boissiera

volume **53**

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Couverture: Boissiera squarrosa (Banks & Solander) Nevski

boissiera

boissiera

volume **53**

Genève, 1997

Mémoires
de
botanique systématique

Systematics of Viola
subsection Boreali-Americanae

by

Nir L. GIL-AD

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ABSTRACT

GIL-AD, N. L. (1997). Systematics of *Viola* subsection *Boreali-Americanae*.

Viola L. subsection *Boreali-Americanae* (W. Becker) Gil-ad (Violaceae), confined to North America including northern México, has long been considered one of the most taxonomically difficult temperate groups of the Angiosperms. A new treatment of the subsection is presented on the basis of comprehensive evaluations and integration of micromorphological, macromorphological, ecological and phytogeographical data. Speciation among the taxa of the subsection has most likely taken place through ecological adaptation, and in a number of taxa by geographic isolation. It is manifested more extensively at the micromorphological level than at the macromorphological level. The role of hybridization in the evolution of the taxa and its effects on the systematics of the subsection are evaluated.

Sixteen taxa are circumscribed as orthospecies: *Viola affinis* LeConte, *V. brittoniana* Pollard, *V. cucullata* Aiton, *V. egglestonii* Brainerd, *V. fimbriatula* Sm., *V. missouriensis* Greene, *V. nephrophylla* Greene, *V. novae-angliae* House, *V. nuevo-leonensis* W. Becker, *V. pedatifida* G. Don, *V. sagittata* Aiton, *V. septemloba* LeConte, *V. septentrionalis* Greene, *V. sororia* Willd., *V. triloba* Schwein., and *V. villosa* Walter. Two changes of rank are proposed: *Viola brittoniana* Pollard f. *pectinata* (E. P. Bicknell) Gil-ad and *Viola novae-angliae* House subsp. *grisea* (Fernald) Gil-ad. New descriptions of the characters delimiting the subsection, keys to the orthospecies at the chasmogamous and cleistogamous phases, descriptions of the orthospecies and discussions, and discussions of names that are commonly recognized as orthospecies, but are hypothesized in this treatment to represent hybrids or introgressants, are provided. A lectotype is designated for *Viola* subsection *Boreali-Americanae*. The type specimens of 15 of the 18 taxa recognized in this research have been located. *Viola affinis*, and *V. septemloba* are lectotypified by illustrations. *Viola nuevo-leonensis* is illustrated for the first time.

RÉSUMÉ

GIL-AD, N. L. (1997). Systématique de la sous-section *Boreali-Americanae* du genre *Viola*.

La sous-section *Boreali-Americanae* (W. Becker) Gil-ad du genre *Viola* L. (Violacées), restreinte à l'Amérique du Nord y compris le Mexique du nord, a été longtemps considérée comme un des groupes taxonomiquement les plus complexes des *Angiospermae*. Un nouveau traitement de la sous-section est présenté sur la base d'une réévaluation complète des données micromorphologiques, macromorphologiques, écologiques et phytogéographiques disponibles. La spéciation parmi les taxons de la sous-section a probablement eu lieu au travers d'une adaptation écologique et, dans le cas de plusieurs taxons, par une isolation géographique. Elle se manifeste plus complètement au niveau micromorphologique qu'au niveau macromorphologique. Le rôle de l'hybridation dans l'évolution des taxons et ses effets sur la systématique de la sous-section sont évalués.

Seize taxons sont reconnus comme bonnes espèces: *Viola affinis* LeConte, *V. brittoniana* Pollard, *V. cucullata* Aiton, *V. egglestonii* Brainerd, *V. fimbriatula* Sm., *V. missouriensis* Greene, *V. nephrophylla* Greene, *V. novae-angliae* House, *V. nuevo-leonensis* W. Becker, *V. pedatifida* G. Don, *V. sagittata* Aiton, *V. septemloba* LeConte, *V. septentrionalis* Greene, *V. sororia* Willd.,

V. triloba Schwein., et *V. villosa* Walter. Deux changements de rang sont proposés: *Viola britto-niana* f. *pectinata* (E. P. Bicknell) Gil-ad et *Viola novae-angliae* subsp. *grisea* (Fernald) Gil-ad. La description nouvelle des caractères qui définissent la sous-section, deux clefs pour les bonnes espèces aux phases chasmogamique et cléistogamique, les descriptions des espèces et les discussions des noms qui sont généralement reconnus comme bonnes espèces, mais qui sont considérés dans ce travail comme des hybrides ou des introgressants, sont fournis. Un lectotype est désigné pour *Viola* sous-section *Boreali-Americanae*. Les spécimens-types de 15 des 18 taxons reconnus dans cette recherche sont désignés. *Viola affinis* et *V. septemloba* sont lectotypifiés par des illustrations. *Viola nuevo-leonensis* est illustré pour la première fois.

ACKNOWLEDGEMENTS

and shipping me live *Viola* species in spring 1992 when I was not able to get out to the field due to my leg injury.

CHAPTER 1

INTRODUCTION

The family *Violaceae* comprises ca. 800 species in ca. 25 genera belonging to three subfamilies: *Violoideae* (world-wide), *Leonioideae* (neotropical), and *Fusispermoideae* (neotropical). Most of the genera and species belong to the subfamily *Violoideae*, which is subdivided into two tribes: *Violeae* (world-wide), and *Rinoreeae* (circumtropical). Tribe *Violeae* comprises ca. 525 species of which ca. 400 (-500) belong to *Viola*, ca. 100 to *Hybanthus*, and ca. 25 are distributed among the neotropical genera *Anchietea*, *Orthion*, *Mayanaea*, *Noisettia*, *Corynostylis*, and *Schweiggeria*, and the oceanic genus *Agatea* (MELCHIOR, 1925a; HEKKING, 1988; VALENTINE, 1962).

Viola L. is a genus of world-wide distribution, centered in the North Temperate Zone, and restricted to mountains in the tropics. A few species occur in the Arctic Zone in the Old World, and in the Subarctic Zone of North America; the southernmost limits are South Africa, New Zealand, and Tierra del Fuego. Endemic species are found in all parts of the generic range. The genus is least represented in Africa. The plants prefer cool climatic conditions of moderate and arctic regions, as well as of montane to alpine zones (BRIZICKY, 1961; GOOD, 1974; HEKKING, 1988; WILLIS, 1966). *Viola* appears to be the most derived genus of the family *Violaceae* (MELCHIOR, 1925b; EXELL, 1925; CAMP, 1947; CLAUSEN, 1951).

One of the most remarkable attributes of *Viola* is that species from different parts of the world, many of which occupy diversified and specialized habitats, have a uniform flower structure that can be readily identified. Conversely, tremendous morphological diversity occurs in the genus in duration, woodiness, growth forms, types of roots, stipule types and attachment, presence and habit of aerial stems, presence of stolons, presence of secondary branches, leaf phases, leaf attachment, blade morphology, inflorescences, calyx and corolla morphology, color patterns on the petals, patterns and colors of the lines on the petals (nectar guides), presence and morphology of petal trichomes, presence and length of the spur, morphology of the gynoecium and androecium, shape and color patterns of capsules, seed dimensions, color and micromorphology, presence and morphology of caruncles, presence of cleistogamy, and habit of the peduncles of cleistogamous flowers. The morphological diversity is compounded by extensive polymorphism, and is coupled with variation in seed dispersal syndromes, chromosome numbers, secondary compounds, and substrate and habitat preferences.

BECKER (1925) provided the first infrageneric classification for supraspecific taxa in the genus, and divided it into fourteen sections. Using Becker's classification as a basal scheme and CLAUSEN's (1929, 1951, 1964) revisions of the classification of section *Nomimium*, fifteen sections are currently recognized (including sections *Plagiostigma* and *Viola* in place of section *Nomimium*). Seven sections of the genus are represented at the northern temperate latitudes: *Dischidium* (circumpolar), *Xylinosium* (Southern Europe, North Africa, and the Cape Region, South Africa), *Delphiniopsis* (Mediterranean), *Melanium* (Eurasia and North America), *Chamaemelanium* (Asia and North America, including México), *Viola* (Eurasia and North America), and *Plagiostigma* (North America and Eurasia) (BECKER, 1925; BRIZICKY, 1961; CLAUSEN, 1951; VALENTINE, 1962; VALENTINE & *al.*, 1968).

Approximately seventy species belonging to four sections: *Melanium*, *Chamaemelanium*, *Viola*, and *Plagiostigma* are native to North America north of México. The exact number will vary, depending upon the delimitation of taxa and upon discoveries of new species as a result of exploration in poorly collected regions. The North American species are mostly perennial herbs, either caulescent or acaulescent (the leaves and peduncles arise directly from the rhizome); possessing or lacking stolons; bearing outcrossing showy chasmogamous flowers with white, yel-

low-white, yellow, violet, violet-blue, or purple corolla. In most of the taxa of sections *Chamae-melanium*, *Plagiostigma*, and *Viola* the chasmogamous flowers are followed by reduced, apeta-lous, closed, highly fertile cleistogamous flowers. Each of these flowers bears 2-5, more or less reduced, spurless stamens, and a curved style. The stigma is brought into contact with the anthers. The pollen grains germinate within the anthers, and the pollen tubes penetrate the anther walls into the stigma (BRIZICKY, 1961).

A number of North American subsections have been recognized as intractable, and have given *Viola* a reputation as one of the most taxonomically difficult genera. These subsections include *Purpureae* and *Nuttallianae* of section *Chamaemelanium*, *Rosulantes* of section *Viola*, and *Stolonosae* and *Boreali-Americanae* of section *Plagiostigma*. Among these subsections, sub-section *Boreali-Americanae* has long been recognized as one of the most taxonomically difficult temperate groups of the angiosperms. This subsection is the focus of this paper.

Numerous forms that do not correspond to any of the species currently defined in standard works, but possess intermediate characters in varying combinations, are frequently encountered in nature (HUBBARD, 1955). One frequently faces the problem of determining whether one is observing extreme variants of taxa others have taken to be distinct species. The borderlines bet-ween species are not clearly defined in spite of the extensive research and observations that have been made on the taxa.

Macromorphological approaches have supplied conflicting data resulting in sharp disagree-ments among authors about the number and delimitation of taxa. Hence, the number of species recognized in previous treatments of the subsection for North America varies between six (Cron-quist *in* GLEASON & CRONQUIST, 1991) and twenty nine (BRAINERD, 1921) (cf. Appendix A).

The difficulties of delimiting the orthospecies have been attributed to several factors inclu-ding: the similarities between the taxa in a relatively large number of floral and certain vegeta-tive characters, extensive variation in blade morphology, heterophylly, extensive hybridization, introgression, polyploidy, phenotypic plasticity, the existence of coenospecies consisting of a large number of ecospecies or possibly even ecotypes that are still actively evolving, and gene-tic drift in isolated populations (BRAINERD, 1904b, 1910b; CLAUSEN, 1929, 1964; STEBBINS, 1950; RUSSELL, 1959; BRIZICKY, 1961; VALENTINE, 1962; RUSSELL & CROSSWHITE, 1963). The com-plexity of subsection *Boreali-Americanae* may be also compounded by the complex breeding system of *Viola*, which includes chasmogamy, cleistogamy, and vegetative reproduction.

CLAUSEN's (1929, pp. 758-759) statement on the nature of subsection *Boreali-Americanae* reflected the state of knowledge about it, and the need for further investigation prior to this research:

"Whether the *Boreali-Americanae* consists of only one Linnean species with many eco-types, or it really forms a number of nearly related and intercrossing species, is a matter of question, about which different opinions can be maintained. But Brainerd's beautiful inves-tigations on hybrids in this critical group...indicate how some of the species might be dif-ferentiated out after crossing of other species."

Previous students of subsection *Boreali-Americanae* and other authors noted the serious problems in the delimitation of taxa, and concomitantly in identification (POLLARD, 1896, 1898; BRAINERD, 1921; NEWBRO, 1936; BAIRD-BRAINERD, 1942; FERNALD, 1950; HUBBARD, 1955; BRI-ZICKY, 1961; MCKINNEY & BLUM, 1978; RUSSELL, 1959, 1965; RUSSELL & RISSER, 1960; VOSS, 1985; CRONQUIST, pers. comm. 1989; MCKINNEY, 1992; BALLARD, 1994; SWINK & WILHELM, 1994). Many of the problems resulted not only from the nature of the plants, but also from the taxonomic treatments that have been published to characterize them. Extensive splitting of taxa by early workers (especially E. L. GREENE) has led to the accumulation of numerous specific and subspecific names and numerous nomenclatural problems. Other treatments lacked thorough-ness, completeness, or consistency in the choice and usage of macromorphological characters, or suffered from a lack of an objective analysis. In addition, the published keys on the subsection do not work well when tried in the field, and most taxa are intractable when these keys are tried

on herbarium specimens. Currently, a broad menu of taxonomic ranks is available in the literature for a large number of the taxa in the subsection. Consequently, one is often forced to make an arbitrary decision, and choose a rank for a plant whose identification is already uncertain.

Two recent studies applied phenetic analyses to delimit taxa, and to clarify variation patterns in two North American subsections of *Viola*. FABIJAN & *al.* (1987) incorporated morphological characters, cytological data, and flavonoid chemistry into numerical and statistical analyses, and produced a revision of subsection *Nuttallianae* of section *Chamaemelanium*. BALLARD (1992) incorporated morphological data into a phenetic analysis of section *Viola*. An application of such approaches to analyze and delimit the orthospecies of subsection *Boreali-Americanae* using macromorphological and cytological data would have been unsuccessful due to the following reasons: **a**. The taxa are closely related, and possess the same chromosome number ($n = 27$); **b**. An effective procedure that would enable the identification and removal of the hybrids and hybrid derivatives prior to any attempt to delimit orthospecies was not available. Even if an adequate number of OTUs (Operational Taxonomic Units) were analyzed without *a priori* judgments of the identity of the taxa, any clustering would have been ineffective and uninformative unless the hybrids had been removed; **c**. The number of macromorphological characters that could effectively be used in a phenetic analysis is too small, and there is an extensive overlap between taxa in a number of important characters.

Given the difficulties of the plants, and the fact that traditional taxonomic methods have proven ineffective in circumscribing them, the following objectives have been established for this research: attempt to identify the evolutionary processes that have shaped subsection *Boreali-Americanae* into such a complex group, and investigate whether it would be possible to unravel the taxonomic difficulties of the taxa.

An independent source of data that would supplement the macromorphological data and provide reference points that would enable sorting out the hybrids and effective analysis of the patterns of variation among the orthospecies, was sought in this research. Micromorphology proved to be the best source of data and was employed in this research. Details on the methodology and results of the micromorphological analyses are given in GIL-AD (1995) and GIL-AD (in press).

In addition to the objectives listed above, this treatment has broader significance. First, in serving as a model for genera with similar problems on how to approach and tackle a group where species limits are greatly confounded by hybridization. Second, the authors of recent revisions of North American floras (VOSS, 1985; Cronquist *in* GLEASON & CRONQUIST, 1991; SWINK & WILHELM, 1994) commented that the treatments of subsection *Boreali-Americanae* in their publications were compromises based on problematic data. Resolving the classification of subsection *Boreali-Americanae* would help to solve this conspicuous gap in our knowledge of the North American flora. Third, a large collection was made of mature seeds of orthospecies, as well as putative hybrids and introgressants, and is deposited at MICH. Future advancements in DNA extraction and amplification techniques might allow the utilization of this collection, and thereby allow the comparison of the morphological data presented in this study with data generated from molecular analyses of the genome. Fourth, taxa belonging to subsection *Boreali-Americanae* have been subjects of numerous ecological and physiological studies. The delimitation of the orthospecies, and the means to sort out hybrids that are presented in Chapter 4, in GIL-AD (1995) and GIL-AD (in press) would ensure that future studies would use orthospecies as subjects for investigations. Consequently, the results reported in such studies would be more reliable, capable of being repeated and tested, and would enable the building of a sound body of knowledge on the ecology and physiology of the orthospecies. Fifth, observing, photographing, and collecting the taxa of subsection *Boreali-Americanae* are very popular activities among professional, as well as amateur, field botanists. A workable and comprehensive treatment would be highly welcomed by them.

CHAPTER 2

MATERIALS AND METHODS

Herbarium Studies. – Initial data on distribution and phenology were compiled from herbarium specimens at MICH, US, NY, GH, VT, UC, NCU, DUKE, FSU, and MO (abbreviations follow HOLMGREN & *al.*, 1990). Specimens of subsection *Boreali-Americanae* bearing cleistogamous seeds were borrowed from GH, NDG, RSA, US and VT to supplement my collections. A total of 530 specimens of the subsection were studied in this research. In choosing specimens for study, emphasis was given to the quality of the specimens, i.e., the presence of informative organs, rather than to quantity. Pohl's solution (POHL, 1965) was applied to soften tissues in order to allow measurements on representative specimens.

Field Work. – Populations of the taxa in their natural habitats were studied during August 1989 in Maryland; May 1990 in Michigan, Pennsylvania, New York, New Jersey, Vermont, New Hampshire, Maine, and Massachusetts; during June 1990 in Modoc County, California; during March-May 1991 in Florida, Alabama, Mississippi, Louisiana, Texas, Nuevo-León, Oklahoma, Arkansas, Tennessee, Missouri, Kentucky, North Carolina, Virginia, and Maryland; during May 1993 in Michigan and northern California; during July 1993 in Maine; and during April 1994 in Tennessee. Observations were made on macromorphological variation, phenology, plant associates, substrate, and habitat specificity. A total of 287 collections of *Viola* (including some numbers consisting of series of specimens from populations of hybrids) were made. From most populations a few plants were pressed, and a number of living plants (usually 1-3) were transferred and cultivated in the greenhouse. The field work covered two types of sites: **a.** sites in which putative orthospecies were discovered; **b.** sites in which instances of hybridization or introgression were suspected.

Cultivation. – Plants collected in the wild were transplanted and grown in four inch pots on a shaded bench under natural day length in the research greenhouse at the Matthaei Botanical Gardens. Plants that grow in the wild on loamy soils tolerated well the commercial potting substrate Sunshine # 4 whose major components are Canadian dolomite, sphagnum peat, perlite, and a wetting agent. For such plants, a clump of soil was retained around the rhizomes and the roots, and was supplemented with Sunshine # 4 soil mixture to assist in anchoring the plants. Conversely, plants that thrive on specialized substrates such as sandy soil were grown only in the substrate taken from their native niche. Such plants do not tolerate the retention of water in commercial potting mixtures. Most plants were cultivated up to three years in the greenhouse. *Viola* requires vernalization in order to produce chasmogamous flowers (EVANS, 1956). Accordingly, the plants were placed in a cold frame in late November. Plants from southern latitudes were covered with mulch in the coldframe and transferred back into the greenhouse in February, and plants from northern latitudes were transferred back into the greenhouse in April.

Growing the plants in the greenhouse has made possible observation of the plants in both the chasmogamous and cleistogamous phases and at comparable developmental stages, and allowed observation of developmental characters, such as heterophylly. Observations were made on macromorphological variation, with a focus on reproductive characters. Characters that are not readily available on herbarium specimens were especially noted. These included: the color of the chasmogamous flowers, the shape of the petal trichomes, the shape and color pattern of the capsules, and the location and habit of the cleistogamous flowers.

Both chasmogamous and cleistogamous seeds are forcibly ejected up to five meters from the capsules of the taxa of subsection *Boreali-Americanae* (BEATTIE & LYONS, 1975). In order to prevent seed scattering, and the establishment of seedlings in wrong pots, cleistogamous capsules were covered prior to their maturation with aluminum foil, and seeds were harvested following

the dehiscence of the capsules. This technique has allowed monitoring the release of seeds, and enabled exact matching of seeds to their respective mother plants. Seeds were harvested from most of the plants, and are deposited at MICH.

The Value of Existing Herbarium Specimens of Subsection *Boreali-Americanae*. – During the preliminary stages of this study I discovered that in spite of the large number of herbarium specimens of *Boreali-Americanae* taxa that are deposited in the major North American herbaria, many are missing important characters, and are not very helpful, except for some of the information provided on the labels, such as locality, phenology, associates, and substrate. On many specimens the plants, especially the chasmogamous flowers, are imbedded in glue on the sheet. Consequently, careful examination of characters, such as reproductive characters, blade shape, and degree of division of divided blades, is not possible unless the integrity of the specimen is disrupted. Most of the specimens available in herbaria consist of plants that were sampled at the chasmogamous phase, and many of these specimens might be hybrids or introgressants. These specimens would not be helpful unless we devise means to identify putative hybrids and hybrid derivatives using the characters available on them. Unfortunately, macromorphological characters of chasmogamous plants are not adequate for the identification of hybrids.

When specimens of cleistogamous plants are available, their capsules are often opened and the pigmentation of the capsules is often faded or absent. In addition these specimens often lack seeds, or carry immature seeds whose pigmentation and micromorphology are incomplete or distorted. Mature seeds provide micromorphological characters that are helpful in distinguishing between orthospecies and nothospecies in subsection *Boreali-Americanae* (GIL-AD, 1995). Other important macromorphological characters that are difficult to depict from cleistogamous specimens are the color patterns of the capsules, the shape of the capsules, and the habit of the peduncles of the cleistogamous flowers.

I hope that future collectors would take the extra effort to re-sample populations from which they collected chasmogamous plants, or would cultivate plants transplanted from the same population from which the chasmogamous specimens were collected.

Preparation of Herbarium Specimens. – In order to overcome these problems, plants collected in this study were carefully prepared prior to pressing. The plants were stored and carried in plastic bags, and were prepared for pressing upon return from the field. The petals of the chasmogamous flowers and representative blades were spread and stabilized by placing over them paper strips that were taped to the newspaper. In a few cases additional flowers were harvested in the greenhouse. The use of a hot air drier was found to destroy the pigments in flowers, capsules and foliage, thus substantially reducing the quality of specimens. In addition, capsules on cleistogamous plants open prematurely upon heat-drying, and release immature, and in some cases, damaged seeds. Most of the specimens were pressed and air dried at ambient temperatures. The plants were mounted onto the sheet without imbedding them with glue. Rather, they were anchored to the sheet with paper strips. When available, a few extra plants were placed in envelopes attached to the specimens without any mounting. Capsules were studied on live plants, and representative capsules and seeds were photographed (see plates *in* GIL-AD, 1995). Seeds were harvested from live plants in the greenhouse, and were not exposed to any drying or pressing procedures. Representative plants at the cleistogamous phase were sampled and pressed to supplement the chasmogamous plants.

