group.

Hybrids. None.

Comments. This species is named for its distinctive extensively tri- to tetraternately dissected summer leaf blades. It was recently detected as a new species in Virginia's Shale Barrens region and was historically interpreted as disjunct populations of *V. pedatifida* or a waif of that species by Platt (1950). It is one of the rarest violets in North America. Essentially nonexistent in national and regional herbaria prior to recent investigation, it is a prime example of the need for intensive fieldwork and integrative taxonomic studies, and of the value of knowledgeable local botanists. Subsequently, Virginia botanists Tom Wieboldt and Johnny Townsend relocated historical sites and determined that Platt's populations represented ostensibly native occurrences representing disjunct populations of *V. pedatifida*. The taxon was completely ignored by violet specialists and lay taxonomists outside that region. Wieboldt and Townsend introduced the first author to the populations in 2012, and shortly afterward graduate student Bethany Zumwalde conducted integrative taxonomic studies on this taxon and others in the *V. pedatifida* and *V. subsinuata* species groups. She demonstrated that the present taxon is a highly distinctive evolutionary species with a unique ecological niche in less acidic soils of woodland borders surrounding open shale barrens and in closed-canopy forest in nearby areas on the same mountain ranges (Zumwalde 2015). It is restricted to three small parallel mountain ranges straddling Allegheny and Bath counties of western montane Virginia, joining other narrow Virginia endemics associated with shale barrens, including *Clematis addisonii* Britton (four counties, G1? S1? status) and *Clematis viticaulis* Steele (two counties, G1 S1S2, federally threatened). Global (G) and state (S) ranks are assigned to species by the provincial and state Heritage Programs, with 1 being most narrowly endemic and imperiled and 5 being widely distributed and of no conservation concern. Macromorphological features, micromorphological traits of lateral petal trichomes and seed coats, and microsatellite diversity demonstrate that this species belongs to the Subsinuata species group and has no close relationship with *V. pedatifida*. Initial studies of this taxon inspired

FIG. 151. *Viola tricolor*. (A) Chasmogamous flowering habit (photo: Madisyn Schultz). (B) Chasmogamous flower front view (photo: Kevin Nixon). (C) Chasmogamous flower profile view (photo: Arieh Tal, Native Plant Trust). (D) Chasmogamous fruit (photo: Arieh Tal, Native Plant Trust).

the extensive integrative taxonomic studies employed by our research group with other violets in our region, leading to detection of much greater evolutionary diversity in our violet flora than previously recognized.

62. *Viola tricolor* L., Sp. pl., ed. 1, 2: 935. 1753; *Ion tricolor* (L.) Medik., Malvenfam.: 102. 1787; *Mnemion tricolor* (L.) Spach, Hist. Nat. Vég. (Spach) 5: 515. 1836. Fig. 151.

Viola grandiflora L., Mant. Pl. 2: 518. 1771.

Viola tricolor L. subsp. *procumbens* Ehrh., Hannover. Mag. 18: 232. 1780.

Viola bicolor Hoffm., Deutschl. Fl. Bot. Taschenb. 4: 170. 1804; *Viola tricolor* var. *bicolor* Hartm., Handb. Skand. Fl.: 110. 1820.

Viola arvensis Murray var. *media* DC., J.B.A.M.de Lamarck & A.P.de Candolle, Fl. Franç., éd. 3, 6: 618. 1815.

Viola banatica Kit. ex Schult., J.J.Roemer & J.A.Schultes, Syst. Veg. ed. 15[bis]. 5: 382. 1819; *Mnemion elegans* Spach, Hist. Nat. Vég. 5: 513. 1836.

Viola parviflora Kit. ex Schult., J.J.Roemer & J.A.Schultes, Syst. Veg. ed. 15[bis]. 5: 383. 1819 [not validly published].

Viola tenella Muhl. ex Schwein., Amer. J. Sci. Arts 5: 78. 1822 [*nomen illegitimum*].

Viola tricolor L. var. *calycina* DC. ex Ging., A.P.de Candolle, Prodr. 1: 303. 1824.

Viola tricolor L. var. *crassifolia* DC. ex Ging., A.P.de Candolle, Prodr. 1: 303. 1824.

Viola tricolor L. var. *degener* DC. ex Ging., A.P.de Candolle, Prodr. 1: 303. 1824.

Viola tricolor L. var. *gracilescens* (DC. ex Ging.), A.P.de Candolle, Prodr. 1: 304. 1824.

Viola tricolor L. var. *hortensis* DC. ex Ging., A.P.de Candolle, Prodr. 1: 303. 1824; *Viola tricolor* L. subsp. *hortensis* (DC. ex Ging.) Corb., Nouv. Fl. Normandie: 80. 1894.

Viola tricolor L. var. *ovatifolia* DC. ex Ging., A.P.de Candolle, Prodr. 1: 303. 1824.

Viola tricolor L. var. *purpurea* DC. ex Ging., A.P.de Candolle, Prodr. 1: 303. 1824.

Viola pratensis var. *humilis* Mert. & W.D.J.Koch, J.C.Röhling, Deutschl. Fl., ed. 3, 2: 267. 1826.

Viola tricolor L. var. *media* Roth, Enum. Pl. Phaen. Germ. 1(1): 763. 1827.

Viola tricolor L. var. *minor* Roth, Enum. Pl. Phaen. Germ. 1(1): 764. 1827.

Viola tricolor L. var. *ramosa* Roth, Enum. Pl. Phaen. Germ. 1(1): 764. 1827.

Viola tricolor L. var. *simplex* Roth, Enum. Pl. Phaen. Germ. 1(1): 764. 1827.

Viola tricolor L. var. *vulgaris* Wimm. & Grab., Fl. Siles. 1: 225. 1827.

Viola mutabilis Rochel, Pl. Banat. Rar.: index. 1828.

Viola tricolor L. var. *grandiflora* Lej. & Courtois, Comp. Fl. Belg. 1: 202. 1828.

Viola micrantha Bertol., Misc. Bot. 1: 15. 1842 [*nomen illegitimum*].

Viola soongorica Fisch. ex Ledeb., Fl. Ross. 1: 257. 1842.

Viola nemausensis Jord., Observ. Pl. Nouv. 2: 18. 1846.

Viola pallescens Jord., Observ. Pl. Nouv. 2: 10. 1846.

Viola sagotii Jord., Observ. Pl. Nouv. 2: 34. 1846; *Mnemion sagotii* (Jord.) Fourr., Ann. Soc. Linn. Lyon, n.s., 16: 342. 1868; *Viola lutea* Huds. var. *sagotii* (Jord.) Nyman, Consp. Fl. Eur.: 81. 1878; *Viola tricolor* L. var. *sagotii* (Jord.) Gaut., Cat. Rais. Fl. Pyr.-Or.: 96. 1898.

Viola vivariensis Jord., Observ. Pl. Nouv. 1: 17. 1846; *Viola lutea* Huds. var. *vivariensis* (Jord.) Nyman, Consp. Fl. Eur.: 81. 1878.

Viola bella Gren., J.C.M.Grenier & D.A.Godron, Fl. France Corse 1: 184. 1847.

Viola virgata Gren., J.C.M.Grenier & D.A.Godron, Fl. France Corse 1: 184. 1847.

Viola flavida Jord., Mém. Acad. Sci. Lyon, Sect. Sci. 1: 25. 1852.

Viola lejeunei Jord., Mém. Acad. Sci. Lyon, Sect. Sci. 1: 27. 1852; *Viola tricolor* var. *lejeunei* (Jord.) P.D.Sell, Fl. Gr. Brit. Ireland 1: 692. 2018.

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Viola luteola Jord., Mém. Acad. Sci. Lyon, Sect. Sci. 1: 27. 1852.

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Viola lloydii Jord. ex Boreau, Fl. Centre France, éd. 3, 2: 80. 1857.

Viola meduanensis Boreau, Fl. Centre France, éd. 3, 2: 80. 1857.

Viola peregrina Jord. ex Boreau, Fl. Centre France, éd. 3, 2: 82. 1857.

Viola provostii Boreau, Fl. Centre France, éd. 3, 2: 82. 1857.

Viola ruralis Jord. ex Boreau, Fl. Centre France, éd. 3, 2: 81. 1857.

Viola derelicta Jord., P.C.Billot, Annot. Fl. France Allemagne: 101. 1859; *Viola tricolor* var. *derelicta* (Jord.) Nyman, Consp. Fl. Eur.: 80. 1878.

Viola mentita Jord., P.C.Billot, Annot. Fl. France Allemagne: 101. 1859.

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Viola foucaudii Sav., A.Tremeau de Rochebrune & A.Savatier, Cat. Pl. Phan. Charente: 49. 1860; *Viola foucaudii* A.Sav., Ann. Soc. Sci. Nat. Charente-Infér. 14: 73. 1878.

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Viola tricolor L. var. *banatica* (Kit. ex Schult.) Rupr., Fl. Ingrica: 141. 1860.

Viola tricolor L. var. *syrtica* Rupr., Fl. Ingrica: 141. 1860.

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Viola leptoceras Schur, Enum. Pl. Transsilv.: 87. 1866.

Viola pseudolutea Schur, Enum. Pl. Transsilv.: 87. 1866.

Viola sicula Schur, Enum. Pl. Transsilv.: 86. 1866.

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Viola mucuzii Orph. ex Nyman, Consp. Fl. Eur.: 80. 1878 [not validly published].

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Viola tricolor L. f. *excelsa* Brenner, Meddeland. Soc. Fauna Fl. Fenn. 19: 80. 1893.

Viola tricolor L. f. *petrophila* Brenner, Meddeland. Soc. Fauna Fl. Fenn. 19: 80. 1893.

Viola tricolor L. var. *polygonata* Brenner, Meddeland. Soc. Fauna Fl. Fenn. 19: 80. 1893.

Viola tricolor L. f. *rupicola* Brenner, Meddeland. Soc. Fauna Fl. Fenn. 19: 78. 1893.

Viola tricolor L. f. *turgescens* Brenner, Meddeland. Soc. Fauna Fl. Fenn. 19: 78. 1893.

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Viola tricolor L. f. *flavescens* Brenner, Meddeland. Soc. Fauna Fl. Fenn. 29: 44. 1904 [*nomen illegitimum*].

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Viola tricolor L. var. *distinctissima* C.G.Westerl., Bot. Not. 1906: 17. 1906.

Viola tricolor L. var. *fulvo-striata* C.G.Westerl., Bot. Not. 1906: 21. 1906.

Viola tricolor L. var. *lacticolor* C.G.Westerl., Bot. Not. 1906: 22. 1906.

Viola tricolor L. f. *luteo-coerulescens* C.G.Westerl., Bot. Not. 1906: 19. 1906.

