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Autor: Gil-Ad, Nir L.
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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 vestiture 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 apices 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. egglesonii*, *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. egglesonii*, *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 egglesonii* 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. egglesonii*, *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. egglesonii* 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 *Chamaemelum* 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).