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CHAPTER 6

TAXONOMIC HISTORY AND TAXONOMY

6.1. Supraspecific Ranks

6.1.1. The Circumscription of *Viola* Section *Plagiostigma*

Viola L. section *Plagiostigma* Godr., Fl. Lorraine ed. 2, 1: 90. 1857. – **Type:** *Viola palustris* L.

De GINGINS (1823) provided the first intrageneric classification of *Viola*. He delimited five sections: *Nomimum*, *Dischidium*, *Chamaemelianum*, *Melanium* and *Leptidium*, primarily on the basis of the morphology of the stigma. Section *Nomimum* (which included in later treatments the taxa of *Viola* subsection *Boreali-Americanae*) was characterized by having a rostrate stigma, with the stigmatic opening at the end of the rostellum. De Gingins typified this section by *Viola odorata*, the type of the genus, and thus it should be called section *Viola*.

GODRON (1857) delimited section *Plagiostigma* by the shape of the capsule (ovoid-triangular), the thickness of the style, and the shape of the style apex (an oblique disk). He listed in it only the circumpolar *Viola palustris*.

REICHE & TAUBERT (1895) modified the original subdivisions of the genus following the addition of a number of South American species. The rank of *Nomimum* Ging. was reduced to a group within series *Herbaceae* in section *Sparsifoliae* Reiche.

KUPFFER (1903) reduced the rank of *Plagiostigma* to a group under section *Nomimum* and delimited *Plagiostigma* by the shape of the style apex. This treatment was followed by BECKER (1910). Becker delimited *Plagiostigma* by the shape of the style apex and the size of the rostellum, which he contrasted with the rostrate apex of the style of members of the other group he recognized in section *Nomimum*, *Rostellatae* Boiss. Becker described a large number of new species and erected new taxonomic groups in a series of worldwide regional treatments published between 1902-1928. In his comprehensive treatment of the genus, BECKER (1925) divided *Viola* into 14 sections, some of which were further divided into groups and subgroups. He characterized section *Nomimum* as comprising mostly perennial herbs bearing blue, white, or rarely yellow flowers and having a style with a curved base and a stigma bearing a rostellum. Furthermore, he abandoned the name *Plagiostigma* (without providing rationale for this decision) and divided section *Nomimum* (ca. 230 species) into 17 groups on the basis of macromorphology and data on geographic distribution.

CLAUSEN (1927) followed de Gingins and Becker in recognizing section *Nomimum*, and listed in it seven groups comprised of taxa with known chromosome numbers. CLAUSEN (1929) employing mainly floral characters (especially the type of the stylar head), chromosome numbers, and to a lesser degree crossing relationships, recognized and divided the species of section *Nomimum* that had purplish blue or bluish white petals into two groups and referred to them as subsections: **a.** *Rostellatae* Boiss. comprising species possessing 10 or 20 chromosome series and styles ending in a more or less curved rostellum, at the end of which the stigma is placed; and **b.** *Plagiostigma* Godr. comprising species possessing 12 chromosome series, having as aberrations 13 and 26 chromosome groups, and clavate styles bearing at the front a small rostellum, at the end of which the stigma is placed. In 1951 he dissolved section *Nomimum* on the basis of additional chromosome counts, and recognized the two subsections at the sectional rank: *Rostellatae* – the caulescent “blue” North American and Eurasian species forming a polyploid series in mul-

tiples of ten, and *Plagiostigma* – the acaulescent white to violet circumboreal species. The species of section *Plagiostigma* belonging to subsections *Adnatae*, *Langsdorffianae*, and *Stolonosae* form polyploid series in multiples of 12, but the species belonging to subsections *Blandae*, *Boreali-Americanae*, and *Pedatae* deviate from the twelve series by having aneuploid numbers (CLAUSEN, 1951, 1964).

BRIZICKY (1961) maintained section *Plagiostigma*. However, he noted that section *Rostelatae* must be called section *Viola*. He listed under section *Viola* subsection *Uncinatae* (which should be called subsection *Viola*) comprising *Viola odorata* and subsection *Rosulantes* comprising North-American and Eurasian caulescent blue species with tufted stems and rosulate basal leaves.

6.1.2. The Circumscription of *Viola* Subsection *Boreali-Americanae*

Viola subsection *Boreali-Americanae* (W. Becker) Gil-ad, **stat. nov.**

BASIONYM: *Viola* section *Nomimium* Ging. “N.” *Boreali-Americanae* W. Becker in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 21: 369. 1925. – **Lectotype**, here designated: *Viola cucullata* Aiton.

Acaulescent perennial herbs lacking stolons; *rhizomes* succulent, thickened, scaly; *stipules* free; *blades* entire or divided, homophyllous or heterophyllous; *bractlets* simple, borne at the same level or staggered; *petals* violet or violet-blue (white in albinic forms) with a white center, and dark violet lines extending from the center to the colored portion of the lower petals; *petal trichomes* borne on the lower lateral petals only, or on the lower lateral petals and the spurred petal; *style* curved at base, clavate, summit flattened, margined, glabrous bearing a flat and short frontal rostellum; *cleistogamous flowers* present in all species; *cleistogamous flower peduncle habit*: prostrate, ascending, or erect; *seeds* ovoid to ellipsoid; dispersed by explosive ejection from the capsule followed by transport and dispersal by ants; *ploidy*: hypertetraploids with an aneuploid chromosome number $n = 27$; *crossability*: the taxa in the subsection interbreed freely; *general distribution*: North America, including northern México.

Subsection *Boreali-Americanae* is monophyletic on the basis of the following synapomorphies: **a.** the common chromosome number: $n = 27$; and **b.** the white corolla center (GIL-AD, 1995).

Discussion. – BECKER (1925) designated the hyphenated epithet *Boreali-Americanae* for an unranked taxon (listed with the letter “N.”) under section *Nomimium*. The name *Boreali-Americanae* is published validly since Becker provided a detailed description referring to the taxon and since the epithet was intended as a name. The criteria for determining that *Viola* “N.” *Boreali-Americanae* was intended as a name (GREUTER pers. comm., 1995) are: **a.** similar groups of North American species in section *Nomimium* and in other sections are designated as unranked groups as *Boreali-Americanae*; **b.** similarly treated groups (of the same, unstated rank) are always designated by epithets. Becker listed in *Boreali-Americanae* twelve North American acaulescent species (see Appendix A) possessing short, horizontal and thickened rhizomes without stolons, free stipules, violet petals, styles curved at the base, having a flattened and margined summit and a short rostellum.

Taxonomic treatments since Becker have dealt primarily with modifications of the ranking of *Boreali-Americanae* as a whole and with its placement among other taxa, but concurrently retained its entity as a distinctive taxon. CLAUSEN (1929) recognized it as an unranked group (numbered “VII.”) under subsection *Plagiostigma*, and listed 20 species for which chromosome counts have been determined. CLAUSEN (1951) cited *Boreali-Americanae* at the rank of subsection (“Subsection *Boreali-Americanae*”), but neither provided a description in Latin nor referred to Becker in the text or among the literature cited. He delimited this taxon by the haploid chromosome number $n = 27$. BRIZICKY (1961) listed this taxon as “Subsection *Boreali-Americanae*

W. Becker,” provided a short list of the main characters of the taxon, and listed BECKER (1925) in the literature cited. However, this combination is not validly published since Brizicky did not provide a complete valid transfer to a subsectional rank including “full and direct reference...with page or plate reference and date” as required by Art. 33.2 of the Tokyo Code (GREUTER & *al.*, 1994) for new combinations published on or after 1 January 1953. Art. 33.2 Note 1 clearly defines “page reference” as “reference to the page or pages on which the basionym was validly published...but not to the pagination of the whole publication...” The transfer of *Boreali-Americanae* to subsectional rank is therefore validated here.

The exclusion or inclusion of *Viola pedata* in subsection *Boreali-Americanae* has been in flux, and varied among authors (cf. Appendix A). BECKER (1925), following POLLARD (1898), placed it in a monotypic group, *Pedatae* in section *Nomimium*. *Viola pedata* is acaulescent, lacks stolons, possesses a thick, succulent, vertical and cylindrical rhizome, stipules adnate to the petiole, deeply divided leaves (as do some of the species of subsection *Boreali-Americanae* with which it might be confused), and chromosome number $n = 27$ (CANNE, 1987). Its adnate stipules, the alignment of its petals in one plane, its protruding stamens, lack of trichomes on the lateral petals, its obliquely concave style apex, lack of a rostellum, and lack of cleistogamous flowers provide ample characters for separating it from subsection *Boreali-Americana*. Additional support for the recognition of *V. pedata* in a separate subsection and its alliance with members of subsection *Adnatae* is provided in a phylogenetic reconstruction of subsection *Boreali-Americanae* in GIL-AD (1995) and GIL-AD (in press). Appendix A provides a comparison of the taxa recognized in treatments of subsection *Boreali-Americanae* since de Gingins.

6.2. An Introduction to the Descriptions of the Taxa of Subsection *Boreali-Americanae*

The descriptions of the species cover the most important taxonomic characters that characterize the plants at the chasmogamous and the cleistogamous phases. Chapter 3 discusses in detail the macromorphological characters and their taxonomic significance. A brief description of the micromorphological characters of the petal trichomes and the seed coat (extracted from GIL-AD, 1995 and GIL-AD, in press) is given for each of the taxa described. Representative specimens are listed in Appendix C.

6.2.1. Types and Typification

The type specimens of 15 of the 18 taxa recognized in this study have been located, and two species, *Viola affinis* LeConte and *V. septemloba* LeConte, are lectotypified here with illustrations. No specimen or other material that could serve as a nomenclatural type could be located for *Viola pedatifida* G. Don.

Some of the plants that were designated as types by their authors might have actually been hybrids or introgressants. For most taxa, seeds that would make it possible to verify the identity of the specimen by SEM are not available. Seeds from the types of two taxa – *Viola nephrophylla* Greene and *V. novae-angliae* subsp. *grisea* (Fernald) Gil-ad (*V. septentrionalis* var. *grisea* Fernald) – were available. They were examined with SEM, and their identity was revealed (see the descriptions and discussions for these taxa below).

6.2.2. Illustrations

For most of the taxa of subsection *Boreali-Americanae*, line drawings (*in* BRAINERD, 1921; ALEXANDER, 1952; RUSSELL, 1965; KLABER, 1976; of *Viola cucullata* *in* CRONQUIST, 1981; and in various regional and local manuals), and color illustrations (*in* BRAINERD, 1921; HOUSE, 1935; BAIRD-BRAINERD, 1942; KLABER, 1976) were published. Most of those illustrations portray the shape of the blades quite well, and vary in their coverage of other characters. The only species for which no illustration has been published is *Viola nuevo-leonensis*. Furthermore, the original description of this species (BECKER, 1922) was rather vague. Therefore, a more detailed description (including descriptions of the style and the stamens that are similar among all taxa of the subsection), and an illustration (Fig. 3) are provided here for this species.

6.2.3. Chromosome Number Counts

The chromosome numbers listed in the descriptions are based on counts made by MIYAJI (1929), CLAUSEN (1929, 1964), GERSHOY (1934), LÖVE & LÖVE (1966, 1982), TAYLOR & BROCKMAN (1966), and CANNE (1987).

6.2.4. Substrate

A number of taxa exhibit specificity to a particular substrate (see the species descriptions for details). It is likely that edaphic specialization has occurred during speciation of a number of taxa of the subsection. The substrate specificity becomes important in corroborating determinations of plants on the basis of suites of morphological characters, especially at chasmogamous anthesis, when a limited number of characters is available. However, a taxon that has been introgressed by another taxon may grow on the same substrate as the orthospecies. Therefore, information about substrate should be used only with a suite of distinct micromorphological and macromorphological characters to identify taxa.

6.2.5. Habitat

A number of taxa in the subsection are adapted to specific habitats. Genetic diversification through habitat adaptation has most likely been one of the major factors in the speciation of these taxa. Yet, hybridization among the taxa counteracts and obliterates the influence of the specific habitats. Most hybrids of the taxa are capable of occupying the habitats of the orthospecies. For example, *Gil-ad* 282 (MICH), a putative introgressant of *V. sororia* and *V. cucullata* (GIL-AD 1995 and GIL-AD, *in press*), grew on *Sphagnum* mats on a slow stream – a typical habitat of *Viola cucullata*. Yet, in many cases they thrive and perpetuate on the margins of those habitats, and gradually move into less specific habitats. This often occurs, for example, among hybrids of *V. cucullata* and *V. sororia* or *V. affinis*. For example, *Gil-ad* 307 (MICH), which displays similarity to *V. cucullata* in its macromorphology, grew in the margins of a swampy area adjacent to a woods in which putative introgressants of *V. sororia* into *V. affinis* (*Gil-ad* 306, MICH) were abundant.

The data on habitat specificity in previous treatments of the taxa often included a wide range of habitats that rendered the information useless. The wide range of listed habitats may reflect

information on the habitats of hybrids, as well as confusion between the taxa and misidentifications. The habitats listed in the descriptions that follow are the habitats of the orthospecies.

Most of the taxa are most likely poor competitors. They grow in openings, or in margins of forests or thickets where they can display their chasmogamous flowers during a brief period in early spring, and sometimes in early autumn, and attract pollinators. Once the chasmogamous phase has ended, most of the taxa become overtopped by the surrounding vegetation.

6.2.6. Phytogeography

Subsection *Boreali-Americanae* is confined to North America, including northern México.

RUSSELL (1959) and RUSSELL & CROSSWHITE (1963) noted that distributions outlined in the literature, as well as ranges extracted from herbarium specimens, are most likely inaccurate due to high frequency of misidentification. Furthermore, the ranges may be skewed as most likely they have been inflated by inclusion of hybrids and hybrid derivatives as orthospecies. This may apply also to Russell's own distribution maps (RUSSELL, 1965), and to MCKINNEY's (1992) distribution maps.

The information on the distribution of the taxa described in this work is provided in order to help the reader predict where the taxa can be expected to be found. For most taxa the information is general, and is not based on extensive mapping of label data from herbarium specimens. Such mapping would not be informative at this time, since many of the specimens available in herbaria cannot be positively identified as most lack mature seeds. Three exceptions are *Viola egglestonii*, *V. nuevo-leonensis*, and *V. novae-angliae* subsp. *grisea*. Distribution data for *V. egglestonii* are available in the references listed under the discussion of this species, and in the citations of the representative specimens. Distribution data for the highly restricted *V. novae-angliae* subsp. *grisea* and for *V. nuevo-leonensis* are available in the citations of representative specimens (Appendix C).

Most of the taxa in subsection *Boreali-Americanae* are distributed in Eastern North America east of the Rocky Mountains. Extensive collecting, followed by positive identifications and mapping, would be required in order to assess the existence of centers of diversity in Eastern North America. Although there is a considerable overlap in ranges for most of the taxa in the subsection, a number of species are geographically isolated from each other, and their distributions can be correlated with the events that have shaped North American floristic regions and vegetation.

The unique characters of *Viola egglestonii* and its distribution can be correlated with its endemism. THORNE (1993) pointed out that the cedar glade habitat of central Tennessee, Kentucky, and Alabama is among the special areas of considerable specific and subspecific endemism in the Appalachian Province of the North American Atlantic Floristic Region. *Viola brittoniana* is confined to the central section of the Atlantic and Gulf Coastal Plain Province, and *V. villosa* and *V. septemloba* occupy the southern section of that province. *Viola pedatifida* is confined to the North American Prairies Province and its extension eastward (the "prairie peninsula"). *Viola novae-angliae* subsp. *grisea* occupies open *Pinus banksiana* stands in northern Michigan. The pines of the Great Lakes Region are believed to have immigrated into the region in the past 10,000 or 11,000 years from refugia to the east (CRITCHFIELD, 1980; WRIGHT, 1968). *Viola nuevo-leonensis* is confined to relatively high elevations of the Madrean Floristic Region in northern México.

General accounts have attributed distribution patterns to the Pleistocene glaciation (BRAUN, 1950, 1955; CRITCHFIELD, 1980; DELCOURT & DELCOURT, 1993). Four discussions correlating the

distribution of North American *Viola* to Pleistocene events have been published so far. RUSSELL (1954) suggested that the results of previous studies on the effect of the Pleistocene could be applied to *Viola*. Those studies have shown that in other plant groups hybridization and introgression have occurred in habitats that were undoubtedly disturbed during the oscillating climates of the Pleistocene. VALENTINE (1962) applied CAMP's (1961) explanation of the distribution and breakdown of isolation between species of *Vaccinium* to the taxa of subsection *Boreali-Americanae*. During the Pleistocene glaciation those species were repeatedly driven southward down the eastern regions of the United States, and repeatedly migrated northward again during interglacial periods. This provided opportunities for the species to become sympatric in their constricted southern area during glaciation, and later the species, modified by hybridization and introgression, spread northward again to occupy new habitats. HARMS & al. (1985) suggested that the occurrence of two species of subsection *Boreali-Americanae*, *Viola sororia* and *V. septentrionalis*, in east central Saskatchewan appears to present an example of relicts from a former post-glacial extension of an eastern deciduous and lake-mixed forest into Saskatchewan. FABIAN & al. (1987) hypothesized that glaciation events during the Pleistocene likely had an effect on speciation in section *Chamaemelum* subsection *Nuttallianae*. Those events drastically affected the climatic conditions on the west coast, and generated two major lineages of species, one adapted to more xeric habitats of the valley bottoms in the rain shadow of the Cascade and Rocky Mountains, and the other adapted to the more mesic forest habitats of coastal and montane forests.

6.2.7. Conservation

Most of the taxa of subsection *Boreali-Americanae* are widespread and common. Yet, three species are relatively uncommon: *Viola brittoniana*, *V. novae-angliae*, and *V. nuevo-leonensis*. Among these species, *V. brittoniana* is suffering the most from human activities along the Atlantic seaboard, and may become rare if measures to protect its known populations are not undertaken. The known populations of *V. novae-angliae* subsp. *grisea* are located in protected areas, and thus are under less threat. Most of the states and Canadian provinces in which *V. novae-angliae* (subsp. *novae-angliae*) occurs list it as endangered, threatened, or of special concern. BALLARD & GAWLER (1994) conducted surveys in New England and the Great Lakes Region, and recommended dropping it from the list of candidates for federal listing in the United States and Canada, but to continue listing it as threatened or endangered for Manitoba and Michigan until additional surveys are conducted. Additional collecting and surveys are needed in order to evaluate and assess the status of *V. nuevo-leonensis* in northern México.

6.2.8. The Names of Hybrids

The names of natural fertile hybrids that have been reported in the literature are listed in the discussion of each species. The purpose of listing the names is to bring to the attention of the interested reader the attempts that have been made to characterize and subsequently to name hybrids, and to recommend that the published names should be considered for naming newly collected hybrids whose identity has been established using modern methods. These listings do not imply that specimens to which the published names were affixed were examined in this work, and that each was proven to represent a genuine intermediate between the two parent orthospecies. Some of the hybrids listed by Brainerd, Dowell, House, and Russell (see references in Chapter 4, Section 4.1 and in the species discussions below) were most likely introgressants, rather than intermediates between orthospecies. Additional names of hybrids of orthospecies with taxa that were recognized by previous authors as orthospecies but determined as putative hybrids in this work are not listed.

6.3. Keys to the Species of *Viola* Subsection *Boreali-Americanae*

6.3.1. Introduction

Two types of keys are provided: a key to plants at the chasmogamous phase, and a key to plants at the cleistogamous phase. These keys employ reproductive characters extensively.

A major difficulty in constructing these keys was the relative scarcity of distinct macro-morphological (especially floral) characters for some species at the chasmogamous phase. Consequently, the couplets of some of the species are shorter compared to the couplets of other species. Habitat specificity and general distribution data were incorporated, and in some cases they compensate for the scarcity of macromorphological characters. Previous keys to North American *Viola*, and to subsection *Boreali-Americanae* in particular, used extensively pubescence patterns on the leaves. These patterns are avoided in the new keys since they are unreliable, and may lead to identification of hybrids and introgressants as orthospecies.

The keys will assist in identifying orthospecies, but the user should be aware that some introgressants will key readily to orthospecies if their deviation from an orthospecies is only slight and undetectable with the characters used. Any plant deviating in one or more characters should be suspected as a hybrid, and should be examined more carefully by consulting the descriptions, and by paying special attention to the color patterns of the seeds and the capsules. Scanning electron microscopy of the seed coat surface of seeds of such plants can provide a positive confirmation of their suspected hybridity, and can also provide confirmation to the identification of orthospecies (GIL-AD, 1995 and GIL-AD, in press).

I have considered including a separate key to the taxa using the micromorphological structures of the seed coats, or at least extending the key to the plants at the cleistogamous phase, and including the micromorphological structures. Such keys could be helpful, but they would suffer from a number of shortcomings. First, these keys would be rather long and cumbersome. Second, they would require the users to have a prior conceptual knowledge of the micromorphological structures of the orthospecies, a good command of the terminology, and ability to distinguish them from features seen on the seed coats of hybrids or introgressants. Third, some taxa possess elaborate structures, and it is difficult to abbreviate and summarize them into concise statements that are required by the dichotomous format. Fourth, some taxa possess a number of character states for characters that are lacking altogether in other taxa. Reproductions of the micrographs of seed coats of representative seeds of the taxa and detailed descriptions are included in GIL-AD (1995) and GIL-AD (in press).

6.3.2. A Key to the Species of *Viola* Subsection *Boreali-Americanae* at the Chasmogamous Phase

- 1a. Plants homophyllous (bearing only one type of blades: entire, lobed, or divided) 2
- 1b. Plants heterophyllous (bearing unlobed blades in early spring, and both unlobed and lobed or divided blades later) 14
- 2a. Blades undivided (including uncleft and unlobed above base) 3
- 2b. Blades divided 13
- 3a. Trichomes borne on the lower lateral petals and the spurred petal 4
- 3b. Trichomes borne only on the lower lateral petals 11
- 4a. Peduncles glabrous; sepals eciliate 5

- 4b. Peduncles pubescent; sepals ciliate or \pm ciliate8
- 5a. Blades more than two times longer than wide, base subtruncate to hastate *V. sagittata*
- 5b. Blades less than two times longer than wide, base cordate or subcordate6
- 6a. Blades narrowly deltoid, margins dentate on the basal lobes to serrate above; apical angle of the largest blades 24° - 38° ; bractlets ciliate; plants of the Atlantic seaboard *V. brittoniana*
- 6b. Blades not deltoid, margins crenate or crenate-serrate; apical angle of the largest blades larger than 40° ; bractlets eciliate; plants widely distributed7
- 7a. Blades narrowly ovate, apex acute to rounded, apical angle of the largest blades 60° - 85° ; upper lateral petals wider than the lower lateral petals; plants of southeastern Canada and eastern and midwestern United States, growing in low shady borders of lakes and streams and low woods on rich loam *V. affinis*
- 7b. Blades cordate to reniform, apex obtuse, apical angle of the largest blades 100° - 145° ; upper lateral petals narrower than the lower lateral petals; plants transcontinental to the western seaboard, growing in cool, shaded wet banks of slow streams, rivers, and lakes or wet soil pockets of protected rock crevices on calcareous loam *V. nephrophylla*
- 8a. Leaves prostrate to ascending, spreading out to form a rosette; apical angles of the largest blades greater than 100° ; upper lateral petals up to 3 mm wide; plants of southeastern United States only *V. villosa*
- 8b. Leaves ascending to erect, not forming a rosette; apical angles of the largest blades less than 100° ; upper lateral petals more than 3 mm wide; plants not confined to southeastern United States9
- 9a. Petiole shorter than the blade; blades ovate to ovate-oblong; margins crenulate; plants growing on gravelly soil or coarse sand *V. fimbriatula*
- 9b. Petiole longer than the blade; blades broadly ovate to cordate, lanceolate-ovate or deltoid ovate; margins crenate or crenate-serrate; plants not growing on gravelly soil10
- 10a. Blades broadly ovate to cordate, length/width ratio of the largest blades 1-1.3, apical angle 74° - 95° ; bractlets ciliate; petal trichomes wide *V. septentrionalis*
- 10b. Blades narrow deltoid, deltoid-ovate, deltoid-lanceolate or lanceolate-ovate, length/width ratio of the largest blades 1.4-2.4, apical angle 29° - 79° ; bractlets eciliate; petal trichomes narrow *V. novae-angliae*
- 11a. Petal trichomes clavate and short; blades light green; plants of swamps, bogs, wet meadows, rock crevices in slow streams; roots often submerged in soaked muck, dark humus or *Sphagnum* mats *V. cucullata*
- 11b. Petal trichomes cylindrical or only slightly expanded at the apex; blades dark green; plants of drier habitats; roots not submerged in a soaked substrate12
- 12a. Blades ovate to orbicular, base cordate; peduncles pubescent; sepals ciliate along the lower half only; petals violet; plants of open mixed woods, shaded ledges, disturbed sites, growing on loam *V. sororia*
- 12b. Blades reniform to deltoid-ovate, base subtruncate to cordate; peduncles glabrous; sepals finely ciliate; petals violet-blue; plants of low woods, floodplains, ravine bottoms, and creek banks, growing on sandy or silty alluvial soils *V. missouriensis*
- 13a. Blades with primary division into three segments, base cordate to subtruncate, middle segment wider than the lateral segments, oblanceolate; petals violet-blue; plants of the Atlantic seaboard, growing in margins or clearings in mixed woods on sandy loam *V. brittoniana*

- 13b. Blades with primary division into three or five segments, base cuneate to subtruncate, middle segment equal to the lateral segments, linear to subspatulate; petals violet; plants of midwestern prairies, growing on clay loam *V. pedatifida*
- 14a. Blades divided or undivided 15
- 14b. Blades subtrilobed, trilobed, or unlobed 16
- 15a. Primary division of the divided blades 3 segments, base of divided blades cordate to reniform in outline; spur 2-4 mm long; spurred petal (including the spur) 20-24 mm long; petal trichomes cylindrical and dense on the lower lateral petals and the spurred petal; plants of openings in pine woods in southeastern United States *V. septemloba*
- 15b. Primary division of the divided blade 3 or 5 (6) segments, base of divided blades cuneate to subtruncate; spur 0.6-1.7 mm long; spurred petal (including the spur) 9-17 mm long; petal trichomes cylindrical, often expanded at the apex, or clavate, dense on the lower lateral petals, sparse on the spurred petal; plants of cedar glades in southern Indiana, Kentucky, Tennessee, Georgia and Alabama *V. egglestonii*
- 16a. Petals violet to purple-violet; lower lateral petals and spurred petal lined with dark violet; petal trichomes dense on the lower lateral petals; apex of the spurred petal subtruncate; sepals glabrous on the adaxial surface, sparsely ciliate or glabrous; stipules irregularly glandular-fimbriate, fimbriae less than 1 mm long; plants of margins and openings in rich woods at low elevations in the United States *V. triloba*
- 16b. Petals pale violet; spurred petal only lined with dark violet; petal trichomes sparse on the lower lateral petals; apex of the spurred petal retuse; sepals irregularly pubescent on the adaxial surface, ciliate; stipules irregularly fimbriate, fimbriae 1-2.5 mm long; plants of margins of chaparral and mixed woods at relatively high elevations in northern México *V. nuevo-leonensis*

6.3.3. A Key to the Species of *Viola* Subsection *Boreali-Americanae* at the Cleistogamous Phase

- 1a. Plants homophyllous (bearing only one type of blades: entire, lobed, or divided) 2
- 1b. Plants heterophyllous (bearing lobed and unlobed blades in the summer, and mostly unlobed blades in late summer and early autumn) 14
- 2a. Blades undivided and unlobed 3
- 2b. Blades divided 13
- 3a. Margin type of the blade base different from the margin type of the blade above base ... 4
- 3b. Margin type of the blade base same as the margin type of the blade above base 5
- 4a. Blades oblong to oblong-ovate; blade base cordate to subcordate, margins of blade base sharply dentate; peduncles of the cleistogamous flowers prostrate; seeds moderate brown; plants of open forests, edges of forests and woodlands, often growing on gravelly soil *V. fimbriatula*
- 4b. Blades lanceolate-deltoid; blade base sagittate, margins of blade base entire to coarsely crenate; peduncles of the cleistogamous flowers erect; seeds deep brown or deep yellowish brown; plants of open grounds, growing on sandy soil *V. sagittata*
- 5a. Peduncles of the cleistogamous flowers prostrate; capsules spotted with red-purple 6
- 5b. Peduncles of cleistogamous flowers erect or ascending, capsules green or yellow-green. 10
- 6a. Seeds orange yellow 7