Viola tricolor L. f. *luteo-roseola* C.G.Westerl., Bot. Not. 1906: 20. 1906.

Viola tricolor L. f. *perobscura* C.G.Westerl., Bot. Not. 1906: 17. 1906.

Viola tricolor L. f. *pulcherrima* C.G.Westerl., Bot. Not. 1906: 21. 1906.

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Viola vectensis (F.N.Williams) Drabble, J. Bot. 65: 47. 1927.

Viola tricolor L. f. *violaceosignata* H.Lindb. ex Hiitonen, Suom. Kasvio (Otava): 412. 1933.

Viola kupffieri Klokov, V.L.Komarov (ed.), Fl. URSS 15: 683. 1949.

Viola tricolor L. f. *alba* Sigunov, Glasn. Prir. Mus. Beogradu, Ser. B, Biol. Nauke 34: 86. 1979.

Common Names. Heartsease, Johnny-jump-up.

Description. Caulescent annuals from slender to somewhat thick taproot, stems erect or declined at base, solitary or multiple, $\leq$ 35 mm tall; stems, foliage, and peduncles light to medium green, quadrate stems recurved-puberulent on the angles, leaves sparsely to moderately hirtellous, peduncles glabrous; leaves cauline and commonly also basal; stipules free, deeply palmatifid, terminal lobe much larger than lateral lobes, elliptical, with (2–)4 or more crenations per margin; leaves ascending, leaf blades undivided, upper $\leq 38 \times 10$ mm, narrowly lanceolate to ovate-lanceolate, middle and lower $\leq 16 \times 15$ mm, smaller and often relatively broader (narrowly ovate to suborbiculate), base narrowly cuneate to broadly rounded (rarely subcordate) and occasionally decurrent onto petiole and indistinct from it, margins crenate or serrate with 4–6 teeth on each side, ciliate, apex occasionally acute to mostly rounded; chasmogamous flower $\leq$ 15(18) mm, petals much longer than sepals; calyx glabrous (occasionally hispidulous), eciliate or ciliate; lowest

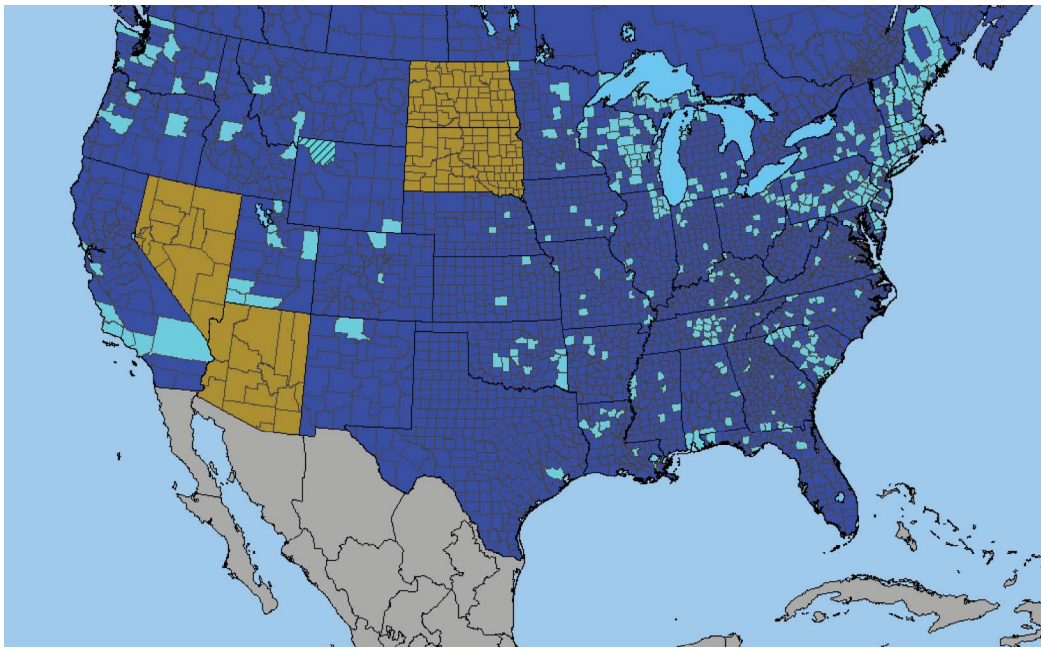

FIG. 152. United States county distribution of *Viola tricolor* (map: Biota of North America Program).

sepals broadly lanceolate to ovate-lanceolate, sharply acute; auricles prominent, entire or erose, not elongating in fruit; corolla commonly with lower three petals cream-white or with yellow, and upper two violet, reddish-purple, purple or purple-black at least in distal half, with a few slender black lines on lateral and spurred petal near base, throat yellow; spur slightly extending beyond the auricles, slender; lateral petals densely bearded with narrowly linear hairs, spurred petal glabrous; cleistogamous flowers lacking; capsule 6–10 mm, green drying tan, unspotted, glabrous; seeds 1.4–1.7 × 0.8–0.9 mm, medium to dark brown, unspotted; 2n = 26.

Similar Species. This species is similar to the other two widely distributed pansies in our region, introduced *V. arvensis* and native *V. rafinesquei*. It differs from *V. arvensis* in the palmatifid stipules, petals well surpassing the sepals, and the upper petals commonly purple-black or occasionally the whole corolla purple. It differs further from *V. rafinesquei* in the common presence of basal leaves, stipules with the terminal leaf-like lobe much larger and with 4 or more crenations per side, leaf blade much longer than broad and with 4 or more teeth per side, and corolla commonly cream with upper petals purple-black or occasionally with all purple petals. It is most similar to the barely escaped garden pansy, *V.* ×*wittrockiana*, distinguished most obviously by its consistently smaller and usually less dramatically colorful flowers and narrower leaves.

Ecology. Infrequently escaped from gardens and cemeteries.

Distribution. Eurasian introduction, transcontinental but especially in the northern region, Newfoundland and Labrador to Alaska, south to Florida, Texas, and California. Fig. 152.

Rarity. None.

Phenology. Chasmogamous flower March–August (October), chasmogamous fruit April–August (September).

Affinities. This species belongs to the Pansy lineage, sect. *Melanium* Ging.

Hybrids. Hybridizes with *V. arvensis*, based on occasional plants in the field and on herbarium specimens with intermediate floral characteristics, such as distally purple-black upper petals but sepals about equaling the petals (Voss and Reznicek 2012; H.E.B., personal observation).

Comments. Brainerd (1921b) did not mention this introduced species, and Brainerd Baird (1942) noted it but did not discuss it. Fernald (1950), Henry (1953a), Alexander (1963), Russell (1965),

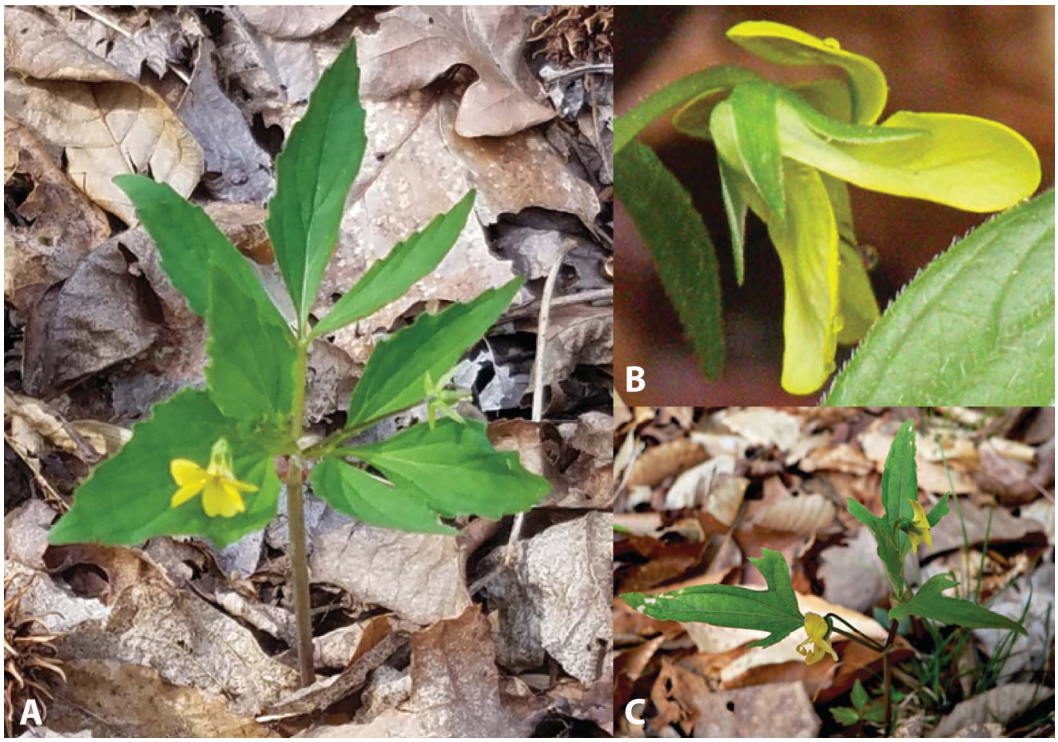

FIG. 153. *Viola tripartita*. (A) Chasmogamous flowering habit (photo: Harvey Ballard). (B) Chasmogamous flower profile view (photo: J. K. Marlow). (C) Leaves during chasmogamous flower (rare "partly lobed" leaf blades) (photo: Richard and Teresa Ware).

Scoggan (1978), Swink and Wilhelm (1979), Gleason and Cronquist (1991), Ballard (1995, 2000, 2013), McKinney and Russell (2002), Haines *et al*. (2011), Voss and Reznicek (2012), and Little and McKinney (2015) reported this species. Russell and McKinney and Russell indicated that it does not persist; and Russell, Scoggan, and Ballard included *V.* ×*wittrockiana* with it. While the latter appears to be rarely collected and almost certainly does not persist very long following abandonment of its garden environment, the same cannot be said of *V. tricolor*. Specimens of *V. tricolor* are widely distributed and often taken in disturbed areas somewhat removed from the nearest likely local seed sources. The first author has observed *V. tricolor* growing plentifully along roadsides near an old cemetery and in a disturbed oak barrens area with *V. rafinesquei* at the back of a cemetery in southern Ohio, for approximately 20 yr with no observable decline.

Along with other members of sect. *Melanium*, this species has contributed genes to the formation of the diverse cultivars of the garden pansy, *V.* ×*wittrockiana*, which barely escapes cultivation. The latter is not treated separately here. Robarts (2013) conducted an extensive phylogenetic study on numerous cultivars of the cultivated pansy and many potential contributors, identifying a number of parental wild species including *V. tricolor*.

