THE COLOURFACTORS OF THE SEEDCOAT IN PHASEOLUS VULGARIS L. AND IN PH. MULTIFLORUS WILLD.

by M. J. SIRKS.

(with 3 coloured plates).

Researches into the various genetic factors, responsible for the different colours and patterns in the seedcoats of *Phaseolus vulgaris* L. and of *Ph. multiflorus* Willd. have already been published by several writers. These researches may be divided into two groups, considering the different ways, by which the results have been obtained.

In the first place it will be possible to study these factors by means of artificial hybridizations between plants, belonging to different races of one of these species or by species-crossing and analyzing the resulting F_2 -generations; if necessary the F_3 - and further generations may be cultivated as well. In this way the differences in genotypic constitutions of both parents may be found out, as papers of MENDEL (1865), TSCHERMAK (1901, 1902, 1904, 1912), EMERSON (1902, 1904, 1909 a and b), SHULL (1908), SHAW and NORTON (1918), TJEBBES and KOOIMAN (1919, 1921) and KOOIMAN (1920) have shown. A great many genetic factors have been discovered by these authors. The artificial hybridization of gardenbeans however is not at all easy, as TSCHERMAK (1901, p. 706) first has pointed out; only a small percentage of crossings will give good results. And in the scarlet-runnerbean artificial crossing seems to be still more difficult.

Therefore another way may be gone with sufficient results: in *Phaseolus* spontaneous hybridization is rather frequent and its products supply us with an excellent material for the study of the genetic factors. In these cases one of the parents only, the motherplant, is known with certainty, but the fatherplant can be indicated frequently with more

or less probability, and moreover in many cases it is perfectly immaterial in these researches that the fatherplant is unknown. For all crosses, made with a white-seeded plant as one of the parents, have the same shortcoming because of the uncertainty in its genotypic constitution of this white plant; one and the same white race of beans may contain plants very different in factorial constitution with regard to the seedcoat-characters; as now known a white-seeded plant is white because of lacking a certain groundfactor, but it may contain a great many other factors, that remain invisible because of the absence of the groundfactor. Thus spontaneous hybridization may offer to us a very welcome subsidiary material for researches; their analysis has been applied by KAJANUS (1914), LUNDBERG and AAKERMAN (1917), TJEBBES and KOOIMAN (1919), SIRKS (1920). Such an analysis is only complete, if all seeds from an F_1 -plant, that originated by spontaneous hybridization, are available and accordingly the *whole* F_2 - and following generations can be grown; only the papers of LUNDBERG and AAKERMAN and my own have been worked out in this manner; KAJANUS as also TJEBBES and KOOIMAN have derived their materials from only one seed with a seedcoat divergent from those of the race of origin. Of course this seed had been developed upon an F_1 -plant, and the embryo contained in it, was thus an F_2 -individual. This does not necessarily involve an essential fault, so less as the little number of F_2 -individuals gives in simple cases only a sufficient result, but notwithstanding a danger remains and an important difficulty may not be disregarded. The posterity of this seed, grown as F_3 -generation, may be wholly uniform, and in that case its importance for a genotypic analysis of the parents fails, and secondly this F_2 -*individual* will in most cases possess only a part of the whole number of genetic factors, that was present in the F_1 -plant and so in the F_2 -*generation*. It will be even conceivable, that the F_2 -plant grown, lacks all seedcoatfactors present in the known motherplant, and the analysis of its F_3 -generation will be therefore very deceiving. In many cases growing the *whole* F_2 -generation is necessary, and growing the *whole* number of F_3 -families obtained very much desired for founding sound conclusions.

In this paper a review will be given of the results obtained by previous authors and of the genetic factors for the seedcoatcolours

in the species above named, as established by them; results of newly grown artificial and spontaneous crossings will build the second part. The previous literature is arranged according to the factors, discussed therein; the results of my own researches will be given in connection with the crosses, by which they have been detected.

PREVIOUS LITERATURE.

a. PHASEOLUS VULGARIS.

In his classic paper MENDEL (1865) has already given some notes upon the results of a cross between *Ph. vulgaris* (*Ph. nanus* L.) as mother and *Ph. multiflorus* Willd. as the male plant. The firstnamed species had white seedcoats, the father showed seeds with a black spotted and marbled pattern upon a peach-red groundcolour. The seeds of the hybrid were like those of the fatherplant; in the F_2 -generation 30 coloured and only one white plants were obtained and this proportion encouraged the genius of MENDEL to establish the now well-known principle of polymeric factors, „if only we might assume that colour of the flowers and seeds of *P. multiflorus* is a combination of two or more entirely independent colours, which individually act like any other constant character in the plant”. MENDEL's rather scarce materials were not sufficient for a more detailed analysis and a more conclusive exposure.

In the first year after the reviving of mendelism, TSCHERMAK as first has tried to obtain numerical proportions from his bean-crossings; a number of papers has been published since by this author relative to these researches. His first contribution (1901) to our knowledge of these colourfactors had only the F_1 -generations in view, and the value of the characters, in which both parents were different; the F_2 -cultures and the numerical proportions resulting from them, were published in 1902. Summarizing papers, giving more new data, have appeared in 1904, and later on, in 1912. With regard to the pair of factors: coloured-white, his results in a very extensive material followed the mendelian proportion 3:1, not only for the whole of his cultures, but also in regard to these cultures, as taken one for one. He found indeed in some of his F_2 -families from crossings between coloured and white races 488 coloured against 161 white

plants; in c-w-splitting F_3 -families 596c : 177w and in c-w-splitting F_4 -cultures 226 coloured: 78 white plants, or totals of 1310 coloured: 416 whites, or 3.15:1. In 1912 TSCHERMAK has indicated this chromogenic groundfactor, the absence of which makes the seedcoat white, while presence or absence of other colourfactors is of no importance, as A. And EMERSON has published like results in his papers (1902, 1904, 1909 a and b), that form excellent complements to TSCHERMAK'S researches. Crosses between coloured and white-seeded plants in *Phaseolus vulgaris* gave in his cultures in F_1 always coloured seedcoats, in F_2 280 with and 111 without pigmentation, and in splitting F_3 -families 191 coloured 70 white plants. Nearly a 3:1- proportion, that led EMERSON to the conclusion of the presence of a factor P for pigmentation: p or the absence of P giving white seedcoats. This factor has since been found by SHULL, SHAW and NORTON and myself and indicated as P; TJEBBES and KOOIMAN (1919) named it F and KOOIMAN (1920) again A. With regard to its absence all authors are unanimous; while it remains uncertain, if its presence without the other colourfactors, involves any observable result. TSCHERMAK (1912) ascribes to the unaccompanied presence of his chromogenic groundfactor a yellowbrown colour (as shown by his yellowish brown race „Non plus ultra” with formula Abcm), while EMERSON (1909, p. 100) is of another opposite opinion: crossing of two coloured beans, that have no common colourfactors, may led to the birth of a certain percentage of white-seeded F_2 -plants, as in these cases the white colour is caused by the absence of all pigment-building factors and presence of the P-factor only. Crossing a white bean, produced in this way with another white one, that lacks the factor for pigmentation, but possesses other colourfactors, will give therefore a coloured F_1 -generation. And SHAW and NORTON (1918, p. 65) have obtained indeed a coloured posterity by crossing two whites (Davis Wax $\times$ Michigan White Wax). It may be regretted, that they have, as far as I know, not yet published more detailed results about the posterities, grown from this important hybrid. The existence of two types of white-seeded plants implies that not all F_2 -generations from a coloured-white crossing will segregate according to 3:1; if the white parent (p) has not all other factors in common with the

coloured (P) one, the proportions in F_2 will vary from 2.4:1 to 3:1, dependant on the presence of a few or more factors in both parents (Pa B $\times$ pAb for instance will segregate in F_2 in the proportion 45 coloured:19 white). White beans lacking the P-factor as also the other colourfactors, will show a segregation when crossed with coloured ones, between 1.3 coloured:1 white and 3 coloured:1 white (e. g. PA $\times$ pa gives in F_2 9 coloured:7 white plants). And finally the splitting after crossing of a white plant, possessing the P-factor but without the other ones, and a coloured bean, will show proportions between ∞ :1 and 3:1; these proportions follow the scheme of polymeric factors 3:1, 15:1, 63:1 and so on.

2. The second character, studied first by TSCHERMAK and since by other writers also, is that of the marble-pattern. In the researches, relating to this character, an essential difference between two types of marbled patterns was discovered. In crossings between beans with marbling as a constant racial character, and self-coloured plants, the marble pattern is dominant, with a segregation of 3 marbled:1 selfcoloured in the F_2 -generation (TSCHERMAK 58:20, EMERSON 331:124, TJEJBES and KOOIMAN 69:22, 130:51 a. o.). But besides the action of this dominant racial character, marbling was found by TSCHERMAK in his first crosses already to appear in another genetic form: some crosses between selfcoloured and white plants gave as „novum” a marbled F_1 -generation and in these cases the segregation in F_2 -families showed to be 1:1, for he found in these cultures 284 marbled:263 selfcoloured, in F_3 -families 218 m:234 s and in F_4 's 91 m:93 s or as totals 593 marbled plants:590 selfcoloured ones. In his F_3 and F_4 -cultures no one marbled individual gave a uniform posterity: all families descended from marbled F_2 - and F_3 -plants segregated according to the proportion 1:1. In crossings, giving whites besides coloured descendants, the proportions were 6 marbled:6 selfcoloured:4 white plants. Moreover this eversporting marbling was observed in crosses between two selfcoloured individuals, as (TSCHERMAK 1904, p. 34 of the separate) the uniform black race „Schwarzer Neger” crossed with the light yellowish brown „Hundert für Eine”. SHAW and NORTON (1918, p. 71) have obtained in their crosses between Blue Pod Butter, with a yellowish brown seedcoat, and

other uniformly coloured races, F_1 -generations with marbled seeds and segregating in F_2 into 1 marbled : 1 selfcoloured (for example 237 m : 239 s).