- 6b. Seeds yellow brown, deep brown or grayish brown8
- 7a. Capsule length/width ratio 2-2.2, sparsely spotted and dotted with red-purple on a yellow-green background, glabrous; sepal length/capsule length ratio 0.2-0.4; seeds dark orange-yellow to strong yellowish brown; blades deltoid, margins crenate-serrate with uneven serrations, base cordate to auriculate, apex bluntly attenuate; growing in low woods, floodplains, ravine bottoms, and creek banks on sandy or silty alluvial soils*V. missouriensis*
- 7b. Capsule length/width ratio 1.5-1.6, densely spotted and dotted with red-purple on a yellow-green background, \pm pubescent; sepal length/capsule length ratio 0.4-0.5; seeds moderate orange-yellow; blades narrowly ovate, margins crenate, base cordate with a deep sinus, apex acute; growing in low shady borders of lakes and streams, and low woods on rich loam*V. affinis*
- 8a. Capsule length/width ratio 1.6-1.8; seeds dark grayish brown, 1.9-2.4 mm long, 1.2-1.5 mm wide, average weight 1.5-2 mg*V. sororia*
- 8b. Capsule length/width ratio 1-1.6; seeds not grayish brown, 1.4-2.1 mm long, 0.9-1.2 mm wide, average weight 0.4-1.1 mg9
- 9a. Capsule length/width ratio 1.4-1.6; seeds dark yellowish brown, length/width ratio 1.6-2.3; blades broadly ovate to cordate*V. septentrionalis*
- 9b. Capsule length/width ratio 1-1.4; seeds deep brown, length/width ratio 1.3-1.7; blades deltoid-lanceolate or lanceolate-ovate*V. novae-angliae*
- 10a. Peduncles of cleistogamous flowers ascending; auricles short, less than 1.5 mm long; sepal length/capsule length ratio 0.3-0.5.11
- 10b. Peduncles of cleistogamous flowers erect, auricles lengthened, more than 2 mm long; sepal length/capsule length ratio 0.5-1.2.12
- 11a. Leaves erect to ascending, not forming a rosette; capsule length/width ratio 1.2-1.5; seeds dark yellowish brown to dark brown; plants transcontinental to the western seaboard, growing in cool, shaded wet banks of low streams, rivers, and lakes, or wet soil pockets of protected rock crevices on calcareous loam*V. nephrophylla*
- 11b. Leaves prostrate to ascending, spreading out to form a rosette; capsule length/width ratio 2-2.5; seeds nearly black; plants of southeastern United States, growing in open pine woodland disturbed sites on dry or well drained sandy soil*V. villosa*
- 12a. Blades broadly deltoid to reniform, base subcordate to truncate, margins coarsely serrate with deltoid serrations; seeds orange-yellow; plants growing on sandy loam in clearings or margins of mixed woods along the Atlantic seaboard*V. brittoniana*
- 12b. Blades ovate to reniform, base cordate, margins crenate-serrate; seeds nearly blackish red, occasionally dark brown; plants growing in swamps, bogs, wet meadows, rock crevices in slow streams, often submerged in soaked muck, dark humus or *Sphagnum* mats throughout southeastern Canada and eastern and midwestern United States*V. cucullata*
- 13a. Blades two times divided; capsule length/width ratio 2-2.5; sepal length/capsule length 0.5-0.7; seeds dark orange-yellow, 1.3-1.8 mm long, average weight 0.6-1.2 mg; plants of the Atlantic seaboard, growing in margins or clearings in mixed woods on sandy loam*V. brittoniana*
- 13b. Blades up to five times divided; capsule length/width ratio 1.8-2; sepal length/capsule length 0.4-0.5; seeds strong yellowish brown, 1.7-2.2 mm long, average weight 1.4-1.9 mg; plants of midwestern prairies growing on clay loam*V. pedatifida*
- 14a. Blades divided, some undivided in late summer and autumn; capsules green15

- 14b. Blades lobed, some undivided in the autumn; capsules blotched, spotted, or dotted with red-purple or greyed-purple 16
- 15a. Cleistogamous flowers and capsules originating above ground, peduncles of cleistogamous flowers erect; capsule surface ridged, length/width ratio 1.5-2; seeds brown black, shining, caruncle 0.3-0.6 mm long; plants of openings in pine woods in southeastern United States *V. septemloba*
- 15b. Cleistogamous flowers and capsules originating underground, peduncles of cleistogamous flowers prostrate; capsule surface subcolliculate, length/width ratio 1-1.5; seeds deep brown or dark brown, dull, caruncle 0.9-1.5 mm long; plants of cedar glades in southern Indiana, Kentucky, Tennessee, Georgia and Alabama *V. egglestonii*
- 16a. Peduncles of the cleistogamous flowers glabrous; capsules blotched and spotted with red-purple on a yellow-green to green background, length/width ratio 1.6-2; seeds dark orange yellow, 1.7-2 mm long, average weight 1.2-1.4 mg; plants of margins and openings in rich woods at low elevations in the United States *V. triloba*
- 16b. Peduncles of the cleistogamous flowers pubescent; capsules yellow-green to green, sparsely spotted and dotted with greyed-purple, length/width ratio 1.4-1.8; seeds deep yellowish brown, 2.1-2.7 mm long, average weight 2.2-2.9 mg; plants of margins of chaparral and mixed woods at relatively high elevations in northern México *V. nuevo-leonensis*

6.4. Descriptions of the Taxa of *Viola* Subsection *Boreali-Americanae* and Discussions

Viola affinis LeConte in Ann. Lyceum Nat. Hist. New York 2: 138. 1828. – **Type:** [locality and date unknown,] *J. E. LeConte* (lectotype, here designated: Plate Number 24! of LeConte's unpublished water-colors, Call number: QK 495 V811 L496f, University of Notre Dame Libraries, Department of Special Collections, Section of Rare Books).

!c.: Species No. 17 [chasmogamous and cleistogamous plants], Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 48. 1921; [color] Plate No. 38 [chasmogamous plant without a rhizome], Baird-Brainerd, *Wild Violets of North America*: 109. 1942.

Acaulescent, homophyllous, perennial herb; *rhizomes* succulent, scaly, vertical to oblique, 1-3 cm long, bearing fibrous roots, roots up to 0.6 mm in diameter, branched into fine fibrous roots; *stipules* lanceolate, densely blotched with red-purple on a yellow-green background, apex acute, margins entire to irregularly fimbriate, ± ciliate; *petioles* green, glabrous; *blades* undivided, glabrous or sparsely pubescent on the adaxial surface, glabrous on the abaxial surface, at chasmogamous anthesis narrowly ovate, base cordate, margins crenate, apex acute to rounded, length/width ratio of the largest blades 1-1.2, apical angle 63°-72°, at the cleistogamous phase blades much larger (ca. 2.5 times longer) basal sinus deep, apex prominently acute, apical angle 40°-56°; *peduncle* green, glabrous, 6-11 cm long; *bractlets* deltoid to lanceolate, densely blotched with red-purple on a yellow green background, apex acute, margins entire, eciliate; *sepals* lanceolate-ovate, green spotted with red-purple, apex acute, margins scarious, eciliate, sepal length/capsule length ratio 0.4-0.5; *auricles* 0.5-1 mm long, green spotted with dark red-purple, apex rounded to subtruncate, eciliate; *spur* 1.5-2 mm long; *petals* violet (RHS # 86) with a white center, lines on the spurred and lateral petals dark violet, spurred petal 14-16 mm long (including the spur), 5-7 mm wide near the apex, apex rounded to subtruncate, lower lateral pair 4-6 mm wide, upper lateral pair 5-7 mm wide; *petal trichomes* borne on the lower lateral petals, and sparsely on the spurred petal, cylindrical, ca. 100 µm wide, visible layers of cuticular folds one, cuticular folds capillary, linear, some convoluted on the apex, most alligned vertically, widely spaced to packed; *cleistogamous flower peduncle habit*: prostrate; *capsule* densely spotted and dotted with red-purple on a yellow-green background, often pubescent, length/width ratio 1.5-1.6; *seeds* moderate orange-yellow (ISCC-NBS # 71), 1.5-1.9 mm long, 0.9-1.2 mm wide,

weight 0.6-1 mg, caruncle 0.7-1.1 mm long; *seed coat*: outer periclinal walls finely striated and delimited by the secondary sculpture's terete thickenings, secondary sculpture with reticulate-terete thickenings with a finely striated or rough surface and randomly distributed semi-circular or slightly elongated plates, solitary or connected, plates with blends of foveate, falsifoveate, and scrobiculate surfaces; *chromosome number*: $2n = 54$.

Substrate. – Rich loam.

Habitat. – Low shady borders of lakes and streams, low woods, wet thickets and meadows.

General Distribution. – Canada: Ontario and Quebec; U.S.A.: Vermont to Wisconsin, south to Georgia, and to Texas.

Typification. – BAIRD-BRAINERD (1938) compiled the history of LeConte's water-colors and their annotations. She noted that LeConte prepared the water-colors to illustrate the papers he read before The Lyceum of Natural History of New York during 1824-1826. However, these paintings were never published, doubtless on the account of the great expense involved.

LeConte most likely described *Viola affinis*, and prepared the illustration (Plate Number 24 of his water-colors), from a living plant. A specimen of this plant is unknown, and no holotype is cited in the protologue.

Examination of Plate Number 24 revealed that it matches the characters listed in the protologue. In addition, it matches in most characters the characters of the chasmogamous phase of the orthospecies, as listed above. The only major character that cannot be clearly depicted is the presence of trichomes on the spurred and lower lateral petals. Very fine horizontal lines that are drawn on the lower lateral petals may have been drawn to represent the trichomes that are listed in LeConte's description for the lower lateral petals. In addition, the color of the blades resembles the light-green color of the blades of *V. cucullata*. Cylindrical trichomes on the spurred petal, which serve as a key character at the chasmogamous phase, are not listed in the description and are not drawn on the spurred petal in the plate. It is conceivable that the plant that served for the illustration might have been a hybrid with *V. cucullata*. Nevertheless, given the match between LeConte's description and the illustration, and the absence of a specimen or strong evidence for hybridity, Plate Number 24 is designated here as the lectotype of *Viola affinis* LeConte.

Etymology. – LeConte erected the specific epithet *affinis* because he considered *Viola affinis* to be of nearest affinity to *V. cucullata* (BRAINERD, 1921).

Discussion. – BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola affinis* as a distinct species. Cronquist (*in* GLEASON & CRONQUIST, 1991) subsumed *V. affinis* into *V. sororia*, and considered it "a form with the spurred petal bearded." MCKINNEY (1992) abolished *V. affinis*. He erected the combination *Viola sororia* var. *affinis*, and later elevated it to subspecific rank: *Viola sororia* subsp. *affinis* (LITTLE & MCKINNEY, 1992; LITTLE, 1993; LITTLE, 1996) to designate the species previously known as *Viola nephrophylla*. The present work demonstrates that each of the following species: *Viola affinis*, *V. nephrophylla*, and *V. sororia*, possesses a number of autapomorphies, as well as distinct suites of characters. Therefore, they should be recognized as distinct species. The major characters that distinguish them are the color of the capsules, the color of the seeds, the micromorphological structures of the seed coat surface, and the size and the micromorphological structures of the petal trichomes.

BRAINERD (1904b, 1906b, 1921, 1924), and DOWELL (1910) reported natural fertile hybrids between *Viola affinis* and other taxa of subsection *Boreali-Americanae*. Seven of those hybrids were named by HOUSE (1924). They included: $\times V. davisii$ (*V. affinis* \times *V. brittoniana*); $\times V. conso-cia$ (*V. affinis* \times *V. cucullata*); $\times V. hollickii$ (*V. affinis* \times *V. fimbriatula*); $\times V. subaffinis$ (*V. affinis* \times *V. nephrophylla*); $\times V. dissena$ (*V. affinis* \times *V. sagittata*); $\times V. champlainensis$ (*V. affinis* \times *V. septentrionalis*); $\times V. consona$ (*V. affinis* \times *V. sororia*); and $\times V. milleri$ Moldenke (*V. affinis* \times *V. triloba*).

Natural hybrids between *Viola affinis* and *V. cucullata* are common. Those hybrids have misled many workers who relied mainly on the shape of the blades to distinguish *V. affinis*, and overlooked the reproductive characters. The blades of those hybrids are narrower than the blades of *V. affinis*, lighter in color, and deltoid with an acute apical angle. The petal trichomes of those hybrids are often slightly clavate or a blend of clavate and cylindrical types. Hybrids and introgressants with other species of subsection *Boreali-Americanae* possessing undivided blades have also contributed to the confusion, and to the difficulties of recognizing unique species-defining character states for *V. affinis*. At chasmogamous anthesis a positive identification of the species may be difficult. Even the seed color may be misleading since putative introgression from other taxa possessing seeds colored orange yellow or a similar color, or even putative introgression from *V. cucullata*, can be detected only by examination of the micro-ornamentation of the seed coat surface. Careful examination of the suite of macromorphological characters that delimit the species, as well as SEM of the seed coat surface, would allow correct identification.

Viola affinis is the only taxon in subsection *Boreali-Americanae* that possesses trichomes on the capsule (BAIRD-BRAINERD, 1942; GIL-AD pers. observation). However, the capsules on some plants may be glabrous. Surveys of additional populations and further investigation are needed in order to assess this character.

Viola brittoniana Pollard in Bot. Gaz. (Crawfordsville) 26: 332. 1898.

REPLACED SYNONYM: *Viola atlantica* Britton in Bull. Torrey Bot. Club 24: 92. 1897, non Pomel, Nouv. Mat. Fl. Atl.: 215 1874. – **Type:** U.S.A. New York: Staten Island, along salt meadows, 8 June 1888, N. L. Britton s.n. (lectotype (also of *Viola atlantica* Britton – designated by MCKINNEY (1992) as “holotype”): NY!).

≡ *Viola pedatifida* subsp. *brittoniana* (Pollard) L. E. McKinney in Sida Bot. Misc. 7: 22. 1992.

= *Viola baxteri* House in New York State Mus. Bull. 254: 500. 1924.

!c.: Species No. 27, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: [color] plate preceding page 65. 1921; reprinted [color] Plate No. 51, Baird-Brainerd, *Wild Violets of North America*: 139. 1942; [color] Plate XXVII [chasmogamous and cleistogamous plants], Klüber, *Violets of the United States*: 71. 1976.

Acaulescent, homophyllous, perennial herb; *rhizomes* succulent, scaly, vertical to oblique, 0.5-3 cm long, bearing fine fibrous roots branched into very fine fibrous roots; *stipules* lanceolate, green blotched with red-purple, apex acute, margins entire to irregularly glandular fimbriate, eciliate; *petioles* green spotted with purple, glabrous; *peduncles* 5-17 cm long, green, finely spotted or dotted with red-purple, glabrous; *bractlets* deltoid, blotched with red-purple on a yellow green background, apex acute, margins entire to irregularly glandular, eciliate; *sepals* lanceolate, green clouded with dark purple, margins scarious, eciliate, apex acute, sepal length/capsule length ratio 0.5-0.7; *auricles* 1-2.5 mm long, becoming 2-3 mm long at the cleistogamous phase, green clouded with dark purple, apex subacute to rounded, truncate, subtruncate or incised, ± irregularly ciliate; *spur* 1-3 mm long; *petals* violet-blue (RHS # 90B/C) with a white center bordered blue, lines on the spurred and lateral petals dark violet, spurred petal spatulate 14-22 mm long (including the spur), 4-7 mm wide near the apex, apex truncate to emarginate, lower lateral pair 4-7 mm wide, upper lateral pair 5-9 mm wide; *petal trichomes* dense on the spurred and lower lateral petals, cylindrical, ca. 60-90 µm wide, visible layers of cuticular folds one, cuticular folds tubular, elongated, and narrow, linear or convoluted, randomly aligned over the apex, vertically aligned below the apex, densely overlapping; *cleistogamous flower peduncle habit*: erect; *capsule* yellow-green, length/width ratio 2-2.5; *seeds* dark orange yellow (ISCC-NBS # 72), 1.3-1.8 mm long, 0.9-1.2 mm wide, average weight 0.6-1.2 mg, caruncle 0.5-1 mm long; *seed coat*: outer periclinal walls ribbed with intercrossed thickening, secondary sculpture with

reticulate-terete thickenings and scattered smooth, circular or elliptical plates, circumscribed by short, segmented thickenings, occasionally by shallow pits; *chromosome number*: $2n = 54$.

Substrate. – Sandy loam.

Habitat. – Margins or clearings in mixed woods, moist banks of roadside ditches and trails.

General Distribution. – The Atlantic seaboard from southern Maine to South Carolina.

A Key to the Forms of *Viola brittoniana*

- 1a. Blades divided, at chasmogamous anthesis lobed, middle lobe oblanceolate, the widest, lateral lobes oblanceolate to linear; base cordate to subtruncate; margins entire at the lower one third of the lobes, irregularly serrulate at the upper two thirds, occasionally bearing lanceolate to narrowly deltoid, linear or curved appendages with acute apices, mucronulate; apical angle of middle lobe 41° - 88° ; during the cleistogamous phase blades lobed, base cordate to subtruncate; dentations on basal lobes none *Viola brittoniana* f. *brittoniana*
- 1b. Blades undivided, at chasmogamous anthesis narrowly deltoid; base cordate; margins crenate-serrate in juvenile blades, becoming dentate on the basal lobes to serrate above, dentations lanceolate, up to 5 mm long on the basal lobes, gradually shorter toward the apex, apical angle 24° - 38° ; during the cleistogamous phase blades broadly deltoid to reniform, base subcordate to truncate; dentations on basal lobes deltoid
 *Viola brittoniana* f. *pectinata*

Viola brittoniana Pollard f. *brittoniana*

Blades two times divided, primary division into three segments, second division: middle segment undivided or divided into three lobes, the lateral segments undivided or divided into 2-4 lobes, base cordate to subtruncate, margins finely ciliate, entire at the lower one third of the lobes, irregularly serrulate at the upper two thirds, occasionally bearing lanceolate to narrowly deltoid, linear or curved appendages with acute apices, adaxial surface finely pubescent along the major veins, abaxial surface often clouded with purple in juvenile blades, veins often clouded with purple in older blades, at chasmogamous anthesis length/width ratio of the largest blades 0.7-1.4, middle lobe oblanceolate, 3-10 mm wide, occasionally subobovate during the cleistogamous phase, at chasmogamous anthesis apical angle 41° - 88° , mucronulate, lateral lobes oblanceolate to linear, 1-5 mm wide, apices acute, mucronulate.

Viola brittoniana f. *pectinata* (E. P. Bicknell) Gil-ad, **stat. nov.**

BASIONYM: *Viola pectinata* E. P. Bicknell in Torrey 4: 129. 1904. – **Type:** U.S.A. New York. [Nassau County:] southwestern Long Island, Woodmere, in low ground near or at the borders of salt marshes with *V. brittoniana*, 21 May 1904, E. P. Bicknell s.n. (holotype: NY!, isotype: GH).

≡ *Viola brittoniana* var. *pectinata* (E. P. Bicknell) Alexander in Gleason, New Ill. Fl. Northeastern U.S. 2: 558. 1952.

!c.: Plate 18 [chasmogamous and cleistogamous plants], House in Bull. Torrey Bot. Club 32. 1905; [no figure number; spring and summer blades] Alexander in Gleason, *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*, Vol. 2: 558. 1952.

Blades entire, narrowly deltoid, margins crenate-serrate in juvenile blades, at chasmogamous anthesis becoming dentate on the basal lobes to serrate above, dentations lanceolate, up to

5 mm long on the basal lobes, gradually shorter toward the apex, adaxial and abaxial surfaces finely pubescent, length/width ratio of the largest blades 1.1–1.5, apical angle 24°–38°, at the cleistogamous phase blades broadly deltoid to reniform, base subcordate to truncate, dentations deltoid, occasionally with one serration on their margins.

Discussion. – *Viola brittoniana* was originally described under the name *Viola atlantica* BRITTON (1897). POLLARD (1898) noted that this name was a homonym of *Viola atlantica* Pomel, and renamed the species after Dr. N. L. Britton. The type of *V. atlantica* Britton serves as the type of *V. brittoniana* Pollard since Pollard did not provide a description and did not cite a specimen when he erected this name. MCKINNEY (1992) stated that a Britton specimen at NY dated 8 June 1888 from Staten Island, New York was the lectotype of *V. brittoniana*. In addition, he stated that the holotype of *V. atlantica* was a Britton specimen from Staten Island dated May 1893. This statement is erroneous. Britton cited no specimens in the protologue. Furthermore, an additional specimen of this taxon from Delaware (*Commons s.n.*, NY) dated 10 June 1880 and mounted on the same sheet as the 1888 specimen was annotated by Britton as *V. atlantica*. Consequently, *V. atlantica* Britton does not have a holotype. *Viola atlantica* and *V. brittoniana* must have the same type, and therefore *Britton s.n.* (NY) dated 8 June 1888 is designated as the lectotype of both.

BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola brittoniana* as a distinct species. Cronquist (*in* GLEASON & CRONQUIST, 1991) subsumed *V. brittoniana* into his broadly defined *V. palmata* as var. *palmata*, and lumped it with the other species possessing strongly divided blades: *V. septemloba*, along with *V. triloba*, the undivided *V. pectinata* (= *V. brittoniana* f. *pectinata*), and taxa that are identified in this work as hybrids: *Viola chalcosperma*, *V. esculenta*, *V. lovelliana*, *V. stoneana*, and *V. viarum*. *Viola palmata* is not recognized as an orthospecies in the present study. MCKINNEY (1992) designated *V. brittoniana* as a subspecies of *V. pedatifida*, adhering to BRITTON's (1897) opinion about their affinity. The rationale for his decision was that these two homophyllous taxa are similar in many respects, but distinct enough (mainly in habitat and distribution) to be considered subspecies of the same complex. The present work demonstrates that *V. brittoniana* differs from *V. pedatifida* in enough characters to justify maintaining it as a separate species. These characters include the color and dimensions of the seeds, the micromorphological structures of the seed coat surface (curvature of the outer periclinal walls ribbed with intercrossed thickenings in *V. brittoniana* vs. unevenly ribbed in various directions in *V. pedatifida*; secondary sculpture: reticulate-terete thickenings with scattered circular or elliptical plates that are smooth and circumscribed by short, segmented thickenings in *V. brittoniana* vs. an irregular, shallow, reticulate secondary wall thickening), the shape of the capsules, sepal length/capsule length ratio, the width of the petal trichomes, the density of the trichomes on the spurred petal, the color of the corolla, the degree of blade division, a number of blade character states, and the diameter of the fibrous roots.

BRAINERD (1921) pointed out that *Viola pectinata* E. P. Bicknell is identical to *V. brittoniana*, except for the shape of the blades. He identified the two types of plants as a case of dimorphism, and did not list the plants named *pectinata* as a distinct taxon. BAIRD-BRAINERD (1942) informally listed them as varieties of *V. brittoniana* in her vernacular description of this species. FERNALD (1950) upheld *V. pectinata* as a distinct species. ALEXANDER (1952) formally changed the rank of *V. pectinata* to variety under *V. brittoniana*. GLEASON & CRONQUIST (1963) listed the two types of blades in the description of *V. brittoniana*, and did not refer to the specific epithet *pectinata*, or to its rank. RUSSELL (1965) briefly described it under *V. brittoniana*, and reiterated that it is presumably a case of genetic dimorphism. Cronquist (*in* GLEASON & CRONQUIST, 1991) listed it in synonymy under his broadly defined *V. palmata* var. *palmata*. MCKINNEY (1992) contended that little variation exists in the taxon he delimited as *V. pedatifida* subsp. *brittoniana* except for a sporadic form described by E. P. Bicknell as *V. pectinata*. A similar dimorphism is found also in two species belonging to section *Chamaemelanium*, *V. tripartita* and *V. lobata*. The plants possessing unlobed blades and associated with *V. tripartita* have undergone a torturous nomenclatural history that was reviewed thoroughly by LÉVESQUE & DANSEREAU (1966). These authors finally corrected the status of this taxon to *Viola tripartita* f. *glaberrima* (Don) Lévesq.

& Dans. The plants of *V. lobata* possessing unlobed blades have been assigned the rank of variety: *Viola lobata* var. *integrifolia* S. Watson. LITTLE (1992) changed the rank of *V. lobata* var. *integrifolia* to subspecies. Neither the rank of subspecies nor the rank of variety seems appropriate in this case given the fact that the only character that distinguishes the two types of plants is blade shape. Examination of the two types of plants of *V. brittoniana* from a number of populations confirmed that the blade shape is the only morphological character that distinguishes them. The secondary cell wall thickenings on the seed coat surface of seeds produced by plants possessing undivided blades are more prominent than their counterparts on the seed coats of seeds produced by plants possessing divided blades, but are similar (GIL-AD, 1995; GIL-AD, in press). Therefore, a change of rank to forms is proposed here for *V. pectinata*. The plants possessing divided blades would be named f. *brittoniana*, and the plants possessing undivided blades would be named f. *pectinata*. *Viola brittoniana* f. *pectinata* is usually syntopic with f. *brittoniana* [e.g., Gil-ad 453 & 454 (MICH)], but occasionally occurs unaccompanied by the other form [e.g., Gil-ad 319 (MICH)]. BRAINERD (1906b, 1921, 1924) reported that the two forms of *V. brittoniana* interbreed, but no intermediates were detected in the populations sampled in this study.

Previous treatments have listed the substrate in which *Viola brittoniana* grows as sandy soil, and the habitat as borders of salt meadows, salt marshes, and low turfy meadows. Field work has revealed that the species grows in margins or clearings in mixed woods. A soil test conducted on a sample taken from the soil that surrounded the roots of Gil-ad 460 (MICH) (*Viola brittoniana* f. *brittoniana*) has revealed that the substrate is sandy loam composed of 65.1% sand, 4.7% silt, and 30.2% clay.

BRAINERD (1906b, 1924) and DOWELL (1910) reported natural fertile hybrids of *Viola brittoniana* with other taxa of subsection *Boreali-Americanae*, some of which were named by HOUSE (1905, 1924). They included: $\times V. davisii$ (*V. affinis* \times *V. brittoniana*); $\times V. notabilis$ (E. P. Bicknell) House (*V. brittoniana* \times *V. cucullata*); $\times V. mulfordae$ (Pollard) House (*V. brittoniana* \times *V. fimbriatula*); $\times V. marylandica$ (*V. brittoniana* \times *V. sagittata*); *V. brittoniana* \times *V. sororia*; and *V. brittoniana* \times *V. triloba*. In addition, he reported a sterile hybrid of *V. brittoniana* with *V. lanceolata* which belongs to subsection *Stolonosae*.

Viola cucullata Aiton, Hort. Kew. 3: 288. 1789. – **Type:** “Hort. Kew 1778” (holotype: BM, photo: MICH!).

lc.: Species No. 21, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 56. 1921; Fig. 4-21a-h, Cronquist, *An integrated System of Classification of Flowering Plants*: 403. 1981; Plate 50, Fig. 1a, b, c [cleistogamous flowers and capsules only], Brainerd in *Rhodora* 7: opposite page 24. 1905.

Acaulescent, homophyllous, perennial herb; *rhizomes* fleshy, scaly, vertical or oblique, often branching, 1-2.5 cm long, bearing numerous fine fibrous roots; *stipules* linear-lanceolate, green sparsely blotched with red-purple, apex acute, margins entire or irregularly glandular toothed, eciliate; *petioles* flat, green, glabrous or sparsely pubescent; *blades* light-green, papery in texture when dried, base cordate, margins crenate-serrate, eciliate, apex acute, becoming obtuse in some older leaves, adaxial surface pubescent in younger leaves to sparsely pubescent in older leaves, the trichomes occurring irregularly throughout or only along the veins, abaxial surface glabrous, at chasmogamous anthesis ovate to reniform, length/width ratio of the largest blades 1-1.4, apical angle 75°-82°; *peduncles* 10-17 cm long, usually longer than the leaves, flat, green, glabrous; *bractlets* lanceolate, green blotched with purple, margins entire, eciliate, apex acute; *sepals* lanceolate, green sparsely spotted with purple, apex acute, margins scarious, ciliate, rarely eciliate, sepal length/capsule length ratio 0.8-1.2; *auricles* 0.3-1.5 mm long at chasmogamous anthesis, becoming 3.1-5.6 mm long on cleistogamous flowers and capsules, subtruncate, truncate, rounded to subacute, or incised to undulate, occasionally narrow at base and wider at the apex, green, sparsely spotted with purple, ciliate; *spur* 1-2.5 mm long; *petals* violet-blue (RHS #

90-93) with a white center bordered by a narrow dark violet-blue area on the lateral petals, lines on the lower lateral petals and the spurred petal dark violet to black, spurred petal narrower in the middle, rounded at the apex, 9-13 mm long (including the spur), 3-4 mm at the widest point near the apex, lower lateral petals (2) 3-4 mm wide, upper lateral pair 3-4 (5) mm wide; *petal trichomes* borne on the lower lateral petals, none on the spurred petal, clavate, 100-130 μ m wide, visible layers of cuticular folds two, cuticular folds tubular, thick, highly convoluted and randomly spaced, overlaid on a layer of thin, highly convoluted, densely packed and overlapping folds, randomly aligned on the apex, vertically aligned below; *cleistogamous flower peduncle habit*: erect; *capsule* green, length/width ratio 2.2-2.5; *seeds* nearly blackish red (ISCC-NBS # 21), occasionally dark brown (ISCC-NBS # 59) when the background color is prominent, often with a flat seed coat on one side, 1.2-1.7 mm long, 0.8-1.2 mm wide, average weight 0.5-0.9 mg, caruncle 0.4-0.8 mm long; *seed coat*: primary sculpture cells isodiametric or elongated in one direction, and superficially tetra-, penta- or hexagonal, outer periclinal walls mostly flat or unevenly flat and relatively smooth, secondary wall thickenings appearing occasionally over the cell boundaries in the form of small, rounded, uneven raised segments; *chromosome number*: $2n = 54$.

