A STUDY OF SOME INTERMOUNTAIN VIOLETS (VIOLA SECT. CHAMAEMELANIUM)

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As a result of a cooperative study between Drs. Milo S. Baker and Jens Clausen, a classification for North American violets of sect. *Chamaemelanium* subsects. *Purpureae, Nuttallianae,* and *Chrysanthae* was proposed in a series of papers (Baker 1935, 1947, 1948, 1949a, 1949b, 1953, 1957, 1960; Clausen 1951, 1964b). This classification, as well as certain other cytotaxonomic, ecological, and evolutionary aspects of these violets, was reviewed by Clausen (1964a). In the review, Clausen expressed the need for an extensive cytological investigation of these violets in order to provide a firmer basis for their classification. This paper includes reports of new chromosome counts and observations of natural hybridization and morphology of some *Chamaemelanium* violets from the Intermountain Region and brief discussion of the taxonomic and evolutionary implications of this information.

METHODS

Field studies were carried out during spring and early summer of 1966, 1967, and 1969. Young flower buds were fixed in Newcomer's solution and chromosome numbers were determined from pollen mother cells using a standard aceto-carmine squash technique. In some cases it was possible to make chromosome counts from mitotic divisions in anther wall cells. Counts were documented with camera lucida drawings from fresh smears. Some slides were made permanent using the carbon dioxide quick-freeze method (Bowen, 1956). Pollen fertility was determined by staining pollen with methylene blue in lactophenol. Voucher specimens for all plants cited in this paper are deposited at UTC.

Herbarium specimens of relevant taxa were studied from the following herbaria: COLO, DS, ISC, JEPS, MO, MONT, RM, UC, US, UT, and UTC.

RESULTS AND DISCUSSION

Subsect. *Purpurea*

Clausen (1964a) placed three species in subsect. *Purpurea*: *Viola purpurea* Kell., $n=6$, with ten, mostly Californian, subspecies; *V. quercetorum* Baker & Clausen, $n=12$; and *V. utahensis* Baker & Clausen, $n=12$. Three of these taxa occur in the Intermountain Region: *V. purpurea* subsp. *atriplicifolia* (Greene) Baker & Clausen, *V. purpurea* subsp. *venosa* (Wats.) Baker & Clausen, and *V. utahensis*.

On the basis of their descriptions and herbarium sheet annotations, Baker and Clausen characterized *Viola purpurea* as a taxon variable in the shape of leaves and in the type of leaf margin. For the Intermountain Region small, purple-leaved plants with margins ranging from serrate to crenate were included under *V. purpurea* subsp. *venosa,* and under *V. purpurea* subsp. *atriplicifolia* were included all those small, purple-leaved forms whose leaf margins were deeply crenate to sublobate. Plants with green or purple leaves and a more or less regularly serrate leaf margin were placed under *V. utahensis*. Treated in this manner, subsp. *venosa* is quite intermediate between the other two taxa making it difficult to separate subsp. *venosa* from subsp. *atriplicifolia* at one extreme, while smaller plants of *V. utahensis* are almost impossible to distinguish from subsp. *venosa* at the other extreme.