In addition to this KOOIMAN (1920, p. 36 ff.) reports to have found that not all F_3 -families, descended from marbled F_2 -plants, show this 1 : 1-proportion. His F_2 -family segregated into 75 marbled : 71 self coloured individuals, but among the F_3 -cultures a great many splitted up according to 2 : 1 (46 marbled : 26 uniformly coloured), so that $66\frac{2}{3}$ of the total had marbled seedcoats, while in other F_3 -families the percentage of marbled individuals was 53.30%, in still others 50%.

The discussions of this phenomenon have gone through a great many changes. At the beginning both types of marbling: the constant and the eversporting form were sharply separated; the firstmentioned type was caused in TSCHERMAKS opinion by only one dominant mendelian factor; the other was an eversporting character, called up from a state of latency, in which it was present in the uniformly coloured race. Afterwards (1908) SHULL has supposed this latent character as being present in the white parent, and this factor M would be observable in heterozygotic condition only; M M as also m m-individuals are therefore uniformly coloured, M m-individuals are marbled. Constant marbling was in his opinion caused by a separate dominant factor. EMERSON had at first accepted this hypothesis as proposed by SHULL, but in a later paper (1909 b) he has changed his opinion and preferred another hypothesis, the proposal of which had been made by SPILLMAN. This author thinks, that races with constant marbling may possess two factors in absolute linkage, that would remain always together in the gametes; being separated from each other these factors would be invisible.

Thus three forms of selfcoloured beans could exist: one with one of these marbling factors, but lacking the other; a second type possessing the other, but missing the first one and as third case a bean, in which both factors fail. If we call with EMERSON these factors Y and Z, so in collaboration with the pigmentation-factor P four types of coloured and four types of white beans may exist, viz.:

1 P Y Z = marbled.

2 P Y z = selfcoloured, with one latent marbling factor.

- 3 P y Z = selfcoloured, the other marbling factor being latent.
- 4 P y z = selfcoloured, both marbling factors being absent.
- 5 p Y Z = white, with both marbling factors latent.
- 6 p Y z = white, with one latent marbling factor.
- 7 p y Z = white, the other marbling factor being latent.
- 8 p y z = white, without any marbling factor.

In this hypothesis of SPILLMAN both types of marbling are taken together; one possessing both absolutely linked factors X and Y in a permanent state, giving thus by their collaboration a constant marbling and pretending the presence of only one dominant factor; the other, inconstant type of marbling would result after crossing two selfcoloured races (or a white race with a selfcoloured one), each of which possesses one of these two factors X or Y. EMERSON did not emphasize the absolute repulsion, that must take action in these crossings, a supposition necessary for an explanation of the numerical proportions (1:2:1) resulting in the F₂-generation. This supposition however seems to be very well tolerable if the cases known from other researches about coupling and repulsion are taken into consideration.

To this seemingly very plausible hypothesis KOOIMAN has objected, that by it the numerical proportions in some of his F₃-families cannot be explained (he observed sometimes 66.60% of marbled, in other cases 53.30% of marbled individuals in the whole of coloured F₃-plants). The firstmentioned proportion was apparent in families, that gave a great number of whites; the segregation followed almost along 1 selfcoloured: 2 marbled: 1 white. The families with 53.30% of marbled individuals showed a segregation of 8 marbled: 7 selfcoloured: 1 white. From these results, KOOIMAN has derived as his opinion, that inconstant marbling may be caused by a special chromogenic factor in a heterozygotic state. He calls A the groundfactor for pigmentation, that alone causes a white seedcoat, but is necessary for the appearance of other colour factors, that remain invisible, if A is absent. A chromogenic factor B gives in collaboration with A a coloured seedcoat, with exception of a small ring around the navel. If only A and B are present, the seedcoat is light lemoncoloured. This chromogenic factor B in KOOIMAN'S opinion would cause in heterozygotic state the inconstant marbling. The F₂-generations from a

hybrid $A A B b$ segregate into three groups : $1 A A B B : 2 A A B b : 1 A A b b$ or 1 selfcoloured : 2 marbled : 1 white. Segregations from an $A A B b C c$ -hybrid, in which C in collaboration with A causes a colouring of the whole seedcoat, the navelring inclusive, go according to $1 A A B B C C : 2 A A B B C c : 1 A A B B c c : 2 A A B b C C : 4 A A B b C c : 2 A A B b c c : 1 A A b b C C : 2 A A b b C c : 1 A A b b c c$; these 16 combinations may be grouped into 8 marbled (all with $B b$), 7 selfcoloured and 1 ($A A b b c c$) white; thus a proportion of 8 marbled : 7 selfcoloured or 53.30% of marbled individuals. These results have led KOOIMAN to his opinion that the factor for constant marbling (called by him M) would be of a character essentially different from his B -factor. This M -factor is dominant over the recessive uniformity in colour, and shows an F_2 -segregation along 3 : 1.

Besides marbling as seedcoatpattern, another design is shown by some races: a striping, by which the colours are restrained to long, almost ellipsoidal stripes with the navel in one of the long sides of these ellipses. This character also may be ascribed to one dominant factor, by most authors indicated as S with monohybridical segregation. TSCHERMAK believes this factor S to be hypostatic to the marbling factor M .

As last factor for special designs the factor or factors for eyedness may be mentioned. This peculiar colourpattern was studied by EMERSON; from his observations on its segregation he concluded to the existence of a pair of factors $T-t$; T causes the extension of the colour upon the whole seedcoat (totality); in t -individuals this colour is restrained to a relatively small part around the navel, as an eye of pigmentation. Totality of colour was dominant in F_1 ; the F_2 segregated into 3 total-coloured : 1 eyed individuals. Concerning this T -factor EMERSON suggested the possibility of its presence in white beans in a state of latency. Thus four genotypes may be found: PT = totally coloured; Pt = eyed, pT and pt whites, one with the other without the latent factor for total colouring.

Of course it will be possible, as EMERSON already has remarked, that more genetic factors are at work in the process of colourextension: for example besides $P-p$ and $T-t$ still another pair $E-e$, that

causes the colourdevelopment in the eye itself. Thus eight different genotypic combinations may be realized: (1) P T E, (2) P T e, (3) P t E, (4) P t e, (5) p T E, (6) p T e, (7) p t E, and (8) p t e. Numbers 1 and 2 are totally coloured individuals (E is supposed to be hypostatic to T); eyed beans occur in number 3, and the other combinations 4—8 have white, colourless seeds. Besides the possibility remains, that different factors (E', E''), are to be accepted for the distinctive types of pigmentextension. For there are races of beans, that show within narrow limits of fluctuations, the pigment restrained to a very small spot around the navel, while in other races the pigmentextension occupies a third or more of the whole seedcoat. And this pigmentextension is an essential character of the race.

By the way it may be mentioned, that in *Vigna sinensis* also a factor for totality has been discovered (SPILLMAN 1913, MANN 1914, HARLAND 1919), leaving in its absence only a part of the seedcoat coloured, while the rest is white.

The further factors, as discovered in researches that have been published till now, are those concerning the various colours and colourintensities, so much characteristic for the seedcoats of *Phaseolus vulgaris*. TSCHERMAK in his earlier papers already has made an effort to divide both groups of coloured individuals: the marbled contained three colourdifferences (black, violet and brown) and these three groups occurred in the proportions of 9:3:4 (92 blackmarbled:33 violetmarbled:38 brownmarbled, thus in more precised proportion 9:3.23:3.72); the selfcoloured ones however showed the reverse proportion of 4 blacks:3 violets:9 brown (39 black:27 violet:101 brown, or 4:2.77:10.36). These results of TSCHERMAK'S paper may be tabulated in this manner:

pigmented 3		:	white 1
marbled 1	:	selfcoloured 1	
Bl. M. 9: V. M. 3: Br. M. 4.		Bl. S. 4: V. S. 3: Br. S. 9.	

A more detailed grouping of the colours met with a great many difficulties and uncertainties concerning the conclusions for the genotypic differences: a few proportions only (brownmarbled: yellowmarbled and full-black: brownish-black) showed to follow a simple mendelian relation 3:1 (30:8 and 29:10); in other cases the proportions of segregation were less clear. For explaining these

segregations, TSCHERMAK has suggested the existence of two colour-factors besides the groundfactor A, that is necessary for the appearance of colour in beans, viz. B causing a violet colouring, and C colouring in coöperation with A alone the seedcoat with a yellowish brown colour; B and C together with A, would give a black seedcoat. The factor B, according to TSCHERMAK, may be divided into two components B_1 and B_2 ; $B_1 B_2$ as also $B_1 b_2$ giving a violet colour, $b_1 B_2$ a red one.

EMERSON has, in the footsteps of SHULL, supposed four colour-changing factors to be present in various races of beans: O changing yellow into orange-brown, D giving darkbrown and B, changing darkbrown into black; R a factor causing a red colour, would be hypostatic to orange-brown, this orange-brown to the other colours a.s.o.

In later years KAJANUS (1914) has given some results of spontaneous crossings, without pointing out the factors concerned therein; LUNDBERG and AAKERMAN (1917) however did so in founding G as the factor for a yellowish-brown colour, and C as that for a chocolate-coloured seedcoat; their coöperation results into darkbrown, the absence of both of them yellowish white. Then $c c g g$ = yellowish white, $c c G G$ = yellowish brown, $C C g g$ = chocolate and $C C G G$ = darkbrown. Both these factors would segregate independently with a segregation in F_2 of 9:3:3:1.

Researches on a large scale at the Massachusetts agricultural experiment station have enabled SHAW and NORTON (1918) to discover a many colourfactors: besides P, the groundfactor for pigmentation, two modifying factors M and M^1 would give rise to two types of colouring; one, M, being present in the beans with yellow-black colours, the other M^1 in those of the red series. In the authors opinion these factors are enzymes, and necessary for the existence of colours. Further the writers have found factors for black (G), for coffeebrown (F), for yellow (C), for darkred (E), lightred (D) and in one race (Creaseback) still another black factor X.

The papers of TJEBBES and KOOIMAN have also unveiled some colourfactors, present in various races of gardenbeans. In their first paper (1919) the cross between a common yellow-brown race and a violet-striped one was studied: the genotypic formula of

the first race was supposed to be FFBBss (F being the groundfactor for pigmentation, B giving the yellowish brown colour), that of the violet-striped bushbean of Prague would be FFBSS; this S indicating a factor that prevents the brown colour in certain regions of the seedcoat from development and changes the remaining brown into violet. In later years (1921) the writers have changed their opinion concerning the functions of these factors: S would not influence B in the manner described above, but its presence alone results in the development of a violet colour, that is locally confined; these factors B, for the brown colour, and S for the violet stripes, show an absolute repulsion in the process of factorial segregation. Further TJEBBES and KOOIMAN have founded the factors Z (black colouring), Bl (blue) and V (corrosive factor causing a marbling and colourdiluting, that may be realised as a constant racial character).