63. ***Viola tripartita*** Elliott, Sketch bot. S. Carolina 1(3): 302. 1817; *Viola hastata* Michx. var. *tripartita* (Elliott) A.Gray, Bot. Gaz. 11(11): 291. 1886. Type: [USA] Georg.[ia], Athens, [no date], *W. Green* [*s.n.*] (holotype: CHARL-BY4773, internet image). Fig. 153.

Common Name, Three-parted yellow violet.

Description. Caulescent perennials from thick rhizome, stems erect, solitary, ≤ 36 cm tall; stems, foliage and peduncles green or gray- to olive-green, with stems, petioles, and lower surface of leaf blades occasionally purple-tinged, glabrous, hirtellous or hirsute; leaves cauline (occasionally 1 basal), spreading, leaves mostly well distributed along the stem; stipules free, entire, weakly erose or moderately incised; leaves spreading, smallest

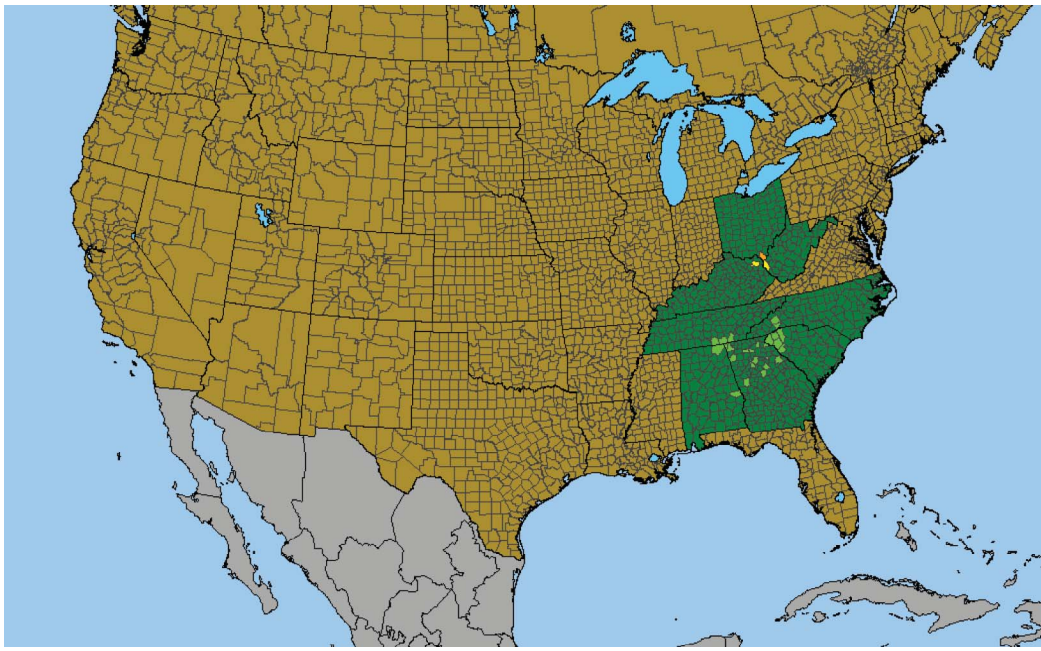

FIG. 154. United States county distribution of *Viola. tripartita* (map: Biota of North America Program).

upper leaf blades undivided, larger lower deeply tripartite (rarely merely shallowly lobed), largest ≤ 103 × 100 mm, upper in outline deltate-lanceolate to narrowly deltate-ovate, lower narrowly to broadly deltate or deltate-ovate to broadly ovate-triangular, base narrowly cuneate to broadly rounded or subtruncate, margins entire or weakly (rarely prominently) serrate, teeth usually restricted to proximal half, eciliate or appressed-ciliate, apex acute to acuminate; chasmogamous flower ≤ 10 mm; calyx glabrous or pubescent, eciliate or ciliate; lowest sepals lanceolate, acute; auricles short and entire, not elongating in fruit; corolla wholly yellow with purple-black lines at base of petals and purple- or brown-tinged on back of petals; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule (7)8–11 mm, green drying brown, unspotted, glabrous or tomentose; seeds 2.5–2.8 × 1.5–2.0 mm, tan to light brown, unspotted.

Similar Species. None. This species is distinctive.

Ecology. Rich sandy loam soils in dry-mesic or mesic forests, probably associated with mafic rocks (Weakley 2015). In the relatively rare sites where the present species occurs sympatrically with *V. glaberrima* or *V. tenuipes* (south of our region), this species typically grows near the ridgetops or on the upper slope. At other sites, in the southern Appalachian Mountains, it often grows at the bottom of the slope near streams.

Distribution. Centered in the southern Appalachian Mountains; western North Carolina to southeastern Tennesse, south to northern Georgia and Alabama, disjunct in southern Ohio, western West Virginia and northeastern Kentucky. Fig. 154.

Rarity. Listed in Ohio; West Virginia (including *V. glaberrima*).

Phenology. Chasmogamous flower March–June, chasmogamous fruit April–July, cleistogamous fruit July–September.

Affinities. This species belongs to the Yellow Violet lineage, sect. *Chamaemelanium* Ging., in the Nudicaules species group.

Hybrids. None.

Comments. Elliott's protologue stated that the species was known "From specimens collected near Athens, Georgia, by Mr. Green. Flowers March–April." Elliott did not designate a type, did

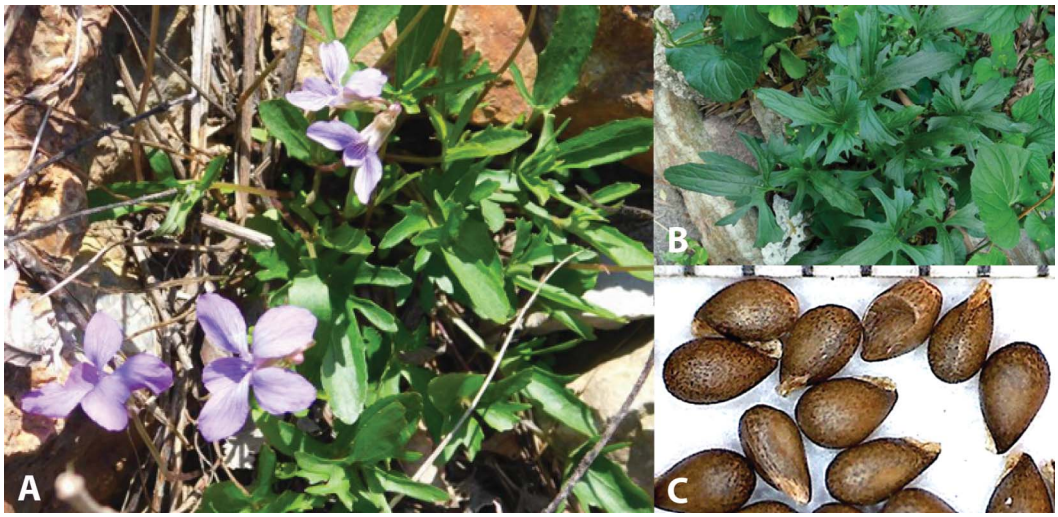

FIG. 155. *Viola viarum*. (A) Chasmogamous flowering habit (photo: Julianna Schroeder). (B) Leaves during cleistogamous fruit (photo: Julianna Schroeder). (C) Seeds from herbarium specimen: Missouri, Eagle Rock, donor B. F. Bush, Ex horto *E. Brainerd 176* (NY).

not indicate a single collection or specify a herbarium. However, according to Stafleu and Cowan (1976), Elliott's herbarium is at the Charleston Museum. A thorough search of the Elliott collection at CHARL revealed a single specimen, which matches the protologue information. It is accepted here as the holotype.

Brainerd (1921b), Russell (1965), Lévesque and Dansereau (1966), Gleason and Cronquist (1991), McKinney and Russell (2002), and Little and McKinney (2015) synonymized *V. glaberrima* under the present species as a mere leaf morph. Fernald (1950) maintained the two as formas under *V. tripartita*; while Alexander (1963), Brainerd Baird (1942), Ballard (2000), and Weakley *et al*. (2012) recognized them as varieties. In all cases, *V. tenuipes* Pollard in the southeastern states has been ignored, being implicitly included in *V. glaberrima*, however the latter was treated. Details supporting segregation of predominately northern *V. glaberrima* and southern *V. tenuipes* as distinct evolutionary species are provided under *V. glaberrima*. Rare shallowly lobed plants, evidently forming small populations in a few localities in Georgia and Tennessee in the range of *V. tripartita*, are not hybrids since they lack intermediate features and are otherwise identical to typical *V. tripartita* elsewhere in the immediate area; they appear to be a product of arrested leaf division. The typical leaf dissection pattern in this species results in some three-lobed or occasionally five-lobed leaf blades, with the uppermost blades often undivided. The present species is one of the rarest violets in our region, now extirpated from sites on the northern periphery of its historical range and uncommon over most of its southern distribution.

64. ***Viola viarum*** Pollard, in Britton, Man. fl. n. states, ed. 1: 635. 1901. Type: USA Missouri. St. Louis, along railroads in dry soil, 15 Jul 1899, *J. B. S. Norton 32* (lectotype (designated by Ballard *et al*. 2020a. Journal of the Botanical Research Institute of Texas 14(2): 227-228): PH00029301 (*n.v.*), internet image); isolectotypes: MO (*n.v.*), NDG33192 (*n.v.*), internet image), NEB-V-0000594 (*n.v.*), internet image), OS0000376 (*n.v.*), internet image), RM0004526 (*n.v.*), internet image), RM0004527 (*n.v.*), internet image), and RSA0006465 (*n.v.*), internet image). Fig. 155.

Common Names. Limestone riverbank violet, wayside violet.

