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HYBRIDIZATION IN THE GENUS VIOLA.

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Certain sections of the genus *Viola*, as is well known, are characterized by that wonderful biological peculiarity, generally termed cleistogamy. The showy flowers of our spring violets generally live but a short time. Although being sexually perfect, i.e., having stamens and pistils normally developed, they generally wither down without producing any seed and the propagation of the individuals and the maintenance of the species are secured through the cleistogamous flowers. These generally appear comparatively late in the season and reach their fullest development after the showy spring flowers have disappeared. As a rule, the cleistogamous flowers are without petals or have them incompletely developed, for which reason they are often in descriptive botany, termed apetalous. The whole flower has the appearance of a half-grown bud arrested in its development. It is often inconspicuous to the eye because of its lack of attractive colours, or even wholly invisible to the casual observer because not rarely it reaches its full development hidden among the decomposed or half-decomposed remnants of plants which cover the ground, or it even flourishes beneath the surface of the soil.

These cleistogamous flowers, however, play the most important part in the life history of the individual as well as of the species. In spite of their seeming incompleteness, they produce, without being aided by outer agencies, all the seed needed for the maintenance of the species. Their pistils are automatically fertilized by the pollen shed from their stamens, the result being the production of an abundance of seed.

This mode of seed production, so different from the ordinary way, did not fail to attract the attention of botanists at least as far back as the 18th century. It was thought to be strange and inexplicable in times when sexuality in plants was still disputed and when the importance of sexual organs as foundations for a scientific plant system was first being discussed.

Linnaeus, in his *Species Plantarum*, described dozens of violets, giving their characters from the shape of the leaves and their general appearance. In only one case, however, did he mention the flower and fruit, and this was done solely because of the extraordinary biological feature encountered in a species which he called *V. mirabilis*. This species, which is found from Southern Sweden to the Alps of Switzerland, was described as follows:— "Viola caule triquetro, foliis reniformi cordatis, floribus caulinis apetalis." To this description was added especially: "Viola floribus radicalibus corollatis abortienatibus, caulinis apetalis seminiferis."[1] The mere description of this violet, which is now known as *V. mirabilis* L. indicates that Linnaeus considered it one of the wonders of the plant kingdom just because of its peculiar mode of fructification. Its showy spring flowers, proving themselves perfectly useless for the propagation of the species, contrasted singularly with the inconspicuous and seemingly imperfect flowers, which were developed later in the season from special shoots. But these inconspicuous flowers, although in their general aspect not betraying their importance, proved themselves capable of safeguarding the existence of the species. Small wonder that the name *V. mirabilis*—The Wonderful Violet—was given to this species.

In North America little attention seems to have been paid to the morphology and the biological and systematical importance of cleistogamy in violets by the early botanists. Its general occurrence in acaulescent violets, as far as the authors have been able to ascertain, was first accentuated by Dr. Edward L. Greene, whose observations dating from 1896, shed much greatly needed light on the morphology and biological relationships of North American violets. In the year 1896 Dr. Greene stated (according to extracts from *Cybele Columbiana* Vol. I, No. 1, 1914, p. 7) that "the very most common of our so called acaulescent violets, continued long after their short season of showy vernal flowering to put forth apetalous flowers from which are produced all or nearly all the seeds by which individuals are multiplied and the species perpetuated."

As the production of seed in the capsules of the apetalous flowers is the result of a process of self-fertilization and as furthermore the flowers in which this takes place, never open, it is evident that the seed developed in the cleistogamous flowers necessarily is perfectly pure, i.e., that it gives when sown a progeny of plants having the characters of the parent plants. In other words, through cleistogamy the pure lineage of the various species is infallibly upheld.

[1] Linnaeus, Sp. Plant. 2, 936. 1753.