The analysis of the posterity from a hybrid, spontaneously originated gave to me (1920) the possibility of concluding the existence of the following characters: P the groundfactor for coloured seedcoat, that in lonely presence develops a yellowish colour; G the factor for yellowish-brown colour; L a factor for darkbrown; V a factor for violet colour, being hypostatic to the L-factor; Gr a factor, that gives a grey glow in addition to the other colours, B a factor changing violet into blue, and S a factor for stripes, that restricts the blue, violet and grey colours into stripes. Some of these factors seemed to be linked somehow.

In another paper concerning this subject, KOOIMAN (1920) has suggested the existence of still other factors in the seedcoats of *Phaseolus vulgaris*: A the groundfactor for colourdevelopment, B a factor that gives a total colouring of the seedcoat, a small ring around the navel excepted, if presence of A makes a coöperation possible; beans with both factors A and B are lemon-yellow. C is a factor that together with A colours the whole seedcoat, the navelring included in a brownish colour, while D in presence of A and absence of B and C causes a brown colour of the navelring only, and an almost unobservable grey dotting on the remainder of the seedcoat. Besides these factors, others still are discovered by KOOIMAN: two factors that influence the intensity of the other colours: E intensifying the brown colours, and F that gives a

violet or grey glow upon them. The B-factor would then, in KOOIMAN's opinion, in heterozygotic state cause the inconstant, eversporting marbled pattern.

b. PHASEOLUS MULTIFLORUS.

About the colourfactors in the seedcoat of the scarlet-runnerbean and its varieties, our knowledge is more restrained and still less clear than it is concerning *Ph. vulgaris*. Besides brief and very incomplete communications of FERMOND and of KOERNICKE (as cited by FRUWIRTH 1919. p. 189), there is an observation of REINKE (1915), that would show the white colour as being dominant over the colouring of the seedcoat; because of the important cross-fertilization in this species (surpassing to a high degree that of the common gardenbean), some doubts about such an observation should always be held. Further indications may be found in the papers, mentioned above, of MENDEL and of TSCHERMAK, who gave (1912. p. 223) some numbers of segregation showing how uniformly coloured F_2 - and F_3 -individuals may give a descendance of marbled and of selfcoloured plants, in proportions near 3:1, while brown-marbled would segregate still blackmarbled, totally blacks and totally violets, and the violet selfcoloured ones gave some descendants with black seedcoats. Coloured seedcoats would, according to TSCHERMAK be dominant over the absence of colour, or whites. And last, TIEBBES and KOOIMAN (1919. p. 334). have told us about a hybrid between the constant marbled *Ph. multiflorus* (black pattern on a violet groundcolour) and a white seeded *Ph. vulgaris*, from which in F_2 a.o. constant-marbled, marbled heterozygotes, constant selfcoloured and segregating selfcoloured individuals descended. The heterozygotes segregated along 3:1.

The complexity of these results and the want of clearness concerning the genotypic factors at work in the seedcoats of these species, made a renewed research very desirable, chiefly in collecting many and precise numbers of segregation in relatively simple crosses. In the present paper these researches are treated in connection with the conclusions, derived from them.

NEW RESEARCHES.

a. PHASEOLUS VULGARIS.

The materials, considered in this paper, came for a part from hybrids artificially obtained, partly from F_1 -individuals that took their origin by spontaneous hybridization. In the first case it was very easy to grow the whole F_2 -generation; in the other cases also the *whole* posterity of an F_1 -individual was taken into cultivation. Part of these materials were obtained by the aid of others: Messrs C. J. Droogendijk (The Hague), J. D. Koeslag (Wageningen), Prof. H. Mayer Gmelin (Wageningen) and N. Raap (Anna Paulowna, N.H.) have supplied me friendly with some hybrids.

The pure races, that have been used in these hybridizations, are:

1. „Witte” (white) beans with a shining white seedcoat, lacking a navelring;
2. „Citroen” (lemon) beans, lemoncoloured, without or at most with a blueish navelring (pl. II, fig. 22);
3. „Wagenaars” have a seedcoat, that immediately after harvesting, is lemon-coloured with a brown navelring, but soon the lemoncolour changes into greyish yellow and a year afterwards the seeds are entirely yellowish-brown (pl. II, fig. 18);
4. „Bruine” (brown) from the moment of ripening yellowish brown on the whole seedcoat and a brown navelring (pl. II, fig. 25);
5. „Rotjes”, a race characterised by a grey-brown seedcolour, that can be discerned in two types: a dark grey-brown (pl. II, fig. 23) and a less intense grey-brown type (pl. II, fig. 24);
6. „Zwarte” (black) with a pure black seedcoat (pl. II, fig. 16);
7. „Kievits” (lapwing) with a constant reddish violet marbling upon a yellowish groundcolour as racial character (pl. II, fig. 21).

Of course in the cultures from artificially obtained hybrids only, both parents were known with certainty; a great many spontaneous hybrids however showed in their posterities proportions of segregation, that were wholly parallel to those from artificial hybrids, and on this ground their descendance gave strong indi-

cations for a certain race as being the fatherplant sought after. In these cases the results of spontaneous crosses are taken together with those of artificial hybrids.

1. CROSS OF CITROEN $\times$ WAGENAAR.

The hybrid obtained between these two races showed the same phaenotype as the Wagenaar: brown navelring and soon colour-changing into brown of the remainder of the seedcoat were dominant. Two families obtained from artificial crossings and one from a spontaneous hybrid came into cultivation; in all cases the Citroen-race was the mother. The segregations in the F_2 -families gave the following numbers of frequency:

Family		Wagenaar-type	Citroen-type	Totals	Proportion in a total of 4
997	Artif. hybr.	33	8	41	3.21 : 0.79
1033	Artif. hybr.	25	9	34	2.99 : 1.01
1034	Spont. hybr.	41	13	54	3.03 : 0.97
	Total	99	30	129	3.06 : 0.94

The segregation follows in a sufficient way the scheme of a monohybrid; the difference between the two races depends upon the presence of a single factor in the Wagenaar, perhaps the same factor, as that indicated by KOOIMAN as D.

2. CROSS OF WAGENAAR $\times$ BRUINE.

The yellowish brown colour of the „Bruine” showed to dominate over the yellow Wagenaar-seedcoat; the F_1 -individuals could not be discerned from the brown race. Two F_2 -families were grown: one originated from an artificial cross, made by Mr. C. J. DROOGENDIJK, the other from a spontaneous hybrid, found as such in a culture of Wagenaar-beans. Some F_3 families, that came from the firstmentioned F_2 -plant and showed the same segregation, may also be taken into consideration and tabulated together:

(Cf table page 111).

Three more F_3 -posterities, grown from F_2 -individuals after artificial hybridization, contained only brownseeded plants (34, 23 and 46); the two Wagenaar-like F_2 -plants gave only Wagenaarseeded

Family		Brown	Wagenaar	Total	Proportion in a total of 4:
1920. 763	Artif. hybr. F ₂	8	2	10	3.20 : 0.80
	F ₃	33	9	42	3.14 : 0.86
	764 F ₃	38	10	48	3.17 : 0.83
	767 F ₃	61	26	87	2.80 : 1.20
	768 F ₃	33	12	45	2.93 : 1.07
	769 F ₃	35	8	43	3.25 : 0.75
1921. 1038. Spont. hybr. F ¹		32	10	42	1.04 : 0.96
		240	77	317	3.02 : 0.98

descendants (33 and 40) with one exception: a brownseeded plant, that was a new spontaneous hybrid.

The numerical proportions allow concluding to a monohybrid nature of the F₁; a single dominant factor being present in the brown race, absent in the Wagenaar, and probably the same factor as that, mentioned in my previous paper as G, perhaps also the same as KOOIMANS C.

3. CROSS CITROEN × BRUINE.

In connection with the results, obtained in the two crosses above, the hybrid Citroen × Bruine was expected to be a dihybrid, segregating according to the scheme 12 brown : 3 wagenaar : 1 citroen, because of the epistasis, according to KOOIMAN, of his factor C (G) for brown seedcoat and brown navelring over the factor D, that causes a brown colour in the navelring only. Individuals with C alone could not be discerned phaenotypically from the CD-plants. The segregation observed however gave other numerical proportions: in some cases the F₂ splitted in only two groups, viz. 3 brown : 1 lemoncoloured, while in others the three phaenotypical groups appeared indeed, but in numbers that deviate strongly from the expected 12 : 3 : 1-proportion. These two groups may be separated in tabular form:

(Cf table page 112).

The monohybrid character of this segregation is beyond doubt; the brown race used in these crosses possessed only one factor that was absent in the lemoncoloured Citroen-individuals.

Monohybrid segregation.

Family	Brown.	Citroen.	Total.	Proportion in a total of 4.
990 Artif. hybr.	3	1	4	3.0 : 1.0
1002 " "	30	7	37	3.24 : 0.76
996 Spont. hybr.	10	3	13	3.08 : 0.92
1003 " "	5	5	10	2 : 2
	48	16	64	3.0 : 1.0

Dihybrid segregation.

Family	Brown.	Wagenaar	Citroen	Total.	Proportion in a total of 16.
987 Artif. hybr.	20	4	10	34	9.41 : 1.88 : 4.71
991 " "	9	2	3	14	10.28 : 2.29 : 3.43
993 Spont. hybr.	20	10	8	38	8.42 : 4.21 : 3.37
999 " "	17	5	9	31	8.80 : 2.58 : 4.62
1004 " "	14	4	3	21	10.67 : 3.05 : 2.28
Total	80	25	33	138	9.28 : 2.90 : 3.82

The results are not at all in agreement with the expected proportion 12:3:1; in all families the numbers of the groups are in defiance of this theoretical supposition. They come nearer to the scheme 9:3:4 and induce thus to another hypothesis, that will be given below in connection with the results from other crosses.