Blade Measurements. – The blade length/width ratio and apical angle were measured on the largest leaves of plants at chasmogamous anthesis, unless indicated otherwise. These blade parameters are illustrated in Fig. 1. Maximum blade length (L) was measured by the distance from the apex to the lowest margin of the basal lobe. In divided blades possessing lobes oriented downward an imaginary line connecting the apexes of the lobes was used to determine the lowest reference point for the length. Maximum blade width (W) was measured at the widest portion of the blade by the horizontal distance between the blade margins, or the apex of the widest horizontal lobe in divided blades. Apical angle (AA) was measured between the two lines extending from the apex and delimiting the margins of the blade, thereby depicting the shape of the apex.

In divided blades the apical angle was measured on the middle segment or lobe. The angle measured in this research differs from the angle measured by Russell (1952, 1956b) and McKinney (1992). They measured the angle of divergence from the horizontal (a line perpendicular to the midrib) of the apical margin of the blade, and designated it as apical angle.

Flower measurements. – The length of the spurred petal (AC) was measured from the edge of the spur base to the edge of the apex of the spurred petal. The length of the spur (AB) was measured from the edge of the spur base to the point of attachment of the nearest auricle (Fig. 2). The other measurements made were width measurements of the spurred petal, the lower lateral petals, and the upper lateral petals. The lengths of the upper and lower lateral petals were not measured since their measurements would have required taking the flowers apart, and thereby damaging the material.

Determination of Corolla Color. – The color of petals was compared in the field or in the greenhouse to color chips of the R.H.S. Colour Chart (1966). The chart was designed for horticultural taxa, and cannot be expected to include the full range of biological colors (Tucker & al., 1991). However, since it provides a better coverage of the variation in color and hue found in *Viola* than the ISCC-NBS Centroid Color Charts, it was selected for the determination of the color of the petals. The chips used for *Viola* belonged to the violet-blue and violet groups. Each chip in a group is numbered and divided into four blocks labeled A through D. When no exact match was found, the closest hue was designated. The major disadvantage of the R.H.S. Colour Chart is that it does not provide value and chroma or sometimes hue for each color chip (Huse & Kelly, 1984). One has to consult the chart in order to get a good perception of the color denoted by a number and a letter. The color name and R.H.S. number listed in the description for each species (Chapter 6) were summarized from determinations of color from plants observed in different geographical areas (when available). Those plants were later determined as orthospecies using the seed micromorphology as one of the primary criteria. The color determinations should not be regarded as absolute since the color of petals may change under environmental stress and modifications in the pH of the substrate. Hybridization and introgression introduce an additional
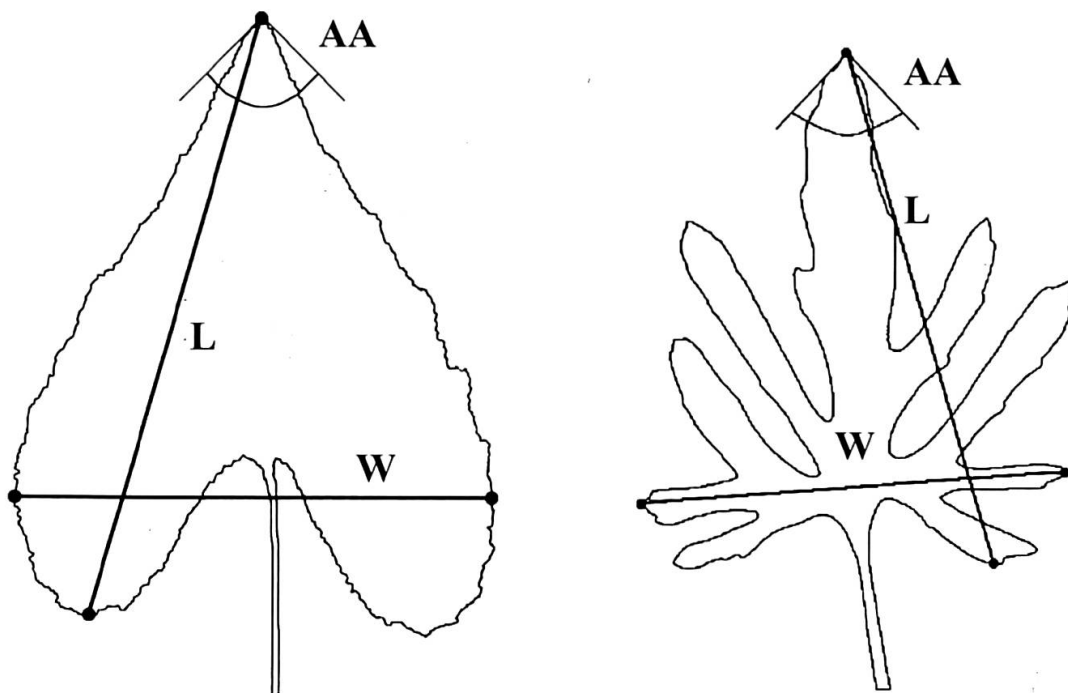
Fig. 1. – Outlines of representative undivided and divided blades, and the parameters measured to characterize the blades. Abbreviations: **L** = maximum length; **W** = maximum width; **AA** = apical angle.
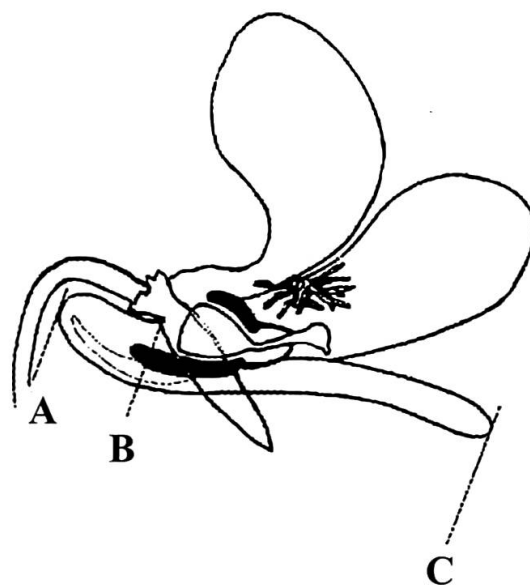
Fig. 2. – A longitudinal section in a representative flower of *Viola* subsection *Boreali-Americanae* (with some of the organs removed), and the parameters measured to characterize the flower: **A-B** = spur length, **A-C** = length of the spurred petal.

variable. Therefore, the color of the petals should be used as an accessory character, and not as a primary character for the delimitation of taxa.

Measurements of Seed Dimensions. – Seeds of the taxa of subsection *Boreali-Americanae* that are produced by chasmogamous and cleistogamous flowers show no significant difference in morphological characters (GIL-AD, pers. observations). In most cases measurements were made on cleistogamous seeds since they were more readily available. Seed length, seed width, and caruncle length were measured using a dissecting microscope equipped with an ocular micrometer (precision 0.1 mm). At least ten seeds were measured per specimen by sampling the range of sizes per sample. When seeds were obtained from live plants, each sample of ten seeds was taken from a different capsule. Ranges for each parameter per specimen were constructed, compared and combined with ranges obtained from other specimens of the same taxon. Caruncle width was found to be too variable even among the seeds of one plant, and caruncles exhibited shape and width variation that would not allow the employment of consistent reference points for measurement.

Measurements of Seed Weight. – A Mettler H-20 analytical balance was employed to determine seed weight. At least ten seeds were weighed per each specimen or live plant, and mean weight was calculated. When enough seeds were available on a specimen, up to ten measurements were conducted, and a range was constructed for the calculated means.

Determination of Seed Color. – The overall seed color of mature *Viola* seeds is comprised of the color of the primary sculpture (background color) and the color of the secondary sculpture (overlaid color). Intraspecific variation in seed color is not common, but may occur when the color of one of the components is more dominant. The overall seed color was determined by using the ISCC-NBS Centroid Color Charts (KELLY, 1965). Each color block is labeled by a number, and a descriptive name. Each color block name consists of the name of a neutral or color hue combined with one or more modifiers with the color hue themselves being used as modifiers, e.g., 72 dark orange yellow (MCKNIGHT, 1977). Five mature seeds were sampled from each specimen. Determination of color was done under a full spectrum light generated by a CHROMALUX ®100W full spectrum bulb. The overall color of the seed surface was compared to the color blocks in the charts, and a matching color was identified. In cases where no exact match could be found, the closest color block names were used to characterize and describe the color.

Ecological and Developmental Observations. – A number of observations on the ecology and development of the taxa have been made throughout this study. Due to limitations of time and resources they were not pursued thoroughly. Therefore, they should be regarded as preliminary observations that require additional studies.

The interested reader is advised to refer to the following publications that cover related aspects of *Viola* biology and ecology: biology of *Viola fimbriatula* in a natural disturbance (COOK & LYONS, 1983), cleistogamy (MADGE, 1929; WEST, 1930; THÉRON, 1939; HOLDSWORTH, 1966; BASKIN & BASKIN, 1975b; MAYERS & LORD, 1983a, b), environmental effects (CURTIS, 1984; CURTIS & KINCAID, 1984; YOST, 1987), floral biology and evolution (BEATTIE, 1969, 1974), pollination and gene flow (BEATTIE, 1971, 1976, 1978), seed dispersal (GATES, 1943; BEATTIE & LYONS, 1975; CULVER & BEATTIE, 1978, 1980; BÜLOW-OLSEN, 1984; OHKAWARA & HIGASHSI, 1994), seed dynamics and longevity of *Viola fimbriatula* (ANDERSON, 1983), photoperiod, vernalization and phenology (BORGSTRÖM, 1939; ALLARD & GARNER, 1940; CHOUARD, 1948; EVANS, 1956; RUSSELL, 1960), population biology (BEATTIE, 1979; SOLBRIG & al., 1980; SOLBRIG, 1981; NEWELL & al., 1981; YOST, 1984).

Determination of Soil Type. – Soil samples (ca. ten cubic centimeters) were removed from the area surrounding the roots of *Gil-ad 389* (MICH): *Viola nuevo-leonensis*, and *Gil-ad 460* (MICH): *V. brittoniana*, and analyzed by Michigan State University Soil Testing Laboratory. Results are reported in the discussion of these species. The substrate for the other taxa was determined by observations in the field and from reports in the literature.

Scanning Electron Microscopy of Seeds and Petal Trichomes. – Details of the sampling procedures of seeds and petal trichomes and the SEM procedures employed to examine them are provided in GIL-AD (1995) and GIL-AD (in press).

CHAPTER 3

MORPHOLOGY

3.1. Introduction

During the course of this research, numerous observations have been made on the macromorphology of the taxa of subsection *Boreali-Americanae*, and on phenomena related to some of the macromorphological characters. A number of observations are reported here for the first time. These observations provided the basis for comprehensive evaluations of the reliability and utility of the macromorphological characters as taxonomic characters. The evaluations presented in this discussion guided the construction of the descriptions of the taxa and the keys that are presented in the taxonomic treatment.

3.2. The Plant

Plant size. – Plant size is subjected to phenotypic plasticity among most of the taxa of the subsection. It is influenced by variables of the habitat, such as the amount of shade exerted by associated plants, the type of substrate, nutrients, and the amount of moisture available. It also increases significantly as the plants progress from the chasmogamous phase into the cleistogamous phase. Plants that are a few centimeters high at chasmogamous anthesis can reach up to 30 cm in height during mid summer. Consequently, plant size is not a good taxonomic character for most taxa of the subsection, with the exception of *Viola fimbriatula* and *V. nephrophylla*, which reach up to 6 cm during chasmogamous anthesis and, at the other end, *V. nuevo-leonensis*, which reaches 25 cm in height. However, data on plant size are provided in the descriptions of a few taxa only as an accessory character to assist in contrasting these taxa with closely related taxa that are not characterized by small size during chasmogamous anthesis.

Habit. – Among all the taxa, only *Viola villosa* possesses a unique habit of the leaves: the leaves are prostrate to ascending, and spread out to form a rosette. In all other taxa the leaves arise sporadically from the rhizome, and most are erect to ascending. Another aspect of habit is the number of crowns arising from the rhizome at chasmogamous anthesis. Most taxa possess only one crown, and are thereby solitary. However, the following taxa often develop multiple crowns and grow in clumps, and are thereby tufted: *Viola brittoniana*, *V. cucullata*, *V. missouriensis*, *V. septentrionalis*, *V. sororia*, and *V. triloba*. Slow ramification of rhizomes over a period of years can obliterate the distinction between tufted and solitary taxa.

Pubescence. – The occurrence, the amount and location of pubescence on the vegetative organs have been used by previous authors as one of the major characters to delimit taxa. The best example is *Viola hirsutula* (determined as a putative hybrid in this study), which was delimited primarily on the basis of pubescence restricted to the adaxial surface of the blades (BRAINERD, 1907b). Presence of pubescence only on the adaxial surface is not unique to this taxon, and was observed also in a number of taxa, such as *Viola cucullata*, during the chasmogamous phase. Early workers erected numerous subspecific taxa to denote the variations in pubescence. BRAINERD (1921) believed that low temperature and high humidity result in pubescence, while high temperature and low humidity result in the lack of, or sparse, pubescence. Consequently, he attributed the inconsistencies in pubescence of some taxa, such as *V. sagittata*, to environmental modification. Pubescence on the vegetative organs is a character that varies extensively both inter- and intraspecifically (MCKINNEY, 1992; MCKINNEY & BLUM, 1978). It also varies with the

development of the plants, and their progression from chasmogamy to cleistogamy. Therefore, pubescence patterns found on plants during the chasmogamous phase may change drastically later in the season. These changes are compounded by hybridization, and especially by introgression. Pubescence patterns of the vegetative organs are consistent and persistent only in the following taxa: *Viola fimbriatula*, *V. novae-angliae* subsp. *grisea*, *V. septentrionalis*, and *V. villosa*. The pubescence patterns outlined in the descriptions of the other taxa are of the chasmogamous phase, and are provided to allow comparison with the taxa in which pubescence is stable. The presence of trichomes is not a good taxonomic character since all the taxa possess strigose vesture at various degrees.

Stipules. – Variations in shape, color pattern, margins, and ciliation of the stipules exist among species. However, there is some variation among plants (and in some cases among stipules on the same plant) in the length of fimbriae, the presence of glandular fimbriae, and in the distribution of these structures along the margins. Consequently, the use of the character states of the stipules as taxonomic characters becomes difficult. One exception where the margins of the stipules is consistent and diagnostic is *Viola nuevo-leonensis*.

3.3. Rhizome

All taxa possess succulent, thickened, and scaly rhizomes. The habits of the rhizomes are vertical, oblique, or horizontal, and may vary among plants of the same species. Occasionally the rhizomes branch, and vegetative reproduction takes place by detachment of rooting lateral, superficial branches of the rhizome of the parent plant. By ramifying freely in the soil the detached segments produce a clonal cluster of separate individuals (GERSHOY, 1934; BRIZICKY, 1961). Most of the character states of the rhizomes, such as size and shape of the scales on the surface, are not taxonomically helpful. The rhizomes are subjected to the variables of the local, immediate substrate that surround them. However, certain character states of the rhizomes can serve as accessory characters since the taxa that possess them differ in those characters from other taxa of the subsection. *Viola nuevo-leonensis* possesses long rhizomes, up to 9 cm long at chasmogamous anthesis, and the roots that branch out of them reach 12 cm, unlike the other taxa of the subsection. Five species possess stout fibrous roots that reach up to 1.5 mm in diameter, whereas the remaining species possess fibrous roots that are usually less than 1 mm in diameter, some of which are very fine.

3.4. Leaf

Petioles. – Variation in the color of the petioles exists among taxa. However, caution is required in using it as a character since it may change as the plant ages. The color of the petioles listed in the descriptions is the color during chasmogamous anthesis. The color can be used as an accessory character in the field, especially when hybrids, which often deviate from orthospecies in the color pattern of the petioles, are suspected. Petiole length is age dependent, and may also vary due to habitat variables, competition from associated plants in sites covered with dense vegetation, and nutrition. One exception is *Viola fimbriatula* (Chapter 6).

Blade Types and Shapes. – Three major categories of blades are found in the subsection: undivided blades (i.e., unlobed and undivided), lobed blades, and divided blades. Blade shape changes as the development of the plants progresses in a number of taxa possessing undivided blades. Therefore, the blade shape, length to width ratio, and the apical angle listed in the descriptions were measured on the largest mature blades at chasmogamous anthesis to allow a uniform reference of phenology and developmental stage. In a few cases the changes in blade shape and the shape of mature blade at the cleistogamous phase are provided. In most cases, more than one blade shape describes the range typical of the taxon. This polymorphism has contributed to

the difficulties previous workers have encountered in delimiting taxa on the basis of blade shape. It is further compounded by intermediate shapes generated by hybridization. The ranges of length/width ratio and apical angle provide better representation of the blade shape. They should be used with caution as accessory characters only after reproductive characters have been evaluated.

The primary division in the taxa possessing divided blades consists of three segments, a single median segment and two lateral segments (one on each side). Each of the segments may be unlobed or divided into additional lobes. BRAINERD (1910b) categorized the divided blades that have five or more lobes into two types, palmately lobed leaves and pedately lobed leaves. Palmately lobed leaves have the median and the lateral segments divided, whereas pedately lobed leaves have the median segment unlobed, and each of the two lateral lobes once or more divided. Furthermore, he correlated these types with the leaf phases, and categorized the taxa possessing divided blades such that plants possessing palmately lobed leaves are homophyllous and plants possessing pedately lobed leaves are heterophyllous. BAIRD-BRAINERD (1942) and SHAVER (1959) pointed out the difficulties that are encountered in distinguishing the two types on some blades, and suggested tracing the veins from the side lobes toward the midvein to determine their origin and placement in relation to the median segment. Examination of these patterns on blades of taxa possessing divided blades revealed that some blades deviated in their veining patterns, and could not be categorized with the other blades on the same plants. Both SHAVER (1959) and I observed that although *Viola egglestonii* was categorized as palmately five lobed, early spring or autumn plants disclose some pedately lobed leaves among the majority of palmately lobed leaves. Some authors have chosen to ignore these categories altogether, and simply provided a range for the number of lobes a divided blade possesses. Those ranges do not provide an accurate representation of the ontogeny of the blade division, and may be misleading since they are not based on a uniform time reference and developmental stage. In some of the taxa the number of blade lobes encountered during the cleistogamous phase is significantly larger compared to the number at chasmogamous anthesis. Compounding these difficulties are hybrids of the taxa possessing divided blades that are often difficult to distinguish from their parents, and obliterate the boundaries of these ranges in the number of lobes. In order to overcome these difficulties, the descriptions of the divided blades (Chapter 6) provide the number of divisions (up to five divisions in *V. pedatifida*), the number of lobes that may be encountered in each division, and the shape of the lobes. The use of the pedate/palmate terminology for the lobing of the blades is abandoned.

Dimorphic Blades. – Three North American species – *Viola brittoniana* of subsection *Boreali-Americanae*, and two species of section *Chamaemelanium*: *Viola lobata* (Western U.S.), and *V. tripartita* (Eastern U.S.) – are comprised of two types of plants: plants possessing only divided blades, and plants possessing only undivided blades (BAIRD-BRAINERD, 1942; BRAINERD, 1921; RUSSELL, 1965). Both types of plants are usually syntopic, but populations comprised of plants possessing only one type of blades have been discovered. The genetic basis for this phenomenon is unknown, and awaits further analyses.

Leaf Phases. – Among the North American taxa of *Viola*, the phenomenon of heterophylly, which was first reported by BRAINERD (1910b, 1921), is unique to subsection *Boreali-Americanae*. Four species are strictly heterophyllous: *Viola egglestonii*, *V. nuevo-leonensis*, *V. septemloba*, and *V. triloba*. In these species some of the blades developing early in the spring are unlobed, the blades developing later are lobed, some of the blades developing in late summer and early fall are unlobed, and most of the blades developing later are unlobed. SHAVER (1959) provided data on the seasonal changes of blade characters states in the heterophyllous *V. egglestonii*. The remaining twelve species of the subsection are homophyllous. In these species all the blades are of one type –undivided or divided. Changes in these species, however, occur in blade size, and in some cases in the amount of growth in one axis. For example, blades of *V. affinis* produced during the cleistogamous phase are longer than blades produced during the chasmogamous phase, and therefore appear narrower compared to the same blades at the chasmogamous phase.

3.5. Flowers

Peduncles. – The comments made on the color of the petioles pertain also to the peduncles. However, pubescence patterns are consistent and persistent when examined at the same developmental stages. Deviations from the patterns exhibited by orthospecies are most likely due to hybridization or introgression.

Bractlets. – Some variation in the shape, margin type, and occurrence of cilia along the margins of the bractlets exists among the taxa. However, a few taxa demonstrate polymorphism in some of these character states. Therefore, caution should be practiced in using them when contrasting taxa. These organs might have evolved in response to foraging insects that ascend on the peduncle and try to reach the flower and its resources, and may deter or even block such insects.

Sepals. – The shape of the sepals is polymorphic in some of the taxa, and consequently it is not always helpful as a character to distinguish between the taxa. The sepal character states that are helpful are the type of margins (scarious or colored), ciliation, and the ratio of sepal length to capsule length. The margins are ciliate, eciliate, or ciliate only along a section of the margins (in *Viola fimbriatula* and *V. sororia*). Comparison of the ratios of sepal length/capsule length is more informative than comparison of absolute sepal lengths. Most of the ranges of sepal length/capsule length of the taxa overlap. However, they are helpful in contrasting pairs of taxa. *Viola cucullata* possesses the largest range of ratios: 0.8-1.2, and *V. missouriensis* the smallest range: 0.2-0.4. The color patterns of the sepals are difficult to delimit. However, *V. septentrionalis* (at the cleistogamous stage), *V . novae-angliae*, and *V. affinis* possess sepals that are densely spotted with red-purple. *Viola nuevo-leonensis* is unique in having trichomes on the adaxial surface of the sepals in addition to the ciliate margins.

Auricles. – The shapes of the auricle apexes are highly polymorphic and are not helpful in distinguishing among the taxa. They may be rounded, subtruncate, truncate, undulate, irregularly incised, or subacute. Some taxa possess more than two apex shapes on one flower. The auricles of three species, *Viola cucullata*, *V. brittoniana* and *V. sagittata*, are longer on the cleistogamous flowers and capsules than on the chasmogamous flowers. The comment on the color of the sepals pertains also to the auricles. In most taxa, ciliation on the auricles is consistent and persistent, and serves as a good character to distinguish among the taxa.

