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INHERITANCE OF COLOUR IN *PHASEOLUS VULGARIS* L. II. A CRITICAL REVIEW

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CONTENTS

1. INTRODUCTION

Thirty years ago the present author wrote 'Inheritance of colours in *Phaseolus vulgaris* L., I' ('PRAKKEN', 1940). In that article he tried to reconcile his own results ('PRAKKEN', 1934 and later) and those of some other investigators, especially KOOIMAN (1920, 1931), with those of the important *Phaseolus* and *Pisum* specialist, the late dr. H. LAMPRECHT. The latter has made many contributions to the study of colour-inheritance in *Phaseolus*, many of which are of a lasting value, because of the accurate colour descriptions and the detailed genetic analysis. On the other hand, however, according to the present writer, LAMPRECHT twice made a fatal misinterpretation in the factorial explanation, resulting in an unnecessarily complicated and, I think, quite faulty factorial scheme of colour inheritance.

Hence my reconciling article ('PRAKKEN', 1940), convinced as I was, thanks to the accurate colour descriptions and, at least in the earlier articles, clear F_2 and F_3 analyses of LAMPRECHT, that we were working with quite the same, or at least strikingly analogous colour types and genes. Part of our races were, moreover, exchanged.

For the sake of clarity, it is desirable to remind of the generally useful (though not strictly objection-free) classification of *Phaseolus* genes for seed coat colour:

a. Groundfactor or *basic gene*

Almost from the beginning of the century (e.g. SHULL, 1908) it became clear that a dominant gene, usually indicated as *P* but sometimes as *A*, is necessary for the plant to be able to produce seedcoat colour. LAMPRECHT (XIII, 1936b) mentions, beside *P*, a second 'groundfactor', *Gri*, but about this gene pair *Gri gri* I do not have personal experience.

b. Chromogenous factors or (complementary) *colour genes*

These are dominant genes which, together or complementary with the basic gene, produce a certain, usually pale, seedcoat colour.

c. Intensifying factors or *modifying genes*

These are genes which, together with the basic gene only, do not produce any seedcoat colour, but which have a darkening influence upon the colour produced by the combined action of basic gene and colour genes. The darkening action is connected with the dominant allele, with but one exception, viz. *rkrk* or $rk^d rk^d$ for recessive red colour (*rk* coming from the variety *R*ed *K*idney; SMITH, 1939 and later). Dominance is in most cases complete or almost complete.

The very core of disagreement in the factorial explanation of colour inheritance centres around the problem whether certain genes act as 'colour genes' or as 'modifying ones'. More precisely: LAMPRECHT conciders the genes *G* and *B* as *colour genes* (*Farbenfaktoren*), each producing, together with *P*, a brown hilumring while leaving the rest of the seedcoat almost colourless, whitish. This type of seedcoat colour is often called 'hilumring type' or H-type. LAMPRECHT describes *PG* as 'speckweiss' (fleshy white) and *PB* as 'veilchenartig weiss' (purplish tinted white), but he often mentions that both types are not clearly distinguishable. PRAKKEN's experience on the contrary is that *G* ('yellow brown factor') and *B* ('greenish brown factor'), together with *P* only, do not produce a brown hilumring, leaving the whole seedcoat pure white: they are but *modifying genes*.

In a comprehensive article of 1951, 'Die Vererbung der Testafarbe bei *Phaseolus vulgaris* L.', LAMPRECHT discussed my objections into some detail and stuck to his interpretation. One might think the problem rather unimportant, but the two different points of view have far reaching consequences.

LAMPRECHT (VI, 1933, p. 251 and later) writes: 'Die verschiedenen Kombinationen der genannten sechs Gene ('Farbenfaktoren', i.e. colour genes: *C*, *J*, *G*, *B*, *V* and *R*) verursachen meistens mehr oder weniger dunklere Töne als einer reinen Mischung der jedem dieser Gene (zusammen mit *P*) entsprechenden Farben zukommen würde. Hier bestehen insofern *keine bestimmte Regeln*, als etwa dem Hinzukommen, eines bestimmten Gens zu irgendwelchen anderen Kombinationen eine bestimmte Wirkung entsprechen sollte. *Es kommt hierbei stets auf die Kombination in ihrer Gänze an, welche Farbe erzielt wird*'. The present author, however, will try to make clear that *every* individual gene has, in all combinations, its own *recognizable and generally describable action*: each gene can even be 'named' according to this general action.

In ascribing 'hilumring-action' to the genes *G* and *B* (according to PRAKKEN purely modifying genes), LAMPRECHT linked actions of complementary colour genes with those of modifying genes. As a consequence, LAMPRECHT in the beginning did not recognize a special colour gene with hilumring-action, but later he *must and did find* such a gene (*Can*, probably also *Ins*). And, conversely, under certain genetical circumstances, he *must and did find* purely modifying genes with actions homologous to those of *G* and *B* (his modifying genes *Ca, Flav, Och* and *Vir*). So the whole thing got very complicated while in fact it is relatively simple.

After the war, the present writer did not find the time or opportunity to re-scrutinize the extensive material of all *Phaseolus* investigators. Nor did he publish results of his own further experiments, but his experimental work was continued. Starting 1930, every year up to 1969 (except for the six years of the world war) thousands of bean plants resulting from hundreds of crossings (usually diallel ones, between 3–8 varieties; or various varieties or lines crossed with the same recessive type) were studied. From the very first *each plant was individually numbered and described for all colour characters*: hypocotyl, cotyledons, flower, fruit and seedcoat, and sometimes the plant as a whole. The experience so gained and the results (for the far greatest part non-published) make it possible to him to compare the conclusions of the various colour investigating authors. Being now retired he finds it worthwhile to continue the work of reconciliation (term of YARNELL, 1965).

2. SCOPE OF THE REVIEW

It is not the author's intention to present a more or less complete historical review of the literature on colour inheritance in *Phaseolus*. For more general reviews there may be referred to KOOIMAN (1931), LAMPRECHT (1941) and YARNELL (1965).

Work on seedcoat colour in *Phaseolus* during the first two decades of the century had to struggle with too many incompletely understood problems at the same time. Very important were (and are) the many correlations between plant-, flower- and seedcoat-colour. Some genetic problems on seedcoat colour can hardly be solved without knowing these correlations. Conversely, it is very inefficient and easily leads to misinterpretations when characters as hypocotyl (or plant) colour, or of colour intensification at the tip of the standard, are analysed genetically without at the same time studying seedcoat colour and pattern of the individual plants. Another troublesome point was that notions about basic gene, complementary colour genes and modifying genes developed slowly. The most complex and difficult problem, even at the moment only incompletely understood, was and is that of seedcoat colour *pattern*: mottling, striping or other more or less regular patterns in two, three or even four different colours, usually covering the whole seedcoat (cf. LAMPRECHT XV, 1940a and LAMPRECHT, 1947).

From the very beginning two types of patterned seedcoat were distinguished. On the one hand '*ever-segregating mottling*': offspring after selfing of the mottled parent always segregating into 2 mottled: 2 selfcoloured, or, with heterozygosity for the groundfactor P, into 6 mottled: 6 selfcoloured: 4 white. On the other hand so-called '*constant mottling*' (or striping, speckling, etc.): offspring after selfing either segregating into 3 mottled (or striped etc.): 1 selfcoloured, or, in case of homozygosity, all mottled (or striped etc.).

An important step was the finding by Kooiman (1920, 1931), corroborated and carefully worked out by Lamprecht (I, 1932a and later), that ever-segregating mottling depends on a definite complementary colour gene, indicated by the first as B and by the latter as C; the heterozygote Cc (Bb) is mottled in a darker and a paler colour, and its offspring after selfing is: 1 selfcoloured in the 'dark pattern colour' (CC, resp. BB): 2 of the ever-segregating mottled type (Cc resp. Bb) : 1 selfcoloured in the paler 'background colour' (cc resp. bb). Prakken (1934), starting from the original explanation (Emerson, 1909) by means of two absolutely linked genes $\overset{\frown}{Xy}$-$\overset{\frown}{xY}$ ($\overset{\frown}{Xy}\ \overset{\frown}{xY}$ showing mottling but $\overset{\frown}{Xy}\ \overset{\frown}{Xy}$ and $\overset{\frown}{xY}\ \overset{\frown}{xY}$ not), proposed the selfcoloured dark pattern type to be $\overset{\frown}{Cm}\ \overset{\frown}{Cm}$, the background colour type $\overset{\frown}{cM}\ \overset{\frown}{cM}$, the hybrid being $\overset{\frown}{Cm}\ \overset{\frown}{cM}$ and therefore mottled: the factor M for mottling locally suppressing the action of the colour gene C, or B of Kooiman).

How this may be, soon all or most experience showed, that the two types of mottling (ever-segregating and constant) *also* are (almost) absolutely linked. Further, that there exist selfcoloured seedcoat types with a dominant red colour (R), and that this same red colour is the dark pattern colour in most (but not all) constant mottled (M) or striped (S) types. Lamprecht (1947) tries to explain the whole rather complicated situation by accepting *two rather closely linked loci* for complementary colour genes, C and R. The heterozygote Cc produces the ever-segregating mottling. In recent years some further c-alleles have been described: c^u (Feenstra, 1960; the suffix u means *u*nchangeable, as it appeared that modifying factors, G, B and V, see chapter 3–5, do not change the pale PJc^u backgroundcolour, neither in selfcoloured c^uc^u nor in mottled Cc^u types), c^{ui} and c^{cr} (Nakayama V-VIII, 1960–'65; c^{ui} means a c^u-allel that also causes an *i*ntense stem and flower colour; in c^{cr} the suffix cr comes from *c*ompletely *r*ecessive, as the heterozygote Cc^{cr} shows the pure dark pattern colour CC, without mottling as in Cc and Cc^u). As regards the locus R for red colour and the various types of constant pattern, Lamprecht (1947) analysed and described a series of seven alleles: $R^{ma} - R^{cir} - R^{res} - R^{st} - R^{rho} - R - r$.

Other investigators as Feenstra and Nakayama always find, with regard to C and R of Lamprecht, only clear monofactorial segregations (1:2:1 or 3:1), without even a single recognizable recombination type. They therefore consider the alleles of C and R as *one multiple allelic series*: $C - C^r - C^m - C^{st} -$ etc. $- c - c^u - c^{ui} - c^{cr}$.

The present author preliminarily prefers to look at C and R as the '*complex locus*' C, hoping to be able to give in following articles an analysis of his own observations over tenths of years and to discuss the character of the certainly very few but actually occurring recombinations.

The problems regarding locus *C* (plus R) are more complex than discussed above. Many other gene symbols than those already mentioned (*C-c* or *B-b*, *M-m*, *S-s*, *R-r*; the multiple allelic series for *C* and for *R*) have been used for characters which, often without it being realized by the author, are linked up with the *C*-complex: *Uc-uc* and *Unc-unc* (Lamprecht) or I_1-i_1 and I_2-i_2 (Nakayama II, 1958) for the presence or not of anthocyanin in hypocotyl and stem; *Inh-inh* (Lamprecht XVII, 1940b) and $I_e i_e$ (Nakayama V, 1960; the recessive alleles *inh* and i_e having an inhibiting influence upon the seedcoat colour action of *V* and some other modifying factors, *G* and *B*; these inhibiting influences are incorporated in the allel c^u, Feenstra, 1960, Nakayama VII and VIII, 1964 and '65); *Nud-nud* (Lamprecht XII, 1936a, p. 163) for an intense anthocyanin colour of the whole plant and flower (cf. Nakayama VII, 1964, the c^{ui} allel); *Aeq-aeq* (Lamprecht, 1948) for colour intensification at the tip of the standard (usually going together with striped seedcoat, C^{st} or R^{st}); *Ro-ro* (Lamprecht, 1951) for intense red (*v*) resp. blackviolet (*V*) striping of the pod wall (also connected with the C^{st} allel).

The problems in connection with red seedcoat colour (*R*-series of Lamprecht) are still more complicated by the existance of a locus for *a recessive red colour*, independently segregating with *R*, the only case, as far as known to me, in which darkening does not depend upon a dominant but upon a recessive allele. Smith (1939 and later) namely described the action of the triple allelic series *Rk* (non-red)-*rk* (pale red)-rk^d (darker red), the symbol *rk* being derived from the red seeded variety *R*ed *K*idney. Prakken in a short article (1938) already described the action of the same modifying recessive Red Kidney gene, without giving it a symbol, but with the further observation that the allele for recessive red seedcoat also produces *a red striping* along the veins of the wing (such red striping was already described by Miyake e.a., 1930, while Lamprecht, XII, 1936a, p. 163, introduced the symbol *Lin-lin* for it).

In order to have this critical review as surveyable as possible this whole field of the 'red' colours, produced by the multiple allelic series of *R* and *Rk*, will further be left out of discussion.

An important point is of course the morphology and anatomy of the various colours and patterns. Many scattered observations exist, but these questions will not be discussed. Also on the chemistry of colours various more or less superficial observations exist, the first profound study on the biochemistry of colour genes being that of Feenstra (1960), who specially investigated the actions of *Sh-sh* (shine-factor, *J-j* of Lamprecht), *V*-v^{lae}-*v* (violet-factor) and of some alleles of the *C*-locus, C^r-*C*-c^u, but also these results will not be discussed.

After so having excluded various fields and complications, the scope of the present review becomes clear. Attention will be concentrated upon the phaenotypical action of *groundfactor*, *complementary colour genes* and *modifying genes* which in their co-operation are responsible for what briefly often is called the group of *yellow-black colour types*, including the ever-segregating mottled *Cc* types. As far as possible the symbols used by different (not all) authors will be homologized, (cf. for this homologization also Prakken, 1940, table 18, p. 405, and FEENSTRA, 1960, table 1, p.6). A rather simple picture, mainly agreeing with KOOIMAN's analysis, will result, and I hope to be able to show, that also the seemingly very complicated results of LAMPRECHT fit into this picture, which may furnish a base or starting point for further renewed genetical, anatomical, developmental and biochemical investigations.