4. CROSS OF CITROEN $\times$ ROTJES.

As indicated above, the race known as „Rotjes” is not always uniform; darker and lighter types of greyish brown can in most cases be discerned. The colour can also come nearer to a reddish brown; besides individuals with a brown navelring, sometimes, though somewhat rarely, others without this racial character appear in cultures of this race. The cause of this mixture of types is for the greater part to be found in the difficulty of discerning them; if spontaneous hybridization has occurred, its results will in most cases remain unobserved, and the hybrids will find occasion to propagation and segregation, while in other races with

light-coloured seedcoats; these crosses are soon detected and may be removed. The grey colour, characteristic for the race „Rotjes” covers all other colours in a high degree, so that only a very sharp selection may discover the differences of types.

The cross Citroen ♀ × Rotjes ♂ (greyish brown as in plate II Fig. 23) was cultivated in only one family; besides two spontaneous hybrids found in a culture of the lemoncoloured race, gave posterities of a wholly analogical composition. The F_1 -individuals were of a reddish brown; the F_2 -generations divided into 8 phaenotypically different groups: I dark redbrown, Ia redbrown (like F_1), II dark greybrown, IIa greybrown (all with a brown navelring), III greybrown with uncoloured or blue navelring, IV yellowbron as the brownseeded race „Bruine”, V Wagenaar-type (yellow with brown navelring) and VI lemoncoloured Citroen-type (without navelring). The types I, II and III are figured in pl. I. figs. 3, 4 and 7; the remaining three agree entirely with fig. 25, 18 and 22 of pl. II. Above those, still two plants with reddish brown seedcoat like that of the F_1 were selected from a culture of the Rotjes-race; they gave progenies segregating in the same way, so that as their father a plant of the Citroen-race may be indicated with a very high probability.

The frequency of the various types in F_2 may be found in the following table:

Type	Ia	Ib	II a	II b	III	IV	V	IV	Total
988. Artif hybr.	5	5	1	3	6	3	1	2	26
994. Spont. hybr. from Citroen	2	7	1	2	11	2	2	3	30
1005. " " " "	1	3	—	1	1	2	—	1	9
1006. " " " Rotjes	3	3	—	—	3	3	2	1	15
1015. " " " "	6	11	2	4	2	2	—	5	32
	17	29	4	10	23	12	5	12	112
	46		14		23	12	5	12	

If the groups Ia with Ib and IIa with IIb are taken together, the segregation shows immediately to be a triheterozygotic: part of the individuals in the F_2 possess the factor for grey (probably the L-factor, as indicated in my previous paper) while the remain-

der is missing this factor; a part of them have a brown navelring (D) the others have not; some show the presence of the factor for a totally yellowish brown seedcoat (G), in the others this factor is absent. Thus the F_1 -individuals had as genotypic formula $G \text{ } g \text{ } D \text{ } d \text{ } L \text{ } l$ and the F_2 -generations would thereby be composed of 8 types of individuals (when homozygotic or heterozygotic presence of a factor is supposed to give the same phaenotype): 1) 27 $G \text{ } D \text{ } L$, 2) 9 $G \text{ } D \text{ } l$, 3) 9 $G \text{ } d \text{ } L$, 4) 9 $g \text{ } D \text{ } L$, 5) 3 $G \text{ } d \text{ } l$, 6) 3 $g \text{ } D \text{ } l$, 7) 3 $g \text{ } d \text{ } L$ and 8) 1 $g \text{ } d \text{ } l$. On the supposition, that the three factors mentioned (G for the yellowish brown seedcoat, D for the brown colour of the navelring, and L for the grey colour) segregate independently from each other, the numbers observed in the F_2 -families give a very strong indication for the hypothesis, that the G-factor can become visible only if the D-factor is also present; in other cases the G-factor may be present but remains in cryptomeric (latent) position. If this may be supposed, the phaenotypes of group 1 ($\frac{27}{64}$ of the whole number) would be reddish-brown (type I), of group 2 yellowbrown (type IV), of groups 3 and 7 grey with uncoloured navelring (type III), group 4 grey-brown (type II), groups 5 and 8 lemoncoloured (type VI) and group 6 Wagenaar-type (type V).

A comparison of the numbers observed with the proportions that were expected on this hypothesis, may be given here:

Type	I	II	III	IV	V	VI
Genotypes	$G \text{ } D \text{ } L$	$g \text{ } D \text{ } L$	$G \text{ } d \text{ } L$ and $g \text{ } d \text{ } L$	$G \text{ } D \text{ } l$	$g \text{ } D \text{ } l$	$G \text{ } d \text{ } l$ and $g \text{ } d \text{ } l$
Theoret. proportion	$\frac{27}{64}$	$\frac{9}{64}$	$\frac{9}{64} + \frac{3}{64}$	$\frac{9}{64}$	$\frac{3}{64}$	$\frac{3}{64} + \frac{1}{64}$
Expected	47.25	15.75	21.0	15.75	5.25	7.0
Observed	46	14	23	12	5	12

The phaenotypic differences, by which group I a could be discerned from group I b, as also II a from II b, have probably their ground in the incomplete dominance of the L-factor; if LL-individuals would show a darker intensity of colour than the heterozygous Ll-plants, this difference will be observable among the individuals of types I, II and III, so that these groups can be

divided again in two parts ($1/3$ and $2/3$). In groups I and II this division was tried with more or less result: I a contained 17, I b 29 individuals (theoretical 15.75:31.5), while II a with 4 and II b with 10 individuals come near to the expectation 5.25:10.5. In group III a further distinction of types was rather impossible.

5. CROSS OF BRUINE $\times$ ROTJES.

Two families of artificially obtained hybrids between greybrown Rotjes and Bruine came into cultivation; two families originating from red-brown individuals found in a Rotjes-culture and showing a segregation parallel to that of the other plants, six families of artificial hybrids Bruine $\times$ Rotjes and eight families of redbrown spontaneous hybrids, found in a culture of the yellowbrown „Bruine”. These 18 F_2 -families could be classified in the same manner as those of the previous cross and gave so the following numbers of individuals per type:

Family	Type	Ia	Ib	IIa	IIb	III	IV	V	VI	Total
1012	Artif hybr. from Rotjes	4	9	2	3	—	4	2	—	24
1013	” ” ” ”	3	7	3	5	—	4	1	—	23
1014	Spont. hybr. ” ”	1	5	2	3	—	2	—	—	13
1016	” ” ” ”	2	4	1	2	—	1	—	—	10
1018	Artif hybr. from Bruine	2	4	2	1	—	4	—	—	13
1019	” ” ” ”	3	13	5	9	—	7	1	—	38
1085	” ” ” ”	4	7	1	6	—	11	—	—	29
1086	” ” ” ”	6	14	2	1	—	4	—	—	27
1087	” ” ” ”	2	9	3	1	—	4	—	—	19
1100	” ” ” ”	1	1	—	—	—	1	—	—	3
1021	Spont. hybr. ” ”	7	15	3	4	—	4	1	—	34
1022	” ” ” ”	4	14	2	2	—	7	2	—	31
1088	” ” ” ”	3	3	1	3	—	5	—	—	15
1089	” ” ” ”	2	7	1	—	—	1	1	—	12
1090	” ” ” ”	3	9	1	—	—	2	3	—	18
1103	” ” ” ”	—	5	1	3	—	3	1	—	13
1104	” ” ” ”	2	1	—	1	—	1	1	—	5
1105	” ” ” ”	3	7	1	4	—	3	—	—	18
		52	134	31	47	—	68	13		345
		186		78		—	68	13		

Both types lacking the D-factor (III and VI) are absent; while the other types come very near to the proportions, that are expected according to the 9:3:3:1- scheme of segregation. In a total number of 345 this expectation would be $194\frac{1}{16} : 64\frac{11}{16} : 64\frac{11}{16} : 21\frac{9}{16}$; the numbers observed were 186:78:68:13. The division into groups I a and I b, II a and II b however is here somewhat deviating from the expectation: the difficulty of discerning these types will be cause of this deviation.

The genotypic formula of the greybrown beans, called „Rotjes”, may thus be written in keeping with the results of the previous cross, as $gg\ D\ D\ L\ L$; that of the gellow-brown race „Bruine” is, here also $G\ G\ D\ D\ l\ l$. The reddish brown hybrid is a diheterozygote $G\ g\ D\ D\ L\ l$, and the F_2 -generation segregates into $9\ G\ D\ L : 3\ G\ D\ l : 3\ g\ D\ L : 1\ g\ D\ l$.

In addition to these families, the segregation of which is entirely in harmony with the theoretical suppositions, in a culture of yellow-brown beans an individual was found with grey-brown seedcoats; its posterity (family 1027) showed a segregation into 4 individuals of type II and 2 of type V. It may be supposed that the mother of this spontaneously born hybrid was a $G\ g\ D\ D\ l\ l$ -heterozygote, that has given with a $g\ g\ D\ D\ L\ L$ -father an F_1 -individual of the genotypic constitution $g\ g\ D\ D\ L\ l$. The mother-plant had been lost and thereby its posterity could not be grown; a decision about its heterozygous nature being thus impossible.

6. OFFSPRING OF OTHER ABNORMAL PLANTS, FOUND IN „ROTJES”.

Some other plants with abnormally coloured seedcoats, found in cultures of the race „Rotjes,” gave as descendants four families, showing a segregation more or less parallel to those of the previous crosses. One of them had grey-brown seedcoats without the brown navelring, while the three others had reddish brown seedcoats. The segregations could be classified in the same groups as in the preceding cases:

(Cf Table page 117.)

The motherplant of family 992 with $g\ g\ d\ d\ L\ l$ as genotypic formula took thus its origin from two gametes $g\ d\ L$ and $g\ d\ l$, either by spontaneous crossing of a phaenotypically identical $g\ g\ d\ d\ L\ L$ with a lemoncoloured ($g\ g\ d\ d\ l\ l$) father, or as off-

Type	I	II	III	IV	V	VI	Total	Supposed formula
992 greybrown without navelring	—	—	26	—	—	7	33	gg dd Ll
1007 reddish brown	11	2	—	—	—	—	13	GgDDLL
1008 reddish brown	6	2	4	—	—	—	12	GgDd LL
1009 reddish brown	7	2	—	—	—	—	9	GgDDLL

spring of a product of segregation after a previous, more complicated crossing. The family 1008 will have descended from a cross $gg\ DD\ LL \times GG\ dd\ LL$, both greybrown parents (one with, the other without navelring) and the origin of families 1007 and 1009 may have been a cross between $GG\ DD\ LL$ and $gg\ DD\ LL$. In every case, the results obtained are not in defiance of the suppositions given above.