Substrate. – Black swamp muck, dark humus saturated with water, or the roots are submerged in water and supported by clumps of *Sphagnum*. pH range: 4.6-6.6 (strongly acid to slightly acid) with a median of 5.1 (McCULLOUGH, 1941).

Habitat. – Swamps (open and forested), bogs, wet meadows, or on rock crevices covered with moss mats and *Carex* spp. in slow streams.

General Distribution. – Canada: Newfoundland and Nova Scotia to Ontario; U.S.A.: Northeastern United States to Minnesota and Nebraska, south to North Carolina, Georgia, Tennessee, Missouri, and Arkansas.

Discussion. – The holotype (BM) consists of a plant missing most of the rhizome and bearing four leaves, a detached leaf, and two detached chasmogamous flowers: “Hort. Kew 1778.” Apparently, this is the cultivated material introduced by Samuel Martin in 1772 (according to the protologue) upon which Aiton based his brief description. On the same sheet is an additional chasmogamous plant: “Hort. Kew 1791,” most likely a different cultivated plant.

BRAINERD (1921) and MCKINNEY (1992) reviewed the troublesome nomenclatural history of *Viola cucullata*. All students of the species since Brainerd have maintained it as a distinct species.

The name *Viola obliqua* HILL (1768: 316) has been thought by some taxonomists to refer to the same species as *Viola cucullata* Aiton, and therefore has priority over *V. cucullata* (GRAY, 1886; POLLARD, 1896). It was resurrected by VALENTINE & *al.* (1968) who accompanied it with a brief and vague description, and listed *V. cucullata* as a synonym. BRAINERD (1907b) pointed out that Hill’s description of *V. obliqua* is “hopelessly vague.” He attributed the variations in the application of the name *V. obliqua* and the confusion that it has caused to some subsequent authors to this vagueness. These authors included PURSH (1813), de SCHWEINITZ (1822), LECONTE (1828), POLLARD (1896), BRITTON (1901), and BICKNELL (1913). GREENE (1896b, 1913) argued that due to the vagueness of Hill’s description, and especially the plate that accompanied the description [Tab. 12 in the second edition of *Hortus Kewensis* (HILL, 1769)], we may never be able to determine what species Hill actually described. Therefore, the application of the name *Viola obliqua* is uncertain, and the name should not be reinstated. HOUSE (1924) pointed out that the status of the name may never be satisfactorily settled, and listed it in synonymy under *V. affinis*. VOSS (1985) echoed the uncertainty among some American authors about the name, and expressed the opinion that upsetting the name for one of our commonest wildflowers seems ill-advised. Greene’s and Voss’ recommendations are followed here.

It is important to note that hybridization of *Viola cucullata* with other species of subsection *Boreali-Americanae* is common in spite of its distinctive habitat. Gene flow apparently takes place during chasmogamous flowering through cross pollination with other taxa of subsection

Boreali-Americanae growing in drier habitats in the vicinity of *V. cucullata* populations (e.g., Gil-ad 307, MICH).

BRAINERD (1904b, 1906b, 1924) reported natural fertile hybrids of *Viola cucullata* with a number of taxa of subsection *Boreali-Americanae* that were named by HOUSE (1924). They included: $\times V. consocia$ (*V. affinis* \times *V. cucullata*); $\times V. notabilis$ (E. P. Bicknell) House (*V. brittoniana* \times *V. cucullata*); $\times V. porteriana$ (Pollard) House (*V. cucullata* \times *V. fimbriatula*); $\times V. insessa$ (*V. cucullata* \times *V. nephrophylla*); $\times V. festata$ (*V. cucullata* \times *V. sagittata*); $\times V. melissaefolia$ (Greene) House (*V. cucullata* \times *V. septentrionalis*); $\times V. conturbata$ (*V. cucullata* \times *V. sororia*); and $\times V. greenmani$ (*V. cucullata* \times *V. triloba*). RUSSELL (1965) reported observations on hybrid swarms between *V. cucullata* and *V. fimbriatula*, and between *V. cucullata* and *V. sagittata* in the eastern states.

RUSSELL (1955) provided evidence for hybridization and possible bi-directional introgression between populations of *Viola cucullata* and *V. septentrionalis*. In many instances, however, introgression appears to be unidirectional. Most of the unique macromorphological characters of *V. cucullata* are maintained, and unless the microstructural ornamentation of the seed coat surface is examined, it is very difficult to distinguish between an introgressant and an orthospecies. A number of the subspecific taxa that have been described (see Appendix B) on the basis of variations, e.g., in pubescence, length of the auricles, are most likely introgressants.

The lengthened auricles on the cleistogamous flowers and capsules that have been described as characteristic of the species (BRAINERD, 1924; BAIRD-BRAINERD, 1942; GLEASON & CRONQUIST, 1963, 1991) are also found in the quite dissimilar *Viola brittoniana* and *V. sagittata*. However, those of *V. cucullata* are longer. The length of the sepals and the ratio of sepal length/capsule length are unique to *V. cucullata*.

Etymology. – The specific epithet – *cucullata* – chosen presumably to describe the ontogeny of the blades (blades expanding in the shape of a hood with involute basal lobes) is not especially appropriate, except for plants growing in the open, and is not unique to *Viola cucullata* (BRAINERD, 1904a).

Viola egglestonii Brainerd in Bull. Torrey Bot. Club 37: 526, plates 34 & 35. 1910. – **Type:** U.S.A. Tennessee. [Davidson County:] West Nashville, limestone barrens, 26 May 1909, W. W. Eggleston 4421 (holotype: not located, isotype: VT!).

lc.: Brainerd in Bull. Torrey Bot. Club 37: Plate 37 [a cleistogamous plant], Plate 35 [a chasmogamous plant]. 1910; Species No. 3 [a cleistogamous plant], Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 18. 1921; Shaver in J. Tennessee Acad. Sci. 34: 41 [Plate IA-C], 43 [Plate IIA-D], 45 [Plate IIIA-C]. 1959.

Acaulescent, heterophyllous, perennial herb; *rhizomes* succulent, scaly, vertical to oblique, ca. 1-2.5 cm long, bearing stout fibrous roots: up to 1.5 mm in diameter, often branched into fine fibrous roots; *stipules* lanceolate to deltoid, green to green blotched with red-purple, apex acute, margins entire to irregularly glandular fimbriate, eciliate; *petioles* green, clouded purple in juvenile leaves, glabrous or sparsely pubescent; *blades* at early spring, late summer and autumn (1-5 in number) entire, ovate, deltoid, occasionally rhomboid, base cuneate or truncate, margins unevenly crenulate, crenulate to entire at base, apex acute or obtuse, juvenile clouded purple on the abaxial surface, at chasmogamous anthesis length/width ratio of the largest blades 1.3-1.6, apical angle 64°-96°, divided blades two times divided: primary division into 3 or 5 (6) segments, second division: middle segment undivided or divided into 2-4 lobes, wider than the lateral lobes, at chasmogamous anthesis 4-8.6 mm wide, apical angle 46°-92°, lobes oblanceolate to subspatulate, up to two thirds of the blade length in developed blades, lateral segments undivided or divided into 2 or 3 lobes, lobes oblanceolate to linear, occasionally falcate, 0.8-3.3 mm wide, internode between the lateral segments and the lobes diverging from the middle segment occasionally up to two thirds of the length of the middle segment, blade base cuneate to subtruncate,

margins entire along the lower one third of the segments, unevenly crenate-serrate above, occasionally or with 1-4 deltoid or deltoid-falcate appendages, apexes acute to rounded, abaxial and adaxial surfaces glabrous, clouded purple in juvenile leaves, length/width ratio of the largest blades 0.8-1.4, midsummer new blades 2-5 lobed. *peduncle* 3-11 cm long, green clouded with red-purple, glabrous; *bractlets* linear-lanceolate, lanceolate, or falcate, blotched with red-purple on a yellow green background, apex acute, margins scarious, entire, eciliate; *sepals* lanceolate or lanceolate-ovate, green irregularly clouded or spotted red-purple along the veins, margins scarious, glabrous or sparsely ciliate, apex acute, rounded or obtuse sepal length/capsule length ratio 0.5 -0.7; *auricles* 0.7-1.5 mm long, green clouded or spotted irregularly with dark red-purple, apex subtruncate to rounded, eciliate, occasionally with a few cilia at the base; *spur* 0.6-1.7 mm long; *petals* violet (RHS # 83B/C) with a white center, often bordered blue, lines on the spurred and lateral petals dark violet, spurred petal narrower at middle, widening toward the apex, 9-17 mm long (including the spur), 4-8 mm wide near the apex, apex subtruncate to rounded, often emarginate, lower lateral pair 3-6 mm wide, upper lateral pair 4-9 mm wide; *petal trichomes* dense on the lower lateral petals, sparse on the spurred petal, cylindrical, ca. 100-110 μ m wide, often expanded at the apex, or slightly clavate, visible layers of cuticular folds one, cuticular folds tubular, unevenly thick, varied in length, linear, twisted or convoluted, randomly aligned on the apex, vertically aligned below the apex, densely packed and overlapping; *cleistogamous flowers* originating underground, achlorophyllous, occasionally arising above ground and becoming chlorophyllous, peduncles habit prostrate; *capsule* origin underground, achlorophyllous, becoming yellow-green when emerging above ground, length/width ratio 1-1.5, seeds often pressed against the inner wall forming an uneven subcolliculate surface, peduncle often wider in the 1-2 cm segment below the capsule attachment; *seeds* color between deep brown (ISCC-NBS # 56), and dark brown (ISCC-NBS # 59), 1.8-2.8 mm long, 1.3-1.7 mm wide, weight 1.9-2.8 mg, caruncle 0.9-1.5 (1.8) mm long; *seed coat*: primary sculpture cells isodiametric or slightly elongated, superficially pentagonal, outer periclinal walls smooth, secondary sculpture structures circular, rosette-like with secondary wall thickenings diverging from a center, or occasionally connected, irregularly spaced (often connected); *chromosome number*: $2n = 54$.

Substrate. – Shallow limestone-derived soil.

Habitat. – Endemic to cedar (*Juniperus virginiana*) glades (limestone barrens). Edges of thickets or woods, in open thickets or on open glades.

General Distribution. – Southern Indiana, north central Kentucky, central and eastern Tennessee, northwestern Georgia, northern Alabama (BASKIN & BASKIN, 1970, 1975a, 1978; BASKIN & al., 1987; MCKINNEY, 1992; RUSSELL, 1958b).

Discussion. – MCKINNEY (1992) listed *E. Brainerd 43* at NY as the holotype. However, BRAINERD (1910c) cited in the protologue *W. W. Eggleston 4421* as the type. Plants that were later distributed as “*Ex Horto E. Brainerd 43*” and “*44*” were transplanted from the same site as *Eggleston 4421*, and cultivated by Brainerd at Middlebury, Vermont. They served to illustrate in Plate 35 a chasmogamous plant, a full grown summer leaf, and a mature capsule. These specimens are deposited in NY, GH, PH, and US. BRAINERD (1910c) indicated that the types of the five new species he described in this paper (including *V. egglestonii*) would be deposited in NY. Yet, the holotype of *V. egglestonii* could not be located in NY (P. K. HOLMGREN pers. comm., 1995).

FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola egglestonii* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) subsumed *V. egglestonii* into his broadly defined *V. palmata* as var. *pedatifida*, and lumped it with *V. pedatifida*. MCKINNEY (1992) subsumed *V. egglestonii* into *V. septemloba* as a subspecies. He contended that the leaf structure and lobing patterns are similar, and since both taxa are habitat specific and their distributions are limited accordingly, a subspecific rank would be appropriate. Examination of the blade divisions reveals that although the blades of both taxa are only divided twice, the degree of division at each level is different, and the blades differ in a number of character states. Furthermore, they differ in a number of additional characters, and each pos-

sesses a number of unique character states. For example, *V. egglesonii* is the only taxon of sub-section *Boreali-Americanae* whose cleistogamous flowers originate underground. Therefore, *V. egglesonii* should be maintained as a distinct species. Additional observations on the seasonal variation in blade shape of *V. egglesonii* were made by SHAVER (1959), and on the ecological life cycle and habitat specificity by BASKIN & BASKIN (1975b).

Viola egglesonii demonstrates polymorphism in the shape of its petal trichomes in some of the flowers. Most of the trichomes on the lower lateral petals are cylindrical, but occasionally a number of trichomes are expanded at the apex. The trichomes on the spurred petal are cylindrical. No evidence for hybridization has been observed in the distinct habitat of this species.

Viola fimbriatula Sm. in Rees, Cycl. 37: *Viola* No. 16. 1817. – **Type:** North America, dry hills from Canada to Virginia, 1817, *Francis Boott s.n.* (holotype: Herb. Smith No. 1380.11, LINN; photo: MICH!).

lc.: [no figure number] Alexander in Gleason, *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*, Vol. 2: 560. 1952; [color] Plate XV [chasmogamous and cleistogamous plants], Klaber, *Violets of the United States*: 45. 1976.

Acaulescent, homophyllous, perennial herb, 2-5 cm high at chasmogamous anthesis; *rhizomes* fleshy, scaly, vertical or slightly oblique, branching, 0.5-2.5 cm long, bearing a few fibrous roots; *stipules* lanceolate, green or green spotted with red-purple, apex acute, margins scarious, entire or irregularly fimbriate, \pm ciliate; *petioles* short: at chasmogamous anthesis 5-12 (21) mm long, green, densely pubescent; *blades* at chasmogamous anthesis widely ovate to ovate-oblong, densely pubescent on the adaxial surface, abaxial surface pubescent and clouded with purple in juvenile leaves, base cordate or subtruncate, margins crenulate, densely ciliate, apex acute-rounded to obtuse, length/width ratio of the largest blades 1.5-1.8 (2.5), apical angle 76°-98° (107°), at the cleistogamous phase oblong to oblong-ovate, base cordate to subcordate with sharply incised dentations, margins above the base shallowly crenate, apex acute; *peduncle* short: 2-4 cm long, green irregularly spotted with dark red-purple, densely pubescent; *bractlets* linear, green dotted with red-purple, apex acute, margins entire, ciliate; *sepals* ovate or lanceolate-ovate, green dotted with red-purple, apex acute, margins scarious, dotted red-purple, and \pm ciliate on the upper half, sepal length/capsule length ratio 0.6; *auricles* 0.5-1.3 mm long, green, \pm dotted with red-purple, apex truncate subtruncate or rounded, glabrous, \pm ciliate on cleistogamous flowers and capsules; *spur* 1.7-2.3 mm long; *petals* violet (RHS # 83B) with a white center, lines on the spurred and lateral petals dark violet, spurred petal 10-15 mm long (including the spur), 4-7 mm wide, apex subtruncate, lower lateral pair 2-6 mm wide, upper lateral pair 4-6 mm wide; *petal trichomes* dense on the spurred and lower lateral petals, cylindrical, ca. 40-50 μ m wide, visible layers of cuticular folds two, cuticular folds tubular, linear, long, and tapering, wider and spaced folds overlaid on densely packed and narrower folds, vertically aligned, convoluted over the apex; *cleistogamous flower peduncle habit*: prostrate; *capsule* yellow-green, length/width ratio 2-2.2; *seeds* moderate brown (ISCC-NBS # 58) comprised of dark brown streaks (59) on a light yellowish brown background (76), 1.3-1.6 mm long, 0.8-1 mm wide, average weight 0.7-0.8 mg, caruncle 0.4-0.6 mm long; *seed coat*: secondary sculpture a blend of semi-circular and elongated-rectangular plates, randomly distributed and connected, and overlaid on the primary sculpture, plates foveate, scrobiculate, or ribbed (often a blends of these types); *chromosome number*: $2n = 54$.

Substrate. – Gravelly soil or coarse sand.

Habitat. – Open *Quercus* forests, edges of forests and forest roads. Frequent associates: *Fragaria* and *Polytrichum*.

General Distribution. – Canada: Nova Scotia to Ontario; U.S.A.: Maine to Wisconsin, south to Georgia and Louisiana.

Discussion. – Two chasmogamous plants on the type specimen are referenced by number to Boott's collection from North America that is listed in Smith's description. Therefore, these plants constitute the holotype. These plants clearly display the characteristic habit and the characters of the species at the chasmogamous phase.

The name *Viola fimbriatula* has often been confused with the name *Viola ovata* that was published by NUTTALL (1818) for the same species. GREENE (1900) clarified the confusion on the priority of Smith's name that resulted from uncertainty about the precise publication date of Rees' Cyclopaedia. He provided the precise date of publication: 23 December 1817, and thus confirmed the priority of the name *V. fimbriatula*.

BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola fimbriatula* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) reduced *V. fimbriatula* to synonymy under *V. sagittata*. MCKINNEY (1992) contended that *V. sagittata* and *V. fimbriatula* are similar in many respects and should be considered as varieties in the same species complex. He reinstated TORREY & GRAY's (1838) varietal status – var. *ovata* – of *V. fimbriatula* under *V. sagittata*.

The boundaries between *Viola fimbriatula* and *V. sagittata* have become obliterated due to vague descriptions of *V. fimbriatula*, the emphasis many authors have put on the similarities between the blade shape of the two species, and the application of the name *V. fimbriatula* to putative hybrids. The name *V. fimbriatula* has become a dumping ground for densely pubescent plants growing in disturbed habitats and possessing short-petioled leaves and blades resembling the shape of the blades of *V. sagittata*. Those plants were most likely hybrids of *V. fimbriatula* with *V. sagittata*, or hybrids and introgressants of *V. sagittata* or *V. fimbriatula* with other taxa of subsection *Boreali-Americanae* possessing undivided blades. *Viola fimbriatula* was a subject of a number of ecological studies (ALLARD & GARNER, 1940; BEATTIE, 1974; ANDERSON, 1983; COOK & LYONS, 1983; BÜLOW-OLSEN, 1984; CURTIS, 1984; CURTIS & KINCAID, 1984; and YOST, 1987) probably because of its frequent occurrence in the northeastern United States. It is likely that at least some of the plants that were used in these studies were identified by using the vague species concepts described above, and did not represent the orthospecies.

BRAINERD (1910a, 1921, 1924) remarked on the confluence of the two species, and provided examples of hybrids between the two species and associated variant forms. He stressed the differences in the pubescence of the leaves, the length of the petiole, blade shape, and the blade base margins as the major characters to distinguish between *V. fimbriatula* and *V. sagittata*. BAIRD-BRAINERD (1942) suggested that *V. fimbriatula* might be distinguished from *V. sagittata* by its ciliate sepals. RUSSELL (1965) stressed the distinction between these species, and added the difference in habitat to the characters provided by Brainerd. VOSS (1985) suggested that *V. fimbriatula* is perhaps only an environmental variant of *V. sagittata*. YOST (1984, 1987) demonstrated, using both cloned plants and plants grown from seed, considerable phenotypic plasticity in petiole length between a putative *V. fimbriatula* that possessed short petioles and was found in an open, grassy field, and a long-petioled form of *V. fimbriatula* (or *V. sagittata*) found in an adjoining shady forest. She concluded that neither the relative nor the absolute length of the petioles can properly be used in trying to distinguish between the two taxa, and left the taxonomic evaluation of the results to others. Voucher specimens were not cited. *Viola sagittata* grows in open grounds on sandy soil, and it is unlikely that it occupied the shady forest habitat and moist substrate described. It is possible that the plants used in Yost's study were hybrids, or belonged to *V. fimbriatula*.

The use of petiole length as the decisive character in distinguishing between the taxa is indeed unwarranted. However, the present study demonstrates that when petiole length is evaluated with additional macromorphological characters, habitat, and substrate, it is one of the characters that clearly distinguish the two taxa. During chasmogamous anthesis there is an overlap in petiole length since the petioles of *Viola sagittata* may be as short as 10 mm. However, later in the season the petioles of *V. sagittata* become longer, up to 10 cm. The major characters and criteria for distinguishing *V. fimbriatula* from *V. sagittata* are listed in Table 1.

The micromorphological structures of the seed coats of the two taxa overlap. The secondary sculpture of the seed coats of *V. fimbriatula* consists of a blend of semi-circular and elongated-rectangular plates that are randomly distributed and connected. These plates are foveate, scrobiculate, or ribbed, and often consist of blends of these types. The secondary sculpture of the seed coats of *V. sagittata* consists of rectangular or semi-circular, foveate to foveolate plates with thickened margins. These plates are usually connected, irregularly oriented, and randomly distributed. However, the petal trichomes of *V. fimbriatula* are narrower than those of *V. sagittata* (ca. 40-50 μm wide vs. 60-70 μm wide), and the ribbed microstructural ornamentation on their surface is different. The overlaid cuticular folds on the trichomes of *V. fimbriatula* are wider and more spaced compared to the capillary and densely packed cuticular folds on the trichomes of *V. sagittata* (GIL-AD, 1995; GIL-AD, in press).

Viola fimbriatula does not display any unique micromorphological characters on the seed coat surface. We cannot rule out the possibility that it might have arisen by speciation of hybrid derivatives, these derivatives then adapting to a different type of habitat than their parents. The morphological data available do not permit speculation about putative ancestors of *V. fimbriatula*; therefore, this hypothesis awaits the inclusion of molecular data.

BRAINERD (1904b, 1906b, 1924), and DOWELL (1910) reported natural fertile hybrids between *Viola fimbriatula* and taxa of subsection *Boreali-Americanae* that were named by HOUSE (1924). They included: $\times V. hollickii$ (*V. fimbriatula* \times *V. affinis*); $\times V. mulfordae$ (Pollard) House (*V. fimbriatula* \times *V. brittoniana*); $\times V. porteriana$ (Pollard) House (*V. fimbriatula* \times *V. cucullata*); $\times V. abundans$ (*V. fimbriatula* \times *V. sagittata*); $\times V. parca$ (*V. fimbriatula* \times *V. septentrionalis*); $\times V. fernaldii$ (*V. fimbriatula* \times *V. sororia*); and $\times V. robinsoniana$ (*V. fimbriatula* \times *V. triloba*).

Table 1. – A Comparison Between *Viola fimbriatula* and *Viola sagittata*

	<i>V. fimbriatula</i>	<i>V. sagittata</i>
<i>During chasmogamous anthesis:</i>		
1. Blade shape	widely ovate to ovate-oblong	elliptic to oblong-lanceolate
2. Blade margins above base	crenulate	entire to crenulate
3. Shape of the blade base	cordate	subtruncate or hastate
4. Blade base margins	crenulate	entire to shallowly crenate
5. Blade length/width ratio	1.5-1.8	2.2-2.8
6. Apical angle	76°-98°	90°-105°
7. Petiole length	5-12 mm	10-30 mm
8. Peduncle length	2-4 cm	4-11 cm
9. Color of the corolla	violet (RHS # 83B)	violet-blue (RHS # 90B/C)
<i>During the cleistogamous phase:</i>		
1. Blade shape	oblong to oblong-ovate	lanceolate-deltoid
2. Blade margins above base	shallowly crenate	entire to shallowly crenate
3. Shape of the blade base	cordate to subcordate	sagittate
4. Blade base margins	sharply dentate	entire to coarsely crenate
10. Habit of the peduncle of the cleistogamous flowers	prostrate	erect
11. Seed color	moderate brown.	deep brown or deep yellowish brown.
12. Habitat:	open <i>Quercus</i> forests, edges of forests and forest roads.	open grounds, mesic sand prairies, open sites in forests
13. Substrate:	gravelly soil or coarse sand.	sandy soil

Viola missouriensis Greene in Pittonia 4: 141. 1900. – **Types:** U.S.A. Missouri. [Jackson County:] Courtney, 30 April 1899, *B. F. Bush* 70 (lectotype: NY! – no. 29621 designated by MCKINNEY (1992) as “holotype”; isoelectotypes: NY! – no. 29619, NDG! – no. 33214/Herbarium Greeneanum no. 38308).

lc.: Species No. 9, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 30. 1921; [color] Plate No. 34, Baird-Brainerd, *Wild Violets of North America*: 99. 1942.

Acaulescent, homophyllous, perennial herb; *rhizomes* fleshy, scaly, vertical to oblique, often branched, 1-6 (8.5) cm long, bearing fibrous roots; *stipules* lanceolate, acute, margins entire to irregularly glandular fimbriate, blotched with red-purple on a yellow-green background, \pm ciliate; *petioles* green, glabrous; *blades* green, glabrous, at chasmogamous anthesis reniform to deltoid-ovate with a subtruncate to cordate base, margins crenate-serrate, apex acute to acuminate, length/width ratio of the largest blades 1.1-1.7, apical angle 43° - 76° (84° - 86°), at the cleistogamous phase deltoid with deeply cordate to auriculate base, margins crenate-serrate with large, uneven serrations on the lower half, and shallow, uneven serrations on the upper half, and bluntly attenuate apex; *peduncle* (3) 4-16 cm long, green, glabrous; *bractlets* lanceolate, blotched with red-purple on a yellow green background, apex acute, margins eciliate; *sepals* lanceolate to ovate, green sparsely dotted with red-purple, apex acute to acuminate, margins scarious and finely ciliate, sepal length/capsule length ratio 0.2-0.4; *auricles* 0.4-0.8 mm long, green, apex truncate to rounded, margins \pm ciliate; *spur* 1.8-2.3 mm long; *petals* violet-blue (RHS # 92A) with a white center, often bordered with a dark violet area around the center, lines on the lateral and spurred petals dark violet, spurred petal 15-19 mm long (including the spur), 3-7 mm wide, apex rounded to subtruncate, lower lateral pair 4-6 mm wide, upper lateral pair 6-8 mm wide; *petal trichomes* borne on the lower lateral petals, absent on the spurred petal, cylindrical, gradually widened toward the apex, ca. 100-120 μ m wide, visible layers of cuticular folds one, cuticular folds capillary to tubular, highly convoluted, varied in length, randomly aligned, densely packed and overlapping; *cleistogamous flower peduncle habit*: prostrate; *capsule* yellow-green sparsely spotted and dotted with red-purple, length/width ratio 2-2.2; *seeds* dark orange yellow to strong yellowish brown (ISCC-NBS # 72 to 74), 1.5-2.2 mm long, 0.9-1.4 mm wide, average weight 0.9 -2.0 mg, caruncle 0.8-1.3 mm long; *seed coat*: outer periclinal walls ribbed with finely intercrossed thickenings, secondary sculpture with reticulate-terete thickenings with a rough surface, and randomly distributed and elongated or semi-circular solitary or connected plates, irregularly overlaid over the surface, plates with blends of scrobiculate, falsifoveate, and foveate surfaces; *chromosome number*: $2n = 54$.

Substrate. – Sandy or silty alluvial soils.

Habitat. – Low woods, floodplains, ravine bottoms, creek banks.

General Distribution. – Indiana to South Dakota, south to Florida, Louisiana and Texas.

Typification. – MCKINNEY (1992) designated *B. F. Bush* 70 at NY as the holotype and an additional specimen bearing the same number as an isotype. There was no designation of the type status by Greene on these specimens, and both were marked later “Co-Type” at NY. However, GREENE (1900) listed in the protologue the following syntypes (the items listed in brackets are added here on the basis of the information on the labels of the specimens at NDG): (1) [Jackson County:] Leeds, 19 April 1895, *B. F. Bush* [231]; (2) [Jackson County:] Courtney, 10 May 1898, *B. F. Bush* [108 and 95]; (3) Courtney, 30 April 1899, *B. F. Bush* [70 and 88]; (4) [Jackson County:] Independence, 24 April 1898, *K. Mackenzie* [8]; (5) [Clay County:] Randolph, 23 April 1899, *K. Mackenzie* [10 and 11]. All these specimens bear chasmogamous flowers except for *B. F. Bush* 95.