3. INHERITANCE IN THE GROUP OF 'SHINY DARK PATTERN COLOURS'

In chapter 2 it was made clear that attention will be centered upon the group of yellow-black seedcoat colours, or slightly more detailed the group of white-yellow-brown-violet-black colours, including both 'dark pattern' *CC* colours and the corresponding paler 'background colours' *cc*, together with the mottled *Cc* types (KOOIMAN: *Bb*).

In the next chapter 4, mainly dealing with the results of KOOIMAN (1920, 1931) it will be learned that a certain number of *colour groups* can be distinguished (depending on the complementary action of three dominant colour genes, together with the groundfactor or basic gene), and that part of these colour groups show a more or less parallel or homologous *colour series* (depending on the action of three dominant modifying genes). The colour groups and series are represented in the scheme p. 39. The gene symbols used are mainly those of LAMPRECHT: to the left the three 'colour genes' *C, D* and *J*, at the top the three 'modifying genes' *G, B* and *V*.

The 'colour groups', represented by the horizontal rows I till VIII in the scheme, are mainly as follows:

I.	white background colour group	(*cc dd jj*),
II.	mat dark pattern colour group without brown hilumring	(*CC dd jj*),
III.	hilumring type background colour group	(*cc D. jj*),
IV.	mat dark pattern colour group with brown hilumring	(*CC D. jj*),
V.	shiny background colour group, always brown hilumring	(*cc dd J.*),
VI.	shiny dark pattern colour group, always brown hilumring	(*CC dd J.*).

Most of the investigations during the first decades of the century were made within the last group, the very common '*shiny dark pattern group or series*', with its deep, lively colours, 'hard colours' called by KOOIMAN (1920, 1931). It is within this series (row VI of the scheme) that the various colours are the most clear and distinct, and the best describable, recognizable and comparable.

Comparing now analyses, descriptions with or without the use of colour systems (OBERTHÜR; KLINCKSIECK et VALETTE; RIDGWAY; MAERZ and PAUL; see after lit. list), or coloured pictures from various authors of the rather early period, *one repeatedly meets the same or very analogous segregations* for colours within this 'shiny dark pattern colour group'. From the palest (the most recessive) to the darkest (the most dominant) types the colours can be grouped under the colours mentioned in VI-1 to VI-8. For comparison LAMPRECHT's perfect analysis of this group (in his article I, 1932), his specific colour names and his gene symbols are also given (cf. row VI of the scheme):

VI-1. *(Pale) greenish yellow*, cream- or canary yellow or greenish buff class.
(cf. LAMPRECHT: *(CdJ)gbv*, 'chamois, oft mehr oder weniger Kanarien- bis Zitronengelb').
VI-2. *Yellowbrown* or orange class, sometimes called yellow.
(cf. LAMPRECHT: *(CdJ)Gbv*, 'bister' or yellowish brown).
VI-3. *Greenish brown*, greyish olive or chocolate class.
(cf. LAMPRECHT: *(CdJ)gBv*, 'münzbronze' or buffy citrine).
VI-4. *Dark brown*, coffee brown or reddish brown class.
(cf. LAMPRECHT: *(CdJ)GBv*, 'mineralbraun' or mineral brown).
VI-5. *Dark violet* or blackviolet class, sometimes almost black.
(cf. LAMPRECHT: *(CdJ)gbV*, 'dunkel veilchenviolett' or violet purple).
VI-6. *Dark brown violet* class, sometimes almost black.
(cf. LAMPRECHT: *(CdJ)GbV*, 'kastanienbraun' or maroon, 'bisweilen zu schwarzviolett').
VI-7. and-8. *Black* colour class.
(cf. LAMPRECHT: *(CdJ)gBV* and *(CdJ)GBV*, 'reinschwarz' or black pure; according to LAMPRECHT, however, and the present author has the same experience, *gg Bb Vv* is 'chromgrün bis schwarz').

Before discussing some typical examples of the older literature a general remark may be made. It has to be mentioned that often the classes VI-5 to VI-8 were taken together as 'black'. Usually, however, with the addition, that some seeds or the seeds of some plants are not really black, but of a very dark blackviolet or brown violet. This grouping together certainly depends on the fact that this 'black' V.-group, seen against the lively yellow and brown *vv*-colours, appears as one complex unity, difficult to subdivide. In more recent analyses, partly with the same varieties as in the early ones, subdivision is always possible, only very few plants being difficult to classify.

The rather extensive study of SHAW and NORTON (1918) will be discussed first. On page 62 they give an enumeration of their colour types (incidentally almost all of the 'shiny dark pattern group', cf. below):

A. White.
B. Buff (including greenish buff).
C. Yellow.
D. Medium or bright red.
E. Dark or purplish red.
F. Coffee brown.
G. Black.
H. Olive.

Leaving out the red colours (D and E) and arranging according to 1–8 above, we receive (cf. scheme row VI):

VI-1(B):	greenish buff (= greenish yellow, schamois)
VI-2(C):	yellow (= yellowbrown)
VI-3(H):	olive (= greenish brown)
VI-4(F):	coffee brown (= dark brown)
VI-5 to-8(G):	black (in the wide sense).

As regards the use of the symbols A, B, C, etc., Shaw and Norton write (p.62) that 'an attempt was made in recording observations to designate the expression of each independent character by a separate letter'. With 'each independent character' they mean each individual recognizable *colour* and *not each gene* or gene action. Therefore it is somewhat difficult to extract *gene symbols* from their list of colours, the more so as they themselves think in terms of epistasis and less in terms of combined gene actions.

It is worthwhile also to look at their list of flower colour types, made according to the same principle:

A. White.
B. Light pink (Lamprecht: pale lilac, $Pv^{lae}nud$; Prakken: pale rose)
C. Pink (Lamprecht: bishopsviolet, $PV\ nud$; Prakken: violet)
D. Crimson (Lamprecht: $PV\ Nud$; Nakayama: $Pc^{ui}V$)
E. Waxy pink (Lamprecht: $Pv^{lae}Nud$; Nakayama: $Pc^{ui}v^{lae}$)

They further state that in their material 'black' beans always go together with pink (= bishopsviolet) or crimson flower (V). Surveying their results within the yellow-black shiny dark pattern series, and comparing them with those of Lamprecht, Prakken, a.o., the results apparently can be explained, quite analogous to Lamprecht's and my own material, by the action of *three dominant darkening factors* (preliminary leaving out of consideration if these are complementary colour genes or merely modifying ones):

C (Lamprecht: G) = *'yellow brown factor'* changing greenish buff to yellow brown).

H (Lamprecht: B) = *'greenish brown factor'*, changing greenish buff to olive; C and H (Lamprecht G and B) together produce dark- or coffee brown.

G (Lamprecht: V) = *'violet factor'*, changing light pink (= pale lilac, $P.v^{lae}v^{lae}$) or white ($P.vv$) flower colour into pink (=bishopsviolet, $P.V.$) and at the same time changing the seedcoat colours VI-1 to -4 into VI-5 to -8, (dark) violets and black.

Shaw and Norton were fortunate with their crossings, as (within the yellow-black series) almost all their parent varieties were of the 'shiny dark pattern' (CC) type, and but one, 'Blue Pod Butter' (pale buff), of the 'shiny background' type, and not of the usual cc type, but $c^{u}c^{u}$, or better $c^{ui}c^{ui}$ (cf. p. 4, alleles C-c-c^{u}-c^{ui}-c^{cr}). As mentioned before, the suffix *u* comes from *u*nchangeable, while *i* relates to the *i*ntensifying action of c^{ui} upon plant and flower colour, for which action Lamprecht (XII, 1936, p.163) choose the symbol *Nud-nud*, an action that in Shaw and Norton's material is expressed by the waxy pink (Nakayama: $c^{ui}.v^{lae}v^{lae}$) and crimson ($c^{ui}.V.$) flower colours. The consequence of the presence in their hybrids of Cc^{ui}, instead of as usual Cc (as e.g. with von Tschermak, 1912, cf. below) is, that in F_2 the $c^{ui}c^{ui}$ all show the same pale buff shiny background colour, not changed by G, B or V (The cc shiny background-colours, on the other hand, especially the V-colours, constitute *the most frustrating colour group*, each colour type showing an extreme variability, therefore being very difficult to describe, to name and to classify; cf. chapters 4 and 5 and row V of the scheme).

VON TSCHERMAK's hybrids (1912 and earlier) apparently were not Cc^u but *Cc*. This means that in F_2 1/4 showed the *CC* shiny dark pattern colour series (row VI), in his case from yellow brown to black, 2/4 the *Cc* mottled series and 1/4 the *cc* shiny background series (row V). At that time, however, the *CC-Cc-cc* relation was still unknown (discovered by KOOIMAN, 1920, sharply worked out by LAMPRECHT, 1932 and later) and therefore VON TSCHERMAN forced the self-coloured dark pattern (*CC*) and background types (*cc*) into the same broad colour classes, resulting in his 'reversal of ratio's', i.e. 9 black : 3 violet : 4 brown among the mottled *Cc*-plants, against about 4 : 3 : 9 among the self-coloured (*CC* + *cc*) ones. The segregating genes in his case at all probability were the 'violet factor' *V* (9 black- + 3 violet mottled against 4 brown mottled) and the 'greenish brown factor' *B* (9 black against 3 violet mottled, brown and yellowbrown taken together), the 'yellowbrown factor' *G* being homozygously dominant in his material.

A very clear older analysis of shiny dark pattern colours was given by JOHANNSEN (1909, p. 53). He crossed a white flowering (*vv*) yellow seeded variety with a violet flowering (*V*) black seeded one. The seeds on the violet flowering F_1-plants were 'schmutzigschwarz' (cf. pres. art. p.7 and LAMPRECHT I, 1932, p.178 and 207–208: *(PPCCJJ)ggBbVv* being 'chromgrünschwarz'). F_2 segregated into 160 'weissblühend' (39 'gelb' + 121 'bronze') and 398 'violettblühend' (105 'violett' + 293 'schwarz' and 'schwärzlich'), corresponding to a 1:3:3:9-ratio. The gene that changes the flower colour into 'violett' and at the same time the seedcoat colour from 'gelb und bronze' into 'violett und schwarz' (*the violet factor*) was later indicated by him as *V*, the gene that changes 'gelb' to 'bronze' and also 'violett' to 'schwarz' (*the greenish brown factor*) as *B*. It is clear that in JOHANNSEN's material *the yellow brown factor* is homozygously recessive. LAMPRECHT (I, 1932, p.207–208) adopted his symbols *B* and *V* from JOHANNSEN; in the scheme p.00 the four colours are VI-1,3,5 and 7.

As a further example of segregation within the group of shiny dark pattern colours the analysis of LUNDBERG and ÅKERMAN (1917) may be mentioned. From a plant of the variety 'Braune Bohne' with chocolate-coloured seed (grey-greenish brown), growing next to a plot with 'Prinzessbohne' (yellow-brown-seeded) they found among the offspring a spontaneous hybrid with dark brown seeds. Its offspring segregated into 47 dark brown, 24 chocolate, 27 yellowbrown and 14 of the new double recessive colour (pale) greenish yellow. Both parents apparently were recessive for the 'violetfactor'. The 'yellowbrown factor' was indicated by them as *G*, the 'chocolate' or 'grey-greenish brown' factor as *C*. LAMPRECHT (I, 1932a, p.207) sent to ÅKERMAN his own colour types 'schamois' (*gg bb vv*; scheme: VI-1), 'bister' (*G. bb vv*; VI-2), 'münzbronze' (*gg B. vv*; VI-3) and 'mineralbraun' (*G. B. vv*; VI-4) for comparison and received the judgement, that his four colours (in reversed order) 'praktisch genommen identisch sind' with those of LUNDBERG and ÅKERMAN. LAMPRECHT therefore used their symbol *G* for the *yellow-brown factor*.

As a last example of the persistent recurrence of the same recognizable colours in the shiny dark pattern group, the analyses of SIRKS (1922) will be shortly discussed, because of their completeness and the good coloured pictures of selfcoloured and mottled types.

On the base of a number of (partly) diallel rather simple crosses within the shiny dark pattern group SIRKS used the following gene symbols:

G for the yellowbrown factor (as LAMPRECHT and PRAKKEN do),
L for the (grey) greenish brown factor (LAMPRECHT and PRAKKEN *B*),
Z for the violet-black factor (LAMPRECHT and PRAKKEN *V*).

On his colour plates I–III are represented among many other colours:

Pl. II no. 18: 'Wagenaar type', canary yellow with brown hilumring:
gg ll zz = *gg bb vv* (scheme: VI-1).
Pl. II no. 25: 'Bruine boon', yellowbrown (= bister):
G. ll zz = *G. bb vv* (scheme: VI-2).
Pl. II no. 23 and 24: 'Rotjes', darker and paler type of chocolate brown:
gg L. zz = *gg B. vv* (scheme: VI-3).
Pl. I no. 3: 'Bruine' × 'Rotjes', dark reddish brown:
Gg Ll zz = *Gg Bb vv* (scheme: VI-4).
Pl. II no. 16: black, all V. colours, the violets in his case apparently being extremely dark (scheme: VI-5, 6, 7 and 8).

The foregoing discussion of the colours belonging to the 'shiny dark pattern' group has, for different reasons, been made rather thoroughly:

1. For making the reader quite acquainted with this frequently occurring colour group and its easily recognizable colours.
2. For making him acquainted with the action and symbols of the three darkening factors (mainly *modifying genes*, not complementary colour genes, as will appear in chapter 4) which bring about this colour series:

indication of action (= name)	symbol used by LAMPRECHT and PRAKKEN	original author of the symbol
'yellow brown factor'	*G*	LUNBERG and ÅKERMAN (1917)
'greenish brown factor'	*B*	JOHANNSEN (1909, 1926)
'violet factor'	*V*	JOHANNSEN (1909, 1926).

3. For using this group as a base for comparison when discussing, in chapters 4 and 5, the remaining colour groups and the work of KOOIMAN and LAMPRECHT.

4. A GENERAL GENETIC SCHEME FOR COLOUR GROUPS AND COLOURS

(mainly according to KOOIMAN's analysis)

Before 1920 many investigators wondered about the kind of action of the generally recognized groundfactor or basic gene *P* (or *A* with other investigators): does *P* itself, without the complementary action of chromogenous factors or colour genes, produce a certain, pale, seedcoat colour or not?

