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JOURNAL OF GENETICS

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, MANAGER
LONDON: FETTER LANE, E.C. 4

LONDON: H. K. LEWIS AND CO., LTD., 136 Gower Street, W.C. 1
LONDON: WHELDON AND WESLEY, LTD., 2-4 Arthur Street,
New Oxford Street, W.C. 2
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(Agent for the United States and Canada)
BOMBAY, CALCUTTA, MADRAS: MACMILLAN AND CO., LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

JOURNAL OF GENETICS

EDITED BY

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Volume XII. 1922

Cambridge
at the University Press
1922

PRINTED IN GREAT BRITAIN

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No. 1 (April, 1922)

No. 2 (October, 1922)

No. 3 (December, 1922)

VOLUME XII APRIL, 1922

VARIEGATION AND ITS INHERITANCE IN *CHLOROPHYTUM ELATUM* AND *CHLOROPHYTUM COMOSUM.*

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(With Plates I—VIII and Three Text-figures.)

CONTENTS.

1. *Introduction.*

THE genetical research, of which this paper gives some account, originated with an observation made in 1912 by the late Mr E. J. Allard, Garden Superintendent of the John Innes Horticultural Institution. He observed that the seedlings springing up around a large clump of *Chlorophytum elatum* var. *albo-marginatum* were wholly green and did not reproduce the albo-marginate character of the presumed parent. The seed was without doubt self sown and pollination had been left quite uncontrolled. From that time onward breeding with the various forms under controlled conditions was undertaken with the view of elucidating the problems relating to the inheritance of the variegation. It has been found necessary to investigate the origin and development of the leaf and flower, as well as the anatomy and histology of the leaf tissues. The earlier records were made by Mr Bateson. Miss M. R. Michell of the South African College, Cape Town, co-operated during the summer of 1916. The writer has been interested in the research since 1915 and is responsible for the collection and presentation of the data as well as the views expressed in the present paper.

2. *Description of the Material.*

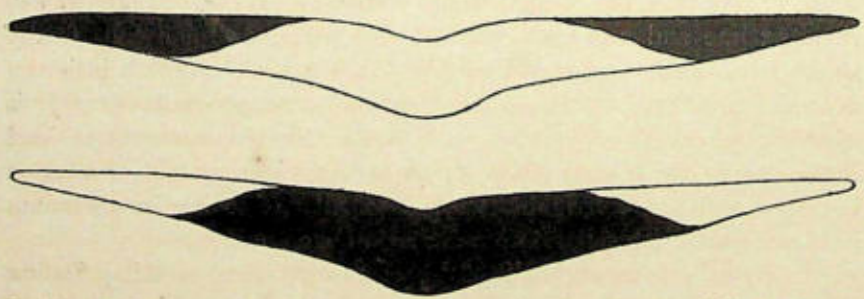
Chlorophytum is a member of the Liliaceae § Asphodeleae. It is characterised by the production of numerous crowns with radical leaves; each crown may throw a long slender stem, upon which are borne the numerous small white flowers, either singly or in groups. Following the production of the flowering shaft the crown gradually dies away. New basal crowns develop and in the course of a few years a large clump may be formed. Vegetative shoots also break out from the points from which flowers have been developed and such shoots under damp conditions push out roots. Plants can therefore be readily propagated vegetatively.

The forms which have been used are *Chlorophytum elatum* R. Br., with its two variegated forms *C. elatum* var. *albo-marginatum* and *C. elatum* var. *medio-variegatum*, and *C. comosum* var. *variegatum*. See Plate I. The type form *C. elatum* is wholly green. Of the variegated forms of this type, one, designated *C. elatum* (W. E.) in the summary of records, has a leaf with a well-marked white edge of variable width. The other form, designated *C. elatum* (W. C.), bears leaves which possess a central longitudinal white band. In *C. comosum* var. *variegatum*[1], which is of smaller growth than *C. elatum*, the leaves also show a central white band. In no case is the central white stripe or the white margin of uniform colour or width, and the separation between green tissue and white is not necessarily sharp. Outwardly, at the zone of junction between chlorophyllous tissue and albinotic tissue, longitudinal strands of white or green colour, varying in tint and width according to the number of layers and rows of the mesophyll cells affected, may frequently be found. In the central white banded leaf forms, the band viewed from the upper surface is more sharply defined, but seen from below it is wider, and the transition is more gradual because the white tissue is extended and thins out gradually over the green. The reverse is the case in the white edged form. These appearances are correlated with the distribution of the albinotic layers and rows of cells of the mesophyll. See Text-fig. 1.

Another feature to which attention must be called is that with increasing age, particularly after the crown has flowered, the white bands of the leaves of the variegated forms assume a green colour and the marked variegation characteristic of the young leaves is lost. Usually

[1] The type form *C. comosum* (Baker), *C. Sternbergianum* (Steud.), *Anthericum comosum* (Thun. Prod. 63) is wholly green. See *Index Kewensis* and *Gard. Chron.* 1873, pages 40 and 75, for the details of the nomenclature.

however the distinction can still be seen as a difference in depth of green. The variegation of the plants also appears to vary in intensity at different times but no continued observation has been made on this point. It is true that a greater intensity of the variegation might well be observed after the rapid development of many new leaves, but apart from this the intensity of the variegation may in some way be related to the amount of light and the degree of heat to which the plant is subjected. With regard to these observations, an examination of the tissues of the leaves, the results of which are described in detail later in the paper, shows that the albinotic cells retain their protoplasmic contents, and plastids[1] embedded in the cytoplasm can be made evident by the use of iodine. Thus the mechanism is present but the power of producing chlorophyll is lacking. This may be due to the working of a bleaching or an inhibitory factor which it is presumed is distributed to the albinotic cells or the plastids at the time of meristematic segregation. The green colour which the albinotic tissue assumes with



Text-fig. 1. Diagrammatic cross sections of leaves showing the general distribution of albinotic and chlorophyllous tissue in the two types of variegated leaves of *Chlorophytum*.

advancing age results from a production of chlorophyll within the plastid. Evidently the power to bleach or inhibit the production of the pigment weakens with age and if the lack of chlorophyll is due to the interaction of a factor with a chemical basis, alteration in the amount of light and heat at different seasons might bring about a variation in the intensity of the variegation.

The long slender flowering stems are wholly green in *C. elatum* and *C. elatum* (W. E.), but in *C. elatum* (W. C.) and *C. comosum* (W. C.) the

[1] The term plastid is here used to denote those granules which stain much more deeply with iodine than the cytoplasmic matrix in which they lie embedded. They are frequently smaller than normal chloroplasts and often of irregular shape; occasionally in unstained preparations they show a slight yellowish green colour.

stems are white. Occasionally faint green lines may occur but their occurrence seems quite haphazard and irregular. The bracts borne on the flowering stem and the leaves of the vegetative axes which develop later upon it are in every way similar to the type of leaf borne by the particular crown from which the flowering stem arises. Hence the flowering stems whether wholly green or wholly white retain in their growing points the power to produce the variegation characteristic of each variety.

Again it must be remembered that with age the creamy whiteness of the white flowering stem in its prime is lost and a pale green colour is assumed.

3. *General Anatomy of the Leaf.*

Fresh material was used throughout. Portions of both the upper and lower epidermis were stripped from the leaf and examined; transverse sections were also made. Mounted in water the chloroplasts swelled, lost their outline and appeared to become dissociated; some cells finally showed more or less homogeneous contents. A ten per cent. solution of salt was then used as the mounting fluid, and although slight plasmolysis of the cells was occasionally found to occur, the chloroplasts remained in good condition for observation. After examination in salt solution the specimens were irrigated with a solution of iodine in potassium iodide, washed with salt solution and again examined.

Chodat(1) has made an interesting observation respecting *Funkia Sieboldiana* var. *albo-marginata*. In it the sub-epidermal layer is green but the epidermis is albinotic. This appears from the fact that the guard cells, whether taken from above the white or from above the green parts of the leaf, are devoid of chlorophyll. On the contrary he found that in the form with the white centre—*F. Sieboldiana* var. *medio-variegata*—the guard cells were green whether taken from the green or the white parts. Hence in consideration of the condition of the epidermis, each variety may be spoken of as a periclinal chimaera. It was this observation which led me to examine the guard cells in detail, and the investigation of the leaves of *Chlorophytum* has shown that in all essential respects *Chlorophytum* agrees with *Funkia*.

It may be mentioned that in 1916 a number of seedlings raised by Bateson, as the result of self fertilisation of the white edged form of *Funkia*, all came green, which from the nature of the sub-epidermal layer might be expected.

C. elatum.

Upper epidermis. Stomata when present confined to the median longitudinal depression; guard cells with chloroplasts and starch.

Lower epidermis. Stomata abundant; guard cells normal.

Mesophyll. The number of cell layers ranges from one at the edge to seven in the thickest part of the leaf. Chloroplasts are closely packed in the cells. No starch is present.

C. elatum (W. E.).

(*a*) An old leaf with a greenish edge but still less green than the central band.

Upper epidermis. Stomata not seen in any preparation.

Lower epidermis. Stomata present over the whole surface; guard cells possess chloroplasts with starch.

Mesophyll. Chloroplasts are not confined to or absent from any particular layer of cells; they appear to be less numerous in the lighter green edge.

(*b*) A well-developed leaf with marked white edging.

Upper epidermis. Stomata not seen.

Lower epidermis. Stomata abundant over both green and white areas; the guard cells are mostly colourless but some possess slightly green and others yellowish plastids of somewhat irregular form. In all, plastids and starch are present.

Mesophyll. In general the chlorophyllous tissue forms a central mass extending towards each edge of the leaf in a rough gradient which is prolonged towards the lower epidermis. The sub-epidermal layer alone finally continues the extension of the chlorophyllous tissue. Albinotic cells retain protoplasm and plastids.

C. elatum (W. C.).

(*a*) An old leaf apparently all green; closer examination showed that the centre lacked the depth of green of the edge.

Upper epidermis. Occasional stomata were seen in the epidermis stripped from the median line; guard cells with chloroplasts and starch.

Lower epidermis. Abundant stomata; guard cells over both green and white areas with chloroplasts and starch.

Mesophyll. In the mid-leaf area the cells are generally larger than those of the leaf edge; the chloroplasts in the former cells are sparse and irregularly distributed in the protoplasmic lining whilst in the latter they are more numerous and closely packed.

(*b*) A well-developed leaf with marked white central band.

Upper epidermis
Lower epidermis } As described under (*a*).

Mesophyll. The chlorophyllous tissue extends from the leaf edges towards the centre in a rough gradient which is prolonged towards the upper epidermis. The sub-epidermal layer finally continues the extension. The albinotic tissue occupies a position similar to that occupied by the chlorophyllous mesophyll of the form *C. elatum* (W. E.). The colourless cells retain both protoplasm and plastids.

C. comosum.

Upper epidermis. No stomata seen in the preparations made.

Lower epidermis. Stomata abundant; guard cells with chloroplasts and starch.

Mesophyll. Cells normal with numerous closely packed chloroplasts.

C. comosum (W. C.).

(*a*) An old leaf in which the central stripe was distinctly green but less green than the edges.

Upper epidermis. No stomata were found.

Lower epidermis. Stomata abundant over both green and white areas; guard cells with chloroplasts and starch.

Mesophyll. The number of cell layers ranges from one to seven, and the average size of the cells approximates throughout. In the central area very few cells are without some chloroplasts but the number in each cell is less than the number in the mesophyll cells of the darker green edges of the leaf.

(*b*) A well-developed leaf with a marked central white band.

Upper epidermis
Lower epidermis } As in (*a*).

Mesophyll. The cells of the central area are without chloroplastids but the protoplasmic contents are retained. Embedded in the protoplasm are plastids—leucoplastids—which appear small and fragmentary. The cells in the green areas are normal.

The green flowering shaft of *C. elatum.*

Epidermis. Guard cells with chloroplasts and starch.

Cortex, outer. Cells with abundant large chloroplasts; some colourless cells.

Cortex, inner. A zone of cells with thickened walls.

Medulla. Cells larger than those of the outer cortex, and usually with small and sparsely distributed chloroplasts.

The green flowering shaft of *C. elatum* (W. E.).

Epidermis. Guard cells without typically green plastids; the plastids contain starch. Many plastids showed traces of green or yellowish colour.

Cortex, outer. Cells with numerous chloroplasts.

In an old flowering shaft, which had produced vegetative growths, the guard cells possessed chloroplasts as well as the three layers of cells forming the outer cortex.

The white flowering shaft of *C. elatum* (W. C.).

Epidermis. Guard cells with chloroplasts and starch.

Cortex, outer. Cells with distinct chloroplasts few and irregularly distributed.

The white flowering shaft of *C. comosum* (W. C.).

Epidermis. Guard cells with chloroplasts and starch.

Cortex, outer. Except for isolated cells with chloroplasts, the tissue was colourless; that the cells retain protoplasm, nucleus and plastids was made evident by the use of iodine.

Cortex, inner. A band of cells with thickened walls.

Medulla. Occasionally cells with chloroplasts were seen; most frequently these were in close proximity to the vascular bundles.

In each case therefore the guard cells of the stem agree with those of the corresponding leaf.

4. *Origin of the Leaves and the Type of Variegation.*

In *Chlorophytum* the leaves originate as successive collars pushed off as it were from the rim of the meristematic zone. They are arranged in a close spiral with a small divergence, and the point of significant interest in the typically variegated forms is the regularity with which the leaves show their type of variegation. Moreover, although new growths are constantly being produced, no wholly green or wholly white crowns have been seen to arise from the typically variegated forms.

Laubert(2) has described a relatively simple case of a sectorial variegation in *Tradescantia cumanensis* where the leaves ensheathe the stem and the phyllotaxy is distichous. Here each pattern is conditioned by the block or blocks of albinotic cells of the growing point as figured in the abstract referred to.

Similar cases which are explicable in much the same way are found in the collection of variegated plants grown at the Institution.

In *Reineckia carnea* var. *variegata* the shoots have a decumbent habit, and as in *Tradescantia cumanensis* the phyllotaxy is distichous,

and the leaves ensheathe the stem. The usual and most striking form of variegation is a sectorial one in which each leaf shows half white and half green throughout its length. The leaves of one rank are thus mirror images of the opposite rank. Although no prolonged observations have been made on this plant, this type of variegation in *Reineckia* appears to be of considerable stability and the shoot may long remain in this condition, the leaves of subsequent growth reproducing the type of variegation. Later however the variegation may give place to some other pattern incidental to a re-distribution of the albinotic and chlorophyllous cells, presumably by further divisions and segregations. Some shoots may run out wholly green while others starting with a slight green banding of the leaf may run out wholly white. The smaller the blocks or groups of albinotic and chlorophyllous cells into which the meristematic tissue of the apex is divided, the finer and apparently the less stable the pattern of the variegation exhibited by the leaf becomes. How the re-distribution of two types of cells forming the meristem of the stem apex is brought about in those instances where the pattern of the variegation changes in one and the same axis can only be conjectured, but in any consideration of the problem the possibility of the existence of a differential rate in the multiplication of the two types of cells in the meristem, or even the recovery or loss of chlorophyll in the albinotic and chlorophyllous cells respectively, must not be overlooked. Anyhow the variegated condition of *Reineckia carnea* can only be maintained by propagation, for if left to form a large clump by natural growth the wholly green condition ultimately predominates.

A variegated plant of *Dactylis glomerata*, which may be mentioned in this connexion, was found and brought to the Institution by Mr M. B. Crane. Text-figure 2 shows the distribution of variegation in this gramineous form. The lowest leaf on the right, and each succeeding member of the same orthostichy, exhibits a central green band, while leaves in the opposing rank show green edges. The distribution of the variegation indicates a division of the apical meristem into two approximately equal masses of cells, the one mass giving rise to the fully chlorophyllous condition, the other to the albinotic condition of the leaf tissue. The position of the two apical masses is such that the leaves of the one rank take out a central white band and green edges, whilst the leaves of the other rank take out a green central band and white edges. An examination of the epidermis of the variegated leaf types borne by this *Dactylis* has shown that the guard cells in all parts are without chloroplasts. Moreover the guard cells of a wholly green plant,

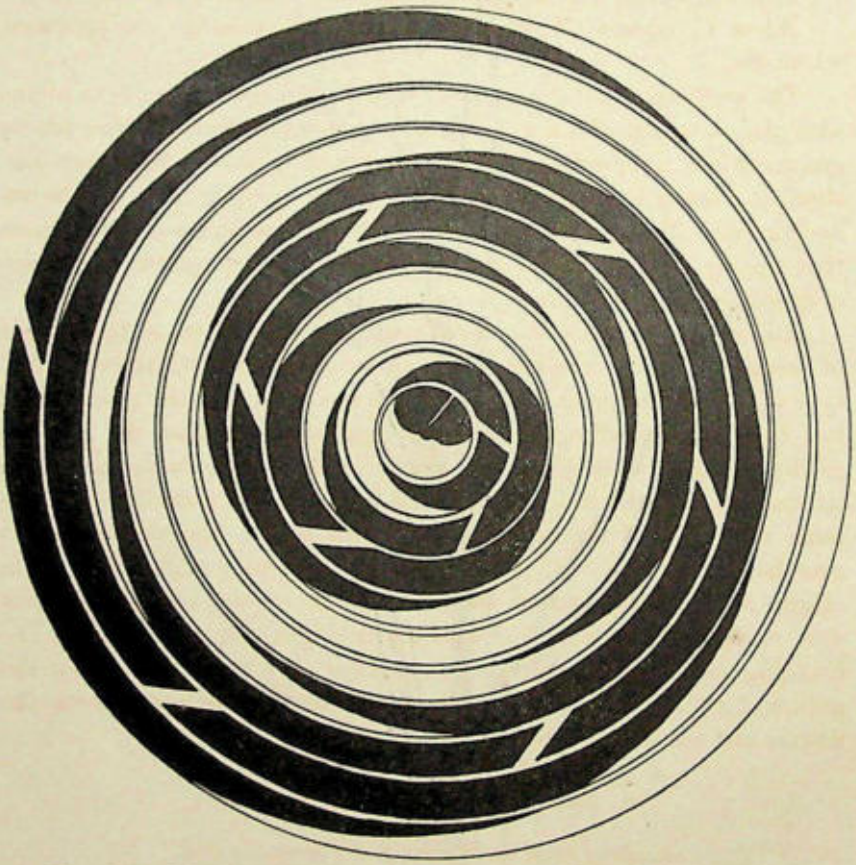
a seedling from the variegated *Dactylis glomerata* in question, were colourless.

No doubt in the variegated forms of *Chlorophytum*, blocks of albinotic cells occur in the apical meristem, but how these contrive to originate the orderly segregation of the albinotic condition to the centre or edges of the leaves having regard to the leaf origin is not clearly evident. On

Text-fig. 2. Variegated shoot of *Dactylis glomerata*. The black areas indicate the chlorophyllous areas.

the assumption that the cells forming an arc of meristematic tissue at the apex are albinotic in character, it will be seen that for the albinotic condition to be passed on to the leaf edges or centre respectively, the arc of albinotic cells must so travel in segregation, that it will trace out a spiral band passing round the apex in correlation with the spiral of

leaf origin. That such a rhythmic distribution of the albinotic conditions occurs is but a conception, for examination of the stem apex has not up to the present revealed any basis of fact for the assumption made. Text-figure 3 which is a diagrammatic representation of the leaf origins will serve to illustrate the conception. This conception of the distribution of albinotic cells to the leaves does not alleviate the difficulty with regard to the nature of the flowering shaft, which in the two



Text-fig. 3. Diagrammatic cross section of the meristematic cone to illustrate the conception of a rhythmic somatic segregation mentioned in the text.

variegated forms is either wholly green or wholly white without visible striping, although as has been mentioned earlier, the bracts borne on these stems are typically variegated. Yet however as will be shown later, where the distribution of the variegation to the leaves is disorderly, the flowering axes arising from such crowns are striped or banded in a

degree which appears related to the character of the leaf variegation. Apparently therefore any displacement of the variegation from the normal type finds expression in the variegated striping of the flowering shaft.

5. *Progeny of the Types and Origin of the Ovule.*

When *C. elatum* (type) is selfed, green seedlings are produced.

When *C. elatum* (W. E.) is selfed, green seedlings are produced.

When *C. elatum* (W. C.) is selfed, *albino* seedlings are produced, which die.

The seedlings from *C. comosum* (W. C.) when selfed have been albino with the exception of a few which were yellowish green and one wholly green. Since a flowering stem may occasionally show a fine green line, there is always the possibility that a green seedling may be thrown among many albinos, while the production of yellowish seedlings suggests that among the cells of the sub-epidermal layer segregation in respect of greenness may be imperfect.

An interesting point was raised with the production of these types of seedlings. It is involved in the question why the white edged leaf type of variegated plant produced green seedlings, and the green edged leaf type white seedlings, when it is generally held that the ovule is produced from the margin of the carpellary leaf, there being no reason to suspect that the differentiation of tissue in the carpellary leaf was other than that of the type of bract borne by the flowering shaft. It was thought possible that in this instance the ovules might be of stem origin, but an investigation showed that the ovules of *Chlorophytum* were normally developed, i.e. carpellary in origin and not cauline. The breeding results however clearly indicate a close relation between the nature of the seedling and the type of flowering stem upon which the flowers and seeds are borne.

6. *Summary of the Genetic Records.*

Progeny from the Species and Varieties selfed.

Ref. No.	Parents. Plate I	Offspring	G.	W.	Var.
A I	*C. elatum* (G.)	8/17	37	—	—
II	*C. elatum* (W. E.)	up to 1914 and 9/17	55	—	—
III	*C. elatum* (W. C.)	13/17, 25/17, 1/18	—	42	—
IV	*C. comosum* (W. C.)	up to 1914 and 5/18	1*	66*	2*

* Among the 66 classed as white, there were 7 with a slight yellowish green tinge of which 5 had sufficient green to give them an existence. The two variegated had but a slight green stripe in the first leaf. The green seedling died.

Progeny from Varietal Crosses.

Ref. No.	Parents	Offspring	G.	W.	Var.
B I	*C. elatum* (G.) × *C. elatum* (W. E.)	1/17	42	—	—
II	*C. elatum* (W. E.) × *C. elatum* (G.) ...	3/17	59	—	—
III	*C. elatum* (G.) × *C. elatum* (W. C.)	2/17, 10/18	51	—	—
IV	*C. elatum* (W. C.) × *C. elatum* (G.) ...	8/18 seed collected before ripe	—	1	—
V	*C. elatum* (W. E.) × *C. elatum* (W. C.)	16/16, 17/17, 11/18	161	1	2*
VI	*C. elatum* (W. C.) × *C. elatum* (W. E.)	18/17, 9/18	—	28	—

* One seedling in 16/16 and one in 17/17 showed slight white markings in the early leaves. These were kept as $16^1/16$ and $17^1/17$ but later became wholly green. An all green form kept as $17^2/17$.

Progeny from C. elatum *and forms* × C. comosum (W. C.).

Ref. No.	Parents	Offspring	G.	W.	Var.
C I	*C. elatum* (G.) × *C. comosum* (W. C.)	10/15	16	—	—
II	*C. elatum* (W. E.) × *C. comosum* (W. C.)	13/16, 15/16	24	—	1*

* One seedling kept as $13^1/16$ showed a white stripe on leaves 5 and 6; later became all green. 5 other seedlings were kept of 15/16

C III	*C. elatum* (W. E.) × *C. comosum* (W. C.)	14/17, 15/17, 16/17	63	—	1†

† One seedling kept as $16^1/17$ showed white stripes on leaves 2 and 3, and after passing through an all green phase, developed new basal crowns showing irregular variegation disposed in lines and narrow bands; now mainly a white edged type.

D I	*C. comosum* (W. C.) × *C. elatum* (W. E.)	8/15	—	11	2‡

‡ These two seedlings $8^{1,2}/15$ grew into forms with an irregular distribution of variegation.

D II	*C. comosum* (W. C.) × *C. elatum* (W. E.)	1914, also 14/16	1§	8	—
	§ Raised in 1914; this plant was *E.* and was used in producing families	11/16, 5/17, 6/17, 22/17	—	—	—
	also by selfing	2/15, 12/16, 11/17, 12/17	83	—	1‖

‖ The variegation came late, and the plant was grown as $2^1/15$.

Derivatives.

Ref. No.	Parents	Offspring	G.	W.	Var.
B III *a*	$10^1/18$ and $10^3/18$ selfed	5/20, 8/20	54	—	—
B V *a*	$16^1/16$ selfed	4/18	13	1	1*
	Grown as $4^1/18$.				
B V *b*	$16^1/16$ × *C. elatum* (W. C.)	3/18	49	—	—
	$3^1/18$ selfed, and $3^3/18$ selfed ...	2/20, 3/20	114	—	1
B V *c*	$16^1/16$ × *C. comosum* (W. C.) ...	7/18	16	—	2*
	* These were grown as $7^{3,3}/18$.				
	Two green forms were also grown as $7^{1,4}/18$.				
	$7^2/18$ selfed; the seeds from the various parts of the plant were kept and sown separately as:				
Plate II	1/19 seed from green stems with slight white lines	—	24	15	6
	2/19 seed from green branch of aerial stem	—	nothing		

Ref. No.	Parents	Offspring	G.	W.	Var.
Plate II	3/19 seed borne directly on white stripe of stem	—	—	15	—
,, ,,	4/19 seed from upper green part of aerial stem	—	6	2	—
	5/19 seed from a green band	—	6	—	—
	6/19 seed from green branch of the aerial stem	—	13	1	—
	Also 7^2/18 selfed, the seed from the various parts of the plant being mixed	4/20	14	18	8
Plates II and III	7^3/18 selfed and seed mixed	8/19	72	20	12†
	This plant had fine white lines on the flowering stem, with a terminal tuft of leaves having white margins and irregularly disposed white stripes.	—	—	—	—
	† Nine variegated plants of 8/19 were grown and observed in detail.				
	7^1/18 and 7^4/18 selfed	—	82	—	1
B V *d*	17^1/17, 17^2/17, 11^1/18 selfed	11/19, 15/18, 6/20	94	—	1?
B V *e*	*C. elatum* (W. C.) × 16^1/16	2/18	—	55	—
B V *f*	*C. comosum* (W. C.) × 16^1/16	6/18	—	14	—
C II *a*	13^1/16 selfed	31/17	29	—	—
C II *b*	15^1/16 × *C. elatum* (W. C.)	23/17	41	—	1
	One seedling had a white stripe in the 3rd and 4th leaves 23^1/17. One became slightly variegated later 23^2/17.	—	—	—	—
	Two other seedlings which showed a variegation in depth of green were grown as $23^{3, 4}$/17.	—	—	—	—
Plate II	$23^{1, 2, 3, 4}$/17 each selfed	12/8, 17/19, 18/19, 19/19	111*	—	3
	* Eleven seedlings arising from 23^2/17 selfed showed variegation in depth of green.				
C II *c*	15^2/16 × *C. comosum* (W. C.)	24/17	34	—	—
C II *d*	*C. comosum* (W. C.) × 15^1/16	20/17	—	5‡	—
	‡ Four were yellowish green.				
C II *e*	*C. comosum* (W. C.) × 15^4/16 ...	21/17	—	27§	4§
	§ One seedling yellow green; the four variegated were grown on and have a detailed history.				
Plate VII	$21^{1, 3, 4}$/17 ran out white and 21^2/17 has stabilised on a slight white edged type of leaf				
C II *f*	*C. elatum* (W. C.) × 15^1/16	19/17	—	36*	—
	* One seedling showed a stripe of green on the second leaf.				
C III *a*	14^1/17 selfed	13/18	30	—	—
C III *b*	16^1/17 selfed	14/19	31	17	36*
Plates II, IV, V	* 14 variegated seedlings grown on.				
	Repeated	7/20	43	—	—
D I *a*	8^1/15 selfed	29/17	71*	—	—
	* Some seedlings with leaves twisted and nicked.				

Ref. No.	Parents	Offspring	G.	W.	Var.
D II *a*	*C. comosum* (W. C.) × green F_1 [*C. comosum* (W. C.) × *C. elatum* (W. E.)]	1/15	—	6*	2*
	* The yellowish green type predominated; 2 variegated were grown as $1^{1,7}/15$				
	$1^1/15$ and $1^7/15$ each selfed	26/17, 27/17	70	—	1*
	* At first all green; then variegated, and finally green; grown as $26^1/17$.				
	$26^1/17$ selfed	14/18	8	—	—
D II *b*	F_1 [*C. comosum* (W. C.) × *C. elatum* (W. E.)] selfed	2/15	24	—	1*
	* This plant threw variegation in its 3rd leaf and subsequently threw several irregularly variegated crowns; it was grown as $2^1/15$.				
	$2^1/15$ selfed	28/17	48	—	3*
	* These three plants were grown as $28^{1,2,3}/17$.				
Plates IV, VI	$28^1/17$ selfed	10/19	30	3	13*
	* 6 variegated seedlings of 10/19 grown.				
Plate VIII	$28^2/17$ selfed. The seeds from the various parts of the plant were gathered and sown separately as:				
	12/19 seed from just below the terminal tuft of leaves ...		42	—	8
	13/19 seed borne directly on the main variegated stem. (Group *B* in the photograph)		8	—	1
Plate III	15/19 seed borne on the basal white branch		—	16	—
	16/19 seed borne on the white fasciated part of the stem near the base		1	21	1
Plates III, VIII	20/19 seed was collected from three flowers, Group *A* in the photograph, borne directly on the variegated stem.				
	From two flowers the seed was mixed...		4	5	10
	The third flower showed a variegated capsule, and the seed from each loculus was sown separately as:				
Plate III	20 *A*/19 5 seeds		1	1	1
	20 *B*/19 3 seeds		1	—	—
	20 *C*/19 5 seeds, from the white loculus		—	3	—
	21/19 seed borne on a green branch of the variegated stem...		12	—	2
D II *c*	*C. comosum* (W. C.) × green F_1 [*C. comosum* (W. C.) × *C. elatum* (W. E.)]	11/16, 6/17, 5/17	—	8	2*
	(Repeat D II *a*)				
	* These were grown as $11^1/16$ and $11^2/16$; the first became wholly green and the second wholly white and died.				
	$11^1/16$ selfed	30/17	15	—	—

7. *General Summary of the Results.*

The number of seedlings raised of which records have been made is 2389, and the summarised tables show in some detail how these seedlings have been bred. Of this total, 1814 seedlings were green, 445 albino and 130 or 5·4 % were recorded as throwing some form of variegation. In no instance was the orderly type of variegation characteristic of the original forms directly reproduced. Attention is particularly called to

the crosses described under the Refs. B III and B V and the derivative forms described under the Refs. B III *a* and B V *a*—*e*. No less important are the breeding details given under Refs. C II and D II and the derivative Refs. C II *a*—*f* and D II *b*. From these results it is clear that the variegation is not distributed on any Mendelian system, and that this property seldom enters the germ cell lineage, or is expressed in the offspring arising from the interbreeding of the typically variegated forms. Nevertheless the green probably owes its character to a factor which the white does not possess and the variegateds may thus be regarded as a special form assumed by the heterozygotes.

