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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 & RISER, 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 heterophyly, 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.