The first clear answer, that *the basic gene A* (= P) alone does *not* produce any seedcoat colour, was given by KOOIMAN (1920) by means of the F_2–F_4 analysis of his cross between the Dutch varieties 'Bruine boon' (seedcoat of yellow brown shiny dark pattern colour) and 'Dubbele Hollandsche spersieboon" (seedcoat white), the F_1 showing a shiny black mottled seedcoat colour. He also came to clear conclusions about the action of *three colour genes*, B, C and D, and *two modifying genes*, E and F. Here it should be anticipated that a third modifying gene, incidentally the 'yellowbrown factor' *G* mentioned in chapter 3, in KOOIMAN's material was present as a homozygous dominant, his F_1 therefore being:

Aa	*Bb Cc Dd*	*Ee Ff GG*
basic gene	colour genes	modifying genes

KOOIMAN's analysis represents, according to the present author, the most complete and coherent genetic analysis of the yellow-black seedcoat colour group. His important work, however, remained relatively unnoticed. For this there are, I think, three main reasons: *a.* it being written (as a doctor's dissertation) in the Dutch language, *b.* the intricacy of the analysis, based on a rather small F_2-family of only 212 plants, and *c.* the homozygously dominant presence of *G*, strongly interfering with homologization by other authors.

KOOIMAN's 212 F_2-plants consisted of 154 coloured seeded plants and 58 white seeded ones (1/4 = 53). LAMPRECHT (I, 1932a, p.105) writes: 'Eine auf den Grund gehende Klarlegung einer Spaltung an der sechs Faktoren teilnehmen scheint bei dieser Individuenzahl wohl ausgeschlossen'. A compensation for the small F_2-number, however, is formed by the extensive, intensively explored F_3-material: KOOIMAN *bred F_3-families of all F_2-plants*, sowing 20 or 21 seeds per plant, usually resulting in 15–20 plants per F_3-family.

In 1931 KOOIMAN published a 'Monograph on the genetics of *Phaseolus*'. His own analysis is systematically reported on pages 341–348, with tables 9–13. When the present author further below discusses KOOIMAN's results, details should be looked for in the Monograph and also in the original article with its coloured plate (partly somewhat misleading as the seeds, when pictured, were almost one year old, with some colour types rather much 'afterdarkened' and other types not, cf. p. 14). See also the scheme p. 39: upper half, jj, non-afterdarkening, lower half, J., afterdarkening.

LAMPRECHT, when writing his first articles, did not have the Monograph at his disposal, which in his literature lists is not mentioned before article VIII of 1934. When making my own first analysis (PRAKKEN, 1934) of the cross 'Fijne tros' (white seeded) with 'Wagenaar' (pale greenish yellow shiny dark pattern type) I scrutinized KOOIMAN's article, but at that time it was better possible for me to find connection with LAMPRECHT's careful colour descriptions and clear analyses, than with KOOIMAN's coloured plate and intricate analysis. Therefore I also chose, as far as possible, my gene symbols in accordance with LAMPRECHT. (At that time, however, I not yet dared to homologize my 'shine factor' *Sh* with LAMPRECHT's *J*, but later it became sure that *Sh-sh* = *J-j*, so now the symbol *J* is used). It was not before later that the common trends and even identities between on the one side the work of KOOIMAN and on the other side that of LAMPRECHT and myself, became quite clear to me (PRAKKEN, 1940).

In this chapter and the next one, I will therefore try to make clear the homology of KOOIMAN's genes *A*, *B*, *C*, *D*, *E*, *F*, [*G*] with, in the same order, those of LAMPRECHT *P*, *C*, *J*, *Can*, *B*, *V*, *G*, the first one being the *basic gene*, the next three *complementary colour genes* and the last three *modifying genes* (about their darkening action cf. the preceeding chapter 3), with the addition, however, that under certain genetic and environmental conditions, *V* (= *F*) has a more or less strong colour gene action, producing a bluish tinge over part of the seedcoat, beginning at the ventral (hilumring) side and from there extending: LAMPRECHT XIV 1939, p.274–277, 'blass glaucescens' (scheme: I-5,6,7 and 8). Ultimately I have decided not to return to KOOIMAN's alphabetic symbols *A* to *F* [*G*], but to stick with those of LAMPRECHT (with the only exception that *D* will be used and not *Can*), partly because these as much as possible are those used by earlier investigators (rule of priority), and partly because they generally are used by the modern investigators.

Returning now to KOOIMAN'a analysis, his F_2, as mentioned, consisted of 154 coloured seeded plants and 58 white ones. In F_3 it appeared that of the 154 families after coloured-seeded F_2-plants no less than 122 segregated at least one white-seeded plant and but 32 not, numbers not at all corresponding with a monogenic 2:1 relation. Moreover, with F_3-families of a size of but 15–20 plants, part of the principally 15 (coloured) : 1 (white) or even 63:1 segregating families (homozygously dominant for the basic gene) will not be recognized as such. KOOIMAN analysed his F_3-material as many-sided as possible, studying a.o. for each F_2-*colour group* (cf. below) the number of white-segregating plants, together with the mean percentage of whites within each 'group' of F_3-families. He of course also analysed the mutual genetic relations between the '*colour groups*' and between the colours within each group, the '*colour series*' (cf. KOOIMAN, 1931, table 13), with the final conclusion that his F_1 possessed the genotype *Aa Bb Cc Dd Ee Ff* [*GG*].

The three *colour genes B*, *C*, and *D*, each single or in their diverse combinations, are, in complementary action with the basic gene *A*, *responsible for the different 'colour groups'*. Theoretically therefore *eight* colour groups exist, their genetic constitution being, leaving out the basic gene and the modifying genes: I. *bdc* and II. *Bdc*; III. *bDc* and IV, *BDc*; V. *bdC* and VI. *BdC*; and finally VII. *bDC* and VIII. *BDC*. With each pair of groups the background colour type *bb* (= LAMPRECHT *cc*) is mentioned first and after it the corresponding dark pattern type *BB* (resp. *CC*), the heterozygote *Bb* (*Cc*) being mottled in both colours (cf. the scheme to the left: **I-VIII**).

The two *modifying genes* E and F (and, in general, also G) are *responsible for the darkening colour series withing the groups.* As shown by a look on KOOIMAN's (1920) coloured plate he could distinguish *four colours* within each group, showing *more or less parallel series, each from pale yellow or yellow-brown to black or almost black*, at least very dark. (KOOIMAN, from his F_2- and F_3-segregations, naturally could not conclude the homozygously dominant presence of the modifying 'yellowbrown factor' *G*; this can only be concluded by a careful comparison with the results of other authors, which comparison will be made below, during the discussion of group VI, the 'shiny dark pattern group', extensively discussed in chapter 3). In the scheme KOOIMAN's colours are indicated with a dot.

Before now characterizing the eight 'colour groups' (row I–VIII of the scheme) depending on the actions of the colour genes B, C and D (together with E, F and G) the 'names' of the three colour genes, derived form their general and most conspicuous action, may be given:

B, *'factor for heterozygous mottling'* (= *C* of LAMPRECHT and PRAKKEN).

D, *'hilumring factor'* (symbol kept by the present author; = *Can* and/or *Ins* of LAMPRECHT).

C, *'shine factor'* (*J* of LAMPRECHT, earlier *Sh* of PRAKKEN).

The description of the *colour groups* as given below mainly depends on KOOIMAN's analysis; some complementary characteristics, e.g. on variability and degree of afterdarkening, at least partly depend on experience of LAMPRECHT and the present author. For the sake of simplicity the symbol *A* for the basic gene is left out. Numbers I–VIII correspond with the rows I–VIII of the scheme.

I. *bb dd cc* (scheme: cc dd jj): *the white group*. In this background colour group the modifying genes are without influence, with the exception, however, that *F* (= *V*) under certain genetic and environmental circumstances produces a pale bluish tinge (LAMPRECHT: 'blass glaucescens'), partly covering the white (cf. schema I-5 to I-8). The white colour group does hardly show any afterdarkening.

II. *BB dd cc* (scheme: CC dd jj): *the group of mat dark pattern colours without brown hilumring*, indicated by KOOIMAN as the group of *soft colours without hilumring*. By the influence of the modifying genes *E* and *F* the series darkens from pale yellow or lemon-coloured to (dark) mouse grey or mat blackish. (II-2, 4, 6 and 8). Colours mat or soft, without or with very little afterdarkening. See KOOIMAN (1920), coloured plate, the four colours in the second row from below to the right, nrs. 24, 23, 22, and 21. KOOIMAN (1920) mentions that the light grey colour of no. 22 sometimes is brownish grey.

Bb dd cc is the mottled group, heterozygous between group I and II, and therefore 'mat or soft colour mottled upon white background', without hilumring; see KOOIMAN (1920) col. plate, the four colours in the second row from below to the left, nrs. 20, 19, 18 and 17. These four types all segregate white seeded plants in the next generation: 3 col. : 1 white (if AA Bb) and 9 coloured : 7 white (if Aa Bb).

III. *bb D. cc* (scheme: cc D. jj): *the hilumringtype group*, by KOOIMAN indicated as *H-type*. This background colour group shows a brown hilumring, but for the rest an almost colourless smoky whitish seedcoat, the colour being not or very slightly influenced by the modifying factors *E*, *F* (or *G*). According to LAMPRECHT and PRAKKEN the gene *F* (= *V*) *can* but need not produce a bluish tinge over part of the whitish seedcoat (LAMPRECHT: glaucescens), cf. colour group I. The hilumring type shows very little afterdarkening. See KOOIMAN (1920), col. plate, left below, no. 25; this, however, is not a typical specimen, the dark coloured part around the narrow dark brown hilumring depending, according to Kooiman and also to Lamprecht ('margo'; art. VI, 1933, p.259), upon a specific genetic situation. A better picture of a hilumringtype is represented in Sirks (1922), Pl. I no. 10, this type certainly being recessive *vv* (or $v^{lae}v^{lae}$) for the violetfactor, because of its lively yellowbrown hilumring, no. 25 of Kooiman certainly being of *V.* (= *F.*) genotype. Prakken (1940) used for the hilumringtype gene the symbol D, taken from Kooiman, as Lamprecht originally did not recognize a specific hilumringtype gene. The type rather accurately corresponds with Lamprecht's genotypes *P G* (speckweiss), *P B* (veilchenartig weiss), *P Can* (speckweiss) and probably also to *P Ins* (hell rohseidengelb). In the next chapter 5, I will try to explain that these four symbols of Lamprecht at all probability represent the action of one and the same hilumringfactor *D*.

IV. *BB D. cc* (scheme CC D. jj): *the group of mat dark pattern colours with brown hilumring*, indicated by Kooiman as the group of *soft colours with hilumring*. Except for the brown hilumring the series shows about the same four colours as group II, *BB dd cc*, slightly darker however (IV-2, 4, 6 and 8). Like the foregoing series (*b d c*, *B d c* and *b D c*) also the present series *B D c* shows little or no afterdarkening. See Kooiman, col. plate, third row from below, nrs. 16, 15, 14 and 13.

Bd D. cc is the mottled group, heterozygous between group III and IV, and therefore 'mat or soft colour mottled upon the whitish background of the hilumring type', and segretating into 1/4 BB mat dark pattern type with hilumring : 2/4 Bb of the mottled type : 1/4 of the bb hilumringtype. For segregating whites too, either the basic gene has to be heterozygous Aa, or, if AA, the hilumring gene must be heterozygous: AA Bb Dd cc.

The colour groups I-IV described above (scheme: rows I-IV),

I. *b d c*, the group of white background colour,
II. *B d c*, the mat dark pattern group without brown hilumring,
III. *b D c*, the hilumringtype background group and
IV. *B D c*, the mat dark pattern group with brown hilumring

all are recessive *cc* with respect to the dominant 'shine factor' *C* (= *J*). All colours belonging to these groups are as mentioned *mat or soft coloured*, at least not pronounced shiny, and all are *non-afterdarkening*. Both characteristics, the *shiny appearence* and the *afterdarkening* apparently depend upon the action of the dominant 'shine factor' *C* of Kooiman (Lamprecht *J*, Prakken originally *Sh*). *C* (= *J*) moreover produces, like the 'hilumringfactor' *D*, a *brown hilumring*. While, however, the almost colourless *(A) b D c* backgroundcolour (the hilumring type) is not or hardly influenced by the modifying genes *E*, *F* (and *G*), the *(A) b d C* shiny backgroundcolour really is influenced, in a more or less *analogous way* as the *(A) B d C* shiny dark pattern type, though always clearly paler and of a somewhat other tone.

One more important observation with respect to the shiny and afterdarkening *C*-colours of Kooiman has to be mentioned here. *If the 'shine factor' C with its hilumring action is present, the action of the 'hilumring factor' D (that hardly* *changes seedcoat colour as a whole) is not observable, or at best it brings about a very slight darkening of the overall seedcoat colour.* The result of it is that *not four* colour groups can be clearly distinguished within the shiny C.-group (as the groups I–IV of the mat cc-groups delt with above), *but only two*:

V. *the shiny background colourgroup* *bb dd C.* (row V in the scheme).
bb D. C. (row VII in the scheme).
VI. *the shiny dark pattern colour group* *BB dd C.* (row VI in the scheme).
BB D. C. (row VIII in the scheme).

As the 'shiny dark pattern series' is extensively delt with in the preceeding chapter 3, and as this series is more easy to describe than the corresponding 'shiny background series', the group or series VI will be described and analysed first, the more so as with the help of this group it is rather easy to connect Kooiman's analysis with the results of other authors, of Lamprecht, Prakken and earlier ones, with respect to the action of the modifying genes *E*, *F* and *G* (cf. chapter 3: *B*, *V* and *G*).