From Greene’s comment (following the protologue) about the cleistogamous flowers on “later specimens” it can be inferred that he also examined the cleistogamous specimens when describing the species. The collection date listed on the labels on *B. F. Bush* 108 and 95 is identical although the plants were collected at different developmental phases in the same area. It is likely that *B. F. Bush* 108 was collected in April and that a wrong date was written on the label

by mistake. In a letter to Greene dated 16 November 1899 (filed in the University of Notre Dame Archives) Bush explained that he used new collection numbers for each year, beginning over again in the spring. He also indicated that "Nos. 70, 88, 150 and 288 are absolutely the same [species]", and then described making specimens from the chasmogamous plants, labeling the patches they were sampled from and collecting summer [cleistogamous] specimens. Although he did not list numbers 95 and 108 in this description, it is likely that he practiced the same collecting methods with these specimens.

The labels of the duplicate syntypes of *B. F. Bush* 70 and 88 at NY and at NDG are similar. Yet, the NDG labels were annotated in handwriting only with the specific epithet "emarginata," whereas the NY labels were annotated in handwriting (most likely Bush's) with "n. sp." This annotation was later crossed-out and re-annotated with the specific epithet *missouriensis* and Greene's name. The label on *Bush* 88 includes also the citation: "Pitt. iv. 142." These annotations on the NY specimens match Greene's handwriting. It is likely that Greene annotated the specimens for Bush, and added the citation on the label of no. 88, so Bush could look up the description in Pittonia. Bush then deposited these specimens at NY. None of the other NDG syntypes is annotated with the specific epithet *missouriensis*. Greene has annotated specimens that he sent to other people, but often left specimens in his herbarium without annotations. He kept these specimens in folders usually bearing the new combinations he erected (B. J. HELLENTAL pers. comm., 1995). The annotations on the NY syntypes are proof that Greene has seen the specimens, but are not sufficient for inferring that Greene regarded them more significant than the NDG specimens. The lectotype should have been selected from Greene's herbarium. However, since Greene has seen the NY specimen it is not possible to overturn McKinney's lectotypification.

Discussion. — BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola missouriensis* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) reduced *V. missouriensis* to synonymy under *V. sororia*. MCKINNEY (1992) transferred it to *V. sororia*, and erected the combination *Viola sororia* var. *missouriensis*. He recognized the blade shape and habitat, in part, as the major criteria for a varietal designation. The present study demonstrates that additional reproductive characters that delimit *V. missouriensis*. These characters include the color of the corolla, the shape of the petal trichomes, the color of the capsule and its length/width ratio, seed color, and the micromorphological structures of the seed coat surface. Therefore, it should be recognized as a distinct species.

Hybrids and introgressants of *V. missouriensis* with *V. sororia* (BRAINERD, 1924; RUSSELL, 1958a, 1965), or with *V. affinis* are common, and may render field and herbarium identifications difficult.

Viola nephrophylla Greene in Pittonia 3: 144. 1896. — **Type:** U.S.A. Colorado: the valley of the Cimarron River, in dry thickets of scrubby willows and *Potentilla fruticosa*, 29 Aug. 1896, E. L. Greene s.n. (holotype and isotype: NDG!).

lc.: Species No. 20, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: [color plate] opposite page 64. 1921; Fig. 2 [habit of a chasmogamous plant], Russell & Crosswhite in Madroño 17: 58. 1963; Plate XII [chasmogamous and cleistogamous plants], Klaber, *Violets of the United States*: 43. 1976.

Acaulescent, homophyllous, perennial herb, 3-6 cm high at chasmogamous anthesis; *rhizomes* fleshy, scaly, vertical to oblique, 0.5-2 cm long, bearing fine fibrous roots; *stipules* yellow-green blotched with red-purple, lanceolate, acute, margins entire irregularly fimbriate, eciliate; *petioles* green or green irregularly dotted with dark red-purple, glabrous; *blades* base cordate, margins crenate to crenate-serrate, eciliate, adaxial and abaxial surfaces glabrous or scarcely pubescent on the adaxial surface on the basal lobes, juvenile blades often minutely pubescent on the adaxial surface, light gray-green on the adaxial surface, clouded with purple on the abaxial

surface, apex obtuse, at chasmogamous anthesis cordate to reniform, length/width ratio of the largest blades 0.7-1.3, apical angle 101°-145°; *peduncles* 3-7 (10-15) cm long, green, often spotted with brown-purple, glabrous; *bractlets* lanceolate, green dotted with red-purple, apex acute margins entire to irregularly glandular fimbriate, eciliate; *sepals* ovate, green sparsely dotted with red-purple, apex obtuse or acute, margins scarious and eciliate, sepal length/capsule length ratio 0.3-0.4; *auricles* 0.5-1.1 mm long, green sparsely dotted with purple, apex truncate, subtruncate, or rounded, eciliate; *spur* 1.2-2.8 mm long; *petals* violet (RHS # 87B/C) with a white center, lines on the spurred and lateral petals violet, spurred petal wider toward the apex, emarginate, 12-18 mm long (including the spur), 6-7 mm wide, lateral petals tapering to almost clawed base, lower lateral pair 5-6 mm wide, upper lateral pair 3-4 (5) mm wide; *petal trichomes* borne on the lower lateral petals and less densely on the spurred petal, cylindrical, 40-50 (60) μ m wide, visible layers of cuticular folds one, cuticular folds tubular to capillary, long, narrow, tapering, vertically aligned, densely packed and overlapping; *cleistogamous flower peduncle habit*: ascending; *capsule* yellow-green, length/width ratio 1.2-1.5; *seeds* dark yellowish brown to dark brown (ISCC-NBS # 78 to 59), 1.3-1.8 mm long, 0.9-1.2 mm wide, average weight 0.5-1.3 mg., caruncle 0.5-1 mm long; *seed coat*: primary sculpture cells penta- or hexagonal, usually elongated in one direction, outer periclinal walls unevenly smooth, secondary sculpture with reticulate-terete, and wide secondary wall thickenings with a smooth surface, overlaid on the outer periclinal walls; *chromosome number*: $2n = 54$.

Substrate. – Calcareous loam.

Habitat. – Cool, shaded, wet banks of slow streams, rivers, and lakes, wet soil pockets of protected rock crevices.

Distribution. – Southeastern to southwestern Canada, northeastern United States extending west to the Pacific Northwest, eastern California, and southeastern United States.

Discussion. – BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963, 1991), and RUSSELL (1965) maintained *Viola nephrophylla* as a distinct species. Several varieties of *V. nephrophylla* and additional species from populations in the Rocky Mountains were named by E. L. Greene and others. BRAINERD (1905) concluded that the plants referred to as *V. cognata*, *V. vagula* and *V. nephrophylla* represent only one species. BAIRD-BRAINERD (1942) noted that *V. cognata* and *V. arizonica* resemble *V. nephrophylla*, and are considered by many botanists to be only genetic variations of it. RUSSELL & CROSSWHITE (1963) analyzed variants collected in Arizona and Colorado, and could not justify the recognition of the names *V. arizonica* Greene, *V. cognata* Greene, *V. prionosepala* Greene, and *V. mccabeiana* Baker. MCKINNEY (1992) listed *V. nephrophylla* in synonymy under *V. sororia* var. *sororia*. Furthermore, he erected the combination *Viola sororia* var. *affinis* to designate the species previously known as *Viola nephrophylla*. This taxon was later elevated to the subspecies rank: *Viola sororia* subsp. *affinis* (LITTLE & MCKINNEY, 1992; LITTLE, 1993; LITTLE, 1996). These changes were made on the basis of observations of herbarium specimens, reports of past workers, and his interpretation of LeConte's description of *V. affinis*.

Viola nephrophylla possesses a distinct suite of both macromorphological and micromorphological characters, including reticulate-terete and wide secondary wall thickenings with a smooth surface that are overlaid on unevenly smooth outer periclinal walls of the seed coat (GIL-AD, 1995; GIL-AD, in press), along with habitat and substrate specificity. Therefore, it is a distinct species.

SEM of the seed coats of the two most mature seeds sampled from the holotype revealed deviation from the features detected on the seed coat surfaces of the orthospecies sampled from two pure populations [*Gil-ad* 317 and *Morefield* 4355 (MICH)]. Both collections are from California where there is no other taxon belonging to subsection *Boreali-Americanae*. The seed coats of the holotype possess scattered plates over the typical reticulate-terete thickenings of the

orthospecies (GIL-AD, 1995; GIL-AD, in press). These plates provide evidence for putative introgression of a taxon of subsection *Boreali-Americanae* possessing plates on the secondary sculpture into *V. nephrophylla*. Although no data on associates is available from the collection site, a likely candidate for the introgressant is *V. novae-angliae*, which possesses similar plates on the secondary sculpture. However, there are no reports in the literature on populations of *V. novae-angliae* in Colorado. WEBER (1987, 1990) listed *V. nephrophylla* and *V. papilionacea* in synonymy under McKinney's *V. sororia* subsp. *affinis*. The brief description in his keys depicting them as having large, cordate, and strongly pointed leaves, and describing their infrequent occurrence in floodplains and piedmont valleys, may indicate plants of hybrid origin. Conversely, it may indicate that more than one species inhabits the area, and thus could have been the introgressant. The possibility that the seeds examined are abnormal is remote since similar structures have been observed on seeds from other samples (e.g., *Gil-ad 488*, MICH). The sheet of the holotype carries 10 plants: one bearing only one chasmogamous flower, three bearing chasmogamous flowers and capsules, and six bearing capsules only. The presence of chasmogamous flowers on the plants in late August is attributed to a second onset of chasmogamy, which occasionally occurs in some of the taxa of the subsection during late summer and early autumn. Superficial observations of the macromorphology may suggest that all these plants fall within the range of the orthospecies. However, careful examination reveals a few deviations: 1. All the seeds (pooled together in one packet) deviate in the color of their seed coats from the typical color of the seed coat of the orthospecies. About half of the seeds (at different degrees of maturity) have orange-yellow surfaces with sporadic darker spots. The other half (including the two most mature seeds that were examined with SEM) have deep to dark brown spots on an olive-green background; 2. The capsules have purple-brown spots on the surface as opposed to the purely green surface in the orthospecies; 3. The sepals are densely and regularly spotted with red-purple as opposed to the sparsely spotted surface and the scarious margin of the sepals of the orthospecies; and 4. Both the adaxial and abaxial surfaces of the blades of the plants bearing capsules are pubescent along the veins as opposed to the mostly glabrous surfaces in the orthospecies. The SEM data provide evidence that the population from which Greene sampled these plants included introgressants, however, the name *Viola nephrophylla* is provisionally maintained, as not all elements of Greene's specimen have been conclusively shown to be genetically impure.

When growing in disturbed habitats, such as moist, grassy fields on rich soil, *Viola nephrophylla* often possesses longer petioles, larger leaves, peduncles 10-15 cm long, and a \pm glabrous spurred petal. With these ranges and character states, it could superficially be confused with *V. sororia*, especially when mounted on herbarium sheets. Distinct populations of *V. nephrophylla* can be found in the western cordillera. East of the western cordillera, hybridization and introgression with other taxa of subsection *Boreali-Americanae* are common, and those with taxa possessing undivided blades could be intractable unless seed micromorphological structures were examined and corroborated with macromorphological characters.

BRAINERD (1906b, 1924) reported natural fertile hybrids of *Viola nephrophylla* with taxa of subsection *Boreali-Americanae*, two of which were named by HOUSE (1924). They included: $\times V. subaffinis$ House (*V. nephrophylla* \times *V. affinis*); $\times V. insessa$ (*V. nephrophylla* \times *V. cucullata*); *V. nephrophylla* \times *V. sororia*; and *V. nephrophylla* \times *V. pedatifida*. RUSSELL (1965) reported hybrids with *V. missouriensis* and *V. sagittata*. *Viola nephrophylla* hybridizes also with *V. septentrionalis*, *V. novae-angliae*, and with *V. fimbriatula* in northeastern United States and Canada.

Viola novae-angliae House in *Rhodora* 6: 226, Plate 59. 1904. – **Type:** U.S.A. Maine. Aroostook County: Valley of the Saint John River, Fort Kent, sandy shore, 15 June 1898, *M. L. Fernald* 2245 (holotype: US!; isotype: NY).

Ic.: Plate 59, House in *Rhodora* 6: opposite page 226. 1904; Species No. 16, Brainerd in *Vermont Agric. Exp. Sta. Bull.* 224: 46. 1921; reprinted [color] Plate 40, Baird-Brainerd, *Wild Violets of North America*: 113. 1942.

A Key to the Subspecies of *Viola novae-angliae*

- 1a. Blades narrow-deltoid to deltoid-ovate, apical angle 40°-77°, margins unevenly crenate, adaxial surface green, sparsely pubescent along the major veins, abaxial surface pale green, pubescent; petioles sparsely pubescent to glabrous; peduncles pubescent below the bractlets, sparsely pubescent above the bractlets; bractlets deltoid to lanceolate; sepals lanceolate-ovate, glabrous or sparsely ciliate; auricles eciliate; seeds 1.4-1.7 mm long, 0.9-1.1 mm wide, average weight 0.4-1 mg, caruncle 0.8-1.3 mm, linear only; habitat river flood shores, ledges on rivers, rock crevices, known from New Brunswick, Ontario, Michigan Upper Peninsula, Wisconsin, and Minnesota *Viola novae-angliae* subsp. *novae-angliae*
- 1b. Blades lanceolate-ovate or deltoid lanceolate, apical angle 29°-79°, margins crenate-serrate, adaxial surface dark-green, densely pubescent, abaxial surface gray-green, densely pubescent; petioles densely pubescent; peduncles pubescent; bractlets deltoid; sepals ovate, densely ciliate; auricles densely ciliate; seeds 1.6-2 mm long, 1-1.2 mm wide, average weight 0.8-1.2 mg, caruncle 1-1.4 mm long, geniculate or linear; habitat grassy glades in open *Pinus banksiana* stands, apparently endemic to northern Michigan
 *Viola novae-angliae* subsp. *grisea*

Viola novae-angliae House subsp. *novae-angliae*

Acaulescent, homophyllous, perennial herb; *rhizomes* fleshy, scaly, vertical, oblique, or horizontal, some branching at the cleistogamous phase, 0.4-3 cm long, bearing fibrous roots; *stipules* linear-lanceolate, green blotched with red-purple, apex acute, margins entire to irregularly fimbriate, eciliate; *petioles* 2-15 cm long, green spotted with purple, sparsely pubescent to glabrous; *blades* narrow deltoid to deltoid-ovate, base cordate, margins crenate with uneven crenations, ciliate, apex acute or rounded, at chasmogamous anthesis deltoid-lanceolate, length/width ratio of the largest blades 1.7-2.4, apical angle 40°-77°, in late summer some blades become wider with a deep sinus at the base, length/width ratio of the largest blades 1.1-1.6, adaxial surface green, sparsely pubescent along the major veins, abaxial surface pale green, pubescent, clouded with purple in juvenile blades; *peduncle* 3-10 (14) cm long, green spotted with red-purple, pubescent below the bractlets, sparsely pubescent above the bractlets; *bractlets* deltoid to lanceolate, apex acute, blotched with red-purple on a yellow green background, margins entire to glandular fimbriate, eciliate; *sepals* lanceolate-ovate, green densely spotted with red-purple, apex obtuse, margins scarious, glabrous rarely sparsely ciliate; *auricles* 0.5-1.6 mm long densely spotted with red-purple on a green background, apex truncate to rounded, eciliate; *spur* 2-3 mm long; *petals* violet with a white center, lines on the spurred and lateral petals dark violet, spurred petal widely spatulate, 14-21 mm long (including the spur), 5-8 (9) mm wide near the apex, apex rounded or emarginate, lower lateral pair 4-6 mm wide, upper lateral pair 5-7 mm wide; *petal trichomes* dense on the spurred and the lower lateral petals, rarely few on the upper lateral petals, cylindrical, narrow, 30-40 µm wide, visible layers of cuticular folds two, cuticular folds capillary or narrow tubular, elongated and randomly spaced in the upper layer, capillary and densely packed in the lower layer; *cleistogamous flower peduncle habit*: prostrate; *capsule* blotched and spotted with red-purple on a yellow-green background, length/width ratio 1.1-1.4; *seeds* close to yellow-brown to deep brown (ISCC-NBS # 56), 1.4-1.7 mm long, 0.9-1.1 mm wide, average weight 0.4-1 mg, caruncle 0.8-1.3 mm long; *seed coat*: secondary sculpture predominantly narrow and flat reticulate secondary wall thickenings overlaid on wide and reticulate-terete thickenings with irregularly distributed circular or elliptical plates possessing a smooth center and circumscribed by short, segmented and rounded thickenings, thickenings occasionally cover the center of the plates; *chromosome number*: $2n = 54$.

Substrate. – Sandy loam, peaty moist substrate with traces of sand and silt in rock-crevices.

Habitat. – River flood shores, rocky river banks, argillite ledges on rivers, in rock-crevices in openings in *Populus-Betula* woods.

General Distribution. – Canada: New Brunswick, western Ontario to southeastern Manitoba; U.S.A.: Upper Peninsula of Michigan, northern Wisconsin, Minnesota.

Discussion. – BRAINERD (1905, 1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola novae-angliae* as a distinct species. Cronquist (*in* GLEASON & CRONQUIST, 1991) reduced it to synonymy under *V. sororia* with a comment indicating that it is a form transitional to *V. sagittata*. MCKINNEY (1992) designated it as a variety of *V. sororia* without providing a clear rationale for his decision. The association of *V. novae-angliae* with *V. sororia* is unwarranted, especially when the reproductive characters are evaluated. BRAINERD (1905, 1921) considered *V. novae-angliae* closely related to *V. septentrionalis*. Brainerd's suggestion is justified on the basis of a number of synapomorphies. The two species possess capsules similar in shape and color pattern, the habit of the peduncle of their cleistogamous flowers is prostrate, and petal trichomes are borne on the spurred petal in addition to the lower lateral petals. *Viola novae-angliae* is a distinct species possessing a suite of characters that distinguish it from *V. septentrionalis*. Most notable are the shape of the blades, the narrow petal trichomes (30-40 μm wide vs. ca. 60-90 μm wide), the shape and color of the seeds, the micromorphological structures on the seed coat surface. The seed coat surface of *V. novae-angliae* subsp. *novae-angliae* consists of narrow reticulate, flat to terete secondary wall thickening and circular or elliptical plates that are smooth, and circumscribed by short, segmented and rounded thickenings whereas the seed coat of *V. septentrionalis* consists of aggregates of intertwined and convoluted terete, narrow thickenings, connected by reticulate-terete, narrow thickenings and irregularly distributed (GIL-AD, 1995; GIL-AD, *in press*). BALLARD & GAWLER's (1994) speculation (on the basis of macromorphology, distribution data and habitat) that *V. novae-angliae* may represent a derivative of hybridization between *V. sagittata* and *V. sororia* is not supported by the micromorphological data.

There are no reports in the literature about hybrids, except for a comment by RUSSELL (1965) about the grading of *Viola novae-angliae* into *V. sagittata* in northern Wisconsin and Minnesota. A population of *V. novae-angliae* subsp. *grisea* growing under a *Pinus banksiana* stand has been recorded in Crawford County, Michigan growing at the vicinity of a population of *V. sagittata* in the open (CHITTENDEN pers. comm., 1992; GIL-AD pers. observations). Plants of *V. nephrophylla* introgressed by *V. novae-angliae* were collected by N. L. Gil-ad (Gil-ad 488, MICH) in the flood-plain zone of the Saint John River, Aroostook County, Maine in 1993. The plants are characterized by blades with acute apical angles, and traces of secondary wall thickenings characteristic of the seed coat surface of *V. novae-angliae* on predominantly secondary wall thickenings characteristic of *V. nephrophylla* (GIL-AD, 1995). An intermediate hybrid of *V. novae-angliae* and *V. nephrophylla* grew near the population of the introgressants.

Fernald collected the holotype of *Viola novae-angliae* at Fort Kent on 15 June 1898, and assigned it the number 2245. The plants bear chasmogamous buds only. Three days later, he collected another specimen at Saint Francis, and assigned it the number 2244. The plants of this specimens bear fully open chasmogamous flowers (BRAINERD, 1921). In spite of the reversed numerical order, and the phenological stage, the earlier collection is the holotype.

***Viola novae-angliae* subsp. *grisea* (Fernald) Gil-ad, stat. & comb. nov.**

BASIONYM: *Viola septentrionalis* var. *grisea* Fernald *in* Rhodora 37: 301, Plate 375. 1935.
– **Type:** U.S.A. Michigan. Schoolcraft County: dry sandy plain near Driggs, 2 July 1934, M. L. Fernald & H. S. Pease 3430 (holotype: GH!; isotype: MICH!).

lc.: Plate 375, Fernald *in* Rhodora 37: opposite page 301. 1935.

Acaulescent, homophyllous, perennial herb; *rhizomes* fleshy, scaly, vertical to oblique, 1-5 cm long, bearing fibrous roots; *stipules* linear-lanceolate, green blotched with red-purple, apex acute, margins entire to irregularly glandular fimbriate, \pm ciliate; *petioles* 4-21 cm long, green spotted with purple, densely pubescent; *blades* lanceolate-ovate or deltoid-lanceolate, base cordate with a deep sinus, often oblique, margins crenate-serrate, densely ciliate, apex acute, at chasmogamous anthesis length/width ratio of the largest blades 1.6-2.3, apical angle 29° - 79° , adaxial surface dark green, densely pubescent, abaxial surface (gray-green), often clouded with purple, densely pubescent; *peduncles* (9) 11-18 cm long, green spotted with red-purple, pubescent to densely pubescent, especially below the bractlets; *bractlets* deltoid, blotched with red-purple on a yellow green background, margins entire to irregularly glandular fimbriate, eciliate, apex acute; *sepals* ovate, densely spotted with red-purple on a green background, apex obtuse, \pm densely pubescent on the adaxial surface, margins scarious, densely ciliate, cilia up to 0.4 mm long, sepal length/capsule length ratio 0.5-0.7; *auricles* 0.4-1.5 mm long, densely spotted with red-purple on a green background, apex truncate to rounded, densely ciliate; *spur* 1-3 mm long; *petals* pale violet (RHS # 85A) with a white center extending up to half of the length of the petals, lines on the spurred and lateral petals dark violet, spurred petal 15-19 mm long (including the spur), 6-9 mm wide near the apex, apex truncate to rounded, lower lateral pair 4-6 mm wide, upper lateral pair 5-10 mm wide; *petal trichomes* dense on the on the spurred and lower lateral petals, rarely a few trichomes on the upper lateral petals, cylindrical, 30-40 μ m wide, visible layers of cuticular folds two, cuticular folds capillary, elongated, and densely packed; *cleistogamous flower peduncle habit*: prostrate; *capsule* blotched and spotted with red-purple on a yellow-green background, length/width 1.0-1.4; *seeds* deep brown (ISCC-NBS # 56), 1.6-2 mm long, 1-1.2 mm wide, weight 0.8-1.2 mg, caruncle 1-1.5 mm long, geniculate or linear; *seed coat*: secondary sculpture consisting of wide reticulate-terete thickenings with deep and wide depressions among them, and irregularly distributed circular to elliptical plates circumscribed by short, segmented and rounded thickenings, plates center smooth or occasionally covered by the thickenings.

Substrate. – Sandy soil saturated with humus.

Habitat. – Moist grassy glades in open *Pinus banksiana* stands.

General Distribution. – Michigan, Schoolcraft and Crawford Counties.

Discussion. – All the authors succeeding Fernald have not recognized *Viola septentrionalis* var. *grisea*. MCKINNEY (1992) reduced it to synonymy under his new combination *V. sororia* var. *novae-angliae*. BALLARD (1994) did not recognize it as a distinct taxon, and listed it as a synonym under *V. novae-angliae*.

FERNALD (1935, 1950) pointed out that this taxon is superficially similar to *V. novae-angliae* on the basis of the blade shape. Yet, he designated it as a variety of *V. septentrionalis* on the basis of the characteristic capsule, the strongly ciliate auricles, the dense pilose-hirsute trichomes on the abaxial surface, and the characteristic seeds of *V. septentrionalis*. He also emphasized the overall pubescence of the plants, which is denser than that of *V. septentrionalis*.

The present study demonstrates that the taxon named *Viola septentrionalis* var. *grisea* shares in addition to blade shape a number of reproductive characters with *V. novae-angliae*, and should, therefore, be recognized as a subspecies of *V. novae-angliae*. Table 2 compares the two subspecies of *V. novae-angliae* and *V. septentrionalis*. All three taxa possess capsules similar in color pattern, but the range of length/width ratio of the capsules of *V. septentrionalis* is larger. The cleistogamous flowers of all three taxa are borne on prostrate peduncles. The auricles of subsp. *novae-angliae* are eciliate compared to the ciliate auricles of *V. septentrionalis* and subsp. *grisea*. However, the pubescence on the foliage of subsp. *novae-angliae* varies with the habitat, and should not serve as a main criterion to delimit taxa at the species level. Furthermore, the seeds of subsp. *grisea* are more similar in color and shape to those of subsp. *novae-angliae*, and not to the seeds of *V. septentrionalis*. The micromorphological structures of the seed coat surface of subsp. *novae-angliae* and subsp. *grisea* are also quite similar. The seed coat of subsp. *grisea* consists of wide reticulate and uneven surface with deep and wide depressions, and sparser plates. The segmented and rounded thickenings often cover the center of the plates or are less cir-

Table 2. – A Comparison Between *Viola novae-angliae* and *Viola septentrionalis*

	<i>V. novae-angliae</i> subsp. <i>novae-angliae</i>	<i>V. novae-angliae</i> subsp. <i>grisea</i>	<i>V. septentrionalis</i>
Seed color	deep brown (56)	deep brown (56)	dark yellowish brown (78)
Seed length (mm)	1.4-1.7	1.6-2	1.6-2.1
Seed width (mm)	0.9-1.1	1-1.2	0.9-1
Seed length/width	1.3-1.7	1.3-1.7	1.6-2.3
Caruncle length (mm)	0.8-1.3	1-1.5	0.8-1.3
Seed average weight (mg)	0.4-1	0.8-1.2	0.6-1.1
Caruncle shape	linear	geniculate or linear	linear
Capsule length/width	1.1-1.4	1-1.4	1.4-1.6
Petal trichomes	narrow	narrow	wide
Spur length (mm)	1-3	1-3	2-3
Petals color	violet?	pale violet	violet
Sepals shape	lanceolate-ovate	ovate	broadly ovate to ovate
Sepals and auricles color	red-purple	red-purple	green/red-purple at the cleistogamous phase
Sepals ciliation	glabrous or sparsely ciliate	densely ciliate	densely ciliate
Auricles ciliation	eciliate	densely ciliate	ciliate
Peduncles	pubescent below the bractlets, sparsely pubescent above	pubescent	pubescent
Bractlets shape	deltoid to lanceolate	deltoid	linear-lanceolate
Petioles	sparsely pubescent or glabrous	densely pubescent	pubescent
Blade shape	narrow deltoid to deltoid ovate/deltoid-lanceolate	lanceolate-ovate or deltoid-lanceolate	broadly ovate to cordate
Blade length/width	1.4-2.4	1.6-2.3	1-1.3
Blade apical angle	40°-77°	29°-79°	74°-95°
Blade margins	unevenly crenate	crenate-serrate	crenate-serrate
Adaxial surface color	green	dark green	green
Abaxial surface color	pale green	gray-green	gray-green
Adaxial pubescence	sparsely pubescent	densely pubescent	pubescent
Abaxial pubescence	pubescent	densely pubescent	pubescent
Substrate	sandy loam, sand and silt in rock crevices	sandy soil with humus	loam mixed with conifer litter
Habitat	river flood shores, ledges on rivers, rock crevices.	grassy glades in open <i>Pinus banksiana</i> stands	openings in coniferous woods, open mixed woods in partial shade

cumscribed and the additional reticulate pattern connecting the plates is less prominent or obscured compared to the seed coats of subsp. *novae-angliae* (GIL-AD, 1995; GIL-AD, in press). In addition, the range of length/width ratio of the seeds of *V. septentrionalis* is larger, and the petal trichomes of both subspecies of *V. novae-angliae* are narrower than those of the petal trichomes of *V. septentrionalis*. The sepals and auricles of *V. septentrionalis* are green at chasmogamous anthesis, but turn into green spotted with red-purple on the cleistogamous flowers. *Viola septentrionalis* differs also in the shape of the bractlets, the shape of the blade, and the apical angle of the largest blades at chasmogamous anthesis. Subspecies *grisea* possesses higher maximum values of seed dimensions than the values of the seeds of subspecies *novae-angliae*, and differs also in the degree of sepal ciliation, auricle ciliation, blade margins, intensity and hue of the blade color, degree of pubescence on the blades, and habitat. Petiole length varies in both subspecies. In open sites the petioles are short, but they become elongated when the plants are shaded and surrounded in grassy situations. Only three populations of subsp. *grisea* have so far been discovered: one in Schoolcraft County, and two in Crawford County, Michigan. A putative *V. novae-angliae* bearing a single chasmogamous flower was discovered by Don Henson in rock-crevices in openings in *Populus-Betula* woods in Schoolcraft County in 1971 (Henson 53, MICH). It is allopatric to the subsp. *grisea* population. This may have been a relict of a larger population disjunct from the two centers of distribution of the species: New England and the Maritime provinces, and the northwestern Great Lakes Region.