Dimensions of the Chasmogamous Flower. – A considerable overlap exists among the taxa in the ranges of the widths of the spurred petals, lower lateral petals, and upper lateral petals, and in the length of the spurred petal. A comparison between the taxa using the length of the spurred petal as a measure of the size of the flowers shows that *Viola cucullata* and *V. villosa* possess the smallest flowers, whereas *V. septemloba* possesses the largest flowers. In most of the taxa the upper lateral petals are wider than the lower lateral petals. The upper and lower lateral petals have the same ranges of width in *V. cucullata*, *V. nuevo-leonensis*, *V. sagittata*, and *V. villosa*. The exception is *V. nephrophylla* whose upper lateral petals are narrower than the lower lateral petals. Additional samplings of populations and flowers are required in order to establish the ranges listed in the descriptions, and to better depict the gaps between the taxa.

Spur Length. – The ranges of spur length of most of the taxa overlap, and fall between 1-3 mm. Yet, the ranges of a number of taxa are set apart. *Viola septemloba* possesses the highest maximum length, 4.3 mm, whereas *V. egglestonii* possesses the lowest minimum length, 0.6 mm.

Petal Trichomes. – The petal trichomes demonstrate interspecific variation in shape, width, micromorphological structures, and presence on the spurred petal. The number of trichomes on the lower lateral petals in most taxa is larger than the number of trichomes on the spurred petal. Most of the taxa of the subsection possess trichomes whose shape is cylindrical. Conversely, *Viola cucullata* distinctly possesses clavate trichomes. *Viola egglestonii* demonstrates polymorphism in the shape of its petal trichomes. *Viola missouriensis* possesses cylindrical trichomes that are gradually widened toward the apex. SEM micrographs of representative trichomes are shown

in GIL-AD (1995) and GIL-AD (in press). The cylindrical trichomes are classified here into three groups according to their maximum width in the area extending up to 100 μm from their apex: a. **narrow**: trichome width up to 50 μm; b. **wide**: trichome width 51-100 μm; c. **broad**: trichome width 100 μm or above. The presence of trichomes on the spurred petal has caused a lot of confusion among previous authors. This confusion was most likely due to sampling of hybrids which often not only possess a blend of trichome shapes, but are also inconsistent in the occurrence of the trichomes on the spurred petal. The orthospecies show consistency in the occurrence of petal trichomes. Five species lack trichomes on their spurred petals: *Viola cucullata*, *V. missouriensis*, *V. nuevo-leonensis*, *V. sororia*, and *V. triloba*.

Color of the Petals of the Chasmogamous Flowers. – The color of the petals demonstrates interspecific variation. The taxa of the subsection are divided here into two major groups by using the color scheme of the Royal Horticultural Society (R.H.S.) Colour Chart (1966): a. taxa possessing violet petals: *Viola affinis*, *V. egglestonii*, *V. fimbriatula*, *V. nephrophylla*, *V. novae-angliae*, *V. nuevo-leonensis*, *V. pedatifida*, *V. septemloba*, *V. septentrionalis*, *V. sororia*, *V. triloba*, and *V. villosa*; b. taxa possessing violet-blue petals: *Viola brittoniana*, *V. cucullata*, *V. missouriensis*, and *V. sagittata*. It is possible to identify additional subgroups within these two groups if chroma and intensity are considered, but additional samplings of flowers in the wild are needed. The color of the petals may be influenced by nutritional imbalance, and changes in the pH of the substrate, and may also change significantly due to hybridization. Consequently, caution should be practiced in the evaluation and use of this character. All the taxa possess a white center on the lower lateral petals and the spurred petal. This center varies in the portion of the total adaxial surface of the petals it occupies. The white center is bordered blue or dark violet-blue in *Viola brittoniana*, *V. cucullata*, *V. egglestonii*, *V. missouriensis*, *V. pedatifida*, and *V. triloba*, but is not bordered in the remaining taxa. It is especially prominent in *V. cucullata*. Most taxa possess dark violet lines (nectar guides) on the lower lateral petals and the spurred petals. Conversely, *V. nuevo-leonensis* possesses dark violet lines on the spurred petal only.

Cleistogamous Flowers. – Early students of the subsection have tried to use differences in the shape of the cleistogamous flowers as an additional character to delimit taxa. In practice, however, it is very difficult to delimit the shape of these reduced flowers since they rapidly change and develop into capsules following self-fertilization. Obtaining a uniform time reference to allow comparison among taxa at the same developmental stage is very difficult. Overall, their shapes are very similar. In color, their sepals and auricles resemble those of the chasmogamous flowers (except for *Viola septentrionalis*). Conversely, the habit of the peduncles of these flowers is a helpful character since it exhibits interspecific variation. The peduncles are either prostrate, ascending, or erect. *Viola egglestonii* has a unique ontogeny of the cleistogamous flowers. These flowers originate underground, they are achlorophyllous, and their peduncles are prostrate. From May to mid-August most of them do not grow above the soil surface (BASKIN & BASKIN, 1975b), but occasionally they arise above ground and become chlorophyllous (GIL-AD, pers. observations).

3.6. Fruit

Capsules. – The color pattern on mature capsules of *Viola* is stable, and serves well to distinguish between species of the subsection in conjunction with other characters. Two major color patterns exist among the taxa: a. one uniform color (usually green or yellow-green); b. a background color upon which a second color is overlaid in the form of irregularly distributed patches or dots. Red-purple overlays are quite common, and variation among taxa exists in their intensity, density and distribution. Color photographs of representative capsules of the taxa are shown in GIL-AD (1995).

Observations on capsules on live plants have instigated a search for a reliable method to characterize their shapes that would also take into account variation among capsules on the same

plant. This search revealed that application of the standard terminology describing the shape of solids obliterates the actual differences in the shapes of the capsules. Conversely, the ranges of length/width ratio, along with a description of the color pattern of a taxon's capsules provide a better representation of the variation and gaps among the taxa, and among capsules on a single plant.

3.7. Seed

Seed Color. – Eight species possess unique seed color patterns. These species are: *Viola cucullata*, *V. egglestonii*, *V. fimbriatula*, *V. novae-angliae*, *V. nuevo-leonensis*, *V. septemloba*, *V. sororia*, and *V. villosa*. The remaining species possess variations of orange yellow, yellowish brown or dark brown. Consequently, seed color can be used in these taxa as an accessory character after careful determination of the color. Color photographs of representative seeds of the taxa of the subsection are shown in GIL-AD (1995).

Seed Dimensions and Shape. – Despite overlaps in the ranges of seed dimensions, the ranges of a number of taxa are clearly set apart, and in some cases are helpful as additional characters that contribute to the delimitation of the taxa. Seed length in the subsection ranges from a minimum of 1.2 mm (in *Viola cucullata*) to a maximum of 2.7 mm (in *V. nuevo-leonensis*). seed width ranges from a minimum of 0.8 mm (in *V. brittoniana*, *V. cucullata*, *V. fimbriatula*, and *V. sagittata*) to a maximum of 1.7 mm (in *V. nuevo-leonensis*). The ranges of seed length/width ratio of most of the taxa overlap, yet the length/width ratio of the seeds of *V. septentrionalis* is higher: 1.7-2.3. Seed weight ranges from a minimum of 0.4 mg (in *V. novae-angliae* subsp. *novae-angliae*) to a maximum of 2.9 mg (in *V. nuevo-leonensis*). Caruncle length ranges from a minimum of 0.3 mm (in *V. septemloba*) to 1.5 mm (in *V. egglestonii* and *V. nuevo-leonensis*). The shapes of most seeds are similar (ovoid to ellipsoid). The seeds of *V. cucullata* have occasionally a flat side. The caruncles of *V. novae-angliae* subsp. *grisea* are polymorphic in shape. Some are linear like the caruncles of the other taxa of the subsection, but some are geniculate.

When compared to the other taxa of *Viola* in North America, the ranges of seed dimensions of the taxa of subsection *Boreali-Americanae* are intermediate between the extreme values. The lowest value of seed minimum length (1 mm) is found in *V. macloskeyi* (section *Plagiostigma* subsection *Stolonosae*), and the highest value of seed maximum length (4.1 mm) is found in *V. beckwithii* and *V. trinervata* (both of section *Chamaemelanium* subsection *Chrysanthae*); the lowest value of seed minimum width (0.6 mm) is found in *V. macloskeyi* and in *V. rafinesquii* and *V. tricolor* (both of section *Melanium*), and the highest value of seed maximum width (2.5 mm) is found in *V. trinervata*; the lowest value of seed minimum weight (0.2 mg) is found in *V. pedata* (subsection *Pedatae*) and in *V. lanceolata* and *V. macloskeyi* (both of subsection *Stolonosae*), and the highest value of seed maximum weight (8 mg) is found in *V. lobata* var. *lobata* (subsection *Nudicaules*); the lowest value of caruncle minimum length (0.1 mm) is found in *V. canadensis* var. *canadensis* (subsection *Canadenses*) and in *V. epipsila* var. *repens* (subsection *Stolonosae*), and the highest value of caruncle maximum length is found in *V. frank-smithii* (2.5 mm) (most likely of section *Viola*), and in *V. odorata* (2.7 mm) (section *Viola*) (complete data *in* GIL-AD, 1995).

CHAPTER 4

HYBRIDIZATION AND ITS EFFECTS
ON THE SYSTEMATICS OF *VIOLA*
SUBSECTION *BOREALI-AMERICANAE*

4.1. Research on Hybridization
in *Viola* Subsection *Boreali-Americanae:* A Historical Perspective

The widespread and frequent natural hybridization in *Viola* is widely known (BRAINERD, 1924; GERSHOY, 1934; RUSSELL, 1954; CLAUSEN, 1951; VALENTINE, 1962). BRAINERD (1906a) noted that the tendency to interbreed has been detected among European species of *Viola* before he focused attention on hybridization in *Viola* in North America and particularly on hybridization among the taxa of subsection *Boreali-Americanae*.

Hybrids of taxa belonging to subsection *Boreali-Americanae* were initially reported by BRAINERD (1904b, 1906b, 1910a, 1912, 1913a, 1921), DOWELL (1910), and HOUSE (1905, 1924). Brainerd studied hybrids of *Viola* in detail in the wild and in cultivation. He summarized his experiments and observations in a series of papers (1906a, 1907a, 1907c, 1910a, 1924), and described and figured 82 natural hybrids (1924). Thirty four of these hybrids were the products of hybridization between taxa that are recognized as orthospecies in this study, nine involved taxa of other subsections, and the remaining were the products of hybridization between orthospecies and taxa that are recognized in this study as of putative hybrid origin.

BRAINERD (1906a) specifically noted that any two *Boreali-Americanae* species that have been growing together for several years are likely to produce hybrids, and hence the observed variability in natural populations. Early in his research (BRAINERD, 1910a) he postulated that hybridization does not add new characters to a group of species, but simply recombines characters that already exist. Yet, he was the first to observe later that natural hybridization among species in the group produces an extraordinary range of blade shapes, many of which are quite different from any found in the parental species. BRAINERD (1924) demonstrated in a number of cases segregation of blade-shape, pubescence (especially in crosses between species possessing divided blades and species possessing undivided blades), and color of capsules and seeds in the F_2 and F_3 generations, and used Mendelian laws to interpret his results. Detailed studies of crosses, such as a cross between *Viola pedatifida* and *V. sororia*, demonstrated that although the principal character differences between the species give simple segregations, and many of the F_2 and F_3 individuals show reversion to one or the other of the parental species, a substantial proportion of these offspring are considerably modified from the condition found either in the parents or in the F_1 individuals, and some of these modified types would eventually breed true (BRAINERD, 1924; STEBBINS, 1950). From his observations of the freedom with which the species cross under natural conditions, he concluded that the limit of hybridization in the genus is set only by the present lack of sympatry of different species (BRAINERD, 1907c, 1921).

GERSHOY (1928) produced experimentally 47 different hybrids between 14 taxa of subsection *Boreali-Americanae*, (including taxa that are recognized as putative hybrids in this study), and 26 reciprocal hybrids, noted their fertility, and determined their common chromosome number ($2n = 54$). GERSHOY (1934) produced additional hybrids, and listed 34 interspecific hybrids of taxa of the subsection. Nearly all the F_1 progeny were vigorous, and most were fertile. His studies did not include analysis of segregation in later generations. On the basis of both Brainerd's and Gershoy's findings, and his own cytological investigations in the genus, CLAUSEN (1951,

1964) characterized the species of the subsection as having weak [intrinsic] barriers to interbreeding.

Russell employed ANDERSON's (1949) hybridization index and pictorialized scatter diagrams on macromorphological measurements to analyze instances of hybridization, and demonstrate, in some cases, putative introgression between taxa of subsection *Boreali-Americanae*: *Viola papilionacea* introgressed into *V. nephrophylla* (RUSSELL, 1952), and *V. sororia* introgressed into *V. sagittata* (RUSSELL & COOPERRIDER, 1955). Later, RUSSELL (1955) provided evidence for hybridization and possible bi-directional introgression between populations of *V. cucullata* and *V. septentrionalis*. He concluded that introgression has proceeded to such an extent in both directions that it has obliterated many of the characteristics of the original species, making it difficult to reconstruct the original phenotypes (RUSSELL, 1955). A major problem he encountered was the determination of characters of the two parents in the preparation of a hybridization index. In some populations it was not possible to identify the orthospecies. Consequently, the ranges of variation assigned to each species were determined from a preliminary visual inspection of the data, and from published taxonomic descriptions (RUSSELL, 1955). Such constraints subject the results of the analyses to bias and jeopardy in analyzing instances of hybridization between the taxa of the subsection. RIESEBERG & WENDEL (1993) compiled a list of examples of introgression in plants, and evaluated Russell's 1955 study. They indicated that evidence for introgression in Russell's study was questionable, and interpretations other than introgression were not adequately ruled out. RUSSELL (1956a) used blade character states to analyze instances of hybridization between *V. pedatifida* and *V. sororia* in populations he sampled in Iowa. He concluded that the hybrid indexes demonstrated, though not conclusively, that hybrids are formed quite commonly between certain species, but the participating species show little evidence of introgression. Furthermore, he hypothesized that these results might reflect the problems of the genus.

Additional cases involving hybrid swarms of taxa belonging to subsection *Boreali-Americanae* were reported by HUBBARD (1955), CAMP (1961), RUSSELL (summarized *in* RUSSELL, 1965), and MCKINNEY & BLUM (1978, 1981). Introgression was also reported among the «stemless white» violets (ANDERSON, 1954; RUSSELL, 1954).

Natural hybridization between taxa of subsection *Boreali-Americanae* and taxa of sister subsections has been detected. BRAINERD (1924) reported natural hybrids between *Viola brittoniana* and *V. lanceolata*, and between *V. cucullata* and *V. primulifolia* (the second species in each of these pairs belongs to subsection *Stolonosae*). These hybrids were absolutely sterile, and could be propagated only by vegetative division.

GERSHOY (1928, 1934) made a large number of crosses to determine the range of hybridization possible within *Viola*. He found that there is apparently no uniform correlation between the chromosome number and the incidence of fertility or sterility. Studies on the rate of pollen tube growth in reciprocal cross-pollinations indicate that inter-sectional crosses are generally unsuccessful because of reciprocal inhibition of pollen tube growth. Species within each subsection are cytologically arranged in smaller subgroups of more closely related species, which are connected by hybrids, which in turn are only partially sterile. For example, crosses between taxa belonging to subsection *Boreali-Americanae* and taxa belonging to subsection *Stolonosae* (both of section *Plagiostigma sensu* Clausen) yielded sterile F_1 hybrids exhibiting hybrid vigor. A cross between *V. missouriensis* ($2n = 54$) and *V. jooi* ($2n = 24$; subsection *Adnatae*) yielded vigorous sterile F_1 hybrids, intermediate in character. By and large, hybrids between taxa of different sections are difficult to produce; many attempts to produce F_1 hybrids fail, and others result in seeds with embryos which are unable to develop, so that the F_1 is not even seen, and some result in weak or dwarf F_1 hybrids (CLAUSEN, 1951).

4.2. The Effects of Hybridization on the Systematics
of *Viola* Subsection *Boreali-Americanae*

Hybridization, followed in some localities by introgression, has made it difficult for previous students of the subsection to discern the "core" species by using only the standard macromorphological characters. Consequently, the systematics of taxa prior to this study was in disarray.

As a result of the research and efforts of Ezra Brainerd and his successors, more data have been compiled on hybrids than on orthospecies of the subsection. However, those ample data are overshadowed by the lack of an effective method to distinguish between the orthospecies and hybrids and hybrid derivatives. Consequently, the data on the hybrids cannot be properly evaluated.

WAGNER (1968) pointed out the taxonomic importance of the recognition of hybrids, and emphasized that if hybrids are excluded from floras and manuals, identification becomes confusing, and the value of taxonomic treatments to advanced students and professional botanists is reduced. In taxonomic (and especially floristic) treatments of subsection *Boreali-Americanae*, the ideal situation would be to include descriptions of hybrids. However, since hybridization is apparently extensive and frequent, and frequently compounded by introgression, it is not possible to provide a complete coverage of all the instances of hybridization that occur in nature. Nonetheless, taxonomic treatments should provide guidelines and recommendations on how to detect and classify those hybrids.

4.3. The Detection of Hybrids

Early investigations in this study revealed that analyses of macromorphological characters are not sufficient to distinguish orthospecies from hybrids. Recognition that the characters of a suspected hybrid or deviant are mainly intermediate or grades between the suites of characters of two orthospecies is most often impossible. Knowledge of the taxa in the locality and a search for the parental taxa when a hybrid is suspected (advocated by McKINNEY, 1992) as the means to discern the hybrids are helpful during the initial stages of the investigation in the field. However, the parental plants in some populations may be extinct or indistinguishable, with a superficial examination of macromorphology, from the hybrids. Consequently, we may have to deal with populations dominated by hybrids or introgressants. A procedure that was developed in this research, and described in below, allows identification of the orthospecies and the discernment of hybrids and putative introgressed taxa by combining analyses of micromorphological characters of the seed coat surface with macromorphological characters, supplemented by ecological and phytogeographic data.

A Procedure for Discerning the Orthospecies. – The survey of the taxa was conducted by iterative examinations of macromorphology and micromorphology until sufficient evidence was gathered to support the delimitation of the orthospecies. In the first round of examinations, specimens were sorted into tentative groups. Specimens in each group shared a suite of macromorphological characters, including reproductive characters, that rendered them as putative representatives of an orthospecies. These groups included specimens that displayed little variation, as well as other specimens that displayed variation in a number of characters, but could still be assigned to a putative orthospecies. Several additional groups, each consisting of specimens putatively representing a taxon recognized by previous authors, were also examined, even though they deviated from the guideline of comprehensive coverage of characters. In the second round, seeds were sampled from the members of a group, and examined under a scanning electron microscope (GIL-AD, 1995; GIL-AD, in press). Then, the micromorphological characters of representative seeds of each specimen were examined using the SEM micrographs, evaluated, and compared

with the micromorphological characters of the other members of the group. Structures and patterns that were consistent were noted, and the specimens that possessed them were hypothesized as being putative orthospecies. In the third round, the macromorphological characters of each specimen in a group were re-examined, and correlations were made between suites of micromorphological characters and suites of macromorphological characters. Attempts were made to identify deviations in macromorphological characters on specimens whose seed coat micromorphology displayed deviations from the structures and patterns characteristic of the seed coats of the putative orthospecies. The fourth round included examination of petal trichomes with SEM. The data on the micromorphology of the petal trichomes was analyzed in the same fashion as the data from seed coat micromorphology, and then combined with the other data. Finally, distinct species were delimited. Specimens from each of the groups were designated as representative of an orthospecies when they displayed a consistent and distinct suite of micromorphological characters, or at least one unique micromorphological character that could be correlated with a consistent and distinct suite of macromorphological characters, as well as with ecological and phytogeographical data.

Furnished with knowledge about the delimitation of the orthospecies, we can examine whether any reliable macromorphological characters can provide reference points that can aid in detecting hybrids. Can we find any characters that would provide grounds for postulating hybridity when we compare a putative hybrid with the suite of characters that delimit an orthospecies?

During the chasmogamous phase, intermediate blade shapes, especially between taxa possessing undivided blades and taxa possessing divided blades, allow the detection of some hybrids in the field, and consequently allow postulation of hybridity. However, in many cases intermediate blade shapes are misleading in heterophyllous taxa. The problems become more acute if the plants are products of hybridization or introgression between two distinct homophyllous taxa possessing undivided blades whose shapes grade into one another. Nevertheless, a number of reproductive characters become available during the cleistogamous phase. Some hybrids produce seeds that exhibit extensive variability in color patterns among the seeds produced by a single plant. Other hybrids produce seeds exhibiting uniform color patterns among the seeds produced by a single plant. Those uniform color patterns may be novel and not match any color found on the seeds of orthospecies, or they may consist of conspicuous blotches or spots on a background color. The use of these patterns in discerning hybrids requires knowledge of the color pattern of the seeds of the orthospecies. These patterns are figured in GIL-AD (1995) and GIL-AD (in press). Capsules of hybrids may exhibit deviations in shape. They may also exhibit blends of colors of different degrees, especially if the hybrid resulted from hybridization of a species possessing green capsules and a species possessing capsules spotted red-purple. Other characters that may exhibit deviations from the characters of the closest orthospecies are the dimensions of the seeds and the habit of the peduncles of the cleistogamous flowers. Introgressants may not show any striking macromorphological deviation from one of the parents. Alternatively, they may show only few deviations, such as a blend of different types of trichomes on the petals, or presence or absence of trichomes on the spurred petal unlike the orthospecies. As noted above, a few reproductive characters can provide us with reference points, but their paucity, especially at the chasmogamous phase, and their complexity renders them difficult to use, especially to those who lack comprehensive knowledge of the taxa.

There are two alternative approaches for the identification of plants of the subsection that we encounter in the field. The first, the traditional way, is using keys and descriptions. We hypothesize that a given plant is an orthospecies. Any deviation from the suite of macromorphological characters listed for an orthospecies that we detect on this plant should lead us to postulate that the plant is a putative hybrid. Accordingly, we should seek additional sources of evidence to support this hypothesis. If we use this approach, we should be aware that any non-deviating plant might still be a cryptic introgressant. Therefore, micromorphological or other data (e.g., molecular data) would be critical for absolute establishment of the plant as an orthotaxon. The alternative approach would be to hypothesize that every plant that we encounter in the field is a putative hybrid, and seek evidence to falsify this hypothesis. Obtaining non-macromorphological

data is critical for using this approach. This approach was employed in the present research that yielded the present treatment.