Variegation in the seedlings must originate in the first instance by some peculiar action which brings about a somatic segregation of the two opposite characters, and the disorderly distribution to the leaves must depend upon the sequence and mode of the subsequent meristematic segregations. Though not at present referable to any cause, it is clear that this pair of allelomorphs, for green and colourless plastids, are especially liable to such somatic segregation, which has brought about the long series of variegated plants. Seedlings exhibiting such disorderly segregation originated in the families described under the Refs. B V, B V *a*, B V *c*, C II *e*, D II *b*, and others, and it will be seen that except for the B V *a* family—an F_2 from a varietal cross—the progeny in these families was derived by the introduction of the second species *C. comosum* (W. C.). These seedlings produced flowering shafts which were striped in white and green bands and lines of variable width. As soon as plants were raised with noticeably striped flowering shafts, variegated seedlings were obtained in larger numbers.

In general the results may be interpreted in the sense that no matter how the pollinations are made the progeny result as follows:

(*a*) Seed carried on wholly green flowering stems produces green seedlings.

(*b*) Seed carried on wholly white flowering stems produces seedlings devoid of chlorophyll and which subsequently die.

(*c*) Seed borne on striped flowering stems gives green seedlings, white seedlings and seedlings showing variegation of irregular pattern.

(*d*) Seed gathered from finely striped flowering stems produces a much larger proportion of these irregularly variegated seedlings, while from those flowering stems showing broad bands of green and white, seed can be isolated which will give wholly green or wholly white seedlings. This isolation of seed has been shown to be possible even to the seed produced in a single variegated capsule. See D II *b*.

A fact of further interest has been revealed by the later growth of the disorderly variegated seedling crowns and the subsequent production of new basal crowns. Where the variegation is of the finely divided order the crowns quite frequently run out wholly green or wholly white. Where the variegation occurs in somewhat broad bands, the variegated basal crowns produced later tend to stabilise on the white edge and the white centre leaf types. Wholly green and wholly white crowns may also be thrown off. By this production of new basal crowns which arise from buds developed on the old crowns at the soil level, forms exhibiting the orderly variegation of the stable types may ultimately result and the disorderly variegation exhibited by the seedling becomes lost. Hence the conditions which lead to the production of disorderly variegation appear to be unstable and temporary and it is presumed that conditions of stability are regained by further segregations in the apical meristems and consequent re-organisation of the distribution of albinotic and chlorophyllous cells.

Grieve(3) writing of variegated zonal Pelargoniums as long ago as 1868 called attention to an ultimate recovery of a stable type of variegation. The passage seems worth quoting in full; it is as follows:

"Although it is by no means uncommon for seedling plants in their early stages to produce numerous leaves, the surfaces of which are irregularly splashed or blotched with white or yellow, still they ultimately resolve themselves into some regular or symmetrical pattern of marginal variegation or otherwise recover, as it were, from their variegated tendencies altogether and become entirely green."

EXPLANATION OF PLATES.

PLATE I.

A. *Chlorophytum elatum*; leaves and flowering shaft.
B. *C. elatum* var. *albo-marginatum*; leaves and flowering shaft.
C. *C. elatum* var. *medio-variegatum*; leaves and flowering shaft.
D. *C. comosum* var. *variegatum*; leaves. The flowering shaft is similar to that of C.

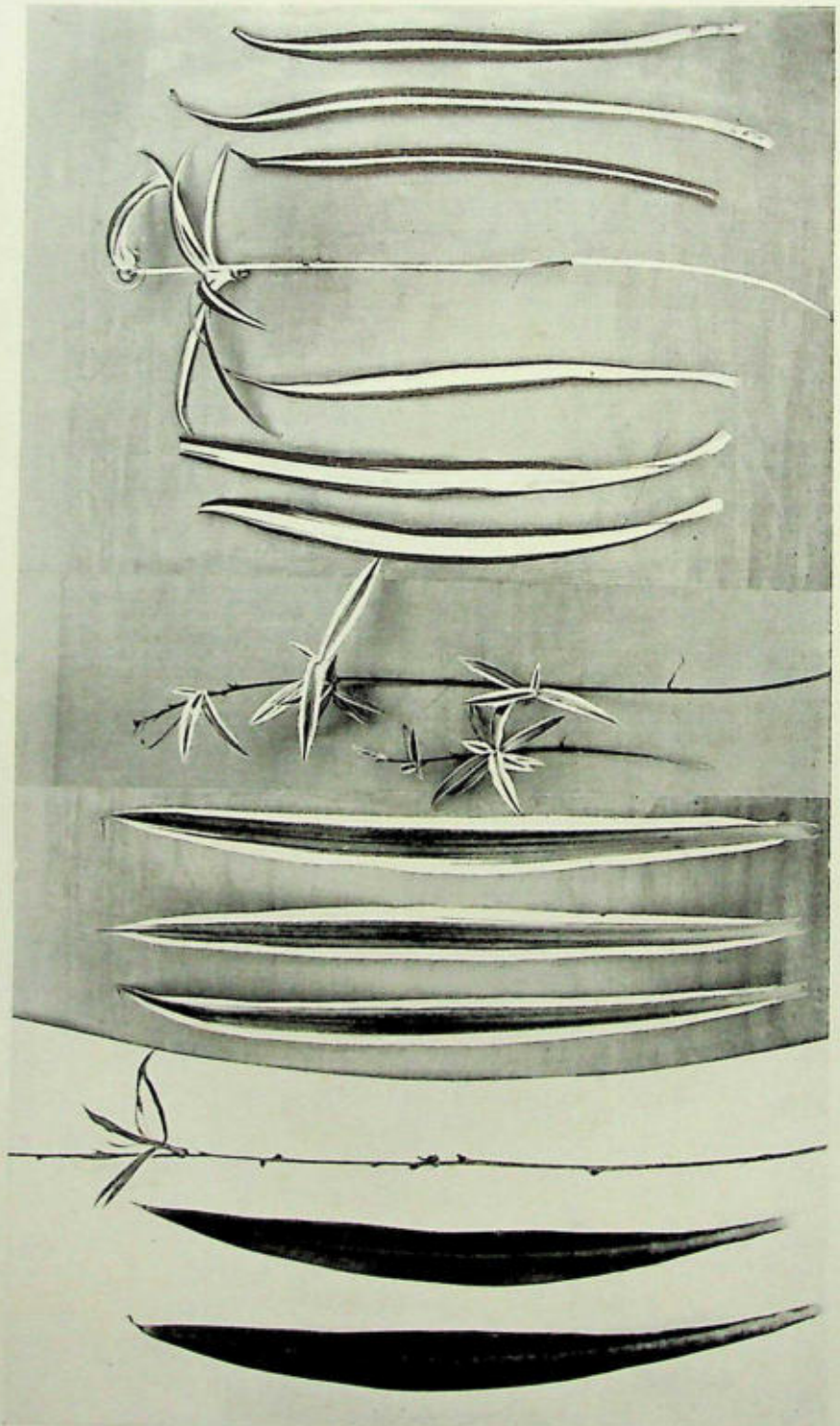
PLATE II.

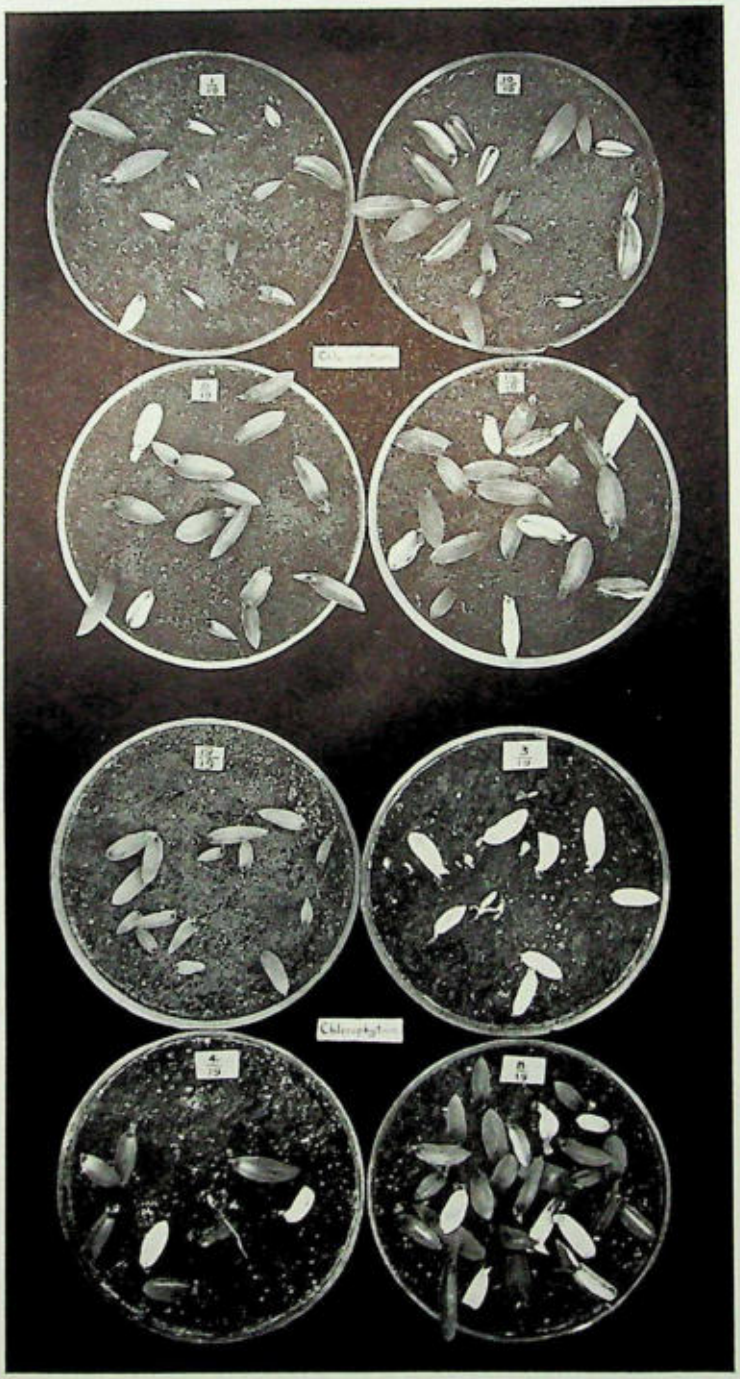
Seedlings in pans; families 1/19, 3/19, 4/19, 8/19, 10/19, 14/19, 19/19.

Reference in Genetic Summary: B V *c* D II *b*, C III *b*, C II *a*.
Family 19/19 of all green seedlings is contrasted with 3/19, a pan of albino seedlings.

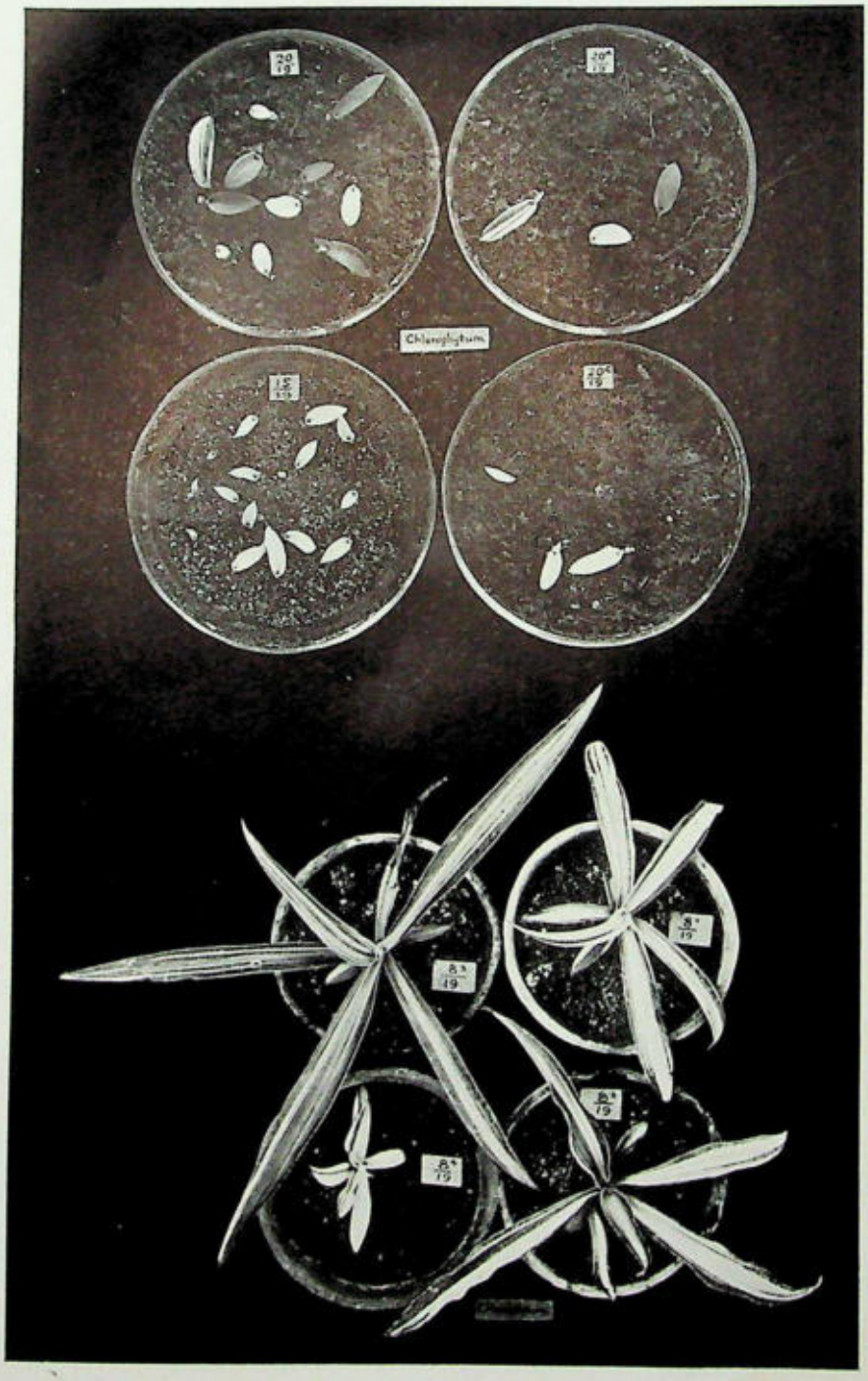
PLATE III.

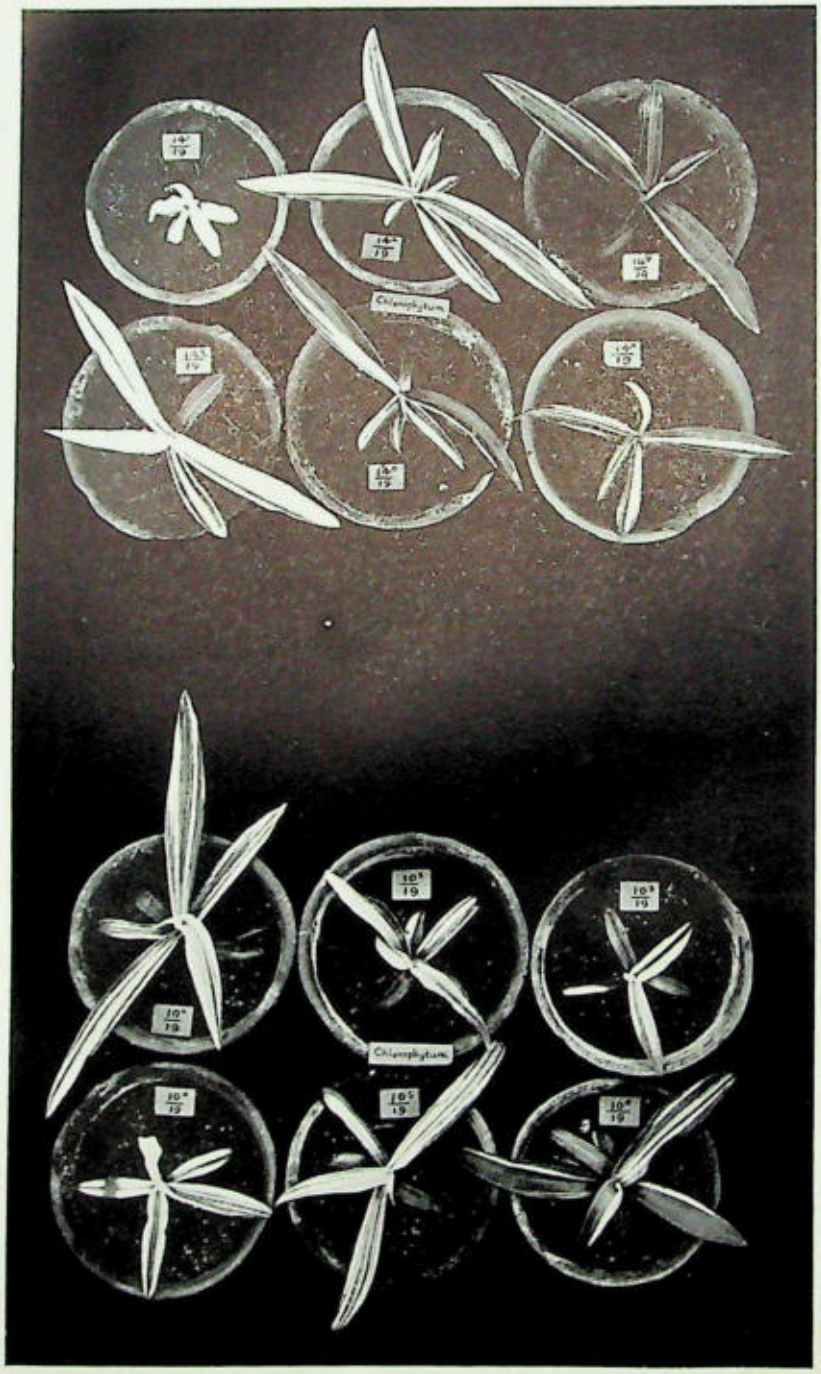
Seedlings in pans; families 15/19, 20/19, 20 *A*/19, 20 *C*/19. Reference D II *b*.
Four seedlings of family 8/19 showing disorderly variegation in the original seedling crowns.

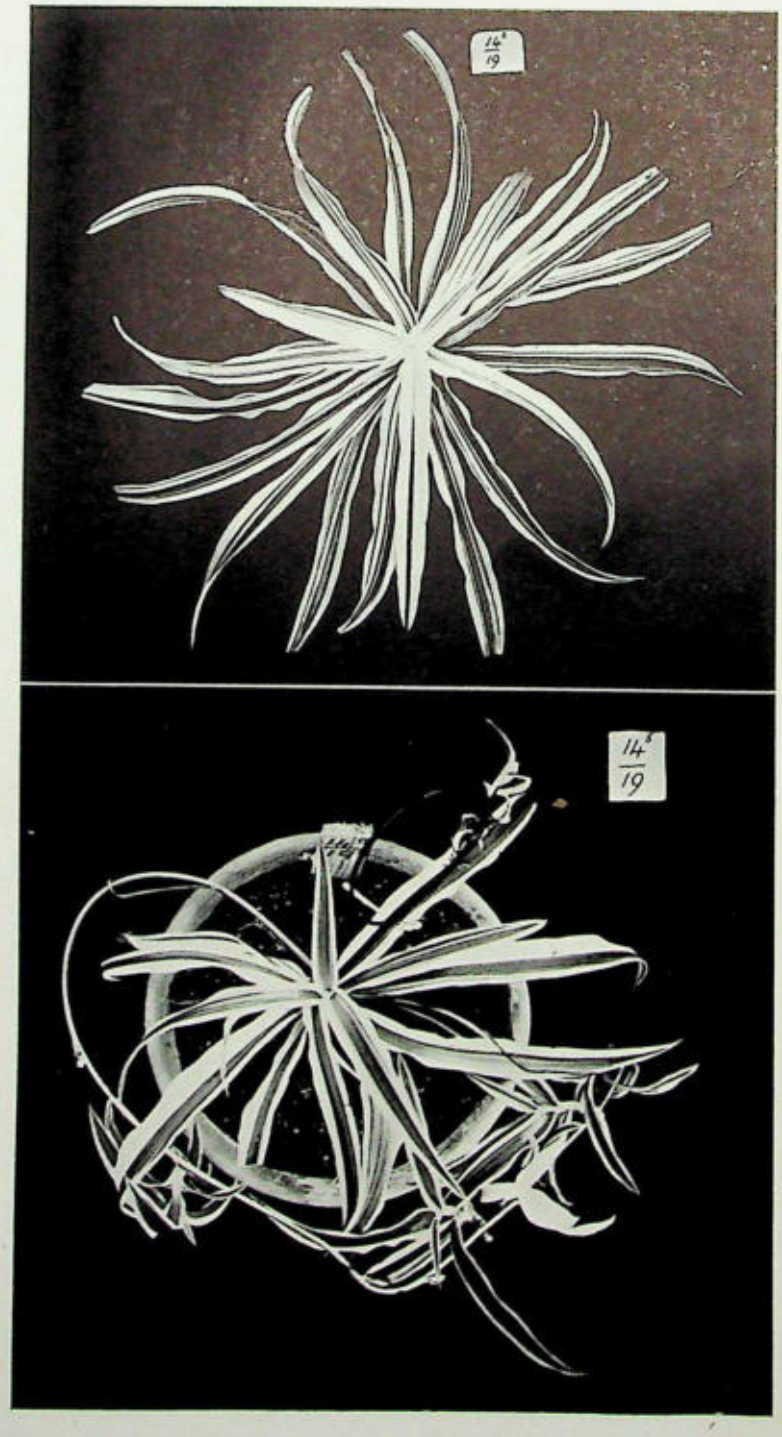

D
C
B
A

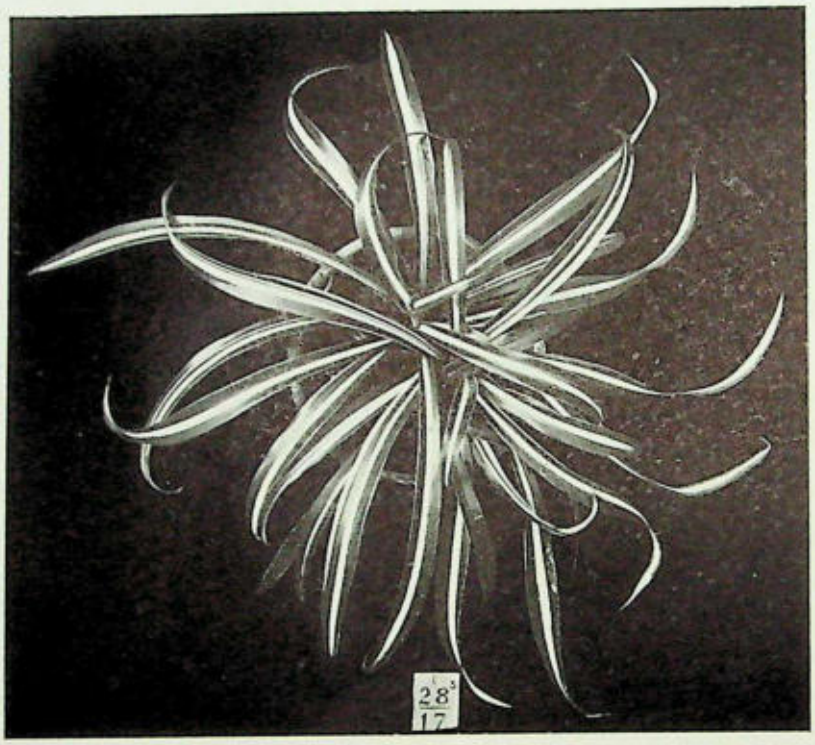


The original seedlings of which the above are photographs were exhibited at the Royal Society's Conversazione in June 1919.

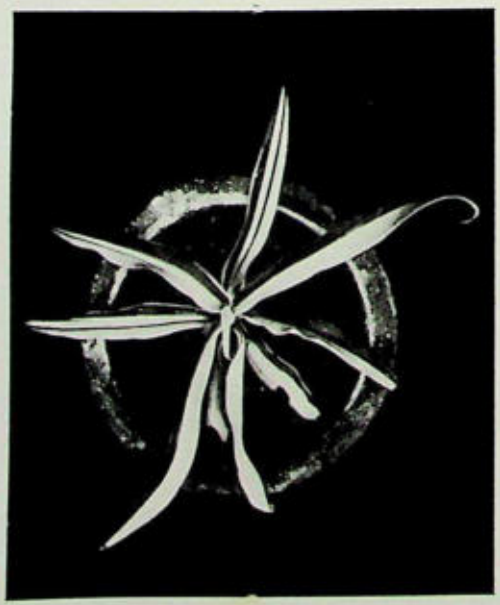

Chlamydomonas


Chlorophytum
Chlorophytum

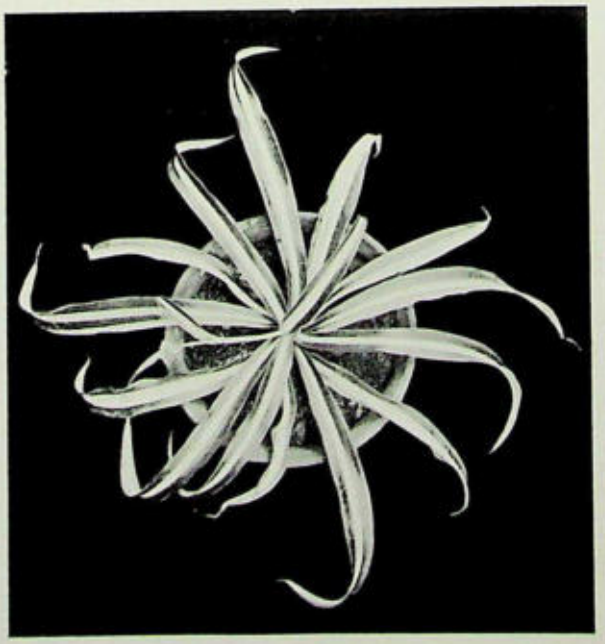

14
19
14
19



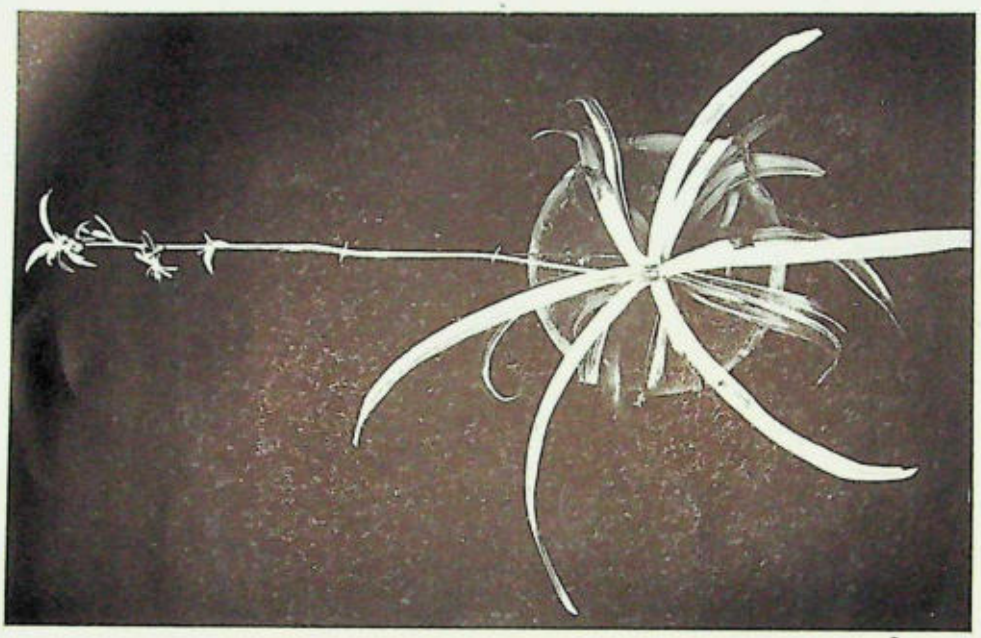
C



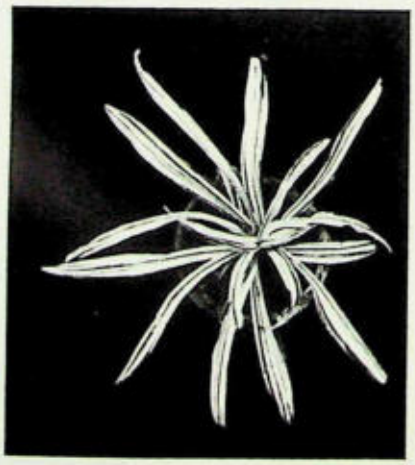
A



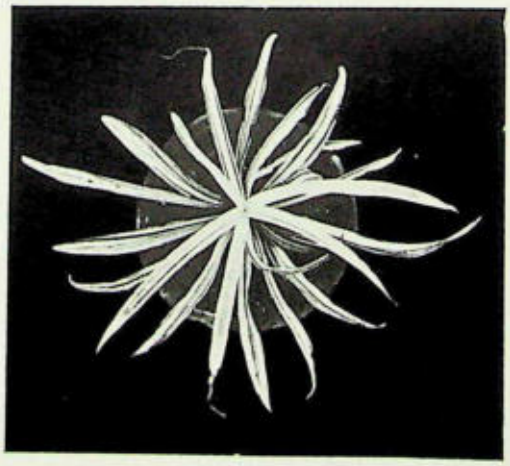
B



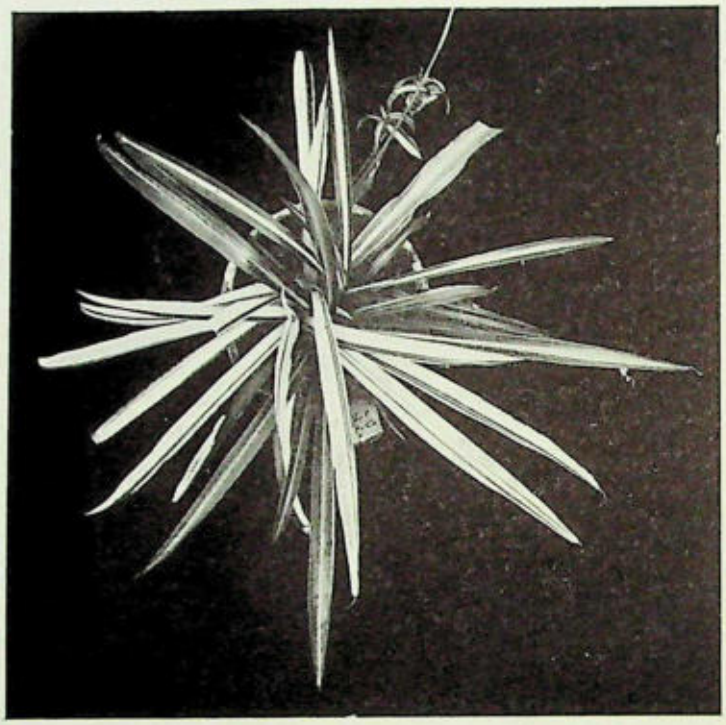
C



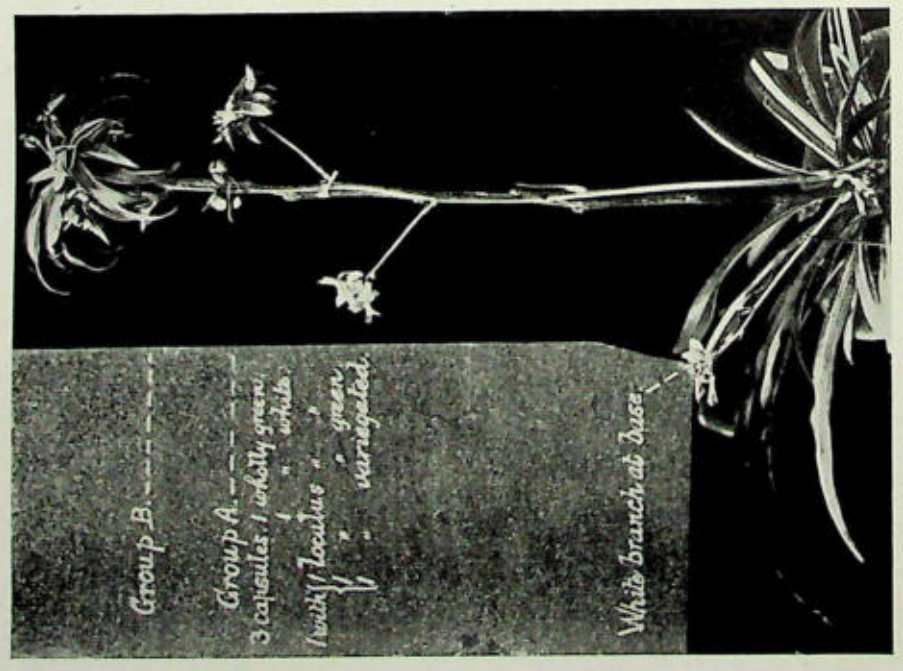
A



B



B


Group B.
Group A.
3 capsules: 1 whitly green.
1 " white.
with 1 locules " green.
" " variegated.
White branch at base.