Viola nuevo-leonensis W. Becker in Repert. Spec. Nov. Regni Veg. 18: 125. 1922. – **Type:** México, Nuevo León: Sierra Madre supra Monterrey, 2800 pedalis, 10 March 1906, *Pringle 10235* (holotype: HBG!; isotypes: BM!, CAS!, CM, F!, GH!, MEXU!, MICH!, MO!, NY!, TEX, US!).

Ic.: Fig. 3A-I.

Acaulescent, heterophyllous, perennial herb, 8-25 cm high; *rhizomes* fleshy, oblique, 2-9 cm long, 0.2-1.0 cm wide bearing stout fibrous roots up to 12 cm in length and up to 1.5 mm in diameter; *stipules* linear-lanceolate, acute, costa shifted to the right on the adaxial, and protruding on the abaxial, green blotched with red-purple, margins scarious, \pm ciliate, irregularly fimbriate, fimbriae 1-2.5 mm long; *petioles*, 4-21 cm. long, green, often spotted or painted with purple, pubescent (especially on the upper half), sparsely pubescent on mature leaves; *blades* at chasmogamous anthesis 2.8-5.5 (7.1) cm long, 2.9-5.4 (9.7) cm wide, early blades cordiform, at anthesis becoming broadly deltoid-reniform or subtrilobed to trilobed with a narrow undivided middle lobe, lateral lobes crescent-shaped, coarsely toothed, apex obtuse to acute, base decurrent, margins crenate-serrate, strigose on the adaxial and abaxial; *peduncle* 10-17 (19) cm long, green, pubescent; *bractlets* borne at about middle to 1/3 of the peduncle, staggered or at the same level, 3.1-5.7 mm long, lanceolate, green with greyed-purple streaks, apex acute, margins scarious, irregularly fimbriate especially at the lower half, ciliate; *sepals* 4-7 mm long, 1-3.9 mm wide, ovate to ovate-lanceolate, green spotted with greyed-purple, especially in a patch over the attachment of the sepals and auricles, apex acute, irregularly pubescent on the adaxial surface, margins scarious and ciliate, sepal length/capsule length 0.3-0.5; *auricles* 0.5-1.5 mm long, green spotted with purple, apex rounded to subacute, or subtruncate, ciliate; *spur* 1.2-1.7 mm long; *petals* pale violet (RHS # 86D) or violet blue (RHS # 90D) with a white patch on the lower one third of all petals and dark violet lines on the spurred petal only, lower lateral pair frequently curled at the apex; spurred petal retuse, 11-20 mm long (including the spur), 4.9-6.1 mm wide, lower lateral pair 4.0-4.7 mm wide, upper lateral pair 4.7-5.6 mm wide; *petal trichomes* borne on the lower lateral petals near the base, none on the spurred petal, short, cylindrical, 60-80 μ m wide, visible layers of cuticular folds one, cuticular folds tubular, elongated, unevenly thick, randomly aligned and densely packed on the apex, vertically aligned, spaced and randomly overlapping below the apex; *stamens* filaments 0.3-0.5 mm long, the anther thecae ca. 2 mm long, the anterior appendages ca. 1 mm long, the posterior (spur) appendages extending into the spur; *style* ca. 2 mm

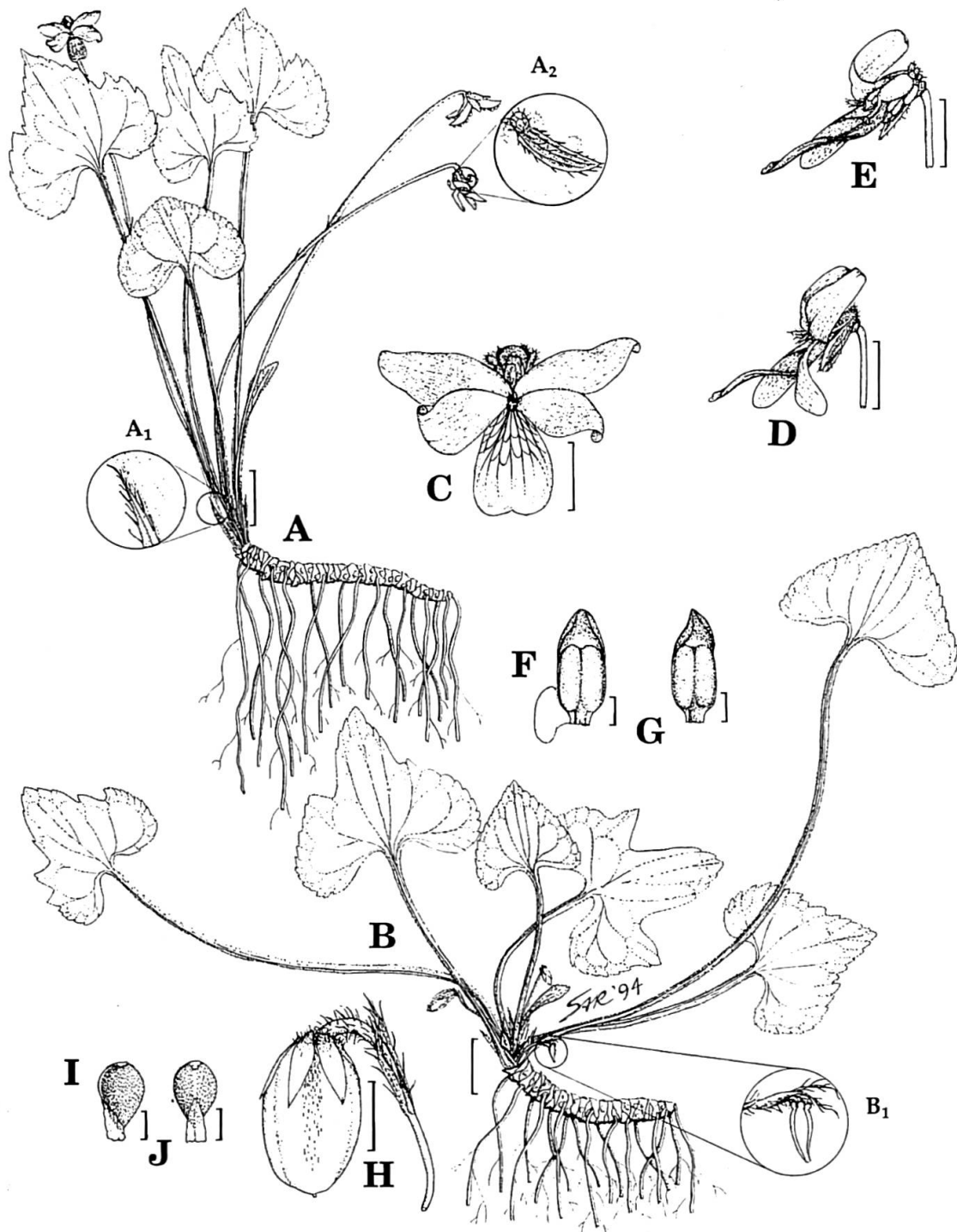


Fig. 3. – *Viola nuevo-leonensis* W. Becker. **A.** Habit of a chasmogamous plant with a blow-up of the upper two thirds of a stipule (**A**₁), and a blow-up of a sepal and an auricle of a chasmogamous flower (**A**₂). **B.** Habit of a cleistogamous plant with a blow-up of a cleistogamous flower (**B**₁). **C.** Face on view of a chasmogamous flower. **D.** Side view of a chasmogamous flower. **E.** Side view of a longitudinal section of a chasmogamous flower. **F-G.** Stamens in adaxial view: **F.** One of the ventral pair with its anterior appendage, anther thecae, filament and posterior appendage (spur appendage or nectary); **G.** One of the posterior three stamens with its anterior appendage, anther thecae, and filament. **H.** Side view of cleistogamous capsule with its sepals, auricles, peduncle, and bractlets. **I-J.** A cleistogamous seed: **I.** A side view of the seed with its caruncle. **J.** A front view of the seed with its caruncle. Bar equals: 2 cm for **A** & **B**; 5 mm for **C**, **D**, **E**, **H**; and 1 mm for **F**, **G**, **I**, and **J**. Drawn by Susan A. Reznicek using *Gil-ad 389* (2 sheets): MÉXICO. NUEVO LEÓN. Municipio de San Pedro Garza García: Parque Chipinque, 9.9 km SE of the intersection of Av. Gómez Morin and Alfonso Reyes, 20 March 1990: CHP, 16 May 1991: CUL, N. L. *Gil-ad 389* (MICH).

long, curved at base, clavate with a rostellum on a margined summit; *cleistogamous flower peduncle habit*: prostrate or occasionally ascending, densely ciliate, especially above the bractlets, spotted or clouded with purple-brown on a green background; *capsule* yellow-green to green sparsely spotted and dotted with greyed-purple, ellipsoid-ovoid with three parallel ridges on each side, ca. 10-17 mm long, 6-9 mm wide, length/width ratio 1.4-1.8; *seeds* deep yellowish brown (ISCC-NBS # 75) comprised of brownish black patches on a moderate to dark orange yellow background, 2.1-2.7 mm long, 1.2-1.7 mm wide, average weight 2.2-2.9 mg, caruncle 0.9-1.5 mm long; *seed coat*: secondary sculpture with randomly spaced verrucate structures, structures superficially foveate, irregularly shaped, connected by irregular, striated or semi-terete folds.

Substrate. – Sandy clay loam.

Habitat. – Margins of chaparral and *Pinus-Quercus-Cercis* forests. Elevation: (853) 1300-2200 meters.

General Distribution. – México: Coahuila and Nuevo León.

Discussion. – The North American students of subsection *Boreali-Americanae* have not incorporated, and (except for GERSHOY, 1934) have not mentioned *Viola nuevo-leonensis* in their treatments since Becker's 1922 description of the species and his 1925 treatment of the subsection in which he listed this species (Appendix A). The species is endemic to northern México, and grows at relatively high elevations. It is one of the four heterophyllous taxa of the subsection, and possesses a number of unique vegetative and reproductive characters. The degree of ciliation of the sepals and the long fimbriae on the stipules serve as good diagnostic characters when other reproductive characters are not available on herbarium specimens.

Another taxon belonging to the subsection that possesses undivided, cordiform and acute blades grows in central México. It was first collected by Pringle (8864) in Hidalgo, and is listed in BECKER's (1922) description as an additional representative specimen of *Viola nuevo-leonensis* (initially identified as *V. ciliata* Schlecht.). Preliminary examination of the vegetative characters available on *Pringle 8864* (MO, GH, US) has revealed that it is not *V. nuevo-leonensis*. SEM of the seed coat of a single, fairly mature seed found on the GH specimen revealed outer periclinal walls ribbed with finely intercrossed thickenings and a secondary sculpture consisting of extensive reticulate-terete thickenings and randomly distributed elongated polygonal or semi-circular plates that are irregularly overlaid over the surface. These plates have blends of scrobiculate, falsifoveate, and foveate surfaces. These surface features are similar to those found on the seed coats of *V. missouriensis*. In addition, a section of the seed coat reveals a primary sculpture in the form of pentagonal elongated cells and occasionally thickened and slightly curved anticlinal walls. These features may be similar to those found on the seed coats of *V. nephrophylla*. Yet, it is difficult to clearly demonstrate a correlation to structures characteristic of *V. nephrophylla* due to the small section available for examination, and the dominance of the secondary sculpture that includes reticulate-terete thickenings found on the seed coats of both *V. nephrophylla* and *V. missouriensis*. The seed color does not match the seed color of *V. missouriensis*. The blades are cordate-ovate, and most leaves are pubescent (especially on the adaxial surface and the petioles) unlike the deltoid and glabrous blades and petioles of *V. missouriensis*. The US specimen has faded pigmentation on the capsules that indicates that the capsules were sparsely spotted with red-purple (similar to the capsules of *V. missouriensis*). These preliminary data provide support to the hypothesis that *Pringle 8864* is not *V. nuevo-leonensis*, but a derivative of a putative hybrid of *V. missouriensis* with another taxon belonging to subsection *Boreali-Americanae*. Plants with a macromorphology similar to *Pringle 8864* (bearing cordate-ovate blades) at the cleistogamous phase were collected in 1989 by Reznicek in Tamaulipas (*Reznicek 8459*, MICH), but their seeds are immature, thereby not suitable for examination with SEM. Currently, our knowledge of the occurrence and distribution of taxa of subsection *Boreali-Americanae* in the temperate zone of México is lacking. Therefore, a discussion of the peculiar occurrence of these plants, which are presumably of hybrid origin, in that region should be postponed until additional collections of plants with mature seeds are obtained, and additional data on their identity are gathered and evaluated.

Viola pedatifida G. Don, Gen. Hist. 1: 320. 1831. – **Type:** “North America...Clt. 1826.” (holotype: not located).

!c.: Species No. 28, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 70. 1921; [color] Plate No. 52, Baird-Brainerd, *Wild Violets of North America*: 141. 1942.

Acaulescent, homophyllous, perennial herb; *rhizomes* succulent, scaly, vertical or occasionally oblique, 0.5-2 cm long, bearing stout fibrous roots: up to 1.2 mm in diameter; *stipules* linear-lanceolate, green blotched with red-purple, apex acute, margins entire, eciliate; *petioles* green often spotted with red-purple, pubescent; *blades* divided up to five times, primary division into three or five segments, in developed blades a second division includes: middle segment divided into three segments, lateral segments divided into two or three segments, third division into one, two, or three segments, fourth division none, or one, two, or three segments, fifth division none or two segments, segments linear to subspatulate, base cuneate to subtruncate, margins entire, segments apexes mucronulate, at chasmogamous anthesis middle segment 1.5-3.8 mm wide, lateral segments 0.8-3.2 mm wide, blade length/width ratio of the largest blades 0.4-1, middle segment apical angle 23°-44° (59°), adaxial surface ± pubescent, abaxial surface of juvenile blades often clouded dark purple, pubescent primarily along the major veins, at the cleistogamous phase blades wider than long; *peduncles* 4-16 cm long, green spotted with red-purple, ± pubescent below the bractlets, sparsely or glabrous above; *bractlets* linear to lanceolate or deltoid, blotched with red-purple on a yellow green background or entirely red-purple, apex acute, margins scarious, entire, eciliate; *sepals* lanceolate to ovate, green often spotted with dark purple along the major veins and over the connection area between the sepal and the auricles, apex acute, margins scarious, ± minutely ciliate, sepal length/capsule length ratio 0.4-0.5; *auricles* 0.2-1.1 mm long on chasmogamous flowers, at the cleistogamous phase 1.9-2.9 mm, green spotted with red-purple, apex rounded to subtruncate, ± ciliate; *spur* (1.8) 2-3.5 mm long; *petals* violet (RHS # 86B/C) with a white center bordered blue, lines on the spurred and lateral petals dark violet, spurred petal 13-19 (22) mm long (including the spur), 6-9 (11) mm wide near the apex, apex subtruncate to rounded, often emarginate, lower lateral pair 4-6 (9) mm wide, upper lateral pair 6-8 mm wide; *petal trichomes* dense on the lower lateral petals, less densely on the spurred petal, cylindrical, 90-100 µm wide, visible layers of cuticular folds two, cuticular folds tubular, unevenly thick, short or elongated, sparsely and unevenly distributed overlaid over densely packed, narrower, elongated folds, folds over the apex densely packed and randomly aligned, most folds below the apex vertically aligned; *cleistogamous flower peduncle habit*: erect; *capsule* yellow-green, length/width ratio 1.8-2; *seeds* color close to strong yellowish brown (ISCC-NBS # 74), 1.7-2.2 mm long, 1.1-1.4 mm wide, average weight 1.4-1.9 mg, caruncle 0.7-1.3 mm long; *seed coat*: outer periclinal walls unevenly ribbed in various directions, secondary sculpture with irregular, shallow, reticulate secondary wall thickenings; *chromosome number*: $2n = 54$.

Substrate. – Clay loam.

Habitat. – Prairies, prairie relicts on banks of railroad tracks and margins of fields.

General Distribution. – Canada: Ontario to Alberta; U.S.A.: Michigan, Ohio to Nebraska, Minnesota to Montana, Wyoming, Kansas south to Oklahoma and New Mexico, and western Arizona.

Discussion. – Don's brief description mentions only that the species is native to North America, but does not provide information on a specimen. Most of Don's types are kept at BM (STAFLEU & COWAN, 1976). However, no type material which might be relevant to the typification of *Viola pedatifida* could be found at BM (VICKERY pers. comm., 1995). Searches in the other herbaria listed by Stafleu & Cowan as repositories of Don's specimens have not uncovered relevant material either.

BRAINERD (1921), CLAUSEN (1929), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola pedatifida* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) subsumed *V. pedatifida* into his broadly defined *V. pal-mata*, and designated it as a variety comprised of the formerly recognized species *V. pedatifida*

and *V. egglesonii*. The macromorphological and micromorphological evidence presented in this work suggests that such lumping at the specific and varietal levels are unjustified, and should therefore be abandoned. MCKINNEY (1992) designated *V. brittoniana* as a subspecies of *V. pedatifida*. This lumping is not justified either, and is discussed under *V. brittoniana*.

BRAINERD (1913a, 1924) and RUSSELL (1953, 1956a) reported natural hybrids of *Viola pedatifida* with *V. sororia*, *V. sagittata*, and *V. nephrophylla*. Introgression of taxa of subsection *Boreali-Americanae* possessing undivided blades into *V. pedatifida* results in forms possessing shallowly divided blades, varying in the depth of the sinuses between the segments. Some of those forms have been reported as *V. palmata*. The color of the seeds, the color pattern on the capsules, and the micromorphological structures of the seed coat surface provide means to discern those hybrids from the orthospecies.

Etymology. – BRAINERD (1911, 1921) pointed out that the specific epithet is inappropriate since the middle segment of the blade is always divided, whereas in a strictly pedate blade it is never divided. In smaller leaves and those that appear in summer, the lateral primary segments are often imperfectly or obscurely trisected, and seem to be somewhat irregularly pedate. He suggested that those observations might have led to the choice of the specific epithet.

Viola sagittata Aiton, Hort. Kew. 3: 287. 1789. – **Type:** “Hort. Fothergill (ex America Pennsylvania)” (holotype: BM, photo: MICH!).

lc.: Species No. 25, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: third [color] plate following page 64. 1921; reprinted [color] Plate No. 47, Baird-Brainerd, *Wild Violets of North America*: 131. 1942; Plate XIX (a cleistogamous plant), Klüber, *Violets of the United States*: 57. 1976.

Acaulescent, homophyllous, perennial herb, 5-8 cm high at chasmogamous anthesis; *rhizomes* fleshy, scaly, vertical 1-2.5 cm long, bearing a few fibrous roots; *stipules* lanceolate, green blotched with red-purple, apex acute, margins entire or irregularly fimbriate, \pm ciliate; *petioles* green, pubescent often becoming subglabrous at the cleistogamous phase; *blades* at chasmogamous anthesis elliptic to oblong-lanceolate, base subtruncate or hastate, margins entire to crenulate, ciliate, apex acute, adaxial surface pubescent, abaxial surface glabrous or pubescent along the veins, veins often painted with purple, length/width ratio of the largest blades 2.2-2.8, apical angle 90°-105°, blades at the cleistogamous phase sagittate, gradually tapering to an acute to rounded apex, base coarsely dentate, dentations large and uneven, margins shallowly crenate above the base, ciliate, adaxial and abaxial surfaces pubescent; *peduncle* 4-(11) 15 cm long, yellow-green, glabrous; *bractlets* linear-lanceolate, yellow-green spotted with red-purple, apex acute, margins entire or irregularly glandular, eciliate; *sepals* green sparsely spotted with red-purple, margins scarious and eciliate, apex acute, sepal length/capsule length ratio 0.4-0.5; *auricles* green, truncate or rounded, 0.5-1.1 mm long, \pm ciliate; 2-3 mm long and ciliate on cleistogamous capsules; *spur* 2-2.3 (2.5) mm long; *petals* violet-blue (RHS # 90B/C) with a white center, lines on the spurred and lateral petals dark violet, spurred petal 9-16 mm long (including the spur), 3-5 mm wide, apex rounded, lower lateral pair 3-4 mm wide, upper lateral pair 3-4 mm wide; *petal trichomes* borne on the spurred and lower lateral petals, cylindrical, 60-70 μ m wide, visible layers of cuticular folds one, cuticular folds capillary, short, convoluted and randomly aligned on the apex, long, vertically aligned, and densely packed below the apex; *cleistogamous flower peduncle habit*: erect; *capsule* yellow-green, length/width ratio 1.9-2.2; *seeds* deep brown (ISCC-NBS # 56) or deep yellowish brown (ISCC-NBS # 75), 1.3-1.5 mm long, 0.8-1 mm wide, average weight 0.3-0.7 mg, caruncle 0.3-0.5 mm long; *seed coat*: secondary sculpture with rectangular or semi-circular, foveate to foveolate plates with thickened margins, plates usually connected, irregularly oriented, and randomly distributed; *chromosome number*: $2n = 54$.

Substrate. – Sandy soil or sandy-loam.

Habitat. – Open grounds, mesic sand prairies, open sites in forests. A common associate: *Viola pedata*.

General Distribution. – Canada: Nova Scotia to Ontario; U.S.A.: Maine to Minnesota, south to Florida and Texas, and west to Kansas and Oklahoma.

Discussion. – The holotype (BM) consists of three sagittate leaves, a cleistogamous flower and its peduncle, and an open capsule with its peduncle (all, apparently, were sampled during the cleistogamous phase). This type is referenced by number to material collected in Pennsylvania and cultivated by Fothergill. Apparently, these detached organs belonged to the original plants introduced by Fothergill in 1775 (according to the protologue) upon which Aiton based his description. On the same sheet are two narrowly-oblong, slightly sagittate leaves and a chasmogamous flower (apparently sampled during the chasmogamous phase) under Hort. Kew 1778, most likely plants cultivated at Kew, perhaps from seeds harvested from the capsule. The absence of seeds on the specimen does not allow further investigation and examination with SEM to reveal whether these plants were orthospecies.

All students of the subsection have maintained *Viola sagittata* as a distinct species primarily due to the unique blade shape this species exhibits. However, its delimitation has become obscure due to confusion about the characters that distinguish *V. sagittata* from *V. fimbriatula* (reviewed in the discussion of *V. fimbriatula*). In addition, opinions vary about numerous sub-specific taxa that have been described on the basis of observations on varying degrees of leaf pubescence, variations of the blade overall shape, and variations in shape and size of the dentations at the blade base. MCKINNEY (1992) presented those variations as typical of the species. BRAINERD (1921) proposed that the varying degrees of pubescence are induced by environmental conditions. RUSSELL (1965) acknowledged the variations in size and pubescence, and suggested that the sagittate blade shape remains constant, except where modified by hybridization. RUSSELL & COOPERRIDER (1955) provided evidence (using pictorialized scatter diagrams) for possible introgression of *V. sororia* into *V. sagittata* that was manifested in variations in blade shape and pubescence, among other characters. RUSSELL & RISSE (1960) established that *V. emarginata* (Nutt.) LeConte, which was first described as a variety of *V. sagittata*, was a hybrid between *V. sagittata* and *V. affinis* or a member of the “*V. affinis* complex.” CAMP (1961) reported observations on a hybrid complex of the two taxa over a five year span, and suggested that genetic recombination followed by environmental modifications were the underlying factors that resulted in numerous forms differing in blade shape and pubescence.

Micromorphological structures of the seed coat have made it possible to identify the orthospecies and sort it out from its hybrids with other taxa of subsection *Boreali-Americanae* (GIL-AD, 1995; GIL-AD, in press). The variations in blade shape and pubescence most likely result from hybridization or from introgression of other taxa into *Viola sagittata*. There is a substantial difference between the size and shape of the blades during the chasmogamous phase compared to the size and shape of the blades during the cleistogamous phase (see the description above). Introgression is manifested by deviations from the typical seed coat surface of *V. sagittata*, as well as seed color.

BRAINERD (1906b, 1913b, 1924) reported natural fertile hybrids of *Viola sagittata* with the following taxa of subsection *Boreali-Americanae*, five of which were named by HOUSE (1924). They included: $\times V. dissena$ (*V. affinis* \times *V. sagittata*); $\times V. marylandica$ (*V. brittoniana* \times *V. sagittata*); $\times V. festata$ (*V. cucullata* \times *V. sagittata*); $\times V. abundans$ (*V. fimbriatula* \times *V. sagittata*); *V. sagittata* \times *V. pedatifida*; *V. sagittata* \times *V. sororia*; and $\times V. caesariensis$ (*V. sagittata* \times *V. triloba*).

Viola septemloba LeConte in Ann. Lyceum Nat. Hist. New York 2: 141. 1828. – **Type:** “Habitat in Carolina et Georgia in pinetis solum, per tractum quae regio inferior vocatur” [only in pineries, through what is called the lowlands], [date unknown,] J. E. LeConte (lectotype,

here designated: Plate number 5! of LeConte's unpublished water-colors, Call number: QK 495 V811 L496f, University of Notre Dame Libraries, Department of Special Collections, Section of Rare Books).

!c.: Species No. 29, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: [color plate] opposite page 68. 1921; reprinted [color] Plate No. 50, Baird-Brainerd, *Wild Violets of North America*: 137. 1942.

Acaulescent, heterophyllous, perennial herb; *rhizomes* succulent, scaly, vertical, often branching, occasionally oblique, ca. 0.5-3 cm long, bearing stout fibrous roots: up to 1.3 mm in diameter, and up to 20 cm long, occasionally branching into fine fibrous roots; *stipules* linear-lanceolate, apex acute, green spotted with red-purple, margins scarious, entire to irregularly glandular fimbriate, eciliate; *petioles* green spotted with dark red-purple, glabrous; *blades* earliest and autumn blades undivided, widely ovate, base cordate-reniform, margins crenate-serrate, apex obtuse, abaxial surface glabrous, often painted with purple, major veins dark purple, at chasmogamous anthesis length/width ratio of the largest blades 0.8-0.9, apical angle 125°-140°, earliest divided blades trilobed, central lobe the widest, occasionally with two linear to falcate appendages borne at the base of the central lobe, at chasmogamous anthesis base cordate to reniform in outline, margins entire to distantly crenate-serrate, ± ciliate, apexes acute and mucronulate, adaxial surface glabrous or pubescent, abaxial glabrous, divided blades two times divided: first division into 3 lobes, central lobe the widest or subequal to the lateral lobes, oblanceolate or linear, 2-13 mm wide, secondary division: 2 lateral lobes borne on the central lobe, linear to linear-oblanceolate, the two basal lobes undivided and coarsely dentate, or divided into 2-4 lobes, the lowest often oriented downward, lateral lobes 1-6 mm wide, basal lobes occasionally undivided, lunate, ca. 10-20 mm wide, length/width ratio of the largest blades 0.9-1.1, apical angle 68°-87°; *peduncle* 8-20 (25-32) cm long, green or green spotted with red-purple, glabrous; *bractlets* linear-lanceolate, yellow green spotted or dotted with red-purple, apex acute, margins entire, often glandular at base, eciliate; *sepals* lanceolate, green or green spotted and dotted with red-purple, especially along the veins, apex acute, margins scarious, eciliate, sepal length/capsule length ratio 0.5-0.7; *auricles* 0.2-2 mm long, rounded, green, apex subtruncate or acute, eciliate; *spur* 2.4-4.3 mm long; *petals* violet (RHS # 83B) with a white center, lines on the spurred and lateral petals dark violet, spurred petal oblong or oblanceolate, (16) 20-24 mm long (including the spur), 6-8 (9) mm wide near the apex, apex subtruncate or emarginate, lower lateral pair 4-7 mm wide, upper lateral pair (4) 5-9 mm wide; *petal trichomes* dense on the spurred and lower lateral petals, occasionally sparse on the upper lateral petals, cylindrical, 70-80 µm wide, visible layers of cuticular folds one, cuticular folds capillary, short and randomly aligned on the apex, long, vertically aligned, and densely packed below the apex; *cleistogamous flower peduncle habit*: erect; *capsule* yellow-green, surface prominently ridged, length/width ratio 1.5-2; *seeds* brown black (darker than ISCC-NBS # 65), luster shining, 2-2.3 mm long, 1.1-1.6 mm wide, average weight 1.6-2 mg, caruncle 0.3-0.6 mm long; *chromosome number*: $2n = 54$.