Description. Acaulescent rosulate perennials from thick rhizome, $\leq$ 30 cm tall; foliage and peduncles green, lower surface of leaf blades occasionally slightly paler than upper, plant glabrous throughout; stipules free, irregularly glandular-fimbriate; heterophyllous, leaves erect or ascending, largest leaf blades longer than broad to as broad as long, moderately to deeply pedately divided into (3)5–7(9) lobes, undivided terminal primary division distinctly broader than any lobes present on the lateral primary divisions and not

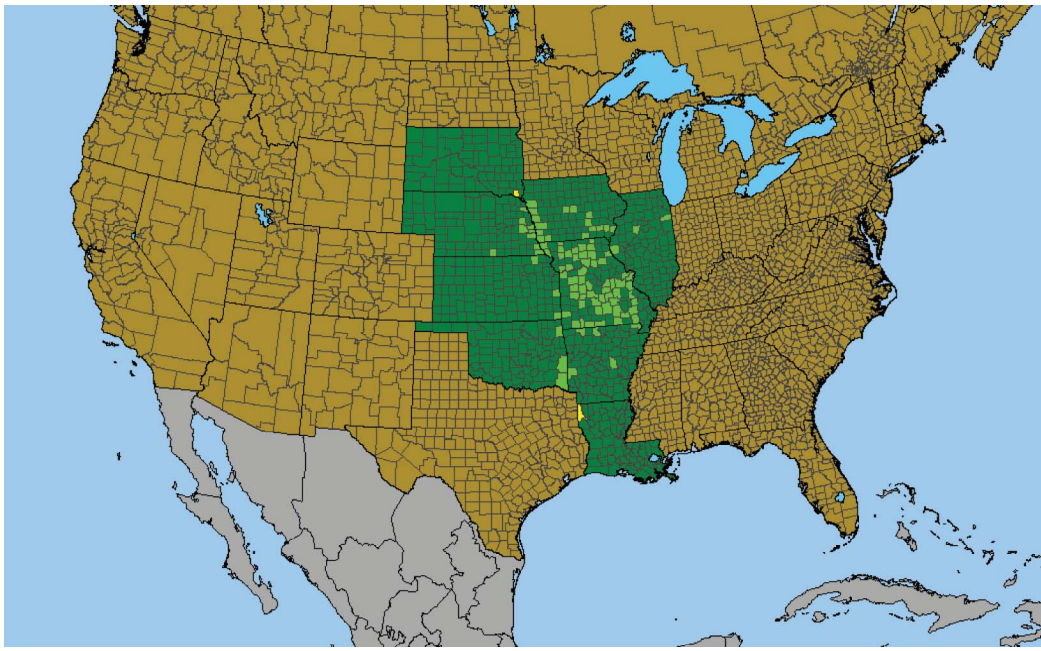

FIG. 156. United States county distribution of *Viola viarum* (map: Biota of North America Program).

distinctly narrowed at its base, the lateral lobes (if present) less than 1/2 the length of the terminal primary division, $\leq 90 \times 85$ mm, outline during chasmogamous flower ovate-triangular to narrowly ovate, in fruit commonly becoming broadly ovate or deltate-triangular, base truncate to shallowly cordate, margins subentire or low-serrate (rarely pronouncedly serrate), eciliate, apex acute to obtuse; chasmogamous peduncle held just above the leaves; chasmogamous flower ≤ 22 mm; calyx glabrous, eciliate; lowest sepals linear-lanceolate to lanceolate, acuminate; auricles somewhat prominent, quadrate and erose, weakly elongating to 2(3) mm in fruit; corolla blue to purple, throat white; spur short-globose; lateral petals densely bearded with slightly clavate hairs, spurred petal sparsely bearded; chasmogamous capsule green; cleistogamous flowers produced after chasmogamous, peduncle ascending to erect, equalling or surpassing shorter petioles; cleistogamous capsule 7–14 mm, green drying tan with fine red or purple spots, glabrous; seeds $1.5–2.1 \times 1.0–1.4$ mm, medium to medium-dark brown with scattered small dark spots.

Similar Species. Among heterophyllous taxa, this species is most similar to others with glabrous foliage in our region, namely *V. edulis* in the Edulis species group and *V. egglestonii* in the Viarum species group. It differs from *V. edulis* in its moderately to deeply pedately divided leaf blades with more slender lateral lobes, the lateral less than 1/2 as long as the terminal primary division, linear-lanceolate to lanceolate sepals acuminate from the base, sparsely bearded spurred petal, and finely spotted cleistogamous capsule. It is easily separated from *V. egglestonii* by its pedately divided leaf blades with the terminal primary division distinctly broader than other lobes, none of the lobes abruptly narrowed at base, acuminate sepals, rather prominent quadrate auricles elongating in fruit, sparsely bearded spurred petal, finely spotted cleistogamous capsule on a taller ascending to erect peduncle, and spotted seeds.

Ecology. Moist to wet limestone gravel and bedrock of riverbanks and streamsides, bluffs, bottomland prairies, persistent along roadsides, lawns, and other disturbed areas formerly in natural habitat.

Distribution. Missouri River basin, Ozark Plateau, and Lower Midwest, northern Illinois to southeastern South Dakota and eastern Nebraska, south to northwestern Louisiana and eastern Oklahoma. Fig. 156.

Rarity. None.

Phenology. Chasmogamous flower April–May, chasmogamous fruit May–June, cleistogamous fruit July–September.

Affinities. This species belongs to the Acaulescent Blue Violet lineage, sect. *Nosphinium* W.Becker, subsect. *Borealiamericanae* (W.Becker) Gil-ad, in the Viarum species group.

Hybrids. Hybridizes with *V. cucullata* (Brainerd 1924), *V. missouriensis* (Russell 1965; Harvey Ballard 2013), and *V. sororia sensu stricto* (H.E.B., personal observation). Hybrids exhibit intermediate or recombinant characteristics in traits of foliage, chasmogamous flower, cleistogamous fruit, and seeds (when these do not abort). Information on reproduction is unavailable.

Comments. Pollard mentioned in his protologue "Type collected by J. B. S. Norton at Valley Park, Mo., July 15, 1899." He cited one collection but did not designate a particular specimen as holotype and did not reference a herbarium. Stafleu and Cowan (1983) noted that Pollard's herbarium and types are at US, with duplicates at several other herbaria. They also stated that Norton's herbarium and types from that time period are at MO. The JSTOR Global Plants database has images of several specimens with the same label information, all bearing a label inaccurately naming them as paratypes (they are syntypes). The US03017761 sheet has the date "Apr. 29 '99," disqualifying it as a syntype. The PH00029301 sheet matches the protologue in all details and is representative of the species in cleistogamous fruit; Ballard *et al*. (2020a) designated that as the lectotype.

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), Alexander (1963), Swink and Wilhelm (1979), and Ballard (2013) accepted this as a distinct species. Russell (1965) presented it among other accepted species but described a situation in his yard where divided-leaved plants appeared to "intergrade" into locally occurring *V. missouriensis*, and he postulated that the present taxon might be a mere genetic variant. Gleason and Cronquist (1991), McKinney (1992), McKinney and Russell (2002), and Little and McKinney (2015) synonymized it in a very broadly delimited *V. palmata*. Gil-ad (1995, 1997, 1998) studied seeds from Brainerd 176, and Brainerd s.n., 7 Oct 1906 (VT) from Eagle Rock, Missouri, and from a hybrid swarm he interpreted as involving *V. viarum* from Gil-ad 415, 416, and 417 in Pettis Co., MO. Gil-ad found no unique micromorphological structures but noted structures were shallow and could not be interpreted accurately. He found similarities of seed micromorphological features with *V. affinis*, *V. missouriensis*, *V. nephrophylla*, *V. pedatifida*, and *V. triloba*. Correlating macromorphological traits with micromorphological features suggested to him a hybrid origin of *V. viarum* involving *V. missouriensis* and *V. nephrophylla* with a taxon possessing lobed or divided leaf blades, such as *V. pedatifida* or *V. triloba*. He excluded *V. viarum* as a species. The several living populations the first author has examined in western and southern Missouri, when putative local hybrids were ignored, were fully fertile via chasmogamous and cleistogamous reproduction and highly uniform in their morphological characteristics. Gil-ad's proposal of a hybrid origin notwithstanding, the taxon as narrowly circumscribed here possesses a distinct suite of macromorphological features, a modally unique habit, and reproduction indicative of a separate evolutionary species. It is distinct in its glabrous foliage and peduncles, largest leaf blades longer than broad to as broad as long, deeply pedately divided into (3)5–7 lobes with the undivided terminal primary division distinctly broader than the lobes on the divided lateral primary divisions, the lateral lobes less than (rarely scarcely more than) 1/2 the length of the midrib, eciliate calyx, slender acuminate sepals, sparsely bearded spurred petal, slightly to moderately elongating auricles in fruit, finely spotted cleistogamous capsule on an ascending to erect peduncle, and brown seeds with scattered small dark spots. Its riverbank limestone habitat is also distinctive. The taxon is accepted here as a distinct species under the unified species concept.

The first author has found that populations of extreme *V. viarum* with deeply pedately dissected leaf blades during later chasmogamous flower and early to midcleistogamous fruit are invariably accompanied by plants with much less deeply divided leaf blades and other macromorphological features, suggesting hybridization with *V. missouriensis* and other locally occurring species with uncut leaf blades. The type of *V. viarum* f. *pilifera* E.J.Palmer & Steyerm. represents a later-generation hybrid involving the present species and *V. sororia*. Russell's example of so-called "intergradation" with *V. missouriensis* probably represented a hybrid swarm. The illustration he chose for this taxon is not typical of the deeply biternate-leaved extreme of *V. viarum* and is likely a hybrid

individual. Hybrids involving *V. palmata* var. *palmata* or *V. pedatifida* with *V. affinis* or *V. missouriensis* would casually resemble the present species in certain features and may also have been misidentified as such. Such putative hybrids commonly end up on herbarium specimens as inadvertent mixed collections or comprise the entire sheet, and some may have passed unnoticed by Brainerd and others, who accepted such specimens as normal components of variation in the present species. Herbarium collections attributed to this species (including Swink and Wilhelm's dubious records) should be reexamined to exclude hybrids, in order to more narrowly circumscribe the taxon and gain a more accurate understanding of its geographic distribution. The present species is similar to *V. egglestonii* in its preference for limestone but it occupies consistently moister microsites, in cobble or crevices of bedrock along streams and rivers, occasionally on the higher ground of riverside bluffs (where it must compete with more mesic-loving hybrids and other species). The infrequently applied common name "plains violet" is a misnomer, since the bulk of the range of this species is in the Lower Midwest and extends only a modest distance westward into the Great Plains region along its preferred river- and streamside habitat. A cumbersome but descriptive new common name, "limestone riverbank violet," is proposed here (better names are encouraged!). Specimens previously referred to this from limestone canyons of the Guadalupe Mountains of New Mexico and Texas have been described as a distinct southwestern species, *V. calcicola* R. A. McCauley & H. E. Ballard, also belonging to the Viarum species group (McCauley and Ballard 2013).

65. ***Viola vittata*** Greene, Pittonia 3: 258. 1898; *Viola lanceolata* L. var. *vittata* (Greene) Weath. & Griscom, Rhodora 36: 48. 1934; *Viola lanceolata* L. subsp. *vittata* (Greene) N.H.Russell, Amer. Midl. Naturalist 54: 484. 1955. Type: USA Florida. [Duval Co.] near Jacksonville, Low rich places, March [no year], *A. H. Curtiss 208* (lectotype (**designated here**): NDG32134 (*n.v.*), internet image; isolectotypes: G (*n.v.*), NY00097606 (*n.v.*), internet image, US03015702 (*n.v.*), internet image, US03015718 (*n.v.*), internet image). Fig. 157.