A

PLATE IV.

Seedlings of families 10/19 and 14/19. Reference D II *b* and C III *b*.

PLATE V.

Seedlings 14^2/19, 14^5/19 more advanced.

PLATE VI.

Seedling plant 28^3/17 at three different periods; A, 15—3—18, B, 9—8—18, and C, 28—1—19. Reference D II *b*. This plant now shows one wholly green crown and two crowns with white centre leaves.

PLATE VII.

Seedling plant 21^4/17 at two different periods; A, 15—3—18, and B, 13—6—18. Reference C II *c*. C, Seedling plant 21^3/17.

These two plants ran out white and died.

PLATE VIII.

Seedling plant 28^2/17 at two different periods. Reference D II *b*.

A. 8—7—18. A white and green striped flowering stem bearing white and green lateral branches is shown. Seed collected from the various parts of this stem gave families as described under D II *b* in the genetic summary.

B. 24—4—19.

At the present date 16—4—21 the plant shows two crowns predominantly white; one crown with white centre leaves and two crowns wholly green except for an occasional leaf with a slight white line in the centre.

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GENETIC ANALYSIS, SCHEMES OF CO-OPERATION AND MULTIPLE ALLELOMORPHS OF *LINUM USITATISSIMUM*.

By TINE TAMMES.

(With Twenty-two Text-figures.)

CONTENTS.

Introduction.

In previous papers[1] I discussed the genetic constitution of *Linum usitatissimum* for the colour and some other characters of the flower and the seed, and the interaction of the hereditary factors or genes, determined by means of crossing. Since that time I have continued my research and I have succeeded in further analyzing that part of the genotypus, especially relating to the characters above mentioned. I should now like to communicate the results obtained by that research. For a good understanding of what follows, however, it is necessary to summarize what has been taught by the crosses previously described. The blue colour of the petals depends upon the interaction of two factors *B* and *C*. If either of the two is absent, the flower is white. In the common blue coloured cultivated flax an intensification-factor is

[1] "Die genotypische Zusammensetzung einiger Varietäten derselben Art und ihr genetischer Zusammenhang." *Rec. d. trav. bot. néerl.* Vol. XII. 1915, p. 217. "Die gegenseitige Wirkung genotypischer Faktoren." *Rec. d. trav. bot. néerl.* Vol. XIII. 1916, p. 44. "On the mutual effect of genotypic factors." *Proc. Kon. Akad. v. Wet.*, Amsterdam, Vol. XVIII. p. 1056.

also present, which by itself cannot produce colour but darkens the light-blue caused by *B* and *C* conjointly. In the absence of *B*, *C* causes the narrower shape and the crumpled condition of the petals and a decrease of seed-formation and germinative-power. *C* therefore acts as a factor inhibiting the development. This inhibiting action of *C* however is neutralised by *B*, which in this respect works as an inhibitor of this inhibitory factor. In the presence of *B*, independent of the presence or absence of *C*, the colour of the anthers is blue, of the seeds brown; while the anthers are yellow and the seeds greyish-green when *B* is absent.

The results above mentioned are deduced from the observations made by crosses between the following strains: the common blue and the common white cultivated flax, a variety with light-blue flowers; all of them with blue anthers and brown seed, and a white-flowering form with narrow crimped petals, yellow anthers and greyish-green seed. These strains were crossed with three others, already mentioned in a previous paper[1]. One of these has lilac flowers, a little darker than those of the common blue flax, and blue anthers, another has pale-blue flowers, a good deal lighter than those of the light-blue variety and yellow anthers, and the third has pink flowers with yellow anthers. All three varieties have broad flat petals and brown seed. The yellow colour of the anther of the narrow-petalled white of the pale-blue and of the pink variety is due to the fact that the yellow pollen is visible through the colourless wall. In the blue anthers however both wall and pollen are blue. Whether there are forms in which the pollen is yellow and the wall blue or the pollen blue and the wall colourless is a matter I have not yet investigated. If in this paper the colour of the anther is mentioned, the whole anther is meant, wall with pollen, as they show themselves in the flower to the naked eye. The filament is white or blue, either the whole or a greater or smaller part, while the intensity of the colour also varies. The style and also the stigma are white or coloured lighter or darker blue[2]. All the differences in colour and in

[1] *L.c.* 1916, pp. 219, 220.

[2] The blue colour of petal, filament, wall of anther, style and stigma is chiefly caused by anthocyanin in solution. Moreover a dark-blue globular body, very probably also containing anthocyanin often occurs in the cells. Addition of hydrochloric acid makes these bodies dissolve in the cell-sap, colouring it red. Addition of ammonia gives a green solution. In the list of plants, composed by Gertz, in which solid or crystalline anthocyanin occurs, quoted in the work of Miss Wheldale: *The anthocyanin pigments of plants*, pp. 30—33, *L. usitatissimum* is not mentioned. In white flower-parts we often find in the cells a group of smaller, usually yellowish-brown globular bodies. I know nothing about the nature of these.

the extension of colour, even the very slight differences, are genetically determined. I shall not discuss this here, as the investigation has not been finished as yet, no more than the one relating to the interdependence between the colour of anther, filament, style, and stigma. I will only mention that blue filament and yellow anther may occur together.

The characters to be fully discussed here, are the colour of the petal, in which the lesser or greater extent of pigmentation towards the base will not be taken into consideration; next the colour of the anther, the colour of the seed, i.e. of the seed-coat, the breadth of the petal and its being flat or not.

There is some difference between the forms with petals that are not flat. Some have not so much crumpled petals as petals which might be called hooded; since their shape reminds us much of the hooded standard of some types of *Lathyrus odoratus* of Bateson, Miss Saunders and Punnett's experiments[1]. In this paper I have not distinguished between the various forms and continued to call them crumpled or crimped. Reciprocal crosses were made between the four strains formerly investigated and the three others mentioned above.

Before discussing the results of the various crosses it seems desirable for the sake of a clear representation to give a preliminary account now.

While through the crosses between the four varieties above mentioned as already stated, three hereditary factors, denoted by *A*, *B* and *C*, could be determined, it was possible through crossing these with the three last forms to analyse the complex *B*, *C* into seven factors. Two of these are necessary for bringing about colour in the petals, they are ground-factors for the colour. In order to agree as much as possible with the previous notation, I shall denote these with *B'* and *C'* and the others with *D*, *E*, *F*, *G* and *H*.

The common blue flax, therefore, has as genetic formula:

AAB'B'C'C'DDEEFFGGHH,

the light-blue, which is distinguished from the common blue flax, because it lacks the intensification-factor *A* is:

aaB'B'C'C'DDEEFFGGHH.

As has been shown by previous crosses the two white-flowering varieties differ from the common blue one, because they lack one single

[1] *Reports to the Evol. Comm. of the Roy. Soc.*, Rep. II. 1905, p. 83 and Rep. IV. 1908, p. 7.

factor. In accordance with the previous indication it is the factor C', which is absent in the common white flax; this therefore has as genetic formula $AA'B'B'c'c'DDEEFFGGHH$; while the narrow-petalled crimped form lacks the factor B' and is $AAb'b'C'C'DDEEFFGGHH$.

The three other forms are: the lilac one $AAB'B'C'C'DDEEffGGHH$; the pale-blue one with yellow anthers $AAB'B'C'C'DDeeFFGGhh$, and the pink one $AAB'B'C'C'ddEEFFGGHH$.

I. Genetic Analysis.

The crosses with the lilac flax with broad flat petals, blue anthers and brown seed.

Common blue × *lilac.* F_1 had flowers very like the common blue flax in colour, only slightly more lilac-tinged. F_2 consisted of 230 blue- and 71 lilac-flowering individuals, i.e. about 3 : 1. Five of the lilac F_2 plants were further cultivated and have given already during five generations a pure lilac offspring, numbering some hundreds of individuals. From three F_2 plants, bearing common blue flowers, but slightly lilac-tinged, an F_3 was raised, segregating into common blue and lilac, superficially estimated at about 3 : 1.

All these observations together point to a monohybrid cross and the factor, in which the two forms differ, I will denote with F.

Since blue dominates over lilac so strongly, that the hybrid is hardly distinguishable from the blue strain, it may obviously be accepted that F is present in the blue-flowering flax F therefore changes the lilac colour into blue and as the blue colour is less intense than the lilac, F appears to act at the same time as a diluting factor.

The lilac flax, which is only distinguished from the blue by the lack of the factor F, possesses like this the factors A, B' and C'. The light-blue flax and each of the two white-flowering varieties are only distinguished, according to a previous investigation, by the lack of one single factor, viz. respectively A or B' or C' of the common blue flax. Like the common blue flax they must therefore possess the factor F. In crossing the lilac with the light-blue variety, and with the two white forms, common blue must arise in F_2, and likewise individuals which, besides F, also lack A or B' or C'..

The observations prove this as will appear below.

Light-blue × *lilac.* F_1 had flowers almost equal to those of the common flax, only slightly more lilac-tinged. F_2 segregated into: common blue 55, light-blue 19, lilac 22, light-lilac 7, a ratio sufficiently agreeing

with the ratio 9 : 3 : 3 : 1, to show that we have to deal with a dihybrid-cross. This was corroborated by the offspring. Among the common blue ones there were those which segregated in F_3 as in F_2. Others gave common blue and light-blue, still others common blue and lilac, in both cases according to an estimate of the plots of about a hundred individuals in a ratio of about 3 : 1; while some common blue-flowering F_2 plants bred true during five generations consisting of some hundreds of individuals. The light-blue F_2 plants were either pure, or segregated in F_3 into light-blue and light-lilac, according to an estimate in a ratio of 3 : 1; likewise did the lilac F_2 plants produce either a pure lilac offspring or segregated into lilac and light-lilac. All of the seven light-lilac F_2 plants produced nothing but light-lilac in some hundreds of individuals during five generations. It is this constant new form which lacks both factors *A* and *F*.

Common white × *lilac*. The flowers of F_1 were coloured blue, a little lighter than the colour of common flax. As in the crosses of common white × common blue, or × light-blue[1], the veins of the petals are no darker than the intervenia, thus contrasting with the homozygous blues and lilacs and with the crosses of narrow-petalled crimped white × blue or × lilac. By the uniform tint of the petals the hybrids are easily distinguishable from the homozygotes.

Previously I denoted the flowers in which the darker colour of the veins was wanting, as "without veins" and I shall continue doing so. While here too it appeared that in the crossing with lilac flax the intensity of the colour of the veins depended on its being homo- or heterozygous for the factor *C'*, I have been able to deduce from experiments, which will however not be treated here, that besides this there exist one or more separate factors for vein-colouring. Intervenia and veins may be coloured quite differently, e.g. the intervenia pink and the veins blue.

F_2 gave :

Common blue	Common blue without veins	Lilac	Lilac without veins	White
42	96	15	30	65
3	6	1	2	4
	9		3	3 1

The theoretical ratio for common dihybrid cross has been given in the bottom row. The ratio observed and the theoretical ratio are sufficiently in accordance, taking into consideration that the behaviour in

[1] *L.c.* 1915, p. 225.

the next generations was similar. Of the blue-flowering F_2 plants some bred true, others segregated into blue and lilac in a ratio of about 3 : 1, according to an estimate of the plots of some hundreds of individuals. The blues without veins again segregated, either as F_2 or only in blue, blue without veins, and white. The lilac-flowering F_2 plants bred true as observed during five generations in some hundreds of individuals. As appears from the above statement, there arose also in F_2 individuals with lilac-coloured flowers, in which the veins were no darker than the intervenia, denoted therefore as lilac without veins. As in the case of the blues, this shows that they are hybrids, heterozygous for the factor *C'*. That this really is the case, appears from the offspring which I shall discuss below.

All whites occurring in F_2 were phaenotypically equal and had flat petals, blue anthers and brown seed. Genetically however they must be of three different compositions, viz. with *FF*, with *Ff* and with *ff*. The first is the common white, the second a hybrid, but the third is a new form, viz. the common white but without the factor *F*. The different whites being externally not distinguishable, this new one could not be directly isolated from F_2. To obtain it various whites would have to be crossed with lilac. In the one which does not produce blue in its offspring, the factor *F* is absent. It is however more convenient to avail oneself of the fact above mentioned, that the lilac-coloured hybrid is distinguished from the homozygous lilac by the deficiency of the dark veins. This lilac without veins, which may easily be isolated from F_2, segregates in F_3 in lilac, lilac without veins and white, and in this white the factor *F* is wanting.

The observations gave: lilac 44; lilac without veins 82; white 44.

The proof that these whites really lack the factor *F*, was given by crossing them with the common blue. There appeared in F_2 individuals with lilac flowers, while in crossing common blue with common white, this is not the case, according to observations previously mentioned.

In all crosses above mentioned all the descendants have flat broad petals, blue anthers and brown seed.

Narrow-petalled crimped white, yellow anthers and greyish-green seed × lilac. As in the case of blue, it is also with lilac, that the hybrid, which is heterozygous for the factor *B'*, is not distinguishable from the homozygote, as in the hybrids the veins are darker coloured than the intervenia. The observations on F_2 gave the following ratio: common blue 411, lilac 141, narrow-petalled crimped white, yellow anthers and greyish-green seed 158. All of the blue or lilac-coloured ones had in

their offspring flat broad petals, blue anthers and brown seed. The proportion of blue and lilac is nearly exactly expressed as 3 : 1. The proportion of the total number of coloured ones to that of the white ones, viz. 552 : 158, or calculated for four individuals 3·11 : 0·89 deviates rather much from the ratio 3 : 1. The mean error for this number amounts to 0·065, the deviation therefore is about twice as great.

I previously[1] demonstrated that in crossing the common blue flax with the narrow-petalled crimped white in F_2 the ratio of the blue and white deviates so much from the ratio 3 : 1, that this deviation cannot be attributed to chance. I was then able to demonstrate that the deviation consists in a deficiency of whites, which is caused by the fact that *C* acts as a semi-lethal factor, when *B* is absent. It is very probable that here we have to deal with a similar case.

The whites occurring in F_2 were phaenotypically alike, having crimped narrow petals, yellow anthers and greyish-green seed. Genetically however they were different, viz. *FF*, *Ff* or *ff*. This appeared from crossing with lilac. Besides white some produced blue and lilac in the offspring, others only lilac besides white. In this latter case the original white one had been homozygous for *f*.

Some of the common blue F_2 plants segregated in F_3 into blue, lilac and white, as was to be expected; others into blue and white, while some bred true. The lilacs segregated into lilac and white or bred true.

The crosses with the pale-blue flax with broad flat petals, yellow anthers and brown seed.

Common blue × pale-blue, etc. The whole of the offspring in all generations had broad flat petals and brown seed. The petals of F_1 were a little lighter in colour than the petals of the common blue flax. The anthers were blue. On close comparison with those of the common flax they appeared to be a shade more greyish-blue. In future these heterozygotes will however be indicated as with blue anthers and counted among the homozygous blue ones.

F_2 segregated as follows: Common blue with blue anthers 58, common blue with yellow anthers 18, pale-blue with blue anthers 18, pale-blue with yellow anthers 7. These latter bred true during five generations observed in some hundreds of individuals. The pale-blue

[1] "The explanation of an apparent exception to Mendel's law of segregation." *Proc. Kon. Akad. v. Wet.*, Amsterdam, Vol. xvi. 1914, p. 1021; also *Rec. d. trav. bot. néerl.* Vol. xi. 1914, p. 54.

types with blue anthers bred true or segregated in F_2 only for the colour of the anthers into blue and yellow in a ratio of about 3:1; likewise did the common blue ones with yellow anthers breed true or segregated in F_2 only for the colour of the petals, viz. into common blue and pale-blue according to an estimate of 3:1. Some of the common blue F_2 plants bred true, some segregated only for the colour of the petals, others only for the colour of the anthers, others again for both characters.

From the preceding it may be concluded, that the two crossed forms are distinguished in two factors, which occur in the common blue flax, but are wanting in the pale-blue type with yellow anthers. These factors will be indicated with E and H.

The pale-blue flax with yellow anthers must possess A, B', C' and F. It has been demonstrated before, that the light-blue, the lilac, the common white, and the crimped narrow-petalled white forms are only distinguished from the common blue type in one single factor. All these strains therefore must also possess E and H.

E is an intensification-factor working in the same way as A; the action however is stronger, for without A the common blue colour is light-blue, without E pale-blue. In crossing the light-blue with the pale-blue, individuals must arise in F_2, possessing A as well as E, common blue ones therefore and individuals lacking both these factors. There actually appeared common blue types and individuals with flowers of a still fainter hue than those of the pale-blue flax. I have called this type very pale blue. They were hardly to be distinguished from white flowers, especially in very hot weather or when the flower had already been open for some hours. In order to be perfectly sure of the absence or presence of pigment in the petals, I watched the slightly-opened buds, because in these the colour is intenser, or I crushed some petals on white paper to make the colour intenser. The best way however appeared to me to treat the petals with an acid. I always used hydrochloric acid for that purpose. White petals put in hydrochloric acid become more or less intense yellow, the very pale blue, apparently white ones, become distinctly pink. By applying this test even to extremely light-coloured offspring of crosses (to be discussed later on) I have always been able to distinguish the really white from the apparently white. But for this, part of the hybrid-analysis discussed here would not have been possible.

Lilac with blue anthers × *pale-blue with yellow anthers.* As far as the colour of the flower is concerned this cross must produce in F_2, besides pale-blue and lilac, individuals possessing both the factors E and F, common blues therefore and individuals in which both factors are

wanting, namely, pale-lilacs. All four actually appeared and in each of the four two forms, namely one with blue and one with yellow anthers. This however remains for the present out of consideration. The proportion of the various phaenotypes was not determined. The blue types bred true or segregated into blue and lilacs, into blue and pale-blue, both according to an estimated ratio of 3 : 1, viz. segregation occurred as in F_2. The ten pale-lilac F_2-individuals further cultivated gave all of them a pure offspring, two individuals followed up for five generations in some hundreds of individuals.

One of these pale lilac-flowering plants was crossed for control with light-lilac proceeding from the cross between light-blue and lilac. When, as must be supposed to be the case, the pale-lilac flax possesses *A*, but lacks *E*, whereas the light-lilac possesses *E*, but lacks *A*, individuals with both *A* and *E* must occur in F_2, which should be lilac-coloured and individuals lacking both factors, therefore very pale lilac ones and these latter ones must breed true. The experiments confirm this.

While the very pale blue flowers are hardly to be distinguished from whites, the very pale lilacs still have a distinctly perceptible colour, which tallies with the fact that the lilac flowers are a good deal darker than the blues.

The second factor *H*, in which the pale-blue flax with yellow anthers is distinguished from the common blue type, influences the colour of the anthers. Previously it has been proved, that for the formation of the blue colour of the anthers the factors formerly called *B* and *C* which together cause the blue colour of the petals, are not both needed, but that one of the two, viz. *C*, may be wanting. The common white flax, namely, which lacks *C*, has blue anthers. When however *B* is wanting, the anthers are yellow. I have already pointed out that the relation must be more complicated, the anthers not always being blue, when *B* is present, as appears from the occurrence of forms with blue flowers and yellow anthers. Now various crosses have shown that for producing the blue colour of the anthers not only the factor *B'* but also the factor *H* must be present and, as will be discussed later on, still a third factor.

Apart from this factor there may be genetically different forms with yellow anthers, viz. without *B'* but with *H*; without *H* but with *B'* and without *B'* and *H*. The first two intercrossed must also produce individuals with *B'* and *H* conjointly, consequently with blue anthers. This indeed happens.

Narrow-petalled crimped white with yellow anthers × *pale-blue with yellow anthers.* The form first mentioned lacks *B'*, the second *H*.

Already F_1 ($B'b'Hh$...) shows blue anthers. Hence the form which lacks both B' and H must occur in this cross. Phaenotypically however this is not to be distinguished from the narrow-petalled crimped white one which only lacks B'. F_2 produced as follows:

	Number observed	Theoretical proportion
Common blue, anthers blue	35	27
Common blue, anthers yellow	9	9
Pale-blue, anthers blue	10	9
Pale-blue, anthers yellow	5	3
Narrow-petalled crimped white, anthers yellow ...	18	16

The ratio of the various phaenotypes agrees fairly well with the theoretical ratio for common trihybrid crosses.

The crosses with the pink flax with broad flat petals, yellow anthers and brown seed.

Besides the six factors A, B', C', E, F, H, another factor could be determined by these crosses, influencing the characters considered above. This factor indicated with D is present in all forms mentioned, but is absent in the pink one.

Common blue × pink. The flower of F_1 was common blue with blue anthers, while F_2 segregated into 150 common blues with blue anthers and 52 pinks with yellow anthers. The pink forms appeared to be homozygous; of the blues some were homozygous, others heterozygous and segregated anew in a ratio 3:1. Thus the common blue and the pink flax differ but in one single factor. From this may be concluded that the pink flax must possess all the factors A, B', C', E, F and H. This is confirmed by the crosses between the pink flax and the forms in which one or more of these factors are absent, since in the offspring common blue is always present. Moreover from the fact that the common blue and the pink flax only differ in one factor, it follows that the factor D must also occur in the light-blue, the lilac, the pale-blue with yellow anthers, the two white forms and all the new forms obtained by crossing these. The crosses between these forms and the common blue flax confirm this. In the offspring there never occurred individuals without D, viz. pinks.

The pink is, notwithstanding its possessing both the factors A and E, much lighter than the common blue. The factor D therefore not only changes pink into blue, but acts at the same time as an intensifier

Light-blue × pink. In this cross individuals must appear in F_2 possessing both factors A and D, common blues therefore, and also indi-

viduals wanting both factors. The experiments produced as follows: common blue with blue anthers 381; light-blue with blue anthers 132; pink with yellow anthers 40; and light-pink with yellow anthers 137. These latter are of a considerably lighter shade than the pink forms.

According to previous observations made in crossing common blue with light-blue flax, the intensity of the colour of the blue-flowering individuals, which are heterozygous for the factor *A*, is fairly equal to that of the homozygotes. With the blue colour therefore the intensifying effect of *A* is the same or almost the same, whether *A* is single or double. This however is not the case with the pink colour. When *A* is present, heterozygous, the colour is much lighter than when the plant is homozygous for *A* and fairly equal to that of the individuals, in which *A* is absent altogether. This appeared from the offspring. None of the eight pinks further cultivated segregated in F_3, of the eight light-pinks five segregated into pink and light-pink, three produced light-pink only.

Thus it appears, that when the factors for blue are present, *A* dominates over *a*; when only the factors for pink are present, *a* dominates over *A*. Consequently the same factor can behave differently in this respect, according to the complex of factors, with which it co-operates. I think I may deduce from my observations, that in neither of the two cases is dominance absolute. On close comparison the homozygotes are presumably distinguishable from the heterozygotes after all.

Pale-blue with yellow anthers × *pink*. This is a trihybrid cross; in the first form the factors *E* and *H* are wanting, in the second *D*. The factor *H* will for the present not be considered. In F_2, individuals must occur, possessing both *D* and *E*, consequently common blues and individuals in which both factors are absent, viz. pinks without *E*. Indeed there occurred besides the two crossed forms, blues and such light pinks that they could only be distinguished from whites by the aid of hydrochloric acid. These have been indicated as pale-pink. They are still lighter than the light-pinks mentioned above; and after treatment with hydrochloric acid it takes much longer for the red colour to become distinctly visible. Just as in the case of blue and lilac, so it appears in the case of pink, that *E* exerts a stronger action than *A*.

The ratio of the various colour phaenotypes was as follows: common blue 81, pale-blue 25, pink 29, pale-pink 9. The number of the pale-pinks is smaller than that of the pinks, the ratio is about 1:3. In F_3 some of the pink forms appeared to breed true, others segregated into pink and pale-pink. All the pale-pinks bred true. From this it appears that of the F_2 pinks some were homozygous for *E*, some heterozygous;

but the pale-pinks were all homozygous for *e*. Consequently the factor *E* exercises in the case of pink as well as in the case of blue, whether single or double, the same intensifying effect and differs in this respect from *A*.

In crossing the light-pinks with the pale-pink types there must also occur in F_2 individuals, in which, besides *D*, both *A* and *E* are absent. It appeared however to be an impossible task, even by means of hydrochloric acid to distinguish these with certainty from the pale-pinks which are apparently white.

As has been stated above pink flax possesses the factor *F*. Besides it was ascertained that in the case of blue flax *F* has a diluting action on the intensity of the colour, for if *F* is absent, the intensity becomes greater, while at the same time blue changes into lilac. The pink flax grows also darker, when *F* is absent; the colour however changes but little, it remains pink. This was deduced from the following cross:

Lilac × *pink*. In F_2 appeared: common blue 94, lilac 31, pink 32, dark-pink 9. The dark-pink types bred true in some hundreds of their offspring observed during five generations. If the dark-pink loses *A* or *E*, which may be the case in some of the F_2 individuals obtained by crossing the dark-pink with light- or pale-pink, the colour becomes still lighter. The dark-pink form without *E* is hardly distinguishable from white to the eye. Individuals in which *A* is also absent, I have not yet produced; without doubt they are so light that the pigment could only be demonstrated with hydrochloric acid or by crushing many petals.

The action of the factor *D* is not limited to the colour of the petals; it also influences the colour of the anthers. For producing the blue colour of these, *D* must be present together with *B'* and *H*. If *D* is absent, the anthers are yellow, even though *B'* and *H* are both present. This is the case with pink flax. The results of the following cross are in accordance with this:

Common white × *pink*. Both forms possess the factors *B'* and *H*, while *D* occurs in the white and is absent in the pink. All the offspring therefore will possess *B'* and *H*, either with or without *D*, likewise the whites. Consequently two genetically different white types must be formed, viz. *B'B'c'c'DD...*, this is the common white with blue anthers and *B'B'c'c'dd....* Now in F_2 there occurred besides common whites with blue anthers also whites with broad flat petals like these, but with yellow anthers. The ratio observed was the following: common blue with blue anthers 406, pink with yellow anthers 146, white with blue anthers 140 and white with yellow anthers 42. These latter appeared to

breed true, observed in some hundreds of individuals during four generations.

All blue and lilac forms, either with or without the factors *A* and *E*, possess *B'* and *D*, while *H* is present or absent. In the former case they have blue anthers, in the latter yellow. The pink-coloured types however always have yellow anthers, because *D* is absent.

Thirdly, *D* influences the shape of the petal and causes, together with *C'*, its crimpiness. Moreover, *D* and *C'* together inhibit the factors for breadth, so that the petal is narrower.

That *C'* by itself does not exercise this action ensues from the results of the cross between pink and narrow-petalled crimped white.