4.4. The Detection of Introgression and Alternative Hypotheses

Ever since the term «introgressive hybridization» was coined by ANDERSON & HUBRICHT (1938), numerous studies documenting introgression have been published. RIESEBERG & WENDEL (1993) refined Anderson and Hubricht's definition of introgression, and characterized it as «the permanent incorporation of genes from one set of differentiated populations into another, i.e., the incorporation of alien alleles into a new, reproductively integrated population system.» Following an initial detection of macromorphological variants in populations of predominantly one species in numerous genera, various sources of data have been employed to analyze them, and to document instances of introgression. They included macromorphology, secondary compounds, isozymes, cytoplasmic markers, nuclear markers, ribosomal RNA genes, and RFLP markers (HEISER, 1973; RIESEBERG & BRUNSFELD, 1992; RIESEBERG & WENDEL, 1993).

The micromorphological data presented in GIL-AD (1995) and GIL-AD (in press), and correlations of those data with macromorphological data provide evidence that allows us to hypothesize that in some cases introgression has taken place among taxa of subsection *Boreali-Americanae*. Thus, evidence for introgression can also be sought from the examination of seed coats. When a blend of micromorphological structures characteristic of two distinct species is detected on the seed coat surface of the seeds of a putative hybrid, and it can be correlated with a blend of macromorphological characters, we can hypothesize that the plant is most likely a product of hybridization and not introgression. Conversely, when the seed coats of seeds of species «A» have structures predominantly characteristic of that species, and only traces of structures characteristic of species «B», we can hypothesize that the plant is a putatively introgressed plant. At the macromorphological level, this plant has predominantly the characters of species «A», and few deviating character states. In some cases, the macromorphological characters of species «B» cannot be readily detected on the introgressed plant, or perhaps cannot be detected at all. The detection of putative cases of introgression using micromorphological data has not been proposed before in the literature.

A major limitation of this evidence is the difficulty of quantifying the data. The seed coats of a putatively introgressed plant can be compared to the seed coats of a corresponding orthospecies, and an intuitive description can be applied to characterize the «imported» structures. Yet, the complexity of these structures and the different combination of suites of structures that characterize each of the orthospecies make it difficult to use common reference points. Thus, we cannot provide a quantitative measure that would represent the extent of the introgression detected, and a measure of the deviation between the character (structure) on the seed coat of an orthospecies and the homologous structure on the seed coat of the seeds of the introgressed plant.

One of the major problems with studies that document putative introgression is that the supporting evidence often has alternative explanations. These include the possibility that remnants of the ancestral population from which two species differentiated might have the appearance of hybrids, primary intergradation, mutations producing results similar to those of introgression, segregation in a polyploid species, the occurrence of hybrid swarms that are no longer in contact with the parental species, the presence of highly variable F_1 hybrids, and inbreeding and selection following hybridization in an autogamous species (GOTTLIEB, 1972; HEISER, 1973; RIESEBERG & WENDEL, 1993).

The last alternative explanation in the list presented above is of special interest for our problem since cleistogamy, a form of autogamy, occurs in subsection *Boreali-Americanae*. GRANT (1981) pointed out that in autogamous plants, introgression-like effects could result from inbreeding and selection of the inbred products following an initial event of outcrossing and hybridi-

zation. It would occur if morphological genes are commonly linked with viability genes, and the species involved differ allelically in respect to these systems of genes. Grant contended that inferring introgression from the observation of introgression-like variations in predominantly autogamous plants (where the probability of a hybrid reproducing by backcrossing is exceedingly low) is unwarranted. These effects would not be introgression *sensu* ANDERSON & HUBRICHT (1938) since no repeated backcrossing is involved. Although the taxa of subsection *Boreali-Americanae* spend a large portion of their seasonal life cycle at the cleistogamous phase, the chasmogamous phase is not sporadic, and the probability of a hybrid reproducing by backcrossing is high. Therefore, the hypothesis that the introgression might follow an initial hybridization event among some of these taxa is viable. The introgression-like effects described by Grant fit RIESEBERG & WENDEL's (1993) definition of introgression since they eliminated (following HEISER, 1973) the requirement for the specification of a specific crossing. GRANT (1981) also pointed out that in plant groups possessing a breeding system intermediate between outcrossing and inbreeding, hybrid reproduction can be expected to follow a mixture of pathways. This may be applicable to the situation among the taxa of subsection *Boreali-Americanae*.

4.5. Why Is Hybridization So Rampant Among the Taxa of *Viola* Subsection *Boreali-Americanae*?

Attempts at quantifying the extent of hybridization among the taxa of subsection *Boreali-Americanae* have not been made in the present study. Such attempts would require extensive and detailed studies of populations throughout the range of the taxa. Yet, frequent encounters in the field of populations consisting of putative hybrids, hybrid swarms, and *a posteriori* determinations of putative hybridity or introgression using SEM of the seed coat surface of seeds of plants that superficially resembled orthospecies support the observations of previous students of the subsection that hybridization among the taxa is rampant in the Eastern United States and Canada.

A number of previous students of the subsection and other authors have grappled with the question of why hybridization is so rampant among the taxa of subsection *Boreali-Americanae* in different contexts. BRAINERD (1906a) proposed a scenario to account for the lack of isolation between the taxa of subsection *Boreali-Americanae*. According to Brainerd, the northeastern United States was entirely covered with forests two or three centuries ago (this has not been proven to be correct, however). The clearing away of those forests by man has extended the range and habitats of *Viola*, which had been previously confined to habitats outside the primeval forests. As a result, the number of individuals has increased, and species which had been isolated before became cohabitant and thereby the opportunities to hybridize increased. RUSSELL (1954) outlined the following suggestions for the difficulties in delimiting species in *Viola* that are applicable to our question. First, the lack of genetic barriers to hybridization between closely related species throughout the genus. Second, the effects of human activities [drawing from ANDERSON's (1948) «hybridization of the habitat»]. Humans have greatly altered the natural habitats of plants over the greater part of the eastern United States, and consequently many species that were formerly separated were brought together. Edaphic situations that were formerly separated by large stretches of intermediate habitats have been brought into contiguity, and new habitats have been created. In addition, competition pressure has been released in habitats formerly closed, allowing hybrids to become established where before this was rarely possible. Third, the oscillating climates of the Pleistocene glaciations have instigated hybridization and introgression. 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*. He attributed the hybridization and the subsequent blurring of species boundaries to the repeated migrations of the species during the inter-glacial periods. Species were supposedly constricted in the South during the glacial maxima, and modified by hybridization and introgression, and then spread northwards to occupy new habitats.

The foregoing suggestions provided a number of important elements of a possible answer to our question. The Pleistocene glaciations have most likely affected the distributions of the taxa. They were followed by additional natural disturbances (e.g., floods, landslides, fire), human activities, or both. Human activities introduced disturbance in old habitats, and opened new ones. All three factors have, most likely, been facilitators in bringing into contact species that were formerly ecologically separated and other species that were also geographically separated. One of the best examples is the well documented (e.g., *in* BRAINERD, 1924) contact between *Viola pedatifida* that occupies prairies and *V. sororia* that occupies margins of open, mixed woods, shaded ledges, and disturbed sites. Many open prairies have become restricted to strips of land along borders of fields and railroads, and thereby have become physically closer to the habitats occupied by *V. sororia*. The decrease in distance between the habitats has probably increased the bi-directional movements of pollinators between the populations of the two species. It also allowed transfer of seeds of one species to the habitat of the other species by ants, and thereby increased the probability of outcrossing.

Furthermore, when we examine the general distributions of the taxa, we find that ecological and geographical barriers are still maintaining distinct and isolated populations of some of the taxa of the subsection. *Viola egglestonii*, endemic to cedar glades in the southeastern United States, is ecologically isolated from the rest of the taxa of the subsection. *Viola nuevo-leonensis*, growing in margins of chaparral and *Pinus-Quercus-Cercis* forests at relatively high elevations in northern México, is both ecologically and geographically isolated. There are no reports of hybridizations involving these species. Another example of geographic isolation is *V. nephrophylla*, which is the only species whose distribution extends to the western seaboard. There are numerous reports on hybridization of this species east of the Rocky Mountains where it has come into contact with other taxa. However, there are no reports on hybrids from the Pacific Northwest and northeastern California where populations of *V. nephrophylla* are geographically isolated. Similar geographic separation is found between the northeastern species *V. novae-angliae* and *V. septentrionalis*, and the species of the southeastern United States, *V. septemloba* and *V. villosa*. Even if we accept the arguments that the disruptions of geographic and ecological barriers promote hybridization, and that hybridization is likely in disturbed habitats, they are still not sufficient to explain why hybridization is so rampant among the taxa. Why do the taxa of subsection *Boreali-Americanae* hybridize more frequently than other taxa occupying the same habitats (including other taxa of *Viola*)?

The answer may be that the plants themselves are exceptionally pre-adapted for hybridization and introgression, and after hybridization or introgression have occurred, are also pre-adapted for maintaining and perpetuating some of the hybrids. These pre-adaptations are accomplished by the following factors. First, the plants have no genetic, structural or phenological barriers for outcrossing. Second, they have a wide spectrum of pollinators, and have not coevolved with specific pollinators. Consequently, gene flow can take place among all the taxa. Third, cleistogamy and vegetative reproduction ensure their perpetuation, and increase the number of fertile individuals (including hybrids and backcrosses) available for outcrossing and subsequent genetic recombination. Fourth, most hybrids are fertile, vigorous, and adaptable to habitat modifications.

4.6. The Consequences of Hybridization in *Viola* Subsection *Boreali-Americanae*

The literature on the evolutionary significance and consequences of hybridization and introgression is voluminous. The discussion that follows highlights some consequences that bear on the systematics of the taxa of subsection *Boreali-Americanae*.

A major consequence of hybridization among the taxa is stabilized hybrids. As outlined in the foregoing discussion, the taxa of subsection *Boreali-Americanae* are equipped with all three

modes of reproduction: chasmogamy, cleistogamy, and vegetative reproduction. Therefore, it should be no surprise that stabilized, homologous hybrids have evolved independently in many separate sites, persisted, and consequently mislead many taxonomists, who interpret them as orthospecies. RIESEBERG & WENDEL (1993) distinguished between recently hybridized or introgressant populations and stabilized introgressants that are reproductively isolated from their parental taxa. There is no evidence of reproductive isolation among the taxa and hybrids of the subsection.

What would be the destiny of the progeny of these hybrids? STEBBINS (1969) pointed out that the progeny of fertile hybrids will either degenerate or revert to their parents if they are unaided by natural selection, or if only selective forces that favor the parental genotypes are present. Furthermore, even if new habitats that change the action of natural selection are available, the emergence of derived populations with new adaptive properties will be greatly retarded by gene flow from their parents unless they achieve some degree of isolation. Most of the progeny of the fertile hybrids of subsection *Boreali-Americanae* do not degenerate (on the basis of Gershoy and Brainerd's studies, and observations made in this study). Some of them might revert to their parents if sufficient outcrossing with the parental plants is maintained, but the process might be slowed down compared to other plants due to their alternative modes of reproduction: cleistogamy and vegetative reproduction. Most of the reproductive portion of the life cycle of the plants is spent at the cleistogamous phase. Cleistogamy retains the sexual mechanism of reproduction – meiosis and recombination are taking place – and enables it to take place without dependency on pollinator availability. Even if outcrossing has not taken place during the brief chasmogamous phase in the spring, the perpetuation of these hybrids is maintained by the production of seeds by cleistogamy. Some of the hybrids in a population would hybridize with other hybrids, and produce hybrid swarms. To complicate the picture, some gene flow may occur between these hybrids and other taxa in adjacent populations depending on pollinator activity and the distances between populations.

Another possible consequence of hybridization is speciation through hybrid derivatives. A hypothesis on such possible evolution of *V. fimbriatula*, the only taxon in subsection *Boreali-Americanae* that does not display unique micromorphological characters on the seed coat surface, is presented in Chapter 6. Another hypothesis on taxa of this subsection was presented by STEBBINS (1950). He noted the various F_2 segregates bearing blades with different degrees of dissection that were illustrated by BRAINERD (1924) (e.g., segregates of the F_1 hybrid of *Viola pedatifida* and *V. sagittata*). He suggested that by comparing these segregates with the stable and constant species in the eastern United States bearing "unusual leaf forms," such as *V. palmata*, *V. brittoniana*, *V. triloba*, *V. stoneana*, and *V. viarum*, one can hypothesize that these species have been derived by stabilization of hybrid derivatives. Therefore, there is a substantial reason for suggesting that the number of stable, recognizable species in subsection *Boreali-Americanae* has been considerably increased by hybridization. The micromorphological data (GIL-AD, 1995) and the correlation of this data with macromorphological and other data (see Chapter 6) revealed that three of the species that Stebbins listed, *V. palmata*, *V. stoneana*, and *V. viarum*, are of putative hybrid origin, and therefore his prediction was correct, in part. Morphological data do not provide evidence to support the hypothesis that the other two species (representing the taxa possessing divided or lobed blades) have been derived from stabilized hybrids. Divided and/or lobed blades have evolved also in the subsections *Chrysanthae* and *Nudicaules* of *Viola* section *Chamaemelanium*, and in subsection *Pedatae* of section *Plagiostigma*. It is more likely that the taxa of subsection *Boreali-Americanae* that possess divided or lobed blades are orthospecies that have evolved by divergence, and not as derivatives of stabilized hybrids. Nevertheless, the final evaluation of Stebbins' hypothesis, as well as the hypothesis concerning the origin of *V. fimbriatula*, await testing by molecular techniques.

4.7. The Nomenclatural Treatment of Hybrids and Introgressants

The frequent occurrence of hybrids and introgressants of the taxa of the subsection raise the question of how they should be treated and subsequently, how their specimens should be annotated.

The nomenclature of hybrids is covered in Appendix I of the International Code of Botanical Nomenclature (ICBN) (GREUTER & al., 1994). Article H.4 (page 85) states that "When all the parent taxa can be postulated or are known, a nothotaxon is circumscribed so as to include all individuals (as far as they can be recognized) derived from the crossing of representatives of the stated parent taxa (i.e., not only the F₁ but subsequent filial generations and also backcrosses and combinations of these). There can thus be only one correct name corresponding to a particular hybrid formula; this is the earliest legitimate name...in the appropriate rank..., and other names to which the same hybrid formula applies are synonyms of it." Thus, when sufficient evidence (e.g., micromorphological or molecular data) is available to support the postulation of the parents of a given hybrid belonging to subsection *Boreali-Americanae*, the published names (see under the discussion of the appropriate orthospecies in Chapter 6, and also Appendix B) for the particular hybrid combination should be used. If a name has not been published, a hybrid formula should be designated (WAGNER, 1983; GREUTER & al., 1994). When hybridity can be postulated (e.g., when the plant's suite of characters does not match that of any orthospecies), but sufficient supporting evidence is not available to allow positive identification of the putative parents, it is better to designate the plant as a putative hybrid, and leave it unnamed. Such procedure would encourage subsequent researchers to seek additional evidence. In addition, it would discourage a common curatorial practice in many herbaria of filing specimens of such plants with one of the stated parents regardless of their morphology. Frequently, this is followed by annotation of such specimens as orthospecies, and consequently, great disarray.

The problem of designating a backcross that closely resembles one of its parents or an introgressant is of special concern when dealing with hybrids of subsection *Boreali-Americanae*. WAGNER (1983) suggested that a hybrid would be classified with its parent if it is so close and cannot be separated from it. This is a workable solution when the putative parents are widely separated, which should be practiced in other taxa. However, in subsection *Boreali-Americanae*, where species are closely related, interfertile, and separated by a relatively small number of characters, and where macromorphological characters (in most taxa) are not sufficient to be used alone to delimit taxa, such a practice would reinstate the obliteration of the species boundaries. When evidence for introgression is available to indicate that, the plant should be annotated properly.

HARDIN (1958) reviewed the many different methods of annotation of introgressants. He pointed out that the use of the symbols > and < as more or less arrows indicating the direction of introgression, or gene flow, might add to confusion, since these symbols are more associated with their mathematical usage. He recommended that the dominant component (the recurrent parental species *sensu* ANDERSON, 1949) would appear first after the genus name or its abbreviation, and would then be followed by the > symbol and the epithet of the second component. For example, if *Viola affinis* introgressed into *Viola cucullata*, the product of the introgressive hybridization would be annotated as *Viola cucullata > affinis*. If the epithets are kept in alphabetical order, e.g., *Viola affinis < cucullata*, the formula might be confusing, and the specimen might be filed under the first epithet rather than under the epithet of the dominant component in this example. TERRELL (1963) favored the usage of the greater than and smaller than symbols, as advocated by Hardin, but suggested that these symbols would be used with a dash to indicate the direction of intergradation (e.g., *Viola cucullata >–V. affinis*). Hardin's and Terrell's suggestions have not been adopted and incorporated into the ICBN (WAGNER, 1983).

An alternative method would be to use the symbol of a simple arrow pointing backwards: ← to designate the direction of introgression. This symbol is widely available in most of the contemporary word processing computer-programs, and would not be confused with mathema-

tical symbols. The dominant component would follow the name or abbreviation of the genus, and would be followed by the arrow, and then by the epithet of the minor component. Using the same example, this notation would be written as *Viola cucullata ← affinis*, and would be read: *Viola cucullata* introgressed by *Viola affinis*. Thus, the notation of the documented case of putative introgression presented in GIL-AD (1995), is *Viola nephrophylla ← novae-angliae*, and it reads: *Viola novae-angliae* introgressed into *Viola nephrophylla*. When there is some evidence for putative introgression, but it is inconclusive (e.g., when foreign micromorphological structures are detected on the seed coat surface, but they can be attributed to more than one orthospecies) a question mark can be interpolated between the arrow and the binomial of the putative minor component to indicate uncertainty.

CHAPTER 5

SPECIES CONCEPT AND SYSTEMATIC APPROACH

5.1. Species Concepts in *Viola* Subsection *Boreali-Americanae:*
A Historical Perspective

The early taxonomic treatments of subsection *Boreali-Americanae* were based on a Linnaean approach that focused on a limited number of conspicuous characters selected from observations on one to few collections of plants, most of which were at the chasmogamous phase. The general outline, dissection, and marginal lobing of the mature blades and pubescence were the major characters that were employed to delimit taxa. In addition, the tendency to collect the unusual from a limited number of populations and to draw general conclusions on species delimitation from those collections, coupled with the obsession of some workers to attach a name to each variant encountered, have resulted in skewed species concepts and taxonomic framework. A large number of taxa have been described, with sharp disagreements among authors on the delimitation of taxa. It is interesting to note that some recognition that the species described were not sharply defined entities became apparent as early as GRAY's (1859) treatment. Gray listed four species of the subsection and *Viola pedata*, and noted that *V. cucullata* var. *cucullata* "passes by intermediate forms of all sorts into var. *palmata.*"

Ezra Brainerd's comprehensive research (published in a series of papers between 1904 and 1924, and followed by vernacular English descriptions of the taxa he recognized by BAIRD-BRAINERD, 1942) was a turning point in the history of our understanding of these taxa. He managed not only to untangle numerous nomenclatural problems that had accumulated, but also introduced a change of course in terms of the study of the taxa and the processes underlying their difficulties. He studied the taxa in major herbaria and in the wild, cultivated transplanted plants, raised seedlings from seeds harvested from cleistogamous capsules and studied the progeny, and studied natural hybrids that have been collected by or sent to him. His approach was a presage to some biosystematic techniques employing common garden studies. The most important contributions he made were his observations that the taxa cross freely under natural conditions, and that characters that appear at the cleistogamous phase are very important in distinguishing between the taxa. His analyses of hybrids enabled him to eliminate many previously described taxa. However, he recognized a large number of species in the subsection (29, including *Viola pedata*), and delimited some of them on the basis of only a few conspicuous characters deemed *a priori* to be of importance, such as blade shape, color of the corolla, and habitat.

GERSHOY (1928, 1934) extended Brainerd's work through comprehensive studies on the breeding system of the taxa. He made chromosome counts that showed that all the taxa of subsection *Boreali-Americanae* possess the same chromosome number ($n = 27$), and thus provided an important character that supports the monophyly of the subsection. In addition, he made 34 different interspecific crosses between taxa of the group using the living collections brought together by Brainerd, and proved that the taxa were not only interfertile, but that the F_1 progeny were vigorous, and most were fertile.

The three floristic treatments that followed Brainerd's treatment maintained earlier species concepts. FERNALD (1950) recognized 27 species and 4 varieties. He derived most of his treatment from Brainerd's studies, and emphasized pubescence and blade character states. However, he did not include two of Brainerd's species, *Viola floridana* and *V. rosacea*, upheld *V. pectinata*, and described a new variety (*grisea*) of *V. septentrionalis*. ALEXANDER (1952) recognized 24 species and 3 varieties, two of which he erected, *V. papilionacea* var. *priceana* and *V. brittoniana*

var. *pectinata*. GLEASON & CRONQUIST (1963) recognized 24 species and 4 varieties, but commented that *V. emarginata* was probably a series of hybrids. In addition, they listed *V. sagittata* var. *subsagittata*.

Russell conducted a number of studies on wild populations of taxa of subsection *Boreali-Americanae* (summarized *in* RUSSELL, 1965), combining observations in the wild with studies of herbarium specimens, and employing numerical methods (RUSSELL, 1956b) to analyze the boundaries between taxa. He conducted detailed macromorphological measurements (especially of blade and pubescence character states), and employed ANDERSON's (1949) hybridization index and pictorialized scatter diagrams to analyze instances of hybridization and demonstrate, in some cases, putative introgression. That approach was successful in establishing that *Viola emarginata* was a hybrid (RUSSELL & RISSER, 1960). Russell also practiced a more critical approach to the delimitation of taxa. He subsumed a number of species and varieties (principally named by E. L. Greene) from the western mountains under *V. nephrophylla* following detailed analyses of herbarium and population samples (RUSSELL & CROSSWHITE, 1963). In addition, he excluded three additional species, *V. latiuscula*, *V. papilionacea* and *V. stoneana*, on the basis of lack of specific characters (RUSSELL, 1965). However, the species concept he used was very similar to Brainerd's species concept. It was based on using a number of key macromorphological characters, primarily blade and pubescence character states, and occasionally including habitat and distribution data. RUSSELL (1965) recognized in the subsection 24 species (including *V. pedata*) and one variety.