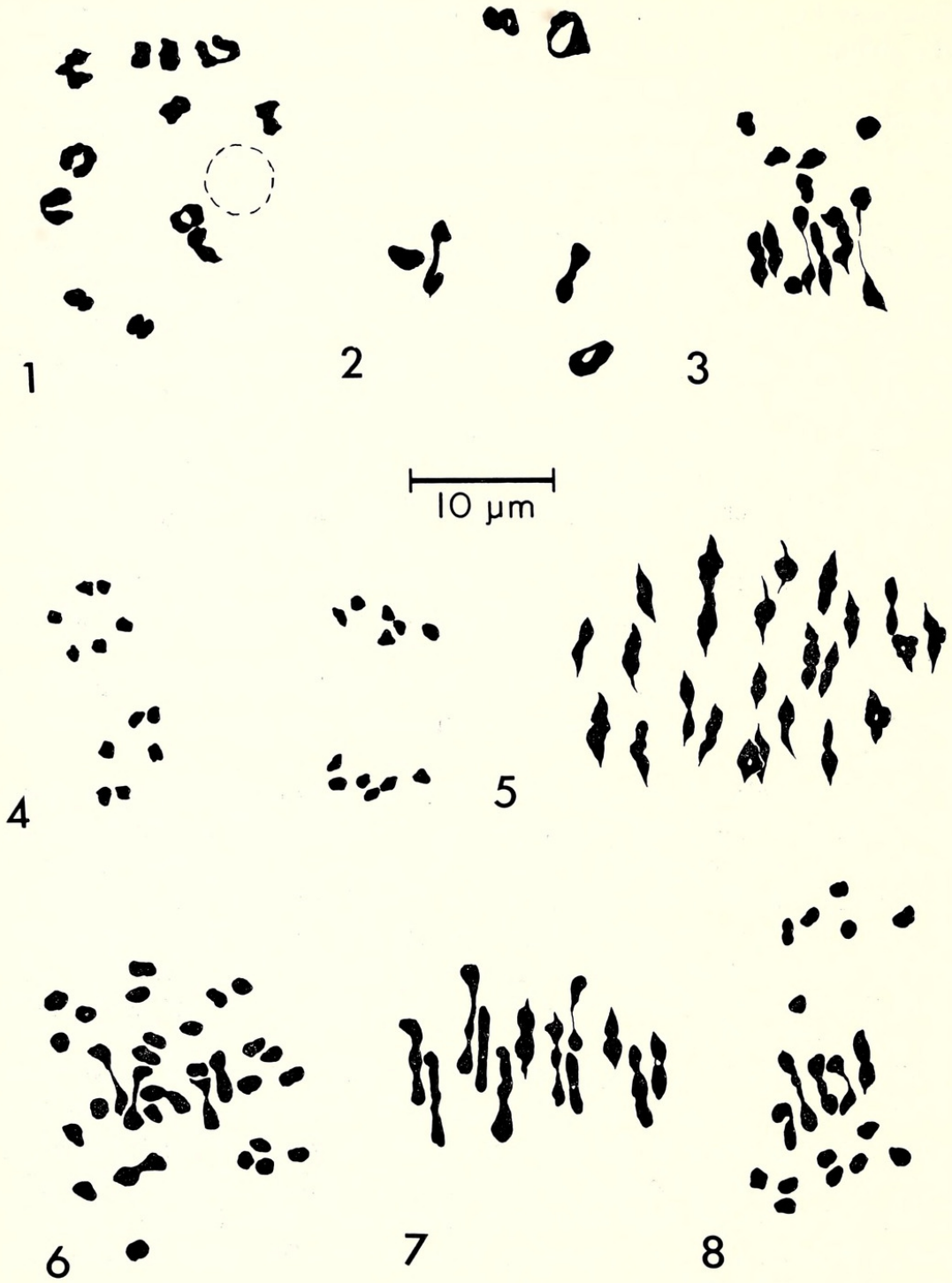
During chromosome number determinations it was discovered that plants with $n=12$ could be distinguished from those with $n=6$ on the basis of leaf margin. Tetraploid plants have serrate margins, whereas diploid plants have crenate margins. The tetraploid plants correspond to *V. utahensis* and the diploid plants correspond to *V. purpurea*. This correlation made it possible to distinguish between these two species with a high degree of confidence.

Meiosis in *Viola utahensis* was always regular with 12 bivalents at metaphase I (fig. 1), and pollen stainability was always well over 95 percent.

The size of plants of *Viola utahensis* is strongly correlated with elevation. Plants of low foothills and valleys are largest and mountain plants decrease in stature with increasing elevation. A distinctive series of green-leaved populations occurs in the Cache and Salt Lake Valleys of northern Utah, whereas mountain populations always have leaves with purple pigmentation. However, in several foothill areas extensive integradation occurs between these color forms, suggesting that they are of no taxonomic significance.

Viola utahensis is found primarily in open sagebrush areas from 1,200 to 2,150 m. In the southern part of its range in central Utah, it is often found growing under scrub oak, *Quercus gambelii* Nutt. Its range extends from Butte County, central Idaho, south to San Pete County, Utah, and from the East Humboldt Mountains, Elko County, Nevada, east to Lincoln County, Wyoming. This extends the range considerably from that delimited by Clausen (1964a).

