MENDEL'S LAW OF DOMINANCE IN THE HYBRIDS OF VIOLA.

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In a recent paper[1] I gave some account of certain experimental cultures of the offspring of violet hybrids. It was shown that these seedlings diverge in a striking manner from the mother plant and from each other, in accordance with the laws of heredity that Mendel found to control the progeny of a hybrid. During the past summer I have been able to trace the operation of these laws in the characters of the petaliferous flowers of these seedlings, and in several cases have raised a second generation of seedlings.

In these experiments it has clearly come to light, that in some particulars at least, Mendel's Law of Dominance finds illustration among violet hybrids. The special instance of this that I wish to present in detail, relates to the inheritance of color of capsules and of seeds in *V. hirsutula* × *papilionacea*, briefly discussed in Rhodora, ix. 93, June 1907.

The putative parents of this hybrid differ from each other as shown in the following table:—

		V. hirsutula	V. papilionacea
Leaves	habit	nearly prostrate	erect
	width	2–4 cm.	5–10 cm.
	upper surface	hirsutulous	glabrous
	petioles	glabrous	somewhat hairy
Flowers	color	reddish purple	deep violet
	spurred petal	villous	glabrous
Capsules	length	6–8 mm.	10–15 mm.
	color	purple	green
	number of seeds	20–30	50–70
Seeds	length	1.6 mm.	2 mm.
	color	buff	dark brown

The offspring of the hybrid present, in the most varied manner, a redistribution of most of these points of difference. Segregation in leaf characters was especially well marked. The differences in size of capsule and in number of seeds were obscured by the impairment

[1] Read before sections F & G of the A. A. A. S., Dec. 27, 1906, and printed in Science June 14, 1907.

of fertility, which though not as great as in many violet hybrids, was yet in some plants sufficient to make the evidence ambiguous. Attention will be here restricted to the two points of color difference, in which Mendelian dominance is plainly manifest.

In the hybrid from the wild the capsules are a reddish purple, like those of *V. hirsutula*. The tendency to produce the green capsules of the other parent is however present, for it appears in some of the offspring; but in the mother hybrid it is overpowered by the conflicting tendency to produce purple capsules. In Mendel's language, the purple color is 'dominant,' the green color 'recessive.' In like manner it appears that the brown seed-color of *V. papilionacea* is dominant over the buff seed-color of *V. hirsutula*. Mendel represented dominant characters by capital letters, recessive characters by the corresponding small letters. Following his practice, we may let **A** stand for the purple capsule-color, and **a** for the green capsule-color; **B** for the brown seed-color, and **b** for the buff seed-color. One parent, *V. hirsutula*, will then be marked as **A.b;** the other, *V. papilionacea*, as **a.B;** and the hybrid resulting from their sexual union as **Aa.Bb.**

The plants from the wild are presumed to have been the immediate result of the crossing of the two species,— what are technically known as F_1's. It may well be that they are removed one or more generations from the original cross; but this is not of especial importance in the present experiment, as it will be seen that these particular plants, so far at least as respects the two color qualities under investigation, are hybrids of exactly the same status as 'first crosses.'

From the close-fertilized seeds of these plants I raised in 1906 11 offspring, F_2's; and in 1907, 10 offspring; in all, 21. Among these all the four Mendelian forms were found to occur, in number and character as follows:

10	plants	had	purple	capsules	and	brown	seeds,	apparently	**A.B.**
3	"	"	"	"	"	buff	"	"	**A.b.**
5	"	"	green	"	"	brown	"	"	**a.B.**
3	"	"	"	"	"	buff	"		**a.b.**

A close approximation to the theoretically required ratio of '9:3:3:1' is to be expected only when there are several hundred individuals; but even in the small number here shown there is a decided plurality of **A.B's.**

The different forms of these capsules and their seeds are shown in

fig. 1, in which the purple capsules and brown seeds are shaded, and the green capsules and buff seeds are left white.