Cronquist (*in* GLEASON & CRONQUIST, 1991) took a radical approach by lumping most of the previously recognized taxa into six species. His rationale (CRONQUIST pers. comm., 1989) was that only taxa possessing a distinct suite of characters should be recognized as species given the current data available. When additional data (including non-morphological characters) become available, the delimitation of the taxa should be re-evaluated and revised. Four of the species he recognized (*Viola sagittata*, *V. cucullata*, *V. nephrophylla*, and *V. villosa*) possess autapomorphies, but the remaining two (*V. sororia* and *V. palmata*) are unnatural assemblages of taxa united primarily on the basis of their general blade shape, undivided or divided respectively.

MCKINNEY's (1992) treatment, based on field observations, extensive examination of herbarium specimens, examination of type material and/or original descriptions, and reports of earlier workers reflects a reversion to pre-Brainerd and Fernaldian concepts in delimiting taxa. Although he provided a critical overview of the taxonomically useful characters he employed in his treatment, some of his conclusions, such as the lack of taxonomic value of character states of capsules and seeds and the lack of consistency in the occurrence of the petal trichomes, are not supported by this research. He contended that his taxonomic concepts were largely based on contemporary works, such as DAVIS & HEYWOOD (1963), but his decisions were primarily based on few characters, lacked empirical evidence, and in some cases relied on comparisons of earlier descriptions, illustrations or type material (some of them selected erroneously) that do not agree well with the real plants. Furthermore, two of the species he re-delimited, *Viola palmata* and *V. subsinuata*, demonstrate extensive blade variation, do not possess clear boundaries in their reproductive characters, and are most likely assemblages of hybrids. This is in spite of his correct assertion that blade structure has probably contributed more taxonomic confusion than any other character due largely to the combined influence of hybridization and environmental modification. Most of his decisions at the subspecific level are unwarranted, since he relied heavily on blade character states, many of the other characters he listed overlap, and the data on reproductive characters is incomplete. McKinney recognized in the subsection 10 species (including *V. pedata*), 2 subspecies, and 4 varieties.

5.2. The Systematic Approach and Species Concept Adopted in This Treatment

In this treatment, sixteen species (*Viola affinis, V. brittoniana, V. cucullata, V. egglestonii, V. fimbriatula, V. missouriensis, V. nephrophylla, V. novae-angliae, V. nuevo-leonensis, V. pedatifida, V. sagittata, V. septemloba, V. septentrionalis, V. sororia, V. triloba,* and *V. villosa*), one subspecies (*Viola novae-angliae* subsp. *grisea*), and one form (*Viola brittoniana* f. *pectinata*) are recognized in subsection *Boreali-Americanae* (Chapter 6; and see also Appendix A for a comparison with previous treatments of the subsection).

Plants were studied in the wild, and were also cultivated and studied in the greenhouse. These studies were supplemented by herbarium specimens (see Chapter 2 for details). All the morphological characters available for examination were evaluated for each putative taxon (see Chapter 3).

SEM of the seed coat surface of seeds of each of the orthospecies revealed a suite of primary and secondary sculpture character states unique to each species that are correlated with a suite of macromorphological characters. In a number of species, SEM of petal trichomes provided additional unique character states. Furthermore, SEM of the surface of seed coats enabled, in most cases, the identification of instances of hybridization and putative introgression by revealing blends of structures of the primary and secondary sculpture typical of different orthospecies and deviations in surface structures from those typical of orthospecies. Thus, hybrids were sorted out by correlating micromorphological characters with macromorphological characters. After unique micromorphological characters have been identified, the reproductive macromorphological characters of the plants from which the micromorphological characters have been sampled were examined. These characters included: seed color (an autapomorphy in seven of the species recognized), seed dimensions, capsule color, capsule shape, ontogeny of the cleistogamous flowers and capsules, habit of the peduncles of the cleistogamous flowers, presence or absence of trichomes on the spurred petal, shape of the petal trichomes, shape of the apex of the spurred petal, color patterns on the petals, presence or absence of cilia on the sepals and auricles, increase in auricle length in the cleistogamous phase, and pubescence on the peduncles. These characters were combined and evaluated for their value as good taxonomic characters with selected vegetative macromorphological characters, presence or absence of heterophylly, the type of substrate, habitat preferences, and in some taxa general distribution data.

Reproductive characters served as primary criteria in detecting the gaps between taxa. Only taxa possessing a distinct suite of character states, including at least one unique reproductive character state were recognized as species. The possession of a number of unique vegetative characters without at least one accompanying unique reproductive character state was not accepted as a justification for the recognition of a species. This criterion was formulated in order to make it possible to overcome two major problems in the subsection: the low divergence among the taxa in macromorphological characters and the nature of the hybrids. Observations conducted in this research on hybrids and orthospecies revealed that some hybrids possess one to few vegetative characters (e.g., blade lobing) which appear to be unique. Yet, these hybrids cannot be distinguished by other macromorphological characters from orthospecies and thus, the vegetative characters do not justify their recognition as orthospecies. Recombination of genetic factors in the offspring of interspecific hybrids may sometimes lead to new types radically different [in vegetative and reproductive characters] than those found in either parent (STEBBINS, 1950). The vegetative characters that appear unique in some hybrids of the subsection may be the outcome of such genetic recombination. The criterion for the recognition of species is restricted to subsection *Boreali-Americanae*. It is not advocated as a criterion that should be practiced in circumscribing species in other taxa (especially those possessing sufficient variation in macromorphology). There are numerous cases of variation in vegetative characters accompanied by a lack of variation in reproductive characters in taxa of other families. Unique vegetative characters often serve well to delimit species in those families. Accepting the circumscription of species in subsection

Boreali-Americanae using only unique vegetative characters would put us back into the species concept that E. L. Greene practiced. This would result in the recognition of a substantial number of taxa as species although they are most likely hybrids or introgressants.

The species concept that forms the foundation for the recognition of species in this research was shaped inductively by examining micromorphological and macromorphological character distributions and the patterns of variation among the taxa. This concept is similar to the phylogenetic species concept advanced by CRACRAFT (1989) and refined by NIXON & WHEELER (1990). Nixon & Wheeler defined species as the smallest aggregation of populations (sexual) or lineages (asexual) for which a unique combination of character states is present in comparable individuals. As stated above, only taxa possessing a distinct suite of character states were recognized as species in subsection *Boreali-Americanae*, and the possession of at least one unique reproductive character state was mandatory for the recognition of species.

These requirements may appear too restrictive to some practicing taxonomists, who would prefer the application of a broader species concept than the species concept applied in this treatment for this subsection. Such a concept would encompass some patterns of variation detected at the macromorphological level regardless of the underlying processes that cause them, and would readily allow the naming of plants. According to this *modus operandi*, general resemblance to an orthospecies would justify assigning the name of the orthospecies to the plant in question. However, given the breeding system of the plants, the major role that reticulate evolution has played in the obliteration of the boundaries between the taxa in this subsection, and the scarcity of distinct macromorphological characters, this broad approach would not allow a clear and objective circumscription of the species, and would therefore be counterproductive. In practice, the identification of the plants would become arbitrary and subjective, many of the putative hybrids or introgressants encountered in the field would readily serve as candidates for recognition as orthospecies, and the disarray that existed prior to this research would be perpetuated.

Furthermore, the species circumscriptions practiced in this treatment may be considered by some taxonomists as erring on the conservative side since they are based on relatively small sample sizes, and rely extensively on evidence from micromorphology. They may argue that if the sample size were larger, some variation at the micromorphological level would be detected, and consequently the circumscription of the taxa would have to be less restrictive. Even if such variation is detected, it would not affect the conclusions of this research and the outcome of cladistic analyses of these taxa. The data obtained in this research suggest that when significant variation occurs at the micromorphological level, it is an outcome of reticulate evolution (GILAD, 1995), and in many cases it is coupled with variation at the macromorphological level in various degrees. Any variation detected by large sample sizes would have to be evaluated first with a third, independent source of data (e.g., molecular data) in order to distinguish it from the effects of reticulate evolution. The reliability and stability of cladistic analyses of the taxa would suffer greatly if a broader species concept were applied.

Speciation among the taxa of subsection *Boreali-Americanae* has most likely taken place through ecological adaptation, and in a number of taxa by geographic isolation. It is manifested more extensively at the micromorphological level where more apomorphies are present than at the macromorphological level where homoplasy is abundant.

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: *Nomimium, Dischidium, Chamaemelanium, Melanium* and *Leptidium*, primarily on the basis of the morphology of the stigma. Section *Nomimium* (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 *Nomimium* 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 *Nomimium* 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 *Nomimium, 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 *Nomimium* 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 *Nomimium* (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 *Nomimium*, 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 *Nomimium* 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 *Nomimium* 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 *Rostellatae* 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 hyphened 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 & BROCK-MAN (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 beapplied to *Viola*. Those studies have shown that in other plant groups hybridization and introgression have occurred in habitats that were undoubtedly disturbed during the oscillatingclimates 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. FABIJAN & *al.* (1987) hypothesized that glaciation events during the Pleistocene likely had an effect on speciation in section *Chamaemelanium* 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 ± ciliate 8

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 subcordate 6

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 distributed 7

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 States 9

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 soil 10

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 substrate 12

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 brown 8

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, ± 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 mg 9

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 green 15

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).

Ic.: 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: ×*V. davisii* (*V. affinis* × *V. brittoniana*); ×*V. consocia* (*V. affinis* × *V. cucullata*); ×*V. hollickii* (*V. affinis* × *V. fimbriatula*); ×*V. subaffinis* (*V. affinis* × *V. nephrophylla*); ×*V. dissena* (*V. affinis* × *V. sagittata*); ×*V. champlainensis* (*V. affinis* × *V. septentrionalis*); ×*V. consona* (*V. affinis* × *V. sororia*); and ×*V. milleri* Moldenke (*V. affinis* × *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-defi-ning 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.

Ic.: 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], Klaber, *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 apexes, 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 apexes, 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, apexes acute, mucronulate.

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

BASIONYM: *Viola pectinata* E. P. Bicknell *in* Torreya 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.

Ic.: 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: ×*V. davisii* (*V. affinis* × *V. brittoniana*); ×*V. notabilis* (E. P. Bicknell) House (*V. brittoniana* × *V. cucullata*); ×*V. mulfordae* (Pollard) House (*V. brittoniana* × *V. fimbriatula*); ×*V. marylandica* (*V. brittoniana* × *V. sagittata*); *V. brittoniana* × *V. sororia*; and *V. brittoniana* × *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!).

Ic.: 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 μm 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: ×*V. consocia* (*V. affinis* × *V cucullata*); ×*V. notabilis* (E. P. Bicknell) House (*V. brittoniana* × *V. cucullata*); ×*V. porteriana* (Pollard) House (*V. cucullata* × *V. fimbriatula*); ×*V. insessa* (*V. cucullata* × *V. nephrophylla*); ×*V. festata* (*V. cucullata* × *V. sagittata*); ×*V. melissaefolia* (Greene) House (*V. cucullata* × *V. septentrionalis*); ×*V. conturbata* (*V. cucullata* × *V. sororia*); and ×*V. greenmani* (*V. cucullata* × *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!).

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

Viola egglestonii 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!).

Ic.: [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, ± 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 ± ciliate on the upper half, sepal length/capsule length ratio 0.6; *auricles* 0.5-1.3 mm long, green, ± dotted with red-purple, apex truncate subtruncate or rounded, glabrous, ± 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 μm 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: ×*V. hollickii* (*V. fimbriatula* × *V. affinis*); ×*V. mulfordae* (Pollard) House (*V. fimbriatula* × *V. brittoniana*); ×*V. porteriana* (Pollard) House (*V. fimbriatula* × *V. cucullata*); ×*V. abundans* (*V. fimbriatula* × *V. sagittata*); ×*V. parca* (*V. fimbriatula* × *V. septentrionalis*); ×*V. fernaldii* (*V. fimbriatula* × *V. sororia*); and ×*V. robinsoniana* (*V. fimbriatula* × *V. triloba*).

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

		V. fimbriatula	*V. sagittata*
During chasmogamous anthesis:			
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)
During the cleistogamous phase:			
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 *Quercus* 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"; isolectotypes: NY! – no. 29619, NDG! – no. 33214/Herbarium Greeneanum no. 38308).

Ic.: 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, ± 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 ± 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 µm 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. HELLENTHAL 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!).

Ic.: 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) μm 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 ± 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: ×*V. subaffinis* House (*V. nephrophylla* × *V. affinis*); ×*V. insessa* (*V. nephrophylla* × *V. cucullata*); *V. nephrophylla* × *V. sororia*; and *V. nephrophylla* × *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!).

Ic.: 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, ± 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, ± 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 µm 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*

	V. novae-angliae subsp. *novae-angliae*	*V. novae-angliae* subsp. *grisea*	*V. septentrionalis*
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 *Pinus banksiana* 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, ± 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 μm 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
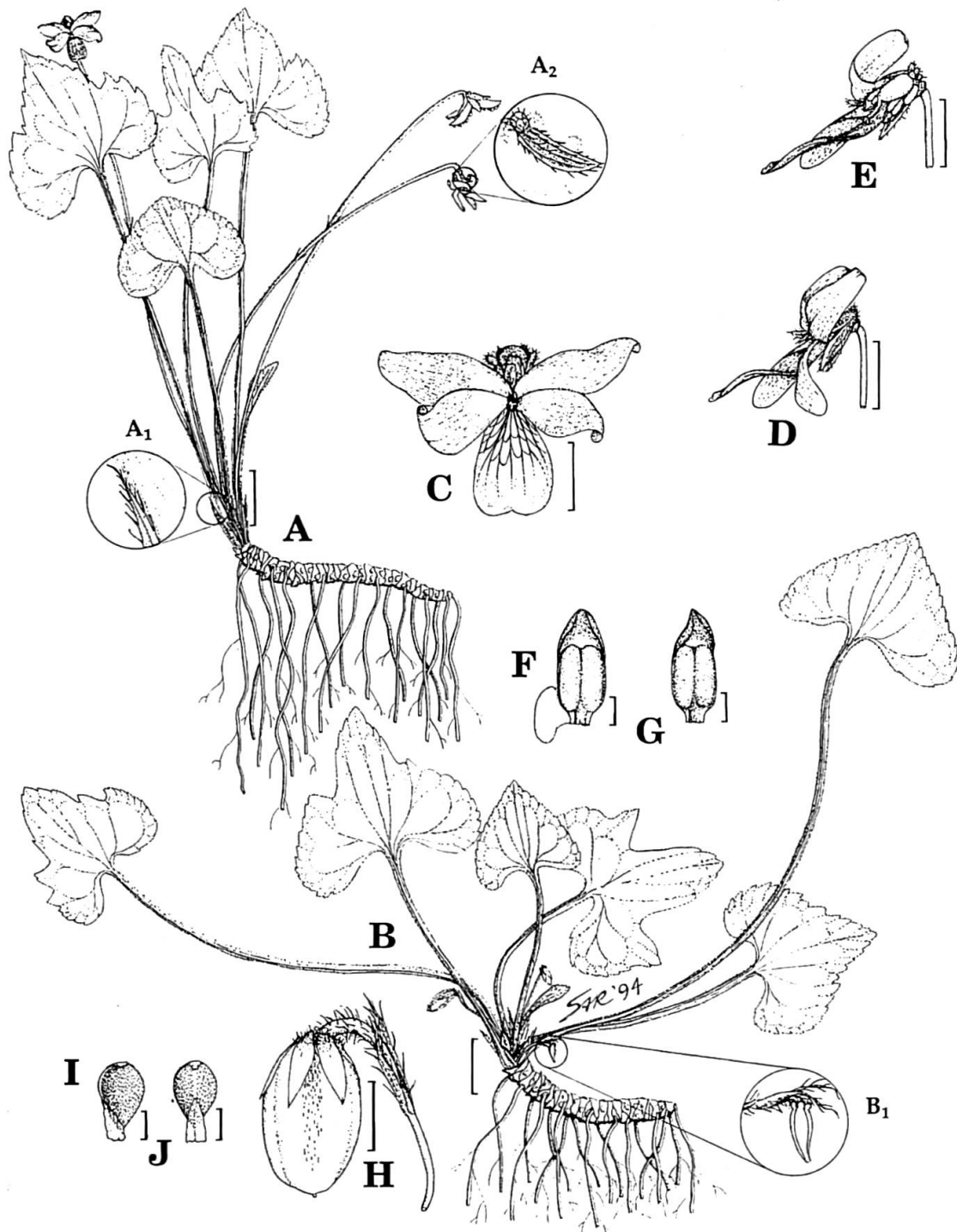
Fig. 3. – *Viola nuevo-leonensis* W. Becker. **A.** Habit of a chasmogamous plant with a blow-up of the upper two thirds of a stipule (**A₁**), and a blow-up of a sepal and an auricle of a chasmogamous flower (**A₂**). **B.** Habit of a cleistogamous plant with a blow-up of a cleistogamous flower (**B₁**). **C.** Face on view of a chasmogamous flower. **D.** Side view of a chasmoga-mous 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 thacae, and filament. **H.** Side view of cleistoga-mous 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* Schlechtd.). 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 semicircular 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).

Ic.: 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. palmata*, and designated it as a variety comprised of the formerly recognized species *V. pedatifida*

and *V. egglestonii*. 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 Pensylvania)" (holotype: BM, photo: MICH!).

Ic.: 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), Klaber, *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, ± 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, ± 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 μm 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 subspecific 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 & RISSER (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: ×*V. dissena* (*V. affinis* × *V. sagittata*); ×*V. marylandica* (*V. brittoniana* × *V. sagittata*); ×*V. festata* (*V. cucullata* × *V. sagittata*); ×*V. abundans* (*V. fimbriatula* × *V. sagittata*); *V. sagittata* × *V. pedatifida*; *V. sagittata* × *V. sororia*; and ×*V. caesariensis* (*V. sagittata* × *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, Secfion of Rare Books).

Ic.: 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. egglestonii* into *V. septemloba* as a subspecies (see the discussion of *V. egglestonii*). 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).

Ic.: 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: ×*V. champlainensis* (*V. affinis* × *V. septentrionalis*); ×*V. melissaefolia* (Greene) House (*V. cucullata* × *V. septentrionalis*); ×*V. parca* (*V. fimbriatula* × *V. septentrionalis*); and ×*V. montivaga* (*V. septentrionalis* × *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, Pensylvania," [date of collection unknown], (lectotype, here designated: sheet No. 3: B-W 4898, photo: MICH!).

Ic.: 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. pratincola*, 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: ×*V. consona* (*V. affinis* × *V. sororia*); *V. brittoniana* × *V. sororia*; × *V. conturbata* (*V. cucullata* × *V. sororia*); ×*V. fernaldii* (*V. fimbriatula* × *V. sororia*); *V. nephrophylla* × *V. sororia*; *V. pedatifida* × *V. sororia*; *V. sagittata* × *V. sororia*; ×*V. montivaga* (*V. septentrionalis* × *V. sororia*); and ×*V. populifolia* (*V. sororia* × *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, ± 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 μm 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., *Gil-ad 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 macromorphological 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!).

Ic.: 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 mate-rial (*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 & RISSER (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 & RISSER'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* Torreya 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. egglestonii*. 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 *subsinuata* 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 periclinal 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 clavelate-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 midwestern 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. ×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.

CHAPTER 7

A PROSPECTUS FOR FUTURE RESEARCH
ON *VIOLA* SUBSECTION *BOREALI-AMERICANAE*

This treatment provides a foundation for a future monograph of subsection *Boreali-Americanae* that would cover in detail the distribution patterns of the taxa and the extent of hybridization among them. Such a monograph would require first extensive collecting throughout North America, including northern México. Due to the apparently broad geographic distributions of some of the taxa and the extent and frequency of hybridization and introgression among the taxa, the monographer would have to cope with an enormous sampling problem when attempting to establish accurate ranges for the orthospecies. This problem involves not only the large number of populations that would have to be sampled, but also the need for a detailed sampling in each population during both the chasmogamous and the cleistogamous phases. Cultivation of some of the sampled plants in a greenhouse may reduce the number of populations that would have to be re-sampled during the cleistogamous phase. However, it may generate another set of difficulties (such as maintenance of the plants and monitoring the release of seeds) due to the large number of plants (perhaps hundreds) that would have to be cultivated for at least one fruiting season. The second requirement for a monograph is a positive identification of each plant to discern the orthospecies. This identification can be done on the basis of the species concept and the circumscription of the taxa presented in this treatment.

There are two alternatives for obtaining positive identifications. One approach, similar to the approach practiced in this research, would require harvesting of mature seeds from each plant for SEM of the seed coat surface. The procedures for SEM and data on the orthospecies that can serve as reference points are outlined in GIL-AD (1995) and GIL-AD (in press). Extensive sampling would compensate for the relatively small sample sizes obtained in the present research, and would therefore enhance the results presented here. The major limiting factors for this approach are SEM machine time and cost.

The alternative approach for positive identifications would require harvesting of mature capsules and seeds for extraction of DNA, followed by molecular analyses of the nuclear genome (e.g., gene sequencing). Pilot studies conducted during the preliminary stages of this research on plants of subsection *Boreali-Americanae* revealed that extraction of total cellular DNA from mature capsules and seeds produces higher yields than extraction from leaves, but the amount of the DNA is relatively low, and requires amplification using PCR (Polymerase Chain Reaction) protocols. Furthermore, the DNA extracted is accompanied by secondary compounds (most likely polysaccharides) and requires further purification prior to conducting analyses. The major limiting factors for this approach are the preliminary costs and time required to locate the gene(s) that would hold promise for demonstration of ample variation between taxa at the species and subspecific levels, as well as the costs involved in subsequent extensive surveys of populations.

The present treatment represents a breakthrough in our knowledge and understanding of the of the taxa of subsection *Boreali-Americanae*. I hope that it would instigate further research on these taxa and other taxa with similar complexity.