7. CROSS OF CITROEN $\times$ KIEVITS.

The so-called „Kievits”-race (kievit = lapwing), pl. II fig. 21, is characterized by a reddish violet marbling on the seedcoat, that has a yellow-white groundcolour; this marbling however does not show any regularity in the distribution of the violet colour, as does the violet striping in other races; but it is a constant racial character like this, and may not be confounded with the inconstant, eversporting marbled type. The other parent of these crosses was the lemoncoloured Citroen-race, mentioned above, with a yellow seedcoat without navelring (pl. II, fig. 22). By means of artificial crossing the hybrid was obtained in 3 F_1 individuals (2 Citroen $\text{♀} \times$ Kievits ♂ and 1 reciprocal). Besides two plants were found in a culture of the Kievits-race that showed to have a seedcoat identical with that of these F_1 -plants and by their manner of segregation to have been born from a spontaneous crossing with Citroen as the father, and last two plants from the Citroen-Race that took their origin from a spontaneous fertilization by Kievits-pollen.

The seedcoat of these F_1 -individuals (pl. I. Fig. 12) was reddish-violet marbled on a yellowbrown groundcolour. Anticipating the results of the next cross, it may be mentioned that these F_1 -plants concerning their seedcoatcolours were phaenotypically identical with those of the cross Bruine $\times$ Kievits, that will be treated below. The segregation in F_2 was much more complicated than those

given above; Type I had a more or less intense reddish violet marbling on a yellowbrown groundcolour as had the F_1 -individuals; according to the prevailance of the violet or of the brown colour, this type has been divided further into five subtypes (I a—e); subtype Ic agrees with the F_1 . Type II was selfcoloured yellowbrown; in some cases however the seedcoat had a violet glow upon the brown colour, so that two subtypes could be discerned: IIa yellowish-brown, and IIb the same with a violet glow. Type IIIa was the same as the well-known Wagenaar-race, while IIIb had the same seedcoat but with a violet glow. The plants, classified as type IV, had the same colours and the same pattern as the Kievits-race; as in type I here also the intensity of violet showed great differences between the various individuals, belonging to this group, so that a division in five subtypes was applied: pl. II fig. 19 shows a bean of the lightest of these subtypes, IVe. Types V, VI, VII and VIII were wholly without violet and without yellowbrown in their phenotypes: V the lemoncoloured like the Citroen-race, VI yellow and white marbled (pl. II fig. 20), VII pure white and VIII a greyish white seedcoat, but possessing a brown navelring (pl. I fig. 10, probably identical with KOOIMANS H-type). The individuals of the seven F_2 -families, that were grown, were distributed over these various types in following frequencies:

(Cf table page 119)

At first sight these numbers may seem to be of little promise; if however the numbers of groups I, II, III a. s. o. are taken one for one, neglecting the further divisions Ia, Ib, Ic, a. s. o., a rather good numerical proportion can be found therein. There are types with and types without the brown navelring (factor D), types with and types without the yellowbrown colour of the whole seedcoat (factor G), types with and types without the Kievits-pattern (violet marbling, that may provisionally be ascribed to a factor K) and finally among the recessive lemoncoloured beans uniformly coloured and marbled individuals. This lastmentioned segregation may be explained rather sufficiently by the supposition of KOOIMAN, that a chromogenic factor B in homozygotic state causes an equal colouring, in heterozygotic presence however the inconstant type of marbling. It is however unclear, why this difference between

	Ia	Ib	Ic	Id	Ie	IIa	IIb	IIIa	IIIb	IVa	IVb	IVc	IVd	IVe	V	VI	VII	VIII	Total
989 Artif. hybr. from Citroen	—	21	—	—	—	6	—	1	1	3	11	—	—	—	4	8	4	—	59
995 " " "	1	2	—	3	—	3	1	1	—	—	—	—	2	—	2	—	3	—	18
998 Spont. hybr. " "	1	2	2	8	2	5	—	4	2	—	2	—	5	—	2	9	2	—	46
1001 " " "	—	11	—	—	2	7	2	1	—	—	3	—	—	—	1	—	—	2	29
978 Artif. hybr. from Kievits	—	—	3	13	2	6	1	2	—	—	—	—	2	3	2	7	3	—	44
979 Spont. " " "	2	—	3	12	5	3	2	1	—	—	—	1	1	2	4	9	1	—	46
980 " " "	—	2	4	4	1	3	—	1	1	—	—	2	—	—	2	2	5	—	27
	4	38	12	40	12	33	6	11	4	3	16	3	10	5	17	35	18	2	269
	106						39			15			37			17			269

BB and Bb-individuals, that was observed by KOOIMAN also among the yellowbrown beans, could not be constated in my materials. If we indicate in his lines the groundfactor for pigmentation as A, and if AA-plants without any other factor have white seedcoats, this complicated cross may be very well presented in a scheme of factorial constitutions. The formula of the Citroen-race may so, corresponding to the suppositions given above about the cryptomeric state of factor G, be written as A A B B G G k k d d, that of the Kievits-race as A A b b g g K K D D and the resulting F₁-generation will thus be A A B b G g K k D d, a tetrahybrid that forms 16 different types of gametes: A B G K D, A B G K d, A B G k D, A B g K D, A b G K D, A B G k d, A B g K d, A b G K d, A b g K D, A b G k d, A b g K d, A b g k D, A b g k d. Consequently the F₂-generation consists of 256 combinations. Supposed, that the factors G, K and D are entirely dominant, while the B b-individuals can be discerned from the B B-plants only if the other factors are missing, and that the K-, as also the G-factor remains invisible, if D is absent, the following groups may be found among these 256 combinations:

27 B B G K D F ₁ -type I	3 B B G k d lemoncoloured V
54 B b G K D F ₁ -type I	6 B b G k d lemonmarbled VI
27 b b G K D F ₁ -type I	3 b b G k d white VII
9 B B G K d lemoncoloured V	3 B B g K d lemoncoloured V
18 B b G K d lemon-marbled VI	6 B b g K d lemonmarbled VI
9 b b G K d white VII	3 b b g K d white VII
9 B B G k D yellowbrown II	3 B B g k D wagenaar III
18 B b G k D yellowbrown II	6 B b g k D wagenaar III
9 b b G k D yellowbrown II	3 b b g k D white with brown navelring VIII
9 B B g K D kievits IV	1 B B g k d lemoncoloured V
18 B b g K D kievits IV	2 B b g k d lemonmarbled VI
9 b b g K D kievits IV	1 b b g k d white VII

In a total of 256 individuals of the F₂-generation there are 108

of phaenotype I, 36 of II, 9 of III, 36 of IV, 16 of V, 32 of VI, 16 of VII and 3 of VIII. In these proportions, one must keep in view the lack of difference between BB- and Bb-plants in the types I, II, III, IV. A comparison of the numbers observed, with the proportions in a total of 269, derived from these theoretical proportions, shows a rather good agreement between them:

Type	I	II	III	IV	V	VI	VII	VIII	Total
Observed numbers	106	39	15	37	17	35	18	2	269
Theoretical proportions	108	36	9	36	16	32	16	3	256
Expectation	113	38	9	38	17	34	17	3	269

Only type III, the Wagenaar-type has occurred in a number somewhat above the expectation, while type I has remained a little below; the deviations however are not strong enough to invalidate the theoretical suppositions. The more detailed divisions into types I a, I b a.s.o. don't allow till now more detailed suppositions; from groups I and IV a polymeric character of the factor for violet marbling could perhaps be concluded to, or from types II b and III b the break of a linkage that existed before the crossing between a factor for violet and a factor for marbling (that are taken together in this paper as one factor K), but without further researches of the F_3 -and following generations these suppositions are far from being justified.

In any case however this cross has shown with sufficient certainty:
 an independent segregation of the four factors B, G, K and D;
 a distinction between BB- and Bb-plants in the individuals that are missing other factors;
 a cryptomeric state of G- and K-factors, if the factor D is absent.

8. CROSS OF BRUINE $\times$ KIEVITS.

In treating the previous cross it was already mentioned, that in their seedcoats the F_1 -individuals from the cross Citroen $\times$ Kievits are phaenotypically identical with those from Bruine $\times$ Kievits. Therefore the products of spontaneous hybridizations with the Kievits-race as mother cannot be determined immediately in so

far it concerns the fatherplant: the segregations in F_2 of Bruine $\times$ Kievits however were of course less complicated, because of the presence of the D-factor in both these races, the F_1 -individuals being thus homozygotes for this factor. In these segregations only types possessing the brown navelring (types I, II, III, IV and VIII) might occur, and from this the fatherplant could be identified as a yellowbrown individual in those cases also, that the father was unknown. Cultures were made of the descendants of three spontaneous and one artificial hybrid with the Kievits-race as mother and one spontaneous and two artificial hybrids that had the yellowbrown race as female parent.

The numbers of segregation may befound in the following table:

(Cf table page 123)

The results of these segregations are in rather good harmony with the hypotheses given above as being derived from the cross Citroen $\times$ Kievits; the hybrid between Bruine and Kievits is a trihybrid $A A B b G g K k D D$ and its segregation will thus show the following groups:

9 B B G K D F_1 -type I	3 B B g K D kievits-type IV
18 B b G K D F_1 -type I	6 B b g K D kievits-type IV
9 b b G K D F_1 -type I	3 b b g K D kievits-type IV
3 B B G k D yellowbrown II	1 B B g k D Wagenaar-type III
6 B b G k D yellowbrown II	1 B b g k D Wagenaar-type III
3 b b G k D yellowbrown II	1 b b g k D white with brown navelring VIII.