Substrate. – Sandy soil with abundant organic material.

Habitat. – Openings in *Pinus* woods.

General Distribution. – North Carolina south to Florida and west to Louisiana.

Typification. – LeConte most likely described this species, and prepared the illustration (Plate number 5 of his water-colors), from a living plant. A specimen of this plant is unknown, and no holotype was indicated in the protologue.

Examination of Plate Number 5 revealed that it matches the characters pertaining to the chasmogamous phase in the description outlined above. The only major character that cannot be seen clearly is the presence of cylindrical trichomes on the spurred and lower lateral petals. Very fine horizontal lines that are drawn on the lower lateral petals may have been drawn to represent the trichomes that are listed in LeConte's description. Yet, none are drawn on the spurred petal. Nevertheless, on the basis of the match between LeConte's description and the illustration, the

absence of a specimen, as well as the match between the illustration and the characters of the orthospecies, Plate Number 5 is designated here as the lectotype.

Etymology. – The specific epithet, *septemloba*, accounts only for divided blades possessing seven lobes. However, blades possessing nine and even eleven lobes are borne on some plants.

Discussion. – BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola septemloba* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) subsumed *V. septemloba* into his broadly defined *V. palmata* as var. *palmata* with the other species with strongly divided blades: *V. brittoniana*, along with *V. triloba*, the undivided *V. pectinata* (= *V. brittoniana* f. *pectinata*), and taxa that are identified in this work as hybrids: *Viola chalcosperma*, *V. esculenta*, *V. lovelliana*, *V. stoneana*, and *V. viarum*. *Viola palmata* is not recognized as an orthospecies in the present work. MCKINNEY (1992) subsumed *V. egglesonii* into *V. septemloba* as a subspecies (see the discussion of *V. egglesonii*). The two taxa are closely related, but should not be combined into one species. *V. septemloba* possesses a number of unique character states (e.g., the color of the seeds, the micromorphological features of the seed coat), as well as habitat and substrate specificity.

There are no reports in the literature of natural hybrids of *Viola septemloba* with other taxa of subsection *Boreali-Americanae*. BRAINERD (1921) and RUSSELL (1965) discussed the confusion between this species and *V. brittoniana* that resulted from superficial consideration of the shape of the blades and the type of substrate the plants grow in. If all characters are examined, there should be no problems distinguishing between the two species. RUSSELL (1965) pointed out the lines of distinction between *V. septemloba* and *V. esculenta* (here considered a putative hybrid). MCKINNEY (1992) contended that *V. septemloba* exhibits blade variation, and interpreted the early trilobed (trifid) blades that occasionally persist into the summer as sources of misidentification. Compounding the confusion is the heterophylly of *V. septemloba*. Early spring, and often autumn, blades are undivided, widely ovate, and possess a cordate base. Plants exhibiting those blades and the early trilobed blades could easily be confused with hybrids of *V. septemloba* with taxa of subsection *Boreali-Americanae* possessing undivided blades. Examination of the macromorphology of seeds from live plants as well as from a number of specimens that exhibited blade shape variation [such as *Brainerd s.n.* (28 March 1909) (VT), *Gil-ad 348* (MICH)] revealed that they are most likely hybrids. Seed color does not match the distinct color and luster of the seeds of the orthospecies, and the dimensions of the seeds deviate from the orthospecies range. The micromorphological structures of the seed coat surface of sampled seeds also suggested a hybrid origin (GIL-AD, 1995; GIL-AD, in press). *Viola septemloba* is often syntopic with *V. villosa*, and it is likely that some of the previous reports on blade variation and misidentifications are due to hybridization or introgression of *V. villosa* into *V. septemloba*.

Viola septentrionalis Greene in *Pittonia* 3: 334. 1898. – **Type:** Canada, Ontario: near Ottawa, Billings Bush, borders of thickets, 30 May 1898, *J. M. Macoun 18,761* (Types: lectotype: NDG No. 33738! – the chasmogamous specimen – 30 May 1898 (MCKINNEY, 1992 designated this specimen as “holotype”); isolectotype: CAN No. 119225 – the chasmogamous specimen – 30 May 1898; syntype: NDG No. 33741! – the cleistogamous specimen – 10 June 1898; isosyntype: CAN No. 119226 – the cleistogamous specimen – 10 June 1898).

lc.: Species No. 15, Brainerd in *Vermont Agric. Exp. Sta. Bull.* 224: [color plate] preceding page 33. 1921; reprinted [color] Plate No. 39, Baird-Brainerd, *Wild Violets of North America*: 111. 1942; Plate 50, Fig. 5a, b, c [cleistogamous flowers and capsules only], Brainerd in *Rhodora* 7: opposite page 24. 1905.

Acaulescent, homophyllous, perennial herb; *rhizomes* fleshy, scaly, vertical or oblique, occasionally branching and green, 1–5 cm long, bearing fibrous roots; *stipules* lanceolate to ovate, densely blotched with red-purple on a yellow-green background, apex acute, margins scarious, irregularly fimbriate, densely ciliate; *petioles* green, pubescent; *blades* broadly ovate to

cordate, green on the adaxial surface, gray-green on the abaxial surface, often clouded with purple in juvenile leaves, pubescent on the abaxial and the adaxial surfaces, trichomes strigose, base cordate, margins crenate-serrate, ciliate, apex acute to obtuse, up to 0.5 mm long, at chasmogamous anthesis length/width ratio of the largest blades 1-1.3, apical angle 74°-95° (114°); *peduncles* 5-12 cm long, pubescent, spotted with red-purple; *bractlets* linear-lanceolate, green painted and spotted with red-purple, margins scarious, entire to irregularly glandular fimbriate, ciliate, apex acute; *sepals* ovate to broadly ovate, apex obtuse, green at chasmogamous anthesis, densely spotted with red-purple on cleistogamous flowers and capsules, margins scarious and densely ciliate, cilia up to 0.4 mm long, sepal length/capsule length ratio 0.5-0.6; *auricles* 0.4-1.5 mm long, color same as the sepals, subtruncate, rounded to acute, incised to undulate, ciliate; *spur* (1.5) 2.1-3.2 mm long; *petals* violet (RHS # 87A) with a white center extending from the center to one third to one half of the length of the petal, lateral petals often whitened on the abaxial surface, spurred and lateral petals dark violet lines, spurred petal 12-21 mm long (including the spur), 4.6-8.5 mm wide, apex rounded to subtruncate, lower lateral pair (3.8) 5.3-7.3 mm wide, upper lateral pair 4.8-8.4 mm wide; *petal trichomes* dense on the spurred and lower lateral petals, cylindrical, ca. 60-90 µm wide, visible layers of cuticular folds one, cuticular folds tubular, a blend of elongated and short folds of varied width, most vertically aligned and randomly spaced with large gaps, wide and short over the apex; *cleistogamous flower peduncle habit*: prostrate; *capsule* blotched and spotted with dense red-purple on a yellow green background, length/width ratio 1.4-1.6; *seeds* dark yellowish brown (ISCC-NBS # 78), 1.6-2.1 mm long, 0.9-1.0 mm wide, average weight 0.6-1.1 mg, caruncle 0.8-1.3 mm long; *seed coat*: secondary sculpture with aggregates of intertwined and convoluted terete, narrow thickenings, connected by reticulate-terete, narrow thickenings, and irregularly distributed, surface between aggregates unevenly smooth; *chromosome number*: $2n = 54$.

Substrate. – Loam, often mixed with coniferous litter.

Habitat. – Openings in coniferous woods, open groves of *Thuja occidentalis*, open mixed woods, in partial shade.

General Distribution. – Canada: Prince Edward Island, Newfoundland and Nova Scotia to Ontario, east-central Saskatchewan (HARMS & *al.*, 1985), southern British Columbia (BRAINERD, 1915, 1921; BAIRD-BRAINERD, 1942); U.S.A.: New England to northern Pennsylvania, southern Wisconsin, northern Illinois, Nebraska, Iowa, and Washington (FERNALD, 1950).

Typification. – GREENE (1898) did not designate a holotype in the protologue. Nevertheless, he listed a chasmogamous specimen with the date 10 May 1898, and a cleistogamous specimen with the vague date designation of “a month later”; both specimens are numbered 18,561. MCKINNEY (1992) listed *V. septentrionalis* in synonymy under *Viola sororia*, and denoted *J. M. Macoun 18,761* at NDG as the holotype.

There are three discrepancies between the protologue and the data listed on the labels of the type specimens. Macoun's collection number listed in the protologue is 18,561, whereas the collection number listed on labels of the specimens is 18,761. This discrepancy was also noted by Greene himself, who wrote to Macoun on 30 December 1898 (the letter is filed at CAN), queried him about the possible number mix-up, and suggested that the printed number might be a typo. Macoun's reply, dated 3 January 1899 clarifies the collection numbers mix-up. This letter, and additional letters sent earlier in 1898 (and filed in the University of Notre Dame Archives), reveal that Macoun regularly sent Greene both living and dried plants under the same collection number. According to Macoun, he first sent Greene the living specimens of *V. septentrionalis* No. 18,761, and by mistake labeled them with the number 18,561. However, he corrected this mistake in a letter, dated 27 May 1898, and by sending him the dried material under the correct number, hence the number on the labels. Apparently, Greene missed the correction and published the wrong collection number in the protologue. Although Macoun encouraged Greene to correct the mistake in print, a correction was not published. The second discrepancy is found in the date of collection of the chasmogamous specimen: 10 May 1898 in the description vs. 30 May 1898 on the labels. It is interesting to note that the 27 May letter – Macoun's first letter of correction –

had been written before the 30 May collection date that we see in Macoun's handwriting on the chasmogamous specimens numbered 18,761. The third discrepancy is the collection date of the cleistogamous specimens. The description lists the collection date for the cleistogamous specimen as "a month later." A month later would be 10 June, which is the date specified on the labels of the cleistogamous specimens. However, using the dates on the labels (written in Macoun's handwriting), a month later would be 30 June. We would expect that with the latitude of Ottawa and the phenology of the plants, they would usually produce chasmogamous flowers during the last week of May or the beginning of June. Yet, weather conditions during that specific collecting season may have been different, and we do not have specific information about the collection site. The Macoun-Greene correspondence does not resolve the mix-up of the dates. For the purpose of reference and typification, the dates on the labels were chosen for the citation of the types.

On the basis of examinations of the specimens numbered 18,761 at NDG and photocopies of the specimens bearing the same number at CAN, and the discussion above, the chasmogamous specimens dated 30 May 1898 are a lectotype (NDG) and an isolectotype (CAN) respectively, and the cleistogamous specimens dated 10 June 1898 are a syntype (NDG) and an isosyntype (CAN) respectively.

Discussion. – BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola septentrionalis* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991), and MCKINNEY (1992) reduced it to synonymy under *V. sororia*. FERNALD (1950) and RUSSELL (1965) pointed out that the underlying problem in the delimitation of *V. septentrionalis* is its resemblance to *V. sororia*. This problem, compounded by the lack of clear criteria on the delimitation of *V. sororia*, and the lack of effective means to sort out hybrids between *V. septentrionalis* and other taxa in the subsection possessing undivided blades, has led most recent authors to eliminate it. Consequently, in many herbaria, specimens of *V. septentrionalis* are filed under the name *V. sororia*.

The best diagnostic macromorphological characters that delimit *Viola septentrionalis* are the color and shape of the seeds (length/width ratio 1.6-2.3) along with the long caruncles, the shape and color of the capsules, the presence of petal trichomes on the spurred and lower lateral petals, and the dense ciliation of the sepals. Pubescence is an unreliable character for most of the taxa in subsection *Boreali-Americanae*. However, *V. septentrionalis* is one of the exceptions, and is characterized by consistent ciliation along the blade margins and the peduncles. The micromorphological structures of the seed coat surface are also unique, and are characterized by aggregates of intertwined and convoluted terete secondary wall thickenings connected by reticulate-terete thickenings (GIL-AD, 1995; GIL-AD, in press).

BRAINERD (1904b, 1924) reported natural fertile hybrids of *Viola septentrionalis* with taxa of subsection *Boreali-Americanae* that were named by HOUSE (1924). They included: $\times V. champlainensis$ (*V. affinis* \times *V. septentrionalis*); $\times V. melissaefolia$ (Greene) House (*V. cucullata* \times *V. septentrionalis*); $\times V. parca$ (*V. fimbriatula* \times *V. septentrionalis*); and $\times V. montivaga$ (*V. septentrionalis* \times *V. sororia*). RUSSELL (1955) provided evidence for hybridization and possible bidirectional introgression between populations of *V. cucullata* and *V. septentrionalis*. Hybrids with *V. nephrophylla* (such as Gil-ad 300, MICH) are difficult to identify using seed coat micromorphological structures since the convoluted, intertwined secondary wall thickenings characteristic of *V. septentrionalis* mask the reticulate pattern characteristic of *V. nephrophylla*. The shape of the seeds and the color of the capsules can help in comparing the putative hybrid to the orthospecies.

Viola septentrionalis var. *grisea* Fernald is transferred here to *V. novae-angliae* and elevated to the rank of subspecies

Viola sororia Willd., Hort. Berol.: Tab. 72. April 1806. – **Type:** “America boreali, Pennsylvania,” [date of collection unknown], (lectotype, here designated: sheet No. 3: B-W 4898, photo: MICH!).

lc.: Plate No. 36 [a chasmogamous plant without a rhizome], Brainerd-Brainerd, *Wild Violets of North America*: 103. 1942; Plate III [a cleistogamous plant], Klaber, *Violets of the United States*: 28. 1976; Plate 50, Fig. 3a, b, c [cleistogamous flowers and capsules only], Brainerd in *Rhodora* 7: opposite page 24. 1905.

Acaulescent, homophyllous, perennial herb; *rhizomes* fleshy, scaly, vertical or oblique, sometimes branching, 1.5–3 cm long bearing fibrous roots; *stipules* linear-lanceolate, green with red-purple, apex acute, margins scarious, entire, irregularly fimbriate; *petioles* ± pubescent, green; *blades* ovate to orbicular, adaxial surface ± pubescent, abaxial surface usually pubescent, base cordate, margins crenate-serrate, ± ciliate, apex acute becoming obtuse later in the season, at chasmogamous anthesis length/width ratio of the largest blades 1–1.1, apical angle 71°–88°; *peduncles* 12–20 cm long, dotted and spotted with red-purple on yellow green to green background, pubescent; *bractlets* lanceolate to lanceolate-ovate, green painted and spotted with purple, margins entire, eciliate, apex acute; *sepals* ovate, green spotted with purple, apex obtuse to acute, ciliate along the lower half; *auricles* 0.5–1.0 mm long (up to 1.5 mm on capsules), green spotted with purple, apex subtruncate to rounded, ciliate, sepal length/capsule length 0.4–0.5; *spur* 1.5–2.6 mm long; *petals* violet (RHS # 86) with a white center and violet lines on the lateral and spurred petals, spurred petal 15–22 mm long (including the spur), 3–6 mm wide, apex rounded, lower lateral pair 4–8 mm wide, upper lateral pair 6–8 mm wide; *petal trichomes* borne on the lower lateral petals, none on the spurred petal, cylindrical, 90–100 µm wide, visible layers of cuticular folds one, cuticular folds tubular, thick and convoluted, randomly aligned over the apex, elongated, dense, overlapped and vertically aligned below the apex; *cleistogamous flower peduncle habit*: prostrate; *capsule* blotched with dark overlapping red-purple patches on a yellow-green background, length/width ratio 1.6–1.8; *seeds* dark grayish brown (ISCC-NBS # 62), 1.9–2.4 mm long, 1.2–1.5 mm wide, average weight 1.5–2 mg, caruncle 0.8–1.3 mm long; *seed coat*: primary sculpture cells superficially tetra- or pentagonal, most elongated in one direction, outer periclinal walls: smooth, uneven, and gradually curve down into the cell boundary, secondary sculpture with superficially tetra-, and pentagonal foveolate plates, usually longer than wide, randomly distributed, and often connected; *chromosome number*: $2n = 54$.

Substrate. – Dry loam.

Habitat. – Margins of open, hardwood and mixed forests, shaded ledges, disturbed sites (considered a weed in rural and urban environments).

General Distribution. – Canada: Quebec to Ontario, east-central Saskatchewan; U.S.A.: Maine west to Minnesota and South Dakota and south to North Carolina, west to Nebraska to Texas.

Typification. – WILLDENOW (1806) did not provide in the protologue information on a specimen and collection data. From the observations he provided in the protologue on the phenology, reproduction, and morphology of plants under cultivation, it can be inferred that he based his description on a cultivated plant. Plate 72 displays a chasmogamous plant devoid of most of the rhizome, and bearing five pubescent leaves and two open chasmogamous flowers. A line-drawing of the plant illustrated in this plate is provided in BRAINERD (1921: 41).

There are 3 sheets of *Viola sororia* (no. 4898) in B-W. These sheets have been numbered 1–3 by Schlechtendal. A label written by Willdenow, and glued to the outside of the species folder, comprises a short description and a note indicating that the habitat was in Pennsylvania.

Willdenow received at least one of the plants from Mühlenberg. Evidence for this is a label bearing Mühlenberg's name that is glued to the inside of the species folder. Schlechtendal made these notes since it was not clear which of the plants was sent by Mühlenberg. Mühlenberg must have also sent seeds since the plant used for the illustration (Plate 72) was a living plant cultivated in the Hortus Botanicus at Berlin. There are no seeds left in the folder. This plant may be the

small plant on sheet No. 1 (HIEPKO pers. comm., 1995). It is composed of the upper segment of the rhizome (which most likely was trimmed from the rest of the rhizome; the latter has not survived) to which two pubescent leaves, a pubescent petiole devoid of the blade, a segment of a peduncle devoid of the flower, a chasmogamous bud, and a chasmogamous flower (glued to the sheet) are attached. The plant on sheet No. 1 is much smaller than the plant illustrated in Plate 72, and does not resemble it.

The plant on sheet No. 2 is composed of the upper segment of the rhizome (which was also trimmed from the rest of the rhizome), four pubescent leaves, a chasmogamous bud, and two open chasmogamous flowers bearing cylindrical trichomes on the lateral petals. This plant was perceived by I. Urban as similar to Plate 72 as indicated in a label written by him in 1898 and attached to the specimen: "Dies ist wohl das Original zu Tab. LXXII" (This is probably the original of Plate 72). Urban added, obviously later: "sed descr. non bene convenit" (but the description does not agree well). This plant does not resemble the plant that is illustrated in Plate 72 in the shape and habit of the flowers and the leaves.

Sheet No. 3 bears the following detached organs: a single open chasmogamous flower bearing trichomes on the lower lateral petals and attached to its peduncle, and a single leaf. The adaxial surface of the blade is glabrous. This blade does not resemble precisely in overall shape and in the shape of the crenations of the margins any of the blades illustrated in Plate 72. A label in Willdenow's handwriting is attached on the bottom of the sheet. This label bears the specific epithet and the initial "W." in parentheses. It is possible that Willdenow sampled one flower and one leaf from the live plant he later used for the illustration, and indicated this by the label bearing his initial. The information available does not clearly establish the identity of the specimen that was used by Willdenow for the illustration. Yet, given the additional information that is provided on the labels in the folder, the lack of resemblance between the material on the other two sheets and Plate 72, and the likelihood that the material on sheet No. 3 represents the type material, sheet No. 3 is designated here as the lectotype.

The apical angles of the blade on sheet No. 3 and of two blades on sheet No. 2 are significantly smaller (48° – 52°) compared to the range typical of the orthospecies during the chasmogamous phase (71° – 88°). In addition, the respective blades are narrower than typical blades at this developmental stage. However, the characters available on these specimens are not sufficient for determination whether the plants were orthospecies.

Etymology. – Willdenow reported in the protologue a resemblance between 'the stamens and related parts' and their counterparts in *Viola odorata*, a Eurasian species that is widely cultivated throughout North America. BAIRD-BRAINERD (1942) speculated (most likely on the basis of this statement) that the specific epithet *sororia*, or "sister" violet, was given because *V. sororia* was thought to resemble *V. odorata*.

Discussion. – BRAINERD (1907b) reviewed the nomenclatural history of *Viola sororia*, and pointed out that the confusion of former botanists regarding Willdenow's *V. sororia* might have resulted in part from a "palpable blunder" in his description. Willdenow described the lowest petal as bearded at the base and the lateral petals as glabrous.

All authors since Brainerd maintained *Viola sororia* as a distinct species. RUSSELL (1965) expressed the opinion that *V. sororia* is the most variable of all the taxa in the subsection in such characters as petal color, size, and blade pubescence. Cronquist (in GLEASON & CRONQUIST, 1991) reduced all the previously recognized species possessing undivided blades (*V. affinis*, *V. papilionacea*, *V. priceana*, *V. novae-angliae*, *V. floridana*, *V. langloisii*, *V. latiuscula*, *V. missouriensis*, *V. pratensis*, and *V. septentrionalis*) to synonymy under *V. sororia*, except for *V. nephrophylla* and *V. villosa*. Cronquist's treatment formalized a widespread practice in which *V. sororia* is the "dumping ground" for all the taxa in the subsection that possess undivided blades and could not be clearly matched with other species. MCKINNEY (1992) echoed Russell's observations, and contended that *V. sororia* is highly variable in habit and pubescence. He erected three varieties (*affinis*, *missouriensis*, and *novae-angliae*) using blade shape as the major criterion for their delimitation. The tortuous nomenclatural history of the species (cleared up by BRAI-

NERD, 1907b, 1921, and outlined by MCKINNEY, 1992) as well as the two most recent treatments reflect the difficulty in finding unique macromorphological defining characters for this widely collected plant. In addition, the alleged variability of this species is most likely a result of the difficulties in sorting out introgressants and hybrids of *V. sororia* with other taxa in the subsection possessing undivided blades from orthospecies by employing analyses of macromorphological characters only.

Seed color along with the micromorphological structures of the seed coat surface enable, in most cases, identification of the orthospecies and recognition of hybrids and introgressants. The seed coat surface is composed of secondary wall thickenings in the form of plates delimited by furrows and smooth rounded edges. Foveolate plates are scattered among them (GIL-AD, 1995; GIL-AD, in press). The seed coat can be misleading if examined without examination and correlation with macromorphological characters since hybridization introduces minor variations that are difficult to detect.

There are more reports of natural hybrids of *Viola sororia* than any of the other taxa in the subsection. This is most likely due to its adaptability to disturbed habitats. The genes provided by *V. sororia* may allow hybrids to thrive in habitats that deviate greatly from the habitats the other parent can tolerate. BRAINERD (1904b, 1924) reported natural, fertile hybrids of *V. sororia* with taxa of subsection *Boreali-Americanae*, five of which were named by HOUSE (1924). They included: $\times V. consona$ (*V. affinis* \times *V. sororia*); *V. brittoniana* \times *V. sororia*; $\times V. conturbata$ (*V. cucullata* \times *V. sororia*); $\times V. fernaldii$ (*V. fimbriatula* \times *V. sororia*); *V. nephrophylla* \times *V. sororia*; *V. pedatifida* \times *V. sororia*; *V. sagittata* \times *V. sororia*; $\times V. montivaga$ (*V. septentrionalis* \times *V. sororia*); and $\times V. populifolia$ (*V. sororia* \times *V. triloba*). RUSSELL & COOPERRIDER (1955) provided evidence, for possible introgression of *V. sororia* into *V. sagittata*, and RUSSELL (1956a) analyzed cases of hybridization of *V. sororia* with *V. pedatifida*. In fact, most of the collections of *V. sororia* collected for this study (Gil-ad 260; 268; 284; 293; 402, MICH); were determined to be putative hybrids or introgressants by correlating the micromorphological structures of the seed coat surface with macromorphology.

Viola triloba Schwein. in Amer. J. Sci. Arts 5: 57. 1822. – **Type:** U.S.A. [North] Carolina: Salem, rich woodland and meadows, [date of collection unknown], L. D. de Schweinitz s.n. (holotype: PH!).

Ic.: Species No. 12a, Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 36. 1921; reprinted [color] Plate No. 28, Baird-Brainerd, *Wild Violets of North America*: 87. 1942.

Acaulescent, heterophyllous, perennial herb; *rhizomes* fleshy, vertical or oblique, 1-4 cm long, bearing fibrous roots, scales often smooth; *stipules* lanceolate, green blotched with red-purple, apex acute, margins scarious, irregularly glandular-fimbriate, ciliate; *petioles* green spotted with red-purple, pubescent; *blades* earliest spring, and autumn blades reniform and trilobed, adaxial surface gray-green, abaxial surface clouded with gray-purple, sparsely pubescent. Reniform blade base cordate, margins crenate-serrate, eciliate apex obtuse to rounded, length/width ratio 0.7-1.1. Largest blades at chasmogamous anthesis trilobed, the middle lobe the widest, early widely obovate or oblong with an obtuse apex, later becoming oblong to elliptic with an acute apex, often with one or two acute side lobes below the middle, (2) 7-12 mm long, basal lobes lunate-obdeltoid at base, one to two lobed, the lower lobe bilobed or coarsely serrate, margins shallowly crenate-serrate, length/width ratio of the largest blades 1-1.3, apical angle 82°-100°; *peduncles* length 7-11 cm long, green spotted with red-purple, \pm glabrous; *bractlets* deltoid, spotted with red-purple on a yellow green background, apex acute, margins entire or irregularly incised, eciliate; *sepals* green spotted and dotted with dark purple, margins scarious, sparsely and irregularly ciliate or glabrous, apex obtuse, sepal length/capsule length ratio 0.3-0.4; *auricles* 0.5-0.8 mm long, green dotted dark red-purple, apex subtruncate to rounded, ciliate, cilia up to 0.4 mm long; *spur* 1.6-2.2 mm long; *petals* violet (RHS # 83B) to purple-violet (RHS # 82A) with

a white center bordered blue, lines on the spurred and lateral petals dark violet, spurred petal spatulate, 12-17 (21) mm long (including the spur), 5-8 mm wide near the apex, apex subtruncate, lower lateral pair 5-7 mm wide, upper lateral pair (5) 6-8 mm wide; *petal trichomes* dense on the lower lateral petals, none on the spurred petal, cylindrical, ca. 90-110 μ m wide, visible layers of cuticular folds two, cuticular folds tubular, short, convoluted, and randomly aligned on the apex, thick, linear or slightly convoluted, vertically aligned, randomly spaced and overlaid on thin, slightly convoluted, and densely packed folds below the apex; *cleistogamous flower peduncle habit*: prostrate; *capsule* blotched and spotted with red-purple on a yellow-green to green background, length/width ratio 1.6-2.0; *seeds* dark orange yellow (ISCC-NBS # 72), 1.7-2 mm long, 1.2-1.5 mm wide, average weight 1.2-1.4 mg, caruncle 1-1.3 mm long; *seed coat*: secondary sculpture with randomly distributed aggregates of variously shaped, elevated plates with blends of foveate and scrobiculate patterns on the surface, occasionally thickened or folded along the margins, surface between the plates uneven and rough; *chromosome number*: $2n = 54$.

Substrate. – Clay loam.

Habitat. – Margins and openings in rich, often rocky woods.

General Distribution. – Vermont and Massachusetts south along the Appalachian Mountains to Georgia, Alabama, and Florida, west to Michigan and south to Texas.

Discussion. – De Schweinitz most likely collected the holotype in Salem, [North] Carolina (indicated by a small annotation label on the specimen at PH). The collection date and collection number are not provided on the specimen's labels and in the protologue (de SCHWEINITZ, 1822). Yet, since his paper was received for publication in July 1821, it is likely that the plant was collected earlier in 1821 or one to few years before. Although seeds are not available for examination, the chasmogamous plant matches in all characters the orthospecies (e.g., *Gilad* 310, MICH).

BRAINERD (1910b, 1921) reviewed the nomenclatural history of the species, and upheld the specific epithet *triloba* on the basis of priority. FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola triloba* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) subsumed *V. triloba* into his broadly defined *V. palmata* as var. *palmata* with *V. brittoniana*, *V. septemloba*, and six other taxa that are identified in this work as putative hybrids.