F_2 produced: common blue with blue anthers 509, pink with yellow anthers 164, narrow-petalled crimped white with yellow anthers 117, white with broad flat petals and yellow anthers 40. Accordingly there arose two phaenotypically different whites. As there are also formed only two genetically different homozygous whites, namely one with both *C'* and *D*, and one with *C'* but without *D*, and the former is the narrow-petalled one, the latter must be the one with common flat broad petals.

The ratio of blue and pink is about 3 : 1, likewise that of the narrow-petalled crimped whites to the whites with broad flat petals. The ratio of the total number of coloured ones to the number of the two white types together, viz. 673 : 157, deviates considerably from the ratio 3 : 1. There too the cause is a deficiency of whites in consequence of the semi-lethal action of *C'* in the absence of *B'*.

That, conversely, *D* without *C'* cannot cause the crimpiness of the petals, and cannot inhibit the factors for breadth, is proved by the results previously described of the cross between the common white and the narrow-petalled crimped white. In this case there arise the F_2 individuals, in which *B'* and *C'* are both absent, but *D* is present. These whites have common flat broad petals.

This action of *C'* and *D* together is neutralised by *B'*; all blue and lilac forms have *B'*, *C'* and *D*, they have broad flat petals; likewise the pinks. In the first place they possess *B'* and secondly they lack *D*.

Fourthly, the factor *D* influences the colour of the seed. With all the forms mentioned, blue, lilac and pink-coloured, the seed is brown, also with the common white flax, while the narrow-petalled crimped white type has greyish-green seed. The former all possess the factor *B'*, while the latter lacks *B'*. It might be deduced from this, that in the presence of *B'* the seed is brown, in its absence greyish-green. The relation however appears to be more complicated. In crossing pink

with narrow-petalled white there arises, besides these whites, also a white, in which both B' and D are absent, and this form has brown seed. The brown colour therefore is not caused by B', but there must exist another factor or group of factors which produces this colour.

From my observations I have been able to deduce that there must be more factors co-operating. As however the analysis of this group has not yet been finished, I will indicate this complex of factors for the present with G. In all the forms above mentioned G occurs. The action of G however is inhibited by D, so that the colour of the seed is greyish-green instead of brown, but B' neutralises the inhibitory action of D.

The pink-coloured forms, either light or dark, all lack D; they have brown seed. All blue and lilac forms, just as the common white, possess D, but likewise B'; they also have brown seed, just as the whites in which B' and D are both present. In the narrow-petalled crimped white, however, and also in the white with yellow anthers and flat petals arising from the cross between common white and narrow-petalled white, D occurs, but B' is wanting. Both of them have greyish-green seed. If G is absent the seed is pure yellow, independent of the absence or presence of B' and D. This colour is caused by the cotyledons which are visible through the perfectly colourless seed-coat. In my cultures I have blue as well as pink-coloured forms with such yellow seed.

From the preceding it has appeared, that at present eight factors have been determined, all of them occurring in the common blue flax. Besides the crosses mentioned I have made several more as controls, the results of which completely confirm the conclusions drawn here. These eight factors give together 256 genetically different homozygous forms, of which, since B' and C' must be present together to produce colour, 64 are coloured and 192 white. From the 64 coloured forms 16 are blue, 16 lilac and 32 pink. The 16 blue and the 16 lilac forms are all phaenotypically different; the 32 pink forms show together 8 phaenotypes, the 192 white genotypes together 7.

The table on p. 33 gives a survey of the different phaenotypes.

Of all these different phaenotypes only two are cultivated for fibre, at least in Holland. These two are the first of the coloured and the first of the white, in the table. The question of the value to agriculture of these forms and whether there exists a relation between the colour of the flower and the characters of the stem and the fibre I have discussed elsewhere[1].

[1] "Der blaublühende und der weissblühende Flachs und ihre Bedeutung für die Praxis." *Mitt. des Forschungs-Instituts Sorau*, Jahrg. 2, 1920, Nos. 6, 7.

TABLE I.

Colour of the petal	Breadth of the petal, flat or crimped	Colour of the anthers	Colour of the seed
Common blue, Light-blue, Pale-blue, Very pale blue	broad, flat	blue	brown, yellow
		yellow	brown, yellow
Lilac, Light-lilac, Pale-lilac, Very pale lilac	broad, flat	blue	brown, yellow
		yellow	brown, yellow
Dark-pink, Pink, Light-pink, Pale-pink (nearly white)	broad, flat	yellow	brown, yellow
White	broad, flat	blue	brown, yellow
		yellow	brown, greyish-green, yellow
	narrow, crimped	yellow	greyish-green, yellow

II. THE CORRELATION OF CHARACTERS.

In the seven original forms, and those which have arisen from them by crossing, several cases of correlation of characters occur. For instance in the case of the petal, broadness is always associated with flatness, and narrowness with crimpiness. There exists however another relation among these forms, which I should like to call a one-sided correlation. This consists in the fact that one definite character only occurs combined with one of two or more possible other characters, while the reverse is not the case. For instance pink colouring of the petals always goes with yellow colour of the anthers, but not all individuals with yellow anthers have pink petals; for as has been stated above, the petals may also be blue, lilac or white. Besides the one case mentioned the one-sided correlations occurring in the various forms are: petal narrow and crimped with petal white; petal narrow and crimped with anther yellow; petal coloured with petal broad and flat: anther blue with petal broad and flat; seed brown with petal broad and flat.

It is not improbable that several of these correlations will yet be broken up, and one or more of the factors at present determined may prove to be still a complex, when other forms again are put at our disposal for crossing-purposes. This I conclude from what follows. With

the four forms, which were originally at my disposal, the one-sided correlation, petal blue with anther blue, occurs. This correlation has been broken up on further investigation; petal blue may also go together with anther yellow. Furthermore in crossing a flat-petalled, white-flowering variety of *L. usitatissimum* with *L. angustifolium* there appeared in F_2 individuals with coloured flowers, blue anthers and brown seed, and also whites with blue anthers and brown seed, the petals of which were not normally flat, but crimped, as the narrow-petalled crimped whites of *L. usitatissimum*.

In the cross mentioned the one-sided correlations, petal blue with petal flat, and anther blue with petal flat, were broken up.

With the individuals mentioned, just as with the narrow-petalled crimped white, the petals did not drop for some hours after the opening of the bud as is the case with *L. angustifolium* and with by far the greater number of forms of *L. usitatissimum*.

The crosses with *L. angustifolium* I shall not further discuss here.

III. Genetic Schemes of Co-operation.

The eight factors that are determined co-operate in a complicated way in order to produce the characters, as has been already shown. This interaction is made clearer by the following representations, which might be called genotypic schemes of co-operation. The topographic representations given by Morgan and his colleagues relate to the reciprocal connection of factors at the forming of the gametes, the factors being considered to be bodily in the chromosomes. In the schemes of co-operation however an attempt has been made to represent the way in which the factors co-operate. The schemes have the advantage that they represent the interaction of the various factors in a simple survey, much quicker and better than by words. I have tried to arrange them in such a way, that they are not only suitable for the cases mentioned here, but also for others. When introducing a special method it seems desirable to me to give a somewhat detailed explanation. Before passing on to this, I want to point out that if any advantage is to be gained by the schemes of co-operation it is absolutely necessary to apply the same principle everywhere. The schemes of co-operation can be extended according to needs, but I hope that what has been given here will be used as a starting-point, considering, that for the sake of unity it is better to sacrifice part of a representation or view, than to lose the unity itself.

In the schemes of co-operation the factor or factors which must be present to produce a character, namely the so-called ground-factors, are surrounded by a double circle. The factors which can only modify the character produced by the ground-factor or -factors, without being able to bring about a character themselves, are placed outside these circles.

A single circle around two or more of these modification-factors, shows that they must necessarily be together to enable them to cause any modification of the ground-character.

The sign $\longrightarrow$ indicates that the action of the factor or the complex of factors to which the arrow points, is intensified by the factor or complex of factors at the other end.

The sign $-<$ indicates the reverse, namely that the factor or factors placed before the open end are diluted or inhibited by those at the opposite end.

In case the modification of the ground-character does not consist in an intensification or dilution, but is of a different nature, e.g. the change of colour, it is indicated by a common connecting line.

The sign $-\!\!+\!\!-$ straight or curved indicates that the factors connected in this way act in the same sense or cumulatively, as for instance the homomeric factors.

The sign $-\!\!\div\!\!-$ straight or curved indicates that the factors thus connected act in a contrary sense.

A dotted line straight or curved indicates that the factors connected by this operate differently.

A double circle, the inner being dotted, indicates that the factor or factors denoted inside have been investigated only partly or not at all.

I shall now give some of the schemes of co-operation for the characters, discussed above.

Colour of the Petal.

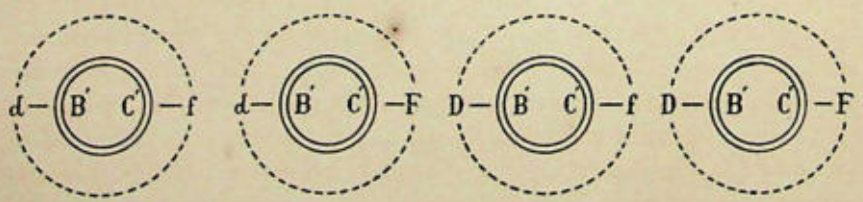

Fig. 1. Pink. Fig. 2. Pink. Fig. 3. Lilac. Fig. 4. Blue.

Above, the schemes of co-operation for the four possible cases for coloured petal have been given. The ground-factors B' and C' together produce pink. D and F act as modifying factors. F does not modify

the pink colour worth mentioning; *D* alters the pink colour into lilac; *D* and *F* together change the pink colour into blue. If one or both of the ground-factors are absent, the petal is white. It is superfluous to give the twelve possible cases. I only want to give one case as an example of what the schemes of co-operation may express.

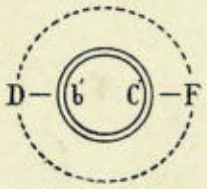

Fig. 5. White.

From this it immediately appears that the petal must be colourless, since one factor inside the double circle is absent.

Intensity of Colour.

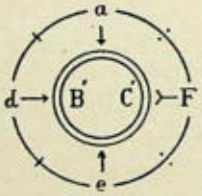

Fig. 6. Slightest intensity pink, nearly white.

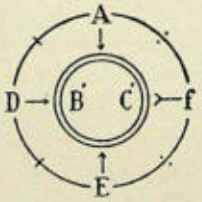

Fig. 7. Greatest intensity lilac.

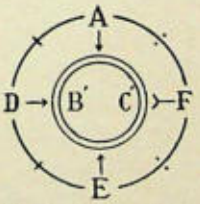

Fig. 8. Intermediate intensity blue.

The intensity of the colour caused by the ground-factors only is extremely slight. Of the 16 possible cases three have been given above. Fig. 6 shows the scheme for the slightest intensity, the intensification-factors are absent, the diluting-factor however is present and consequently the intensity of the colour is still slighter than the one produced by the ground-factors alone. Fig. 7 is the scheme for the greatest intensity. The three intensification-factors are present, the diluting-factor is absent. This is the scheme for the lilac flax. Next to it in Fig. 8 has been given the scheme for the common blue flax. From this it appears that because of the presence of the diluting-factor, the intensity of the colour is slighter than that of the lilac-flax.

The 16 possible cases in which the intensity of the colour differs may be divided into three groups, viz. a group of eight with pink flowers, a group of four with lilac flowers and one of four with blue, while the three groups according to intensity may be arranged in an ascending row.

In the 48 cases, in which the colour is white, the intensification- and diluting-factors exercise no influence in consequence of the lack

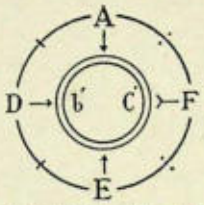

Fig. 9. No intensity, white.

of colour. Just one of these schemes of co-operation may serve as an example (Fig. 9).

Colour of the Anther.

Fig. 10. Blue.

Fig. 11. Yellow.

The double circle round the three factors shows clearly that all three of them must necessarily be present to bring about colour. This is blue, Fig. 10. If one of these ground-factors is absent, Fig. 11, or two or three, the colour is yellow. Factors modifying the colour caused by the ground-factors have not been determined.

The representation is so simple that it is not necessary to represent more than two of the eight possibilities.

Colour of the Seed-coat.

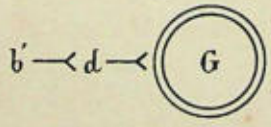

Fig. 12. Brown.

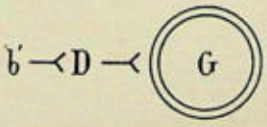

Fig. 13. Greyish-green.

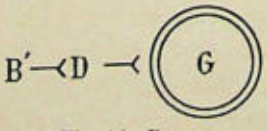

Fig. 14. Brown.

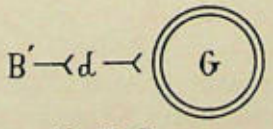

Fig. 15. Brown.

From these schemes it appears that *G* is the ground-factor, and *B'* and *D* the modifying-factors. When these latter are absent, as in Fig. 12, the colour is brown. Fig. 13 shows that beside the ground-factor only

D is present, which acts as an inhibitory-factor. The colour is then greyish-green. That *B'* neutralises the inhibitory action of *D*, appears from Fig. 14. The colour is again brown, *B'* influences *D* only, not *G* directly, and is therefore unable to inhibit *G*, if *D* is absent, which fact is represented in Fig. 15. If the ground-factor *G* is absent, there is no colour, quite independently of the presence or absence of *B'* and *D*. Fig. 16 gives an example of one of these four possibilities.

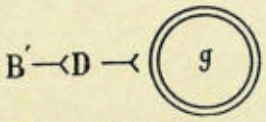

Fig 16. Colourless.

The flat or crimped Condition of the Petal.

With the common flax and with many other varieties the petal is flat, and the edge lies exactly in the same plane as the middle. The factor or factors for this character unknown to me I have indicated with *Z*.

From the schemes it appears that *C'* and *D* have a modifying influence upon *Z*, and that they exercise this action only in co-operation. If both of them are present as in Fig. 17 the petal is crimped. If one or both are absent the petal is flat. Fig. 18 gives one of these cases. The action of the complex *C'D* is neutralised by *B'*. Fig. 19 illustrates this.

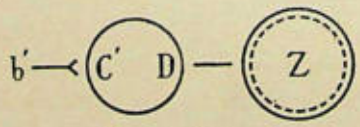

Fig. 17. Crimped.

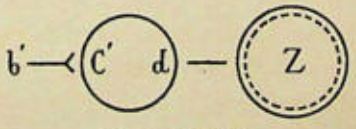

Fig. 18. Flat.

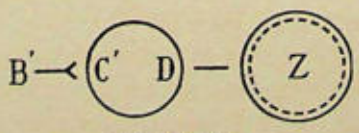

Fig. 19. Flat.

Besides it appears from this that only in one of the eight possible cases will the petal be crimped.

Breadth of the Petal.

I have previously[1] shown that the breadth of the petal of *L. usitatissimum* is partly caused by some homomeric factors. I shall indicate these, as well as the factors not yet further examined, by *Y*. This complex, or part of it, is influenced by *B'*, *C'* and *D* in a way illustrated by the following schemes. Of the 16 possible cases three have been given.

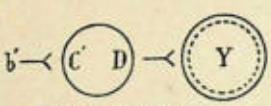

Fig. 20. Narrow.

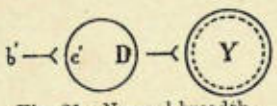

Fig. 21. Normal breadth.

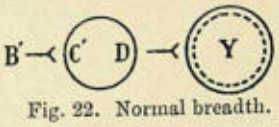

Fig. 22. Normal breadth.

Y by itself causes a certain breadth of the petal, which I shall indicate as normal. As appears from Fig. 20, *C'* and *D* have an inhibitory influence on *Y*, but only conjointly. In this case the petal is narrow. If one or both are absent, Fig. 21, the petal is normal in breadth.

B' neutralises the inhibitory action of the complex *C'D*. Fig. 22 shows this. From the schemes of co-operation it appears that only in one of the eight possible cases is *Y* inhibited and the petal narrow.

A comparison of the schemes of co-operation given above shows at once that the co-operation of factors for various characters is very different. It further shows that one and the same factor takes part in bringing about wholly divergent characters. For instance *B'* and *D* occur in all six, *C'* in four of the cases.

IV. THE DISTRIBUTION OF FACTORS AMONG THE CHROMOSOMES.

While in the preceding pages the various factors and their co-operation have been treated, it must now be discussed whether anything may be deduced from the observations, concerning their connection at the forming of the gametes. The question is whether from the proportions found in F_2 either a perfect independence, or a certain degree of coupling of the factors, may be inferred in the various cases. In this I want to leave the factor *G* out of consideration, because I have very few data concerning it. The remaining seven factors give 21 combinations of two, consequently 21 different crosses are possible, in which the parents differ from each other in two of these factors.

The following table gives a survey of this and the ratio in F_2 as found for the various cases. For some of them this has been given

[1] "Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung." *Rec. d. trav. bot. néerl.* Vol. VIII. 1911, p. 201.

above, while for 1, 2 and 3 the figures given have been derived from observations previously made[1].

The number of individuals with two dominants is always mentioned first, that with the two recessives last. Only in the cross of light-blue with pink (4) is, as explained above, the ratio of dominant and recessive other than usual. In some cases only three phaenotypes can be distinguished, the theoretical ratio is then 9 : 3 : 4 instead of 9 : 3 : 3 : 1. In numbers 1, 3, 8 and 10, all relating to crosses with the narrow-petalled crimped white, the number of phaenotypes denoted with an * is too small. The cause of this deficiency has been discussed above. In 9 and 11 numbers are too small to be certain that the slight deficiency is due to the cause mentioned.

TABLE II.

Number	Factors	Number of Individuals representing the 4 [or 3] classes of phaenotypes in F_2				
1	*A* and *B'*	298	96	—	91*	—
2	*A* and *C'*	287	96	—	125	—
3	*B'* and *C'*	610	203	167*	—	74
4	*A* and *D*	381	132	40	—	137
5	*A* and *E*	25	8	9	—	2
6	*A* and *F*	55	22	19	—	7
7	*A* and *H*	29	10	5	—	3
8	*B'* and *D*	509	164	117*	—	40*
9	*B'* and *E*	44	15	—	18	—
10	*B'* and *F*	411	141	—	158*	—
11	*B'* and *H*	45	14	—	18	—
12	*C'* and *D*	406	146	140	—	42
13	*C'* and *E*	44	15	—	18	—
14	*C'* and *F*	138	45	—	65	—
15	*C* and *H*	41	13	12	—	6
16	*D* and *E*	81	29	25	—	9
17	*D* and *F*	94	31	32	—	9
18	*D* and *H*	46	15	—	23	—
19	*E* and *F*	32	12	14	—	4
20	*E* and *H*	58	18	18	—	7
21	*F* and *H*	45	17	16	—	7

In none of the 21 possible cases does the F_2 ratio deviate enough from the theoretical 9 : 3 : 3 : 1 or 9 : 3 : 4 to make a coupling of two factors a certainty. In a few cases numbers are too small to deduce anything with certainty, though the ratio found makes us presume that the true ratio is 9 : 3 : 3 : 1. In most cases however the ratio 9 : 3 : 3 : 1 is sufficiently evident.

Can we now conclude from this, that the pairs of factors for which this holds good, are actually completely independent of each other?

Some years ago this conclusion would certainly have been drawn; according to more recent investigations however, another possibility

[1] *L.c.* 1915.

cannot be excluded. The ratio 9 : 3 : 3 : 1 will also be obtained, when the two factors are not independent of each other, but lie in the same chromosome, a distance equal to half the length of the chromosome between them and that no double crossing over occurs. If at the formation of the gametes, crossing over always takes place, the two factors will be separated in half the cases and each will be united with the allelomorph of the other factor in the same chromosome. In the other half of the cases the factors will remain together as in complete coupling. The number of gametes with the original combination of factors and that with the new combination will be equal and consequently give the ratio 9 : 3 : 3 : 1 in F_2. The same will be the case, and F_2 will also show the ratio 9 : 3 : 3 : 1, when each of the two factors lies at an end of the same chromosome, so that in crossing over they are always separated, and if moreover at the formation of the gametes in half the number of cases crossing over occurs, in the other half not. The third possibility, namely that the two factors lie in the same chromosome, but not with half the length between them, or each at an end, while a percentage of crossing over takes place in accordance with this, I will leave out of consideration here. For each separate pair of factors, therefore, it cannot be concluded from the ratio 9 : 3 : 3 : 1, whether the two factors occur in the same chromosome or not. For the pairs of factors collectively however at least something may be deduced from it.

Let us take the first case, viz. that crossing over always occurs and the factors are at a distance equal to half the length of the chromosome. This, e.g. holds good of *A* and *B*, and also of *A* and *C*. It is possible, when *A* lies in the middle of the chromosome and *B* and *C* each at an end. *B* and *C* however are assumed to lie with a distance of half the length of the chromosome between them. The three factors therefore cannot lie together in the same chromosome, but must be distributed among at least two chromosomes.

The same holds good for the case when two factors lie each at an end of the same chromosome.

If for all the 21 combinations the ratio 9 : 3 : 3 : 1 had been observed, the seven factors would have to occupy at least four chromosomes. In some cases the number of observations is too small. For the ten possible combinations of the factors *A*, *B*, *C*, *D* and *F* (Nos. 1, 2, 3, 4, 6, 8, 10, 12, 14 and 17), however, the ratio expected has been attained within a reasonable limit of error. It follows that even in the greatest possible number of couplings these five factors must be distributed among at least three chromosomes.

It appears from the preceding, that even when the ratios found in F_2 are 9 : 3 : 3 : 1, but little can be determined about the distribution among the chromosomes. A starting point cannot be obtained until cases occur in which the F_2 ratio shows definite coupling.

For researches on the situation of the factors in the chromosomes *L. usitatissimum* however is no suitable object, for according to Mr Reynder's investigation, made in the Botanical Laboratorium here, the diploid number of chromosomes is 30.

V. Multiple Allelomorphs.

The analysis of factors described above has revealed six factors, influencing the colour of the flower. For this character the number of forms genetically distinct amounts to 64. Of these there are 16 coloured and 48 white. The 16 coloured types are blue, lilac or pink in various grades.

Now I have known for a long time that the number of forms of *L. usitatissimum* of a genetically distinct flower-colour is much greater than 16. Besides these I have 46 additional forms in culture, all different in flower-colour from the 16 above mentioned and from one another[1]. They may be joined into three groups. The first group contains the forms in which the flower-colour resembles most that of common flax; the second is of a much lighter shade of blue, the third bears lilac flowers. Forms belonging to the different groups can easily be distinguished in normal circumstances; the differences between the forms of one and the same group however are sometimes extremely slight. Only by comparing flowers newly opened is the distinction perceptible. The differences refer to the intensity of the colour only, or to the tint only, or to both. Such slight differences in colour as are dealt with here are not represented in any work on the determination of colour that I know of. Out of the 54 blue or lilac-coloured types, belonging to the first and the third groups, only six can be found in the *Code des Couleurs* of Klincksieck et Valette, and at most eight in Baumann's *Neue Farbentonkarte*.

[1] These forms are of various origin. Some of them I have isolated from the blue-flowering flax that is cultivated in Holland for the fibre. Before the war the seed was regularly imported from Russia. This seed however was not pure, it produced a crop consisting of a great number of forms, not only differing in the colour of the flower but also in many other characters. One of the colours predominated very strongly with respect to the number of individuals that show it. It is this colour form that I chose several years ago as a starting-point for my investigations, and which I have in my papers indicated as common blue, or dark blue.

The differences however small are perfectly hereditary; some forms I have already had in culture for eight years and every summer the differences can be recognized anew.

By means of crossing I have further examined three forms of each of the three groups. It appeared that these three forms of the common blue group, crossed with the common blue flax, gave monohybrid segregation in F_2. Crossed among each other however they produced the same, and not the dihybrid segregation, as was to be expected from the fact that each of them differs in one and not the same factor from the common flax. This relation deviating from the common rule has repeatedly been observed of late. Since the researches of Morgan and his colleagues the phenomenon is explained by assuming that in these cases we have to deal with so-called multiple allelomorphs, i.e. a group of more than two factors, each factor of which can form an allelomorphic pair with every other, while in any one individual two at most can be present at one time, one in each of the two homologous chromosomes. Accordingly the number of hereditary factors for which the locus in the chromosome is the same, amounts to more than two.

For the blue-flowering *L. usitatissimum* a group of four allelomorphs has been determined through the crosses above-mentioned.

The three lilac forms crossed with each other or with the lilac which was used for the extensive investigations reported above, always gave monohybrid segregation; so did the three light-blue forms when crossed with each other or with the light-blue previously mentioned. By this the existence of a group of four allelomorphs has also been demonstrated for both.

Now the question is which of the factors causing the flower-colour occur in an allelomorphic series? For those forms, in which the difference only refers to intensity of colour, it may be A as well as E for the blue and the lilac group; for the light-blue, which lacks A, only E. If it is a difference in tint, it may be the consequence of slight differences in the factors B', C', D or F, for the blue and light-blue group; in the factors B', C', or D for the lilac group. To decide which factor it is the various forms of a group with multiple allelomorphs must be crossed with all those forms, in which one of the factors is absent. Suppose it is the factor B' which belongs to the group of multiple allelomorphs and accordingly is different in the different forms. This will be indicated by B', B^2, B^3, and B^4. In crossing these four forms with the narrow-petalled crimped white $b'b'C'C'$..., there arises in F_2 in the first case, i.e. when the blue form possesses B', only the blue $B'B'C'C'$..., in the

second case only $B^2B^2C'C'$..., in the third case only $B^1B^1C'C'$..., and in the fourth only $B^1B^1C'C'$. In every case only one blue homozygote. When however the same four forms are crossed with a form lacking another factor, there arises only in one case a single blue type in F_2, in all other cases there appear two different ones, e.g. the crossing with pink, $B'B'dd$..., gives with $B'B'DD$... only $B'B'DD$, but with B^2B^2DD both $B'B'DD$... and B^2B^2DD. Consequently that factor which is absent in the form, which in all crosses with the group of forms with multiple allelomorphs in F_2 gives but one blue-coloured homozygote, occurs as multiple allelomorph.

From the foregoing it appears, that it is a very extensive labour to attain results. Though some work has already been done in that direction, it has not yet advanced far enough to draw definite conclusions. For the 37 remaining forms, only the heredity of the mutual differences has been determined, genetically they have not yet been further examined. Whether each of the three groups comprises but one single series of allelomorphs, or some series differing in the factors for which they are multiple allelomorph, or whether some forms possess quite different factors not yet determined, is so far unknown. Such an investigation, where such extremely slight differences are taken into account, is attended with great difficulties.

It has been proved recently that the presence or absence of a single factor does not always produce a striking character, nor does it cause it to disappear, but the difference produced may be so extremely slight, that it is hardly perceptible, even in circumstances most favourable for its manifestation. Where a greater difference is observed between two individuals, only differing in one hereditary factor, it is often caused by the fact that the lack of a single factor renders the co-operation of a whole complex of factors impossible; or conversely, one single factor may complement an incomplete complex. How small the power of one factor may be, will probably be more apparent as the analysis of the genotypes advances, and as knowledge of the interaction of hereditary characters increases.

Conversely, investigations have taught that many hereditary factors are much more dependent for their manifestation on external circumstances than was originally expected. Flower-colour of flax too is very variable; the nutritional condition of the plant, temperature and light have a great influence on it. The variety showing the darkest flowers in normal circumstances, that is a little darker than those of the common flax, has, at a low temperature, flowers which are almost white. The

range of variation of this one form embraces the phaenotypes of all blue-flowering genotypes occurring in my cultures. The differences caused by external circumstances are much greater here, than those which are the consequence of differences in hereditary factors, and this makes the genetic investigations still more difficult.

That I have nevertheless succeeded in determining something about these hereditary factors is due to the fact that I have tried with the utmost care to cultivate and observe the plants in completely similar circumstances.

SUMMARY OF RESULTS.

1. For *Linum usitatissimum* eight factors have now been determined: *A*, *B'*, *C'*, *D*, *E*, *F*, *G* and *H*, influencing the colour, shape and breadth of the petal and the colour of the anther and the seed-coat.

2. These factors co-operate in various ways to bring about the characters mentioned.

3. Some of these factors influence several characters together and their action in producing those various characters is quite different.

4. For the colour of the petal six of the factors, namely *A*, *B'*, *C'*, *D*, *E*, and *F* co-operate.

5. Of those factors mentioned under 4 only *B'* and *C'*, and then only when combined, can produce colour.

6. The colour caused by *B'* and *C'* is extremely light pink, hardly distinguishable to the eye from white.

7. *A* and *E* are intensification-factors of the colour. In each other's presence they act accumulatively. The action of *E* is stronger than that of *A*.

8. The intensifying action of *A* is different for various complexes of factors. When *B'*, *C'*, *D* and *F* are present, *A* dominates *a*, when *B'*, *C'*, and *F* are present *a* dominates *A*.

9. *D* modifies the pink colour caused by *B'* and *C'* into lilac, acting at the same time as an intensification-factor.

10. *F* does not appreciably modify the pink colour caused by *B'* and *C'*, but it changes the lilac colour produced by *B'*, *C'* and *D* into blue. In both cases *F* acts simultaneously as a diluting-factor.

11. The blue colour of the anthers is dependent on the co-operation of the factors *B'*, *D* and *H*; if one of these is absent the anthers are yellow. Consequently blue and lilac-coloured flowers have either light or dark anthers, and likewise white flowers may have blue or yellow; pink flowers only yellow ones.

12. The brown colour of the seed-coat is produced by a complex of factors not yet further analysed, indicated with *G*. If *G* is absent the

seed-coat is colourless and transparent and the seed yellow in consequence of the yellow colour of the cotyledons.

13. The action of G is inhibited by D; in the presence of both G and D the seed is greyish-green.

14. The inhibitory action of D is neutralised by B'.

15. C' and D together cause the crimpiness of the petal, an action neutralised by B'.

16. C' and D together inhibit the factors for breadth of the petal, an action which is prevented by B'.

17. The 64 genetically different forms with coloured flowers show 40 different phaenotypes; the 192 white coloured genotypes show 6 different phaenotypes.

18. With the different phaenotypes occur six one-sided and one common correlation. Probably some of these correlations may still be broken up.