As mentioned above, all small, crenate-leaved plants examined of *Viola purpurea* have $n=6$. Meiosis is regular and pollen stainability high (fig. 2). When all tetraploid, serrate-leaved plants are included under *V. utahensis,* there is no further basis for distinguishing subsp. *atriplicifolia* and *venosa,* so that subsp. *atriplicifolia* should be considered synonymous with subsp. *venosa*. Recognized in this sense, *V. purpurea* subsp. *venosa* occurs throughout the Intermountain Region, north into Washington, Idaho, Wyoming, and Montana, and south into



FIGS. 1–8. Camera lucida drawings of meiotic chromosomes of *Viola*. 1. *V. utahensis,* diakinesis, $n = 12$, *Davidse 1722A*. 2. *V. purpurea* subsp. *venosa,* late diakinesis, $n = 6$, *Davidse 1725*. 3. *V. purpurea* subsp. *venosa* × *V. utahensis,* metaphase I, $6_{II} + 6_{I}$, *Davidse 1722*. 4. *V. vallicola,* telophase II, $n = 6$, *Davidse 1720*. 5. *V. praemorsa* subsp. *major,* metaphase I, $n = 24$, *Davidse 1739*. 6. *V. praemorsa* subsp. *major* × *V. utahensis,* metaphase I, $6_{II} + 24_{I}$, *Davidse x-44C*. 7. *V. beckwithii,* metaphase I, $n = 12$, *Davidse x-5*. 8. *V. utahensis* × *V. beckwithii,* metaphase I, $5_{II} + 14_{I}$, *Davidse 1006*.

the higher mountains of Arizona. Altitudinally, it ranges from 1,800 to 3,050 m. It is associated with sagebrush or relatively open spaces in forested areas up to timberline.

Subsect. *Nuttallianae*

Clausen (1964a) recognized the following six species in subsect. *Nuttallianae*: *Viola vallicola* A. Nelson, $n=6$; *V. tomentosa* Baker & Clausen, $n=6$; *V. nuttallii* Pursh, $n=12$; *V. linguaefolia* Nutt., $n=18$; *V. bakeri* Greene, $n=24$; and *V. praemorsa* Dougl. ex Lindl. with three subspecies, $n=18$ and 24. This treatment is similar to that of Baker (1957), except that Baker considered *V. linguaefolia* to be a subspecies of *V. praemorsa* and he recognized one more subspecies of *V. praemorsa*. Three taxa, *V. vallicola, V. linguaefolia,* and *V. praemorsa* ssp. *major* (Hook.) Baker & Clausen occur within the Intermountain Region and were studied.

The chromosome number of *Viola vallicola,* $n=6$, was confirmed for a large number of populations (Table 1; fig. 4). This number had previously been based on a single determination. *Viola vallicola* has usually been considered to be closely related to the more eastern *V. nuttallii* and Russell (1965) considered the two species indistinguishable. However, from field observations and a comparison of a large number of herbarium specimens, it is clear that the diploid *V. vallicola* can be reliably separated from the tetraploid *V. nuttallii* on a morphological basis. *Viola vallicola* has cordate to truncate leaf bases, whereas *V. nuttallii* has cuneate leaf bases. *Viola vallicola* is very widely distributed from east of the Cascades and Sierra Nevada to the Great Plains just west of the Missouri River, and from the Canadian Plains south to Colorado. *Viola nuttallii* is found only east of the Continental Divide. It would be highly desirable to study the two species cytologically in their area of sympatry. Clausen (1964a) speculated that a diploid race of *V. nuttallii* may exist somewhere in this area, but there is no evidence for this.

Clausen (1964a) indicated that *Viola linguaefolia* was very similar morphologically to *V. praemorsa* subsp. *major* and he considered the difference in chromosome number to be the most reliable means of distinguishing the two taxa. *Viola linguaefolia* was reported to have $n=18$ on the basis of two counts, one from Latah County, Idaho, and another from Cache County, Utah (Baker, 1949b; Clausen, 1964a; Gershoy, 1934). Four counts of $n=24$ were reported for *V. praemorsa* subsp. *major* (Baker, 1949b; Clausen, 1964a). However, the hexaploid number for *V. linguaefolia,* $n=18$, could not be confirmed for plants from nine populations from Utah, Nevada, and Idaho, all within the range of *V. linguaefolia*. All plants had $n=24$ with regular meiosis and high pollen fertility (Table 1; fig. 5). For this reason and because no reliable morphological differences could be found, *V. linguaefolia* should be considered synonymous with *V. praemorsa* subsp. *major*.