McKINNEY (1992) reduced the specific epithet *triloba* to synonymy under *Viola palmata*, and used the specific epithet *palmata* to designate a heterophyllous species encompassing an artificial assemblage of taxa that are recognized as putative hybrids in the present research. BALLARD (1994) accepted McKinney's arguments that the name *V. triloba* is superfluous, and listed it as a synonym under *V. palmata*. McKinney based his decision on interpretations of the descriptions of LINNAEUS (1753), PLUKENET (1705) and Clayton (listed but not referenced), examinations of Plukenet's plate and of a photograph of the type of *V. palmata* (LINN) at GH, and the use of heterophylly as the major criterion to delimit *V. palmata* from another name that he resurrected: *Viola subsinuata* Greene. McKinney contended that the violet that Plukenet and Linnaeus described is what has been called *Viola triloba*. His first supporting argument, based on his interpretations of Plukenet's plate, is irrelevant since there is a specimen at LINN that appears to be the basis of Linnaeus' description, and bears the number of this species ("1") in Species Plantarum. Another argument of McKinney is based on his assertion that *V. palmata* exhibits throughout its wide range a considerable amount of variation in both the shape of the undivided blade segments and the amount and location of pubescence. Furthermore, it is based on his assertion that *V. esculenta*, *V. viarum*, and *V. lovelliana* (identified as putative hybrids in this study) represent some aspect of the overall phenotypic plasticity associated with the species. His argument that the type specimen of *V. palmata* at LINN more closely resembles the midseasonal cut-leaved aspect of the heterophyllous species may be correct under his broad interpretation of the delimitation of the species, but is not correct if strictly applied to *V. triloba*. Examination of the microfiche of the type of *V. palmata* (LINN 1052.1) showed three leaves and three chasmogamous flowers (whose petal trichomes are not revealed). One detached leaf has a blade with relatively wide cen-

tral lobe and a wide right side lobe, but no lobe on the left side (apparently it has been broken off and lost). The other two leaves of the same plant have blades with five lobes. Their central lobe is not significantly wider than the side lobes, and the sinuses between the lobes are deep. These blades do not resemble the typical trilobed blades of *V. triloba*. Rather, they resemble the blades of putative hybrids described under *V. palmata* (see Section 6.5). Furthermore, no typical undivided and cordate-reniform blades, which usually accompany the trilobed blades of the heterophyllous species, are present. Although the evidence is scanty, the type of *V. palmata* likely represents a putative hybrid rather than an orthospecies. The evidence presented in this research, based on studies of live plants, including SEM of seed coats (see Section 6.5), provides support to the delimitation of *V. triloba* as an orthospecies, and consequently maintaining the specific epithet *triloba* in spite of the priority of the specific epithet *palmata*.

Both Cronquist and McKinney's treatments are unwarranted since the single vegetative character they employed – the shape of the blades – does not clearly circumscribe *V. palmata*. In addition, McKinney did not take into account the possibility that the variation in blade shape he detected is a product of hybridization or introgression rather than phenotypic plasticity as he asserts.

Another problem associated with the delimitation of *Viola triloba* is that some authors, such as FERNALD (1950) and RUSSELL (1965), found it very similar to *V. sororia*, except for the lobing of the blades, and some earlier authors regarded them as forms of the same species (BRainerd, 1912). Variation in the color and size of seeds of heterophyllous plants bearing trilobed blades that were sampled in this study provided the first indication that the species as construed by previous workers is not uniform, but included many individuals of hybrid origin. The micromorphological structures of the seed coat surface revealed at least in one population (Gil-ad 310, MICH) a pattern of secondary wall thickenings on the seed coat surface that is not blended with structures characteristic of other taxa, and that could be correlated with a unique suite of macro-morphological characters, including shape and seed color. The seed coat of seeds from other populations [Brainerd 167 (US), Deam 23479 (VT), Gil-ad 262; 344; 355, 439 (MICH)] revealed secondary wall thickenings characteristic of *V. affinis*, *V. sororia* or both on the same seed coat (GIL-AD, 1995; GIL-AD, in press). This evidence suggests that introgression from *V. affinis* and *V. sororia* into *V. triloba*, and in some cases possible backcrossing to *V. sororia*, are the underlying processes that generated the obliteration of the characters of *V. triloba*, and consequently the difficulties previous workers have encountered in delimiting the species and comments about similarities between them.

Viola triloba var. *dilatata* (Elliott) Brainerd (1910b) was delimited from var. *triloba* on the basis of the narrower middle lobe, the number of lobes, their deeper incisions, and the shape of the basal lobes. The varietal status was upheld by FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965). PALMER & STEYERMARK (1958) reduced it to the rank of form since it was lacking a definite geographical range. They cited specimens from Missouri indicating both varieties frequently occur together, and have practically the same geographical range. They also mentioned extremes and intermediates in blade shape. MCKINNEY (1992) reduced it to synonymy under the taxon he delimited as *V. palmata*. RUSSELL (1965) contended that although the ranges of var. *triloba* and var. *dilatata* overlap broadly, he has never found populations of both. Observations on populations sampled in this study confirm that they are not syntopic. Plants examined in this study grew on limestone outcrops in woods dominated by *Quercus*, and deviated from var. *triloba* in a number of characters in addition to character states of the blades. The capsules are globose (length/width ratio 1-1.3), the seeds are longer (1.8-2.4 mm) and wider (1.3-1.6 mm), the petals are blue-violet, the sepals are densely ciliate, the auricles are longer (0.5-1.1 mm) and densely ciliate, the petal trichomes are often expanded toward the apex, and the plants are more pubescent than in var. *triloba*. Only partially mature seeds were available for SEM examinations. The seed coat surface of those seeds exhibited, in addition to porous plates found on the seed coats of var. *triloba*, reticulate secondary wall thickenings that are also found on the seed coats of *V. affinis*, *V. missouriensis*, and *V. nephrophylla*, and curvature of the periclinal walls characteristic of *V. missouriensis*. The data available cannot rule out

the possibility of a hybrid origin of var. *dilatata*, and do not shed light on its affinity to *V. triloba*. The absence of firm micromorphological data does not permit a taxonomic decision. Therefore, further studies are needed in order to determine the status of this taxon.

BRAINERD (1912, 1913b, 1924) reported natural fertile hybrids of *Viola triloba* with taxa of subsection *Boreali-Americanae*, some of which were named by HOUSE (1924). They included: *Viola affinis* × *V. triloba*; *V. brittoniana* × *triloba*; ×*V. greenmanii* (*V. cucullata* × *V. triloba*); ×*V. robinsoniana* (*V. fimbriatula* × *V. triloba*); ×*V. caesariensis* (*V. sagittata* × *V. triloba*); ×*V. populifolia* (Greene) House (*V. sororia* × *V. triloba*). Gil-ad 355 (MICH) is apparently *V. triloba* introgressed by *V. villosa*, which grew in the same site.

Viola villosa Walter, Fl. Carol.: 219. 1788. – **Type:** [locality and date of collection unknown] Thomas Walter 136 (holotype: BM, photo: MICH!).

lc.: Species No. 23b [chasmogamous and cleistogamous plants], Brainerd in Vermont Agric. Exp. Sta. Bull. 224: 60 and second [color] plate following page 64. 1921; reprinted [color] Plate No. 45, Baird-Brainerd, *Wild Violets of North America*: 127. 1942.

Acaulescent, homophyllous, perennial herb, leaves prostrate to ascending, spreading out to form a rosette, at chasmogamous anthesis 4–7 cm high; *rhizomes* fleshy, scaly, vertical or oblique to horizontal, 0.5–5 cm long, bearing stout fibrous roots: up to 1.5 mm in diameter; *stipules* lanceolate to broadly lanceolate, green, apex acute, margins irregularly glandular fimbriate, glabrous ± ciliate; *petioles* green, short (petiole length/blade length ratio up to 2.2), ± pubescent; *blades* ovate to elliptic-ovate or orbicular, base cordate, margins shallowly crenate to crenate-serrate, ciliate, apex obtuse to rounded (acute in some juvenile blades), densely pubescent on the adaxial surface, sparsely pubescent or glabrous on the abaxial surface, major veins often dark purple rendering a variegated pattern to the adaxial surface, at chasmogamous anthesis length/width ratio 0.8–1.4, apical angle 105°–132°; *peduncle* 2–4 (7) cm long, green, pubescent, especially below the bractlets; *bractlets* lanceolate, densely spotted with red-purple on a yellow-green background, margins narrow and scarious, irregularly glandular fimbriate, ciliate, apex acute; *sepals* ovate to lanceolate, green or green sparsely spotted with purple, apex acute or obtuse, margins scarious and finely ciliate, sepals length/capsule length ratio 0.3–0.5; *auricles* 0.3–1.2 mm long, green or green sparsely spotted with purple, apex truncate, subtruncate to rounded, finely ciliate; *spur* 1.7–2.5 mm long; *petals* violet (RHS # 87A) with a white center, abaxial surface often whitened, violet lines on the lateral and spurred petals, 9–13 mm long (including the spur), 2–4 mm wide, lower lateral pair 2 mm wide, upper lateral pair 2–3 mm wide; *petal trichomes* borne on the lower lateral petals and the spurred petal, cylindrical, 30–40 µm wide, visible layers of cuticular folds one, cuticular folds capillary, elongated, narrow, tapering, linear or slightly convoluted over the apex, most vertically aligned, widely and randomly spaced; *cleistogamous flower peduncle habit*: ascending; *capsule* yellow-green, length/width ratio 2–2.5; *seeds* nearly black, occasionally with a flat side, 1.6–2.2 mm long, 1.1–1.6 mm wide, average weight 1.3–2.1 mg, caruncle 0.5–1.1 mm long; *seed coat*: secondary sculpture with folded, segmented, or aggregated and irregularly shaped verrucate structures, and irregularly distributed on reticulate, ring-like terete thickenings or a rough surface; *chromosome number*: $2n = 54$.

Substrate. – Dry or well drained, often sandy, soil. The soil is often covered with pine litter.

Habitat. – Open *Pinus* woods, disturbed sites.

General Distribution. – Southeastern United States from Texas to Florida, north to Virginia, Tennessee, and southern Indiana.

Discussion. – The type at BM consists of a single cleistogamous plant bearing a rosette of leaves typical of the species, and an open capsule. WALTER's (1788) brief description is not accompanied by information about the locality and date of collection. The plant was most likely collected in South Carolina where Walter lived (BRAINERD, 1921). Walter's herbarium was pur-

chased by BM in 1863, and contains many of the plants described in *Flora Caroliniana* (STAFLEU & COWAN, 1988). The specimen is labeled with the number 136, an early annotation: “*Viola pubescens*,” and “in Flora, Villosa” in handwriting that matches Walter’s handwriting as published in EWAN (1979). Therefore, it is apparently the specimen upon which Walter based his description.

All students of the subsection since BRAINERD (1921) have maintained *Viola villosa* as a distinct species due to a number of unique species-specific macromorphological characters. BRAINERD (1907b) reviewed the nomenclatural history of the species and clarified the confusion and misconceptions of previous authors regarding the distinction between *V. villosa*, *V. hirsutula* (abandoned in this study), and *V. sororia*.

The seed color is unique, and could not be matched with the color charts consulted. The overall color of the seeds is nearly black, but color varies since the background color is not uniform. The micromorphological structures of the seed coat surface are also unique. They are most difficult to describe since they vary in shape and are not uniformly distributed. The major secondary wall thickenings are often verrucate, protruding from the surface, and connected by a network of rings or linear thickenings on a rough and uneven surface (GIL-AD, 1995; GIL-AD, in press).

BRAINERD (1907b) reported that much of the autumn foliage remains green throughout the winter, and that cleistogamous flowers and capsules are borne in the winter and early spring in addition to the regular summer crop found in the other taxa of subsection *Boreali-Americanae*. Observations on plants in the field and the greenhouse confirmed Brainerd’s report. In addition, they revealed that the chasmogamous phase is very brief in this species (up to two weeks), and is readily switched to the cleistogamous phase when temperatures rise and the photoperiod lengthens.

There are no reports in the literature on hybrids of *Viola villosa* with other taxa of subsection *Boreali-Americanae*. Putative hybrids of *V. villosa* with *V. septemloba* are reported in the discussion of *V. septemloba*.

6.5. Names Commonly Recognized as Orthospecies, but Hypothesized to Represent Hybrids or Introgressants in This Treatment

6.5.1. Introduction

The following section provides a summary of previous treatments of taxa recognized as distinct species by Brainerd and his predecessors, discussions correlating the micromorphological data obtained by SEM of seed coats (GIL-AD, 1995; abbreviated in GIL-AD, in press) with the macromorphological and other data, and evaluating their distinctness, and recommendations to abandon the recognition of these names.

The types of these names have often not been studied. These types, however, would not be useful for evaluation of their status unless they carried mature seeds that were available for examinations with SEM. The material examined can be divided into four categories, and the corresponding taxa are given in parentheses:

- a. seeds from the holotype (*Viola pratincola*);
- b. seeds harvested in cultivation by Brainerd from plants gathered with the type material (*Viola chalcosperma*, *V. floridana*, and *V. lovelliana*);

- c. seeds from plants cultivated by Brainerd or sampled from specimens examined by him (*Viola papilionacea*, *V. stoneana*, *V. triloba* var. *dilatata*, and *V. viarum*);
- d. seeds from other material (*Viola hirsutula*, *V. palmata*, and some of the taxa listed in the previous categories). Detailed descriptions of the micromorphological structures of the seed coat surface of each taxon and reproductions of micrographs "are provided in GIL-AD (1995). The specimens that were examined are listed in Appendix D.

6.5.2. Discussions

Viola chalcosperma Brainerd in Bull. Torrey Bot. Club 37: 523. 1910.

≡ *Viola affinis* var. *chalcosperma* (Brainerd) Griscom in Rhodora 38: 49. 1936.

FERNALD (1950), and GLEASON & CRONQUIST (1963) maintained *Viola chalcosperma* as a distinct species. FERNALD (1950) listed the habitat as Cypress swamps, wooded bottoms and rich slopes, and the range as the coastal plain from Florida to Virginia. ALEXANDER (1952) did not include it in his treatment. RUSSELL (1965) contended that he was not able to distinguish it from *V. floridana*, and therefore excluded it. Cronquist (in GLEASON & CRONQUIST, 1991) subsumed it into his broadly defined *V. palmata* var. *palmata*. MCKINNEY (1992) did not refer to it in his treatment.

BRAINERD (1910c) and BAIRD-BRAINERD (1942) listed the color of the seeds ("old bronze", hence the specific epithet), heterophylly, pedately trilobed blades at chasmogamous anthesis, and a habitat of wet soil in wooded ravines, as the primary criteria that delimit this species. In addition, they listed long auricles (3-4 mm long), peduncles of the chasmogamous flowers overtopping the leaves, light violet petals, purple sepals, presence of petal trichomes on the lower lateral petals and occasionally on the spurred petal, cleistogamous flowers on ascending peduncles, and gray capsules that are tinged purple at base.

The micromorphological data – a primary sculpture similar to the primary sculpture of seeds of *Viola cucullata* and a secondary sculpture consisting of plates that are unevenly smooth, sparsely and irregularly foveate to falsifoveate in the center, and circumscribed by segmented thickenings – provide evidence that this taxon was most likely derived from putative introgression of another taxon belonging to subsection *Boreali-Americanae* into *V. cucullata*. It is possible that the plants Brainerd described derived from introgression of *V. triloba* or (the putative hybrid previously described as) *V. lovelliana* into *V. cucullata*. These taxa are heterophyllous, possess trilobed blades and capsules spotted with red-purple, and are found in the area *V. chalcosperma* was described from.

The plants were collected in a wet wooded ravine along the Jacksonville highway in Florida (BRAINERD, 1910c; BAIRD-BRAINERD, 1942). That area is south of the southernmost state from which *V. cucullata* was reported – Georgia. It is possible that the conditions that prevailed during the oscillating climates of the Pleistocene, as noted in Section 6.2.6 above, promoted migrations and contact between the taxa, and consequently hybridization or introgression. A more remote possibility is that the occurrence of the plants in an urban area in Florida was associated with dispersal along a dispersal corridor along the Jacksonville highway.

The corroboration of the micromorphological and macromorphological data provides evidence that this taxon is a putative *Viola cucullata* introgressed by a heterophyllous taxon, and therefore, should not be recognized as an orthospecies

Viola emarginata (Nutt.) LeConte in Ann. Lyceum Nat. Hist. New York 2: 142. 1828.

≡ *Viola sagittata* var. *emarginata* Nutt., Gen. N. Amer. Pl. 1: 147. 1818.

POLLARD (1896) asserted that a plant possessing “glabrous and somewhat flaccid, deltoid-cordate, or even panduriform in outline, irregularly crenate [blades], and in general so unlike those of the ordinary violets with which it is associated” (page 90) has been considered as a hybrid. Yet, concurring with Britton [pers. comm.] he considered it as a distinct species that is mainly of southern range, reinstated for it Pursh’s name *Viola dentata*, and listed *V. sagittata* var. *emarginata* and *V. emarginata* in synonymy under this species. BRAINERD (1921), FERNALD (1950), and ALEXANDER (1952) recognized *Viola emarginata* as a distinct species. RUSSELL & RISSE (1960) employed pictorialized scatter diagrams and hybrid indexes, and established that *V. emarginata* was a hybrid of *V. sagittata* with *V. affinis*, or a member of a complex they named the “*V. affinis* complex.” GLEASON & CRONQUIST (1963) listed it as a species, but commented that it might be a series of hybrids. RUSSELL (1965) excluded *V. emarginata* on the basis of Russell & Risser’s study. Cronquist (in GLEASON & CRONQUIST, 1991) reduced it to synonymy under *V. sagittata*, and reiterated its putative hybrid origin. MCKINNEY (1992) contended that the suite of characters he saw on the type specimen of this taxon justified subsuming it into the taxon he delimited as *V. sagittata* var. *sagittata*.

Mature seeds were not available for examination with SEM, but RUSSELL & RISSE’s (1960) analyses and the lack of a distinct suite of characters justify the exclusion of this taxon.

Viola esculenta Elliott ex Greene in Pittonia 3: 314. 1898.

≡ *Viola heterophylla* Muhl. ex LeConte in Ann. Lyceum Nat. Hist. New York 2: 139. 1828, non Poir. in Lam., Encycl. 8: 646. 1808.

BRAINERD (1921) pointed out that the label on the type specimen [CHARL] reads “*Viola esculenta* mihi:” and underneath “*Heterophylla* Muhl.” ELLIOTT (1817) described the taxon under the name *Viola palmata* L. var. *heterophylla*, and remarked that he named it [on the sheet] “*V. esculenta*” since the plants [blades] are very mucilaginous and much used by members of the black community [in the southeastern U.S.A.] in their soups. He also remarked that it is *V. heterophylla* Muhl., and thus did not accept the name *V. esculenta*. According to Elliott, it differs from the other varieties listed under *V. palmata* in size and by and glabrous and rugose leaves, and grows in river swamps. LECONTE (1828) provided a detailed description for the name *V. heterophylla* Muhl. (nom. nud.), but it is a homonym. The name *V. esculenta* was validated by GREENE (1898) who outlined its main characters.

BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola esculenta* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) listed it as a synonym under his broadly defined *V. palmata* var. *palmata*. MCKINNEY (1992) listed it in synonymy under the taxon he delimited as *V. palmata*, and contended that it represents some aspect of the overall phenotypic plasticity associated with this species.

BRAINERD (1921) pointed out that *Viola esculenta* is heterophyllous, and grows in river swamps and on wet borders of slow streams in the southeastern coastal plain. BAIRD-BRAINERD (1942) listed the glabrous and succulent foliage and the crimson colored rhizome as unique characters of *V. esculenta*. RUSSELL (1965) pointed out that it might be confused with *V. septemloba*, and presented the shape of the blade lobes as the main character that distinguishes them. According to Russell, *V. esculenta* usually possesses 3-5 broadly obovate lobes, whereas *V. septemloba* possesses 7-9 slightly oblanceolate lobes. Furthermore, he noted that the two species are often syntopic, and that he had not seen any evidence for hybridization between the two. However, he contended that hybridization between *V. esculenta* and *V. floridana* is responsible for many variations in blade lobing.

The data from SEM of seed coats [Brainerd *s.n.*, 21 March 1909 (VT) and Gil-ad 357 (MICH)] do not demonstrate that this taxon possesses unique micromorphological structures. The micromorphological structures of the seed coat provide evidence that *Viola missouriensis* might have contributed structures to this taxon. However, these structures deviate from the typical combination found on the seed coats on *V. missouriensis*, and may be overlaid on the secondary sculpture of another taxon. The identity of the other taxon cannot be depicted from the micromorphological data. The shape of the blades, heterophylly, and the distribution limited to the southeastern United States narrow down the identity of the other taxon that contributed characters (perhaps by introgression) to the heterophyllous species *V. septemloba* and *V. triloba*, or to hybrids of these species with other taxa. The habitat reported for *V. esculenta* is similar to the moist habitats that *V. missouriensis* prefers. *Viola esculenta* does not possess a unique suite of reproductive characters. The vegetative characters that Baird-Brainerd described as unique are not reliable. Pubescence on vegetative organs is a character that varies extensively both inter- and intraspecifically (Chapter 3, Section 3.2). The determination of the color of the rhizome may be influenced by subjective perception of color. In addition, the substrate or soil organisms may modify the surface features and the color of the rhizome. The effects of these factors on the morphology of rhizomes should be further investigated. The succulent foliage may be an example of a character that appears in an interspecific hybrid but is not found in either parent (STEBBINS, 1950). Succulence of the foliage among the taxa of subsection *Boreali-Americanae* is also liable to subjective delimitation. It is not confined only to plants bearing lobed blades which were circumscribed by previous workers as *V. esculenta*. A number of putative hybrids collected for this research [e.g., Gil-ad 348 and 355 bearing lobed blades, and Gil-ad 354 and 401 bearing undivided blades (MICH)] had succulent foliage.

Viola esculenta most likely originated by hybridization or introgression, and does not possess a distinct suite of characters that would justify maintaining it as an orthospecies.

***Viola floridana* Brainerd in Bull. Torrey Bot. Club 37: 524. 1910.**

FERNALD (1950), ALEXANDER (1952), and GLEASON & CRONQUIST (1963) did not include it in their treatments. RUSSELL (1965) maintained *Viola floridana* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) reduced it to synonymy under *V. sororia*, and MCKINNEY (1992) reduced it to synonymy under the taxon he delimited as *V. sororia* var. *sororia*. BRAINERD (1910c) contended that in flower and fruit it resembles *V. esculenta*, but its undivided leaves on erect petioles and its habitat, well drained soil, mark it as distinct. RUSSELL (1965) contended that *V. floridana* is very similar to *V. affinis*, but differs in slightly smaller leaves that are slightly fleshy and in peduncles overtopping the leaves. Furthermore, he noted instances of hybridization with *V. esculenta* and *V. sororia*, and contended that both *V. floridana* and *V. esculenta* show the effects of introgression.

SEM of seeds of Brainerd 61 (US) revealed that the micromorphological structures on the seed coat are similar to those on the seed coat of *Viola missouriensis*. A number of macromorphological characters – the color of the seeds (strong yellowish brown), the color of the petals (pale violet), the absence of trichomes on the spurred petal, the color and shape of the capsules, and the dimensions of the seeds – support the hypothesis that this taxon is similar to *V. missouriensis*. The habitat described by BRAINERD (1910c), moist, rich woods on well drained soil, can conform with the habitat of *V. missouriensis*. However, *V. floridana* differs from *V. missouriensis* in its pubescent petioles. *Viola floridana* has been collected only in two southern states (BAIRD-BRAINERD, 1942): Florida and South Carolina. It is possible that *V. floridana* resulted from slight introgression of *V. sororia* into *V. missouriensis*, but there is no evidence for this in micromorphological structures on the seed coat.

Viola floridana does not possess a unique suite of characters. Therefore this name should be abandoned.

Viola hirsutula Brainerd in Rhodora 9: 98. 1907.

– *Viola villosa sensu* Nutt., Gen. N. Amer. Pl. 1: 148. 1818, non Walter 1788.

BRAINERD (1907b, 1921) reviewed the long and tortuous nomenclatural history of *Viola hirsutula*, and clarified the confusion between it and *V. villosa*. FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *V. hirsutula* as a distinct species. Cronquist (in GLEASON & CRONQUIST, 1991) listed it in synonymy under *V. villosa*, and indicated that it is “a form with the blades glabrous beneath.” MCKINNEY (1992) maintained it as a distinct species on the basis of its smaller, prostrate appearance, a silvery mottling on the adaxial surface of the blade, and pubescence limited only to the adaxial surface.

Seeds from collections of Brainerd were not available. SEM of seed coats of *Reznicek s.n.* (MICH), possessing a similar suite of characters, did not reveal unique micromorphological structures. The structures observed could be attributed to a number of taxa. The primary sculpture is composed of cells that could be attributed to *Viola nephrophylla* or to *V. cucullata*. Some of the seeds examined displayed outer periclinal walls and reticulate-terete thickening that could be attributed to *V. missouriensis*. The secondary sculpture has porous plates that could be attributed to *V. sororia* or to *V. missouriensis* and *V. affinis*.

The vegetative characters that previous authors used to delimit *Viola hirsutula* are not sufficient to justify maintaining it as a distinct species. The habit of the plants, the shape of the blades at chasmogamous anthesis, the gray-green adaxial surface, and veins suffused with purple on the abaxial surface of early blades can be attributed to *V. nephrophylla*. The assertion that this taxon is the only stemless violet with pubescence confined only to the adaxial surface of the blade (BRAINERD, 1921; BAIRD-BRAINERD, 1942) is erroneous. This pubescence pattern can be found in *V. cucullata*, in juvenile blades of *V. nephrophylla*, and in *V. selkirkii* (subsection *Adnatae*). Reproductive macromorphological characters are not sufficient either to delimit this taxon. The petal trichomes display variation in shape (a blend of cylindrical and clavate trichomes), the seeds’ overall color is close to dark grayish brown but is variable and the capsules resemble in shape the capsules of *V. nephrophylla* but are spotted with red-purple. The habitat is variable as well: undisturbed pine forests, or rich, relatively dry, deciduous forests (BAIRD-BRAINERD, 1942; RUSSELL, 1965).

On the basis of the lack of unique micromorphological characters, and the lack of a clear, distinct suite of macromorphological characters, it is most likely that this taxon is a putative hybrid. Therefore, it should not be considered as an orthospecies, and the name should be abandoned.

Viola langloisii Greene in Pittonia 3: 87. 1896.

≡ *Viola affinis* var. *langloisii* (Greene) Griscom in Rhodora 38: 49. 1936.

= *Viola langloisii* var. *pedatiloba* Brainerd in Bull. Torrey Bot. Club 38: 2. 1911.

In spite of GREENE’s (1896a) vague description, BRAINERD (1921) maintained *Viola langloisii* as a distinct species. He pointed out that *V. langloisii* is distinguished by the lengthened auricles, and occupies wet, often flooded borders of bayous from Florida to Texas. He also speculated that it is closely related to *V. affinis*. BAIRD-BRAINERD (1942) elaborated on the characters of *V. langloisii*, and distinguished it from *V. affinis* by its glabrous foliage, the spreading auricles, the clavate trichomes borne on the lower lateral petals, and seeds mottled with dark green. Furthermore, BRAINERD (1911) erected a variety and named it *pedatiloba* for a heterophyllous plant possessing 3-5 lobes that appears in the range of the species. BAIRD-BRAINERD (1942) distinguished this variety from *V. lovelliana* by its glabrous leaves. Subsequent authors did not list the variety, and it is most likely a hybrid.

FERNALD (1950) and RUSSELL (1965) maintained *V. langloisii* as a distinct species. RUSSELL (1965) pointed out that it is delimited by the tiny triangular blades and large ratio of peduncle

length to petiole length. He also remarked that it is more similar to *V. missouriensis*, and grades into *V. floridana* in Mississippi and west Florida. ALEXANDER (1952) and GLEASON & CRONQUIST (1963) did not include it in their treatments. Cronquist (*in* GLEASON & CRONQUIST 1991) reduced it to synonymy under *V. sororia*, and MCKINNEY (1992) reduced it to synonymy under the taxon he delimited as *V. sororia* var. *sororia*.

Mature seeds from Greene's collections and Brainerd's distribution were not available. The characters provided by Brainerd, Baird-Brainerd, and Russell are not sufficient to delimit this taxon and to rule out the possibility that it is a hybrid involving *V. cucullata* and *V. affinis* or *V. missouriensis*. Therefore, it should not be considered an orthospecies until mature seeds become available for examination with SEM, or other supporting data are obtained.