VI. *BB dd C.* (scheme: CC dd J.): *the group of shiny dark pattern colours*, indicated by Kooiman as the group of *hard colours.* All colours show a brown hilumring, shiny appearance and intense afterdarkening, all colours, even the palest ones, changing in the course of some years to about the same intense very dark brown to black. See Kooiman's (1920) col. plate, upper row to the right, nrs. 8, 7, 6 and 5. As the picture is made after seeds of about *one year old* there already is a considerable degree of afterdarkening. The all-important question now is: how to compare Kooiman's shiny dark pattern series of *four* colours (his four hard colours) with the complete series of *eight* (or better seven) colours derived from the literature and described in general terms in the preceeding chapter 3 (p.7)? As will be seen below the comparison is possible and even *completely fitting*:

the 8 (7) colours as descr. in literature	genotype acc. to Lampr. and Pr.	the 4 colours of Kooiman	genotype acc. to Kooiman
1. (pale) greenish yellow (Lampr.: schamois)	*(PCdJ) g b v*	–	
2. yellow brown (orange) (Lampr.: bister)	*(PCdJ) G b v*	orange brown	*(A B d C) (G) e f* (scheme: VI-2)
3. greenish brown (chocolate) (Lampr.: münzbronze)	*(PCdJ) g B v*	–	
4. dark- or coffeebrown (Lampr.: mineralbraun)	*(PCdJ) G B v*	coffee brown	*(A B d C) (G) E f* (scheme: VI-4)
5. dark violet (Lampr.: dunkel veilch. viol.)	*(PCdJ) g b V*	–	
6. dark brown violet (Lampr.: kastanienbraun)	*(PCdJ) G b V*	violet brown	*(A B d C) (G) e F* (scheme: VI-6)
7. black (Lampr.: reinschwarz)	*(PCdJ) g B V*	–	
8. black (Lampr.: reinschwarz)	*(PCdJ) G B V*	black	*(A B d C) (G) E F* (scheme: VI-8)

V. *bb dd C.* (scheme: cc dd J.): *the group of shiny background colours*, indicated by Kooiman as the group of *half-hard colours.* As mentioned (p.14) the colour series of this group runs more or less parallel with the dark pattern series just described, though always paler and of an other tone, all of course with a brown hilumring, shiny appearance and strong afterdarkening. See KOOIMAN, col. plate, the series of four colours below to the right, nrs. 29, 28, 27 and 26; already much afterdarkened, no. 28 probably pictured to greyish. For this group too the four colours of KOOIMAN are below compared with the complete series of eight as described or 'named' by LAMPRECHT and PRAKKEN (genotypes as 1–8 above, but *cc* resp. *bb* instead of *CC* resp. *BB*):

LAMPRECHT	PRAKKEN	KOOIMAN
1. 'rohseidengelb' (cartidge buff)	pale yellowish	–
2. 'maisgelb' (maize yellow)	pale orange	sallow yellow
3. 'havannabraun' (snuff brown)	grey brown	–
4. 'rhamninbraun' (buckthorn brown)	(pale) brown	half-hard brown
5. 'eisenhutviolett' (bluish violet)	pale yellowish t.w. plumbago violet	–
6. 'ageratumblau' (ageratum blue)	pale orange t.w. ageratum blue	half-hard violet brown
7. 'dunkles indigo' (dark indigo)	grey brown t.w. slate blue	–
8. 'graulich indigo' (greyish indigo)	(pale) brown t.w. greyish indigo	reddish brown t.w. violet (greenish black)

As mentioned before (cf. p.8) especially the four *V*-colours of this shiny background series (nrs. 5–8; t.w. = tinged with) are *extremely variable* and difficult to describe and to name, depending on the fact that the blue or violet tinges caused by *V* (as 'blass glaucescens' in the *V*-colours of the white background group, row I, and 'glaucescens" in the hilumringtype background group, row III; cf. above) do not begin to develop before a relative late stage of seed ripening, first at the ventral (hilumring) side and from there more or less far extending over the already developed *vv*-colours (PRAKKEN: pale yellowish, pale orange, grey brown and brown); on some seeds of a plant this 'covering' process hardly begins or stops very soon, on other ones it proceeds to complete covering, resulting in a tremendous lot of pure and mixed colours on one and the same plant. Also genetic factors influence the degree of tinging, but a genetic analysis has appeared to be extremly difficult. This tinging or covering process has by PRAKKEN been expressed in the namegiving of the colours, no. V-1 being called 'pale yellowish' and no. V-5 'pale yellowish tinged with plumbago violet', etc., cf. the table. LAMPRECHT, however, derives the name from the most intense covering colour, no. V-1 being called 'cartridge buff' and no. V-5 'bluish violet', etc. If, however, the tinge has not or hardly developed, the two colour types are practically indistinguishable and the flower colour white (*vv*) or pale lilac ($v^{lae}v^{lae}$) as against violet (*V*.), has to help to make the decision. KOOIMAN at last makes use of both namegiving methods, calling no. 6 half-hard violet brown and no. 8 reddish brown tinged with violet (in KOOIMAN's plate a very dark type is pictured, almost greenish black).

Bb dd C. is the mottled group, heterozygous between group V and VI, and therefore 'shiny or hard dark pattern colour mottled upon the paler shiny or half-hard background colour'. The group is pictured in KOOIMAN, col. plate, upper row to the left, nrs. 4, 3, 2 and 1, but not in a very satisfactory way: the background in no. 2 e.g. is much too pale, also when taking into consideration that the *V*-tinge upon the background colour usually develops less strongly in the mottled Cc than upon the selfcoloured cc type. The three investigators, KOOIMAN, LAMBRECHT and PRAKKEN, quite agree in calling the 'shiny background colour' group the most exasperatingly difficult group.
The groups
VII. *bb D. C.* (scheme: cc D. J.), shiny background group as V, but because of D. probably slightly darker, and
VIII. *BB D. C.* (scheme: CC D. J.), shiny dark pattern group as VI, but because of D. probably slightly darker, need no further discussion.

Because of all the foregoing, and especially because of the very good agreement between the results of KOOIMAN, LAMPRECHT and PRAKKEN with respect to the shiny background and the shiny dark pattern group (rows V and VI), it seems very probable that the following homologies exist (cf. also the scheme):

basic gene *P* (LAMPR. and PR.) = *A* of KOOIMAN = groundfactor.

compl. colour gene *C* (LAMPR. and PR.) = *B* of KOOIMAN = mottling factor.
compl. colour gene *D* (LAMPR. *Can*) = *D* of KOOIMAN = hilumring factor.
compl. colour gene *J* (LAMPR. and PR.) = *C* of KOOIMAN = shine factor.

modifying gene *G* (LAMPR. and PR.) = homoz. dom. w. K. = yellowbrown factor.
modifying gene *B* (LAMPR. and PR.) = *E* of KOOIMAN = greenish brown factor.
modifying gene *V* (LAMPR. and PR.) = *F* of KOOIMAN = violet factor.

With the remark that, under special genetic and environmental conditions, *V* showns some complementary colour gene action. And with the further remark that, because of the homozygous GG constitution in KOOIMAN's F_2, the columns *1.* pale greenish yellow, *3.* grey- to greenish brown, *5.* diverse violet colours and *7.* dark greenish to black, are in his material not represented (cf. the scheme).

5. RECONCILIATION BETWEEN DIVERGENT EXPLANATIONS
KOOIMAN – LAMPRECHT – PRAKKEN

The history of growing disagreement with respect to seedcoat colour inheritance in *Phaseolus vulgaris* is rather long, As already mentioned in the 'Introduction' the disagreement centers around the question if the 'yellowbrown factor' *G* and the 'greenish brown factor' *B*, together with the groundfactor *P*, *do or do not produce a brown hilumring*, in other words if they are complementary 'colour genes' (Farbenfaktoren) as LAMPRECHT finds or but 'modifying genes'

(Modifikationsfaktoren) as concluded by Kooiman (1920) and Prakken (I, 1940).

In the first article of a long series Lamprecht (I, 1932a) made perfect F_2 and F_3 analyses, mainly in the group of shiny dark pattern colours, *CC JJ*, and he made quite clear the action of the factors *G*, *B* and *V* upon this group (cf. pres. art. p.7 and 15; see scheme p. 39, row VI).

In that first article he also delt with the highly informative cross no. XII (p.196–201):

L 27, 'De Digoin'	×	L 29, 'De la Chine'
'rohseidengelb'		'geschwefeltes weiss'
(PP) cc JJ (gg bb vv)		*(PP) CC jj (gg bb vv)*
scheme: V-1		scheme: II-1

F_1: 'schamois' mottled upon 'rohseidengelb' (schamois/rohseidengelb)
= *(PP) Cc Jj (gg bb vv)*

F_2-segregation (*CC*, dark pattern, and *Cc*, mottled, taken together):

schamois plus schamois/roh. s.g.	rohseiden-gelb	geschw. weiss plus geschw. weiss/weiss	rein = weiss	total
(CC J. + Cc J.)	*cc J.*	*CC jj + Cc jj*	*cc jj*	
696(9)	263(3)	235(3)	95(1)	1289
scheme: VI-1	schem: V-1	scheme: II-1	scheme: I-1	

This analysis was the first one which in the most simple way showed that the basic gene *P* itself does not produce any seedcoat colour, while it at the same time showed that:

C, the 'factor for ever-segregating mottling' (= *B* of Kooiman) and
J, the 'shine factor' (= C of Kooiman) both are real 'colour genes'.

About the character of the genes *G*, *B* and *V*, colour genes or modifying ones, nothing was proved. According to the present author the beginning of misinterpretation about the action of *G* and *B* may be found on the first page of Lamprecht III, 1932b, where he writes: 'Die in der genannten Arbeit (Lamprecht I, 1932a) mitgeteilten Resultaten bezogen sich auf Kombinationen

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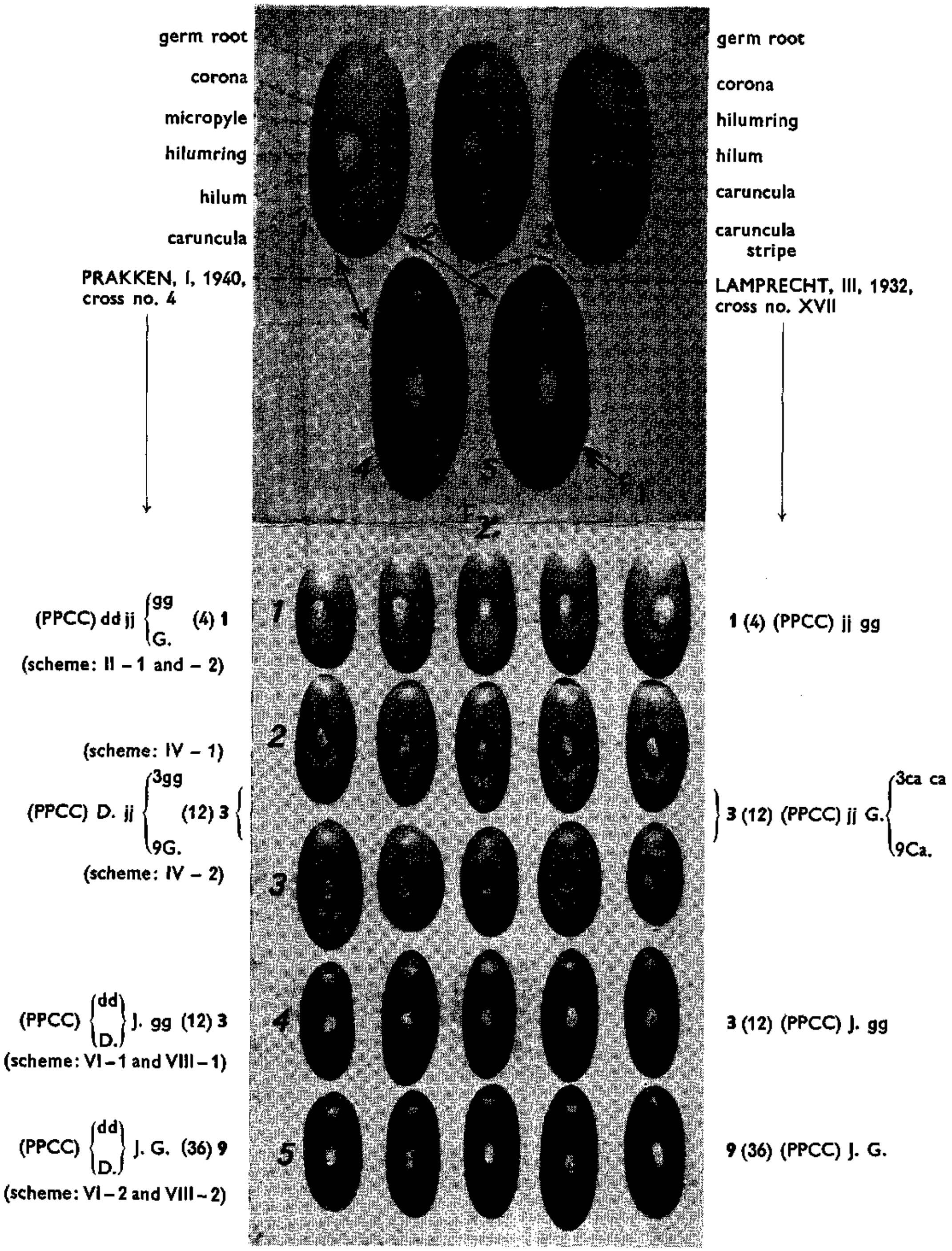
Fig. 1. Parents, F_1 and F_2 of Lamprechts's cross no. XVII (III, 1932b) and of Prakken's cross no. 4 (I, 1940).

1. (mat and non-afterdarkening) greenish yellow without hilumring (scheme: II-1 or II-2). Lamprecht variety 'De la Chine' ('geschwefeltes weiss').
   Prakken variety 'Citroen' (greenish yellow).
2. (mat and non-afterdarkening) greenish yellow with brown hilumring, without caruncula stripe ('ambra'; scheme: IV-1).
3. (mat and non-afterdarkening) greenish yellow with brown hilumring, with yellowbrown caruncula stripe ('steinfarbig'; scheme: IV-2).
4. (shiny and afterdarkening) greenish yellow, with brown hilumring ('schamois'; Prakken variety 'Wagenaar'; scheme: VI-1 or VIII-1).
5. (shiny and afterdarkening) yellowbrown, with brown hilumring ('bister'; Lamprecht variety 'Braune Bohne; scheme: VI-2 or VIII-2).