According to this scheme, in a total number of 64 individuals in F_2 there are belonging to type I 36, II 12, III 3, IV 12 and VIII 1. The proportions derived therefrom for a total number of 175 may be compared with the observations in this way:

Type	I	II	III	IV	V	VI	VII	VIII	Total
Observed numbers ^a	92	43	11	28	—	—	—	1	175
Theoretical proportions	36	12	3	12	—	—	—	1	64
Expectation	98	33	8	33	—	—	—	3	175

This comparison of the results obtained with the numbers that

Type	Ia	Ib	Ic	Id	Ie	IIa	IIb	IIIa	IIIb	IVa	IVb	IVc	IVd	IVe	V	VI	VII	VIII	Total
974 Spont. hybr. from Kievits	1	4	10	4	2	10	—	1	1	1	1	1	3	—	—	—	—	—	39
975 " " "	—	4	8	6	4	10	1	4	1	1	—	—	3	1	—	—	—	—	43
976 " " "	1	3	5	8	2	10	—	1	1	1	—	2	3	1	—	—	—	—	38
982 Artific. " " "	1	—	2	6	3	4	—	—	1	—	—	1	1	—	—	—	—	—	19
1093 Spont. hybr. from Bruine	—	—	1	3	—	1	—	—	—	—	—	—	1	—	—	—	—	—	8
1096 " " "	—	—	—	—	5	2	—	—	—	—	3	—	—	—	—	—	—	1	11
1099 Artific. " " "	—	—	1	8	—	5	—	1	—	—	1	3	—	—	—	—	—	—	19
	3	11	27	35	16	42	1	7	4	3	5	7	11	2	—	—	—	1	175
	92			43			11			28									175

were theoretically expected, is a sufficient corroborative of the suppositions given above; the further details of types I and IV and the violet glow in types IIb and IIIb are, here also, still too complicated for allowing conclusions on their genotypic nature.

9. CROSS OF ROTJES $\times$ KIEVITS.

In a culture of the Rotjes-race two plants were found, the seeds of which were different from those of the other plants by a marbling of the grey-brown colour, and besides by a blueviolet marbling that covered here and there the greybrown groundcolour. Artificial hybrids between the Rotjes-race and Kievits were not available so that a decision could not be founded upon the phaenotype of the F_1 -individuals, but the segregation of both F_2 -families made the paternity of a redviolet-marbled individual (like the Kievits-race) very probable; in only one of them however the Kievits-race as such seems to have been the pollenparent, in the other a race with reddish-violet striped beans, as had the striped bushbean of Prague, used by TIEBES and KOOIMAN in their crosses.

The F_2 -posterity of the firstnamed spontaneous hybrid segregated into five well-discernable types, of which three again could be divided in subtypes: type I corresponded in phaenotype very well to the F_1 , some individuals however being darker of colouring (type Ia) than the others (Ib); type II was phaenotypically the same as the reddish-violet-marbled Kievits-race, the colour however being changed into blue-violet; here also two types of intensity could be discerned: one darker (IIa, plate II fig. 11) and the other, IIb, with a lighter and more matblue. The third type was apparently the same as the Kievits-race, and could again be divided into five subtypes (IIIa—e) according to the intensities of colouring; IV was identical with the grey-brown Rotjes-race, while V had the same phaenotype as the Wagenaar-race. The distribution of the individuals among these types, was the following:

Type	Ia	Ib	IIa	IIb	IIIa	IIIb	IIIc	IIId	IIIe	IV	V	Total
1010 Spont. hybr. from Rotjes	3	23	7	8	1	3	2	2	4	9	5	67
	26		15		12					9	5	67

Conclusions regarding the genotypical constitutions, that are realized in these phaenotypical groups, by which the segregation may be explained, are not at all easy because of the relatively little number of individuals. From the previous crosses however some suppositions have been derived, that may be justified here too: the Kievits-race would possess a factor K responsible for the red-violetmarbling, while in it the factor L for grey-brown is absent; this Kievitsfactor does not occur in the Rotjes-race, but the L-factor is one of its characteristics. The segregation however shows to be more complicated than a dihybrid, for the K- and L-factors only are not sufficient for explaining the occurrence of phenotype II (blue-violet colouring). Probably the Rotjes-race is in possession of still another factor: Bl, a factor that is changing the reddish violet into blue, and that remains invisible in the Rotjes-race. This Bl-factor would be visible only, if reddish-violet is present and thus it cannot make its appearance in types IV and V, remains therein in a cryptomeric state. Now, if types with and those without L are grouped, those with and those without Bl, those with and those without K, one would expect to find a 3:1— segregation in each of these cases. The results dont agree with this expectation:

Type	with L I and IV	without L II, III and V	with Bl I and II	without Bl III	with K I, II and III	without K IV and V
Number	35	32	41	12	53	14

These numerical proportions may be considered as rather sufficient with regard to the factors Bl and K (expectation 40:13, resp. 50:17); those of the L-factor however show a considerable deviation from the expected 3:1-proportion, so that they lead to the conclusion, the L-factor must be in a cryptomeric state in some individuals. Probably this will be found to be the case in the bl-individuals, where thus the Bl-factor is missing, for the utterance of the L-factor cannot be dependent upon the presence of the K-factor, because of its phaenotypical perceptibility in the Rotjes-race, where the K-factor is entirely absent. So the case will find a rather good explanation, if one supposes the Bl-factor to be cryptomeric in those beans, that are missing the K-factor and the L-factor as cryptomeric when the Bl-factor is absent. Type I will be represented than by the

combination K L B l (27 from 64), type II contains K l B l (9 from 64), type III K L b l (9) and K l b l (3), type IV k L B l (9) and type V k L b l (3), and k l b l (1). A comparison of the frequencies obtained with those expected according to these suppositions gives a rather good agreement:

Type	I	II	III	IV	V	Total
1010 Observed frequencies	26	15	12	9	5	67
Theoretical proportions	27	9	12	9	7	64
Expected numbers.	29	3	13	9	7	67

Type II is the only one, that does not wholly accord with the expectation; the cultures of F_3 -families that are grown in this year, will decide if these provisional suppositions are well-founded or if they are not; the meaning of the more detailed divisions of the types into subtypes may be kept also for further research.

The second of both spontaneous hybrids gave a more limited descendance; its examination gave therefore less results than the first one. Here also a grouping into five different types could be made; type I was divided into two subtypes: one darker Ia (pl. I fig. 5), the other lighter (pl. I fig. 6); type II was a blueviolet striped bean with a yellowish-white groundcolour (pl. I fig. 1); type III the same but the striping in reddish-violet (pl. I fig. 2), IV the Rotjes-race, and V the Wagenaar-race. Type III may be supposed to be identical with the unknown father. The segregation observed in this F_2 -family did not agree very well with the theoretical expectations, as is indicated by the following table:

Type	I	II	III	IV	V	Total
1011 Observed frequencies	3	9	5	3	2	22
Theoretical proportions	27	9	12	9	7	64
Expected numbers.	10	3	4	3	2	22

If here again the types with and those without one of the visible factors are taken together, the same phenomenon as that in the previous cross is met with: with K^1 (= the factor for violet *striped* pattern on the yellowish-white groundcolour), types I, II and III,

there are 17, without K^1 (IV and V) 5 individuals; with Bl. (I, II) 12, without Bl. (III) 5 plants; with L (I, IV) 6, without L (II, III, V) 16 individuals. With regard to K^1 and Bl the segregations come very near the monohybrid 3:1-proportion; those for the L-factor are here also very deviating from the expected proportion. The cryptomeric state of the L-factor in those types, that do not possess the Bl-factor, is here the probable cause. But besides the deviation in types I and II is highly remarkable; here the cause may perhaps been found in a possible coupling or repulsion between one of the factors L or Bl and the K^1 -factor. The cultures of this year will probably give certainty about this problematic factorial relation.

10. CROSS OF BRUINE $\times$ ZWARTE.

Only one F_1 -plant of this hybrid was available; its seedcoats were intense black. The F_2 -family segregated very simply into three groups: I black (39 individuals), II reddish-brown (phaenotypically identical with the F_1 of cross 4, Citroen $\times$ Rotjes; 6 individuals) and III yellowish brown, as the common yellow-brown race „Bruine” (3 plants). The hybrid did not segregate further than the yellow-brown type; it may thus be concluded, that the G-factor was present in both parents. Besides this one, the black parent seems to have possessed the L-factor and a factor Z, that is responsible for the black colouring. The hybrid has been GG Ll Zz and segregates thus into 9 GLZ, 3 GlZ, 3 GLz and 1 Glz; giving so 12 blacks: 3 reddish-brown: 1 yellow-brown, and this is in good accordance with the numbers observed:

Type	I	II	III	Total	Remark
1028 Observed frequencies	39	6	3	48	Among the 39 blackseeded individuals there were 4, that had besides black, also reddish-brown beans; their classification in type I may thus be doubtful.
Theoretical proportions	12	3	1	16	
Expected numbers.	36	9	3	48	

11. CROSS OF KIEVITS $\times$ ZWARTE.

In a culture of the Kievits-race, one spontaneous hybrid was found with blackmarbled pattern upon a greyish white groundcolour. The F_2 -generation of this hybrid consisted of 53 individuals, all coloured, so that the supposition: the unknown father was a white bean, may be con-

sidered to be very feeble. Most probably a blackseeded bean had functioned as pollenparent; the segregation fell into 11 phaenotypic groups:

- 977 I black marbling upon greyish white groundcolour (28 individuals);
 II matblue marbling upon greyish white groundcolour (1 ind.);
 III darkblueviolet marbling upon yellowish white groundcolour (1 ind.);
 IV matblueviolet marbling upon yellowish white groundcolour (1 ind.);
 V greyish brown marbled, here and there somewhat violet (3 ind.);
 VI reddish brown marbled, here and there somewhat violet (1 ind.);
 VII red marbling, here and there somewhat violet (2 ind.);
 VIII yellowish brown marbling, here and there somewhat violet (2 ind.);
 IX selfcoloured black (9 ind.);
 X reddish brown selfcoloured (1 ind.);
 XI Wagenaar-type (1 ind.);

Such a complicated segregation with very little groupnumbers does not allow a detailed analysis of the factorial constitutions, if, as is here the case, only one F_2 -family is available; the F_3 -cultures in this year will perhaps give the possibility of a decision. The results given above however are sufficient for argumenting a provisional hypothesis about the genotypic factors that are present in the parents and in the hybrid. There are types possessing the factor for black, Z, and other types without this factor; there are types with L, the factor for grey-brown and types missing this one; there are types with G, the factor yellow-brown and types, where this factor is failing and last types with K, the factor for Kievits-pattern besides types without K. The probable genotypic constitution of the Kievits-race can thus be supposed to be $ggll$ $bl.bl.zzKK$, while the black race had, in harmony with the suppositions in the foregoing cross $GGLLBl.Bl.ZZkk$ as genotypic formula. The segregation will thus be that of a pentaheterozygote and cannot be studied in detail in the few materials till now available. In some respects the numerical proportions are

clear enough; four groups may be found that are rather good in accordance with a 9:3:3:1-segregation: blackmarbled, blackunicoloured, no-black-marbled; no-blackunicoloured are represented by 28:14:9:2 individuals, while a segregation according to 9:3:3:1 would give as expectation 30:10:10:3 in a total of 53. It seems however to be useless to go further into details about such conclusions, before more materials are available.