Viola denticulosa Pollard, Bull. Torrey Bot. Club 28: 475. 1901.

Common Names. Southern water violet, strapleaf violet.

Description. Acaulescent perennials from slender rhizome, nonstoloniferous or producing poorly developed surficial nonreproductive stolons with few leaves in summer (plants north of North Carolina occasionally with leaves and a few flowers or fruits); foliage and peduncles green, glabrous or leaves more commonly moderately to densely hirtellous; stipules free, finely glandular-fimbriate; leaves erect, leaf blades undivided, largest $\leq$ 153 $\times$ (2–)4–9(–13) mm, 8–15 $\times$ as long as broad, often abruptly tapering to the petiole, narrowly linear to linear-lanceolate, base narrowly attenuate, gland of marginal teeth abruptly widely ascending to spreading, margins appearing denticulate, eciliate, apex narrowly acute to narrowly attenuate; chasmogamous peduncle held among the leaves; chasmogamous flower $\leq$ 10 mm; calyx glabrous, eciliate; lowest sepals narrowly lance-triangular, acuminate; auricles short and entire, not elongating in fruit; corolla white, throat greenish-white; spur short-globose; all petals glabrous (occasionally lateral petals with sparse beard of narrowly linear to slightly clavate hairs); cleistogamous flowers produced after chasmogamous, on erect peduncle nearly to quite as long as petioles; capsule 9–14 mm, green drying light brown, unspotted or with fine red spots, glabrous; seeds 1.0–1.2 $\times$ 0.7–0.9 mm, dull gray-brown, unspotted; $2n = 24$.

Similar Species. This species is so distinctive that it could only be confused with a few long-leaved species in subsect. *Stolonosae*. It differs from *V. lanceolata* in its rather commonly moderately to densely hirtellous foliage, summer stolons usually absent or nonreproductive with few leaves, proportionally longer and narrower linear to linear-lanceolate leaf blades with a narrowly attenuate base and denticulate margins; and from *V. primulifolia* in its proportionally very long and narrow leaf blades attenuate at base with denticulate margins. Preliminary examination of the few seeds available suggests that seeds in this species are smaller and darker than in *V. lanceolata*.

Ecology. Margins of steep-sided ponds in the north; depression ponds, Carolina bays, other wetlands lacking flowing water in the south (Ballard *et al*. 2020b).

FIG. 157. *Viola vittata*. (A) Chasmogamous flowering habit (photo: Janet Wright. (B) Chasmogamous flower front view (photo: Janet Wright). (C) Chasmogamous flower profile view (photo: Janet Wright). (D) Seeds from herbarium specimen: North Carolina, Scotland Co., 17 Frogs Pond, *H. Ballard et al. 15-011Y* (BHO).

Distribution. Atlantic and Gulf Coastal Plains, New Jersey south to Florida, west to southeastern Oklahoma and eastern Texas. Fig. 158.

Rarity. Listed in New Jersey (as *V. lanceolata* subsp. *vittata*).

Phenology. In our region, presumably similar to *V. lanceolata*; in the Southeast it blooms throughout the year and sets fruit shortly thereafter.

Affinities. This species belongs to the Acaulescent White Violet lineage, sect. *Plagiostigma* Godr., subsect. *Stolonosae* (Kupffer) Kupffer.

Hybrids. Hybridizes with *V. lanceolata* (Brainerd 1924; Russell 1955c; Harvey Ballard, pers. obs.) and *V. primulifolia* (Brainerd 1924; Russell 1955c).

Comments. Greene's protologue state "Florida, collected by Canby and by Curtis [sic!-Curtiss]; also in southeastern Texas, E. Hall." He makes vague reference to at least three different collections, gives no indication that these consisted of single sheets, designates no type, and mentions no particular herbarium. The JSTOR Global Plants database and the US specimen database have several duplicates of Curtiss 208.

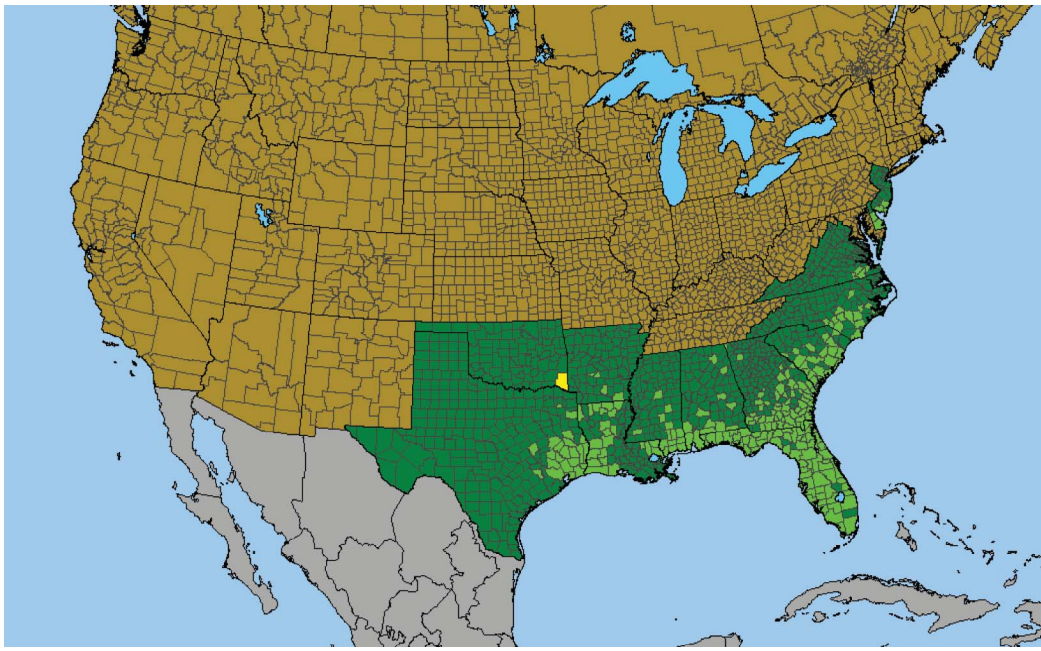

FIG. 158. United States county distribution of *Viola vittata* (map: Biota of North America Program).

McKinney erroneously annotated the NDG sheet in 1994 as holotype but his designation was not published. The NY sheet has an anonymous label stating "co-type," plus an annotation (possibly by Ezra Brainerd) confirming it as *V. vittata*. Norman Russell annotated the NY sheet and the US sheets as *V. lanceolata* subsp. *vittata*. None of the sheets bears an indication by Greene as to type status. Russell (1955c) cites the G, NY, and US sheets in his revision of the North American white-flowered *Stolonosae*. The NDG sheet is selected here as lectotype, making the other sheets isolectotypes.

Russell (1955c) cites specimens of this species (as *V. lanceolata* subsp. *vittata*) from Massachusetts but later doesn't include records from anywhere farther north than extreme southeastern Virginia. He also mentions examining "several" specimens from northwestern Indiana and cites one, and maps two, records from extreme northwestern Indiana and two from adjacent Illinois, as well as one record from southeastern Indiana. The few specimens examined by the first author from northern Indiana all appear to be depauperate *V. lanceolata*. Dave Snyder (personal communication) at the New Jersey Natural Heritage Program noted that the distinctive leaf morphology and atypical deep pond habitat of collections he made of this species struck him as quite different from the common *V. lanceolata* in the area. In North Carolina, where both species have been documented and often grow in the same general area, the two inhabit somewhat different ecological niches and do not generally co-occur at the same site. Given a number of unambiguous morphological differences, strong tendency to occupy divergent habitats, and rare putative hybrids that do not represent "intergrades," *V. lanceolata* and *V. vittata* are treated here as distinct evolutionary species. As with other members of the *Stolonosae* they are most distinct during summer fruit, when the leaf blades have attained their maximum size and shape, presence and morphology of summer stolons is apparent, and cleistogamous seeds are available.

66. ***Viola walteri*** House, Torreya 6: 172. 1906 [replacement name for *Viola canina* Walter]; *Viola canina* Walter non L. (1753), Fl. carol.: 219. 1788. Type: USA South Carolina. Berkeley Co., near Goose Creek, woods, 30 Mar 1933, *F. W. Hunnewell 12638* (neotype (designated by Daniel Ward, J. BRIT 2: 485. 2008): GH00277012 (*n.v.*), internet image). Fig. 159.

Viola muhlenbergii Torr. var. *multicaulis* Torr. & A.Gray, Fl. N. Amer. 1(1): 140. 1838; *Viola canina*

FIG. 159. *Viola walteri*. (A) Mat-forming prostrate stems (photo: J. K. Marlow). (B) Leaves during chasmogamous flower (leaf blades with red-purple veins) (photo: J. K. Marlow). (C) Chasmogamous flower front view (photo: Clayton Ziemke).

Walter var. *multicaulis* (Torr. & A.Gray) A.Gray, Bot. Gaz. 11(11): 292. 1886; *Viola multicaulis* (Torr. & A.Gray) Britton non Jord. (1851), Mem. Torrey Bot. Club 5: 227. 1894.

Common Names. Prostrate blue violet, Walter's violet.