To the right Lamprecht's genetic explanation, to the left that according to Prakken.


germ root
corona
micropyle
hilumring
hilum
caruncula
PRAKKEN, I, 1940, cross no. 4
germ root
corona
hilumring
hilum
caruncula
caruncula stripe
LAMPRECHT, III, 1932, cross no. XVII
4
5
1
F2
1
2
3
4
5
(PPCC) dd jj {gg G. (4) 1
(scheme: II – 1 and – 2)
1 (4) (PPCC) jj gg
(scheme: IV – 1)
(PPCC) D. jj {3gg 9G. (12) 3
(scheme: IV – 2)
3 (12) (PPCC) jj G. {3ca ca 9Ca.
(PPCC) {dd D.} J. gg (12) 3
(scheme: VI – 1 and VIII – 1)
3 (12) (PPCC) J. gg
(PPCC) {dd D.} J. G. (36) 9
(scheme: VI – 2 and VIII – 2)
9 (36) (PPCC) J. G.

von sechs verschiedenen Faktoren, einem Grundfaktor für die Ausbildung von Farbe überhaupt *(P)* sowie fünf Farbenfaktoren (*C*, *J*, *G*, *B*, *V*)'.

In this article III Lamprecht extensively deals with cross no. XVII (p.8–19), from which cross he concludes to the hilumring-action of the 'yellowbrown factor' G. The discussion here will be made with the help of figure 1, taken from Prakken, 1940, p.352. Lamprecht's cross was (cf. fig. 1):

L.25, 'Braune Bohne'	×	L.29, 'De la Chine'
'bister' or yellowbrown		'geschwefeltes weiss' (without hilumring)
(PP CC) JJ GG (bb vv)		*(PP CC) jj gg (bb vv)*
scheme: VI-2 or VIII-2		scheme: II-1

F$_1$: 'bister' or yellowbrown, (PP CC) Jj Gg (bb vv).

F$_2$ (1507 plants) according to Lamprecht:

1/16 *(PP CC) jj gg* = 'geschwefeltes weiss' (without hilumring; in the fig.: 1)

$$3/16\,(PP\ CC)\,jj\quad G. = \text{`steinfarbig'} \begin{cases} \text{3/64 without caruncula stripe (in the fig.: 2)} \\ \text{9/64 with caruncula stripe (in the fig.: 3)} \end{cases}$$

3/16 *(PP CC) J. gg* = 'schamois', shiny greenish yellow (in the fig.: 4)

9/16 *(PP CC) J. G.* = 'bister', shiny yellowbrown (in the fig.: 5).

As the difference between 9/16 'bister' and 3/16' schamois' among the shiny *J.*-types (all with brown hilumring) depends upon the *G-g* gene pair, Lamprecht easily accepted that among the mat *jj*-types the difference between 3/16 'steinfarbig' (with brown hilumring) and 1/16 'geschwefeltes weiss' (without hilumring) also depends upon the *G-g* gene pair, i.e. the 'yellowbrown factor' G has hilumring-action and *is a colour gene*. For the segregation, clear within the 'steinfarbig' type only, into 'steinfarbig' *with* and *without* a yellowbrown caruncula-stripe he makes the new gene pair *Ca-ca* responsible, which at the same time changes the general seedcoat colour from greenish yellow towards a more yellow or even a faint orange colour (cf. in the scheme: IV-1 and IV-2). Lamprecht's factorial explanation is be be found at the right in the picture. It must, however, not be left out here that among the 1/16 (93) 'geschwefeltes weiss' individuals Lamprecht found 5 which were slightly less greenish and by him were called 'gelblich weiss' (cf. in the scheme II-1 and II-2). Lamprecht's opinion about the real genetic character of 'gelblich weiss' *has changed often*: double recessive, single recessive, mutated individuals? In his article of 1951, later to discuss, he comes to the conclusion that it is a *dominant gene*, indicated with *Flav*, that brings about the slight change from 'geschwefeltes weiss' to 'gelblich weiss'.

Now I must compare my own cross no. 4 (Prakken I, 1940, p. 351–364) with Lamprecht's cross no. XVII. See scheme p. 39 and fig. 1 to the left. Lamprecht crossed a type like 1 of the figure (De la Chine) with type 5 (Braune Bohne, *JJ GG*). *My* cross no. 4, however, was between a type like 1 of the figure ('Citroen'; greenish yellow without hilumring; scheme: II-1 or II-2) and a type like 4 in the figure ('Wagenaar', gg; scheme: VI–1 or VIII–1).

In both cases the F_1 was of type 5, 'bister' or yellowbrown, and moreover the F_2-segregations were absolutely identical, into the last detail.

Such identical results at all probality have the same genetical explanation. In my case it is quite clear that the 'yellowbrown factor', recessive *gg* in 'Wagenaar'', is (cryptomerically) present in the variety 'Citroen' (scheme: II-2, and not II-1), and *therefore has no hilumring action.* And it is as clear that in my variety 'Wagenaar' *two genes with hilumring action are present,* viz. the 'shine factor' *J* (formerly *Sh* of PRAKKEN; *C* of KOOIMAN) and (cryptomerically) the 'hilumring factor' *D* of KOOIMAN (scheme: VIII-1, and not VI-1). Cross no. 4 of PRAKKEN therefore was:

'Wagenaar''	×	'Citroen'
(PP CC) DD JJ gg (bb vv)		*(PP CC) dd jj GG (bb vv)*
Scheme: VIII-1		scheme: II-2

F_1: 'bister' or shiny yellowbrown, *(PP CC) Dd Jj Gg (bb vv)*, scheme: VIII-2. F_2: easy to be read to the left of the seedcoat types 1–5 in fig. 1. The *bifactorial ratio* 9:3:3:1 in an F_2 segregating for *three gene pairs* is caused by D-d having no or hardly any influence upon shiny *J.*-types, and *G-g* having but a slight influence upon the mat *jj*-types with or without a brown hilumring: the 9:3 ratio is caused by gene pair *G-g*, the 3:1 ratio however by *D-d.*

If the above reasoning is right, it means that LAMPRECHT uses three different symbols for one and the same action of the 'yellowbrown factor' G:
Flav-flav, in mat d.p. without hilumring (*CC dd jj*; scheme: II-2 and II-1),
Ca-ca, in mat d.p. with brown hilumring (*CC D. jj*; scheme: IV-2 and IV-1),
G-g, in shiny dark pattern ($CC^{D.}_{dd}\,J.$; scheme: VI-2 and 1, VIII-2 and 1).

In LAMPRECHT's case the explanatory value as regards the F_1 and the F_2 ratio is quite the same for both explanations, but in my case LAMPRECHT's explanation was a priori impossible. The F_3-generation of PRAKKEN (I, 1940, tables 8–13, p.355–358) completely agrees with the expectations. It is a pity that LAMPRECHT discusses his F_3-results (1400 individuals) but superficially. Especially the F_3-offspring of 'bister' (shiny yellowbrown; scheme VI-2 and VIII-2) would have been of much importance, as according to PRAKKEN's explanation 'bister' can have *two* genes for brown hilumring (being *PP CC D. J. G.*; scheme: VIII-2) *or but one* (being *PP CC dd J. G.*; scheme: VI-2), while according to LAMPRECHT's explanation *it always has two* (*PP CC J. G.*). But 'für eine Demonstration der Aufspaltung der zahlreichen Genotypen von Bister ...ist das Material wie erwähnt zu klein' (LAMPRECHT, 1932b, p...).

In the discussion above it has become clear, I think, why LAMPRECHT could make his faulty explanation: because the one parent (De la Chine) was double recessive jj gg and the other (Braune Bohne) double dominant JJ GG and moreover (cryptomerically) possessed the 'hilumring factor' *D. It is in an analogous situation that* LAMPRECHT *made his quite analogous misinterpretation with respect to the pretended hilumring-action of the 'greenish brown factor' B.* It happened in two crosses, delt with in his article VI of 1933 (p. 295–312).

Cross VI:

L.28, 'Favoriet'	×	L.29, 'De la Chine'
white seeded		'geschwefeltes weiss'
pp cc [*DD*] *JJ gg BB vv*	×	*PP CC* [*dd*] *jj gg bb vv*

Cross XLVIII:

L.11, 'Graue Spargel'	×	L.29, 'De la Chine'
'havannabraun'		'geschwefeltes weiss'
PP cc [*DD*] *JJ gg BB vv*		*PP CC* [*dd*] *jj gg bb vv*
scheme: VII-3		scheme: II-1

F_1: 'münzbronze/havannabraun' (buffy citrine/snuff brown):

$\left.\begin{matrix}Pp\\PP\end{matrix}\right\}$ *Cc* [*Dd*] *Jj gg Bb vv* (heterozygous: *Cc* [*Dd*] *Jj Bb*)

A complication with respect to cross XVII discussed above is that both F_1's are not *CC*, but *Cc*, the F_2 thus showing both a *CC*-dark pattern group and a *cc*-background group, together with the mottled *Cc*-group. Looking at these three groups, LAMPRECHT found within each of them an F_2-segregation of 1:3:3:9, interpretated by him as shown in the table (see gene symbols to the left):

background color group (*cc*)

jj mat	*bb* (1) pure white	*Vir-vir* without influence upon $^{jj}_{J.}$*cc*-backgr. colours
	B. (3) hilumring type (whitish)	
J. shiny	*bb* (3) 'rohseidengelb' (= cartidge buff)	
	B. (9) 'havannabraun' (= snuff brown)	

mottled colour group (*Cc*)

jj mat	*bb* (2) mat without h.r./white	'geschwef. weiss'/white	*vir vir*
		'*russgrün*'/white	*Vir.*
	B. (6) mat with h.r./whitish	'ambra'/whitish	*vir vir*
		'*mattmünzbr.*'/whitish	*Vir.*
J. shiny	*bb* (6) 'schamois/rohseidengelb'	*Vir-vir* without influence upon shiny *J.*-colours	
	B. (18) '*münzbronze*/havannabraun'		

dark pattern colour group (*CC*)

jj mat	*bb* (1) mat without hilumring	'geschwefeltes weiss'	*vir vir*
		'*russgrün*'	*Vir.*
	B. (3) mat with hilumring	'ambra'	*vir vir*
		'*mattmünzbronze*'	*Vir.*
J. shiny	*bb* (3) 'schamois' (greenish yellow)	*Vir-vir* without influence upon shiny *J.*-colours	
	B. (9) '*münzbronze*' (greenish brown)		

From the symbols to the left it is clear that, similar as in cross XVII with respect to *G*, LAMPRECHT now reasoned with respect to *B* (a priori apparently *convinced* about the colour gene character of *B* too, and again *overlooking* the possibility of a special 'hilumring factor'): *if* among the shiny *J.*-type the 9:3 ratio (resp. 18:6) is caused by the gene pair *B-b*, *then* also the 3:1 ratio (resp. 6:2) between the mat *jj*-types with and without hilumring is caused by *B-b*, the 'greenish brown factor' *B* therefore being a 'colour gene'.

In cross XVII, with respect to *G-g*, the mistake could easily be made, because of the slight influence of *G* upon the mat *CC jj* types. In these crosses VI and XLVIII however, with respect to *B-b*, the type of F_2-segregation ought to have been a warning to LAMPRECHT. Here there is not only among the shiny *J. CC-* and *J. Cc*-types a clear segregation into 1/4 greenish yellow (chamois, *bb*) and 3/4 greenish brown (*münzbronze, B.*), but also among the mat *jj*-types without and with a brown hilumring: 'geschwefeltes weiss' against '*russgrün*' and 'ambra' against '*mattmünzbronze*', see to the right in the table. Having disposed of the 'greenish brown factor' *B* for the hilumring-action (see at left of the three groups of the table), LAMPRECHT is obliged to make another (new), modifying gene pair responsible for the change of greenish yellow into greenish brown among the mat groups without and with a brown hilumring, and he calls it *Vir* (see to the right). A remarkable situation, for according to LAMPRECHT himzelf (VI, 1933, p.298) '...bestehen zwischen den Farben '*münzbronze*' (shiny dark pattern), '*mattmünzbronze*' (mat dark pattern with hilumring) and '*russgrün*' (mat dark pattern without hilumring) Übergänge in Bezug auf die Farbe selbst'. LAMPRECHT moreover has to suppose that *Vir-vir* not at all influences the shiny dark pattern colours (*J.C.*), nor the background colours (*cc*), just only the *jj C.* colours, i.e. mat dark pattern.

Concluding, it seems to the present author that LAMPRECHT again *overlooked* the hilumring factor D, *ascribed wrongly* the hilumring-action in the mat *jj*-types to B, and *unnecessarily introduced* the modifying gene *Vir*. The F_2-segregation acc. to me depends on the heterozygous F_1-constitution *Cc Dd Jj Bb* and the F_2 contains all types I to VIII of the columns 1 and 3 of the scheme p.123. It has to be remarked that, as in the case of *G*, the F_2-ratio's according to both explanations do not differ, the many consequences not appearing before F_3, but also in the crosses VI and XLVIII LAMPRECHT does hardly or not present F_3-offspring from shiny dark pattern types: e.g. 'schamois' with (hypostatically) the gen *Vir* (*PP CC Jj gg bb vv Vir Vir*) should produce an F_3 of 3/4 'schamois' (*greenish yellow*) and 1/4 *greenish brown* ('*russgrün*': *PP CC jj gg bb vv Vir Vir*). Such segregations, however, are never observed in *Phaseolus*.

In LAMPRECHT's article XIII (1936) we again are confronted with the hilumring-problem, but now in a certain sense from the opposite side. In this article LAMPRECHT uses as one parent the white-seeded *PP cc jj* lines 146 and 147, both derived from his cross no. XII, *PP CC jj* ('geschwefeltes *weiss*') × *PP cc JJ* ('rohseidengelb'). It is in his article XIII that he proves the existence of the 'second groundfactor' *Gri*, but this need not to be discussed here. From p.255 he discusses his cross no. 162:

L.146, rec. white	L.60, 'graulich weiss'
PP Gri Gri cc jj (*gg bb vv*)	*PP gri gri CC JJ* (*gg bb vv*)

F_1 being *PP Grigri Cc Jj* (*gg bb vv*), mottled 'schamois/rohseidengelb'.
F_2 segregates into 1/4 *PP grigri* and 3/4 PP Gri. In this latter part C and J show their normal action, resulting however not into 3/4 *J.* against 1/4 *jj*, but into 718 *J.* against ± 53 *jj* (non-shiny without hilumring; *CC*, *Cc* and *cc*).