19. The co-operation of the various factors in producing the characters may be represented in a simple synoptic way, by what I have called genetic schemes of co-operation.

20. The common blue-flowering flax possesses all of the eight factors. All other forms mentioned in this paper are loss-mutants; they are distinguished by the lack of one or two factors of the common blue-flowering type.

21. The seven factors: A, B', C', D, E, F and H may lie in seven different and must lie in at least three different chromosomes, the haploid number of chromosomes being 15.

22. Besides the 16 different forms obtained by different combinations of the factors A, D, E and F with the complex $B'C'$ there exist for the colour of the petal a great number of others, which are genetically distinct from these 16 and from one another. So far I have isolated 46 different blue, light-blue or lilac forms, and I have observed several others. The total number is unknown to me.

23. Three series of multiple allelomorphs, each series consisting of four, have been determined.

24. For the flower-colour the genetic differences between some forms are so slight that they are scarcely perceptible. The fluctuating variability of the flower-colour on the other hand is very great; the range of variation of one single form comprises the phaenotypes of many others.

This paper is dedicated to my honoured master Prof. Dr J. W. Moll on his 70th birthday.

GRONINGEN. 3 *June*, 1921.

THE LAW OF HOMOLOGOUS SERIES IN VARIATION.

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Director of the Bureau of Applied Botany and Plant Breeding, Petrograd, Russia.

(With Plates IX and X.)

CONTENTS.

Introduction.

Evolution of the study of systematics of plants.

The characteristic feature of the history of plant investigation, from Tournefort up to the present, has been the varied conception of systematical units. Further investigation did away with the former conception of species, as introduced by Linné. The history of systematics of plants gives a vivid illustration of attempts to arrange in a convenient and harmonious system all newly discovered morphological and physiological characteristics, the number of which grows rapidly with improved methods of discerning hereditary forms, and with the study of new specimens of the same plants, gathered in different regions. The Linnean species had to be divided into subspecies and varieties (*in sensu bot.*); varieties into races. Genetical studies of the last decades have proved even the divisibility of the minutest morphological and physiological units in systematics (races, Elementararten of de Vries), and established that, although outwardly similar, they can be different genotypically. The same is applicable to the animal world.

Lotsy, in his book *Evolution by Means of Hybridization* (1916), proposes to introduce a new terminology to distinguish fundamental units in the classification of hereditary forms. He proposes to call the old Linnean species, which, as was shown in the nineteenth century, are of collective nature—"Linneons"; races, varieties, which make up the elementary species of Jordan and de Vries he proposes to define as "Jordanons." The term "species," Lotsy would retain (as it seems to us not very successfully) for the modern conception of genetics—the genotype, as a fundamental unit covering similar hereditary groups of individuals.

Statistics of the diversity of the plant world.

Up to the present, statistics of the plant and animal world are available only for "Linneons." According to Hooker and Engler there are known altogether about 130,000—140,000 Linnean species of higher seed plants, including *Coniferae*. Families most abounding in Linneons are, according to Engler[1], those of *Compositae* (ca. 13,100), *Leguminoseae* (ca. 12,000), *Gramineae* (ca. 4000).

Although these numbers of Linneons are quite large, they give a very superficial representation of the real diversity of the plant world.

[1] Engler, *Syllabus der Pflanzenfamilien*, 8te Auflage, 1919.

Only a closer study of Jordanons and genotypes would give a true idea of this diversity.

The systematic study of numerous varieties among Linnean species, which was initiated by Lindley (Monograph on Roses), de Candolle (*Brassica*), Kraus, Metzger, and Alefeld on cultivated plants, and by Séringe[1], Jordan and Naegeli on wild plants, and is continued nowadays by plant breeders and by botanists (Swedish school of systematists: Wittrock, Dalstedt, Almquist and others), has revealed a total absence of monotypical Linneons. Linnean species, which, in the nineteenth century were regarded as uniform, in the twentieth century were separated by plant breeders and systematists into large numbers of Jordanons, easily distinguishable both morphologically and physiologically; e.g. many species of *Gramineae*, *Compositae*, *Cruciferae*, *Leguminoseae*, *Sesamum indicum*, *Viola tricolor*, *Linnea borealis*, etc. Up to the present, not many Linneons of wild and cultivated plants have been studied thoroughly, but still the data available shows an immense diversity of Jordanons among Linneons.

Thus, after investigations of local Russian and Asiatic wheats at our experimental station, the existence was proved of about 3000 Jordanons of *Triticum vulgare* Vill., perfectly recognizable morphologically and physiologically[2]. This number does not include many hundreds of varieties of hybrids created artificially by plant breeders of Western Europe during the last thirty or forty years, but only the natural local varieties of wheat.

For barley we know at least 600 to 700 Jordanons, for oats more than 600. In Rye, *Secale cereale*, many hundreds of forms, differing in hereditary morphological and physiological characters, were collected by Mrs V. P. Antropova, from different parts of Persia, Bokhara, Asiatic and European Russia. Hundreds of easily distinguished forms are found in sorghum by American investigators. Investigations in Japan and India discovered thousands of varieties in rice. Thousands of varieties might be established in Indian corn, *Zea mays*. Hundreds of varieties were found in peas, *Pisum sativum*; vetches, *Vicia sativa*; lentils, *Ervum Lens*; beans, *Phaseolus vulgaris*. Hundreds of varieties are found among Soya beans, *Soya hispida*. Jordan and Rosen found about 200 constant varieties in wild *Draba verna*. Miss Sinskaja, at our experimental station, found more than 300 well recognizable varieties

[1] *Musée helvétique*, p. 115 (Aconitum).

[2] This data is given in the address by the author and his co-workers at the All-Russian Conference on Plant Breeding, 1920. Saratov. Now in the press.

of *Eruca sativa*, a weed occurring in fields of flax in Turkestan and Bokhara. Thousands of forms, perfectly distinguishable, exist among species of *Cucurbita Pepo*, *Cucurbita maxima*, *Citrullus vulgaris*—water-melon, *Cucumis sativus*, and *Cucumis Melo*[1]. Hundreds of forms are found among wild *Linnea borealis* (Wittrock), *Picea excelsa* (Wittrock), etc.

Wild and cultivated plants.

The majority of cultivated and wild Linneons propagated by seeds, are represented by hundreds of well-defined Jordanons. There is no essential difference in this respect between wild and cultivated plants. Wild Linneons, like clover (*Trifolium pratense*), *Agropyrum cristatum*, *Agropyrum repens*, yellow alfalfa (*Medicago falcata*), *Alopecurus pratensis*, *Brassica elongata*, studied in detail at Russian Experimental Stations by plant breeders (Roudzinski, Lorch, Jegalov, Bogdan), proved to be no less variable than cultivated wheats, barleys, oats, and peas. The monotypic nature of many wild Linnean species is kept only so long as they are studied by a few specimens in the herbarium. The individual study in cultures of many samples of the same Linneon inevitably discovers its polymorphic nature.

Still greater diversity is observable in plants multiplying vegetatively or apogamically, like roses, potatoes, apples, *Hieracium* (Naegeli), and *Dahlia*.

We do not exactly know if there are really monotypic Linnean species in nature, fairly well specific and separated from other Linnean species and represented by one variety, one Jordanon only. The whole impression is that the more we study our plants and animals, the more variable they are, the more varieties we find among Linnean species. Several Linnean species of plants and animals, like roses, wheats, Indian corn, rice, squashes, *Drosophila*, seem to be extremely variable, but these have attracted more attention than others. We easily notice sharp differences in colour, size, and shape of several organs and are rather inattentive to others.

The differences of Jordanons within the limits of the same Linneon, in the shape and colour of their flowers, form and size of leaves, fruits and other organs, are very often no less marked than the differences between Linneons themselves. For instance, some varieties of *Cucurbita Pepo* are characterized by fruit the size of hen's eggs; other varieties, growing under the same conditions, bear fruit three and four feet in

[1] These plants were studied at our experimental station by Mr S. M. Boukasov and Mrs S. A. Kartashov.

diameter. Some varieties of *Sesamum indicum* have opposite leaves and fruits, others have alternate. Some varieties of wheat and rye have simple leaves, without differentiation into vaginae and plates, having no "ligula," or "auriculae"; others have the usual complicated leaves, with "ligula," and "auriculae."

Plants self-fertilized, as wheat, barley, peas, soya, etc., and cross-fertilized, as rye, maize, beet, are alike polymorphous. The seeming uniformity of several cross-fertilized wild and cultivated plants is only apparent when they are not studied carefully. The difference consists only in the heterozygotic nature of many characters in cross-fertilized plants, and in the homozygotic nature of self-fertilized plants. Some recessive characters may be hidden in cross-fertilized plants by the dominance of other characters, but by artificial self-fertilization of these plants, and by inbreeding, it is possible to re-establish them. From what we know at present from the study of Indian corn (Emerson, Collins, and others), of rye, beetroot, *Drosophila*, man himself, cross-fertilized organisms are not less variable than self-fertilized.

The above-mentioned numbers of Jordanons are in reality still greater, because, up to the present time, African and Asiatic varieties of even the most important cultivated plants, like wheat, oats, barley, peas, lentils, *Cruciferae*, are almost unknown.

Problems of the future.

There is a real need for the study and systematizing of these Jordanons, especially in cultivated plants and domesticated animals, for the benefit of geneticists, as well as systematists and agriculturists. Only the closest study of Jordanons and genotypes will give a real representation of what a Linneon is. To construct the general genetic schemes, it is necessary to know the composition of Linnean species. Before creating new varieties by crossing we ought to know what exists in nature. Even for cereals, *Leguminoseae*, and other most important plants, we have no adequate knowledge of even easily recognizable botanical varieties. Regions of ancient culture in Asia, Africa, and America still preserve numbers of varieties unknown to systematists and plant breeders.

In 1880, Alphonse de Candolle wrote in his remarkable book *La Phytographie*: "Un jour la science traitera les éléments de l'espèce comme les éléments des genres, comme ceux de la famille et tous ces groupes seront coordonnés, les uns au-dessus des autres d'une manière parfaitement uniforme" (p. 80). This day has arrived, but the task is not

very simple. The closest study of some Linneons of cereals, *Leguminoseae*, *Cruciferae*, *Compositae*, and *Cucurbitaceae*, persuades one of the immensity of this work. The diversity of plants and animals is too great to admit of giving a complete list of existing forms. There comes the necessity to establish some principles and schemes of classification.

The near future promises to differentiate the Linneons still more, and to multiply the number of Jordanons and species in Lotsy's sense. Artificial hybridization threatens considerably to enlarge the external diversity of forms.

It may be expedient to define even at the present time the multiformity in Linneons, not by the number of described and possible combinations, but by the number and list of *varietal characters* through which Jordanons differ from each other, not forgetting that separate characters can be dependent on several hereditary factors or genes, involving complicated genotypical formulae. The complete genotypical composition of Linneons is a problem for the future.

The multitudinous chaos of innumerable forms obliges investigators to look for some way of simplification. The process of differentiation will go on inevitably, adding to the records of existing forms, and giving a true conception of Linneons. But parallel to differentiation it is natural to search for ways of *integration* of our knowledge of Jordanons and Linneons themselves. If some 130,000 Linneons are difficult to manage for investigation, the work with tens and hundreds of millions of Jordanons will be still more complicated.

As formerly, in the study of dead organic and inorganic worlds, so at the present, the problem before the investigator of the animal and plant world is to explore the regularities in polymorphism, and to establish its classes.

The object of this work.

Below is an attempt to integrate the phenomena of polymorphism which we define as "The Law of Homologous Series of Variation." These regularities were noted by the author during the study of innumerable varieties of cultivated and wild plants.

The ideas expounded below in some part are not foreign to biological literature. Separate facts of regular variation were known long ago. Naudin noticed them in his classical study of *Cucurbitaceae*. Darwin[1], who was in general rather the adherer of fortuitous variations in all directions in his *Origin* and *Variation*, paid attention to regular varia-

[1] Darwin, *Variation of Animals and Plants*, Part 2; "Analogous or Parallel Variation."

tion, which, as he states, "occasionally" happens in plants and animals. M. J. Duval-Jouve collected a great many data on the variation of wild Linnean species of *Gramineae, Juncaceae* and *Cyperaceae* in his paper on "Variations parallèles des types congenères" published in 1865 in *Bull. de la Sté. Botanique de France*, Vol. XII. His conclusions in some part come near to the statements of our study. De Vries notices in his *Mutationstheorie* the existence of series of variation. Eimer[1] in his study of Orthogenesis approached the same subject from a different point of view. Several palaeontologists (Cope, Osborn) noticed regular variation in animals. More recently Saccardo[2] and Zederbauer[3] gave extremely instructive instances of regular variation in fungi and *Coniferae*.

The detailed study of variation among many different groups, and the great number of new facts permits us to take this subject anew and to bring all known facts into the form of a general law to which all organisms are submitted.

I. VARIATION OF CLOSELY ALLIED LINNEONS.

In studying the varietal composition of the plant world, and in investigating in detail Linnean species, one can observe some regularities in their varietal diversity, in spite of their enormous polymorphism.

The first regularity one meets with is the similarity in series of morphological and physiological characters, which distinguish varieties and races (Jordanons) of nearly allied Linneons; also a parallelism in the series of genotypical as well as phenotypical variation in Linnean species of the same genus. Let us consider some examples.

Wheat. There are eight Linnean species of wheat, which represent typical collective units, well determined by their specific characters. Numerous investigations have shown that these Linneons form three genetical groups, as follows:

I. (1) *Triticum vulgare* Vill.
(2) *T. compactum* Host.
(3) *T. Spelta* L.

II. (4) *T. durum* Desf.
(5) *T. polonicum* L.
(6) *T. turgidum* L.

III. (7) *T. monococcum* L.

[1] G. H. T. Eimer, *Die Entstehung der Arten auf Grund von erworbener Eigenschaften nach den Gesetzen organischen Wachsens*, Vols. I—III. 1888—1901, Iena.

[2] P. A. Saccardo, "I Prevedibilli Funghi Futuri secondo la Legge d' Analogia." *Degli Atti del R. Instituto Veneti de Scienze, Lettere ed Arti*, Tomo VIII. Ser. 7.

[3] E. Zederbauer, "Variationsrichtungen der Nadelhölzer." *Sitzberichte d. Akademie d. Wissenschaften, Wien, Math. Nat. Klasse*, 116, Abt. I. 1907.

The eight species, *T. dicoccum* Schrank, occupies a place between the first and the second groups[1]. *Triticum vulgare* is represented by a multitude of Jordanons (varieties and races), which differ in the following characters:

1. Bearded, beardless, semi-bearded ears.
2. Ears white, red, gray, black.
3. Ears smooth, hairy.
4. Seeds white, red.
5. Winter, spring varieties; and so on.

T. compactum, *T. Spelta*, genetically closely related to *T. vulgare* repeat exactly all its varieties. So we have a complete similarity in the series of varieties in all three Linneons.

The second group of wheats, separated from the first by a considerable sterility of hybrids between them, repeats, in general, the series of variation of the first group. In *T. durum*, *T. polonicum*, *T. turgidum*, there are white, red and black eared varieties, smooth hairy eared, white and red grained, winter and spring varieties. Only beardless forms are still unknown. All existing varieties of this group of Linneons are bearded or semi-bearded. By artificial crossing, beardless durum wheats have been obtained during the last few years, at Saratov Experimental Station.

The third group of *T. monococcum*, in its wild and cultivated forms, completely repeats the former group in its variability[2].

T. dicoccoides Kcke, a wild Linnean species nearly allied to cultivated wheat, and found in great quantities by Aaronsohn in Syria, consists of a large number of varieties parallel to varieties of *T. durum*, *T. dicoccum* and other Linneons.

Numerous races included in different botanical varieties of *T. vulgare*[3], and investigated at our experimental station, showed the minutest likeness in their series. For instance, among the botanical variety *T. vulgare* var. *ferrugineum* A1, studied by Miss E. I. Baroulina, about

[1] N. I. Vavilov, "Immunity of Plants to Infectious Diseases," 1919, Ch. v. *Annales de l'Académie Agronomique Petrovskoé (près Moscow)*, Année 1918. (With a résumé in English.) "Immunity to Fungous Diseases as a Physiological Test in Genetics and Systematics, exemplified in Cereals." *Journal of Genetics*, Vol. IV. No. 1, June, 1914.

[2] K. A. Flaksberger, "*Triticum monococcum* L." *Bulletin of Applied Botany*, 1914, Petrograd.

[3] This Linnean species is divided, according to F. Koernicke (*Handbuch der Getreide*, 1885) and K. A. Flaksberger ("Determination of Wheats." *Bulletin of Applied Botany*, Petrograd, 1915), into 26 botanical varieties, each of which is of collective nature and consists of a number of races.

220 Jordanons were established, differing in structure of ears, glumes, rachis, grain, leaves, in physiological characters (immunity to fungous diseases, early ripening, etc.). The same series of morphological and physiological races were found in *T. vulgare* var. *erythrospermum* Kcke, *T. vulgare* var. *graecum* Kcke, T. var. *erythroleucon* Kcke.

Barley. Cultivated varieties of barley are represented by two genetically closely allied Linneons, which can easily be crossed: *Hordeum vulgare* L. and *H. distichum* L. The first of these has the varieties:

1. With dense and loose ears.
2. With black, yellow and red (anthocyanin) ears.
3. With hairy and smooth empty glumes.
4. With kernels hulled and without hulls.
5. With awns smooth and rough.
6. With " Kapuze " instead of awns.
7. Winter and spring varieties; and so on.

The second Linneon (*H. distichum*) completely repeats the whole series of varieties of the first one.

Until late years, only one variety of wild barley (*H. spontaneum* C. Koch), closely allied to cultivated *H. distichum*, was known. This was a winter variety, with yellowish ears. In 1916, we found in Persia and Transcaspic Province and Bokhara, a number of spring varieties of wild barley, with typical bristle spikelets, varieties with black ears, with smooth as well as with hairy, empty glumes.

Oats. Let us take a larger group of Linneons, belonging to the botanical section *Euavena*, which includes genetically nearly related Linnean species of cultivated and of uncultivated oats. A closer investigation of their numerous varieties, studied in our Bureau of Applied Botany, Petrograd, by Mr. A. I. Malzev, showed that *Avena diffusa* Asch. and Gr., *A. orientalis* Schr., *A. fatua* L., *A. Ludoviciana* Dur., *A. sterilis* L. are represented by similar series of varieties with white, yellow, gray and brown (black), flowering glumes, with hairy and smooth glumes; all these Linneons include spring as well as winter varieties, those susceptible to crown rust (*Puccinia coronifera*), as well as those which are immune, etc.

Millet. The same parallelism may be observed in Linneons which, although nearly related, are still quite distinct and cannot be crossed. *Panicum italicum* and *P. milliaceum* give an example of such distinct Linnean species, represented by a large number of botanical varieties, studied by Koernicke (*Handbuch der Getreide*, 1885), and by Russian

plant breeders Arnold, Syriousov, and others at our experimental station. The series of varieties differing in compactness of panicule, in colour of flowering glumes, in the presence or absence of anthocyanin pigment in panicules, and in the size of the plants, etc., are extremely alike in both Linneons.

Cotton. If we compare the variability of Asiatic cotton, *Gossypium herbaceum*, cultivated on a large scale in Turkestan, Persia and India, with the variability of American cotton, *Gossypium hirsutum* (Upland), we notice a striking similarity in both Linnean species. Asiatic cottons were studied in detail by Leake, Gammie and others, in India, and by Zaitzev in Turkestan. In their manner of branching, in the variation of the shape of their leaves, colour of stem, and in all details of structure of fruit, colour of fibre, and other characters, one Linneon repeats the other. At the same time, these Linneons differ not only geographically but also physiologically in their origin. They can only be crossed with great difficulty, and then give mostly plants which are completely sterile[1].

Agropyrum repens and Agropyrum cristatum.

Let us take two distinct Linnean species, grown in typical wild conditions. *Agropyrum repens* and *A. cristatum*, two typical wild Linneons, meadow grasses, widely distributed over European and Asiatic Russia. These grasses were studied in detail by V. S. Bogdan, at the Krasny Kout Experimental Station (Samara Government), and by the author, in Moscow and in Saratov Government. On comparing their polymorphism we must acknowledge a striking likeness between the series of varieties represented by both plants. Both have—

1. Bearded and beardless ears.
2. Hairy and smooth glumes.
3. Yellow, red and black eared varieties.
4. Varieties with anthocyanin in ear (violet, and without anthocyanin).
5. Varieties with spreading (lying) and erect form of seedlings.
6. With thin and thick straw.
7. Loose and dense ears.
8. Ears covered with wax, and without wax.
9. With yellow and violet anthers.
10. With short and with long stems.

[1] G. S. Zaitsev, "The Results of Crossing *Gossypium hirsutum* and *G. herbaceum*." *Bulletin of Applied Botany* (Petrograd). At present in the press.

11. Hairy and smooth leaves.
12. With narrow and broad leaves.
13. Early and late varieties.
14. Hydrophilous and xerophilous types.

Agropyrum cristatum, also, has varieties with straw full of pith, as well as the ordinary varieties with hollow straw. The former varieties are not found yet in *A. repens*, but it has not been sufficiently studied to say definitely that these forms are absent.

Brassica Napus and B. rapa.

A clear parallelism of series of varieties is to be observed in *Brassica Napus* and *Brassica rapa*. Both have annual and biennial varieties; the diversity in colour and shape of flowers and leaves, form of plants, shape and colour of fruit and seed is quite similar in both Linneons.

Cucumbers and melons, Cucurbita maxima and C. Pepo.

A striking parallelism of a series of varieties is observed in cucumbers and melons, belonging to two different Linnean species, *Cucumis sativus* and *C. Melo*, which are physiologically distinctly separated, as was shown by Naudin. Both in shape and colour of their fruit, seeds and leaves, in details of flower structure, and habits of plants, one must notice the astonishing similarity in series of variation of these Linneons, represented by a large number of well distinguished Jordanons. Some varieties of melons are quite similar in appearance and flavour to several varieties of cucumbers. This parallelism has already been mentioned by Darwin in his *Variation of Animals and Plants under Domestication*.

Very similar variability in Jordanons might be observed in *Cucurbita maxima* and *Cucurbita Pepo*, and *C. moschata*, three Linneons represented by a large number of varieties. "Three species of *Cucurbita* have yielded a multitude of races which correspond so closely that Naudin insists they may be arranged in an almost strictly parallel series[1]." These Linneons, notwithstanding their similarity in variation, cannot be crossed together, as was shown by Naudin and confirmed at our experimental station by Mrs Kartashov.

An immense number of other similar examples could be given for wild and cultivated plants. So far as we know, this kind of variation is not "occasional," as Darwin supposed it to be, *but quite general*. The data were not available in his time, but the detailed study of hundreds

[1] Darwin, *Variation*, Part II. New York edition, 1876, p. 341.

of Linnean species belonging to different families shows that there are no plants which are an exception to this rule. *Therefore, we may conclude that, in general, closely allied Linnean species are characterized by similar and parallel series of varieties; and, as a rule, the nearer these Linneons are genetically, the more precise is the similarity of morphological and physiological variability. Genetically nearly related Linneons have consequently similar series of hereditary variation.*

II. Variation of Different Genera.

Rye and wheat.

In the study of Linneons and Jordanons of closely allied genera, one can notice the same regularity in polymorphism. To compare wheat and rye—

The varietal composition of rye—*Secale cereale*—until recently has only been studied in a fragmentary and insufficient manner, notwithstanding the great importance of the culture of this cereal in Europe. As a typical cross-fertilized plant, rye has no definite constant varieties, and the separation and definition of different hereditary forms is more difficult than in wheat, which is usually self-fertilized. The predominant view met with in literature is that rye is a uniform plant, as compared with wheat.

Investigations made by Mrs V. P. Antropova and Mrs A. J. Toupikova, at our experimental station, of many samples of rye collected from different regions of European and Asiatic Russia, from Persia, Bokhara, Pamir, and Afghanistan, showed a sharp polymorphism in rye no less than in wheat. The most interesting result of these studies is that the characters which distinguish the different forms of rye appear to be strikingly similar to those marking the different forms of wheat. So it appears that rye, just as wheat, is represented by:

1. Varieties with bearded, beardless (almost), and semi-bearded ears.
2. With hairy and smooth ears.
3. By white (yellowish), red and dark brown eared varieties.
4. By varieties with violet ears (with anthocyanin), and without anthocyanin.
5. With not only the common green seeds, but also seeds of white, red or brown[1].

[1] Several varieties of Abyssinian wheat (*Triticum durum*) have brown-purple seeds, cf. A. St C. Caporn, *Journ. Gen.* VII. 1918, p. 261.

6. As in wheat, varieties with grains easily shed from flowering glumes, or *vice versa*, with seeds entirely covered in glumes.

7. Forms with hollow straw, and with straw full of pith.

8. Varieties with fragile rachis, as well as with strong rachis (as in ordinary varieties of European rye).

9. Varieties with long and short ears.

10. „ „ dense and loose ears.

11. „ „ hairy and smooth rachis.

12. „ „ broad and narrow glumes.

13. „ „ bearded and beardless empty glumes.

14. „ „ many flowers on their spikelets, or with only two flowers in a spikelet.

15. Varieties with rough or tender beards.

16. „ „ starchy or flinty seeds.

17. „ „ small and with large seeds.

18. „ „ nerves highly developed on glumes, with nerves weakly developed on glumes.

19. Varieties with smooth leaf sheaths, or with hairy sheaths.

20. „ „ ligula, or without ligula.

21. „ „ well-developed auriculae, or without auriculae.

22. „ „ smooth auriculae or with hairy auriculae.

23. „ „ violet seedlings[1] or with green seedlings.

24. „ „ broad and narrow leaves.

25. „ „ hairy and smooth leaves.

26. „ „ thin and thick straw.

27. „ „ short and long straw (stems).

28. „ „ procumbent and erect form of seedlings.

29. Early and late varieties.

30. Winter and spring varieties.

31. Resistant to and susceptible to brown and yellow rusts.

32. Varieties with ordinary simple ears, or with complicated branchy ears.

33. Varieties with leaves covered with wax inflorescence, or without wax.

34. Cross-fertilized or self-fertilized forms[2], etc.

In general, the genus *Secale* repeats in detail the series of variation

[1] In wheat some Persian varieties belonging e.g. to *Triticum vulgare* var. *ferrugineum* Al. are characterized by seedlings in colour and shape not distinguishable from seedlings of ordinary violet rye.

[2] In wheats, several varieties of *T. vulgare* are inclined to cross-fertilization.

of the genus *Triticum*, a result which was unexpected at the beginning of our studies. In the same investigation, a search was conducted for varieties similar to those of wheat previously known to us; and our presuppositions concerning the forms of rye which theoretically ought to exist were, in most cases, exactly corroborated.

Prediction of existence of rye without "ligula."

Thus we found in 1916, in Shugnan (Pamir) and in Afghanistan, several varieties of wheat (*T. vulgare*), the leaves of which were without "ligula," unknown before that time, so far as we know, in botanical literature. (See Pl. IX.) *A priori*, basing our opinion on the principle of homologous variation in nearly allied plants, we expected to find these curious forms without "ligula" in rye too; and in 1918, it was actually found among Pamirian spring rye, sown at our experimental station. (See Pl. IX.)

In literature there is no mention of the existence of varieties of rye with hairy ears. *A priori*, their existence was very probable, for in the genus of *Triticum*, all Linneons are represented by smooth eared, as well as by hairy eared, varieties. In 1918, such hairy forms were found by examining thoroughly ears of Pamirian spring rye.

Wheat, as we have seen before, is represented by bearded and beardless Jordanons. Even in Linneons, which usually are represented only by bearded varieties, as e.g. *T. durum*, there are known semi-bearded varieties (var. *Arraseita* Hochst.). *A priori*, we should expect to find the same differences in rye, and, in 1919, there were found typical long-bearded (Astrakhan rye), semi-bearded, and almost beardless varieties (the latter among specimens from Pamir and Afghanistan).

Rye and wheat belong to two genera comparatively closely allied. In some cases they produce many natural hybrids, as has happened in recent years in south-eastern Russia, some of which may even be partially fertile (single seeds)[1]. Most striking is their complete parallelism in variation down to the minutest characters.

Aegilops.

The genus *Aegilops*, which is related to *Triticum*, and grows in large quantities in natural wild conditions in southern Russia, Turkestan and Persia, as was shown by our observations, repeats in general all varieties of the genus *Triticum*. In *Aegilops squarrosa* and *Ae. cylindrica*, there

[1] G. K. Meister, "Hybrids of Wheat and Rye." *Report of the Third All-Russian Conference of Plant Breeding*, Vol. I. 1920.

are beardless as well as bearded varieties, varieties with yellow, red and black ears, hairy and smooth ears; and we know winter as well as spring varieties of these Linneons. The same division of the genus *Aegilops* into collective Linneons seems to be similar to that of *Eutriticum* (cultivated wheats). The Linnean species, *Aegilops cylindrica* and *Ae. squarrosa*, are akin to *Triticum vulgare* and to other Linneons of the same group of wheat. Both are characterized in general by hollow stems, susceptibility to yellow and brown rusts (*Puccinia glumarum* and *P. triticina*), to mildew (*Erysiphe graminis*), and to smut—*Tilletia tritici*. Other Linneons, like *Aegilops triuncialis*, correspond more to *Triticum durum* or *T. monococcum* in their immunity to these parasites, and the similarity of their straw, which is full of pith, and in the absence of completely beardless varieties[1].

As is known, Godron produced artificially hybrids of wheat and *Aegilops*, which proves the relative affinity of these genera.

Agropyrum.

The genus *Agropyrum* belongs to the group of genera closely allied to *Triticum* and to *Secale*. In 1919, we produced a sterile hybrid (F_1) by crossing *Secale fragile* with *Agropyrum villosum*. As we have shown before in the example of polymorphism of *Agropyrum repens* and *A. cristatum*, this genus in general repeats, even in detail, the series of variation of *Triticum* and *Secale*.

Vicieae.