CHAPTER 8

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CHAPTER 9

APPENDICES

9.1. Appendix A

A Comparison
of the Classifications of *Viola* Subsection *Boreali-Americanae*
and its Taxa as recognized by Various Authors

DE GINGINS (1824)
    Section *Nomimium* Ging.
    Group I

    V. pedata
    V. palmata
    V. asarifolia
    V. papilionacea
    V. cucullata
    V. ovata
    V. sagittata
    V. villosa
    (plus additional *Viola* species)

GRAY (1848)*	GRAY (1856)*	GRAY (1889)*
V. cucullata	*V. cucullata*	*V. palmata* var. *cucullata*
V. palmata	*V. cucullata* var. *palmata*	*V. palmata*
V. sagittata	*V. sagittata*	*V. sagittata*
	V. delphinifolia	*V. pedatifida*
V. pedata	*V. pedata*	*V. pedata*

REICHE & TAUBERT (1895)
Sparsifoliae Reiche
    Ser. 2 *Herbaceae*
        Nomimium Ging. (*sensu stricto*)
            Rostellatae
                Stemless Plants

        V. pedata
        V. sagittata
        V. palmata var. *palmata*
        V. palmata var. *cucullata*
        V. pedatifida
        (plus additional *Viola* species)

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* = no supraspecific ranking is provided; additional *Viola* species are listed.

BRAINERD (1921, 1924)*	**BECKER (1925)**
	Section *Nomimium* Ging.
	"N." *Boreali-Americanae* W. Bckr.
29 species, 3 varieties	12 species

V. affinis	
V. brittoniana	*V. brittoniana*
V. chalcosperma	
V. cucullata	*V. cucullata*
V. egglestonii	
V. emarginata	*V. emarginata*
V. emarginata var. *acutiloba*	
V. esculenta	
V. fimbriatula	*V. fimbriatula*
V. floridana	
V. hirsutula	
V. langloisii	
V. langloisii var. *pedatiloba*	
V. latiuscula	
V. lovelliana	
V. missouriensis	
V. nephrophylla	
V. novae-angliae	
	V. nuevo-leonensis
V. palmata	*V. palmata*
V. papilionacea	*V. papilionacea*
V. pedatifida	*V. pedatifida*
V. rosacea	
V. sagittata	*V. sagittata*
V. septemloba	
V. septentrionalis	*V. septentrionalis*
V. sororia	*V. sororia*
V. stoneana	
V. triloba	
V. triloba var. *dilatata*	
V. viarum	
V. villosa	*V. villosa*
	"O." *Pedatae* Pollard
V. pedata	*V. pedata*

---

* = no supraspecific ranking is provided.

CLAUSEN (1929)	BAIRD-BRAINERD (1942)
Section "*Nominium*" [*sic*] Ging.	Section *Nomimium*
Subsection *Plagiostigma* Godr.	
"VIII." *Boreali-Americanae* W. Beckr.	*Boreali-Americanae*
20 species	28 species, 2 varieties

V. affinis	*V. affinis*
V. brittoniana	*V. brittoniana*
	V. chalcosperma
V. cucullata	*V. cucullata*
	V. egglestonii
V. emarginata	*V. emarginata*
	V. esculenta
V. fimbriatula	*V. fimbriatula*
	V. floridana
V. hirsutula	*V. hirsutula*
V. langloisii	*V. langloisii*
	V. langloisii var. *pedatiloba*
V. latiuscula	*V. latiuscula*
V. lovelliana	*V. lovelliana*
V. missouriensis	*V. missouriensis*
V. nephrophylla	*V. nephrophylla*
	V. novae-angliae
V. papilionacea	*V. papilionacea*
V. palmata	*V. palmata*
V. pedata	
	V. pedatifida
	V. rosacea
V. sagittata	*V. sagittata*
V. septemloba	*V. septemloba*
V. septentrionalis	*V. septentrionalis*
V. sororia	*V. sororia*
	V. stoneana
V. triloba	*V. triloba*
	V. triloba var. *dilatata*
	V. viarum
V. villosa	*V. villosa*

CLAUSEN (1951, 1964)	BRIZICKY (1961)
Section *Plagiostigma*	Section *Plagiostigma* Godr.
1951: Subsection *Boreali-Americanae*	Subsection *Boreali-Americanae* W. Becker
–20 species (not listed)	25 species (a few species listed as
1964: Subsection *Boreali-Americanae*	examples)
W. Beckr.–approximately 30 species	
(a few species listed as examples)	
1951: Subsection *Pedatae*	Subsection *Pedatae* Pollard
–1 species	*V. pedata*

FERNALD (1950)*	ALEXANDER (1952)*	GLEASON & CRONQUIST (1963)*	RUSSELL (1965)
			Stemless Blue Violets
27 species	24 species	24 [23] species	24 species
4 varieties	3 varieties	4 [3] varieties	1 variety
V. affinis	*V. affinis*	*V. affinis*	*V. affinis*
V. brittoniana	*V. brittoniana*	*V. brittoniana*	*V. brittoniana*
	var. *brittoniana*		
V. pectinata	var. *pectinata*		
V. chalcosperma		*V. chalcosperma*	
V. cucullata	*V. cucullata*	*V. cucullata*	*V. cucullata*
V. cucullata var. *microtitis*			
V. egglestonii	*V. egglestonii*	*V. egglestonii*	*V. egglestonii*
V. emarginata	*V. emarginata*	*V. emarginata*	
V. emarginata var. *acutiloba*		[*V. emarginata* var. *acutiloba*]	
V. esculenta	*V. esculenta*	*V. esculenta*	*V. esculenta*
V. fimbriatula	*V. fimbriatula*	*V. fimbriatula*	*V. fimbriatula*
			V. floridana
V. hirsutula	*V. hirsutula*	*V. hirsutula*	*V. hirsutula*
V. langloisii			*V. langloisii*
V. latiuscula	*V. latiuscula*	*V. latiuscula*	
V. lovelliana	*V. lovelliana*		*V. lovelliana*
V. missouriensis	*V. missouriensis*	*V. missouriensis*	*V. missouriensis*
V. nephrophylla	*V. nephrophylla*	*V. nephrophylla*	*V. nephrophylla*
V. novae-angliae	*V. novae-angliae*	*V. novae-angliae*	*V. novae-angliae*
V. palmata	*V. palmata*	*V. palmata*	*V. palmata*
V. papilionacea	*V. papilionacea*	*V. papilionacea*	
	var. *papilionacea*	var. *papilionacea*	
	var. *priceana*	var. *priceana*	
			V. pedata
V. pedatifida	*V. pedatifida*	*V. pedatifida*	*V. pedatifida*
			V. pratincola
V. sagittata	*V. sagittata*	*V. sagittata*	*V. sagittata*
		var. *subsagittata*	
V. septemloba	*V. septemloba*	*V. septemloba*	*V. septemloba*
V. septentrionalis	*V. septentrionalis*	*V. septentrionalis*	*V. septentrionalis*
V. septentrionalis var. *grisea*			
V. sororia	*V. sororia*	*V. sororia*	*V. sororia*
V. stoneana	*V. stoneana*	*V. stoneana*	
V. triloba	*V. triloba* var. *triloba*	*V. triloba* var. *triloba*	*V. triloba* var. *triloba*
V. triloba var. *dilatata*	*V. triloba* var. *dilatata*	*V. triloba* var. *dilatata*	*V. triloba* var. *dilatata*
V. viarum	*V. viarum*	*V. viarum*	*V. viarum*
V. villosa	*V. villosa*	*V. villosa*	*V. villosa*

* = no supraspecific ranking is provided.

CRONQUIST (*in* GLEASON & CRONQUIST, 1991)	MCKINNEY (1992)	GIL-AD (1995, 1997)
No supraspecific ranking provided	Section *"Nominum"* [*sic*] Ging. Subsection *Plagiostigma* Godr.	Section *Plagiostigma* Godr. Subsection *Boreali-Americanae* (W. Becker) Gil-ad
6 species 1 variety	10 species 2 subspecies, 4 varieties	16 species 1 subspecies, 1 form
		V. affinis
[*V. palmata* var. *palmata*] [*V. palmata* var. *palmata*]	*V. pedatifida* subsp. *brittoniana*	*V. brittoniana* f. *brittoniana* *V. brittoniana* f. *pectinata*
V. cucullata	*V. cucullata*	*V. cucullata*
[*V. palmata* var. *pedatifida*]	*V. septemloba* subsp. *egglestonii*	*V. egglestonii*
	V. sagittata var. *ovata*	*V. fimbriatula*
	V. hirsutula	
	V. sororia var. *missouriensis*	*V. missouriensis*
V. nephrophylla	*V. sororia* var. *affinis*	*V. nephrophylla*
	V. sororia var. *novae-angliae*	*V. novae-angliae* subsp. *novae-angliae* *V. novae-angliae* subsp. *grisea*
		V. nuevo-leonensis
	V. pedata	
V. palmata var. *palmata*	*V. palmata*	
V. palmata var. *pedatifida*	*V. pedatifida* subsp. *pedatifida*	*V. pedatifida*
V. sagittata	*V. sagittata* var. *sagittata*	*V. sagittata*
[*V. palmata* var. *palmata*]	*V. septemloba* subsp. *septemloba*	*V. septemloba*
		V. septentrionalis
V. sororia	*V. sororia* var. *sororia*	*V. sororia*
	V. subsinuata	
[*V. palmata* var. *palmata*]		*V. triloba*
V. villosa	*V. villosa*	*V. villosa*

9.2. Appendix B

Synonyms and Published Combinations of Albinos, Putative Hybrids and Putative Introgressants of *Viola* Subsection *Boreali-Americanae*

Introduction

This appendix outlines synonyms and published combinations of albinos, putative hybrids and putative introgressants of *Viola* subsection *Boreali-Americanae*. Although the citations provided here could be divided into four categories: names published for albinos, nomenclatural synonyms, putative taxonomic synonyms, and names that apparently have been given to putative hybrids and introgressants, the names that could be placed in one of the first three categories could also be placed in the last category. A search for mature seeds that would allow SEM examinations of the seed coats of seeds was conducted at NDG on the specimens of names published by E. L. Greene. The results indicated that most do not carry mature seeds, and therefore the identity of these taxa could not be revealed. Since *Viola* is usually collected during chasmogamous anthesis, this will likely turn out to be true for the specimens of the other combinations outlined here that have not been examined. For ease of reference, the citation of a combination published for albinos is given just after homotypic combinations if it has been published. Some of the combinations listed under *Viola fimbriatula* may be applicable to *V. sagittata* and vice versa. The list is not intended to be complete. It does not include synonyms and names that are affiliated with taxa that are hypothesized to be of hybrid origin (e.g., *V. papilionacea*) in this treatment.

Viola affinis LeConte *in* Ann. Lyceum Nat. Hist. New York 2: 138. 1828.
  Viola sororia subsp. *affinis* (LeConte) R. J. Little *in* Phytologia 80: 295. 1996.
  Viola sororia var. *affinis* (LeConte) L. E. McKinney *in* Sida Bot. Misc. 7: 39. 1992.

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

  Viola affinis var. *subarctica* J. Rousseau *in* Canad. J. Res. 28 C: 245. 1945.
  Viola crenulata Greene *in* Pittonia 4: 295. 1901.
  Viola nepetaefolia Greene *in* Pittonia 5: 92. 1902.
  Viola venustula Greene *in* Pittonia 3: 335. 1898.

Viola brittoniana Pollard *in* Bot. Gaz. (Crawfordsville) 26: 332. 1898.
  Viola atlantica Britton *in* Bull. Torrey Bot. Club 24: 92. 1897, non Pomel. 1874.
  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.

Viola cucullata Aiton, Hort. Kew. 3: 288. 1789.
  Viola palmata var. *cucullata* (Aiton) A. Gray *in* Bot. Gaz. (Crawfordsville) 11: 254. 1886.

Viola cucullata f. *albiflora* Britton *in* Bull. Torrey Bot. Club 17: 124. 1890.
Viola cucullata δ *alba* Torr. & A. Gray, Fl. N. Amer. 1: 137. 1838.

Viola cucullata ε *reniformis* Torr. & A. Gray, Fl. N. Amer. 1: 137. 1838.
Viola cucullata var. *macrotis* (Greene) W. Stone *in* Proc. Acad. Nat. Sci. Philadelphia 55: 673. 1903. *Viola macrotis* Greene *in Pittonia* 5: 97. 1902.
Viola cucullata var. *leptosepala* (Greene) W. Stone *in* Proc. Acad. Nat. Sci. Philadelphia 55: 674. 1903. *Viola leptosepala* Greene *in* Pittonia 5:98. 1902.
Viola oconensis House *in* Torreya 7: 137, Fig. 4. 1907.
Viola cucullata var. *microtitis* Brainerd *in* Rhodora 15: 112. 1913.
Viola cucullata f. *prionosepala* (Greene) Brainerd *in* Rhodora 15: 112. 1913. *Viola priono-sepala* Greene *in* Pittonia 5: 99. 1902.
Viola cucullata f. *thurstonii* (A. Twining) House *in* New York State Mus. Bull. 254: 504. 1924. *Viola cucullata* var. *thurstonii* A. Twining, Fl. N.E. Pennsylvania: 52. 1917.

Viola egglestonii Brainerd *in* Bull. Torrey Bot. Club 37: 526, plates 34 & 35. 1910.
Viola septemloba subsp. *egglestonii* (Brainerd) L. E. McKinney *in* Sida Bot. Misc. 7: 33. 1992.

Viola fimbriatula Sm. *in* Rees, Cycl. 37: *Viola* No. 16. 1817.

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

Viola alleghaniensis Roem. & Schult., Syst. Veg. 5: 360. 1819.
Viola sagittata var. *ovata* (Nutt.) Torr. & A. Gray, Fl. N. Amer. 1: 138. 1838. *Viola ovata* Nutt., Gen. N. Amer. Pl. 1: 148. 1818.
Viola sagittata Paine, Cat. Pl. Oneida Co.: 63. 1865, non Aiton. 1789.
Viola sagittata var. *hicksii* Pollard, Bot. Gaz. (Crawfordsville) 20: 326. 1895. *Viola ovata* var. *hicksii* (Pollard) Pollard *in* Proc. Biol. Soc. Washington 10: 92. 1898.
Viola amorphophylla Pollard *in* Proc. Biol. Soc. Washington 13: 129. 1900.
Viola aberrans Greene ex W. Stone *in* Proc. Acad. Sci. Philadelphia 55: 683, pl. 37, Fig. 4-6. 1903.
Viola fimbriatula var. *glabra* Pennell *in* Bartonia 12: 19. 1931.

Viola missouriensis Greene *in* Pittonia 4: 141. 1900.

Viola candidula Nieuwl. *in* Amer. Midl. Naturalist 3: 85, pl. 2-3. 1913.
Viola lucidifolia Newbro. *in* Stud. Nat. Hist. Iowa Univ. 17: 56, pl. 4 Fig. 3, pl. 8 Fig. 24-25. 1936.
Viola sororia var. *missouriensis* (Greene) L. E. McKinney *in* Sida Bot. Misc. 7: 42. 1992.

Viola nephrophylla Greene *in* Pittonia 3: 144. 1896.

Viola nephrophylla f. *albinea* Farw. *in* Amer. Midl. Naturalist 11: 64. 1928.

Viola vagula Greene *in* Pittonia 4: 67. 1899.
Viola austinae Greene *in* Pittonia 5: 30. 1902.
Viola galacifolia Greene *in* Pittonia 5: 30. 1902.
Viola subjuncta Greene *in* Pittonia 5: 31. 1902.
Viola peramoena Greene *in* Pittonia 5: 94. 1902.
Viola subrotunda Greene *in* Pittonia 5: 118. 1902.

Viola mccabeiana M. S. Baker *in* Madroño 5: 226, Pl. 22 Fig. 5, Pl. 23. 1940.
Viola nephrophylla var. *arizonica* (Greene) Kearny & Peebles *in* J. Wash. Acad. Sci. 29: 487. 1939. *Viola arizonica* Greene *in* Pittonia 5: 33. 1902.
Viola nephrophylla f. *bicolor* Boivin *in* Nat. Canad. 87: 49. 1960.
Viola nephrophylla var. *cognata* (Greene) C. L. Hitchc., Vasc. Pl. Pacific Northwest 3: 445. 1961. *Viola cognata* Greene *in* Pittonia 3: 145. 1896.

Viola novae-angliae House *in* Rhodora 6: 226, Plate 59. 1904.
Viola sororia var. *novae-angliae* (House) L. E. McKinney *in* Sida Bot. Misc. 7: 44. 1992.

Viola pedatifida G. Don, Gen. Hist. 1: 320. 1831.
Viola palmata var. *pedatifida* (G. Don) Cronquist *in* Gleason & Cronquist, Manual Pl. Northeastern U.S. ed. 2: 864. 1991.

Viola delphinifolia Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 136. 1838.
Viola pedatifida var. *bernardi* Greene *in* Pittonia 3: 259. 1898.
Viola indivisa Greene *in* Pittonia 5: 124. 1903.

Viola sagittata Aiton, Hort. Kew. 3: 287. 1789.

Viola dentata Pursh, Fl. Amer. Sept.: 172. 1813.
Viola sagittata var. *subsagittata* (Greene) Pollard *in* Bot. Gaz. (Crawfordsville) 26: 340. 1898. *Viola subsagittata* Greene *in* Pittonia 3: 315. 1898.
Viola sagittata var. *secedens* (Greene) Farw. *in* Amer. Midl. Naturalist 12: 68. 1930. *Viola secedens* Greene *in* Pittonia 5: 121. 1903.
Viola sagittata var. *glabra* Pennell *in* Bartonia 12: 19. 1931.
Viola sagittata f. *carlii* Creutz *in* Wild Flower 35: 9, Fig. 2. 1959.
Viola sagittata f. *umbelliflora* (Fernald) Scoggan, Fl. Canada 1: 52. 1978. *Viola fimbriatula* f. *umbelliflora* Fernald *in* Rhodora 51: 56. 1949.

Viola septemloba LeConte *in* Ann. Lyceum Nat. Hist. New York 2: 141. 1828.

Viola vicinalis Greene *in* Pittonia 4: 9. 1899.
Viola insignis Pollard *in* Bot. Gaz. (Crawfordsville) 26: 344. 1898, non Richter. 1886.

Viola septentrionalis Greene *in* Pittonia 3: 334. 1898.

Viola septentrionalis f. *alba* Vict. & J. Rousseau *in* Contr. Inst. Bot. Univ. Montréal 36: 20. 1940.

Viola macounii Greene *in* Pittonia 3: 335. 1898.
Viola subviscosa Greene *in* Pittonia 4: 293. 1901.
Viola fletcheri Greene *in* Pittonia 4: 296. 1901.
Viola nesiotica Greene *in* Pittonia 5: 102. 1902.

Viola sororia Willd., Hort. Berol.: Tab. 72. April 1806.
Viola cucullata γ *sororia* (Willd.) Torr. & A. Gray, Fl. N. Amer. 1: 137. 1838.
Viola palmata var. *sororia* (Willd.) Pollard *in* Bot. Gaz. (Crawfordsville) 26: 332. 1898.

Viola sororia f. *beckwithae* House *in* New York State Mus. Bull. 243-244: 40. 1923.
Viola sororia f. *pallida* F. Seymour, Fl. New England: 395. 1969.
Viola asarifolia Pursh, Fl. Amer. Sept.: 732. 1813.
Viola cuspidata Greene *in* Pittonia 3: 314. 1898.
Viola dicksonii Greene *in* Pittonia 4: 65. 1899.
Viola sororia var. *incognita* Lacey *in* Sida 3: 312. 1969.
Viola sororia f. *priceana* (Pollard) Cooperr. *in* Michigan Bot. 23: 167. 1984. *Viola priceana* Pollard *in* Proc. Biol. Soc. Washington 16: 127. 1903.

Viola triloba Schwein. *in* Amer. J. Sci. Arts 5: 57. 1822.

Viola triloba f. *albida* Steyerm. *in* Rhodora 54: 256. 1952.

Viola cucullata β *congener* (LeConte) Torr. & A. Gray, Fl. N. Amer. 1: 137. 1838. *Viola congener* LeConte *in* Ann. Lyceum Nat. Hist. New York 2: 140. 1828.
Viola vespertilionis Greene *in* Leafl. Bot. Observ. Crit. 1: 217. 1906.
Viola ornithodes Greene *in* Leafl. Bot. Observ. Crit. 1: 218. 1906.
Viola triloba f. *dilatata* (Elliott) E. J. Palmer & Steyerm. *in* Brittonia 10: 115. 1958. *Viola triloba* var. *dilatata* (Elliott) Brainerd *in* Bull. Torrey Bot. Club 37: 587. 1911. *Viola palmata* var. *dilatata* Elliott, Sketch Bot. S. Carolina 1: 300. 1817.

Viola villosa Walter, Fl. Carol.: 219. 1788.

Viola alabamensis Pollard *in* Proc. Biol. Soc. Washington 13: 169. 1900.
Viola carolina Greene *in* Pittonia 3: 259. 1898.

9.3. An Introduction to Appendices C and D

Abbreviations for the reproductive phases in the citations of representative specimens. – The reproductive phase of the plants mounted on a given specimen of *Viola*, and consequently the type of organs available for examination, are important in determining the type and value of information that could be extracted from the specimen. Therefore, a listing of the reproductive organs available on each representative specimen cited was added to the standard format. Following the abbreviation of the herbarium that is given in parentheses, the following abbreviations may be listed: **CH** = chasmogamous flowers; **CL** = cleistogamous flowers; **C** = capsules; **S** = mature seeds; **IMS** = immature seeds (the pigmentation of the seeds is missing, and they may also be shrunken); **CUL** = cultivated. In cases in which both chasmogamous and cleistogamous plants are mounted on the same sheet (or on serial sheets) and dates are listed, abbreviations for the reproductive phase: **CHP** = a chasmogamous plant; **CLP** = a cleistogamous plant, follow the respective date within the standard citation, and the abbreviations for the reproductive organs follow the herbarium abbreviation. In most cases when only chasmogamous (CH) and seeds (S) are listed, a chasmogamous specimen was made at the time of collection, and seeds were harvested in the greenhouse from a sibling plant cultivated in the greenhouse.

Specimens of putative hybrids and introgressants cited in Appendix C. – For some taxa, citations of specimens whose seeds were examined under SEM and were determined as putative hybrids or putative introgressants, follow the citations of the representative specimens of the orthospecies. These putative hybrids or introgressants were initially grouped with the respective orthospecies (see the procedure for discerning the orthospecies outlined in Chapter 4, Section 4.3). Specimens whose putative association with orthospecies could not be determined, and are cited in the text, are listed at the end of Appendix C.