Lamprecht further writes: 'Das bestehen eines zweiten Genpaares mit wenigstens praktisch genommen gleichen Effekt wie *J-j* habe ich eben in noch einer Kreuzung (no. 133) feststellen können (988 *J.* against 71 *jj*) ...weshalb also kein Zweifel über das Vorhandensein eines zweiten Genpaares mit dem Effekt von *J-j* bestehen kann'. This second gene pair he calls *Ins-ins*, derived from *insericoloratus* (= non-silkcoloured or non-shiny). – In the next article however (Lamprecht XIV, 1939), an important supplementing observation about this discovered 'second shine factor' *Ins* is made. Lamprecht writes: 'Die Testafarben 'schamois' und 'schamois/Rohseidengelb' (CC resp. Cc, with at least one of the two genes *J* or *Ins*) zeigten etwa die übliche Variation. Unter den rohseidengelben Samen (cc, with at least *J* or *Ins*) war die Variation indessen grösser als gewöhnlich. *Namentlich wurde ein Teil der Samen dieser Farbe als besonders hell bezeichnet.* Die hatten auch eine *mattere Oberfläche* als die sonst stets stark glanzenden J-Samen. Diese (hellen; present author) Samen wurden nun, nachdem sie drie Jahre aufbewahrt gewesen, neuerdings durchgegangen. Hierbei stellte sich heraus, dass sie von *J*-Samen und damit auch von *J Ins*-Samen ganz verschieden waren: *...die 'hellrohseidengelben' Samen behielten ihre Farbe anscheinend ganz unverändert bei*'; i.e. they did not at all show the strong afterdarkening of the *J*-group (Kooiman: C-group). 'Die Farbe hell rohseidengelb ist also auf das Gen *Ins* zurückzuführen. *Dieses steht in seiner Wirkung ... jener der Gene G und B näher als der von J*'. All three genotypes of Lamprecht, *PG*, *PB* and *P Ins* therefore have four characters in common:

1. the brown hilumring,
2. for the rest almost colourless, whitish,
3. not very shiny and
4. no afterdarkening.

Therefore *Ins* is, according to the present author, very probably *identical* with the 'hilumring factor' *D* of Kooiman, just as the alleged hilumringaction of *G* and *B* also depends upon the action of *D*. Lamprecht *did find* 'hellrohseidengelb' (hilumringtype; scheme: row III), but in the same cross he *did not find* (and therefore apparently *not save*) 'hell schamois', which not at all need wonder, because the difference between *newly harvested* $CC^{D.}_{dd}J.$ ('schamois'; scheme: VI-1 and VIII-1) and $CC\ D.\ jj$ ('ambra'; scheme: IV-1) is extremely slight, much less clear than that between 'rohseidengelb' ($cc^{D.}_{dd}J.$; scheme: V-1 and VII-1) and 'hilumring type' ($cc\ D.\ jj$; scheme III-1). – As a last remark with respect to cross no. 162: the special hilumringfactor, *Ins* = *D*, *must* be discovered here, because the hilumring action could not be ascribed to *G* or *B*, the whole F_1 and F_2 being *gg bb*.

In Lamprecht XIV, 1939, further important aspects with respect to hilumring action are to be found. In its title all Lamprecht's results regarding the yellow-black group (inclusive his misinterpretations as I think) are collected: 'Über die Wirkung der Gene *P*, *C*, *J*, *Ins*, *Can*, *G*, *B*, *V*, *Vir*, *Och* und *Flav*'. The first cross analysed in it is no. 107:

'bister' × 'weiss'
(PP GriGri) CC [DD] JJ GG bb vv *(PP GriGri) cc [dd] jj gg bb vv*
F_1: bister/maisgelb = *(PP GriGri) Cc [Dd] Jj Gg bb vv* (*D-d*, between square brackets, has been added by the present author).

The situation is *the same* as that in cross no. XVII (cf. pres. art. p.20), except that cross no. XVII was homozygous *CC*. Therefore the situation is *quite analogous* to that in crosses VI and XLVIII just delt with (p.22): F_1 there *Cc [Dd] Jj **Bb*** and here *Cc [Dd] Jj Gg*. Hilumring action in the present cross no. 107 again is wrongly ascribed to *G*. Segregation among the mat types (*jj*) with (*D. jj*) and without hilumring (*dd jj*) is not mentioned by Lamprecht, though according to my experience the *G-g* action there *must* have been visible: in the presence of not only 'steinfarbig mit carunculastrich' (Lamprecht: *CC jj G. Ca*; Prakken: *CC D. jj G.*; scheme: IV-2) but also 'steinfarbig ohne carunculastrich' (Lamprecht: *CC jj G. ca ca*; Prakken: *CC D. jj gg*; scheme: IV-1), and in the presence of not only 'gelblich weiss' (Lamprecht: *CC jj gg Flav*; Prakken *CC dd jj G.*; scheme: II-2) but also 'geschwefeltes weiss' (Lamprecht: *CC jj gg flav flav*; Prakken: *CC dd jj gg*. scheme: II-1). My explanation of this not-mentioning is that 'carunculastrich' is considered by Lamprecht as but an 'Abzeichen', not at discussion here, and that the difference between 'gelblich weiss' and 'geschwefeltes weiss' is very inconspicuous (cf. the many changes in the genetic explanation of this difference, see pres. art. p.20).

Lamprecht's next cross, no. 337 (XIV, 1939, p.260), shows, except for being *Pp*, accurately the same F_1-genotype and F_2-segregation, needs therefore no discussion. More discussion, however, needs the following one, cross no. 126 (p.262):

'geschwefeltes weiss' 'rhamninbraun'
(primrose yellow) (buckthorn brown)
(PP GriGri) CC [dd] jj gg bb vv *(PP GriGri) cc [DD] JJ GG BB vv*
(scheme: II-1) (scheme: V-4 or VII-4)
F_1: 'mineralbraun/rhamninbraun'
(PP GriGri) Cc [Dd] Jj Gg Bb vv

Observe that this F_1 is heterozygous for the 'shine factor' pair, *Jj*, and at the same time heterozygous *Gg Bb*. Therefore among the mat *jj*-types, with and without brown hilumring (*D.* resp. *dd*) *not one but two modifying genes* have to be found by Lamprecht. He indicates them as *Och* and *Vir*. *Vir* has been discussed before (pres. art. p.22). About *Och* he writes (p.265): 'Über das zweite Modifikationsgen *Och* wurde von mir kurz erwähnt (VI, 1933, p.253) dass es 'geschwefeltes weiss' in 'gelblich weiss' (*ochraceous*) umwandelt. Diese Angabe ist zu berichtigen. Die von mir (1932^b, p.3) beschriebene Farbe 'gelblich weiss' wird durch ein rezessives Modifikationsgen (ev. zwei) bedingt. Dieses Gen will ich, abgeleitet von *flavus* = gelb, mit dem Symbol *flav* belegen'. It seems quite certain to the present author that *Och* too, like *Flav* and *Ca*, *a new symbol is for the action of the 'yellowbrown factor' G within the field of mat colours*, shaped because of the overlooking of the real character of *Flav-flav* and because of the special difficulties met in connection with the (pseudo-) existence of *two* 'hilumring factors', *G* and *B*. To analyse thoroughly LAMPRECHT's whole analysis would take too much space. I only cite his statement on p.265 about the hilumring types *PB* (veilchenartig weiss), *PG* (speckweiss) and *PGB* (graulich speckweiss): 'Alle drei Farben können gemeinhin als *weisslich* bezeichnet werden. Bei der Beurteilung von Kreuzungen, wo fast stets noch eine Reihe von anderen Genen spaltet und verschiedener Grad von Reifung sich geltend macht, *lassen sie sich nicht sicher unterscheiden*'. According to the present author there is but *one* hilumring gene acting in the cross, viz. *D*. A clear indication for this is also found in the number of F_2 recessive white (*PP*) individuals. According to LAMPRECHT, there should be 1/256 (*PP cc jj gg bb*, after F_1 *PP Cc Jj Gg Bb*), according to my hypothesis however 1/64 (*PP cc dd jj*, after F_1 *PP Cc Dd Jj*). With an F_2 of 1127 individuals there occur 10 recessive whites, D/m for 1/256 (= 4.40) being (+) 2.7, and for 1/64 (= 17.6) being (–) 1.8. It looks very improbable that a quadruple recessive should appear so much too frequent (cf. also p.32 of the present article).

LAMPRECHT's endconclusion about the two parents in cross no. 126 is:
L. 156, 'geschwefeltes weiss' = *P C j g b v (r) vir och Flav.*
L. 157, 'rhamninbraun' = *P c J G B v (r) Vir Och Flav.*
According to the present author the situation is much simpler:
L. 156, 'geschwefeltes weiss' = *P C d j g b v (r)* (scheme: II-1).
L. 157, 'rhamninbraun' = *P c D J G B v (r)* (scheme: VII-4),
the F_2-whites not being quadruple recessive (after *Cc Jj Gg Bb*), but *triple recessive* (after *Cc Jj Dd*). *Flav, Ca, Och and Vir apparently do not exist.*

Still one cross of LAMPRECHT XIV has to be discussed, no. 378, p.280. It is between the recessive white line 214, *P c j ins g b v r*, and line 62, a type very near *P C J*, 'schamois', but with the canary yellow colour (always to be found at the ventral side of 'schamois', more or less far extending over the seedcoat) very pronounced, so that LAMPRECHT indicated line 62 as 'kanariengelb' (canary yellow; scheme: VI-1, or better VIII-1). F_1 has the genotype *PP Cc Jj gg bb*, i.e. a constitution where an extra hilumringfactor, if present, *must* be discovered: heterozygote *Jj* and recessive *gg bb*, cf. his cross no. 162, pres. art. p.23. The F_2-segregation (522 plants, table p.283) learns that an extra hilumringfactor *is* really present, *is* discovered by LAMPRECHT, and named *Can* (from *canus* = 'graulich weiss' or 'speckweiss'). The F_1 genotype therefore was, according to LAMPRECHT, *PP Cc Jj Can can* (= *Dd*), and the F_2-whites are triple recessive: 5 (exp. 8.2).

About this fifth gene (*J* included) to which LAMPRECHT ascribed hilumring action he writes (XIV, p.282) that *Can* 'weder mit *Ins*, noch mit *G* oder *B* identifiziert werden kann'. But all his evidence is *indirect or depends on quite uncertain small differences in action*, so the present author is rather sure that all four symbols (*G, B, Ins* and *Can*), as far as their pretended (*G, B*) or real hilumring action (*Ins, Can*) concerns, *represent one and the same gene*, viz. KOOIMAN's *hilumringfactor D* (= *Can* = *Ins*), in the scheme row III-1:

1. *P Ins* = 'hell rohseidengelb', but according to Lamprecht (XIV, p.281) it is nearer to *PG* and *PB* than to *PJ*,
2. *P Can* = 'speckweiss', typical hilumring type.
3. *P G* = 'speckweiss' (not caused by *G*, but by the hilumring factor *D* = *Can*)
4. *P B* = 'veilchenartig weiss' (not caused by *B*, but by the hilumring factor).

Or, together with *PC* (*PC* = 'geschwefeltes weiss'; scheme: II-1):

1. *P C Ins* = 'schamois' (no, '*ambra*', then overlooked by Lamprecht; scheme: IV-1).
2. *P C Can* = '*ambra*' (scheme: IV-1).
3. *P C G* = 'steinfarbig' (steinfarbig without car. stripe, *ca ca* = *gg*, = '*ambra*'; scheme: IV-1).
4. *P C B* = '*ambra*' (in 3 and 4 *G* and *B* represent the hilumringfactor *D*).

Or, together with *PJ* (*PJ* = 'rohseidengelb'; scheme: V-1):

1. *P J Ins* = 'rohseidengelb' (scheme: VII-1). } not to distinguish,
2. *P J Can* = 'dunkel rohseidengelb' (scheme: VII-1) } both *P J D*.
3. *P J G* = 'maisgelb' (here it is the real modifying action of *G*)
4. *P J B* = 'havannabraun' (here it is the real modifying action of *B*)
   (In the scheme: 3 = V-2 or VII-2 and 4 = V-3 or VII-3).

Lamprecht's article XIV, 1939, was the last one the present author took into consideration when writing the article (Prakken, I, 1940) in which he, on the ground of his own results reported there and earlier (Prakken, 1934), tried to reconcile Lamprecht's results with those of Kooiman and Prakken, reasoning along about the same lines as above. Sharply formulated Prakken's suggestions were (and are) as follows:

Lamprecht's genes *G* and *B* do not cause a brown hilumring, they are but *modifying genes*, which, in addition to their very wellknown influence upon the colour of the shiny *J. C.* and *J.cc* types, *cause parallel changes* upon the mat *jj D. C.* and *jj dd C.* colours (with resp. without brown hilumring), changes for which Lamprecht makes the non-existing genes *Flav*, *Ca*, *Och* and *Vir* responsible; the hilumringtype action, wrongly ascribed to *G* and *B*, depends upon the special 'hilumring factor' *D* of Kooiman, which at all probability is homologous with the genes *Can* and *Ins* of Lamprecht.

As already mentioned in the introduction, Lamprecht however became not convinced and in a comprehensive article containing numerous crosses (Lamprecht, 1951) he opposed my suggestions and completely stuck to his original opinions about the 'colour genes' *C*, *J*, *Ins*, *Can*, *G* and *B* and the 'modifying genes' *Flav*, *Och* and *Vir*, considering *Ca* as but a gene for 'Abzeichen'.

The present author has read and re-read Lamprecht's article of 1951 and scrutinized every cross from the diverse points of view, but *he finds no real or tenable arguments against his own explanation*, neither here nor in some more recent articles (Lamprecht, 1960, 1964). Discussing every cross would take too much space, therefore but a few crosses and some general points will shortly be mentioned.

1. *Mat colours without brown hilumring* (*CC*; *with action of Flav*, *Och* and *Vir*).