Description. Caulescent mat-forming perennials from somewhat slender rhizome, flowering stems short and ascending, later prostrate, persistent and node-rooting, commonly ≥ 2, ≤ 7 cm tall; stems, foliage, and peduncles gray-green strongly tinged or finely spotted with red-purple, leaf blades with upper surface gray-green and veins dark green or red-purple, foliage and peduncles densely puberulent; leaves cauline and basal, cauline distributed along stem; stipules free, deeply laciniate with marginal processes $> 1/2$ as long as the stipule; leaves ascending to spreading, leaf blades undivided, largest $\leq 32 \times 29$ mm, broadly ovate to reniform (rarely ovate), base deeply cordate, margins crenulate to serrate, ciliolate, apex broadly rounded to obtuse; chasmogamous flower ≤ 16 mm; calyx glabrous, eciliate; lowest sepals lanceolate, acute; auricles short and entire, not elongating in fruit; corolla medium to dark blue, with white throat extending onto base of lateral and spurred petal; spur moderately elongate, slender, 3–5 mm, white to medium or dark blue; lateral petals densely bearded with filiform to narrowly linear hairs, spurred petal glabrous; cleistogamous flowers produced after chasmogamous; capsule 5.0–7.0 mm, green drying tan, unspotted or with fine red spots or faint blotches, glabrous; seeds

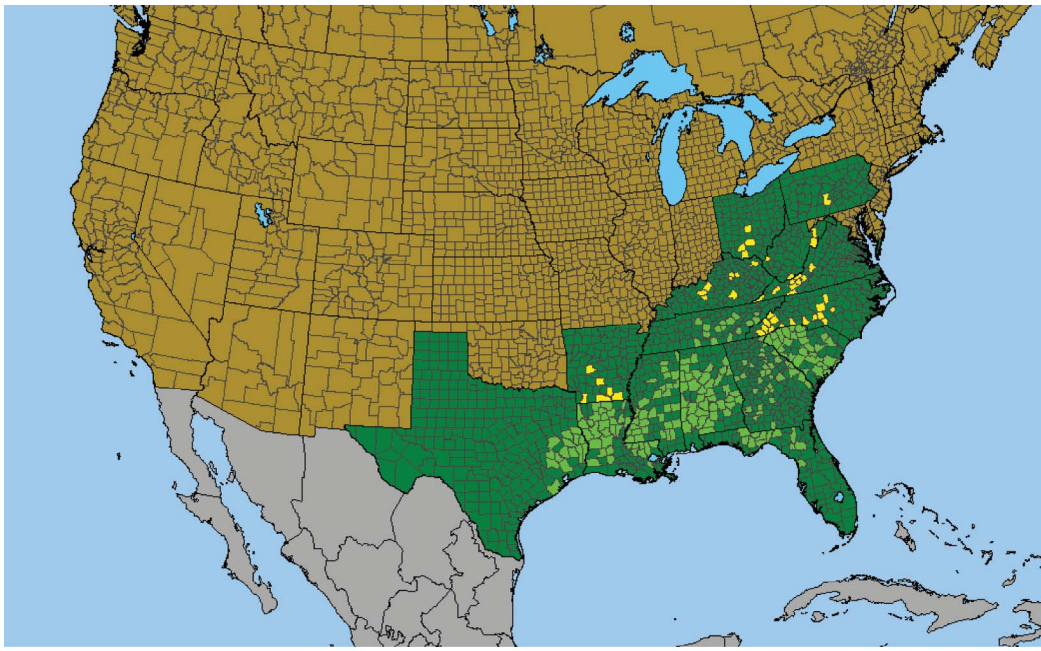

FIG. 160. United States county distribution of *Viola walteri* (map: Biota of North America Program).

1.7–2.4 × 1.0–1.4 mm, medium to dark brown, unspotted; 2n = 20.

Similar Species. This species and *V. appalachiensis* are our only mat-forming members of subsect. *Rostratae*. It is distinct from *V. appalachiensis* in its densely puberulent foliage and peduncle, typically "variegated" or bicolorous leaves with gray-green or silvery-green lamina and darker green veins, deeply lacerate to laciniate stipules, and other features as noted in the key. Its mat-forming nature and puberulent foliage resemble *V. odorata*, but the usually variegated upper surface of the leaf blades, longer spur, short bent style, and small brown seeds separate it. If the mat-forming stems and elongate spur went unnoticed or flowers were not present, this species could potentially be confused with *V. hirsutula* on the basis of the relatively short broad variegated leaves, but its densely puberulent foliage would distinguish it.

Ecology. Nutrient-rich woodlands and forests, dolomite bluffs and ledges, especially on mafic or calcareous rocks, growing beneath *Juniperus*, in the northern half of its range; in sandy or rocky and often somewhat acidic soils in dry or dry-mesic forests under *Pinus* and/or *Quercus* in the Southeast.

Distribution. Widely distributed in the southern Appalachian Mountains, southern Piedmont and southern Atlantic and Gulf Coastal Plains, sporadic and rare northward into the central Appalachians, Western Allegheny Plateau, and Interior Lowland Plateau, central Pennsylvania to central Ohio, south to Florida, southern Arkansas, and eastern Texas. Fig. 160.

Rarity. Listed in Kentucky, Ohio, and Virginia.

Phenology. Chasmogamous flower (late January–)March–May, chasmogamous fruit May–June, cleistogamous fruit July–August.

Affinities. This species belongs to the Rostrate Violet lineage, sect. *Viola*, subsect. *Rostratae* (Kupffer) W.Becker.

Hybrids. Hybridizes with *V. labradorica* (Ballard 1992, 1993) and *V. striata* (Ballard 1992, 1993). The first author has observed the hybrids and have found the features of chasmogamous flowers and foliage to be more or less precisely intermediate. Hybrids fail to reproduce by chasmogamous flowers, and cleistogamous capsules fail to produce viable seeds.

Comments. Walter misapplied the name *V. canina* L., belonging to a European violet, to a totally different North American species. Nearly

120 yr later, House provided a replacement name. Ward (2007) presented evidence that the collections in the Walter Herbarium are not necessarily those on which Walter's names were based. He subsequently neotypified Walter's basionym *V. canina* to fix the application of that name (as well as House's *V. walteri*).

Brainerd (1921b), Brainerd Baird (1942), Fernald (1950), and Alexander (1963) recognized *V. walteri* narrowly, although Brainerd Baird mentioned a Maryland locality that is undoubtedly a misidentification of *V. appalachiensis*, a species that had not yet been recognized. Davis and Davis (1949) and Platt (1950) drew attention to anomalous populations of a mat-forming node-rooting rostrate violet in West Virginia, Pennsylvania, and Maryland that differed in several macromorphological features from *V. walteri*, and Henry (1953a, b) promptly studied and named them *V. appalachiensis*. Russell (1965) later studied populations of *V. appalachiensis* and pronounced them either depauperate *V. conspersa* (= *V. labradorica* as treated here) or *V. walteri* bordering on the former. Ballard (1992) and Ballard and Wujek (1994) conducted a full-scale systematic study on the complex and related rostrate violets, and documented many consistent macromorphological differences and a different style micromorphology, as well as modally different habitat, to support recognition of both as distinct evolutionary species. Strausbaugh and Core (1978) and Ballard (2000) continued to recognize both as distinct species; Gleason and Cronquist (1991) merged the two without recognition of infraspecific taxa, while McKinney and Russell (2002), Grund and Isaac (2007), Weakley *et al*. (2012), and Little and McKinney (2015) demoted *V. appalachiensis* to a variety under *V. walteri*. Given the several consistent macromorphological and morphological distinctions and clearly different ecological niches as evidence, the two taxa are accepted as distinct species here. While the two share a mat-forming habit by persistent prostrate node-rooting stems, the present species is easily distinguished by its puberulent foliage and peduncles, conspicuously bicolorous upper leaf blades, and deeply laciniate stipules. It occupies consistently drier habitats than *V. appalachiensis* and other rostrate violets in its range.

Potential Taxa. Six taxa, briefly described with figures below, have been documented within three counties of our region. They may be found here in future searches.

Pombalia verticillata (Ortega) Paula-Souza (baby slippers, nodding green violet) (Fig. 161A) is a distinctive caulescent violet with long linear to lanceolate subentire leaves, and very small nodding yellowish flowers. It grows in grasslands and deserts of the Southwest and southern Great Plains, occurring within three counties of western Missouri.

Viola aduncoides A.Löve & D.Löve (Canada hooked violet) (Fig. 161B) is similar to *V. adunca* but is distinguished by foliage indument and style features noted in the keys. It was studied by McPherson (1972) and McPherson and Packer (1974), who documented it as a tetraploid cytotype of *V. adunca* showing some morphological differentiation, reproductive isolation in its sterile triploid hybrids with *V. adunca*, and partially allopatric northerly distribution; they withheld formal taxonomic decisions pending additional investigation. Löve & D.Löve (1976) later published the species name, referencing one of McPherson and Packer's specimens. Thus far its range is restricted to central and western Canada, nearing our region in the Thunder Bay District of Ontario; while McPherson and Packer's distribution map shows a northeastern Minnesota record, that remains unconfirmed (G. McPherson, personal communication).

Viola emarginata (Lower Midwest variant) (Fig. 161C) is similar to *V. emarginata* (Kentucky variant) in its narrowly winged petioles and broadly rounded petals, but it differs in leaf blades convexly tapering to the narrowly rounded apex, and its wet prairie habitat. It has been documented immediately south of the Missouri River in Missouri to southeastern Nebraska, south to southern Arkansas and northeastern Texas.

Viola "*impostor*" (Fig. 161D) is an undescribed species most similar to several other homophyllous undivided glabrous species with leaves longer than broad in chasmogamous flower but broadening significantly in fruit. It differs in chasmogamous flower from *V. affinis* and *V. retusa* in its glabrous spurred petal and prominent to elongate auricles; from *V. cucullata* by the often even more elongate auricles, longer lateral petal beards, and lack of dense strongly contrasting eyespot around the throat; and from *V. langloisii* (southeastern, just outside of our region), *V. missouriensis*, and *V. retusa* in the prominent to elongate slender or

FIG. 161. Potential taxa. (A) *Pombalia verticillata* (photo: Max Licher). (B) *Viola aduncoides* (photo: Bev Ramey). (C) *Viola emarginata* (Lower Midwest variant) from herbarium specimen: Oklahoma, Muskogee, *E. Brainerd 45* (NY). (D) *Viola* "*impostor*" (photo: Bina Sitepu). (E) *Viola langloisii* (photo: John Kees). (F) *Viola vallicola* (photo: Steven Van Kampen-Lewis).

obtrapezoidal dentate or lobate auricles. In cleistogamous fruit it differs from all the above species (except *V. langloisii* with spotted capsules) in the finely spotted cleistogamous capsule on short declined peduncle, conspicuously elongate auricles, and unspotted dark brown seeds with a white raphe. It is distributed on the Lower Atlantic Coastal Plain from northeastern North Carolina to Savanah area of Georgia. Specimens from southeasternmost Virginia may be this undescribed species but require further study to confirm their identity. This, *V. langloisii* below, and other members of the Affinis species group are currently under study by Remington Burwell at Ohio University.

Viola langloisii Greene (Langlois's violet) (Fig. 161E) is similar to *V. affinis*, *V. missouriensis*, and other uncut-leaved *Borealiamericanae* taxa (as noted in the keys and taxon accounts) but can be distinguished by flowers overtopping the spreading to horizontal leaves, slender narrowly acuminate sepals, prominent trapezoidal entire auricles elongating somewhat in fruit, and an unspotted or occasionally finely spotted cleistogamous capsule on a short declined peduncle. It grows in bottomlands of the Gulf Coast watersheds, confirmed thus far from western Florida to Texas, and sporadically northward along the west side of the Mississippi Embayment through eastern Arkansas and southeastern Missouri (the latter records recently confirmed). It has been misidentified most frequently as, and inaccurately synonymized with, *V. missouriensis*, and most geographic distributions are suspect; based on our preliminary studies, Russell's (1965) distribution map is generally representative for *V. langloisii*. Fernald's (1938) report of *V. langloisii* var. *pedatiloba* Brainerd from Southampton Co., VA, is excluded here as a misidentification. This member of the Affinis species group and others are under study by graduate student Remington Burwell at Ohio University.

