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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 *Chamaemelanium*, *Plagiostigma*, and *Viola* the chasmogamous flowers are followed by reduced, apetalous, 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, subsection *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 between 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 disagreements 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 (Cronquist *in* GLEASON & CRONQUIST, 1991) and twenty nine (BRAINERD, 1921) (cf. Appendix A).

The difficulties of delimiting the orthospecies have been attributed to several factors including: the similarities between the taxa in a relatively large number of floral and certain vegetative 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 genetic drift in isolated populations (BRAINERD, 1904b, 1910b; CLAUSEN, 1929, 1964; STEBBINS, 1950; RUSSELL, 1959; BRIZICKY, 1961; VALENTINE, 1962; RUSSELL & CROSSWHITE, 1963). The complexity 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 ecotypes, 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 investigations on hybrids in this critical group...indicate how some of the species might be differentiated 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; BRIZICKY, 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 thoroughness, 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.