TABLE 1. CHROMOSOME NUMBERS OF INTERMOUNTAIN VIOLA SPECIES. Collection numbers without name refer to Davidse collections.

V. beckwithii T. & G.; $2n = 12_{II}$.
IDAHO: Butte Co.: 2 mi NE of Butte Co. border along U.S. Hwys. 20 and 26, *1755*.
UTAH: Cache Co.: Millville, *1019;* 0.3 mi W of Wellsville, *x-4, x-5, 286*.

V. beckwithii × *V. utahensis;* $2n = 6_{II}+12_{I}$.
UTAH: Cache Co.: 0.3 mi W of Wellsville, *x-6, 1002, 1003, 1004, 1005, 1006*.

V. praemorsa Dougl. ex Lindl. subsp. *major* (Hook.) Baker & Clausen; $2n = 24_{II}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *1046*. Franklin Co.: 20.5 mi W of Ovid, *x-39, 1033*. Owyhee Co.: Silver City Range, *1746*.
NEVADA: Elko Co.: 10 mi NW of jct. Nev. Hwy. 51 and Nev. Hwy. 11, *1738, 1739;* Chicken Creek Summit between Jack Creek and Deep Creek, *1742;* Columbia Creek along road between Deep Creek and Mountain City, *1744*. Humboldt Co.: Lye Creek, Santa Rosa Range, *Gentry & Davidse 1640*.
UTAH: Cache Co.: mouth of Wellsville Canyon *x-22, x-24, 1015;* 20.5 mi up Logan Canyon, *1041*.

V. praemorsa subsp. *major* × *V. utahensis;* $2n = 6_{II} + 24_{I}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *x-44C*.

V. purpurea Kell. subsp. *venosa* (Wats.) Baker & Clausen; $2n = 6_{II}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *x-44B, x-45, 1047A*. Camas Co.: Silver City Range, *1748*.
NEVADA: Elko Co.: Chicken Creek Summit between Jack Creek and Deep Creek *1740, 1741;* Pequop Summit along U.S. Hwy. 40, Pequop Mts., *1731;* 9 mi S of Wells, *1735;* 10 mi NW of jct. Nev. Hwy. 51 and Nev. Hwy. 11, *1737*. Humboldt Co.: 14 mi N of Winnemucca, *Gentry & Davidse 1553*.
UTAH: Cache Co.: 31 mi NE of Logan, Logan Canyon, *1724, 1725*. Rich Co.: 4 mi W of Garden City, *382, 1721;* 2 mi W of Garden City, *1038*.

V. purpurea subsp. *venosa* × *V. utahensis;* $2n = 6_{II} + 6_{I}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *1047B*.
NEVADA: Elko Co.: 9 mi S of Wells, *1734*.
UTAH: Cache Co.: 31 mi NE of Logan, Logan Canyon, *1723A*. Rich Co.: 4 mi W of Garden City, *1722A*.

V. utahensis Baker & Clausen; $2n = 12_{II}$.
IDAHO: Bannock Co.: 5 mi E of Inkom, *1759*. Bear Lake Co.: 8 mi W of Ovid, *x-44D*. Butte Co.: Big Southern Butte, *1756*. Franklin Co.: 18.8 mi W of Ovid, *1035;* 20.5 mi W of Ovid, *x-43, 1034;* just N of Franklin Cemetery, *x-29, x-31, x-36, x-37*.
NEVADA: Elko Co.: 9 mi S of Wells, *1733*.
UTAH: Box Elder Co.: 0.5 mi E of Deweyville, *x-18, x-19, 992;* 1 mi SE of Honeyville, *x-21, 308, 994, 995, 996*. Cache Co.: 14 mi up Logan Canyon *302*; 20.5 mi up Logan Canyon, *1042*; 30 mi up Logan Canyon, *1723;* 0.5 mi W of Mendon, *x-13, x-17*; Richmond, *1030*; mouth of Wellsville Canyon, *1017*; 0.3 mi W of Wellsville, *x-1, x-2, 1051*; 1.5 mi NW of Wellsville, *x-7, x-8*. Rich Co.: 4 mi W of Garden City, *1722*; 1 mi W of Garden City, *1044*. Salt Lake Co.: between Mt. Olympus and Big Cottonwood Canyon, *1713, 1716;* 3 mi up Lamb's Canyon, *1760*. Utah Co.: 4 mi NW of Alpine, *1719*.