Cross no. 163 (p.26):

L.23, geschwefeltes weiss	×	L.155, gelblich weiss
PP CC flavflav		*PP CC FlavFlav*
(scheme: II-1)		(scheme: II-2)

F_1: *PP CC Flavflav* (gelblich weiss).

F_2: 376 gelblich weiss (*Flav.*) : 143 geschwefeltes weiss (*flavflav*).

This is the first analysis in which LAMPRECHT plainly recognized Flav as a *dominant gene* for 'gelblich weiss', while before the genetics of this colour was very unclear (cf. pres. art. p.20 and 25): double recessive? single recessive? mutants? It looks as if one has to 'learn to see' the difference (the present author never learned it quite clear).

Cross no. 576 (p.27):

L.427, weiss	×	L.155 gelblich weiss
PP cc flavflav		*PP CC FlavFlav*
(scheme: I-1)		(scheme: II-2)

F_1: *PP Cc Flavflav* (mottled, 'gelblich weiss/weiss').

F_2: colour	number	ratio	genotype acc. to LAMPRECHT	genotype acc. to PRAKKEN
gelblich weiss	47	3	(*PP*) *CC Flav.*	(*PP*) *CC G.*
geschwefeltes weiss	16	1	(*PP*) *CC flavflav*	(*PP*) *CC gg*
gelblich w./weiss	73	6	(*PP*) *Cc Flav.*	(*PP*) *Cc G.*
geschwef. w./weiss	24	2	(*PP*) *Cc flavflav*	(*PP*) *Cc gg*
weiss	48	4	$(PP)\ cc\begin{cases}Flav.\\ flavflav\end{cases}$	$(PP)\ cc\begin{cases}G.\\ gg\end{cases}$

Again Flav appears clearly dominant, and moreover not a colour gene but *a modifying gene*. But now, *the origin* of L.155, 'gelblich weiss' (*P C Flav*), parent in both above crosses, is very important. It comes from LAMPRECHT's cross XVII, extensively discussed on p.20 of the present article. Among 93 'geschwefeltes weiss' individuals (*CC jj gg* according to LAMPRECHT; $CC\ dd\ jj \begin{cases}G.\\ gg\end{cases}$ according to PRAKKEN) LAMPRECHT found 5 which were less greenish and indicated by him as 'gelblich weiss'. From one of these individuals, then supposed to be homozygously double recessive, the more so because *all five bred true*, line 155 has been derived. *Now* LAMPRECHT (1951, p.26) writes: 'Das Auftreten in Kreuzung Nr. XVII kann daher *nicht als Ausspaltung* aufgefasst werden sondern ist sicherlich *durch eine Mutation* von *flav* zu *Flav* verursacht'. To this the present author asks: but why in that case would all 5 individuals have been homozygous *FlavFlav* (= true breeding 'gelblich weiss')? And he comes to the conclusion that LAMPRECHT at that time *not yet had learned to sharply distinguish* between *Flav.* and *flavflav*, and had picked out 5 extreme types, all being homozygously dominant ... *GG*, and not *FlavFlav*. LAMPRECHT

(1951, p.23) as a matter of fact writes: 'Aufschlussreich ist PRAKKEN's Beschreibung der Farbe seiner Rasse 'Citroen'. Diese wird als Ambra = R.C. (Répertoire de Couleurs) 12, 3 und 4, sowie zuweilen Gelblich Weiss = R.C. 13, 4 angegeben. Im C.S. (Color Standards, RIDGWAY, 1912) entsprechen diese Farben XVI 23'e = Barium Yellow and Naphthalene Yellow bzw. XVI 21'e = Straw Yellow and Massicot Yellow. *Diese Farben entsprechen demnach keineswegs meinem Geschwefelten Weiss sondern meinem Gelblich Weiss*'.

Cross no. 575 (p.34):

L.155, gelblich weiss	×	L.230, russgrün
PP CC FlavFlav virvir		*PP CC flavflav VirVir*
(scheme: II-2)		(scheme: II-3)

F_1: *PP CC Flavflav Virvir* (hell antiquabraun).

F_2: colour (scheme: II-4, 3, 2, 1)	number	ratio	genotype according to LAMPRECHT	genotype acc. to PRAKKEN
hell antiquabraun	134	9	*(PP CC) Flav. Vir.*	*(PP CC) G. B.*
russgrün	50	3	*(PP CC) flavflav Vir.*	*(PP CC) gg B.*
gelblich weiss	44	3	*(PP CC) Flav. vir vir*	*(PP CC) G. bb*
geschwefeltes weiss	8	1	*(PP CC) flavflav virvir*	*(PP CC) gg bb*

The parallel between these mat *CC dd jj*-colours (without brown hilumring) and the corresponding shiny *CC dd J.*-colours is rather clear:

mat *PP CC dd jj*-colours (scheme: II-4, 3, 2, 1)	shiny *PP CC dd J.*-colours (scheme: VI-4, 3, 2, 1)	genotype
'hell antiquabraun'	'mineralbraun' or dark brown	G. B.
'russgrün'	'münzbronze' or greenish brown	gg B.
'gelblich weiss'	'bister' or yellow brown	G. bb
'geschwefeltes weiss'	'schamois' or greenish yellow	gg bb

A few segregations among the mat colours present serious difficulties for my attempt to bring back the action of LAMPRECHT's *three* genes *Flav*, *Och* and *Vir* to that of the *two* genes *G* and *B*, e.g. crosses 323 (1951, p.30) and quite analogous cross 477 (p.33).

Cross no. 323:

L. 153, hell lohfarben	L.155, gelblich weiss
PP CC flavflav Och Och	*PP CC FlavFlav ochoch*
(scheme: II-11)	(scheme: II-2)

F_1: *PP CC Flavflav Ochoch* (hell antiquabraun).

F_2: colour	number	ratio	genotype according to LAMPRECHT	genotype acc. to PRAKKEN
hell antiquabraun	279	9	*(PP CC Flav. Och.*	*(PP CC G. B.*
hell lohfarben	85	3	*(PP CC) flavflav Och.*	*(PP CC) gg B.?*
gelblich weiss	102	3	*(PP CC)Flav. ochoch*	*(PP CC) G. bb*
geschwefeltes weiss	26	1	*(PP CC)flavflav ochoch*	*(PP CC) gg bb*

The present author wonders if the first parent, PC flav Och, might really have been PC flav Vir. According to his experience the difference between 'brown' and 'greenish brown' among the mat colours sometimes is rather inconspicuous. In this connection LAMPRECHT (1951, p.35) may also be cited: 'Russgrün zeigt bei schlechter Ausbildung und auch nach einiger Zeit Lagerung nach Hell Lohfarben ziehende Töne. Normal ist Hell Lohfarben bräunlicher und leicht von Russgrün zu unterscheiden. Hell Antiquabraun lässt bei schlechter Ausfärbung im Grund einen an Hell Lohfarben erinnernden Ton erkennen'. These difficultes and variabilities should also be thought of when LAMPRECHT (1951, p.35) presents (but only theoretically, without segregation-numbers) the types in the offspring of a triple heterozygote *(PP CC) Flavflav Ochoch Virvir*:

colour	genotype acc. to LAMPRECHT	genotype acc. to PRAKKEN
antiquabraun	(*PP CC*) Flav . Och . Vir .	(*PP CC*) G. B. (scheme: II-4)
hell antiquabraun	(*PP CC*) Flav . Och . virvir	(*PP CC*)
hell antiquabraun	(*PP CC*) Flav . ochoch Vir .	(*PP CC*)
hell lohfarben	(*PP CC*) flavflav Och . Vir .	(*PP CC*)?
hell lohfarben	(*PP CC*) flavflav Och . virvir	(*PP CC*) ?
russgrün	(*PP CC*) flavflav ochoch Vir .	(*PP CC*) gg B. (scheme: II-3)
gelblich weiss	(*PP CC*) Flav . ochoch virvir	(*PP CC*) G. bb (scheme: II-2)
geschwefeltes w.	(*PP CC*) flavflav ochoch virvir	(*PP CC*) gg bb (scheme: II-1)

It is a pity that LAMPRECHT does not analyse or discuss a cross P C *Och* × P C Vir, which might have been enlightening.

2. *Mat colours with and without a brown hilumring.*

As LAMPRECHT concluded that among the mat (*jj*) colours the genes *G* and *B* are responsible for the appearance of a brown hilumring, he had to introduce the special modifying genes (*Flav*, *Och*, *Vir*) responsible for the colour variation in the mat types with and without hilumring. The most complete discussion of their action within both types is made with the help of his cross no. 126 (LAMPRECHT XIV, 1939, p.262–271; 1951, p.64–65):

L. 156, geschwefeltes weiss	L.157, rhamninbraun
PP CC, further recessive	*PP cc* [*DD*] *JJ GG BB vv*
scheme: II-1	scheme: VII-4

F_1:*PP Cc* [*Dd*] *Jj Gg Bb* (mineralbraun/rhamninbraun; hypostatically, according to LAMPRECHT, also *Ochoch Virvir*). On page 25–26 of the present article the cross is shortly discussed and it was pointed out that the F_2-ratio of recessive white-seeded individuals is much nearer to a trifactorial segregation (after *Cc Dd Jj*) than to a quadrifactorial one (after, as LAMPRECHT had to suppose, *Cc Jj Gg Bb*). The (theoretical) factorial explanation for *the mat jj colours* given by LAMPRECHT (1951, p.64) is reproduced below. To the right in the table the suggested factorial explanation of the present author has been placed.

genotype	colour	genotype	remarks
acc. to LAMPRECHT	acc. to LAMPR.	acc. to PRAKKEN	remarks
(PC) G. B. Och . Vir .	lohfarben	(PC) D. G. B.	
(PC) G. B. Och . virvir	lohfarben	(PC) D. G. B.	
(PC) G. B. ochoch Vir .	mattmünzbronze	(PC) D. gg B.	
(PC) G. B. ochoch virvir	steinfarbig	(PC) D. G. bb (=*with* car.stripe!)	

(PC) G. bb Och . Vir .	lohfarben	(PC) D. G. B.
(PC) G. bb Och . virvir	lohfarben	(PC) D. G. B.
(PC) G. bb ochoch Vir .	mattmünzbronze	(PC) D. gg B.
(PC) G. bb ochoch virvir	steinfarbig	(PC) D. G. bb (=*with* car. stripe!)
(PC) gg B. Och . Vir .	lohfarben	(PC) D. G. B.
(PC) gg B. Och . virvir	lohfarben	(PC) D. G. B.
(PC) gg B. ochoch Vir .	mattmünzbronze	(PC) D. gg B.
(PC) gg B. ochoch virvir	ambra	(PC) D. gg bb (= steinf. *without* car. str!)
(PC) gg bb Och . Vir .	hell lohfarben	(PC) dd G. B.
(PC) gg bb Och . virvir	hell lohfarben	(PC) dd G. B.
(PC) gg bb ochoch Vir .	russgrün	(PC) dd gg B.
(PC) gg bb ochoch virvir	geschwefeltes w.	(PC) dd gg bb (incl. dd G. bb = gelblich weiss).

In Lamprecht's scheme 'gelblich weiss' is not represented, because he thinks of it as caused by *Flav*. Moreover, as Lamprecht disposes of *two* hilumringtype genes (*G* and *B*), while the present author thinks there acts only *one* (*D*), the scheme is in a sense *doubled* and has to be simplified as follows (*Och* and *Vir* can be left out):

Colours of Lamprecht	genotype acc. to Prakken	corresp. colours of Kooiman	genotype acc. to Kooiman
lohfarben	(PCj) D. G. B. vv (scheme: IV-4)	soft brown with h.r.	(ABc)D. (GG) E. ff (scheme: IV-4)
mattmünzbronze	(PCj) D. gg B. vv (scheme: IV-3)	–	–
steinf. with car.str.	(PCj) D. G. bb vv (scheme: IV-2)	lemon coloured with h.r.	(ABc)D. (GG) ee ff (scheme: IV-2)
ambra	(PCj) D. gg bb vv (scheme: IV-1)	–	–
hell lohfarben	(PCj) dd G. B. vv (scheme: II-4)	soft brown without h.r.	(ABc)dd (GG) E. ff (scheme: II-4)
russgrün	(PCj) dd gg B. vv (scheme: II-3)	–	–
gelblich weiss	(PCj) dd G. bb vv (scheme: II-2)	lemon coloured without h.r.	(ABc)dd (GG) ee ff (scheme: II-2)
geschwef. weiss	(PCj) dd gg bb vv (scheme: II-1)	–	–

According to the present author therefore the genes *G* and *B* act *in an identical* or at least *in a quite analogous way* among the three dark pattern (CC) colour groups. Below the colours of the three groups, under the 'names' they received from Lamprecht, are placed side by side (the vv colours only):

genotype	*shiny dark pattern CCD.J. and CC dd J.* (scheme: VIII- and VI-4 to 1)	*mat d.p. with h.r. CC D. jj* (scheme: IV-4 to 1)	*mat d.p. without h.r. CC dd jj* (scheme: II-4 to 1)
G. B. vv	mineralbraun	lohfarben	hell lohfarben
gg B. vv	münzbronze	mattmünzbronze	russgrün
G. bb vv	bister	steinf. (*with* car.str.)	gelblich weiss
gg bb vv	chamois	ambra (*without* car.str.)	geschwefeltes weiss

After thus having tried to make probable that *G* and *B* are modifying factors which in an analogous way influence the colours of the three dark pattern groups $CC\genfrac{}{}{0pt}{}{D.}{dd}J.$, *CC D. jj* and *CC dd jj*, also in LAMPRECHT's material, a few remarks of more general importance have to be made.

3. *The number of segregating PP cc... recessive whites is always too high* when F_1 is *Gg Bb* (and at the same time $\genfrac{}{}{0pt}{}{D.}{dd}Jj$), just because *G* and *B* do not have hilumringtype action and are but *modifying genes*. The present author indicated it already (pres. art. p.25–26) in connection with cross no. 126 in LAMPRECHT XIV, 1939, with the F_1-genotype *PP Cc [Dd] Jj Gg Bb*. In the article of 1951 LAMPRECHT *himself is struck by it*. He mentions three F_2-families after F_1 of the genotype *PP cc Jj [Dd] Gg Bb*:

no. of cross	total number F_2	number rec. whites	expected 1/64 (*jj gg bb*)	expected 1/16 (*jj dd*)
582, p.43	288	26	4.5	18.0
408, p.44	446	35	7.0	27.9
533, p.45	443	21	6.9	27.7
total	1177	82	18.4	73.6

As a possible 'explanation' either linkage between G and B (generally, however, segregating quite independently) or mutation from G to g or B to b are suggested by LAMPRECHT (1951, p.44).