Viola vallicola A.Nelson (Fig. 161F) is a distinctive member of the caulescent yellow-flowered Nuttallianae group, similar to *V. nuttallii* but differing in its short ovate-lanceolate to narrowly ovate leaf blades with broadly cuneate to cordate base. It is found in the Rocky Mountains and northern and central Great Plains, ranging eastward up against the western border of Minnesota.

EXCLUDED TAXA. Two species were reported previously from our region, but no confirmed records of them have been found despite intensive searches. They are excluded from our region.

Viola chalcosperma Brainerd was described from Jacksonville, FL. Fernald (1938) reported it (as *V. affinis* var. *chalcosperma* (Brainerd) Griscom) from Southampton and Nansemond counties in southeastern Virginia. Graduate student Remington Burwell and the first author have examined Fernald's specimens and concluded that they are misidentifications of other species; *Viola chalcosperma* has not been found outside of the Jacksonville area, and it is excluded from our region.

Viola villosa Walter was first reported by Brainerd in the early stages of his investigations, before he realized that all northeastern populations represented a new violet, which he named *V. hirsutula*. *Viola villosa* does not approach our region nearer than south-central North Carolina and the northwestern and north-central border of Arkansas.

UNCERTAIN NAMES. The following 26 names attributed to plants in our region have not been interpreted as to taxonomic identity or status.

1. *Viola caricetorum* Greene ex Farw., Pap. Michigan Acad. Sci. 2: 31. 1923 ['1922'].
2. *Viola cucullata* Aiton var. *alba* Torr. & A.Gray, Fl. N. Amer. 1(1): 137. 1838.
3. *Viola cucullata* Aiton var. *congener* (Leconte) Torr. & A.Gray, Fl. N. Amer. 1(1): 137. 1838 [Jul 1838].
4. *Viola cucullata* Aiton var. *cordiformis* Ging., in DC., Prodr. 1: 292. 1824.
5. *Viola cucullata* Aiton var. *hispidula* Ging., in DC., Prodr. 1: 292. 1824.
6. *Viola cucullata* Aiton var. *minor* Hook., Fl. bor.-amer. 1: 75. 1830.
7. *Viola cucullata* Aiton var. *obliqua* (Schwein.) Ging., in DC., Prodr. 1: 292. 1824.
8. *Viola cucullata* Aiton var. *reniformis* Torr. & A.Gray, Fl. N. Amer. 1(1): 137. 1838 [Jul 1838].
9. *Viola elegantula* Greene, Pittonia 4: 66. 1899.
10. *Viola emarginata* (Nutt.) Leconte var. *simulata* Greene, Leafl. Bot. Observ. 1(4): 217. 1903–1906.
11. *Viola filicetorum* Greene, Leafl. Bot. Observ. 1(4): 215. 1903–1906.
12. *Viola filicetorum* Greene var. *parthenica* Greene, Leafl. Bot. Observ. 1(4): 216. 1903–1906.

13. *Viola fontana* Greene, Leafl. Bot. Observ. 1(4): 218. 1903–1906.
14. *Viola laetecaerulea* Greene, in Steele, Proc. Biol. Soc. Washington 14: 70. 1901.
15. *Viola muhlenbergiana* Ging., in DC., Prodr. 1: 297. 1824.
16. *Viola obliqua* Pursh, Fl. Amer. sept. 1: 172. 1813.
17. *Viola palmata* L. f. *albiflora* E.L.Rand & Redfield, Fl. Mt. Desert Isl.: 80. 1894.
18. *Viola palmata* L. f. *variegata* E.L.Rand & Redfield, Fl. Mt. Desert Isl.: 81. 1894.
19. *Viola palmata* L. var. *cordata* Britton, Sterns & Poggenb., Prelim. Cat.: 6. 1888.
20. *Viola palmata* L. var. *obliqua* Hitchc., Trans. Acad. Sci. St. Louis 5: 487. 1891.
21. *Viola papilionacea* Pursh f. *albiflora* Grover, Ohio J. Sci. 39: 148. 1939.
22. *Viola papilionacea* Pursh f. *michaelii* Creutz, Wild Fl. 35: 9, fig. 3. 1959.
23. *Viola sagittata* Aiton f. *albescens* Farw., Amer. Midl. Naturalist 12: 127. 1930.
24. *Viola sandbergii* Greene, Pittonia 5: 119. 1903.
25. *Viola secedens* Greene, Pittonia 5: 121. 1903.
26. *Viola tricolor* L. f. *tenella* Farw., Pap. Michigan Acad. Sci. 2: 35. 1923 ["1922"].

Hybrids. Below is a list of 113 wild hybrids that are tentatively or confidently identified in our region, including a few cases (*e.g.*, *Viola palmata* species complex) where more than one infraspecific taxon has served as a parent. All hybrids are listed by formula, presented by the name of the alphabetically earlier parent taxon. Where binomials are published, these are also listed. Where both are known for a particular hybrid, the two representations are listed below. Synonyms of binomials are also listed, with the earliest valid name following.

Viola ×*aberrans* (Greene ex W.Stone) House–*Viola communis* × *Viola fimbriatula*; synonym: *Viola fimbriatula* Sm. var. *aberrans* Greene ex W.Stone

Viola ×*abundans* House–*Viola fimbriatula* × *Viola sagittata*

Viola adunca × *Viola labradorica*

Viola affinis × *Viola baxteri*

Viola affinis × *Viola brittoniana–Viola* ×*davisii* House

Viola affinis × *Viola communis–Viola* ×*columbiana* House

Viola affinis × *Viola cucullata–Viola* ×*consocia* House

Viola affinis × *Viola emarginata sensu stricto*

Viola affinis × *Viola fimbriatula–Viola* ×*hollickii* House

Viola affinis × *Viola hirsutula–Viola* ×*consobrina* House

Viola affinis × *Viola missouriensis*

Viola affinis × *Viola nephrophylla–Viola* ×*venustula* Greene; synonyms: *Viola* ×*crenulata* Greene, *Viola* ×*subaffinis* House, *Viola obliqua* Aiton var. *crenulata* Farw.

Viola affinis × *Viola palmata* (*pseudostoneana* variant)

Viola affinis × *Viola palmata* var. *triloba*

Viola affinis × *Viola sagittata–Viola* ×*dissena* House

Viola affinis × *Viola septentrionalis sensu stricto–Viola* ×*champlainensis* House

Viola affinis × *Viola sororia–Viola* ×*consona* House

Viola affinis × *Viola subsinuata–Viola* ×*discors* House

Viola ×*angellae* Pollard–*Viola palmata* var. *triloba* × *Viola subsinuata*

Viola appalachiensis × *Viola striata–Viola* ×*wujekii* H.E.Ballard

Viola baxteri × *Viola fimbriatula–Viola* ×*excerpta* House

Viola baxteri × *Viola sagittata*

Viola baxteri × *Viola sororia*

Viola ×*bernardii* (Greene) Greene–*Viola pedatifida* × *Viola sororia*; synonyms: *Viola pedatifida* G.Don var. *bernardi* Greene, *Viola* ×*fallacissima* Greene, *Viola* ×*perpensa* Greene

Viola ×*bissellii* House–*Viola communis* × *Viola cucullata*

Viola blanda × *Viola incognita*

Viola ×*brauniae* Grover ex T. S. Cooperr.–*Viola rostrata* × *Viola striata*

Viola brittoniana × *Viola communis–Viola* ×*insolita* House

Viola brittoniana × *Viola cucullata–Viola* ×*notabilis* E.P.Bicknell

Viola brittoniana × *Viola emarginata sensu stricto–Viola* ×*holmiana* House; synonym: *Viola emarginata* (Nutt.) Leconte var. *acutiloba* Brainerd

Viola brittoniana × *Viola fimbriatula–Viola* ×*mulfordiae* Pollard

Viola brittoniana × *Viola lanceolata*

Viola brittoniana × *Viola palmata* var. *triloba*

Viola brittoniana × *Viola pectinata*—*Viola* ×*lesmehrhoffii* A.Haines

Viola brittoniana × *Viola sagittata*–*Viola* ×*marylandica* House

Viola brittoniana × *Viola septemloba*

Viola brittoniana × *Viola sororia*–*Viola* ×*egregia* House

Viola brittoniana × *Viola subsinuata*–*Viola* ×*eamesii* House

Viola ×*caesariensis* House–*Viola palmata* var. *triloba* × *Viola sagittata*

Viola ×*cestrica* House–*Viola emarginata sensu stricto* × *Viola sagittata*

Viola ×*champlainensis* House–*Viola affinis* × *Viola septentrionalis sensu stricto*

Viola ×*columbiana* House–*Viola affinis* × *Viola communis*

Viola communis × *Viola cucullata*–*Viola* ×*bissellii* House

Viola communis × *Viola emarginata sensu stricto*–*Viola* ×*greenei* House

Viola communis × *Viola fimbriatula*–*Viola* ×*aberrans* (Greene ex W.Stone) House; synonym: *Viola fimbriatula* Sm. var. *aberrans* Greene ex W.Stone

Viola communis × *Viola hirsutula*

Viola communis × *Viola nephrophylla*

Viola communis × *Viola palmata* var. *triloba*

Viola communis × *Viola sagittata*–*Viola* ×*conjugens* Greene

Viola communis × *Viola sororia*–*Viola* ×*grandis* Greene; synonym: *Viola* ×*napae* House

Viola communis × *Viola stoneana*

Viola communis × *Viola subsinuata*–*Viola* ×*modica* House

Viola ×*conjugens* Greene–*Viola communis* × *Viola sagittata*

Viola ×*consobrina* House–*Viola affinis* × *Viola hirsutula*

Viola ×*consocia* House–*Viola affinis* × *Viola cucullata*

Viola ×*consona* House–*Viola affinis* × *Viola sororia*

Viola ×*conturbata* House–*Viola cucullata* × *Viola sororia*

Viola ×*convicta* House–*Viola fimbriatula* × *Viola subsinuata*

Viola ×*cooperrideri* H.E.Ballard–*Viola striata* × *Viola walteri*

Viola ×*cordifolia* (Nutt.) Schwein.–*Viola hirsutula* × *Viola sororia*; synonyms: *Viola villosa* Walter var. *cordifolia* Nutt., *Viola* ×*perpera* House

Viola ×*crassula* Greene–*Viola nephrophylla* × *Viola sororia*

Viola ×*crenulata* Greene–*Viola* ×*venustula* (*Viola affinis* × *Viola nephrophylla*); synonym: *Viola obliqua* Aiton var. *crenulata* (Greene) Farw.