V. vallicola A. Nelson; $2n = 6_{II}$.
IDAHO: Bear Lake Co.: 1.3 mi W of Ovid, *x-38, x-40, x-41, x-42A*. Blaine Co.: 3 mi W of Carey, *1754*. Camas Co.: 12 mi E of Fairfield, *1753*. Franklin Co.: just N of Franklin Cemetery *x-30, x-32, x-34, x-35*. Owyhee Co.: 13 mi NE of Riddle, *1745*.

TABLE 1. *Continued.*

NEVADA: Elko Co.: Pequop Summit along U.S. Hwy. 40, Pequop Mts. *1731*; 2 mi S of Wells, *1732*; 10 mi NW of jct. Nev. Hwy. 51 and Nev. Hwy. 11, *1736*. Humboldt Co.: Lye Creek, Santa Rosa Range, *Gentry & Davidse 1639*.

UTAH: Box Elder Co.: 0.5 mi E of Deweyville, *x-20, 993*; S end of Howell Valley, *Davidse & Hatch 1009*; 2 mi S of Stanrod, *Davidse & Hatch 1011*. Cache Co.: Spring Hollow, Logan Canyon, *282*; 20.5 mi up Logan Canyon, *1040*; 0.5 mi W of Mendon, *x-14, x-15*; mouth of Wellsville Canyon, *x-27, x-28*; 0.3 mi W of Wellsville, *1053*. Rich Co.: 2 mi W of Garden City, *1037*. Utah Co.: 0.5 mi NE of Alpine, *1720*.

The previous count of $n=18$ for *V. linguaefolia* from Utah may well have been based on a hybrid between *V. praemorsa* subsp. *major* and *V. utahensis,* similar to the one reported below in the section on hybridization. The count for *V. linguaefolia* from Latah County, Idaho, may represent an inland extension of the typically coastal hexaploid (Clausen, 1964a) *V. praemorsa* subsp. *praemorsa* along the Columbia-Snake River drainage system.

Subsect. *Chrysanthae*

In subsect. *Chrysanthae*, characterized by rosettes of deeply dissected leaves, Clausen (1964a) recognized five species: *Viola sheltonii* Torr., $n=6$; *V. douglasii* Steud., $n=12$ and 24; *V. hallii* Gray, $n=36$; *V. trinervata* Howell, $n=12$ (Carr, 1969); and *V. beckwithii* T. & G. *Viola bonnevillensis* was described from Utah by Cottam (1939). This name was not discussed by Baker and Clausen but was treated as a synonym of *V. beckwithii* by Holmgren and Reveal (1966). *Viola beckwithii* and plants corresponding to *V. bonnevillensis* (see below under hybridization) have been studied.

Chromosome counts from three populations in Utah and Idaho show that *Viola beckwithii* is a tetraploid, $n=12$, with regular meiosis (Table 1; fig. 7). This is the first count for this species.

Hybridization

Viola purpurea subsp. *venosa* × *V. utahensis*.—In Cache County, Utah, Elko County, Nevada, and Bear Lake County, Idaho, hybridization between *V. utahensis* and *V. purpurea* subsp. *venosa* has been observed. In the Utah and Idaho localities the parent species grew in mixed populations, but in Nevada, *V. purpurea* subsp. *venosa* grew on the west slope of a ridge while *V. utahensis* occupied the drier east slope. The hybrid was found on the summit of the ridge where the two species overlapped.