4. *The segregation for the would-be modifying genes Flav, Och and Vir among the mat C. jj-types is generally quite predictable* (just because *Flav*, *Ca* and *Och* = *G*, and *Vir* = *B*):

$PP\ C.\genfrac{}{}{0pt}{}{D.}{dd}Jj$ Gg segregates for *Flav* (and/or *Ca*) = G;
$PP\ C.\genfrac{}{}{0pt}{}{D.}{dd}Jj$ Bb segregates for *Vir* = *B*;
$PP\ C.\genfrac{}{}{0pt}{}{D.}{dd}Jj$ Gg Bb segregates for *Och* and *Vir* = *G* and *B*;

Och in the latter case, however, does not represent the real but *a deformed G*, as certain (weak) action of *G* is ascribed to *Flav* (or *Ca*) and moreover that weak action was not always noticed. Cross no. 28 (LAMPRECHT, 1951, p.47) is said to have the F_1-genotype *Pp Cc Jj Gg Bb Vv Flavflav Ochoch Virvir*, which according to the present author should be *Pp Cc Dd Jj Gg Bb Vv*. LAMPRECHT's F_2 of this cross contained 1600 plants, F_3-F_7 about 15000, but segregation numbers of individual F_3-families are hardly given, only F_2-genotypes concluded from groups of F_3-families. This cross is of a special value because it learns much about the influence of V-v upon the mat types (complete homologization, however, remains difficult, esp. as regards the *jj V.* colours, right upper quarter of the scheme).

From more recent work of LAMPRECHT (1964), SMITH (1961) and NAKAYAMA

(IX, 1968) the modifying character of *G* and *B* can also be concluded, e.g. by the segregation of not 1/16 recessive *PP* whites but 1/4, or by the presence of *G* or *B* in a white seeded *PP* parent plant. Because of space, however, these crosses will not be discussed.

5. LAMPRECHT himself too sometimes is confronted with some quite unexpected action of e.g. the modifying gene *Flav*: generally the modifying genes *Flav*. *Och* and *Vir* are without influence upon shiny *J*.-types, but in some crosses *Flav* appears to change (hell) 'rohseidengelb' (*PcJ*; scheme: V–1) into (hell) 'maisgelb' (*PcJG*; scheme: V-2), or 'schamois' (*PCJ*; scheme: VI-1) into (hell) 'bister' (*PCJG*; scheme: VI-2), thus behaving like *G* (what it, according to the present author, *really is*). For saving the character of *Flav* (as not influencing shiny *J*-colours), LAMPRECHT suggests *that in the pertinent cases the shiny J-parent is not really J but Ins*, while *Ins*, according to him, obviously *is* influenced by *Flav*. LAMPRECHT (1951, p.54) in this connection writes: 'In Bezug auf die Wahl von Symbolen für die polymeren Gene *J* und *Ins* bzw. *Can* und *G* (zum Teil vielleicht auch B) sei hier auf eine einstweilen bestehende Schwierigkeit hingewiesen. In spaltendem Material kann auf Grund der Farbenwirkung allein oft nicht entscheiden werden, um welches von diesen Gene (*J* oder *Ins*, bzw. *G* oder *Can*) es sich handelt. Es ist daher damit zu rechnen, dass die genotypische Konstitution von Linien auf Grund späterer Kreuzungsergebnisse *einmal geändert werden muss.* Die Zugehörigkeit zu einer bestimmten Koppelungsgruppe würde hier sogleich klaren Bescheid geben; aber hiervon sind wir noch weit entfernt. Einstweilen soll in Bezug auf *J* und *Ins* so vorgegangen werden, dass *wenn Modifikationsgene auf eine Testfarbe keinen Einfluss haben, so soll das Symbol J benutzt werden, im umgekehrten Fall wird J durch Ins ersetzt*'. To this however, it has to be remarked that LAMPRECHT himself only at the time of the first analysis (cross no. 162, LAMPRECHT XIII, 1936) supposed that *Ins* was a more or less duplicate gene of *J*, but that a few years later he became aware that in reality *Ins* produces not a shiny and afterdarkening J-phaenotype, but a whitish, not very shiny and non-afterdarkening *hilumringtype* (cf. pres. art. p.24).

In agreement with the 'principle' cited above the genotype of line 199 (originating precisely from his cross no. XII, *PP CCjj* × *PP cc JJ*!) is changed from *PP cc JJ flavflav* (cf. LAMPRECHT 1951, cross no. 582, p.43) into *PP cc InsIns flavflav* (1951, cross no. 574, p.54). And line 62, *PP CC JJ CanCan* in cross no. 378, p. 46, becomes *PP CC InsIns CanCan* in cross no. 551, p.57:

PP CC Ins Ins CanCan flavflav × *PP CC insins cancan FlavFlav*,

F_1: *PP CC Insins Cancan Flavflav*. According to the present author this F_1 has the same genotype (and the same F_2-segregation) as LAMPRECHT's cross no. XVII at the beginning of this chapter (*PP CC Dd Jj Gg*, cf. fig. 1), both parents in this case also having the same genotype as those in PRAKKEN's cross no. 4:

PP CC DD JJ gg (chamois) × *PP CC dd jj GG* (gelblich weiss), Ins being *J*, *Can* being *D* and *Flav* being *G*.

In this chapter (and the foregoing ones) I think to have made clear that the results of Kooiman (1920, 1931), Lamprecht (1932–1964) and Prakken (1934, 1941) are essentially the same, see also next chapter 6, Conclusions. It should be pointed out, however, that these conformities *relate to one rather generally occurring genetic situation*, and that various complications due to further genes exist.

In this respect the already mentioned high variability in extension and intensity of violet or bluish covering tinges in *cc V.* background colour types, partly caused by environmental and partly by genetic influences, has to be reminded of first (the corresponding *CC V.* dark pattern colours seeming hardly to be influenced). The present writer has paid careful attention to the subject, but he never came to a complete solution. – Secondly, according to all literature, these (partly) covering violet tinges occur in violet flowering *cc V.-types* only. Some years ago, however, the present author has found more or less analogous partly covering rose-violet tinges, also extremely variable, in pale lilac flowering cc $v^{lae}v^{lae}$-types too. Crosses for explaining the situation were made, but unfortunately the seed produced by the various F_1-types (1969) has been completely destroyed by a severe attack of the common bean weevil (*Acanthoscelides obtectus* Say). – As a third complication of the general scheme to be given in chapter 6, a gene pair met with by the present author, but not yet described and named, has to be mentioned: in its (apparently seldom occurring) recessive state it partly to almost completely locally suppresses the action of the yellowbrown gene *G*, which normally e.g. changes greenish yellow or 'schamois' (*CC JJ gg*) into yellowbrown or 'bister', (*CC JJ G.*, cf. the scheme). – Also Lamprecht's 'second basic gene' *Gri* has to be mentioned in this connection.

6. Conclusions

The author has tried to show the strong relationship between the seemingly divergent results obtained with respect to seedcoat colour inheritance in the yellow-black colour group of *Phaseolus vulgaris* L. by Kooiman, Lamprecht, Prakken and other authors.

The disagreements depend, according to the present author, upon the wrong conclusions Lamprecht drew about the action of the genes *G* (yellowbrown factor) and *B* (greenish brown factor). These are, according to Kooiman and Prakken, purely modifying genes which change the colour within the shiny and afterdarkening *J.*-group (J causing, according to all investigators, at the same time a brown hilumring) *and* in the mat and non-afterdarkening *jj*-groups with and without a brown hilumring, in a quite analogous way. Lamprecht, however, recognized their colourchanging action within the shiny *J.*-group only, ascribing to them within the mat *jj*-colour group *hilumring-action*, mat without hilumring according to him being *jj bb gg* and mat with a brown hilumring being *jj G.*, *jj B.* or *jj G. B.* (at those moments he overlooked the special hilumring-factor *D* of Kooiman); as a consequence Lamprecht had to introduce special, but in reality non-existing, modifying genes (*Flav*, *Ca*, *Och* and *Vir*). for the colour changing actions within the mat *C. jj*-groups. Ultimately, in *gg bb* types, he discovered the special *hilumring-gene*, which received the symbols *Ins* and *Can*, both at all probability identical with KOOIMAN's hilumring factor *D*. With LAMPRECHT's needlessly complicated system, it becomes impossible to ascribe one characteristic action to each gene (the result depending upon their combination), and one and the same colour can depend on many different combinations of dominant genes (cf. e.g. 'Lohfarben', with eight different genotypes, LAMPRECHT 1951, p.78).

According to the present author all investigations together, and primarily those of KOOIMAN (1920, 1931), suggest a relatively simple explanation of seedcoat colorer in the yellow-black group of *Phaseolus vulgaris*, *each gene showing a clear specific action* and generally *each colour being caused* (except for a few simple cases of epistasis) *by one definite combination of dominant genes.*

Three complementary colour genes, together with *the basic gene*, are responsible for the various *'colour groups'* (see cheme p.123, **I-VIII**), while *three modifying genes* are responsible for the (parallel!) *'colour series'* within the groups (see scheme, **1-8**; for some further complications cf. p.34).

The hitherto identified (main) genes, indicated with the symbols used by LAMPRECHT (only the symbol *D* for the hilumringfactor has been taken from KOOIMAN) are:

1. *P* (= *A* of KOOIMAN) *groundfactor* or *basic gene* (left out in the scheme; the factor *Gri*, according to LAMPRECHT a second basic gene, has been left out of discussion).

   Three *chromogenous factors* or *complementary colour genes* (in the scheme to the left):
2. *C* (= *B* of KOOIMAN), the 'factor for ever-segregating mottling', CC being greenish yellow ('geschwefeltes weiss') and Cc greenish yellow mottled upon white.
3. *D* (symbol of KOOIMAN, = *Ins* and *Can* of LAMPRECHT[1]), the 'hilumring factor', producing a brown hilumring, but for the rest leaving the seedcoat almost whitish (hilumringtype) or unchanged.
4. *J* (= *C* of KOOIMAN), the 'shine factor', producing a brown hilumring and making the seedcoat of a shiny and highly afterdarkening pale yellowish colour ('rohseidengelb' or cartridge buff). All *jj*-colours are non- (or less) shiny, i.e. mat or dull, and non-afterdarkening.

   Three *intensifying factors* or *modifying genes*, together causing changes from greenish yellow or pale yellow to dark grey, near black or pure black (above in the scheme):

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[1] An indication that *Can* = *Ins* might also be taken from the fact that according to LAMPRECHT (1961a, p. 329), *both genes show linkage with the same gene Cor* (from *corona*):
crossing over *Ins-Cor* = 27.6 ± 2.6,
crossing over *Can-Cor* = 34.7 ± 2.8; as far as known to the present author the crossing - over *Ins-Can* has not been studied directly. The difference between the two values does not exclude that *Ins* and *Can* are at the same locus.

5. *G* (= homozygously dominant in KOOIMAN's material), the 'yellowbrown factor', changing greenish yellow or pale yellowish to yellow or yellowbrown.
6. *B* (= *E* of KOOIMAN), the 'greenish brown factor', changing greenish yellow or pale yellowish to grey-greenish brown.

   G and *B* together produce a brown colour.
7. *V* (= *F* of KOOIMAN), the 'violet factor', changing white (vv) or pale lilac ($v^{lae}v^{lae}$) flower into violet, also changing pink anthocyanin of all plant parts into violet, while at the same time producing bluish or violet (to black) colours in the seedcoat. Under special (genetic and environmental) conditions *V* acts as a colour gene, producing together with *P* a 'glaucescent' tinge over (part of) the white seedcoat, cf. the scheme, I-5 to I-8. The difference between vv and $v^{lae}v^{lae}$ is in the flower colour only: white resp. pale lilac.

7. SUMMARY

The genetics of the group of white-yellow-brown-violet-black seedcoat colours (briefly: the yellow-black group) in *Phaseolus vulgaris* L. is discussed. A genetical explanation based on seven loci accounts for the seemingly contradictory results obtained by the different authors (cf. the scheme p. 39). The scheme is closely related to the genetic analysis of KOOIMAN (1920, 1931), while the symbols used (except that for the hilumringfactor, *D* of KOOIMAN), are those of LAMPRECHT (1932–1964). See further chapter 6, Conclusions.

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COLOUR SYSTEMS

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Scheme for the inheritance of the group of yellow-black seedcoat colours in *Phaseolus vulgaris* L.

The *horizontal rows* **I-VIII** represent the 'colour groups' caused by the action of the (complementary) 'colour genes' *C*, *D* and *J*, together with the 'basic gene' *P* (left out); to the left are the genotypes (in **bold letter**) and above in each row is the general character of the group.

Within the groups are (except for I and III) more or loss '*parallel series*' of principally eight colours, **1–8**, caused by the action of the 'modifying genes' *G*, *B* and *V* (the latter sometimes having a slight action as colour gene, see I-4 to 8); at the top of each column is the genotype (in **bold letter**), together with an attempt to a general colour description.

Below the genotype in bold letter is the genotype written in KOOIMAN's symbols A, B, C, D, E, F, (G); the colours occurring in his analysis, columns 2, 4, 6 and 8, are indicated with a dot.

Uppermost in each of the 64 compartments ia a colour describing name, mainly derived from the results of KOOIMAN and PRAKKEN; in the lower half of each compartment is, between quotation marks, the corresponding (according to the present author) german colour name of LAMPRECHT, together with, between brackets, his english translation; in the right upper quarter (*jj V.*) the correspondence is uncertain in some cases.

The 'ever-segregating' mottled types (*Cc*) are not represented in the scheme: they are mottled in the colours of I and II, III and IV, V and VI, VII and VIII.

Abbreviations: K. = KOOIMAN; yell. br. f. = yellow brown factor; t.w. = tinged with; car. str. = Caruncula Strich (caruncula stripe).