9.4 Appendix C

Representative Specimens of *Viola* Subsection *Boreali-Americanae*

Viola affinis LeConte

CANADA. ONTARIO, Essex County: Mersea Township, Point Pelee National Park, 26 July 1977, *A. A. Reznicek, P. F. Maycock, & D. R. Gregory s.n.* (MICH) CL, C, IMS. **U.S.A.** – PENNSYLVANIA. Philadelphia: near Tacony Creek, 3 June 1899, *C. L. Pollard 6* (MICH) C. Chester County: woods adjacent to the intersection of PA Route 82 and German Hollow Road, 11 May 1990: CHP, 20 May 1991: CLP, *N. L. Gil-ad 271* (MICH) CH/CL, C, S. – VERMONT. Grand Isle County: North Hero, borders of Lake Champlain, 20 May 1904, *E. Brainerd 1* (US) CH; *E. Brainerd 2* (US) C, S.

Additional specimens examined (putative hybrids): NEW JERSEY. Monmouth County: Allaire State Park, 0.3 miles NW of the park's main office on NJ Road 524A, 12 May 1990, *N. L. Gil-ad 274* (MICH) CL, C, S. Burlington County: Mount Laurel Township, 0.3 mile S of the intersection of Walton Avenue and Union Mill Road, 29 April 1991: CHP, 20 May 1991: CUL, *N. L. Gil-ad 461* (MICH) CH, C/ CL, C, S. – PENNSYLVANIA. Berks County: Union Township, 0.1 mile E of 464 Park Road, 11 May 1990, 23 May 1991: CUL, *N. L. Gil-ad 270* (MICH) CL, C, S.

Viola brittoniana Pollard f. *brittoniana*

U.S.A. CONNECTICUT. Fairfiled County: Stratford, 31 May & 25 June 1901, *E. H. Eames 135/135a* (MICH) CH, CL, C, S. DELWARE. Kent County: Bombay Hook, 10 June 1880, *A. Commons s.n.* (NY) CL. – MARYLAND. Prince Georges County: Hyattsville, 25 June 1899, *W. R. Maxon & C. L. Pollard 3* (MICH) CL, C. – MASSACHUSETTS. Middlesex County: Town of Bedford, Great Meadows National Wildlife Refuge, 2.3 miles SW of the intersection of Routes 225 and 62, W of the west end of Bonnievale Drive, 17 June 1990, CUL–14 May 1991: CHP, 11 Aug. 1991: CL, *N. L. Gil-ad 323* (MICH) CH/ CL, S; Town of Carlisle, Greenough Conservation Land W of Concord River off 528 Maple Street, 17 June 1990, CUL–14 May 1991: CHP, *N. L. Gil-ad 324* (MICH) CH/ S. Norfolk County: Dedham, meadow along the Charles River, 22 May 1910 & 23 Aug. 1910, *Ex Horto Brainerd 17* (US, VT) CH, CL, C, S. – NEW JERSEY. Burlington County: 2.6 miles SW of the intersection of County Roads 616 and 630, 25 meters S of County Road 663, 30 April 1991 *N. L. Gil-ad 463* (MICH) CH, CL, S. Mercer County: Princeton Junction, 28 May 1907, *E. B. Bartram 5515* (MICH) CH. Ocean County: 0.85 mile E of the intersection of NJ Route 9 and Game Farm Road in Forked River, 28 April 1991: CHP, 9 Aug. 1991: CLP, *N. L. Gil-ad 460* (MICH) CH/CL, S. – NEW YORK. Staten Island, 8 June 1888, *N. L. Britton s.n.* (lectotype: NY!) CH, C; May 1893, *N. L. Britton s.n.* (NY) CH. – NORTH CAROLINA. Bertie County: one mile SE of the intersection of NC Route 42E/11 Bypass and NC Route 305 in Aulander, 22 April 1991: CHP, 9 Aug. 1991: CUL, *N. L. Gil-ad 452* (MICH) CH/ CL, C, S. Currituck County: 2.3 miles N of Grandy on U.S. Highway 158, 8 May 1958, *H. E. Ahles 40163* (MICH) CH, C. Gates County: 2.6 miles NE of the intersection of U.S. Route 13 and U.S. Route 158 NE of Winton, 22 April 1991: CHP, 9 July 1991 and 11 June 1992: S, *N. L. Gil-ad 454* (MICH) CH, C, S. – SOUTH CAROLINA. Horry County: 2 miles SE of Conway by U.S. Highway 701, *W. W. Thomas 741* (MICH) CH, C.

Additional specimen examined (putative hybrid): NEW JERSEY. Atlantic County: 0.3 mile N of the intersection of NJ Route 49 and Hunters Mill Road, 28 April 1991, *N. L. Gil-ad 459* (MICH) CH, CUL: S.

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

U.S.A. CONNECTICUT. Fairfield County: Stratford, 30 June 1905, *E. H. Eames 5257* (MICH) CL, C. – MASSACHUSETTS. Norfolk County: Dedham, Charles River meadow, 25 July 1904, *F. F. Forbes s.n.* (MICH) C, S. Suffolk and Norfolk Counties Line: Blue Hills Reservation (Neponset River Reservation), ca. 0.5 mile W of Blue Hill Road along the north edge of Burma Road, 14 June 1990: CHP, 14 May 1991/11 Aug. 1991: CUL, *N. L. Gil-ad 319* (MICH) CH/ CL, S. – NEW YORK. [Nassau County:] southwestern Long Island, Woodmere, 21 May 1904, *E. P. Bicknell s.n.* (holotype: NY!, isotype: GH) CH. – NORTH CAROLINA. Gates County: 2.6 miles NE of the intersection of U.S. Route 13 and U.S. Route 158 NE of Winton, 22 April 1991, *N. L. Gil-ad 453* (MICH) CH, CL, C, S.

Viola cucullata Aiton

U.S.A. MASSACHUSETTS. Bristol County: Caratunk Wildlife Refuge, 0.5 mile W of the intersection of Pine Street and Brown Avenue, 14 June 1990, *N. L. Gil-ad 321* (MICH) CH, CUL: S. – NEW JERSEY. Sussex County: High Point State Park, 0.3 miles NW of the intersection of NJ Route 23 and Kuser Road W of Kuser Road, 13 May 1990, *N. L. Gil-ad 276; 277* (MICH) CH, CL, C, S.

Additional specimens examined (putative hybrids): MAINE. Aroostook County: 5.1 miles W of the eastern townline of Allagash, on the southern flood shore of the Saint John River, 11 July 1993, *N. L. Gil-ad 485* (MICH) CL, S. Penobscot County: Eddington Township, 2.9 miles N of the intersection of ME Routes 178 and 9 in Eddington, 20 May 1990, *N. L.*

Gil-ad 298 (MICH) CH, CUL: S. – MICHIGAN. Hillsdale County: 0.4 mile S of the intersection of Mosherville Road and Concord Road E of the Kalamazoo River, T.5S., R.3W, Sec. 9, NE¼, 27 May 1989, *N. L. Gil-ad 223* (MICH) CUL: C, S. Delta County: Cornell. T.40N., R.23W., Sec. 6, N½, NE¼, on the SW bank of the Escanaba River, *N. L. Gil-ad 340* (MICH) CH, CUL: S. – NEW YORK. Onondaga-Cortland Counties Line: 0.3 miles SW of the intersection of Route 91 and Labrador Crossing Road, 23 May 1990, *N. L. Gil-ad 305* (MICH) CH, C, S; *N. L. Gil-ad 307* (MICH) C, S. Ulster County: Minnewaska State Park, 5.5 miles S of the intersection of NY Routes 209 and 299, 14 May 1990, *N. L. Gil-ad 282* (MICH) CH, CUL: S.

Viola egglestonii Brainerd

U.S.A. TENNESSEE. [Davidson County:] West Nashville, 26 May 1909, *W. W. Eggleston 4421* (isotype: VT!) CL, C; 10 May 1910, *Ex Horto Brainerd 43* (NY, US) CH; 14 July 1910, *Ex Horto Brainerd 44* (NY) C, S, (US) CL, C, S. Rutherford County: Ca. 0.2 miles NW of the intersection of Richland Road and Factory Road, 5 April 1994, *N. L. Gil-ad 494* (MICH) CH, C; LaVergne, 2.6 miles N of the intersection of Murfreesboro Road and Mason Road, ca. 0.1 miles S of Mason Road, E of Hurricane Creek, 5 April 1994, *N. L. Gil-ad 495* (MICH) CH; between Stones River Road and J. Percy Priest Lake, NW of Hollandale Road, 19 April 1992, *A. G. Moore s.n.* (MICH) CH, C, CUL: CL, C, S. Wilson County: 0.5 miles NW of the intersection of US Highway 231 and Fall Creek Road, E of Gwynn Road, 5 April 1994, *N. L. Gil-ad 493* (MICH) CH.

Viola fimbriatula Sm.

North America, dry hills from Canada to Virginia, 1817, *Francis Boott s.n.* (photo: MICH!) CH, C. **U.S.A.** NEW JERSEY. Sussex County: High Point State Park, 0.3 mile N of the intersection of NJ Road 23 and Kuser Road, 13 May 1990, *N. L. Gil-ad 279* (MICH) CH, C, S. – NEW YORK. Tioga County: at south limit of Cayuga Basin, NW of station at North Spencer, 10 May 1914, *L. H. MacDaniels & A. J. Eames 2853* (MICH) CH. – OHIO. Jefferson County: Springfield Township, Sec. 4, SW¼, 0.2 miles SE of OH Route 164, 6 May 1983, *A. W. Cusick 22403* (MICH) CH.

Additional specimens examined (putative hybrids): MAINE. Orono, gravel, 5 Sep. 1898, *Fernald s.n.* (VT) CL, C, S. – MASSACHUSETTS. Berkshire County: 3 miles W of the intersection of MA Route 2 and U.S. Route 7 in Williamstown, 18 June 1990, *N. L. Gil-ad 332* (MICH) CH, CUL: S. Hampden County: Mount Tom State Preservation, Kay-Bee Trail, 17 June 1990, *N. L. Gil-ad 327* (MICH) CUL: CL, C, S. Norfolk County: Dedham, 507 Bridge Street on Route 109, 22 May 1990, *N. L. Gil-ad 302* (MICH) CH, C, S. – MICHIGAN. St. Claire County: near Port Huron, 16 May 1909: CHP, 4 July 1909: CLP, *C. K. Dodge s.n.* (MICH) CH/CL, C, S. Wayne County: Sumpter Township, T.4S., R.8E, Sec. 31, N½, field SW of old borrow pits; nearly 0.5 mile SW of the intersection of Arkona Road and Sherwood road, 1 Sep. 1990, *W. W. Brodowicz 776* (MICH) C, S. – NEW JERSEY. Cumberland County: Bridgeton City Park, 0.8 miles N of the intersection of Commerce Street and Park Drive, 28 April 1991, *N. L. Gil-ad 458* (MICH) CH, CUL: S. Sussex County: High Point State Park, 1.5 miles NE of the intersection of NJ Road 23 and Kuser Road, 0.5 mile NE of the intersection of Kuser Road and Monument Drive, 13 May 1990, *N. L. Gil-ad 281* (MICH) CH, CUL: S. – NEW YORK. Long Island. Nassua County: Westbury, along the old deserted road between Roosevelt Airport and Stewart Avenue, 6 June 1950, *L. A. Charette 784* (VT) CL, C, S. – VERMONT. [Rutland County:] Brandon, 14 May 1922: CHP, 28 July 1923: CLP, *N. L. Dutton s.n.* (MICH) CH/C, S. – VIRGINIA. Wythe County: Jefferson National Forest, Stony Fork campground, south side of VA Highway 601, ca. 4 miles W of the intersection with I-75, ca. 7 miles N of Wytheville, 28 May 1992, *A. A. Reznicek s.n.* (MICH) CUL: C, S.

Viola missouriensis Greene

U.S.A. ILLINOIS. Champaign County: Urbana Township, 3 May 1914, *Crane 1471* (VT) CH, C, S; Champaign Township, 9 June 1914, *Crane 1627* (VT) CL, C, S. – MISSOURI. Clay County: Randolph, 23 April 1899, *K. Mackenzie 10* (NDG) CH; Randolph, 23 April 1899, *K. Mackenzie 11* (NDG) CH. [Jackson County:] Leeds, 19 April 1895, *B. F. Bush 231* (NDG) CH. Jackson County: Courtney, 10 May 1898, *B. F. Bush 108* (NDG) CH; Courtney, 10 May 1898, *B. F. Bush 95* (NDG; 2 sheets) C; Courtney, 30 April 1899, *B. F. Bush 70* (NDG) CH, (NY; 2 sheets); CH; Courtney, 30 April 1899, *B. F. Bush 88* (NDG) CH, (NY) CH. [Jackson County:] Independence, 24 April 1898, *K. Mackenzie 8* (NDG) CH. – TEXAS. Travis County: 0.9 miles SE of US Route 183, S of Burleson Road: at the west end of Precint 4 County Park Parking, Lat. 30°10'28", Long. 97°40'31", 22 March 1991: CHP, 16 May 1991: CLP, *N. L. Gil-ad 390* (MICH) CH/CL, C, S; E of a clearing with navigation posts, Lat. 30°10'30", Long. 97°40'40", 16 May 1991: CHP, 16 May 1991: S, *N. L. Gil-ad 391* (MICH) CH, C, S.

Additional specimens examined (putative hybrids): NORTH CAROLINA. Nash County: 2.5 miles S of the intersection of U.S. Route 64 Alt. and NC Route 5815 in Spring Hope, 22 April 1991, *N. L. Gil-ad 449, 451* (MICH) CL, C, S.

Viola nephrophylla Greene

U.S.A. ARIZONA. Gila County: 20 miles NE of Payson, 9 April 1960, *Russell 11492* (MICH) CH. – CALIFORNIA. Modoc County: Modoc National Forest, T.44N., R.14E., Sec 14, 1.5 miles NW of the intersection of Forest Road 30 and Plum Valley Road, 6 June 1990: CHP, 28 July 1991: CLP, *N. L. Gil-ad 317* (MICH, UC) CH/CL, C, S. Mono County: White Mountains, T.2/3S., R.33E., Sec. 32/5, along Pellisier Creek 3.1 miles S80°W of Mount Hogue Summit, 22 Aug. 1986, *J. D. Morefield 4355* (MICH) C, S (RSA) C, IMM. – COLORADO. the valley of the Cimarron River, 29 Aug. 1896, *E. L.*

Greene s.n. (holotype: NDG!) CH, C, S, (isotype: NDG!) C. Leyden, 1 Aug. 1911: CLP, 19 May 1912: CHP, *Cross 152* (VT) CL, C, S/CH. – NEW MEXICO. Las Vegas, Gallinas Canyon, 16 May 1934, *Studhalter & Marr 1661* (MICH) CH, C. – SOUTH DAKOTA. Lawrence County: 4 miles down Box Elder Creek from Nemo, Greek Bank, 12 June 1940, *P. Johnson 162* (MICH) CH. – UTAH. Washington County: T.39S., R.13W., E slope of Pine Valley Mountains, between Browse guard station and Syler Spring, 16 May 1984, *Atwood 9653* (BRY) CH; T.39S., R.14W., Sec. 19, Pine Valley Reservoir, 16 June 1986, *Warrick 1972* (BRY) CH, C.

Additional specimens examined (putative hybrids): CANADA. QUEBEC: Grand Cascapedia River, gravel bars and beaches, 15 July 1905, *Collins & Fernald 108* (VT) CL, C, S. **U.S.A.** MAINE. Aroostook County: 21.3 miles E of the intersection of ME Route 11 and County Road 161W in Fort Kent, 5-15 meters S of the St. John River, 11 July 1993, *N. L. Gilad 488* (MICH) CL, C, S/CUL: CH. – VERMONT. Grand Isle County: Providence Island, transplanted July 1905, 31 May 1910, *Ex Horto E. Brainerd 83* (US) CH; rocky shores of Lake Champlain, 4 & 22 July 1905, *E. Brainerd 84* (US) CL, C.

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

CANADA. ONTARIO. Thunder Bay District: Paipoonge Twp., SW of Fort William, 12 June 1966, *Allin s.n.* (MICH) CH; **U.S.A.** MAINE. Aroostook County: Saint Francis, Valley of the St. John River, 18 June 1898, *M. L. Fernald 2244* (US) CH; Fort Kent, Valley of the Saint John River, 15 June 1898, *M. L. Fernald 2245* (holotype: US!) CH buds; gravelly beach 1 mile below Fort Kent, 25 Aug. 1905, *M. L. Fernald s.n.* (VT) C, S; 21.3 miles W of the intersection of ME Route 11 and County Road 161W in Fort Kent, the southern floodshore S the Saint John River, 11 July 1993, *N. L. Gil-ad 487* (MICH) CL, C. Penobscot County: Veazie, by the Penobscot River, 22 August 1908, *M. L. Fernald 243* (MICH, US) CL, C, S; Old Town, on a rocky island on the Penobscot River NE of the intersection of North Main Street and Stillwater Street, 12 July 1993, *A. A. Reznicek & N. L. Gil-ad 490* (MICH) C. – MICHIGAN. Schoolcraft County: T.42N., R.16W., Sec. 23, S¹/₂, NW¹/₄, NE¹/₄, 27 May 1971, *D. Henson 53* (MICH) CH. – MINNESOTA. Koochiching County: 9 miles NE of Big Falls, 20 May 1952, *J. W. Moore 21588* (US) CH.

Additional specimens examined (putative hybrids): CANADA. ONTARIO. Thunder Bay District: Devon Twp., 2 km. N of Fallingsnow Lake, 26 May 1980, *C. G. Garton 19377a* (MICH) CH; Right bank of Weikwabinonaw Road at crossing of Great Lakes Forest Products Access Road to Buda Lake, 27 May 1981, *C. G. Garton 19945* (MICH) CH.

Viola novae-angliae subsp. *grisea* (Fernald) Gil-ad

U.S.A. MICHIGAN. Crawford County: T.27N., R.4W., Sec. 32, NE¹/₄ & SW¹/₄ of SE¹/₄, W of Howes Lake, 21 May 1992, *E. M. Chittenden 421* (MSC); 23 May 1993, *N. L. Gil-ad 470* (MICH) CH, CUL: S. Schoolcraft County: dry sandy plain near Driggs, 2 July 1934, *M. L. Fernald & H. S. Pease 3430* (holotype: GH!; Isotype: MICH!) C, S; Seney National Wildlife Refuge, T.45N., R.16W., Sec. 14, SW¹/₄, ca. 4 miles S of Creighton, 10 June 1986, *D. Henson 2024* (MICH) CH; 22 June 1987, *A. A. Reznicek 7940*; 16 Aug. 1987, *D. Henson 2387A* (MICH) CL, C; 13 June 1990, *N. L. Gil-ad 334* (MICH) CH, C, S.

Viola nuevo-leonensis W. Becker

MÉXICO. COAHUILA : Ca. 35 (air) km W of Cuatro Cienegas, in Canyon de la Madera, 5 August 1973, *Henrickson 11962* (TEX) C, IMS; Cañon Desiderio ca. 9.4 miles by road W from Rancho Cerro de la Madera, 27°07'35"N, 102°31'37"W, *Wendt & Lott 1809* (LL) CH, C, IMS. NUEVO LEÓN. Chipinque, near branch of roads 25°55'N, 100°23'W, 7 April 1960, *Ford Smith M69* (TEX) CH, C; Municipo de San Pedro Garza García: Parque Chipinque, 9.9 km SE of the intersection of Av. Gómez Morin and Alfonso Reyes, 19 March 1990, *N. L. Gil-ad 384* (MICH) CUL: CL, C, S; 20 March 1990: CHP, 16 May 1991: CUL, *N. L. Gil-ad 389* (MICH) CH, C/ CL, C, S; Mountains near Monterrey above La Mina, 6000 feet, July 1933, *Mueller & Mueller 67* (F) CL, C; Sierra Madre Mountains, Monterrey, 23 July 1933, *Mueller & Mueller 67* (GH) C, IMS; Sierra Madre supra Monterrey, 10 March 1906, *Pringle 10235* (holotype: HBG!, isotypes: BM!, CAS!, F!, GH!, MEXU!, MO!, NY!, US!) CH, C, (isotype: MICH!) CH.

Viola pedatifida G. Don

U.S.A. IOWA. Mills County: one mile N of Hastings at Wearin Prairie, West Nishnabotna River floodplain, 3 May 1992, *B. L. Wilson s.n.* (MICH) CH, CUL: S. Page County: Palmquist Prairie, one mile W and 0.25 mile N of Bethesda, 12 May 1992, *B. L. Wilson s.n.* (MICH) CH, CUL: S. Poweshiek County: SE of Grinnell, near Jasper County line, N of Scoutland, 13 May 1952, *Russell NR513521* (MICH) CH, C. – MICHIGAN. Kalamazoo County: T.4S., R.11W., Sec. 30, ca. 250 meters SE of the intersection of Highway 131 and XY Avenue West, June 1980, *H. E. Ballard, Jr. s.n.* (MICH) CH; 28 June 1990, *N. L. Gil-ad 333* (MICH) S. Delta County: T.39N., R.16W., Sec. 26, N¹/₄, NE¹/₄, 13 miles SW of the intersection of M183 and Route 2, W of M183, 3 July 1990, *N. L. Gil-ad 337* (MICH) C, S. Schoolcraft Township, 8 June 1935, *C. R. Hanes s.n.* (MICH) CH, CL, C. Washtenaw County: Lima Township, Sec. 26, SW¹/₄, near Mill Creek, 13 May 1973, *C. B. Nimke s.n.* (MICH) CH. – MINNESOTA. Ottertail County: Perham, 24 May 1910, *Z. L. Chandonnet s.n.* (MICH) CH. – WISCONSIN. Waukesha County: Delafield, north end of "Government Hill", 13 May 1906, *Ogden 85* (VT) CH, C.

Additional specimens examined (putative hybrids): MICHIGAN. Delta County: T.39N., R.19W., Sec. 26, W¹/₂, NE¹/₄, NW¹/₄, at the top of a limestone bluff, 9 June 1971, *D. Henson 114* (MICH) CH; T.39N., R.16W., Sec. 26, NE¹/₄, NW¹/₄,

ca. 0.4 mile W of the intersection of route 1122 and M183, 3 July 1990, *N. L. Gil-ad 338* (MICH) CH, CUL: S. Iowa. Page County: one mile N of Hastings at Plamquist Prairie, one mile west and 0.25 mile N of Bethesda, CUL: 3 May 1992; Field: 12 May 1992, *B. L. Wilson s.n.* (MICH) CH, C, S/ CH, S.