Morphologically the hybrids appear almost identical with *V. utahensis*. In the field they can best be recognized by their vigorous growth compared to surrounding plants. However, definitive confirmation of their hybrid nature can be obtained only from chromosome or pollen

stainability studies. Hybridization is apparently limited to the areas where the parent species occur in mixed stands. Frequency of hybridization is difficult to judge, but it is probably not high. The hybrids were triploid with usually $6_{II}+6_{I}$ at metaphase I, although in occasional PMC's configurations of $5_{II}+8_{I}$ or $4_{II}+10_{I}$ were observed (fig. 3). Pollen stainability varied from 0–29 percent. Unequal distribution of chromosomes at anaphase I and lagging univalents were frequent irregularities. Stainable pollen was probably not all fertile since some of the grains were not as well filled with starch and cytoplasm as those of non-hybrid plants. Pollen grains also differed widely in size. This results from abnormal pollen formation caused by meiotic irregularities. In those instances where lagging univalents do not become incorporated into the four newly formed nuclei at telophase II, ensuing cytokinesis forms cell walls around micronuclei creating chromosomally deficient microspores. The size of these microspores is probably correlated with the number of chromosomes that are included in the micronuclei. This phenomenon, termed polyspory, has previously been reported in widely different groups of *Viola* (Bamford and Gershoy, 1930; Manch, 1937; Pettet, 1964; Schmidt, 1961). In rare instances, the unpaired chromosomes may be totally excluded from one of the daughter cells after the first division. In such a case there is a potential for the formation of two fertile pollen grains and this mechanism may account for the low percent of apparently normal pollen that is observed in the hybrids.

Baker and Clausen (Baker, 1949a) have suggested that *V. utahensis* is an allopolyploid derivative of hybrids between *V. purpurea* subsp. *venosa* and *V. vallicola*. If this were true, the hybrid between *V. purpurea* subsp. *venosa* and *V. utahensis* should have a $6_{II}+6_{I}$ configuration at metaphase I. This was the maximum pairing observed in the hybrids and, therefore, tends to confirm Baker's hypothesis. Unfortunately, the second unpaired genome of the hybrid cannot be positively identified as the *vallicola* genome on the basis of these few natural hybrids. *Viola vallicola* is the logical choice, however, since this is the only diploid plant now known that occurs in the same area with *V. purpurea* subsp. *venosa* and *V. utahensis*. Moreover, morphologically *V. vallicola* appears to be the only diploid species that could have been a parent.

Although on the basis of leaf morphology alone, *V. utahensis* and *V. purpurea* subsp. *venosa* would, perhaps, not be considered distinct at the species level, the barrier to gene exchange through sterile, or nearly sterile, triploids indicates that these two taxa are best maintained as closely related, but distinct, species.

Viola praemorsa subsp. *major* × *V. utahensis*.—One plant similar to *V. praemorsa* subsp. *major*, but with purple coloration of the leaves, was discovered to have the hexaploid number $n=18$. Unfortunately only a few PMC's were suitable for chromosome counts and meiotic interpretation. These showed a configuration of $6_{II}+24_{I}$ at late metaphase I (fig. 6). Stainable pollen was only 58 percent. The single plant was

found in Bear Lake County, Idaho, in the same mixed population of *V. purpurea* subsp. *venosa* ($n=6$), *V. utahensis* ($n=12$), and *V. praemorsa* subsp. *major* ($n=24$) where a *V. purpurea* subsp. *venosa* × *V. utahensis* hybrid was discovered. The chromosome number of each of the parent species from this population was reconfirmed and all had normal stainable pollen. The intermediate chromosome number, irregular meiosis, and lowered pollen fertility of the single hexaploid plant in a population of normal parent plants leaves little doubt that the hexaploid was a hybrid between *V. praemorsa* subsp. *major* and *V. utahensis*. It may have been on a similar plant that the previous record of $n=18$ for *V. linguaefolia* (=*V. praemorsa* subsp. *major*) from Utah was based, since both plants of *V. praemorsa* subsp. *major*, $n=24$, and *V. utahensis*, $n=12$, occur in the locality.

Clausen (1964a) stated that *V. vallicola* might have been one of the parents of *V. linguaefolia* (=*V. praemorsa* subsp. *major*). If this were indeed true, then the paired genome observed in the hybrid probably corresponds to a commonly shared *vallicola* genome in *V. utahensis* and *V. praemorsa* subsp. *major*. However, only controlled hybridization can confirm this speculation.