Let us turn to the family of *Papilionaceae*. Four Linneons—*Pisum sativum*, *Lathyrus sativus*, *Ervum Lens*, and *Vicia sativa*—belonging to the systematical section *Vicieae*, were studied in detail at our experimental station. All four Linneons manifest a similar homologous series of variation like cereals. Each Linneon was represented by a large number of varieties collected from different European and Asiatic countries. All four genera proved to have varieties with white, red (pink), and violet (purple) flowers, and all manifested a striking phenotypical similarity of variation in the shape and colour of their seeds and cotyledons. In all genera were found varieties with yellow-green cotyledons, also with orange-red, and with black, brown, green, yellow, and white seeds. (See Plate X.) In all Linneons there are varieties with spotted, as well as with unicoloured seeds. In all genera were

[1] For details see N. I. Vavilov, *Immunity of Plants to Infectious Diseases*, 1919, Ch. 4.

discovered varieties with small and large seeds. The variation in the shape of seeds is found to be alike in peas, lentils and vetches, as well as in *Lathyrus sativus*; they may be flat, angular, or round. In all genera we found varieties with narrow and broad leaves, with leaves covered with wax, with coloured (violet) seedlings, and with ordinary green seedlings. All four genera have tall and dwarf varieties, early and late forms. The variation in fruits in all of them tends in the same direction.

This similarity in *Vicieae* is so clearly expressed that sometimes it was difficult to say, from an external view of the seeds, to which genus they belonged. This is the more striking as all these genera are physiologically quite independent and cannot be crossed together, in spite of many attempts made by Fruwirth[1], and at our experimental station.

Cucurbitaceae.

The most cultivated genera and Linneons of the family *Cucurbitaceae* are *Citrullus vulgaris* (water-melon), *Cucumis Melo* and *C. sativus* (melons and cucumbers), and *Cucurbita Pepo*, *C. maxima* and *C. moschata* (squashes, gourds and pumpkins). After the investigations of Naudin, it was found that these three genera, although quite distinct, belong to the closely related botanical sections *Cucumerinae* and *Cucurbitinae*, and their variability can therefore be compared.

The numerous varieties of these genera, collected from different parts of Russia, Persia and Bokhara, were studied at our experimental station during 1919 and 1920.

All three genera in their Linneons have varieties with round, oblong, and flat, simple, as well as segmented fruits. The variation of the colour of fruits is relatively similar in all genera, whether monochrome, streaked or spotted, white, green, yellow, brown, or black. Their parenchyme can be colourless, or with coloured plastids. The fruit may be sweet or bitter. Variation in the size of fruits is extremely great in all genera, beginning with small fruits of the size of apples and even smaller, and ending with the gigantic fruits, such as the ordinary squashes, melons and water-melons. The diversity in flower structure, colour and hairiness of petals and calyx, is very great in different varieties, and varies similarly in all genera. The leaves vary greatly in all three genera. Most varieties of melon have simple leaves, very different from those of the water-melon, but some resemble, in the dissection of their leaf

[1] *Pflanzenzuchtung*, Dritte Auflage, 1919.

plates, varieties of water-melon. At the same time, we know several varieties of water-melon which approach other melons in the shape of their leaves. Varieties of gourds (*Cucurbita Pepo*) have leaves differing from the simple undissected shapes to those similar to ordinary water-melons.

Probably there are not many plants which vary so greatly, or at least so conspicuously, as these genera of *Cucurbitaceae*. Sometimes it is difficult from the exterior, and even from the interior, of their fruits, to decide positively to which genus they belong. The similarity of variation in separate characters is so sharp that several very careful botanists, such as S. I. Korshinski, have classified some varieties of melon as being natural hybrids of water-melon (*Citrullus vulgaris*), and melon (*Cucumis Melo*)[1]. It is often stated quite wrongly in agricultural and horticultural literature that melons are fertilized by pollen of squashes, and give intermediate forms.

The experiences of Naudin, repeated on a large scale at our experimental station by Mrs S. A. Kartashov, have proved the impossibility of crossing these three genera. Even separate Linneons, within the limits of the same genus, e.g. *Cucurbita moschata*, *C. maxima*, and *C. Pepo*, cannot be crossed together.

The so-called intermediate forms of these plants, accepted erroneously as being natural hybrids of these genera on account of the shape of their leaves and seeds, and the flavour and shape of their fruits, are only a beautiful illustration of similar variation of these distinct genera, and of their overstepping their characters[2], including the "hybrids" of water-melon and melon described in detail by Professor S. I. Korshinski. The same phenomenon evidently is observed in the case of *Gramineae* in so-called varieties of *Festuca loliacea* supposed to be hybrids of *Festuca* and *Lolium*.

The most essential point is that, notwithstanding an exceptional diversity of varieties in these genera, their variation is very regular, and not accidental. Knowing in detail the series of variation of water-melons, we could find a similar series of varieties among melons and gourds (*Cucurbita Pepo* and *C. maxima*).

[1] S. I. Korshinski, "Bastarde zwischen *Citrullus vulgaris* and *Cucumis Melo*." *Bulletin de l'Académie des Sciences de St Pétersbourg*, 1897.

[2] A detailed article on this subject, entitled: "Hybrids between melons, water-melons and squashes," was given by the author (N. I. Vavilov) at the First All-Russian Congress on Applied Botany, Veronej, Sept. 1920, and will be published in the Report of this Congress.

Cruciferae.

Observations have also proved the striking likeness of varieties of different genera of *Cruciferae*, belonging to the section *Brassicinae*, namely—of Linneons *Eruca sativa*, *Brassica campestris*, *B. elongata*, *B. juncea*, *B. rapa*, and *B. Napus*, *Sinapis alba*, and *Raphanus sativus*. Linneons of these four genera show a complete repetition of a series of varieties, differing in the shape and colour of their petals and calyx, shape of leaves, presence and absence of wax on stems and leaves, shape and hairiness of fruits, colour of seedlings, hairiness of stems and leaves, as well as by many minute characters. Linneons of all four genera are differentiated into early and late varieties, into spring and winter (or biennial) varieties. In general, it was found that the more specimens of the same Linneon were studied, the closer was their parallelism of variation to that of other Linneons of the same generic section.

Capsicum and Solanum.

A clear repetition of variation can be observed in *Solanaceae*. The genera *Capsicum* and *Solanum* belong to the same botanical section, *Solaninae* (Engler). In comparing series of varieties of pepper—*Capsicum annuum*, with tomatoes—*Solanum lycopersicum*, the similarity of their hereditary variation in different organs and different characters becomes evident.

The phenomena of homologous variation in related genera may be observed in quite different botanical families of monocotyledonous, and dicotyledonous plants, as well as in *Coniferae* (Zederbauer). Notwithstanding the extinction of many links during the millennial existence of most genera and Linnean species, the rôle of natural selection and extinction, there is no difficulty, by careful study, in tracing the similarity in variation in most of the related genera.

Therefore, in general, *the second rule or law in polymorphism, as a sequence to the first one, is that not only genetically closely related Linnean species, but also closely allied genera, display similarity in their series of phenotypical, as well as genotypical, variability.*

III. Variation of Whole Systematical Families.

Closer investigation of many genera within the limits of different systematical families, discloses the fact that all genera of a given family are subject to common tendencies in variation.

Gramineae.

Let us take the family of *Gramineae*, and consider the schemes of division into varieties of quite distinct genera, belonging to different generic sections of the same family. All genera and Linneons might be divided into varieties according to their density of inflorescence. Millet—*Panicum miliaceum*—is divided by systematists into three groups, according to its density of panicule:

1. Loose (branchy)—*Effusum.*
2. Densed—*Compactum*, and
3. Intermediate—*Contractum*[1].

In just the same way *Andropogon Sorghum* might be divided. Oats (*Avena sativa*) are represented by varieties with one-sided, compact panicules (*A. orientalis* Schr.), as well as by varieties with loose, branchy panicules (*A. diffusa* Asch. & Gr.). The latter are divided into varieties with more or less crowded panicules (*Steifrispe, Schlafrispe*). In general, the division of oats corresponds to that of millet and *Andropogon*. Cereals with ear-inflorescence might be divided into compact, loose, and intermediate varieties. In wheat, barley, and rye, there are all these kinds of ears among their different varieties. Varieties of maize might be distinguished quite clearly through the density of their ears. There are varieties of rice with compact vs. loose grain arrangement. Many food grasses, studied from a varietal point of view, as *Festuca pratensis, Lolium perenne, Agropyrum cristatum, A. repens, Phleum pratense, Alopecurus pratensis, Dactylis glomerata, Bromus inermis*, and others, all proved to be composed of varieties with loose and dense ears and panicules.

In the family of *Gramineae*, almost all the varieties may be divided into bearded and beardless forms.

The type of wild barley—*Hordeum spontaneum*, and wild oats—*Avena fatua*, characterized by spikelets which are brittle at the time of ripening, repeats itself in many different genera belonging to various sections, as *Secale* (*Secale montanum*), *Triticum* (*T. dicoccoides*), *Agropyrum, Oryza*, etc.

Branching ears are common not only to different Linneons of wheat, e.g. *Triticum turgidum* var. *mirabile* Kcke, but other Linneons belonging to quite different genera, with ear-shaped inflorescence, as barley, rye, *Agropyrum, Lolium, Panicum italicum*, etc.

[1] F. Koernicke, *Handbuch der Getreide*, Vol. I. Bd. 1885.

Varieties of entirely different genera of *Gramineae* might be divided into forms which have hulls and those which are hull-less, i.e. with grains tightly held by glumes, or with grains loose and easily shed out of glumes. We know such varieties in wheat (compare *T. vulgare* and *T. Spelta*), in barley (i.e. *Hordeum distichum* var. *nutans* and *H. distichum* var. *nudum*, or *H. vulgare* var. *coeleste*), in rye, in maize, in millet, in *Andropogon*.

A great many Linneons, belonging to quite different genera of *Gramineae*, studied in detail, have manifested a similar variation in the colour of their glumes. Varieties may usually be divided into white, yellow, red, gray and black (or black-brown) coloured forms. These varieties are known in wheat, barley, rye, oats, rice, millet, *Andropogon*, *Aegilops*, *Alopecurus pratensis*, *Panicum italicum*, and other genera.

Nilsson-Ehle has found among cultivated oats a variety with leaves which are entirely lacking in "ligula," called by us var. *eligulatum*. We found such varieties in wheat and rye, and hope to find them also in barley. Dr Emerson and Dr Collins in America recently found aligulate maize[1]. Prof. Janishevski found such varieties among different forms of *Poa bulbosa*. Several varieties of *Panicum Crus Galli* have a small, almost undeveloped "ligula."

Most Linneons belonging to different genera may be divided into smooth and hairy varieties. Hairiness may be connected with the stems, leaves, or glumes of spikelets.

Probably all Linneons of *Gramineae* might be divided into varieties with anthocyanin in stems, and those without it; into varieties with stems and leaves covered with wax, and those without wax.

In many Linneons belonging to quite different genera, we find varieties with procumbent forms of seedlings, and those with erect seedlings.

In a great number of Linneons belonging to different sections of *Gramineae*, cases of "vivipara" were observed. (See Penzig, *Teratologie*.) Duval-Jouve in his old paper (*l.c.*) gives many examples of similarity in variation of different genera of wild grasses (*Poa*, *Festuca*, *Bromus*, *Brachypodium*, *Agropyrum*).

Even the rare and isolated characters, which are regarded as confined to distinct Linneons, could be found in other genera, as e.g. the so-called "Kapuze," or "hoods," in several varieties of barley, that is, the special metamorphosis of beards into short, thick projections. (See *Hordeum*

[1] Dr R. A. Emerson, "The inheritance of ligule and auricules of corn-leaves." *Ann. Rpt. of Nebraska Expt. Sta. Res. Bull.* 25, pp. 81—88.

trifurcatum.)[1] Thus, some varieties of wheat (*Triticum vulgare*), found by us in Persia, as well as some varieties of Chinese wheats described by Mr K. A. Flaksberger[2] under the name "*inflatum*," are by their morphological as well as their genotypical nature very similar to "Kapuze," "hooded" in barley. (We crossed them with ordinary bearded and beardless wheats.)

If we compare the following series of variable characters distinguishing different hereditary forms of wheat with those distinguishing varieties of other genera of the same family, we notice a similarity in most of them.

A Series of Characters Distinguishing Varieties (Races, Jordanons) of Wheat—*Triticum vulgare* Vill.

I. *Characters of Ears (Spikes):*

1. Bearded, semi-bearded, beardless.
2. Colour of ears: white (yellow), red, gray, black (brown).
3. Hairiness of glumes: absence, presence, the degree of pubescence, the character of hairs.
4. The shape of glumes: narrow, broad, cuspidated, "hooded," etc.
5. Hairiness of the rachis: presence, absence, the degree of pubescence, the character of hairs.
6. Density of ears: loose, compact, intermediate.
7. Length of awns.
8. Length of the glume-tooth.
9. Length of the ear.
10. Number of flowers in spikelets.
11. Wax efflorescence: presence, absence, the degree.
12. The character of awns: smooth, rough.
13. Grains easily shed out of glumes, grains tightly covered by glumes.
14. Nerves of glumes: highly developed, or weakly developed.
15. Dents of nerves: weak, rough, present, absent.
16. Presence or absence of undeveloped spikelets at base of ears: presence or absence of additional spikelets in ears (very typical for several varieties of wheat).
17. Branched and simple ears.

[1] G. V. Ubisch, "Beitrag zu einer Faktorenanalyse von Gerste." *Zeitsch. f. induktive Abstammungs- und Vererbungslehre*, 1921, Cb. 25, H. 3/4.

[2] K. A. Flaksberger, "Wheats of Sounpan" (China). *Bulletin of Applied Botany*, Petrograd, 1910. John Percival, *Wheat Plant.* A monograph, 1921.

II. *Characters of Grains (Seeds):*

18. Shape of seeds: oblong, short, round, angular.
19. The size of seeds.
20. Colour of seeds: white, yellow, red, brown.
21. Character of the internal structure of seeds: farinaceous or flinty (glassy).
22. The characters of hairs on the top of grains (brush): long, short, dense, rare, etc.

III. *Characters of Plants (Vegetative Organs):*

23. Colour of seedlings: violet (presence of anthocyanin), or green (absence of anthocyanin).
24. Hairiness of leaves: presence, absence, the character of pubescence (short hairs, long hairs, rare, dense hairs, etc.).
25. Borders of leaves are ciliated, non-ciliated.
26. Leaves and stems covered by wax efflorescence, without wax efflorescence.
27. Colour of leaves: dark green, light green, variegated.
28. Length and width of leaves.
29. Length of stems (straw): tall, short, intermediate plants.
30. Straw thick, thin.
31. Straw full of pith, hollow straw.
32. Presence and absence of "ligula."
33. Presence and absence of "auriculae," size of "auriculae."
34. Colour of "auriculae."
35. Hairiness of "auriculae," presence, absence.
36. Nodes of stems: hairy, smooth.
37. Seedlings procumbent, erect, or intermediate.
38. Straw smooth and hairy.
39. The number of nodes, leaves.
40. Stems coloured by anthocyanin, without anthocyanin.
41. Leaf-sheaths hairy or smooth.
42. The number of tillers, stems, i.e. the degree of branching.

IV. *Physiological Characters:*

43. Winter and spring varieties.
44. Late and early varieties.
45. Susceptibility to brown rust (*Puccinia triticina*).
46. „ „ yellow rust (*P. glumarum*).
47. „ „ mildew (*Erysiphe graminis*).

48. Closed and opened flowering.
49. Number and length of stomata.
50. Xerophytic types, hydrophytic.

This list of variable characters is not complete; further investigation will undoubtedly increase the number of dissimilarities between different varieties of wheat. Nevertheless, it gives an idea of the great variability within the limits of one Linneon in the family of *Gramineae*. Many of the enumerated characters are independent of others in their inheritance, and in their different combinations form thousands of varieties. Those who are engaged in the study of different genera of cereals, as well as of different wild grasses, cannot deny that in *Gramineae* of quite distant genera variation manifests itself on the same lines. The knowledge of the details of a series of varieties of a single Linneon or genus might help to discover new varieties among other genera and Linneons.

The nearest families to *Gramineae* from a systematical point of view, as *Juncaceae* (Duval-Jouve) are characterized by a series of varieties similar to those of *Gramineae*.

Papilionaceae.

The same similarity of variation can be seen in *Papilionaceae*. The detailed study of variation among distant genera of this family discloses a striking unity in their differentiation into varieties, in scores of different characters of seeds, fruits, flowers, and vegetative organs. For example, if we compare the differentiation into varieties of the above-mentioned section—*Vicieae*, including *Vicia*, *Ervum*, *Pisum*, *Lathyrus* and *Cicer*[1], with differentiation of Linneons belonging to sections—*Trifolieae* (*Trifolium pratensis*, *Medicago sativa*), *Loteae* (*Lotus corniculatus*), *Galegae* (*Caragana arborescens*), *Phaseoleae* (*Phaseolus vulgaris*, *Soya hispida*), we cannot help noticing the great resemblance in their mode of variation. They vary in colour of seeds (from white to black), from unicoloured to those covered with small spots or large spots), in colour of cotyledons (from green-yellowish to orange-red), in shape of seeds (from round to oblong and to flat or angular), in size of seeds, in colour of flowers (from white to violet), in shape of fruits, in structure of leaves and flowers, in pubescence of stems and leaves, in shape and colour of seedlings (green or violet, spreading or erect, etc.), and in many other characters (notwithstanding the specific nature of these genera, and the

[1] *Cicer arietinum*. *Memoirs of the Department of Agriculture of India*. Bot. Ser. Vol. VII. 1915.

botanical sections to which they belong). These variations are tending in the same direction, and the completed series of varieties of separate genera show a clear and evident regularity and likeness. It is possible to speak about systems of varieties for different genera and families.

Cruciferae and Papaveraceae.

An astonishing parallelism of variation might be observed in the family of *Cruciferae*. At our experimental station we studied in detail varieties of some Linneons belonging to the section *Sinapeae*, namely, of *Eruca sativa*, *Brassica campestris*, *B. juncea* and *B. napus* (studies carried on by Miss E. N. Sinskaja). The first Linneons established a great number of varieties differing in hairiness of fruits (presence, absence), in colour of flowers (petals) and calyx, in colour and form of seeds, in shape of leaves (beginning with quite simple forms and ending with complicated, dissected varieties), in the shape of petals, form of plants (spreading, erect), in the colour of seedlings (with anthocyanin, without anthocyanin), in structure of fruits (long, short, round, broad, narrow), in density of florescence, etc. In *Eruca sativa* we established more than 250 fixed varieties.

The Jordanons of *Brassica juncea* were studied recently by the Howards in India[1]. Comparing the varieties studied by the Howards and our varieties of *Eruca* and *Brassica*, belonging to the section *Sinapeae*, with Linneons of a quite different botanical section—*Hesperideae* (several Linneons of which (*Draba verna*, *Capsella Bursa pastoris*) were studied in detail by Jordan, Rosen, Lotsy, Shull, and others—it is impossible not to notice the striking similarity of their series of variation. We have no doubt the same series will be found in other genera, and other sections of *Cruciferae*. The mere examination of lists of varieties in "Keys to Determination of Species," in different "Floras" occasionally indicated by some authors for single Linneons, proves this regularity in variation.

The nearest family to *Cruciferae*, from a morphological and anatomical point of view, *Papaveraceae*, is characterized, as far as we can judge, from the study of varieties of *Papaver somniferum*, *Chelidonium majus* and *Corydalis solida* (sub-fam. *Fumarioideae*) by a series of variation very similar to that of *Cruciferae*.

[1] *Memoirs of the Department of Agriculture of India.* Botanical Series, 1915.

Compositae.

The numerous family of *Compositae* displays quite distinctly common tendencies in forming varieties within the limits of different genera. If we compare numerous varieties of *Hieracium*, studied carefully by Naegeli, numerous varieties of sunflower (*Helianthus annuus*), studied in detail by Miss E. M. Plachek in Russia at the Saratov Experimental Station[1], and by Dr Cockerell in America, and varieties of *Carthamus tinctorius*, studied by the Howards in India[2], we cannot help noticing the general character of varietal differentiation. Dahlias, cornflowers (*Centaurea cyanus*), *Cichorium Intybus* manifest similar series of variation in the shape and colour of flowers. The examination of catalogues, horticultural literature, and exhibitions of flowers, shows an extremely instructive similarity in direction of variation in chrysanthemums, asters, dahlias, sunflowers. The similarity is not only superficial and exterior, e.g. there are some varieties of sunflower characterized anatomically by the presence of a layer of dark cells in the skin of seeds, which prevents the seeds from attacks of larvae of sunflower moths—*Homeosoma nebulella*. The same varieties exist in *Carthamus tinctorius*, as well as in some other genera of *Compositae*. The colour of plastids in flowers of *Helianthus*, *Carthamus*, and *Hieracium*, varies in different varieties from pale yellowish to bright orange; there are known varieties with anthocyanin in petals (red sunflower and red *Hieracium*) and without anthocyanin.

The same unity of variation, with the same series of varieties, could be observed as a general rule in families of *Solanaceae*, *Cucurbitaceae*, *Chenopodiaceae*, *Caryophyllaceae*, and, we believe, in all families of the plant world. A beautiful example of parallel variation in different genera and families of *Coniferae*, is given by Mr E. Zederbauer[3].

IV. Prediction of Existence of New Forms.

The immediate future will define modes of variation in different families. The series of variation specific for single families will become more exact as the varietal studies of genera become more differentiated.

[1] Miss E. M. Plachek and Prof. A. I. Stebout, "Sunflower." *Report of Saratov Experimental Station*, 1915. Miss E. M. Plachek, "Materials for the Classification of Sunflowers." *Report of the third All-Russian Conference on Plant Breeding*, Saratov, 1920.

[2] *Memoirs of the Department of Agriculture of India.* Botanical Series, 1915.

[3] E. Zederbauer, "Variationsrichtungen der Nadelhölzer." *Sitzber. d. Akad. Wiss. Wein. Math. Nat. Klasse* 116, Abt. 1, 1907.

But it is already evident that the similarity in series of polymorphism of allied Linneons, genera, and even of nearly related families, is so regular that it becomes possible to forecast, on this basis, the existence of forms and of varieties (and even Linneons), not yet discovered. Some such unknown forms might be obtained by artificial hybridization of corresponding varieties, or Linneons.

We have mentioned already some instances where predictions were fulfilled in the finding of forms of rye without "ligula," and of hairy, bearded and beardless varieties of rye. We have met many times with convincing occurrences in forecasting, according to the law of homologous variation, the existence of forms not yet described. To give some more examples—

Linnean species of wheat: *Triticum vulgare, T. compactum, T. Spelta, T. dicoccum, T. monococcum, T. turgidum,* are represented equally by winter and spring varieties[1]. But *T. durum* is usually described in literature as a species represented exclusively by spring varieties, notwithstanding its great polymorphism in many other characters. In literature, occasionally, we find remarks about the existence of one variety of wheat belonging to *T. durum*[2], but even these statements are discounted by other authors.

A priori, one would expect that such winter varieties ought to exist in great numbers, in *T. durum*, if they exist in *T. monococcum, T. Spelta*, and *T. vulgare*. Investigations were begun, and in 1918 we actually received from Mr D. D. Boukinich a large number of specimens of *T. durum*, brought from an isolated, mountainous region of Soumbar, in North Persia, near the Transcaspian Province. And, among these specimens, we found a considerable number of real winter varieties of *durum* wheats, as was shown by sowings of these samples in the spring.

On the other hand, wild Linnean species of *Triticum dicoccoides* Kcke, as well as of wild barley (*Hordeum spontaneum*), are characterized exclusively as winter plants; no spring varieties of these species being known[3]. The study of many specimens of wild barley, collected by the author in 1916 in Persia, Transcaspic Province, and in Bokhara, and sown at the experimental station, resulted in the discovery of a series of

[1] N. I. Vavilov and Miss E. S. Kouznetzov, "On the Genetic Nature of Spring and Winter Varieties of Plants." *Annals of Agricultural College of Saratov University*, Vol. 1. 1921. (Résumé in English.)

[2] F. Koernicke, *Handbuch der Getreide*, 1885, Bd. 2.

[3] K. A. Flaksberger, "*Triticum dicoccoides* Kcke-Wild Emmers." *Bulletin of Applied Botany*, 1913 (Petrograd). R. Regel, "Les Orges Cultivées de Russie." *Bulletin of Applied Botany*, 1910 (Petrograd).

wild spring barleys. Among a number of varieties of *Triticum dicoccoides* obtained by us from Mr A. Aaronsohn, from Syria, we found a typical spring variety of wild wheat. Theoretically, it is very likely that spring varieties will be found eventually in *Secale montanum* Guss., which is characterized in botanical literature as a perennial plant.

Several genera of *Gramineae* contain varieties with naked grains (hull-less), as well as the ordinary hulled varieties, with grains tightly covered by glumes. Systematists know naked barley, oats, wheat. We searched for naked varieties in other genera, and found them among millet (*Panicum milliaceum*), and *Andropogon sorghum*.

It seemed probable that in *Aegilops*, *Secale*, and *Agropyrum*, as in *Triticum*, there would be forms with hollow straw, and with straw full of pith. Indeed, such varieties and Linneons were found in these genera.

Melons and squashes (*Cucurbita*) are characterized by varieties with round, oblong, flat, and segmented fruits. In literature we could find no indication of the existence of segmented varieties of water-melons (*Citrullus*), but after special search for them they were found in south-eastern European Russia, in the Astrakhan Government.

Knowing the scheme of variation of colour and shape of seeds and cotyledons, and in colour and shape of stems and leaves in *Pisum* and *Vicia*, we could establish just such a series of similar varieties in *Ervum Lens* and *Lathyrus sativus*, as well as in other genera of *Papilionaceae*. Most Linnean species of *Papilionaceae* are characterized by hairy as well as by smooth fruits. *Soya hispida* in all botanical literature is always characterized by hairy fruits. *A priori*, we expected to find sometimes a variety of *Soya* with smooth fruits. On visiting the United States we saw such a variety in the collection of the Illinois University.

Similar examples are very numerous. We are accustomed at our experimental station to investigate the varietal composition of a plant according to a scheme based on the law of homologous series in variation, and this makes it possible for us to determine many differences and to note many varieties which otherwise would escape a systematist.

V. PHENOTYPICAL AND GENOTYPICAL VARIATION.

We have spoken, so far, strictly about phenotypical differences. Jordanons, Linneons, genera, botanical families in the sense of Johannsen, are phenotypical units. But we have no doubt that the same rules apply

to genotypical variation as well. The majority of differences between varieties established by old and new systematists are hereditary differences, and although all our morphological and physiological systems of organisms are systems of phenotypes, they imply genotypical differences too.

There is no doubt that under the same external aspect different genotypes may be concealed. The red colour of wheat grains may be dependent on one, two, three or more hereditary factors (genes), as was shown by Nilsson-Ehle. But genes for colour of grain may vary in different varieties. We know, e.g., two types of yellow cotyledons in peas, one dominant, the other recessive (Love); and different types of hairiness. In barley the character of crenatures depends upon five or six different genes in different varieties[1].

But this only obliges us to be careful and to study varietal differences not externally but genetically as well. It complicates the scheme of differences but does not change the statements settled before; it merely requires further and more detailed genetical investigation.

Until now, only single plants and animals, like one or two Linneons of *Antirrhinum*, or peas, maize, *Drosophila*, have been studied in detail, from a genetical point of view; and not even these in all their varietal characters and existing varieties. The study of genetics of many characters and of all types of varieties of a Linneon is not an easy task, and even for single plants looks almost hopeless to carry out in detail. The number of phenotypes by itself is so large in most Linneons (e.g. for wheat, barley, potatoes, etc.), that it looks an incredible task to accomplish. Up to the present, and for a long time yet, the knowledge will be fragmentary. So far, we have had no adequate system of phenotypes, even for most important plants like cereals. There are no complete scientific classifications for varieties of cultivated plants. In their systematical and geographical study, the investigators still work as in the pre-Columbian time. Very few Asiatic or African varieties of cultivated plants have as yet been discovered or described. The attainment of complete genetical monographies for single Linneons will still be more difficult.

At the same time, the relation of these laws to genotypical variation enables us to use them for purely genetic purposes. After the period of differential work in genetics a period of integration of all data for single plants will inevitably come.

[1] N. I. Vavilov, "On Origin of Smooth Awned Barleys." *Bulletin of Applied Botany*, 1919. (Petrograd.) Not yet published, on account of state of affairs in Russia.

The existence, e.g., in wheat, of two kinds of beards, dominant and recessive, obliges us to search for the same division in other genera of *Gramineae*. And in reality two types of bearded varieties were recently found in oats: one dominant, another recessive in crossing with the same variety[1], two different kinds of beardless varieties of oats: one recessive, another dominant.

In our crossings of *Avena nuda* var. *biaristata* Arch. & Gr. with *A. brevis* and *A. strigosa* (two hulled varieties with gray flower-glumes), all plants in F_2 as well as in F_3 of hull-less type, proved to be colourless (yellowish), showing repulsion between genes of hull-less and grey colour of flowering glumes.

On observing this, we began to study the crossings of black, hulled, with yellow hull-less varieties of barley. Here again was clearly seen the partial repulsion between genes in black (coloured) glumes, and genes of naked grain.

Moreover, all varieties of millet with naked grains, which are cultivated in Afghanistan and Bokhara, proved to be white, that is, colourless.

The genetical behaviour of the special kind of awns in barley—"Kapuze" (var. *trifurcatum*)—is very similar to that for the character of awns in wheat called "inflatum."

Many suggestions of this kind might be found by the systematical comparison of varieties of different genera of the same families, which would facilitate the comprehension of phenomena of segregation, and give useful generalizations, necessary for differential work in genetics.

In summarizing the above regularities, we state also that:

1. *Linneons and genera more or less nearly related to each other are characterized by similar series of variation with such a regularity that, knowing a succession of varieties in one genus and Linneon, one can forecast the existence of similar forms and even similar genotypical differences in other genera and Linneons. The similarity is the more complete as the Linneons and genera are more nearly allied.*

2. *Whole botanical families in general are characterized by a definite cycle (series) of variability which goes similarly through all genera of the family.*

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[1] Prof. S. I. Jegalov, "Hybrids of Oats." *Report of the Third All-Russian Conference on Plant Breeding*, pp. 80—86, 1920, Vol. I.