Viola sagittata Aiton

U.S.A. Iowa. Johnson County: T.80N., R.8W., Sec. 5, S of Williams Cemetery, 17 May 1992: CUL, *B. L. Wilson s.n.* (MICH) CL, C, S. – Michigan. Hillsdale County: Litchfield Township, T.5S., R.4W., Sec. 23, NE¹/₄, 4.2 miles N of the intersection of MI Highway 12 and Cronk Road, 27 May 1989, *N. L. Gil-ad 222* (MICH) CH, CUL: S. Lenawee County: Deerfield Township, T.7S., R.5E., Sec 24, SW¹/₄, of SE¹/₄, N of Carroll, W of County Line Highway, 6 May 1987, *R. W. Smith 2096* (MICH) CH. – Wisconsin. Marquette County: Vicinity of Silver Lake, 29 Aug. 1990, *A. A. Reznicek s.n.* (MICH) CH, CUL: S.

Additional specimens examined (putative hybrids): Illinois. Kankakee County: Wichert, along the C&EI Railroad, 5 June 1908, *F. C. Gates 2431* (MICH) CH, CL, C, S. – Kentucky. Boyle County: 2 miles W of Junction City, 3 July 1937, *M. E. Wharton 661* (MICH) C, S. Michigan. [Cass or Van Buren County:] Magician Lake, 13 Aug.1915, *L. M. Umbach s.n.* (MICH) CL, C, S. Washtenaw County: Lyndon Township, T.1S., R.3E., Sec. 27, ca. 180 meters N of Long Lake, 6 May 1990, *N. L. Gil-ad 251* (MICH) CH, CUL: S. – Missouri. Barton County: Prairie State Park, 2.1 miles S of the intersection of the park's main road and County Road P, T.32N., R.33W., Sec. 20, NE¹/₄, NE¹/₄, 10 April 1991, *N. L. Gil-ad 421* (MICH) CH, CUL: S. – North Carolina. Avery County: 2.7 miles S of the intersection of U.S. Road 19E and NC Road 194 in Ingalls, 18 April 1991, *N. L. Gil-ad 441* (MICH) CH, CUL: S. – Wisconsin. Waukeska County: Nashotah, near Fair Oaks Pine Lake: 18 May 1906, *Ogden 31* (MICH) CH; 18 May 1906: CHP, 29 July 1906: CLP, *Ogden 38* (VT) CH/CL, C, S. – Texas. Newton County: 30.7 miles N of the intersection of I-10 and TX Route 87, 17 March 1991: CHP, 16 May 1991: CUL, *N. L. Gil-ad 381* (MICH) CH/CL, C, S.

Viola septemloba LeConte

U.S.A. Florida. Marion County: Ocala National Forest, SE corner of the intersection of Road 88 and Highway 314, 1 April 1984, *Brunton & McIntosh 4889* (MICH) CH, C, IMM. Washington County: Falling Waters State Recreation Area, 2.4 miles SE of the intersection of I-10 and FL Route 77, ca. 43 meters N of the Picnic Area Parking Lot, 11 March 1991: CHP, 16 May 1991: CUL, *N. L. Gil-ad 366* (MICH) CH, C/ CL, C, S; Ca. 280 meters SW of the Picnic area Parking Lot, 11 March 1991: CHP, 14 May 1991: CUL, *N. L. Gil-ad 368* (MICH) CH, C/CL, C, S.

Additional specimens examined (putative hybrids): Florida. Franklin County: Apalachicola National Forest, 0.6 miles from FL Route 65, T.5S., R.7W., Sec. 31, SW¹/₄, SW¹/₄, 5 March 1991: CHP, 9 May 1991: CUL, *N. L. Gil-ad 348* (MICH) CH, C/ CL, C, S. Liberty County: T.3S., R. 8W., Sec. 2, SW¹/₄, SW¹/₄, ca. 7 meters N of FL Road 379, 11 Aug. 1991: CUL, *N. L. Gil-ad 346* (MICH) CL, C, S. [Volusia County]: between DeLand and Deep Creek, 28 March 1909, *E. Brainerd s.n.* (VT) CH, S; Between DeLand and DeLeon Springs, 30 March 1909, *E. Brainerd s.n.* (VT) CH, C, one S. – Mississippi. Jackson County: Shepard State Park, 10.6 miles S of U.S. Route 90, 13 March 1991: CHP, 16 May 1991: CUL, *N. L. Gil-ad 372* (MICH) CH, C/CL, C, S.

Viola septentrionalis Greene

CANADA. Ontario. Algoma District, east side of Highway 17 at Blacktrout L., 4 miles N of the intersection of Highways 17 and 101, *C. G. Garton 14294* (MICH) CL, C. **U.S.A.** Maine. [Locality not listed,] woods, Sep. 1907, *Ex Horto E: Brainerd* (V. 200) (VT) C, S. Hancock County: Birch Island, 27 June 1971, *McVaugh 25689* (MICH) CH. Penobscot County: 2.9 miles N of the intersection of ME Routes 178 and 9 in Eddington, 20 May 1990, *N. L. Gil-ad 299* (MICH) S. Waldo County: Moose Point State Park, 3.8 miles E of the intersection of U.S. Route 1 and County Road 141, 20 May 1990, *N. L. Gil-ad 301* (MICH) CH; 12 July 1993, *N. L. Gil-ad 492* (MICH) CL, C, S. – New Hampshire. Grafton County: White Mountain National Forest, ca. 4 miles E of the intersection of Trudeau Road and Main Street in Bethlehem, 18 May 1990, *N. L. Gil-ad 295* (MICH) CH, CUL: S.

Additional specimens examined (putative hybrids): Maine. Penobscot County: Milford, 9 miles NE of the intersection of Routes 9 and 178 on the east bank of the Penobscot River, 20 May 1990, *N. L. Gil-ad 300* (MICH) CH, CUL: S. – Massachusetts. Worcester County: Wachusett Mountain State Reservation, ca. 3 meters N of the intersection of Bicentennial and Loop Trail, 16 June 1990, *N. L. Gil-ad 326* (MICH) C, CUL: S. – New Hampshire. Carrol County: 17 miles SE of the intersection of U.S. Highway 302 and NH Route 16, 18 May 1990, *N. L. Gil-ad 296* (MICH) CH, CUL: S.

Viola sororia Willd.

U.S.A. Kentucky. Nelson County: 2 miles N of Trappist Monastery, 13 & 31 May 1941, *M. E. Wharton 6003* (MICH) CH, C. – Maryland. Montgomery County: ca. 3 meters E of Lock 20 of the Chesapeake and Ohio Canal, *N. L. Gil-ad 226* (MICH) C, S. – Massachusetts. Berkshire County: ca. 0.2 miles S of Great Barrington town boundary, NW of Route 7, 22 May 1990, *N. L. Gil-ad 303* (MICH) S. – Ohio. Seneca County: T2, R15, Sec. 6, NE¹/₄, 3.5 miles N of Heidelberg College, 12 May 1963, *R. K. Scaife s.n.* (MICH) CH. – Vermont. Addison County: Middlebury, 12 June 1902, *E. Brainerd 51b* (MICH) CL.

Additional specimens examined (putative hybrids): ILLINOIS. [Kendall County:] Yorkville, collected by Miss Pollard, transplanted May 1909, 31 Aug. 1910, *Ex Horto E. Brainerd 160* (US) C, S. – KENTUCKY. Bullitt County: 3.4 miles W of the intersection of US Route 31E and KY Route 480, 2 April 1991, *N. L. Gil-ad 402* (MICH) CH, CUL: S. – MICHIGAN. Washtenaw County: Lima Township, T.2S., R.4E., Sec. 26, SW¹/₄, NW¹/₄, woods at the back of 989 Dancer Road, 2 May 1990, *N. L. Gil-ad 246*; along the southern bank of Mill Creek, 7 May 1990, *N. L. Gil-ad 260* (MICH) CH, CUL: S. – NEW YORK. Onondage-Cortland county line, 2.4 miles SE of the intersection of routes 81 and 80, in woods NW of Labrador Hollow Wetland Boardwalk, 23 May 1990, *N. L. Gil-ad 306* (MICH) CH, CUL: S. – PENNSYLVANIA. Bradford County: Smithfield Township, 2.2 miles S of the intersection of Springfield Road and Benwick Turnpike, 10 May 1990, *N. L. Gil-ad 268* (MICH) CH, CUL: S. Chester County: Kennett Square, N of a driveway leading to 540 N. Walnut Road, 11 May 1990, *N. L. Gil-ad 273* (MICH) CH, CUL: S. – TEXAS. Travis County: City of Austin, ca. 0.1 mile E of Route 360, south side of Barton Creek, 22 March 1991, *N. L. Gil-ad 392* (MICH) CH, CUL: S. – VERMONT. Addison County: 4.4 miles E of the intersection of VT Routes 22A and 73 in Orwell, 15 May 1990, *N. L. Gil-ad 284* (MICH) CH, CUL: S. Lamoille County: 6 miles S of the intersection of Lower Valley Road and Main Street in Cambridge, 17 May 1990, *N. L. Gil-ad 293* (MICH) CH, C, S.

Viola triloba Schwein.

U.S.A. MICHIGAN. Washtenaw County: Ann Arbor Township, T.2S., R.6 E., Sec. 12, E¹/₂, 0.7 mile NW of the intersection of Dixboro Road and Ford Road, 29 May 1990, *N. L. Gil-ad 310* (MICH) CH, CUL: S. – NORTH CAROLINA. Salem, [date of collection missing], *L. D. de Schweinitz s.n.* (holotype: PH!) CH, C (immature).

Additional specimens examined (putative hybrids): FLORIDA. Gasdsden County: Town of Chattahoochee, Chattahoochee Nature Park, 5 March 1991: CHP, 14 May 1991: CUL, *N. L. Gil-ad 355* (MICH) CH/ CL, C, S. – INDIANA. Crawford County: 2 miles E of Marengo, in beech woods, *C. C. Deam 23479* (VT) CL, C, S. – MICHIGAN. Hillsdale County: Jefferson Township, Lost Nation State Game Area, T.7S., R.2W., Sec. 25, SE¹/₄, NE¹/₄, NW of the intersection of Pittsford Road and Skuse Road, 6 July 1990, *N. L. Gil-ad 344* (MICH) CH, CUL: S. Washtenaw County: Ann Arbor Township, T.2S., R.6E., Sec. 1, SW¹/₄, NE¹/₄, ca. 0.5 mile E of 4984 Earhart Road, 8 May 1990, *N. L. Gil-ad 262* (MICH) CUL: S; *Gil-ad 264* (MICH) CH. – TENNESSEE. Wilson County: 3.2 miles E of the intersection of U.S. Highway 231 and Cedar Forest Road, 18 April 1991: CHP, *N. L. Gil-ad 439* (MICH) CH, C/ S. – VERMONT. Addison County: Orwell, wooded ledge of limestone, 30 July 1905, *E. Brainerd 167* (US) CL, C, S. – VIRGINIA. Alexandria County: Lima Park, 5 Sep. 1908, *P. Dowell 5535* (VT) C, IMS.

Viola villosa Walter

U.S.A. FLORIDA. Gadsden County: Town of Chattahoochee, Chattahoochee Nature Park, 5 March 1991: CHP, 16 May 1991: CLP, *N. L. Gil-ad 353* (MICH) CH/CL C, S. Liberty County: Torreya State Park, end loop of FL Route 271 S of Gregory House, 8 March 1991: CHP, 8/16 May 1991: CUL, *N. L. Gil-ad 362* (MICH) CH/ CL, C, S. – NORTH CAROLINA. Onslow County: 40 miles S of New Bern, 25 April 1913, *House 5093* (VT) CL, C, S. – TEXAS. Traves County: Bastrop State Park, 3 miles NE of the intersection of TX Highway 71 and Loop 150S of Park Road 1A, 24 March 1991: CHP, 20 May 1991: CLP, *N. L. Gil-ad 395* (MICH) C/ CL, C, S. – VIRGINIA. Norfolk County: Gilmerton, 19 April 1913, *House 5079* (VT) CL, C, S.

Additional Specimens Examined and Cited in the Text: Putative Hybrids

MÉXICO. HIDALGO: Baranca below Trinidad Iron Works, 5500 feet, 2 June 1904, *C. G. Pringle 8864* (GH) C, S (1); (MEXU) C, IMS (1); (MO) C, IMS (1); (US) C, IMS;. TAMAULIPAS. Municipio Gómez Farías, vicinity of Rancho del Cielo Biological Station, ca. 7 km WNW of Gómez Farías along logging road from Indian Springs to Aqua Linda turnoff, 1400 m., 1 June 1989, *A. A. Reznicek 8459* (MICH) CL, C, IMM. **U.S.A.** FLORIDA. Gadsden County: Town of Chattahoochee, Chattahoochee Nature Park, 5 March 1991, *N. L. Gil-ad 354* (MICH) CH, S. Kentucky. Nelson County: 1.2 miles SE of the intersection of U.S. Route 31E and KY Route 46E, 2 April 1991: CHP, 16 May 1991: CLP, *N. L. Gil-ad 405* (MICH) CH/ C, CL, S. VIRGINIA. Lee County: 0.25 SE of a bridge connecting U.S. Route 58 and VA Road 664, 27 March 1991, *N. L. Gil-ad 401* (MICH) CH, S.

9.5 Appendix D

Representative Specimens of Names in *Viola* Subsection *Boreali-Americanae* Commonly Recognized as Orthospecies, but Hypothesized to Represent Hybrids or Introgressants in This Treatment

Viola chalcosperma Brainerd

FLORIDA. Jacksonville, March 1907, *E. K. Comstock s.n.*, 15 Oct. 1909: CUL, *E. Brainerd s.n.* (VT) C, S; Jacksonville, off Lackawana Avenue, 22 March 1914, *E. Brainerd s.n.* (VT) CH, C.

Viola esculenta Elliott ex Greene

FLORIDA. Jacksonville, transplanted April 1909, 30 Aug. 1910: CUL, *Ex Horto E. Brainerd s.n.* (VT) C, S; Jacksonville, along bayou in shade near Lincoln Park, 21 March 1909, *E. Brainerd s.n.* (VT) CH, C, S; Jacksonville, Highway Avenue, Bridge, 10 Sep. 1909, *Ex Horto* [from seeds] *E. Brainerd s.n.* (VT) CL, C, S. Jefferson County: T.4S., R.3E., Sec. 11, NE¼, 1.6 mile N of the Jefferson-Taylor county line, N side shoulder of U.S. Route 98, 7 March 1991: CHP, 14/16 May 1991: CLP, *N. L. Gil-ad 357A & B* (MICH) CH/CL, C, S.

Viola floridana Brainerd

FLORIDA. Jacksonville: in moist woodland, 13 & 22 March 1907, *E. Brainerd 60* (US) CH; transplanted March 1909, 7 Sep. 1910, *E. Brainerd 61* (US) CL, C, S. Daytona (?): 16 Feb. 1911, *N. F. Flynn 318* (VT) CH, C; 17 Feb. 1911, *N. F. Flynn. s.n.* (VT) CH.

Viola hirsutula Brainerd

MISSOURI. St. Clair County: Taberville Prairie, 1.8 miles S of the intersection of county roads B and H; ca. 141 meters east of County Road H, 9 April 1991, *N. L. Gil-ad 420* (MICH) CH, CUL: S. – TENNESSEE. Sevier County: 2.5 miles SE of the intersection of U.S. Route 441 and Little River Road, 27 March 1991, *N. L. Gil-ad 398* (MICH) CH/CUL: S. – VIRGINIA. Wythe County: Jefferson National Forest, Stony Fork campground, south side of VA Highway 601, 4 miles W of the intersection with I-75, ca. 7 miles N of Wytheville, 28 May 1992, *A. A. Reznicek s.n.* (MICH) CH/CUL: C, S.

Viola lovelliana Brainerd

LOUISIANA. Crowley: hillocks under young pines, 25 March 1910, *E. Brainerd 77* (US) CH, C; transplanted March 1908, 11 Sep. 1909, *Ex Horto E. Brainerd 78* (VT, US) CL, C, S; transplanted Feb. 1911, 28 Aug. 1911, *Ex Horto E. Brainerd s.n.* (VT) CL, C, S; St. Tammany Parish: Fountainebleau State Park, 0.7 miles S of the intersection of the access road to Group Camp III Lodge and U.S. 190, 13 March 1991: CHP, 16 May 1991: CLP, *N. L. Gil-ad 375* (MICH) CH/CUL: CL, C, S; Vermilion Parish: 5.4 miles N of the intersection of LA Route 13 and I-10, 17 March 1991, *N. L. Gil-ad 380* (MICH) CH, S.

Viola palmata L.

NEW JERSEY. Burlington County: Mount Laurel Township, 1.5 miles SW of the intersection of NJ Route 38 and Briggs Road, and 0.3 miles S of the intersection of Walton Avenue and Union Mill Road, 29 April 1991, *N. L. Gil-ad 462* (MICH) CH, CUL: S; Sussex County: High Point State Park, 1.4 miles NE of the intersection of NJ Route 23 and Kuser Road, 0.5 miles NE of the intersection of Scenic Drive and Monument Drive, 12 May 1990, *N. L. Gil-ad 280* (MICH) CH, CUL: S. – MICHIGAN. Washtenaw County: Lima Township, T.2S., R.4E., Sec. 26, SW¼, NW¼, S of Mill Creek, 7 May 1990, *N. L. Gil-ad 258* (MICH) CH, CUL: S.

Viola papilionacea Pursh

CONNECTICUT. Glastonbury, transplanted by C. H. Bissell, 18 May 1902, 20 Sep. 1903, *Ex Horto E. Brainerd s.n.* (VT) CH, C, IMS. – ILLINOIS. Yorkville, transplanted May 1909, 9 Sep. 1910, *Ex Horto E. Brainerd 107* (VT) CL, C, S. – INDIANA. Washington County: ca. 6 miles SW of Salem, wooded flood plain of Mill Creek, 6 June 1917, *C. C. Deam 23497* (VT) C, S. – MASSACHUSETTS. Brookline, dooryard, 25 Sep. 1905, *F. F. Forbes s.n.* (VT) CH, C, S; Brookine, corner of Freeman and Powell streets, collected by F. F. Forbes, May 1906, 31 Aug. 1906, *Ex Herb. E. Brainerd s.n* (VT) CL, C, S; Cambridge, transplanted from Mr. Brewster's garden, May 1909, 21 Sep. 1910, *Ex Horto E. Brainerd 108* (VT) CL, C, IMS. – VIRGINIA. Lee County: 0.25 mile SE of a stone bride connecting U.S. Route 58 and VA Route 664, NW of Jonesville, 27 March 1991, *N. L. Gil-ad 401* (MICH) CH, C, S.

Viola pratincola Greene

IOWA. Page County: Plamquist Prairie, one mile west and 0.25 mile N of Bethesda, 12 May 1992, *B. L. Wilson s.n.* (MICH) CH, CUL: S; Johnson County: Williams Prairie, S of Williams cemetery along a gravel road, T.80.N., R.8W., 17 May 1992, *B. L. Wilson s.n.* (MICH) CH. MINNESOTA. Near Windom, 1 July 1898, *E. L. Greene s.n.* (holotype: NDG!) CL, C, S. WISCONSIN. Prairie du Chien, 24 June 1898, *E. L. Greene s.n.* (NDG) C, S. Additional hybrid examined: IOWA. Page County: Palmquist Prairie, one mile west and 0.25 mile north of Bethesda, 12 May 1992, *B. L. Wilson s.n.* (MICH) S.

Viola stoneana House

DISTRICT OF COLUMBIA: Brookland, May 1907, Collector Holm, *Ex Horto E. Brainerd 163* (VT) CL, C, S. – NORTH CAROLINA. Nash County: 2.5 miles S of the intersection of U.S. Route 64 Alt. and NC Route 581S in Spring Hope, west bank of the Tar River, 22 April 1991, *N. L. Gil-ad 450* (MICH) CH, C/ CUL: CH, S.

Viola subsinuata Greene

TENNESSEE. Cocke County: within three miles of Wolf Creek Station, 11 Sep. 1897, *T. H. Kearney, Jr. 615* (holotype: NDG!) CH.

Viola triloba var. *dilatata* (Elliott) Brainerd

ARKANSAS. Hempstead County: Fulton, 14 April 1905, *B. F. Bush 2313* (VT) CL, C, IMS. – MISSOURI. Christian County: Chadwick, 31 miles N of the Missouri-Arkansas border, 14 May 1907, *B. F. Bush 4435* (VT) CH, C, IMS. Dallas County: 11.9 miles E of the intersection of Missouri Route 73 and Missouri Route 64, T,35N., R.18W., Sec. 26, N1/2, 10 April 1991, *N. L. Gil-ad 424* (MICH) CH, CL. C, S; 12 miles E of the intersection of Missouri Routes 73 and 64, S of Route 64, 10 April 1991, *N. L. Gil-ad 425* (MICH) CH, IMS. Iron County: 4.6 miles S of the intersection of Routes 21 and 72 in Arcadia, 7 April 1991, *N. L. Gil-ad 411* (MICH) CH, CL, C, S; Bufford Mountain, 0.6 miles NE of the intersection of County Road U and Buford Mountain gravel road, 7 April 1991, *N. L. Gil-ad 412* (MICH) CH, CL, C, IMS.

Viola viarum Pollard

IOWA. Montgomery County: T.12N., R.39W., Sec. 19, SW quarter, prairie between H34 and a railroad, 7 April 1992, *B. L. Wilson s.n.* (MICH) CUL: C, S. – MISSOURI. Eagle Rock, 10 June 1910, collector B.F. Bush, *Ex Horto E. Brainerd 176* (VT) C, S; Seedling from *Bush 3144*, 16 & 19 May 1911: CHP, 7 Oct. 1906: C, *Ex Horto E. Brainerd s.n.* (VT) CH, C, S; Pettis County: 2.7 miles W of the intersection of U.S. Route 50 and County Road T in Dresden, 8 April 1991, *N. L. Gil-ad 415* (MICH) CH, S.

Additional putative hybrids cited in the discussion on *Viola viarum*:

MISSOURI. Pettis County: 2.7 miles W of the intersection of U.S. Route 50 and County Route T in Dresden, 8 April 1991, *N. L. Gil-ad 416A-H & 417* (MICH) CH.

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*Synonyms and names that are no longer recognized are printed in *italics*.