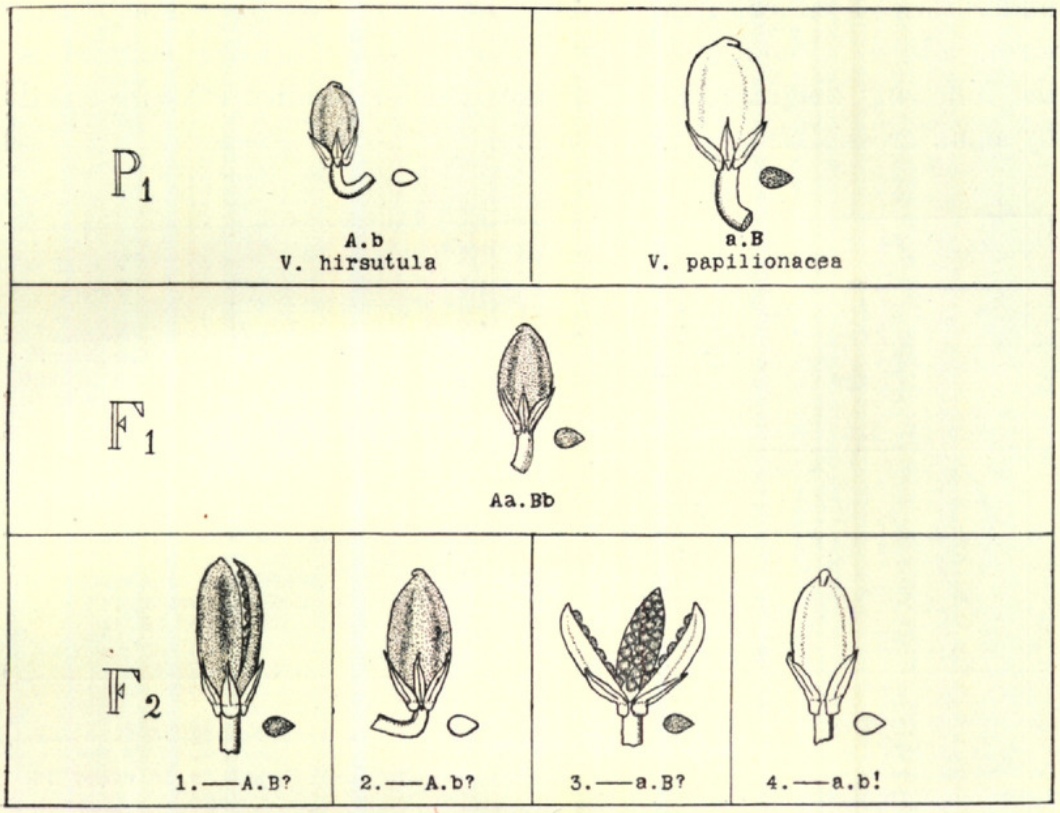

Fig. 1.—Capsules and Seeds of Viola hirsutula × papilionacea, and of its Parents and Offspring.

In 1907 offspring were obtained of six different plants of the eleven raised in 1906. In order to interpret the results, the reader who is not familiar with the laws of Mendel, will be helped by a brief preliminary discussion of the real nature of the four forms of F_2 that appear as the product of the first sowing. As a matter of fact there are five other forms, that masquerade under one or another of the first three forms shown above. We are not sure, among these, in a plant with purple capsules, but that there is also a latent tendency to produce green capsules, kept in check in this individual plant by the dominance of the purple tendency, but able to assert itself in some of the offspring That is, we do not know whether the **A** is pure **A** or **Aa**. Similarly we are not sure in a plant that bears brown seeds but that there is also a latent tendency to bear buff seeds, repressed in this individual plant by the stronger tendency to bear brown seeds, but able to

assert itself in some of the offspring; **B** may be simply **B** or **Bb**; it may be pure or hybrid. Accordingly, under form 3 above we may have either **a.B.** or **a.Bb**; under form 2 either **A.b** or **Aa.b**; and under form 1 either **A.B**, **A.Bb**, **Aa.B**, or **Aa.Bb**. The fourth form, **a.b**, is without ambiguity. These possibilities are pictured in the following diagram, in which the latent hybridity is represented by small crosses on capsule or seed.

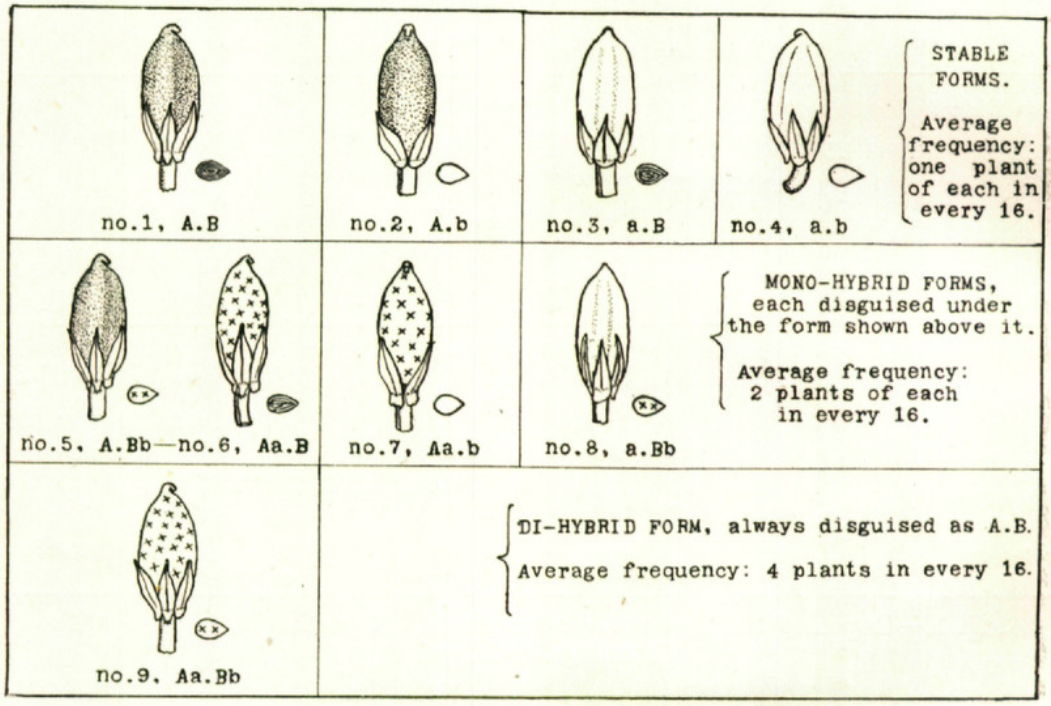

Fig. 2.—Color Forms in Offspring of V. hirsutula × papilionacea.