VI. Formulas of the Law of Homologous Variation.

The above conception may be represented by symbols in the following way. As we have seen, different Linneons and different genera are composed of an immense number of varying distinctions; at the same time this variability is similar in nearly allied Linneons and genera. For purposes of abbreviation let us call these different varying characters by letters $a, b, c, d, e, f, g, h, i, j, k$, etc. Their different expressions let us signify by a_1, a_2, a_3, a_4, a_5, etc., b_1, b_2, b_3, b_4, b_5, etc. For instance, the colour of glumes we signify by a, for white we shall use a_1, for yellow a_2, for red a_3, for gray a_4, and so on.

Linneons and genera consequently differ, not by these characters, but by their specific complexes of morphological and physiological nature. These differences we shall call *radicals*. There might be radicals for Linneons, as well as for genera, and whole families too.

Thus we have for two different but nearly allied Linneons of the same genus the following expression of their morphological and physiological peculiarities:

$$L_1(a+b+c+d+e+f+g+h+i+k.....),$$
$$L_2(a+b+c+d+e+f+g+h+i+k.....),$$
$$L_3(a+b+c+d+e+f+g+h+i+k.....).$$

L_1, L_2, L_3 are radicals distinguishing these Linneons one from another, a, b, c, d are different varying characters, as colour and shape of glumes, of leaves, stems, etc. Each of these characters is complicated and accordingly may be divided into two, three, or more morphological and physiological units—a_1, a_2, a_3, a_4, a_5, etc. Each of these morphological units may be, if necessary and possible, represented in terms of genotypical composition.

If we compare, e.g., the three Linneons of wheat, *Triticum vulgare*, *T. compactum*, *T. Spelta*, we can say that the radicals L_1 and L_2 are distinguishable from the morphological side, simply by the density of the structure of ears and stems, for L_2 (*T. compactum*) from L_1 (*T. vulgare*). *Triticum Spelta* (L_3) will be distinguished by the density of its spikelets, grains tightly covered by glumes and extremely loose ears. The varying characters a, b, c, d, etc., are the same in all these Linneons.

The same determination might be given to different genera. Let us take rye and wheat. As we have seen, their resemblance in the mode of variation is extremely close. Although every one will say there is no difficulty in distinguishing rye and wheat, there are, as a matter of fact, very few characters really specific to each of these genera which

cannot be met with, although perhaps in some rare varieties, in the other, and which could be considered radicals. Let us signify the radicals of different genera by G_1, G_2, G_3, G_4, G_5, etc. We can express by formulas the composition of rye and wheat as follows:

$$G_1(a+b+c+d+e+f+g.....)$$
$$G_2(a+b+c+d+e+f+g.....).$$

The contents of the brackets are the same in both genera. The difference between their radicals, from a morphological standpoint, consists, in this case particularly, in the differences of empty glumes and flowering glumes of rye and wheat, narrow seed of rye, and a few other characters not so conspicuous and stable. As the different genera include many ordinary Linneons, some of which might be very distant phylogenetically, the more correct representation of a genus in symbols would be as follows:

$$G_1[(a+b+c+d+e+f+g+h+i+k...)\,L_1, L_2, L_3, L_4, L_5].$$

But practically, at least in a good many cases, Linneon radicals might be taken in some cases into simple brackets, as they are often not divisible from ordinary alternative characters of Jordanons. In the same way the composition of different families might be represented.

Radicals of Linneons and genera could be understood as morphological and physiological complexes specific for single genera and Linneons; they could be of special genetic nature, but in this direction our knowledge is at present too limited.

If we consider from this point of view the modern classifications of plants by systematists into Linneon species and genera, we notice that in many cases they are perfectly correct, through intuition, as the specific characters of radicals were taken as a basis for the division into Linneons and genera. Several systematists like Linné, Jussieu, de Candolle, and Boissier, were very sagacious in this respect. But in many other cases it was quite different. Varietal alternative characters were often mixed with those of radicals; particularly was this the case when descriptions of new genera and Linneons were made on single plants and samples collected in one district.

From this representation of systematical units it is clear that for systematics and classification of genera and Linneons, as well as for phylogenetical purposes, only characters of radicals ought to be taken as a basis of separation.

A great number of examples of such an unsuccessful division can be seen in the family of *Cruciferae*. Such genera as *Sinapis* and

Brassica are not divisible by radicals; their division is based on varietal alternative characters, and as a result it is difficult, and even impossible, to say to which genus some varieties are related. Many Linneons of *Cruciferae* appear to be simply different varieties of the same Linneon. In the near future there must be a revision of such doubtful species, and a consequent reduction. Many new "species" described by botanists in recent systematical literature as new species are only new Jordanons.

Sometimes the characters of radicals are very sharp, as for instance in the family of *Ranunculaceae* (genera *Paeonia*, *Aquilegia*, *Aconitum*, *Nigella* and others), and in many *Gramineae*.

Certainly our conceptions of "Linneons," "genera," are conventional—only schemes. Characters which are alternative for most "higher" plants, are taken often as generic in mycology. But without "systems," without "schemes," it is impossible to grasp the phenomena of multiform life. Science itself is in many respects a schematization of the phenomena of nature. The adoption of the above point of view of the systematical study of variation seems inevitable. Except for some individual observations in this direction, it has not so far been taken seriously into account.

VII. Variation in Distant Families.

We have considered variation within the limits of different genetical groups united into Linneons, genera and families. But, besides, the parallelism of varietal polymorphism displays itself also in different and distant botanical families, even in different orders and classes.

Albinism.

For instance, the phenomena of albinism, or the appearance of plants without chlorophyl, or partly deprived of chlorophyl, occurs in most different families. It was observed in hundreds of genera of *Gramineae*, *Compositae*, *Papilionaceae*, *Chenopodiaceae*, *Polygonaceae*, *Onagraceae*, *Rosaceae*, *Scrophulariaceae*, *Caryophyllaceae*, *Cannabinaceae*, *Coniferae*, etc.

Gigantism, nanism.

In most different and distant families, as *Gramineae*, *Papilionaceae*, *Urticaceae*, *Solanaceae*, *Rosaceae* (*Pisum*, *Phaseolus*, *Triticum*, *Hordeum*, *Zea*, *Rubus*, *Myosotis*, *Oenothera*, *Primula*, *Humulus*, *Nicotiana*, etc.), there were established dwarf and gigantic forms.

Fasciation.

In almost all families there exists a tendency to form fasciations or enlargements of different organs, e.g. from *Compositae* to *Equisetum* (de Vries). We have seen it in peas, flax, beet, barley, sunflower, wheat, maize, buckwheat, squashes, water-melon, and several different *Cruciferae.*

Dwarfism, gigantism, albinism, and fasciation occur in the whole plant world, as well as in the animal world.

Root formation.

On a level with these general types of variation there are also narrower kinds of variability, inherent, nevertheless, to many families genetically rather distant. So, e.g., many genera of some families are apt to form swelling of their roots, as beet, turnips, radish, carrots. This peculiarity is a trait of many families, but what is more remarkable is that in the process of their formation the varietal differences repeat themselves in most distant families. For example, beet, belonging to *Chenopodiaceae,* has varieties with oblong, cylindrical, rhombic, spherical, and flattened and segmented roots. Similar varieties can be found among turnips (*Brassica rapa*) belonging to *Cruciferae,* in carrots belonging to *Umbelliferae,* etc., which means that forms of roots are crystallized in definite directions in genetically different families.

Shape of fruits.

The same may be seen in fruits of different families, e.g. apples, melons, tomatoes, peppers, squashes, water-melons. In all these quite distinct plants, varieties differing in the shape of fruits give the same series of variation—round (spherical), oblong, flattened, cylindrical, pyriform and segmented (cantaloupes in melons, "scrijapel" in apples).

Colour of flowers and fruits.

The colour of flowers is determined chiefly by two groups of pigments—yellow or orange, of plastids and pink (rose-red) or violet anthocyanin pigments dissolved in cell-sap; the last group is often accompanied by a special kind of pigment—flavone, pale yellow, also soluble in cell-sap. Series of varieties in anthocyanin colouring, from white (absence of anthocyanin), through pink (rose), to dark violet and blue, are similar in most different Linneons belonging to quite distinct families. Compare variation in cornflowers, *Iris, Aquilegia, Linum,*

Cichorium, *Hysopus*, *Myosotis*, *Matthiola*, peas, vetches, lilac, *Hyacinthus*, etc.

Red, pink or white cornflowers (*Centaurea cyanus*), pink flax (*Linum usitatissimum*), and pink lilies of the valley are rare, but still they exist, as do many rare minerals, and one has to consider them in constructing a system of genotypes and phenotypes in plants.

Varietal differences in colour of plastids are similar in a great many Linneons: pale yellow, yellow, orange. Compare e.g. varieties of *Hieracium*, *Nasturtium*, *Helianthus*, and many other genera.

When a Linneon is characterized by the presence of both pigments, of anthocyanin as well as of coloured plastids like flowers of dahlias, tulips (*Tulipa Gesneriana*), *Cheiranthus cheiri*, *Viola tricolor*, *Helianthemum vulgare*, we have more complicated but also regular series of polychroism.

The distribution of pigments is not altogether irregular, and it is possible to recognize types in different varieties and plants, and these types repeat themselves in different families.

A similar variation in anthocyanin colouring is observed not only in flowers, but in fruits of many distant genera: *Atropa belladonna*, *Daphne mezereum*, *Fragaria vesca*, *Ribes rubrum*, *Rubus idaeus*, *Solanum nigrum*, *Vitis vinifera*, and many others (Wheldale).

Nearly all seedlings in some varieties are coloured by anthocyanin, in others they are colourless. The same is observable with the stems.

Variation in other characters.

Linneons of nearly all families are divided into varieties with hairy leaves, stems, fruits, and petals, and those with smooth organs. Almost all plants could be divided into dense and loose varieties, according to the density of their inflorescence. Many plants are characterized by varieties with procumbent as well as erect form of seedlings.

Zederbauer (*l.c.*) points out that several types of varieties in shape of stem and branches (vv. *pendula*, *pyramidalis*, *nana*) are common in *Coniferae* and dicotyledonous families *Salicaceae*, *Betulaceae*, *Fagaceae*, *Juglandaceae*, and, we believe, they are common in herbaceous plants too.

Thousands of Linneons are represented by both single and double flowers.

Most families with zygomorphic flowers have peloric varieties (*Labiateae*, *Scrophulariaceae*, *Papilionaceae*).

Winter and spring varieties, genetically distinct, are common in most herbaceous families and genera of plants.

Teratology gives thousands of clear examples of common variation in most plants[1].

In general parallelism is noticeable in organs having the same form and function. To this category are related the phenomena of "unabhängiger Entwicklungsgleicheit" or "Homogenesis" of Eimer by which he accounts for the acquiring of similar characters by different groups of plants and animals.

Series of varieties in distant families.

We have observed in detail large numbers of varieties among different genera of *Gramineae, Cucurbitaceae, Papilionaceae, Cruciferae, Compositae, Linaceae, Urticaceae.* In general, we came to the conclusion that a great many varietal morphological and physiological differences are similar even in most distant families. There is e.g. very little in common in phylogeny between squashes (*Cucurbita Pepo*) or water-melons (*Citrullus vulgaris*) and wheat or barley. Nevertheless, there are many common varying morphological and physiological characters which vary in the same direction in both families. The shape of petals varies in *Cucurbitaceae* very similarly to that of glumes in cereals—there are varieties in both families with pointed petals of perianth (in case of wheat of glumes) as well as with blunt petals. In both families we know varieties with sharply developed nerves in perianth, or *vice versa*, with very weakly developed nerves. Types of hairiness in different varieties, although at first sight very unlike in both families, are strikingly alike in *Cucurbitaceae* and *Gramineae* on close examination of varieties. There are varieties of squashes (*C. Pepo*) with naked seeds, similar to the naked varieties of cereals. In the shape and form of seedlings, there are common varietal differences in both families.

Homologous and analogous variation.

The origin of these organs might not be quite the same in different families—they might, from a formal morphological point of view, be only analogous and not homologous. The same genotypical difference in the sense of modern genetics, might vary in different families. But, nevertheless, the similarity in variation allows us to construct simple general schemes of morphological and physiological variation.

The difference between homologous and analogous organs, as well as between homologous and analogous variation, is in many cases not easily discernible. Some authors, competent enough to know the

[1] Penzig, *Teratologie*, 1, 2, Bd. Second edition, 1920.

difference between homology and analogy, are prepared to deny the essential difference of these two kinds of variation (Lotsy, *Evolution by Means of Hybridization*). In any case, the great majority of varietal characters, not only within the limits of single genera and families but even in distant families, are homologous from a morphological point of view (colour, shape, etc.).

If we follow the above-mentioned symbolic designation, we must own that although the radicals for families might be extremely different, as in the case of *Cucurbitaceae* and *Gramineae*, the contents of brackets will be similar for both families in a considerable degree.

Origin of new forms and the law of homologous variation.

Summarizing all above said, it is clear that after detailed study of any particular Linneon it would be possible, according to the law of homologous variation, to forecast the division into varieties (Jordanons) of other genera and Linneons. To some extent the same divisions into Linneons, and even genera too, are subject to the same rules.

Moreover, this concerns not only the existing diversity of forms, but also new forms appearing from hybridizing distant forms or through mutation.

The origin of new forms was studied in *Oenothera Lamarckiana*, where a great number of varieties originated during observation. If one compares the series of varieties obtained from *Oenothera* by de Vries with that obtained from *Rubus* by Lidforss[1], in hybrids of different Linneons, one cannot help noticing the remarkable parallelism in the varietal composition of *Oenothera* mutants and *Rubus* hybrids.

The same similarity in the series of new forms (we mean forms not representing simple combinations), obtained as a result of distant crossings, could be observed in hybrids of different Linneons of wheat, and of hybrids of wheat and rye. In both crossings hybrids showed new forms with extremely narrow leaves, or with extremely broad leaves, plants with very hairy stems and leaves, the appearance of very late, as well as of very early forms, varieties with branching ears, the development of awns on empty glumes, dwarf plants, as well as giant forms, albino plants, etc., partly as a result of "cryptomery" in the sense of Tschermak, partly as a result of abnormal development very common in the offspring of distant hybrids. *Helianthus* and *Oenothera* are very little related—

[1] *Zeitschrift für induktive Abstammungs und Vererbungslehre*, 1914.

writes T. D. A. Cockerell—yet in breeding and studying sunflowers one is constantly reminded of phenomena previously recorded in connection with evening primroses. The parallelism in variation is such that one is led to ask what, precisely, do we mean by a "new variation[1]."

Mutations in closely related Linnean species and genera all tend in the same direction. T. H. Morgan, C. B. Bridges, A. H. Sturtevant, A. Weinstein and H. J. Muller[2], found it for different species of *Drosophila*, E. B. Babcock for *Juglans*[3]. De Vries, R. Gates, Stomps and other investigators established the same for different species of *Oenothera*[4].

E. Baur, in the fourth edition of his *Einführung in die experimentelle Vererbungslehre*, 1919 (pp. 193—194), in the Chapter on Mutations, notices the remarkable parallelism of mutations in different related Linnean species of plants and animals, homologous series of mutations, "ganz merkwürdige homologe Reihen."

In general, in comparing mutations in different plants and animals, one notices general lines of variation even in distant groups of organisms.

VIII. VARIATION IN FUNGI AND IN ANIMALS.

Doubtless the same regularity in variation manifests itself not only in "higher" but also in "lower" plants, as well as in animals.

Ascomycetes and Basidiomycetes give a complete parallel series of Linneons and genera. The same differentiation into the smallest units, "biologic species," is noticeable in both classes. P. A. Saccardo in his article "I Prevedibili Funghi Futuri secondo la Legge d'Analogia[5]" has noticed the existence of series of forms in fungi, and has given a system for their division according to a series of variation in single families. In general his system has proved to be too artificial; he took for the basis of classification the characters of varieties of "higher plants"; his division of great groups as genera is based, not on separation

[1] "Suppression and Loss of Characters in Sunflowers." *Science*, Vol. XL. No. 1025, 1914, p. 283.

[2] T. H. Morgan, *Physical Basis of Heredity*, 1919. A. H. Sturtevant, "A Parallel Mutation in *Drosophila funebris*." *Science*, 1918, Vol. XLVIII. A. Weinstein, "Homologous genes and linear linkage in *Drosophila virilis*." *Proc. of the National Acad. of Sciences*, Vol. VI. No. 11, 1920.

[3] "Studies in *Juglans*, III. A parallel mutation in *Juglans hindsii*." *U. C. Pub. Agr. Sci.* 2. 3, 1916.

[4] R. R. Gates, *Mutations and Evolution*. London, 1921.

[5] *Degli Atti del R. Instituto Veneti de Scienze, Lettere ed Arti*. Tomo, VIII. Ser. VII. Or in *Tabulae Analogical Omnium Gener. Fung. Syll.* Vol. XI. 1896—97.

of radicals, but pre-eminently on varietal characters. But still some of his predictions were afterwards justified. And, undoubtedly, Saccardo's beginnings in this direction are of great importance in systematics.

Comparative animal and plant anatomy discovered a common plan of construction for distant classes and families. The facts of hereditary variation among Linneons, genera and families of animals, known nowadays in great numbers, are a proof of the general plan in variation. Exterior characters of many animals show an evident subordination to the law of homologous variation. Colour of hair, the same structure of hairs, and horns, in their variation, show a similarity not only in near Linneons and genera, but also in different families; and, as genetics has shown, from a genotypic as well as from an external point of view[1]. The series of known mutations in rabbits, rats, and mice are extremely alike.

The systematical division of many genera into Linneons in zoology, shows in some cases a clear series of homologous variation. Palaeontology gives many examples of this kind. Gastropoda, Goniatites, and in general, fossil-molluscs, show beautiful examples of the existence of these series of variation. Many examples could be taken from Rotatoria, etc.

Looking over botanical and zoological, as well as palaeontological literature on variation and systematics, one could find many data for parallel series of variation in different genera and families. In *Pangenesis* and *Mutationstheorie*, we find many facts signifying the existence of parallel variation. "Suchen wir in irgend einer Flora," writes de Vries in *Mutationstheorie*, p. 454, "diese abgeleiteten Varietäten zusammen, so fällt sofort auf, dasz dieselbe Abweichung in der verschiedensten Familien, Gattungen, und Arten widerkehrt. Überall bilden die Varietäten Reihen von parallelen Formen." *Mutationstheorie*, I. p. 454. Variation does not take place in all directions, by chance and without order, but in distinct systems and classes analogous to those of crystallography and chemistry. The same great divisions into orders and classes manifest regularities and repetitions of systems.

IX. Phenomena of Mimicry and Convergence.

Phenomena of mimicry.

The so-called mimicry—the imitation by one genus of another in shape and colouring, which may be of some profit in living beings, undoubtedly is in most cases only a repetition of similar cycles of variation

[1] A. Lang, *Ergebnisse der Mendelforschungen.* Jena, 1914. Castle, *Genetics and Eugenics*, 1920.

in different families and genera. Eimer was quite right when he explained the phenomenon of mimicry in butterflies by independent development of the same types of variation in different genera and families. Mimicry may be regarded as a general phenomenon of repetition of form characteristic for the whole organized world, and by no means as an exception, illustrating the rôle of selection in creation of forms, as was supposed by Darwinists[1].

At our experimental station we observed a striking case of such mimicry in plants, namely in *Papilionaceae*, studied in detail by Miss E. I. Baroulina[2]. Vetch (*Vicia sativa* L.) is often found as a weed in sowings of lentils. Several varieties of vetches are so similar to ordinary lentils in the shape, colour and size of their seeds, that they cannot be separated by any sorting machine. Most of these varieties flower and ripen simultaneously with lentils, and are perfect mimics of their "models"—lentils. We began to study both plants in detail. Many samples of lentils (*Ervum Lens*) and vetches (*Vicia sativa*) were gathered from different parts of Russia and from Persia, Bokhara and Afghanistan. As a result it was found that not only vetches exist which in shape, colour, and size of seeds are inseparable from ordinary lentils, but also that there exist varieties of lentils which are quite similar in their seeds to ordinary round black seeded vetches. The whole series of varieties (a number of which are represented on Plate X) showed clearly that the similarity between these two different genera is so great that it would be difficult, even for an expert eye, to divide several varieties of vetches from lentils by their seeds. This example gives one of the best illustrations of the idea of homologous series in variation which we have in the plant world. In the colour of their flowers and in many other characters lentils show similar series of variation to vetches.

The rôle of natural selection in this case is quite clear. Man unconsciously, year after year, by his sorting machines separated varieties of vetches similar to lentils in size and form of seeds, and ripening simultaneously with lentils. The same varieties certainly existed long before selection itself, and the appearance of their series, irrespective of any selection, was in accordance with the laws of variation.

The phenomena of "mimicry," from our point of view, are general for all classes and families, and those usually impressive forms of mimicry,

[1] See R. C. Punnett, *Mimicry in Butterflies*. Cambridge, 1915.

[2] E. I. Baroulina, "On Vetches (*Vicia sativa*) weeds in lentils." (Mimicry in Plants.) *Report of Third All-Russian Conference on Plant Breeding*, held in June, 1920, Vol. 1.

which are found, for example, in butterflies, give an excellent illustration of the law of homologous variation[1].

The phenomena of convergence, or similarity in characters, which is known in many existing and fossil animals and plants found in similar or sometimes in different surroundings, represents also the phenomena of parallel variation, if not homologous, at least analogous. These phenomena are also of general character and no exception. There are already many data on convergence in most different groups of plants and animals, and their number increases every year. The same division of placental mammals into various orders of carnivorous and insectivorous is parallel to the orders of implacental beasts. Countess Linden established many cases of convergence in Gastropoda[2], without any relation to their affinity and biological surroundings. Dr F. Alverdes recently published a work on parallel development of birds and mammals[3]. It seems as though nature cannot differ indefinitely, but creates analogous or similar forms in different families and orders.

St G. Mivart, in his book *On the Genesis of Species* (New York, 1871), devoted much attention to the coexistence of closely similar structures of diverse origin. He regarded these phenomena as contradictory to Darwin's theory of "Natural Selection." It seems that Mivart was the first who used the expression "The Law of Homologous Variation" (see p. 196).

External conditions to which naturalists of the last century ascribed phenomena of convergence, acted as a factor in selection and elimination without creating forms, but leaving and sorting those which were best suited to their surroundings.

X. General Conclusions.

Parallelism in varietal polymorphism, and the existence of regularity in differentiation of greater groups as Linnæons, genera, and families, is a great help in the study of varieties in self- and cross-fertilized plants and animals. Instead of searching for unknown forms, the investigator can definitely look for, and foresee, forms lacking in a system, by noticing

[1] R. Punnett, *Mimicry in Butterflies*. Cambridge, 1915. H. Eltringham. "On Specific and Mimetic Relationships in the genus Heliconius." *Trans. of the Entomological Society of London*, 1916.

[2] Linden, Gräfen U. v. "Unabhängiger Entwicklungsgleicheit bei Schneckengehäusen." *Biologisches Centralblatt*, Bd. xviii. 1898.

[3] Dr F. Alverdes, "Die gleichgerichtete stammesgeschichte Entwicklung der Vögel und Säugetiere. *Biologisch. Centr.* 39 Bd. September, 1919.

the similarities with the nearest known Linneons and genera. In this respect a biologist places himself in the position of a chemist, who classifies substances according to their place in a system, and creates them through synthesis.

The investigation of polymorphism and the description of new forms become full of scientific meaning and interest. New forms have to fill vacancies in a system. The collections of immense numbers of butterflies and beetles in our museums and herbariums will play a more worthy rôle in the immediate future than ever before. For a systematist is not a man who knows all the curiosities of nature, but one who grasps the order and sense of it all.

The existing systems of Linneons and varieties ought to be fundamentally changed, and constructed according to a general plan. Instead of occasional characters, which usually determine species and varieties, it would be more rational to follow a general system. The greatest problem of systematists is to build up a general well sustained monotypical system, where similarity and homological series of variation would be considered as the fundamental basis, instead of an indefinite tangle of names impossible to remember. This may seem rather revolutionary for systematists, and it must be done very carefully, in consideration of existing orders. It would be easier to arrange in general systems of minutest systematical units, varieties and races which are as yet almost untouched by systematists. We have tried this for cultivated plants, and have found it expedient. Instead of remembering endless forms, usually named after occasional places of origin or in honour of persons, we have the possibility of studying a system and introducing into it individual additions, where it may be necessary to do so, for single Linneons and genera. We realize well the size and difficulty of the whole problem. Without a differential work, and without studying in detail, the integral work will be groundless. To integrate it is necessary to differentiate. We know that perhaps a century will pass before botanists and zoologists will create, through collective work, an organized world system; but this way is historically necessary and inevitable.

Analogy with chemistry.

The above-mentioned analogy of the present day position of the biologist and chemist is deeper than it might seem at first. We have spoken conventionally about characters, colours, hairiness, beardedness, etc. Chemistry says little about the exterior of its substances; it

considers the chemical nature of its compounds and their formulas. Numerous chemical substances are reduced to a harmonious system of combinations of a few elements. The biologist is still far behind. During the last decades, however, genetics has advanced greatly and is rapidly overtaking chemistry—at least the old chemistry of complicated organic compounds. Genetics is creating a laconic language of signs for hereditary factors, determining external characters. The biologist has learned to analyze organisms, and to get a hold on methods for the synthesis of new forms.

The regularities in polymorphism of plants, established by a minute examination of variation in different genera and families which we have examined, can be compared to homologous series of organic chemistry, e.g. carbohydrogen (CH_4, C_2H_4, C_3H_6, ...). Its series of compounds differing from each other, are still characterized by many common properties in reactions, by definite cycles of compounds, by definite reactions of exchange and adhesion. Every single hydrocarbon gives a series of compounds similar to that of other hydrocarbon.

In general, genera (G_1, G_2, G_3, ...) and Linneons (L_1, L_2, L_3, ...) of plants and animals display, in just the same manner, their homologous series of varieties, corresponding to different homologous series of hydrocarbons.

$$\begin{array}{ll} G_1L_1(a+b+c\ldots) & G_2L_1(a+b+c\ldots) \\ G_1L_2(a+b+c\ldots) & G_2L_2(a+b+c\ldots) \\ G_1L_3(a+b+c\ldots) & G_2L_2(a+b+c\ldots) \end{array}$$

$$\begin{array}{lll} L_1a_1, & L_1a_2, & L_1a_3, \ \ldots \\ L_2a_1, & L_2a_2, & L_2a_3, \ \ldots \\ L_3a_1, & L_3a_2, & L_3a_3, \ \ldots \end{array}$$

Where a, a_1, a_2, a_3, ... are different characters which distinguish different varieties. The series of forms are strikingly analogous to homologous series of organic chemistry.

Besides their chemical structure, different forms of organized nature are characterized by physical structure, and perhaps it would be better to trace also the analogy of homological series of plants and animals, with systems and classes of crystallography with definite chemical structures (Crystallo-Chemistry of Fedoroff).

We leave the question, in detail, of these analogies, which is already discussed in literature (Johannsen, Lehmann, Tischler).

Further investigations will establish more precisely the law of homologous variation in plants and animals, and it may be possible to bring

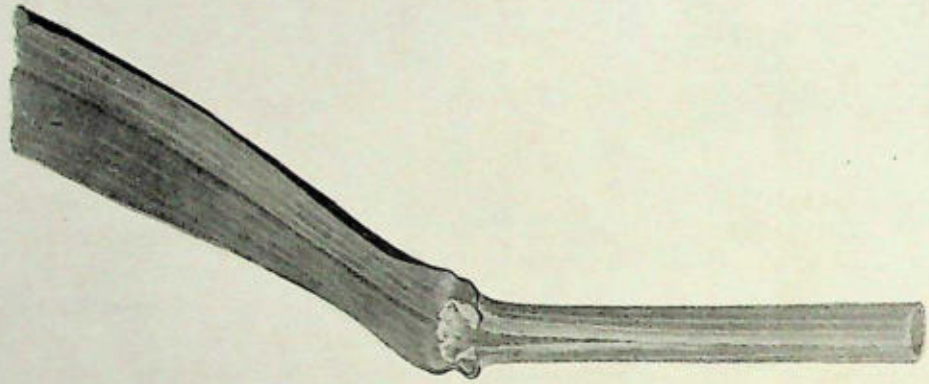


Fig. 4.

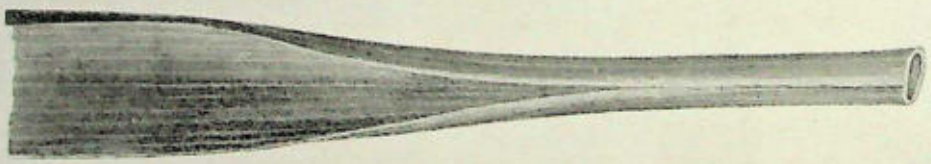


Fig. 3.