12a. CROSS OF BRUINE $\times$ WITTE.

Four F_1 -plants were obtained by artificial hybridization: one from the white-seeded plant as mother, three from the brown race as seedparent. Besides four spontaneous hybrids were found in a culture of white-seeded plants and five others from a culture of the brown race, and recognised from their manner of segregation to have been born as hybrids with white as pollenparent. Those, in total thus thirteen, F_1 -plants showed not only to have the same phaenotype, but also they segregated in their F_2 -generations in one and the same manner, giving the same phaenotypically distinctive groups, so that the genotypical identity of the F_1 -individuals might be concluded to with rather great probability. The segregation resulted into the occurrence of nine phaenotypes: the first, I, had the same seedcoatpattern as the F_1 -individuals, blackmarbled upon a yellowbrown ground-colour (pl. II. fig. 13); II had a reddish brown marbling upon yellowish brown; III had a grey-brown marbling upon a greyish white ground (pl. II. fig. 14), IV was yellow-brown-marbled upon a light yellow groundcolour (pl. II fig. 15); as parallels to these four groups could be considered four others: V selfcoloured black (fig. 16), VI selfcoloured redbrown, VII selfcoloured grey-brown (fig. 17) and VIII selfcoloured yellow-brown; as last a group (IX) of whitedseeded plants without coloured navelring.

The distribution of the descendants among these nine groups results from the table given below; the good harmony between the theoretical suppositions and of the proportion observed of coloured: white (279:87 with an expectation of 275:91) is striking immediately. All white parents seem to have been of an aa-constitution and from this absence of the A-factor to have derived their white colour; relative to their other genotypic factors, nothing can be said. Therefore, if the little numbers of each family allow a con-

clusion, one might suppose the genotypical identity of the white parents in their whole genotypic constitution, because of the parallelism between the various segregations, that have shown all the same scheme:

Type	I	II	III	IV	V	VI	VII	VIII	IX	Total
Artif. hybrid from Witte	7	1	1	3	5	2	4	2	6	31
983 Spont. hybrid from Witte	9	2	—	1	3	—	2	3	5	25
984 " " " "	19	5	—	—	7	2	3	—	15	51
985 " " " "	10	—	4	5	8	1	6	2	8	44
986 " " " "	7	4	—	2	3	1	5	4	12	38
1020 Artif. hybrid from Bruine	1	2	—	—	1	1	1	—	3	9
1024 " " " "	1	1	—	—	—	—	1	—	1	4
1025 " " " "	4	3	1	1	2	—	—	—	—	11
1029 Spont. hybrid from Bruine	23	4	4	3	19	9	7	11	30	110
1094 " " " "	1	1	—	—	2	2	—	3	3	12
1097 " " " "	4	1	—	—	1	—	3	—	2	12
1098 " " " "	8	—	—	—	—	—	1	—	—	10
1102 " " " "	3	—	—	—	4	—	—	—	2	9
	97	24	10	17	55	18	33	25	87	366
	148				131				87	366

Though these numerical proportions do not meet in details the theoretical suppositions given above, there are certain conclusions, that may be drawn from these segregations. The F_1 -plants may be considered to have been heterozygotes in five genotypic factors: A (groundfactor for pigmentation), D (factor for coloured navelring), G (yellow-brown colour of the seedcoat), L (grey-brown seedcoat) and Z (black seedcoat). Probably they were also heterozygotes in the factor B, that causes according to KOOIMAN in heterozygotic state the eversporting marbled pattern. In every case the segregation is in perfect accordance with the classical proportion 6:6:4, mentioned above, because of the numbers observed to be 148 marbled: 131 selfcoloured:87 whites (expected in a total of 366: $137\frac{1}{4}$ m: $137\frac{1}{4}$ s: $91\frac{1}{2}$ w.). The absence of yellowish brown plants however (not only marbled, but also selfcoloured) in the rather comprehensive family 984 indicates with some probability that its F_1 -plant was a homozygote in respect to the L-factor, so that the fatherplant seems to have been not a yellow-brown, but a

red-brown (Rotjes)-plant. The segregation of white-seeded aa-plants results from the heterozygotic state of the A-factor; the D-factor, that is visible more or less in all coloured individuals, is missing entirely in these white-seeded descendants, so that no one individual of the so-called H-type has occurred. Therefrom one might conclude to a linkage of very high degree between the factors A and D; all aa-plants were also dd, while all AA-plants, insofar one could discern it phaenotypically, possessed the coloured navelring D. The conclusion of the heterozygotic state of the G-factor might perhaps be met with some doubt, because of the segregation going not farther than the yellow-brown type; the previous crosses however have led to the genotypic formula $g g L L$ for beans of the grey-brown type (like the Rotjes-race) and the occurrence of such grey-brown descendants in these F_2 -families can only be explained by supposing a heterozygotic state of the G-factor.

TSCHERMAK already had found a difference in proportions of colourtypes between the marbled beans and the selfcoloured ones; the numbers given above seem to show the same. Here also, as in TSCHERMAK's researches, the blackselfcoloured beans are too few in number in relation to the numbers of grey-brown and yellow-brown types; among the marbled groups these proportions seem to have been reversed. The further study of the F_3 -families will give more confirmed conclusions.

12b. CROSS OF BRUINE $\times$ WITTE?

Besides the black-yellow-brown marbled F_1 -plants, the posterities of which gave entirely parallel segregations, one plant, originated as spontaneous hybrid in a culture of „Bruine” and showing the same phaenotype as the others, segregated in F_2 in another way, especially regarding the little number of white-seeded descendants. The distribution of its F_2 -descendants among the same phaenotypes as in the previous crossings was found to be as follows:

Type	I	II	III	IV	V	VI	VII	VIII	IX	Total
1023 Spont. hybrid from Bruine	11	4	—	—	8	2	7	5	3	40

If truly the pollenparent in this case has been a white-seeded individual, this white-seeded plant will probably have been an A-individual, that missed all other colourfactors or in which all other colourfactors were in a kryptomeric state. The formula of the hybrid will perhaps have been A A B b G g L l Z z; a further research of the F₃-families will give here the correct explanation.

12c. CROSS OF BRUINE × WITTE.

The black-yellow-brown marbled phenotype is of course not the only one, that can take its origin after the cross Bruine × Witte. Other spontaneous crossings were found, though in remarkable less numbers. So for example reddish brown-yellowbrown marbled individuals; their segregation was of course less complicated than that of the blackmarbled F₁-plants. Five phaenotypical groups only were observed in these segregations: I redbrown marbled, II yellow-brown-marbled, III redbrown selfcoloured, IV yellow-brown selfcoloured and V white. The frequencies of these groups in the F₂-generations that were grown and in some F₃-families, that were the posterities of redbrown marbled F₂-individuals, coming from a cross Bruine × Witte, and segregating along the same lines, are tabulated in the following table:

Type	I	II	III	IV	V	Total
1044 Spont. hybr. from Bruine	8	2	11	4	7	32
1047 " " " "	4	1	6	1	5	17
1048 F ₃ after spont. hybr. from Bruine	20	7	19	6	19	71
1049 " " " " " "	11	4	18	5	11	49
1050 " " " " " "	18	7	14	4	12	55
	61	21	68	20	54	224

Other F₃-families, derived from redbrown marbled F₂-plants segregated in still less phaenotypical groups; these may also be given here in a table:

Cf table page 133

The whole segregation indicates a trihybrid nature of the F₁-plants, the formula of which can be written as A a B b G G L l; its descendants segregate thus in five phaenotypical groups: I A B b G L, II A B b G l, III A B B (or b b) G L, IV A B B (or b b) G l and V white a-plants.

Type	I	II	III	IV	V	Total	Probable genotype of the F ₂ -plant
1045 F ₃ -family	6	—	9	—	5	20	A a B b G G L L
1046 "	11	—	14	—	—	25	A A B b G G L L
1053 "	15	3	17	7	—	42	A A B b G G L l
1054 "	12	5	16	3	—	36	A A B b G G L l
1057 "	18	—	21	—	12	51	A a B b G G L L

The F₃-families 1048, 1049 and 1050 are descendants from plants with A a B b G G L l as genotypic formula; the Families 1045 and 1057 from A a B b G G L L-individuals, 1046 from an A A B b G G L L-plant, while 1053 and 1054 have had an A A B b G G L l-individual as ancestor.

12d. CROSS OF BRUINE × WITTE.

A third phaenotype was also found in a culture of Bruine as spontaneous hybrid from a white seeded pollenparent: a plant with yellow-brown-marbled seeds, identical with the phaenotype of group II in the previous crosses. In the same manner as the F₂, raised from this F₁-plant, some other F₃-posterities, grown from the yellow-brown-marbled F₂-individuals mentioned under 12c, segregated into 6 yellow-brown-marbled : 6 yellow-brown selfcoloured : 4 white. For the numbers of segregation were in these cases : 8 : 5 : 3; 12 : 14 : 9; 21 : 19 : 14; 9 : 11 : 5 and 26 : 22 : 17, or as totals 76 : 73 : 48, being expected the proportions of $73\frac{7}{8} : 73\frac{7}{8} : 49\frac{1}{4}$. This spontaneous hybrid, as also the F₂-plants in the foregoing cross had the genotypic formula of A a B b G G and segregated into 6 A B b G : 6 A B B (or b b) G and 4 a-plants.