It will be seen at once that to determine the real nature of any one of the first three of the F_2's in fig. 1, we need to grow its seeds. The apparent forms of the six plants whose seeds were sown, and of their offspring, are given in the following table:

Form of F_2	A.B	A.B	A.B	A.b	a.B	a.b
Seed-number	340	337	339	334	333	338
Forms of F_3 obtained, and the number of plants of each form.	A.B–4	A.B–4				
		A. b–1		A.b–4		
	a.B–2	a.B–3			a.B–6	
			a.b–1			a.b–5

The plants raised from these six sowings were so few (largely from lack of time to transplant) that the numerical results are unimportant;

but in no instance is there a failure to comply with the laws of Mendel. The following points should be noted:—

1. In the sowing numbered 338 all five offspring are like the parent **a.b**,— have green capsules and buff seeds; a recessive character (in this case a double recessive) must always breed true. Here we have a new and stable form, which as a whole is unlike either of the original species.

2. We may infer that the plant from which seeds numbered 333 were obtained was probably pure, that is, was really **a.B** and not **a.Bb**; had it been the latter, one or more of the six offspring would probably have had buff seeds, or been **a.b**. Perhaps as regards capsule-color 334 was also pure,— **A.b** and not **Aa.b**. If so, we should have here in color characters complete reversions to the respective grandparents, *V. papilionacea* and *V. hirsutula*.

3. In sowing 339, though only one seed germinated, it tells the whole story regarding the form of the parent,— it must have been the di-hybrid **Aa.Bb**, and thus exactly like the immediate parent F_1. A plant with purple capsules and brown seeds produces one with green capsules and buff seeds; a feat to be expected of a di-hybrid, though only once in every sixteen plants that it reproduces.

4. The proof is equally clear that in sowing 337 we have the seeds of another di-hybrid; it throws both sorts of capsules and both sorts of seeds.

5. In sowing 340 the result is somewhat ambiguous;— the mother may be either **Aa.Bb** or **Aa.B**; it could not be **A.Bb** or **A.B**.

6. Though three apparent **A.B**'s were sown, none proved to be pure or stable like no. 1 of fig. 2. But in the offspring of a di-hybrid the chances are that only one in nine, that have the form **A.B**, will turn out to be that in reality.

I much regret that the experiment was not conducted on a larger scale; but it should be borne in mind that the object was not to verify the Laws of Mendel,— that is now quite unnecessary; but, conversely to prove that as these seedlings in their metamorphoses obey the laws of Mendel, their parent was of hybrid origin. Disappointed in my expectation that the artificial production of violet hybrids would be attempted at a certain 'biological laboratory,' it occurred to me over two years ago that equally valuable results might be gotten by observing the behavior of the offspring of the supposed

hybrids. As pointed out by Dr. McDougal,[1] the test of a suspected natural hybrid may often be better made by the Method of Analysis than by the Method of Synthesis. In the genus Viola the analytic method has proved unexpectedly successful. Over thirty putative hybrids have produced offspring that segregate in accordance with Mendelian principles.

An objection recently made to the occurrence of hybrids in Viola is based on the supposed fact "that 99 out of 100 seeds of these plants"[2] are from self-fertilized flowers. This led me last June to examine with reference to this matter plants of some eighteen species of our stemless violets, and revealed the fact that all but two of these plants produced seed freely from the petaliferous flowers; in some instances over 300 such seeds were produced by a single plant.[3] The structure of the flower, in style stamens and petals, shows a most ingenious arrangement to prevent self-pollination; and it is now evident that the ovules are readily fertilized by the pollen of an allied species. The coexistence of this habit with the opposite habit of producing in summer self-fertilized flowers is apparently the cause of the multiplicity of forms in this group of plants. Hybridism gives rise to numerous intergradient types; cleistogamy preserves them from further intermixture more skilfully than the artificial hybridizer with his paper bags, and permits the laws of Mendel to work out their natural results, giving rise often to new varieties and races. The behavior of violet hybrids and their offspring under cultivation presents many striking illustrations of this procedure, and awakens the hope that with this clew to guide us we may solve some of the long-standing perplexities of the genus.

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[1] Hybridization of Wild Plants, Bot. Gazette xliii. 11–44, Jan. 1907.

[2] Prof. E. L. Greene, Leaflets i. 214.

[3] Five plants of *V. nephrophylla* furnished at one time from the capsules of petaliferous flowers 1227 ripe seeds.