Viola cucullata × *Viola fimbriatula*–*Viola* ×*porteriana* Pollard

Viola cucullata × *Viola nephrophylla*–*Viola* ×*insessa* House

Viola cucullata × *Viola palmata* var. *triloba*–*Viola* ×*greenmanii* House

Viola cucullata × *Viola pectinata*

Viola cucullata × *Viola primulifolia*–*Viola* ×*lavandulacea* E.P.Bicknell

Viola cucullata × *Viola sagittata*–*Viola* ×*festata* House

Viola cucullata × *Viola septentrionalis sensu stricto*–*Viola* ×*melissifolia* Greene

Viola cucullata × *Viola sororia*–*Viola* ×*conturbata* House

Viola cucullata × *Viola subsinuata*–*Viola* ×*ryoniae* House

Viola cucullata × *Viola viarum*

Viola ×*davisii* House–*Viola affinis* × *Viola brittoniana*

Viola ×*dimissa* House–*Viola emarginata sensu stricto* × *Viola hirsutula*

Viola ×*discors* House–*Viola affinis* × *Viola subsinuata*

Viola ×*dissena* House–*Viola affinis* × *Viola sagittata*

Viola ×*dissita* House–*Viola hirsutula* × *Viola palmata* var. *triloba*

Viola ×*dowelliana* House–*Viola* ×*consobrina* (*Viola affinis* × *Viola hirsutula*)

Viola ×*eamesii* House–*Viola brittoniana* × *Viola subsinuata*

Viola ×*eclipes* H.E.Ballard–*Viola labradorica* × *Viola striata*

Viola ×*egglestoniana* House–*Viola fimbriatula* × *Viola latiuscula*

Viola egglestonii × *Viola sororia*

Viola ×*egregia* House–*Viola brittoniana* × *Viola sororia*

Viola emarginata sensu stricto × *Viola fimbriatula*–*Viola* ×*erratica* House

Viola emarginata sensu stricto × *Viola hirsutula*–*Viola* ×*dimissa* House

Viola emarginata sensu stricto × *Viola sagittata*–*Viola* ×*cestrica* House

Viola emarginata sensu stricto × *Viola sororia*

Viola emarginata sensu stricto × *Viola stoneana*

Viola ×*erratica* House–*Viola emarginata sensu stricto* × *Viola fimbriatula*

Viola ×*excerpta* House–*Viola baxteri* × *Viola fimbriatula*

Viola ×*fallacissima* Greene–*Viola* ×*bernardii* (*Viola pedatifida* × *Viola sororia*)

Viola ×*fernaldii* House–*Viola fimbriatula* × *Viola sororia*

Viola ×*festata* House–*Viola cucullata* × *Viola sagittata*

Viola fimbriatula × *Viola hirsutula*–*Viola* ×*redacta* House

Viola fimbriatula × *Viola latiuscula*–*Viola* ×*egglestoniana* House

Viola fimbriatula × *Viola nephrophylla*–*Viola* ×*nephrophylloides* Farw.

Viola fimbriatula × *Viola palmata* var. *triloba*–*Viola* ×*robinsoniana* House

Viola fimbriatula × *Viola sagittata*–*Viola* ×*abundans* House

Viola fimbriatula × *Viola septentrionalis sensu stricto*–*Viola* ×*parca* House

Viola fimbriatula × *Viola sororia*–*Viola* ×*fernaldii* House

Viola fimbriatula × *Viola subsinuata*–*Viola* ×*convicta* House

Viola ×*grandis* Greene–*Viola communis* × *Viola sororia*; synonym: *Viola* ×*napae* House

Viola ×*greenei* House–*Viola communis* × *Viola emarginata sensu stricto*

Viola ×*greenmanii* House–*Viola cucullata* × *Viola palmata* var. *triloba*

Viola hirsutula × *Viola palmata* var. *triloba*–*Viola* ×*dissita* House

Viola hirsutula × *Viola sagittata*

Viola hirsutula × *Viola sororia*–*Viola* ×*cordifolia* (Nutt.) Schwein.; synonyms: *Viola villosa* Walter var. *cordifolia* Nutt., *Viola* ×*perpera* House

Viola hirsutula × *Viola stoneana*

Viola hirsutula × *Viola subsinuata*–*Viola* ×*ravida* House

Viola ×*hollickii* House–*Viola affinis* × *Viola fimbriatula*

Viola ×*holmiana* House–*Viola brittoniana* × *Viola emarginata sensu stricto*; synonym: *Viola emarginata* (Nutt.) Leconte var. *acutiloba* Brainerd

Viola incognita × *Viola lanceolata*

Viola incognita × *Viola minuscula*

Viola incognita × *Viola renifolia*

Viola ×*indivisa* Greene–*Viola pedatifida* × *Viola pratincola*

Viola ×*insessa* House–*Viola cucullata* × *Viola nephrophylla*

Viola ×*insolita* House–*Viola brittoniana* × *Viola communis*

Viola labradorica × *Viola rostrata*–*Viola* ×*malteana* House

Viola labradorica × *Viola striata*–*Viola* ×*eclipes* H.E.Ballard

Viola labradorica × *Viola walteri*

Viola lanceolata × *Viola minuscula*–*Viola* ×*sublanceolata* House

Viola latiuscula × *Viola palmata triloba*–*Viola* ×*slavinii* House

Viola latiuscula × *Viola palmata* var. *triloba*

Viola latiuscula × *Viola sororia*–*Viola* ×*vermontana* House

Viola ×*lavandulacea* E.P.Bicknell–*Viola cucullata* × *Viola primulifolia*

Viola ×*lesmehrhoffii* A.Haines—*Viola brittoniana* × *Viola pectinatea*

Viola ×*malteana* House–*Viola labradorica* × *Viola rostrata*

Viola ×*marylandica* House–*Viola brittoniana* × *Viola sagittata*

Viola ×*melissifolia* Greene–*Viola cucullata* × *Viola septentrionalis sensu stricto*

Viola minuscula × *Viola primulifolia*–*Viola* ×*mollicula* House

Viola missouriensis × *Viola pedatifida*

Viola missouriensis × *Viola sororia*

Viola missouriensis × *Viola viarum*

Viola ×*mistura* House–*Viola sagittata* × *Viola subsinuata*

Viola ×*modesta* House–illegitimate homonym of *Viola modesta* Fenzl, 1842 (*Viola lanceolata* × *Viola primulifolia* Dowell)

Viola ×*modica* House–*Viola communis* × *Viola subsinuata*

Viola ×*mollicula* House–*Viola minuscula* × *Viola primulifolia*

Viola monacanora × *Viola sororia*

Viola ×*montivaga* House–*Viola septentrionalis sensu stricto* × *Viola sororia*

Viola ×*mulfordiae* Pollard–*Viola brittoniana* × *Viola fimbriatula*

Viola ×*napae* House–*Viola communis* × *Viola sororia*

Viola nephrophylla × *Viola pedatifida*

Viola nephrophylla × *Viola pratincola*

Viola nephrophylla × *Viola sagittata*

Viola nephrophylla × *Viola sororia*–*Viola* ×*crassula* Greene

Viola ×*nephrophylloides* Farw.–*Viola fimbriatula* × *Viola nephrophylla*

Viola ×*notabilis* E.P.Bicknell–*Viola brittoniana* × *Viola cucullata*

Viola palmata (*pseudostoneana* variant) × *Viola sororia*

Viola palmata var. *triloba* × *Viola sagittata*–*Viola* ×*caesariensis* House

Viola palmata var. *triloba* × *Viola sororia*–*Viola* ×*populifolia* Greene

Viola palmata var. *triloba* × *Viola stoneana*

Viola palmata var. *triloba* × *Viola subsinuata*–*Viola* ×*angellae* Pollard

Viola ×*parca* House–*Viola fimbriatula* × *Viola septentrionalis sensu stricto*

Viola ×*peckiana* House–*Viola sororia* × *Viola subsinuata*

Viola pedatifida × *Viola pratincola*–*Viola* ×*indivisa* Greene

Viola pedatifida × *Viola sagittata*

Viola pedatifida × *Viola sororia*–*Viola* ×*bernardii* (Greene) Greene; synonyms: *Viola pedatifida* G.Don var. *bernardii* Greene, *Viola* ×*fallacissima* Greene, *Viola* ×*perpensa* Greene

Viola ×*perpensa* Greene–*Viola* ×*bernardii* (*Viola pedatifida* × *Viola sororia*)

Viola ×*perpera* House–*Viola* ×*cordifolia* (Nutt.) Schwein. (*Viola hirsutula* × *Viola sororia*)

Viola ×*populifolia* Greene–*Viola palmata* var. *triloba* × *Viola sororia*

Viola ×*porteriana* Pollard–*Viola cucullata* × *Viola fimbriatula*

Viola pratincola × *Viola sororia*

Viola primulifolia × *Viola vittata*

Viola ×*ravida* House–*Viola hirsutula* × *Viola subsinuata*

Viola ×*redacta* House–*Viola fimbriatula* × *Viola hirsutula*

Viola ×*robinsoniana* House–*Viola fimbriatula* × *Viola palmata* var. *triloba*

Viola rostrata × *Viola striata*–*Viola* ×*brauniae* Grover ex T. S. Cooperr.; synonym: *Viola* ×*braunii* Grover

Viola ×*ryoniae* House–*Viola cucullata* × *Viola subsinuata*

Viola sagittata × *Viola sororia*

Viola sagittata × *Viola subsinuata*–*Viola* ×*mistura* House

Viola septentrionalis sensu stricto × *Viola sororia*–*Viola* ×*montivaga* House

Viola ×*slavinii* House–*Viola latiuscula* × *Viola palmata* var. *triloba*

Viola sororia × *Viola stoneana*

Viola sororia × *Viola subsinuata*–*Viola* ×*peckiana* House

Viola sororia × *Viola viarum*

Viola striata × *Viola walteri*–*Viola* ×*cooperrideri* H.E.Ballard

Viola ×*subaffinis* House—*Viola* ×*venustula* Greene, (*Viola affinis* × *Viola nephrophylla*)

Viola ×*sublanceolata* House–*Viola lanceolata* × *Viola minuscula*

Viola ×*venustula* Greene–*Viola affinis* × *Viola nephrophylla*; synonyms: *Viola* ×*crenulata* Greene, *Viola obliqua* Aiton var. *crenulata* Farw., *Viola* ×*subaffinis* House

Viola ×*vermontana* House–*Viola latiuscula* × *Viola sororia*

Viola ×*wujekii* H.E.Ballard–*Viola appalachiensis* × *Viola striata*

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