13. CROSS OF CITROEN × WITTE?

As last cross among *Phaseolus vulgaris* a spontaneous hybrid may be mentioned, found in a culture of the Citroen-race, that gave a segregation somewhat parallel with those of the hybrids, treated under 12b. The red-brown and yellow-brown types are missing here entirely; in other directions the hybrid however shows a more detailed segregation. The F₁-plant had greyish black-marbled seeds with a greyish-white groundcolour (pl. I fig. 9) and segregated in F₂ into eight phaenotypical groups. I was identical with the F₁-type;

II was grey-marbled upon white; III greyish black selfcoloured; IV grey selfcoloured, V H-type (white with brown navelring); VI Wagenaar-type, VII lemoncoloured and VIII white. The frequencies in F_2 were as follows:

Type	I	II	III	IV	V	VI	VII	VIII	Total
1000 Spont. hybr. from Citroen	10	4	5	2	5	1	1	1	29

If here the same blackfactor Z has played a rôle, as in the previous crosses, one might conclude, that it gives the phaenotype of bright black only when the factor for yellowbrown, G, is also present; if this factor is absent, the Z-factor will give only a greyish-black colour. Further conclusions may be reserved for the future.

b. PHASEOLUS MULTIFLORUS.

The scarletrunnerbean is in many respects less favourable for a genotypic analysis of its varieties than the races of the common gardenbean; first in individual cultures the plant requires a stalk and a square metre each, and second the cross-fertilization in this species is certainly more important than in the other, so that isolation of the inflorescences seems to be a necessary condition for obtaining exact results. This isolation however is very difficult and has given in my researches in a few cases only some seeds, but never more than four in a whole inflorescence. Obtaining of reliable numbers in these researches is thus much less probable than in those concerning *Phaseolus vulgaris*.

The number of varieties in this species is only a few; the most common form with red flowers has blackmarbled seeds upon a light-violet ground (pl. III fig. 2); besides there are redflowering forms with black marbling and a darkviolet groundcolour (fig. 3), redflowering ones with light-violet colour and here and there little black spots (fig. 4), redflowering plants with shining black seeds (fig. 5), a red-and-white flowering (socalled Papillon) type with yellow-white and brown-marbled seeds (fig. 6), red-and-white flowering with yellowish-white and grey-marbled seeds (fig. 7) and last a white-flowering race with pure white seeds (fig. 1), which race is used on a great scale as vegetable in our country. The redflowering

PLATE I

and red-and-white ones are used more as ornamental plants.

The whitedseeded race was cultivated during four years (1918—1921) always in the neighbourhood of redflowering individuals; it has given however never coloured descendants; artificial hybridizations though made on a rather great scale, have never yielded any result.

The redflowering race, obtained as such from a seedgrower, has shown from the beginning a rather important multiformity; in the first year of cultivation already the types 2, 3, 4 and 5 could be discerned. In later years plants of types 6 and 7 were obtained. The posterities of these plants have for the greater part shown to be constant; some of them however segregated into more types. These segregations are given in the following table:

Type of motherplant :	Type of descendants.							Total
	1	2	3	4	5	6	7	
1. White	42	—	—	—	—	—	—	42
"	20	—	—	—	—	—	—	20
"	31	—	—	—	—	—	—	31
2. Lightviolet marbled	—	27	—	—	—	7	—	34
" "	2	12	—	—	11 ¹⁾	—	—	25
" "	3	52	—	—	2 ¹⁾	—	—	57
" "	—	73	4 ¹⁾	—	3 ¹⁾	—	—	80
" "	—	56	1 ¹⁾	—	8 ¹⁾	—	—	65
" "	10	45	7 ¹⁾	—	14 ¹⁾	—	—	76
" "	8	59	—	—	9 ¹⁾	—	—	76
" "	—	45	—	3 ¹⁾	—	—	—	48
3. Darkviolet marbled	—	9	21	—	—	—	—	30
" "	—	16	59	—	3 ¹⁾	—	—	78
4. Lightviolet spotted	—	9	—	21	—	—	—	30
" "	—	17	—	44	1 ¹⁾	—	—	62
5. Black	—	7	—	—	23	—	—	30
"	—	9	—	—	31	—	—	40
"	—	18	—	—	60	—	—	78
"	4	14	—	—	47	—	—	65
"	17	15	—	—	43	—	—	75
6. Brown-white marbled	—	6 ¹⁾	—	—	—	10	3	19

1) = probably new spontaneous hybrids,

Though these numerical proportions are not entirely proving, they seem to indicate the correctness of following conclusions:

1. White is the recessive form, that is missing a groundfactor for pigment;

2. Lightviolet-marbled plants do segregate white descendants; the monohybrid nature of this segregation, however, is uncertain (168:23);

3. Darkviolet-marbling dominates lightviolet marbling; the difference is caused by only one factor (80:25);

4. The spotted type dominates the lightviolet marbling, as may be concluded from the segregation 63 spotted: 26 lightviolet marbled;

5. Black is dominant over lightvioletmarbled, as also over white seedcoat; 204 blacks: 63 lightvioletmarbled; one of the segregations seems to segregate into 12 black: 3 lightvioletmarbled: 1 white, the other into 9:3:4;

6. Brownmarbling (Papillonpattern) is recessive to lightviolet marbling (27:7); besides an absolute linkage be mentioned between this pattern of the seedcoat and the red-and-white colour of the flower (these characteristics may also be considered as to be caused by one pleiotropic factor);

7. The brown papillonpattern is dominant over the grey-white marbling (segregation 10:3).

13

13

14

14

15

15

16

16

17

17

18

18

19

19

20

20

21

21

22

22

23

23

24

24

25

25

LITERATURE CITED.

- EMERSON R. A., 1902. Preliminary account of variation in bean hybrids (15th. Ann. Rept. Nebr. Agr. Expt. Stat. S. 30—43).
- EMERSON R. A., 1904. Heredity in bean hybrids (17th. Ann. Rept. Nebr. Agr. Expt. Stat. p. 33—68).
- EMERSON R. A., 1909^a. Factors for mottling in beans (Ann. Rept. Am. Breeders Ass. V. p. 368—376).
- EMERSON R. A., 1909^b. Inheritance of color in the seeds of the common bean (22 d. Ann. Rept. Nebr. Agr. Expt. Stat. p. 67—101).
- FRUWIRTH C., 1919. Handbuch der landwirtschaftlichen Pflanzenzüchtung. Band III. Dritte Auflage (Berlin, P. Parey, 1919).
- HARLAND C. S., 1919. Inheritance of certain characters in the cowpea, *Vigna sinensis* (Journ. Genetics. VIII. p. 101—132).
- KAJANUS B., 1914. Zur Genetik der Samen von *Phaseolus vulgaris* (Zschr. f. Pflanzenzüchtung. II. P. 377—388).
- KOOIMAN H. N. 1920. Over de erfelijkheid van de kleur der zaadhuid van *Phaseolus vulgaris* (Diss. Univ. Utrecht. Bussum C. A. J. v. Dishoeck, 1920).
- LUNDBERG J. F. och AAKERMAN A., 1917. Jakttagelser rörande fröfärgen hos avkommen av en spontan korsning mellan tvenne former av *Phaseolus vulgaris* (Sveriges Utsädesfören. Tidsskr. XXVII, p. 115—121).
- MANN A., 1914. Coloration of the seedcoat of cowpeas (Journ. agr. Research II. p. 33—56).
- MENDEL G. J., 1865. Versuche über Pflanzenhybriden (Verhandl. naturf. Ver. Brünn. IV. p. 3—47).
- REINKE J., 1915. Eine bemerkenswerte Knospenvariation der Feuerbohne nebst allgemeinen Bemerkungen über Allogonie (Ber. Deutsch. Botan. Gesellsch. XXXIII p. 324—348).
- SHAW J. K. and J. B. NORTON, 1918. The inheritance of seed coat colours in garden beans (Mass. Agr. Expt. Stat. Bull 185, p. 59—104).
- SHULL G. H., 1907. Some latent characters in a white bean (Science 1907, p. 828—832).
- SHULL G. H., 1908. A new mendelian ratio and several types of latency (Amer. Natural. XLII, p. 433—451).
- SIRKS M. J., 1920. De analyse van een spontane boonenhybride (Genetica II, p. 97—114).
- SPILLMAN W. J., 1913. Colour correlations in cowpeas (Science XXXVIII, p. 302—304).
- TJEBBES K. en H. N. KOOIMAN, 1919. Erfelijkheidsonderzoekingen bij boonen I en II (Genetica I, p. 323—346).
- TJEBBES K. en H. N. KOOIMAN, 1921. Erfelijkheidsonderzoekingen bij boonen,

IV. Over den strepingsfactor. Een geval van volkomen afstooting tusschen twee factoren. V. Analyse eener spontane kruising van de stokkievitsboon (*Genetica* III, p. 28—49).

TRACY W. W. JR., 1907. American varieties of garden beans (U. S. Dept. Agr. Bur. Plantindustry. Bull. 109. 173 pp.).

TSCHERMAK E., 1901. Weitere Beiträge zur Verschiedenwertigkeit der Merkmale bei Kreuzung von Erbsen und Bohnen (*Zschr. f. d. Landw. Versuchswesen Oesterr.* IV. p. 641—735).

TSCHERMAK E., 1902. Ueber die gesetzmässige Gestaltungsweise der Mischlinge (*Zschr. f. d. landw. Versuchswesen Oesterr.* V. Sep. 80 pp.).

TSCHERMAK E., 1904. Weitere Kreuzungsstudien an Erbsen, Levkojen und Bohnen (*Zschr. f. d. landw. Versuchswesen Oesterr.* VII. p. 533—638).

TSCHERMAK E., 1912. Bastardierungsversuche an Erbsen, Levkojen und Bohnen (*Zschr. und Abstamm. v. Vererb. Lehre* VII. p. 81—234).

TSCHERMAK E., 1919. Bastardierungsversuche mit der grünsamigen Chevrier-Bohne (*Zschr. f. Pflanzenzüchtung* VII. p. 57—61).

PLATE III

A. S. Zimerly