***Viola latiuscula* Greene in Pittonia 5: 93. 1902.**

GREENE (1902) distinguished this taxon from *Viola affinis* by having blades with a firmer and more succulent texture, by the size of the chasmogamous flowers, and by the breadth of the blades. In addition, he listed the petal trichomes of the lateral petals as "calculate." BRAINERD (1904a, 1921), FERNALD (1950), ALEXANDER (1952), and GLEASON & CRONQUIST (1963) maintained *V. latiuscula* as a distinct species. CRONQUIST (*in* GLEASON & CRONQUIST, 1991) reduced it to synonymy under *V. sororia*, and MCKINNEY (1992) reduced it to synonymy under the taxon he delimited as *V. sororia* var. *sororia*.

BAIRD-BRAINERD (1942) elaborated on the characters of this taxon. She pointed out that the broadly cordate-ovate or deltoid mature blades, which are purplish on the abaxial surface, distinguish it from the other members of a group of taxa possessing purple capsules and prostrate cleistogamous flowers. In addition, she suggested that it is closely related to *Viola papilionacea*, limited in its distribution to the northeastern United States, and grows on dry soils. FERNALD (1950) listed an additional character, granulose-angled petioles, but RUSSELL (1965) pointed out that this character appears sporadically on specimens of other taxa, and excluded it.

Mature seeds from Greene's or Brainerd collections were not available. Russell's decision is justified since this taxon does not possess a distinct suite of characters, and is most likely a hybrid involving *V. sororia*, and *V. affinis* or *V. cucullata*.

***Viola lovelliana* Brainerd in Bull. Torrey Bot. Club 37: 526. 1910.**

BRAINERD (1921) considered *Viola lovelliana* a species closely related to *V. triloba* since they are heterophyllous and possess trilobed blades. The two species were distinguished by a different pubescence pattern on the leaves, the color of the petals, and the limited range of *V. lovelliana* (Mississippi, Louisiana, Arkansas, Missouri, Oklahoma, and eastern Texas). *Viola lovelliana* was maintained by FERNALD (1950), ALEXANDER (1952), and RUSSELL (1965), omitted by GLEASON & CRONQUIST (1963), reduced to synonymy under the broadly defined *V. palmata* var. *palmata* by Cronquist (*in* GLEASON & CRONQUIST, 1991), and listed in synonymy under the taxon MCKINNEY (1992) delimited as *V. palmata*.

Examination of the micromorphological structures of the seed coat surface of Brainerd 78 (US), Brainerd s.n. (28 Aug. 1911, VT), and Gil-ad 375 and 380 (MICH) revealed on some seeds outer periclinal walls characteristic of *V. missouriensis*, and secondary wall thickenings characteristic of *V. triloba* and *V. missouriensis* that are distributed unevenly and vary among seeds. No unique micromorphological structures were detected.

A number of macromorphological characters of *V. lovelliana* support the hypothesis that *V. triloba* and *V. missouriensis* were involved in the evolution of *V. lovelliana*. A blend of cylindrical and slightly clavate trichomes is found on the lower lateral petals only. Field observations

revealed variation in the color of the petals among populations. The seeds of *V. lovelliana* are spotted and banded with strong yellowish brown on an orange-yellow background, but vary in the intensity of the streaks and the background. The cleistogamous flowers are borne on prostrate peduncles. The capsules are similar to those of *V. missouriensis* in shape (length/width ratio ca. 2) and in color pattern. The plants thrive on clay-loam. In addition, the ranges of *V. missouriensis* and *V. lovelliana* overlap.

The evidence presented above combined with the heterophylly of the plants supports the hypothesis that *V. lovelliana* is a stabilized introgressant of *V. missouriensis* into *V. triloba*. Therefore, it should not be recognized as an orthospecies.

***Viola palmata* L., Sp. Pl.: 933. 1753.**

- ≡ *Viola cucullata* var. *palmata* (L.) A. Gray, Manual ed. 2: 43. 1856.
- = *Viola variabilis* Greene in Pittonia 5: 90. 1902.
- ≡ *Viola palmata* var. *variabilis* (Greene) W. Stone in Proc. Acad. Nat. Sci. Philadelphia 55: 677. 1903.
- = *Viola angellae* Pollard in Torrey 2: 24. 1902.
- ≡ *Viola palmata* var. *angellae* (Pollard) W. Stone in Proc. Acad. Nat. Sci. Philadelphia 55: 678, Plate 34, Fig. 2. 1903.

BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola palmata* as a distinct species. VOSS (1985) (following unpublished opinions of Ballard and others) and BALLARD (1994) treated *V. palmata* as “a broad complex” encompassing plants previously referred to as *V. triloba*, and plants of probable hybrid origin with *V. pedatifida* (×*V. sororia* and/or *V. sagittata*) or hybrids of *V. sagittata* and *V. sororia*. Cronquist (in GLEASON & CRONQUIST, 1991) took a radical approach, and lumped under the binomial *Viola palmata* all the taxa possessing divided or lobed blades. Furthermore, he erected two varieties: variety *palmata* comprising *V. brittoniana*, *V. septemloba*, *V. chalcosperma*, *V. esculenta*, *V. lovelliana*, the undivided *V. pectinata* (= *V. brittoniana* f. *pectinata*), *V. stoneana*, *V. triloba*, and *V. viarum*; and variety *pedatifida* comprising *V. pedatifida*, and *V. egglesonii*. He contended that the eastern var. *palmata* passes westward into var. *pedatifida*, and that extreme plants of var. *palmata* from well outside the area of var. *pedatifida* would pass as var. *pedatifida* in the absence of geographic data.

MCKINNEY (1992) outlined the troublesome nomenclatural history of *Viola palmata*. He concluded, after examining a photograph of the holotype and a number of early treatments, that the taxon Linnaeus described was the heterophyllous taxon that has been called *V. triloba*. On the basis of priority he reduced *V. triloba* to synonymy under the binomial *Viola palmata*. Furthermore, he applied the specific epithet *subsiniata* to a homophyllous taxon that authors since POLLARD (1898) treated as *V. palmata*. Furthermore, he contended that the taxon he delimited as *V. palmata* exhibits a considerable amount of variation in both the shape of the undivided [middle] blade segments, and the amount and location of pubescence. He also asserted that *V. esculenta*, *V. viarum*, *V. lovelliana*, and *V. triloba* var. *dilatata* represent some aspect of the overall phenotypic plasticity that this species exhibits.

The major macromorphological character that has been used by authors since POLLARD (1898) to delimit *Viola palmata* is the 5-11-lobed homophyllous blade, possessing a middle segment wider than the lateral segments. Other characters that were cited were petal trichomes borne only on the lower lateral petals, the prostrate peduncles of the cleistogamous flowers, the color of the capsules (blotched and spotted with purple), and the color of the seeds (brown). In addition, a wide distribution was attributed to this species covering eastern and midwestern United States, and the southern Atlantic States (BAIRD-BRAINERD, 1942; FERNALD, 1950; GLEASON & CRONQUIST, 1963). However, RUSSELL (1965) contended that *Viola palmata* is essentially Appalachian, and is relatively uncommon. BAIRD-BRAINERD (1942) commented that geographic varia-

tion has been detected in the number of blade lobes, pubescence of the leaves, and blade margins. The habitat attributed to this species was rather general: wooded hills or ravines on dry rich soil (BAIRD-BRAINERD, 1942; ALEXANDER, 1952; GLEASON & CRONQUIST, 1963). BRAINERD (1913a, 1924) demonstrated segregation in blade characters in the F_1 hybrid, and segregating F_2 offspring hybrids of *V. pedatifida* and *V. sororia*. The blade dissection and additional characters listed for some of the offspring correspond to the suite of characters assigned to *V. palmata*. Brainerd also reported and demonstrated the segregation of offspring of a hybrid of *V. pedatifida* and *V. sagittata*. The sinuses in the blades of the F_1 hybrid in this case were deeper than those of the hybrid between *V. pedatifida* and *V. sororia*, and the blades of the F_2 offspring were longer than wide. However, Brainerd and other authors did not detect the putative correlation between the characters of these hybrids and the species – *Viola palmata* – they chose to recognize.

Mature seeds from earlier collections were not available. Therefore, seeds were obtained from plants possessing blades characteristic of *Viola palmata* that were collected during the course of this study. The seed coat surfaces of seeds obtained from those plants revealed extensive variation among populations, and lack of consistent and unique micromorphological characters that could delimit this taxon.

The seed coat surface of *Gil-ad 258* (MICH) (Michigan) revealed features suggesting that *Viola pedatifida* and a taxon (most likely *Viola affinis*) possessing striations on the outer periclinial walls and a secondary sculpture consisting of porous plates and reticulate-terete thickenings were most likely the parents. The seed color – light yellowish brown banded by moderate yellowish brown – is close in range to the color of the seeds of the orthospecies (ca. strong yellowish brown in *V. pedatifida*, and moderate orange-yellow in *V. affinis*). The presence of a few cylindrical trichomes on the spurred petals also supports the hypothesis that *V. affinis* is the second parent of this hybrid. A previous collection (*Nimke s.n.*, MICH) displays blades typical of *V. pedatifida*, and documents that *V. pedatifida* has previously occupied the site where *Gil-ad 258* was collected. The prairie habitat that most likely formerly dominated this site has been replaced by open woods. The orthospecies has become extinct, and hybrid derivatives that are more adapted to the new habitat persist in it (W. H. WAGNER, JR. pers. comm., 1990). *Viola sororia* and hybrids of *V. sororia* and *V. nephrophylla* were observed and collected in the vicinity of the plants as well.

The seed coat surfaces of seeds of *Gil-ad 280* (MICH) (New Jersey) that displayed aggregates of porous plates support the hypothesis that *Viola triloba* might have been one of the putative parents. The identity of the second parent could not be clearly depicted from the structures observed on the seed coat. Both *V. nephrophylla* and *V. affinis*, which possess reticulate-terete thickenings, could be hypothesized as the second putative parent. Some of the plants in the population were homophyllous and possessed blades with narrow lobes and deep sinuses, and others were heterophyllous and possessed blades with a wider central lobe and narrow lateral lobes, as well as undivided cordate-ovate blades. Additional reproductive macromorphological characters did not shed light on the identity of the second parent. The cleistogamous flowers were borne on prostrate peduncles, the capsules were spotted red-purple, and only the lateral petal trichomes bore cylindrical trichomes. The color pattern of the seeds – gray yellowish brown banded by darker shades – does not match the color of any orthospecies.

The seed coat surface of *Gil-ad 462* (MICH) (New Jersey) indicated that *Viola brittoniana* and a taxon possessing porous plates on the seed coat were the putative parents. A large population of hybrids of *V. affinis* and *V. cucullata* was detected in the vicinity. Therefore, it is likely that one of these plants or one of the parental orthospecies was the other putative parent. The color of the seeds (dark orange yellow) is close to the color of the seeds of the putative parents.

The number of blade lobes, the presence or absence of trichomes on the spurred petal, and the color of the seeds varied among these populations. This macromorphological variation as well as the micromorphological evidence supports the hypothesis that the taxon named *Viola palmata* and characterized by multi-lobed blades represents homophyllous hybrids of *V. pedatifida*

or *V. brittoniana* (both homophyllous species) with taxa possessing undivided blades and porous plates on the seed coat surface. It may also represent heterophyllous hybrids of *V. triloba* with taxa possessing undivided blades and porous plates on the seed coat surface. Therefore, *V. palmata* should not be recognized as an orthospecies.

The circumscription of *Viola palmata* by recent authors (Cronquist in GLEASON & CRONQUIST, 1991; MCKINNEY, 1992) is not supported by the data. The use of the specific epithet with a multiplication sign (*V. ×palmata*) to designate an assemblage of putative hybrids derived from various combinations of orthotaxa (advocated by BALLARD, 1994) is not recommended either, since it does not represent a single combination of putative parents, it would cause confusion with previous species concepts and the circumscriptions of the orthospecies, and is contrary to the code.

***Viola papilionacea* Pursh, Fl. Amer. Sept.: 173. 1813.**

Viola papilionacea has long been considered a species closely related to *V. sororia*, and has puzzled students of the group and field botanists. BRAINERD (1921) reviewed its troublesome nomenclatural history and upheld it on the basis of the flower shape (supposedly resembling the flower of the garden pea in the shape of the spurred petal) and characters mentioned in Pursh's description. These characters were: cordate-deltoid, crenate, acute, nearly glabrous blades, peduncles equal in length to the leaves, obovate petals, upper two petals reflexed, green yellow center on the spurred petal, and the presence of trichomes on the three lower petals. BAIRD-BRAINERD (1942) provided a more detailed summary of the characters of the species and listed petal trichomes on the lower lateral petals only, prostrate peduncles of the cleistogamous flowers, dark brown seeds, and glabrous foliage except for soft pubescence on the early petioles. One of the reproductive characters she listed, the dimorphic color of the capsules (green or dark purple) provides reason to suspect that the plants described were not orthospecies. Subsequent authors, FERNALD (1950), ALEXANDER (1952), and GLEASON & CRONQUIST (1963), maintained it as a distinct species and listed the habitat as moist fields, low damp woods, meadows, roadsides, and dooryards. RUSSELL (1965) asserted that *V. papilionacea* has been a catch-all for almost any glabrous or near-glabrous taxon possessing undivided blades in the group, and that populations of *V. sororia* often have glabrous or near glabrous plants in the eastern states, due to normal variation or introgression. He concluded that Pursh must have described one of these variants. Cronquist (in GLEASON & CRONQUIST, 1991) followed Russell and reduced *V. papilionacea* to synonymy under *V. sororia*, and considered it a subglabrous form.

Seeds from herbarium specimens identified by Brainerd as *Viola papilionacea* – Brainerd 107 (VT), Brainerd s.n. (31 Aug. 1906, VT) and Deam 23497 (VT) – exhibited extensive variation in their color patterns among specimens, and in some cases among seeds of one specimen. The micromorphological structures of the seed coats provide evidence that plants that were named *V. papilionacea* lack any unique micromorphological structures and are hybrids of *V. cucullata* and *V. affinis*, *V. cucullata* and *V. sororia*, or *V. sororia* and *V. affinis*. All of these putative hybrids involved taxa possessing undivided blades that are very similar in their overall blade shape. These hybrids possess combinations of macromorphological characters that resemble the suite of characters of *V. sororia*, but differ in a few characters, such as the shape of the petal trichomes, the color of the seeds, the color pattern of the capsules, ciliation on the sepals and auricles, and the dimensions and color of the petals. These hybrids are more likely to occupy the mesic habitats that have been attributed to *V. papilionacea* since two of the putative parents, *V. cucullata* and *V. affinis*, prefer those habitats.

On the basis of the micromorphological data and the lack of distinct suite of morphological characters the name *Viola papilionacea* should be abandoned.

***Viola pratincola* Greene in Pittonia 4: 64. 1899.**

GREENE (1899) described this species from a collection of plants that grew on rich black prairie soil near the banks of the Des Moines River at Windom, Minnesota. Most of the characters he listed in the description are standard and do not clearly delimit the species. Yet, the following characters should be noted: cuspidately acuminate and cordate-reniform and glabrous blades, and terete and cylindric or abruptly clavellate-dilated trichomes on the lateral petals. This wide range in trichome shape suggests putative hybridity.

BRAINERD (1921) contended that *Viola pratincola* appears not to be specifically distinct from *V. papilionacea*, and therefore he did not recognize it. FERNALD (1950) subsumed it into *V. papilionacea*. ALEXANDER (1952) and GLEASON & CRONQUIST (1963) did not include it in their treatments. RUSSELL (1965) maintained it as a distinct species. He described it as a distinct mid-western prairie margin violet that grows as a weed beside or in disturbed prairie tracts or urban settings, and possesses entirely glabrous blades that are uniformly toothed to the acute apex. Cronquist (in GLEASON & CRONQUIST, 1991) listed it as a synonym under *V. sororia*. MCKINNEY (1992) listed it in synonymy under the taxon he delimited as *V. sororia* var. *sororia*.

Seed micromorphological structures provide evidence that this taxon is most likely a hybrid between *V. nephrophylla* and another taxon possessing porous plates. The micromorphology of the seeds sampled from the holotype: *Greene s.n.* (1 July 1898, NDG) suggests that the other taxon is most likely *V. affinis*. The micromorphology of seeds sampled from a recent collection – *B. L. Wilson s.n.* (MICH) (12 May 1992) – suggests that the other taxon is most likely *V. sororia*. The micromorphological data are corroborated by a number of macromorphological characters. These characters include glabrous sepals, auricles, and peduncles, narrow cylindrical trichomes on the spurred petal (as in *V. nephrophylla*, but unlike the plants described by Greene), smaller flowers than the flowers of *V. sororia* and *V. affinis*, and the predominantly green background of the capsules. A number of characters have most likely been contributed by either *V. sororia* or *V. affinis*: the prostrate peduncles of the cleistogamous flowers, red-purple spots on the capsules, and the red-purple blotched sepals, auricles, and peduncles.

Wilson s.n. was collected in Palmquist Prairie, Page County, Iowa. That prairie is significantly disturbed, dominated by sedges, and parts of it are very wet (B. L. WILSON pers. comm., 1992). The wetness has most likely enabled *V. nephrophylla* to enter this habitat, but apparently only its hybrids with *V. sororia* have survived. Putative hybrids of these hybrids with *V. pedatifida* bearing lobed blades were also collected at the same site (*B. L. Wilson s.n.*, MICH).

On the basis of this evidence *Viola pratincola* is most likely a hybrid, and should not be recognized as an orthospecies.

***Viola rosacea* Brainerd in Bull. Torrey Bot. Club 37: 525. 1910.**

BRAINERD (1910c) collected this homophyllous taxon in two sites, near Crowley, Louisiana, and near Biloxi, Mississippi, and delimited it by the color of the petals, rose-purple or rosy violet (petunia violet) (BAIRD-BRAINERD, 1942). BRAINERD (1924) described also a hybrid between *V. rosacea* and *V. sagittata* that possessed lobed blades similar to those of *V. lovelliana*. Most subsequent authors did not mention *V. rosacea* in their treatments. RUSSELL (1965) pointed out that this taxon is merely a color form of *V. affinis*, and did not recognize it as a distinct species. MCKINNEY (1992) listed it in synonymy under the taxon he delimited as *V. sororia* var. *sororia*.

Mature seeds were not available for examination with SEM. Russell's decision to exclude this species is justified since the characters outlined by Brainerd and Baird-Brainerd are not sufficient to delimit it as a species

Viola stoneana House in Bull. Torrey Bot. Club 32: 253, Plate 16. 1905.

- *Viola septemloba sensu* W. Stone in Proc. Acad. Nat. Sci. Philadelphia 55: 678, Plate 35 Fig. 2, Plate 39 Fig. 3. 1903, non LeConte. 1828.

The major character that authors used to delimit *Viola stoneana* is the shape of the blades. The blades are divided into three segments, the middle one divided into three lobes, and the lateral segments divided into 2-3 lobes. The lobes are cuneate or oblanceolate, and their margins are unevenly and coarsely crenate-serrate on the upper half. STONE (1903) and BRAINERD (1921) noted that the plants often bear one or more small undivided leaves in early spring, thus the plants are heterophyllous. HOUSE (1905) and BRAINERD (1921) considered it closely related to *V. palmata*, and noted that *V. stoneana* is less pubescent (minute trichomes on the blade margins and adaxial surface). BAIRD-BRAINERD (1942) mentioned the light brown seeds and the longer petioles of *V. stoneana* as additional characters distinguishing it from *V. palmata*. FERNALD (1950) contended that habitally *V. stoneana* suggests *V. triloba* var. *dilatata*, but noted that *V. stoneana* is glabrous. In addition he listed the seed color as buff to olive-brown. ALEXANDER (1952) and GLEASON & CRONQUIST (1963) maintained *Viola stoneana* as a distinct species. RUSSELL (1965) noted that he could not find any specific characters for this taxon. He suspected that it represented an assemblage of hybrids, and consequently excluded it. Cronquist (in GLEASON & CRONQUIST, 1991) listed it as a synonym under his broadly defined *V. palmata* var. *palmata*. MCKINNEY (1992) listed it in synonymy under the taxon he delimited as *V. palmata*.

The micromorphological data, obtained by examination of seeds of *Brainerd 163* (VT) and *Gil-ad 450* (MICH), did not provide evidence for unique structures on the seed coat. The shape of the secondary sculpture plates of *Brainerd 163* is quite similar to the shape of the plates found on the seed coat surface of *Viola triloba*, but the plates are sparser and less aggregated. Other species, such as *V. sororia* and *V. affinis*, possessing porous plates on the seed coat could have been also involved in the evolution of this plant. Correlations of micromorphological and macromorphological data of *Gil-ad 450* and the data on the other hybrid derivatives in the same locality (*Gil-ad 449* & *451*, MICH) suggest that *Gil-ad 450* is likely a hybrid derivative of *V. triloba* with either a hybrid of *V. missouriensis* and *V. sororia* or an introgressant of *V. sororia* into *V. missouriensis*. Thus, the micromorphological data available cannot clearly identify the other putative parent.

Viola stoneana shares a number of macromorphological characters with *V. triloba*: heterophylly, presence of cylindrical trichomes on the lateral petals only, the prostrate peduncles of the cleistogamous flowers, and orange yellow seeds. *Viola stoneana* differs from *V. triloba* in the shape of the blades, by the color pattern on the capsules (densely blotched with overlapped red-purple patches), and the shorter seed caruncle (0.6-0.9 mm). *Viola stoneana* was reported from New Jersey, Pennsylvania, the District of Columbia, Virginia, Kentucky and North Carolina (BAIRD-BRAINERD, 1942; FERNALD, 1950; GIL-AD pers. observations). It is likely closely related to *V. triloba*, and perhaps should be recognized as a variety on the basis of macromorphology and distribution alone. However, the micromorphological data do not provide clear evidence to rule out the possibility that *V. stoneana* has derived from hybridization or introgression from other taxa of subsection *Boreali-Americanae* into *V. triloba*. Seed samples from additional populations and molecular data may provide additional evidence to resolve this problem. Nonetheless, the data available do not support maintaining *V. stoneana* as an orthospecies.

Viola subsinuata (Greene) Greene in Pittonia 4: 4. 1899.

- ≡ *Viola emarginata* var. *subsinuata* Greene in Pittonia 3: 313. 1898.

GREENE (1898) erected this species based on a specimen (*Kearney 615*, NDG) collected in the mountains of eastern Tennessee. The character he used to delimit the species is the lobing of the blades (subpinnately and subsinuately deeply toothed or parted, including the small broad early blades). This species was ignored by the authors who followed Greene, but the specific epi-

thet was resurrected by MCKINNEY (1992). McKinney contended that a homophyllous taxon that has been treated by most authors under the misapplied binomial *Viola palmata* should be renamed *V. subsinuata*, and considered it related to the "*V. pedatifida* complex of homophyllous violets." BALLARD (1994) commented that the morphology of *V. subsinuata* is essentially identical to the morphology of *V. x palmata* except for the homophyllous blades that are moderately to deeply lobed including the central segment. In addition, he contended that many individuals from populations of *V. subsinuata* in southeastern Michigan approached *V. pedatifida* in morphological features, and occupied more prairie-like microhabitats within broader forest habitats. He designated *V. subsinuata* as a hybrid encompassing *V. palmata* (auct. not L.) and hybrids of *V. pedatifida* and *V. sororia*. His assertion that the binomial *V. subsinuata* represents a putative hybrid is most likely correct, but the evidence that it has derived from hybridization between *V. pedatifida* and *V. sororia* is not substantial.

MCKINNEY (1992) characterized the blades of *Viola subsinuata* as homophyllous, triangular, ovate to widely ovate in outline, and cleft or parted into 5-9 (-16) segments, each separated by wide sinuses, and having a larger middle segment. The middle segment is narrowly triangular or narrowly elliptic and the lateral segments lanceolate to narrowly elliptic or falcate. Most of the other characters that McKinney listed, especially the reproductive characters, are polymorphic and do not delimit this taxon clearly. Furthermore, he mentioned and illustrated variation in the lobing of the blades and in pubescence that suggests that this taxon represents an assemblage of hybrids. Examination of the holotype (NDG) revealed glabrous sepals and auricles, cylindrical trichomes on the spurred and lower lateral petals, peduncles of the cleistogamous flowers ascending and shorter than the petioles, and traces of red-purple spots on the opened capsules. These reproductive characters are not sufficient to delimit this taxon as an orthospecies. Seeds from plants named *V. subsinuata* by Greene or McKinney were not available. Yet, evidence from SEM of seed coats of seeds derived from plants bearing blades with similar lobing are presented under *V. palmata* in this section. The use of homophylly as the major criterion to name and subsequently delimit this taxon is unjustified. *Viola subsinuata* should not be considered as an orthospecies, and is likely of hybrid origin.

Viola viarum Pollard ex Britton, Man. Fl. N. States: 635. 1901.

BRAINERD (1921), FERNALD (1950), ALEXANDER (1952), GLEASON & CRONQUIST (1963), and RUSSELL (1965) maintained *Viola viarum* as a distinct species. Cronquist (*in* GLEASON & CRONQUIST, 1991) listed it as a synonym under his broadly defined *V. palmata* var. *palmata*. MCKINNEY (1992) listed it in synonymy under the taxon he delimited as *V. palmata*.

Viola viarum was reported as a species occupying alluvial banks, moist ledges of bluffs, gravel bars along streams, and moist low ground (STEYERMARK, 1963) in Missouri, Indiana, Kansas, Nebraska, and Arkansas (ALEXANDER, 1952; BRAINERD, 1921; BAIRD-BRAINERD, 1942; GLEASON & CRONQUIST, 1963). RUSSELL (1965) reported observing a few plants of *V. viarum* and intermediates in a large population of *V. missouriensis*, and hypothesized that *V. viarum* might be "a simple genetic form" of *V. missouriensis*.

Two sources of evidence can aid in hypothesizing the putative hybridity of *Viola viarum*: **a.** correlation of the micromorphological structures of the seed coat surfaces of seeds of Brainerd 176 (VT), Brainerd s.n. (7 Oct. 1906, VT), and Gil-ad 415 (MICH) (both from Missouri) with micromorphological structures of orthospecies found in the area of distribution of *V. viarum*; **b.** macromorphological characters of a hybrid swarm [Gil-ad 416 & 417 (MICH); Missouri] consisting of plants with undivided blades, plants with trilobed blades, and intermediates at the vicinity of Gil-ad 415 with similar macromorphology to *V. viarum*.

The seed coats examined did not display any unique structures, and the structures present were shallow. It is not possible to accurately and definitely correlate the shallow structures on the

seed coat surface of seeds of *Viola viarum* with structures characteristic of orthospecies. However, it is possible to hypothesize and correlate structures characteristic of putative orthospecies found in the geographical range of this taxon with the structures and features observed on the seed coat of this taxon. The polygonal cells of the primary sculpture are found also on the seed coats of *V. nephrophylla*. The unevenly ribbed outer periclinal walls are found on seed coats of *V. pedatifida*. The shallow porous plates can be attributed to *V. missouriensis*, *V. triloba* or *V. affinis*. The reticulate-terete, secondary wall thickenings is found on the seed coats of *V. missouriensis* and *V. nephrophylla*.

The macromorphological characters that were used to delimit *V. viarum* were the 3-7 lobed blades with distinctly long, broad, acute, and serrate middle lobe and serrate lateral lobes that become broadly triangular and incised-serrate at the cleistogamous phase, short cylindrical to clavate trichomes (matching *V. missouriensis*) on the lower lateral petals and on the spurred petal, the erect peduncles of the cleistogamous flowers (matching *V. pedatifida*), the green capsule (matching *V. nephrophylla* and *V. pedatifida*), and dark to olive-brown seeds. Three taxa that can be proposed as putative parents possess orange-yellow or yellow-brown seeds: *Viola missouriensis*, *V. pedatifida*, and *V. triloba*. *Viola nephrophylla*, however, possesses dark yellowish brown to dark brown seeds as well as a conspicuous reticulate-terete pattern and polygonal cells of the primary sculpture on the seed coat surface. The plants that possessed undivided blades in the hybrid swarm, mentioned above, were most likely hybrids of *V. missouriensis* and *V. nephrophylla*, and some of them have most likely crossed with a taxon possessing divided or lobed blades and formed the intermediates.

These sources of evidence support the hypothesis that *V. viarum* is most likely a hybrid involving *V. missouriensis*, *V. nephrophylla*, and a taxon possessing divided or lobed blades, such as *V. pedatifida* or *V. triloba*. Thus, *Viola viarum* should not be recognized as an orthospecies.