Although much more conspicuous and pretentious in aspect the ordinary showy petaliferous flowers of our violets are of far less importance for the propagation of the individuals than are the cleistogamous ones. This is evident from the fact that only in few cases do they produce any seed. Their life generally ends with the withering of their petals, shortly after which all traces of the whole flower are gone. In most cases, there is no postfloral maturing of capsules because the ovules are incapable of developing into germinable seeds. The reason for this sterility is simply that, as a rule, the petaliferous flowers are not fertilized. They lack the ability of self-fertilization and are consequently dependent for their fertilization on outer agencies. Furthermore, special arrangements and morphological peculiarities of the sexual organs, the nature of which need not be described in this connection, tend to make self-fertilization extremely difficult, if not wholly impossible.

Under these circumstances it is evident that when seed is found developed in the capsule of a petaliferous violet flower, it must be regarded as the result of a cross-fertilization between two flowers. These two flowers may belong to the same individual, to two different individuals of the same species or to two individuals of distinct species. To which one of these three possibilities the development of seed in the capsules of petaliferous flowers is to be attributed in individual cases can only be determined by a study of the progeny raised from this seed.

That the capsules of petaliferous flowers in most species of our violets frequently produce germinable seed, is beyond doubt. Actual observation supporting this statement are, however, rather scant. Brainerd[2] states that though the infertility of the petaliferous flowers has often been observed, he has "during the past season (1903) found these capsules to be usually fertile." In the vicinity of Ottawa the same observations have been made on *V. Macounii* Greene and the writers believe they could be easily made on practically all species of acaulescent violets were these more closely observed.

That fertilization of petaliferous flowers really often takes place, is demonstrated beyond a doubt, by the frequent occurrence of hybrids between different species of violets. As the formation of hybrids through cross-fertilization of the cleistogamous flowers is wholly out of the question the mere fact of their occurrence must necessarily prove that fertilization of and seed formation from petaliferous flowers often occur.

[2] Rhodora, Vol. 6., p. 10.

In this paper the authors will endeavour to give a brief account of the general characteristics of violet hybrids and also a list of the hybrids recorded from the North American continent.

To the amateur botanist who has neither time nor inclination to study with earnest perseverance the multitude of violets occurring in our woods and meadows, the existence of intermediate forms between different species is at first apt to provoke confusion and discouragement. A closer study of those intermediate forms which at first may seem to blur the systematic boundaries between well defined extremes belonging evidently to different specific units will, however, instead of causing confusion, help most comprehensively to avoid it. In other words, the recognition of certain intermediate forms as casual hybrids will prove one of the most helpful means to the botanist endeavouring to arrive at a well founded understanding of the systematic value and relationship of our violets.

The hybrid nature of puzzling forms, apparently intermediate between two species, can be most easily determined.

The general appearance of hybrid plants, their vigorous vegetative development, their bright and abundant flowers and, generally speaking, their air of strength and splendour is often very characteristic. When odd plants displaying these marks are found in violet colonies composed of two or more species, they very often prove to be typical hybrids between well defined species.

The vegetative superiority of hybrids in plants is, however, a too well known feature to warrant a lengthy discussion. It is sufficient to say for the sake of illustration, that for instance hybrids in the genus Epilobium and in grasses are always characterized by their conspicuously vigorous vegetative organs. Not only do they display a most luxuriant growth as far as foliage and profusion of shoots are concerned, but their ability to survive and hold the ground is far more pronounced than that of any of their parents. Several observations have thus been recorded to the effect, that hybrids between species of Epilobium, originating in a ditch or any other area of limited extension, are able on account of the superior strength of their vegetative organs, after a few years, to take possession of every inch of the ground, killing every plant of the species from which they originated. Similar observations have been made on violet hybrids. In botanic gardens, where several species of violets are grown in close proximity, it has been recorded that species, after a few years, often have been killed and replaced by more vigorous hybrid plants.