Viola beckwithii × *V. utahensis*.—Plants corresponding to the type of *V. bonnevillensis* were found growing in a large mixed population of *V. beckwithii* and *V. utahensis* near Wellsville, Utah. Another single plant of *V. bonnevillensis* was found near Providence, Cache County, Utah. Cottam (1939), when describing *V. bonnevillensis*, mentioned the possibility that this species was a hybrid between *V. beckwithii* and *V. purpurea* subsp. *venosa* (= *V. utahensis* of this treatment). This seems indeed to be the case. Morphologically the hybrids are intermediate in leaf shape and flower color. The leaves of *V. utahensis* are entire and those of *V. beckwithii* are palmatisect with many lobes, while those of *V. bonnevillensis* are palmatifid with few lobes. Flowers of *V. utahensis* are deep yellow on the face and brown on the back, especially on the upper two petals. *Viola beckwithii*, in this population, had very dark violet upper petals, white lateral and spur petals, and a deep yellow center. The hybrid had purplish brown upper petals, very light yellow lateral and spur petals, and a yellow center. The lower petals also had variable amounts of brown pigments.

Seed was not set during the 1966 to 1968 growing seasons either in garden transplants or in plants growing in the field. Stigmas of the hybrids were artificially pollinated with *V. beckwithii* and *V. utahensis* pollen, but no seed was produced in either case, although the ovaries markedly increased in size for about a week.

The chromosome number of the hybrid was $n=12$, but meiosis was highly irregular. Up to 6 bivalents were observed at metaphase I, although the number was usually lower (fig. 8). Pollen stainability was only 9 percent and fertility may well be lower. Polyspory was also very frequent. Although homology of one genome of *V. beckwithii* and *V.*

utahensis may be indicated by the pairing, it is probably not a very close homology. Chromosomal bridges were often observed, indicating that the chromosomes of these genomes differed in a number of rearranged segments. The incomplete homology may indicate that an originally similar genome has had time to differentiate through gross chromosomal rearrangements in each of the parent species. The origin of these presumably partially homologous genomes cannot be identified at the present time but may be hypothesized to represent the genome of an ancestral diploid species that eventually gave rise to the several subsections of *Chamaemelanium* violets in the western United States.

A parallel to the Utah hybrid has been described from California where *V. quercetorum* and *V. douglasii* hybridize to produce offspring morphologically similar to the Utah hybrids and also having a $6_{II}+12_{I}$ chromosome configuration. Clausen (1964a) did not speculate on the origin of the paired genome but hypothesized that autosyndesis may have been involved.

Nondiscriminate insect pollinators, especially bee flies, syrphids, and flower flies, are no doubt largely responsible for interspecific hybridization among these *Viola* species. An interesting example of contrasting pollinator behavior was observed in the mixed *V. beckwithii-V. utahensis* population near Wellsville, Utah. This population also contained the hybrid between these two species. Two species of bees were important pollinators in this population. The honey bee, *Apis mellifera* L., was species specific, i.e., individual bees visited either *V. utahensis* or *V. beckwithii* flowers, but not both. In contrast, individuals of *Anthophora ursina* Cresson visited both violet species indiscriminately, thus creating the opportunity for hybridization through cross pollination. In other populations flies of the genera *Eristalis* and *Bombylius* have been frequently observed to visit the yellow flowered species *V. vallicola, V. utahensis,* and *V. praemorsa* subsp. *major* indiscriminately and insects such as these probably play a major part in the interspecific pollination that leads to occasional hybridization among these species.

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TAXONOMY OF MENTZELIA MOLLIS AND ALLIED SPECIES (LOASACEAE)

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Mentzelia mollis Peck is a small annual endemic to the Succor Creek region in the Owyhee Desert of southeastern Oregon and southwestern Idaho. During a taxonomic and ecological study designed to clarify the relationship of *M. mollis* to other members of the genus, two poorly understood taxa came under investigation (Glad, 1975). One had been found in Leslie Gulch, a few kilometers west of Succor Creek, by Patricia L. Packard; the other had been noted in Colorado and Utah by Henry J. Thompson, who tentatively identified it as *M. mollis*. This paper reports conclusions reached concerning taxonomy of the three taxa.

Within *Mentzelia* sect. *Trachyphytum* T. & G., taxonomic interpretations are often difficult, because differences in morphology from one