The conspicuous vegetative development of certain wild violet forms, the systematic value of which may at first seem difficult to understand, may therefore often indicate, to the student of violets, their hybrid value. It must be understood, though, that however helpful be the general characteristics briefly hinted at above for the recognition of hybrids, the decision as to whether a suspected form be really a hybrid or not can be satisfactorily reached only through a minute study of its morphological and sexual characteristics. This means not only that a violet in order to be classified as a hybrid, should be intermediate between supposed species as far as vegetative characters are concerned, but also, and particularly, that the morphological and cytological development of its sexual organs should most strongly support its supposed hybrid nature. In doubtful cases, the functional capacity of the pollen and the ovula must really furnish the final decision on the question whether a certain individual should be regarded as a hybrid or not. Space will not permit that in this article European literature bearing upon the subject of hybridization as influencing the development of sexual organs in violets be quoted. This is also, in fact, unnecessary as numerous observations relating to the subject have been recorded in North America. This is especially true as far as the development of seeds in hybrid violets are concerned, in other words, as far as the development of, or rather the failure of development of the female organs is concerned.

Strangely, but as a matter of fact most naturally, contrasting with the luxuriant growth of the vegetative organs of a violet hybrid stands its more or less marked sexual impotence, i.e., its incapability, to a greater or less degree, of reproducing itself sexually. Generally a violet hybrid is markedly barren and although developing numerous capsules and ovules fails to produce an adequate number of germinable seeds.

A few quotations from one of the excellent papers of Dr. E. Brainerd[3] on the subject will suffice. Thus, describing the hybrid plants between *V. septentrionalis* and *V. fimbriatula* Dr. Brainerd says that "in the late summer they produce numerous cleistogamous flowers and fruit, but nine-tenths of the ovules remain unfertilized."[4] Observations on hybrid plants of the combination *V. cucullata* x *fimbriatula* also reveal the fact that specimens of the same in their cleistogamous flowers, develop capsules which either contain only a few ripened seeds or even become "brown and withered as though

[3] Rhodora, Vol. 6. pp. 213–223.

[4] l.c. 216.

entirely unfertilized."[5] The hybrid *V. fimbriatula* x *sororia*, according to Dr. Brainerd, is less sterile than most hybrids, but never was a capsule found that contained more than half the normal number of seeds.[6] Also in other hybrids, the characteristic sterility of the capsules is most typical. Thus, *V. cucullata* x *septentrionalis* was found to bear only from one to six seeds[7] and, in the hybrid *V. septentrionalis* x *sororia*, "the uniformly stunted and often distorted capsules containing mostly aborted ovules"[8] clearly betrayed its mongrel origin. In *V. affinis* x *sororia* the capsules of the cleistogamous flowers were found to be small and often one-sided and relatively infertile[9] and in *V. cucullata* x *sororia* although numerous, proved to be all small, imperfect and few seeded."[10]

The above quotation will suffice to substantiate what was stated without confirming evidence on a previous page, namely, that in a hybrid between two violet species, the faculty of producing the normal amount of germinable seed is most conspicuously reduced. To avoid misconception, it may be pointed out, especially, that the degeneration of the sexual organs mentioned above refers to the cleistogamous flowers, that is to say the flowers, which in specimens belonging to a "good" species normally produce an abundance of well developed seed. As the cleistogamous flowers are always self-fertilized this failure, in hybrid plants, to bear seed of normal reproductive vigour, cannot be explained by assuming that the pollen necessary for the fertilization of the ovules has not been available. It can be explained only by recognizing the fact that the mixing of and unnatural union of sexual units, belonging to distinct species, in the reproductive organs of the hybrids, is causing a disturbance of the functions of the sexual cells which manifests itself in partial or total sterility.

The inability of the cleistogamous flowers of hybrid plants to produce seed of normal vitality is thus very pronounced. This being the case, it is evident that when violet plants are found having sterile cleistogamous flowers they may be looked upon as possible hybrids. In fact, such plants in most cases are really hybrids. The sterility of the capsules of the cleistogamous flowers in violets is therefore a character which will prove most helpful for the identification of critical forms as hybrids.

[5] l.c. 217
[6] l.c. 218
[7] l.c. 220
[8] l.c. 221
[9] l.c. 222
[10] l.c. 222

(To be continued)