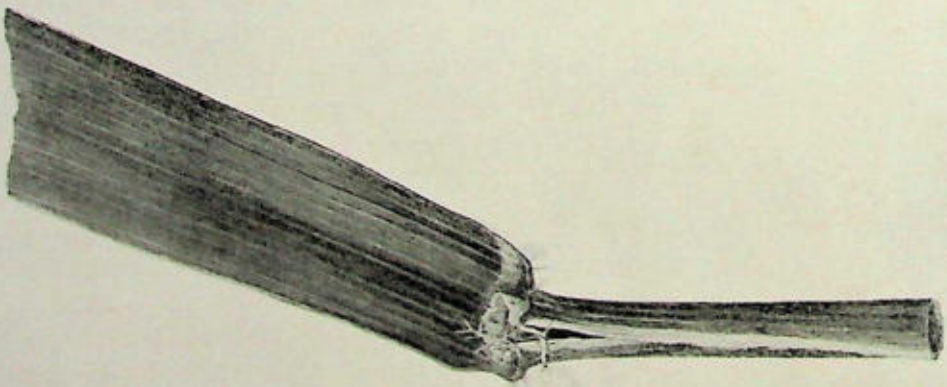
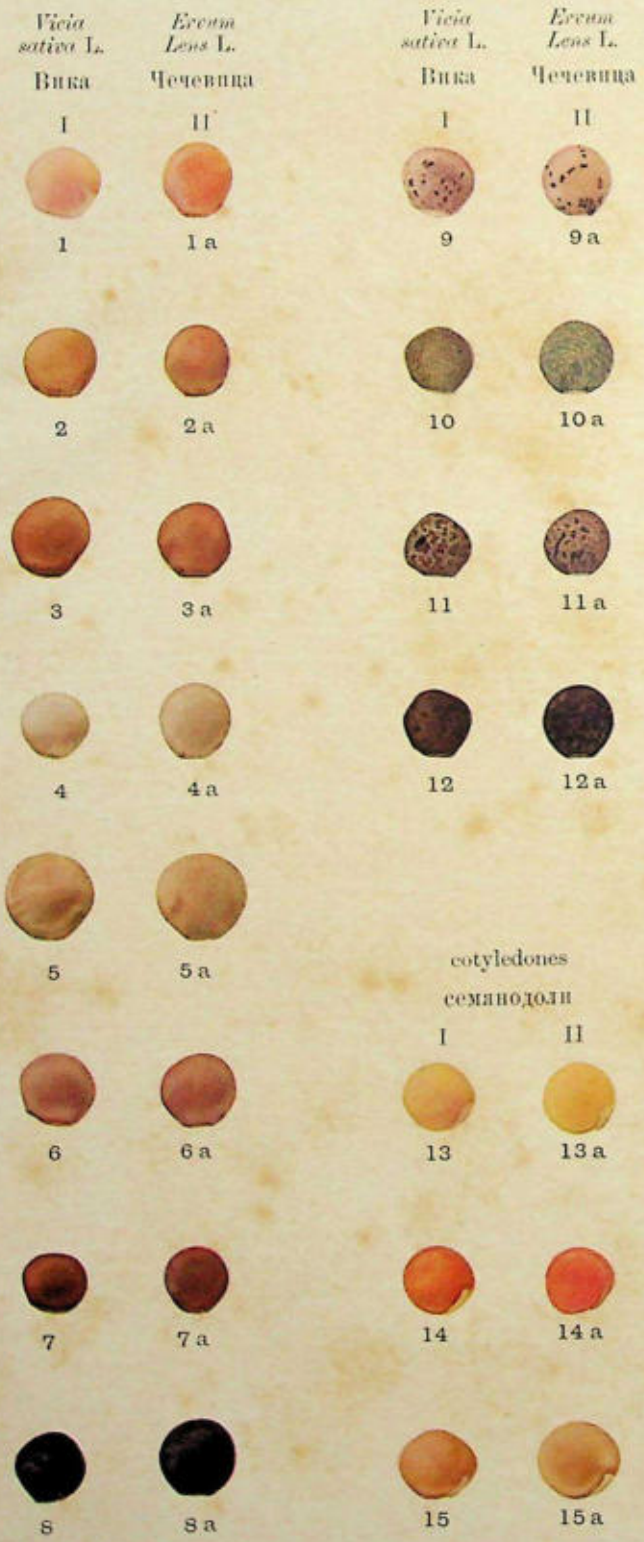


Fig. 2.

Fig. 1.


Vicia sativa L.
Вика
Ervum Lens L.
Чечевица
I
II
1
1a
2
2a
3
3a
4
4a
5
5a
6
6a
7
7a
8
8a
Vicia sativa L.
Вика
Ervum Lens L.
Чечевица
I
II
9
9a
10
10a
11
11a
12
12a
cotyledones
семянодоли
I
II
13
13a
14
14a
15
15a

the same series into mathematical expression. The variation in form might be reduced to some geometrical scheme.

The problem of the origin of species cannot be separated from the problem of variation. A great many forms are undoubtedly only different combinations of the same genes, some primary types. The study of variation will give us the possibility of establishing these primary types, the fundamental series of variation of organisms.

The idea of the homologous series in variation in its essence is only a development of the general idea of Goethe's "Metamorphosis of plants," the idea of the unity in variety of C. Dresser[1].

In conclusion, we take the liberty of expressing our strong conviction that the most rational and expedient method of studying the diversity of plants and animals open to breeders of both, even for practical purposes, is through the establishment of parallelism and homologous series of variations.

[1] Christopher Dresser, *Unity in Variety*. London, 1860. Recently there appeared several works devoted to the general uniformity of phenomena of life, history, psychology. See f. i. K. Marbe, *Die Gleichförmigkeit in der Welt*. Bd. I and II. München 1916—1919. P. Kammerer, *Das Gesetz der Serie*, 1919.

DESCRIPTION OF PLATES.

PLATE IX.

Fig. 1. *Triticum vulgare eligulatum*—found in North Afghanistan and Shugnan (Pamir).

Fig. 2. *Triticum vulgare ligulatum*—ordinary wheat.

Fig. 3. *Secale cereale eligulatum*—found in North Afghanistan and Shugnan (Pamir).

Fig. 4. *Secale cereale ligulatum*—ordinary rye.

PLATE X.

Parallel variation in colour and in shape of the seeds and cotyledons of vetches (*Vicia sativa* L.) and lentils (*Ervum Lens* L.).

Drawn by Miss M. P. Lobanova.

A NOTE ON THE INHERITANCE OF THE "STEEL" COAT-COLOUR IN RABBITS.

By H. ONSLOW,
Trinity College, Cambridge.

THE work of Punnett, Hurst, Castle and others has treated of many colour varieties in the domestic rabbit, but the inheritance of the peculiar ticking of the hairs which produces the colour known as "steel" has apparently not yet been fully investigated. There appear to be more kinds of "steel" than one almost the same in appearance, though no doubt genetically quite different. Such, for example, are Punnett's "agouti-black," modified to steel by being heterozygous for *B*, the factor which converts chocolate into black. Again, there are the "*eisengrau*" of Pap, mentioned later, and no doubt more than one type of steel among Flemish and other breeds. The relationship of the various forms of "steel" to each other will no doubt be a problem of some difficulty, but it is one that calls for immediate solution.

The following communication deals with certain experiments which have been in progress for a considerable time, but owing to the many difficulties caused by the war, the results have not hitherto been published. The original animals were of the variety known as "steel Dutch," i.e. the coloured portions of the Dutch pattern were steel and the remaining portions white. The chocolate, black and yellow barring on a steel hair is not unlike that on the hairs of the common wild rabbit, except that steel hairs contain more black pigment, especially in the distal portions. These steel Dutch when crossed with some black English rabbits, produced, in addition to agouti, black self and English, a certain number of rabbits, in which the entire coat, including the belly and scut, had the same steel colour as the pigmented portions of the original Dutch parents. The rabbits were in fact steel selfs, and they supplied the material used in the following experiments.

A pair of these steels was first tested by crossing them with blues, to see whether they carried the dilution factor, which it was feared would complicate the results. When a number of steels had been obtained, which did not carry the dilution factor, they were mated

together, to see if it were possible to produce a rabbit homozygous for steel. On the supposition that steel is produced by the interaction of two factors *A* and *B*, steel, agouti and black would be produced in the ratio of 9 : 3 : 4. The steels would be of four types; 4 would produce all three forms, 2 would give steel and agouti, 2 would give steel and black, and 1 would give all steel. It was, however, found quite impossible to produce a homozygous steel, and although 28 rabbits of both sexes were tested, they all gave black and agouti as well as steel. In consequence of this it seemed probable that steel was itself a heterozygous form. A number of litters were accordingly obtained from matings of steel × steel, the results of which were as follows:

TABLE I.

Steel × *Steel.*

Mating ♀ × ♂	Steel	Agouti	Black
11 × 24 *a*	3	3	1
11 × 24 *a*	1	3	1
11 × 70	3	—	4
25 × 24 *a*	4	1	1
25 × 26	1	1	1
25 × 70	2	1	6
29 *a* × 24 *a*	3	1	3
32 *b* × 24 *a*	4	1	1
32 *b* × 24 *a*	3	3	—
32 *b* × 49 *b*	2	1	1
32 *b* × 49 *b*	3	1	1
38 *a* × 85 *a*	1	3	—
44 *b* × 24 *a*	3	2	—
44 *b* × 49 *b*	2	4	1
50 *a* × 28 *b*	2	2	1
50 *a* × 49 *b*	1	1	1
52 *c* × 28 *b*	4	1	3
54 *a* × 24 *a*	2	—	2
54 *a* × 49 *b*	2	—	—
54 *a* × 49 *b*	2	1	—
55 *b* × 24 *a*	3	—	1
56 *a* × 24 *a*	2	—	3
56 *a* × 24 *a*	4	2	1
56 *a* × 49 *b*	6	—	—
56 *a* × 49 *b*	—	—	4
60 *a* × 28 *b*	2	4	—
60 *a* × 28 *b*	1	1	2
70 *a* × 85 *a*	3	—	1
70 *a* × 85 *a*	1	—	1
79 × 28 *b*	3	—	—
80 × 28 *b*	1	—	—
80 × 24 *a*	4	2	—
84 × 57 *b*	4	1	—
87 *b* × 86 *a*	2	2	1
110 × 49 *b*	2	1	1
Totals	86 (50 %)	43 (25 %)	43 (25 %)
Expectation on 9 : 3 : 4 ratio	*96·75*	*32·25*	*43·0*
Expectation on 1 : 2 : 1 ratio	*86*	*43*	*43*

The figures fit perfectly a 1 : 2 : 1 ratio of agouti, steel and black, and diverge considerably from the 9 : 3 : 4 ratio. The sex of every rabbit was not recorded, but as the ratio of males to females in the large majority which were determined showed nothing abnormal, the sexes were omitted from the tables. The steels were for the most part self-coloured, but, as is usual, a few animals showed traces of the white Dutch markings.

The following hypothesis, which, as Professor Punnett pointed out, makes the case parallel with that of his "agouti-blacks[1]," appears to afford an adequate explanation of the phenomena. An agouti-black is a black rabbit with a slight development of agouti hairs at the nape of the neck. The main feature in the case of the agouti-blacks was the existence of a factor *D*, which deepened the melanic pigment. It behaved differently, according to whether it was present in the homozygous or the heterozygous condition. If heterozygous, it would turn an agouti into an agouti-black; if homozygous, it converted an agouti into a full black, which in appearance was indistinguishable from a normal black.

In the case of the steel rabbits, the factor comparable to *D* may be called *X*. Like *D* it appears to have a darkening effect, but to a less degree. It is a darkening factor which (1) in the heterozygous condition turns agouti into steel; and (2) in the homozygous condition converts agouti into black. Thus, if *A* is the factor for agouti and *a* the factor for black, then:

$AAxx$ = agouti,
$AAXx$ = steel,
$AAXX$ = black extracted from steels,
$aaxx$ = normal black.

In other words "one dose" of *X* turns agouti into steel, and "two doses" of *X* turn agouti into black. This obviously means that there are two forms of black, which are the same in appearance but genetically quite different. These two forms may be represented as already shown. Moreover, an animal cannot be steel or agouti unless it is at least heterozygous for *A*.

From these considerations it follows that:

(1) Steel × steel will, as has already been shown, give the 1 : 2 : 1 ratio of a heterozygous form.

(2) Black (extracted from steels) having the constitution $AAXX$, mated to normal agouti ($AAxx$), will give nothing but steel ($AAXx$).

[1] Punnett, R. C., *Journal of Genetics*, Vol. II. p. 227, 1912.

(3) Steel ($AAXx$) mated to agouti ($AAxx$) will give equal numbers of steel and agouti.

(4) Finally, black (extracted from steels) having the constitution $AAXX$ mated to steel ($AAXx$) should give equal numbers of steel and black.

These matings were accordingly made with the following results:

TABLE II. *Black* (extracted from steel) × *Agouti* (homozygous).

Mating ♀ × ♂	Steel	Agouti	Black
66 *c* × 51 *b*	5	—	—
77 × ,,	3	—	—
77 × ,,	6	—	—
77 × ,,	2	—	—
77 × ,,	7	—	—
78 × ,,	5	—	—
78 × ,,	6	—	—
78 × ,,	4	—	—
83 *a* × ,,	6	—	—
84 *a* × ,,	5	—	—
91 × ,,	5	—	—
91 × ,,	6	—	—
92 × ,,	6	—	—
92 × ,,	5	—	—
101 × ,,	6	—	—
65 *c* × 45 *b*	6	—	—
57 *c* × 109	5	—	—
Total	88	—	—

Most of these matings were made with the ♂ 51*b*, kindly given by Professor Punnett, a homozygous agouti whose ancestry was known for a number of generations. The male parents in the last two matings of the table were agoutis extracted from steels. These agoutis were presumably of the supposed composition $AAxx$, since they gave nothing but steel. It appears, however, as will be shown later, that more than one type of agouti can exist. The same male, 51*b*, when mated to steels, produced, as was expected, equal numbers of steel and agouti.

TABLE III. *Steel* × *Agouti* (homozygous).

Mating ♀ × ♂	Steel	Agouti	Black
11 × 51 *a*	3	3	—
11 × ,,	4	2	—
25 × ,,	3	5	—
54 *a* × ,,	3	3	—
56 *a* × ,,	1	2	—
55 *b* × 51 *b*	1	—	—
55 *b* × ,,	2	1	—
44 *b* × ,,	4	3	—
79 × ,,	3	1	—
38 *a* × ,,	2	3	—
60 *a* × 45 *b*	4	—	—
68 *b* × 85 *a*	3	2	—
Totals	33 (57 %)	25 (43 %)	—
Expectation	*29*	*29*	—

The agouti ♂ 51 *a* used for some of these matings also came from Professor Punnett, and was believed to be of the same breeding as the agouti 51 *b*. With both males the numbers of steel and agouti were approximately equal. In the last two matings the agouti parents were extracted from steels, 68 *b* being a ♀ and 45 *b* a ♂.

TABLE IV.

Black (extracted from steels) × *Steel*.

Mating ♀ × ♂	Steel	Agouti	Black
66 *c* × 85 *a*	—	—	1
66 *c* × 86 *a*	3	—	1
73 *b* × 70 *a*	1	—	3
73 *b* × 38 *a*	1	—	3
77 × 86 *a*	1	—	2
84 *a* × ,,	2	—	2
Totals	8 (40 %)	—	12 (60 %)
Expectation	*10*	—	*10*

The figures in Table IV diverge rather widely from the expected ratio, but the number of animals bred was small. Otherwise it will be seen that all the four suppositions on pp. 93–94 have been fulfilled with sufficient accuracy.

A number of matings were also made in order to test the question whether steels which were made by mating blacks (extracted from steels) to agoutis (Table II), behaved in the same way as the original steels. The following table shows that this was the case.

TABLE V.

Steels (from black × agouti) mated *inter se*.

Mating ♀ × ♂	Steel	Agouti	Black
50 *b* × 97	—	2	1
50 *b* × ,,	1	3	—
50 *b* × ,,	1	1	1
103 *a* × 67 *c*	2	1	—
106 *a* × ,,	4	—	—
106 *a* × ,,	5	—	—
107 *a* × ,,	4	1	—
115 × 118	2	1	3
115 × ,,	2	—	1
115 × ,,	2	3	2
116 × ,,	2	1	—
116 × ,,	2	1	2
116 × ,,	3	2	1
116 × ,,	3	1	—
117 × ,,	1	3	2
117 × ,,	3	—	3
Totals	37 (51 %)	20 (27 %)	16 (22 %)
Expectation	*36·5*	*18·25*	*18·25*

These proportions are nearly the same as those in Table I, and need no further comment.

If normal blacks are expressed by the formula *aaxx*, and blacks extracted from steels by the formula *AAXX*, as has been suggested, an interesting result should follow the mating of these two forms of black with each other. All the offspring of such matings (*aaxx* × *AAXX*) should have the composition *AaXx*, and must therefore all be steel. As the result of an experiment, in which a strain of homozygous chocolates was used in place of the normal blacks, the following families were bred:

TABLE VI.

Black (extracted from steels) × *Chocolate*.

Mating ♀ × ♂	Steel	Agouti	Black
57 *c* × 31 *a*	2	—	—
57 *c* × 31 *a*	3	—	—
57 *c* × 31 *a*	4	—	—
56 *c* × 73 *b*	3	—	—
66 *c* × 31 *b*	4	—	—
84 *a* × 31 *b*	3	—	—
Total	19	—	—

In all matings but one of the above table, a chocolate was used as the male parent. In the mating 56 *c* × 73 *b*, the female parent was a chocolate. The fact that two blacks to all outward appearance exactly the same (but genetically different) should produce nothing but steel offspring, seems to be explicable on some such hypothesis as that already outlined.

Since the families in Table VI were bred, some of the same blacks have been mated to blues, i.e. blacks carrying the dilution factor. In these three litters the black ♀♀ 66 *c* and 84 *a* and the black ♂ 73 *b* gave 7 steel and 4 black young. An explanation of this unexpected result can only be looked for in the constitution of the blues. Thus it is possible that the blues used were heterozygous for Punnett's *D* factor, in which case we should expect equal numbers of animals with the constitution *AaXxdd* (= steel) and *AaXxDd*. An animal of the constitution *AaxxDd* is an agouti-black, i.e. not far removed from a full black in appearance, and on the addition of a further dose of *D* such an animal becomes a full black. It seems not unlikely that the addition of a dose of *X* to an animal heterozygous for *D* may have the effect of producing the full black coat.

As was said above, mating together the two forms of black produces steels as in Table VI, having the composition *AaXx*. The result of

pairing two of the latter individuals has not yet been ascertained, although the matings are now being effected. It is clear, however, that as the four gametes are AX, Ax, aX, ax, when these meet, sixteen rabbits will be produced consisting of black, steel and agouti, in the ratio 7 : 6 : 3. This assumes of course, as previously stated, that to be steel an animal carrying X must also be at least heterozygous for A—thus $aaXx$ will be black. In an exactly analogous manner Professor Punnett's[1] agouti-blacks of the constitution $DdEEAa$ produced black, agouti-black and agouti in the same ratio of 7 : 6 : 3.

It was mentioned on p. 94 that more than one type of agouti might exist, because a certain agouti male did not behave in the same manner as the others, when mated to blacks of the constitution $AAXX$. The explanation of this anomalous behaviour has not been discovered, but the work is being continued in the hope that some light may be thrown on the matter.

From Table II it will be seen that blacks of the form $AAXX$ mated to homozygous agoutis produced, as was expected, nothing but steel. This male, however, 51*a*, bred by Professor Punnett in the same way as the ♂ 51*b*, gave in addition to steels a number of agoutis, as follows:

TABLE VII.

Black (extracted from steel) × *Agouti* ♂ 51 *a*.

♀	Steel	Agouti	Black
46 *a*	5	2	—
46 *a*	—	6	—
47 *a*	3	4	—
48 *a*	2	4	—
48 *a*	2	4	—
Totals	12	20	—

The figures are very small, but it appears as if an equal number of steel and agouti might have been expected. At the same time it must be carefully noticed that this ♂ 51*a*, when mated to steels, behaved in exactly the same way as the ♂ 51*b*, which produced equal numbers of steel and agouti (see Table III). Unfortunately, until another agouti can be found which behaves in the same way as ♂ 51*a*, the question must remain unsolved. So far, the few animals tested have behaved quite normally.

As this is going to press, a paper by Pap[2] has been received which reviews most of the work on the coat-colour of rabbits, and contributes

[1] *Loc. cit.*

[2] Pap, Endre. *Zs. f. induktiv. Abstammungs- und Vererbungslehre*, xxvi. p. 185, 1921.

certain new facts. The author says that some of his unpublished experiments confirmed in every particular the work of Punnett on the extension and deepening factors *D* and *E*, and he gives data which show that in agreement with Punnett[1], these two factors are completely linked. Punnett observed that the factor *B* which converts the chocolate series into the black, had an interesting effect upon his agouti-blacks. If instead of an ordinary agouti-black (*DdEEBB*) he produced a similar animal heterozygous for *B*, the coat would have far more of the wild character. In fact, so far as the back is concerned, the excellent figure in Punnett's Plate[2] is not at all unlike a steel. Such rabbits were bred by Pap, and to them he gives the name of "*eisengrau*", which he says is the term used by breeders of Flemish Giants to denote this particular colour. The bellies of Pap's rabbits often had much of the wild character, but could always be distinguished from those of true wild rabbits. This I understand is also the case with Flemish steels.

The main point of interest is that Pap says rabbits carrying *D* and *E*, and also homozygous for *B*, which should be full black, can still be modified by another factor to *eisengrau*. These *eisengrau* are heterozygous for the dilution factor, which converts black into blue and chocolate into lilac. In fact, all Pap's rabbits with *D* and *E*, which should have been agouti-black or full black, varied from a dark form of agouti, through *eisengrau*, to a form not quite so dark as agouti-black. This divergence from Punnett's results was proved, it is said in a note at the end of Pap's paper, to be due to the fact that all these rabbits were heterozygous for the dilution factor.

It is very difficult to give an opinion as to the relation of these *eisengrau* rabbits to the steel of the present paper, but it seems doubtful whether Pap was dealing with rabbits of the same constitution. In the first place, so far as is known, all the animals in the author's experiments were in the black and not the chocolate series; and secondly, as was said on p. 91, special care was taken to remove the dilution factor from the strain used. It is of course possible that Pap may be mistaken in the interpretation of his results, which may have been due to an extension factor similar to Punnett's *D*, or to the one described in this paper, and not, as he thought, to the dilution factor.

[1] Punnett, R. C. *Journal of Genetics*, Vol. v. No. 1, p. 37, July, 1915.
[2] Punnett, R. C. *Journal of Genetics*, Vol. II. 1912. Plate XII, fig. 1.

CONCLUSIONS.

1. The peculiar ticking which causes the coat pattern known as "steel" in Dutch rabbits may be represented as a heterozygous character.

2. The factor for this character, called *X*, may be considered as a darkening or melanising factor, similar to *D* in the "agouti-blacks" of Punnett, but rather weaker in its effect. In a heterozygous condition, it converts an agouti rabbit into a steel; and in a homozygous condition, it converts an agouti into a black.

3. The data show that blacks extracted from steels, and therefore homozygous for *X*, when mated to agoutis (homozygous for *x*) give nothing but steel; and moreover, the same blacks when mated to normal blacks or chocolates (*aaxx*) give nothing but steel.

4. There is some evidence to show that there may be more than one type of agouti, for two agouti males were used, which when mated to steels gave equal numbers of steel and agouti, but when mated to extracted blacks, one gave nothing but steel, the other both steel and agouti. On this point, further investigations are being made.

I should like to thank Professor Punnett for his help and encouragement throughout the experiments, and Mr W. Auton for his management of the rabbits in extremely difficult circumstances.

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SEX RATIO AND UNISEXUAL STERILITY IN HYBRID ANIMALS.

BY J. B. S. HALDANE, M.A.
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Many observers have noted that the crossing of different animal species produces an offspring one sex of which is rare or absent, or if present sterile, whilst occasionally the missing sex is represented by intermediate forms. Doncaster(1) concluded that the missing sex was generally the female, but, as will be shown later, this is by no means always the case. I believe, however, that the following rule applies to all cases so far observed, with one certain, and a few doubtful exceptions:—

When in the F_1 offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous sex.

By the heterozygous sex is meant that sex which is known to be heterozygous for sex factors and sex-linked factors, to contain an odd pair or an odd number of chromosomes, and to produce two different classes of gametes, which normally determine the sex of the offspring. The heterozygous or digametic sex is in most groups the male, but in birds and Lepidoptera the female. Groups in which the male sex is haploid are only extreme cases of the normal type, in that all the chromosomes here behave like the sex-chromosomes of other groups.

Disturbances of sex-ratio and unisexual sterility have been observed as the result of crosses in Lepidoptera, Aves, Diptera, Mammalia, Anoplura, and Cladocera. I have here recorded all cases known to me in which (*a*) the animals were bred in captivity; (*b*) more than 10 offspring were raised, and (*c*) one sex was absent or sterile, or the sex-ratio was more than 2 : 1. In the tables *F* denotes fertility, *S* sterility established by testing several individuals. Of course the fertility is often subnormal.

Table I summarizes the data for Lepidoptera. Goldschmidt's results were each obtained with several different races. In the other crosses there were 24 cases where females were absent or rare, 10 where males were fertile and females sterile, and a number where there was an

unstated excess of males; or else the males, though not known to have been fertile, were anatomically normal, whilst the females were clearly sterile.

Of exceptions to the rule there is first the case described by Goldschmidt (20) where crosses between two races of *Lymantria* gave

TABLE I.

Lepidoptera.

Mother	Father	Offspring	Offspring of reciprocal cross	Reference
Cerura erminea ...	*Cerura vinula*	9 ♂, 1 *S* ♀	—	Guillemot (2)
Clostera curtula ...	*Clostera anachoreta* ...	21 *F* ♂, 3 ♀, 2 *S* ♀	Excess *F* ♂'s, *S* ♀'s	Tutt (3)
Deilephila galii ...	*Chaerocampa elpenor* ...	>20 ♂, 8 ♀ [1]	—	Castek (4)
				Grosse (5)
Smerinthus ocellata ...	*Mimas tiliae*	20 ♂, no ♀	—	Standfuss (6)
,, ,, ...	*Calasymbolus astylus* ...	25 ♂, no ♀ [2]	—	Neumögen (7)
Amorpha populi ...	*Smerinthus ocellata* ...	490 ♂, 10 ♀ and ♀ [3]	2 ♂, no ♀	Tutt (8)
				Standfuss (6, 9)
,, ,, ...	,, *atlanticus* ...	9 ♂ : 1 ♀	>20 ♂, no ♀	,, (9)
				Dannenberg (10)
,, *austauti* ...	,, *ocellata* ...	93 ♂ : 7 ♀	—	,, (10)
,, ,, ...	,, *atlanticus* ...	45 ♂, 5 ♀	Excess ♂'s	Standfuss (9)
				Austaut (11)
				Dannenberg (10)
Saturnia spini	*Saturnia pavonia* ...	113 *F* ♂ : 100 *S* ♀	Excess ♂'s, *S* ♀'s	Standfuss (6, 12)
,, *pyri*	,, ,, ...	106 *F* ♂ : 100 *S* ♀	No ♂, 2 ♀	,, (6, 12)
Malacosoma franconica .	*Malacosoma neustria* ...	12 ♂, no ♀ [4]	No ♂, 1 ♀	,, (13)
Nyssia graecaria ...	*Lycia hirtaria*	65 *S* ♂, no ♀	—	Harrison (14)
,, *zonaria* ...	,, ,, ...	208 *S* ♂, no ♀	181 *F* ♂, 279 *S* ♀ [5]	,, (16)
,, ,, ...	*Poecilopsis isabellae* ...	32 ♂, no ♀	—	,, (16)
,, ,, ...	,, *pomonaria* ...	90 ♂, no ♀	44 ♂, 102 ♀	,, (16)
,, ,, ...	,, ,, (inbred)	71 ♂, 7 ♀	—	,, (16)
,, ,, ...	,, *lapponaria* ...	93 ♂, no ♀	Excess ♀'s	,, (16)
,, ,, ...	,, ,, (inbred)	62 ♂, 3 ♀	—	,, (16)
Lycia hirtaria (English)	,, *pomonaria* ...	86 *F* ♂, 75 *S* ♀	98 *F* ♂, 92 *F* ♀	,, (14)
,, (Scottish)	,, ,, ...	190 *F* ♂, 14 *S* ♀	—	,, (14)
Poecilopsis isabellae ...	*Lycia hirtaria*	38 *F* ♂, 32 *S* ♀	—	,, (14)
,, *lapponaria* ...	*Poecilopsis pomonaria* ...	38 *F* ♂, 1 ♀, 39 *S* ♀	—	,, (15)
Oporabia dilutata ...	*Oporabia autumnata* ...	6 ♂, no ♀ [6]	52 *F* ♂, 47 *S* ♀	,, (17)
Tephrosia bistortata ...	*Tephrosia crepuscularia*	378 *F* ♂, 12 *F* ♀	313 *F* ♂, 327 *F* ♀	,, (18)
				Tutt (19)
Lymantria dispar ...	*Lymantria dispar* ...	*F* ♂'s, *S* ♀'s	1 *F* ♂ : 1 *F* ♀	Goldschmidt (20)
,, ,, ...	,, ,, ...	*F* ♂'s, ♀'s	,,	,,
,, ,, ...	,, ,, ...	*F* ♂'s, no ♀	,,	,,
Fumea affinis	*Fumea nitidella* ...	♂'s, no ♀ [7]	♂'s, no ♀ [7]	Standfuss (12)
Basilarchia archippus ...	*Basilarchia arthemis* ...	>9 ♂, no ♀ [8]	—	Field (21)

[1] Grosse obtained 20 ♂, 8 ♀, Castek a number of ♂'s and no ♀'s.

[2] 20 chrysalides wintered over. Their sex was not recorded owing to the author's death, so they may have been the missing ♀'s.

[3] Out of about 500 imagines 98 % were ♂'s, the remainder ♀ s, never normally developed, often with ♂ appendages.

[4] "Ein reichliches Dutzend."

[5] I have described the male as fertile, though several males between them only fathered one egg which hatched.

[6] 6 out of 400 pupae, all ♂, survived.

[7] "Eine Anzahl."

[8] These 9 were bred in captivity. All the wild examples were also ♂.

intersexual males, and an excess of males. This took place in two broods only. Goldschmidt's other intersexual males occurred either sporadically or in generations later than F_1, and are therefore not exceptions. It seems just possible that the intersexuality of the two aberrant broods may have been due to disease or other external conditions, or to unsuspected heterozygosis of one parent. His theoretical explanation of them is not convincing, since he ascribes to the race "Fukuoka" on p. 103 (*loc. cit*) a formula which, according to the analysis on p. 66, is entirely inconsistent with its being a "weak" race as stated on p. 12 and borne out by its behaviour in other crosses.

In two of Harrison's reciprocal crosses noted in the table there was a moderate excess of females, though in one of them these females were sterile. Standfuss(6, 12) mentions five cases where a species-cross gave only females. In three of these the numbers of females recorded were two, one, and one, which are insignificant; one (*Drepana falcataria* ♀ × *D. curvatula* ♂) was subsequently shown by him to give both sexes in equal numbers. In the last (*Malacosoma castrensis* ♀ × *neustria* ♂) Bacot(22) found that the males emerged a year after the females, but in only slightly smaller numbers.

Finally Fletcher(23) obtained a brood of 33 females and no males from a *Cymatophora or* ♀, supposed to have been fertilized by a *C. ocularis* ♂, but he was himself dubious of their paternity. There are thus no undoubted exceptions outside *Lymantria*.

The data for Aves are summarized in Table II.

TABLE II.

Aves.

Mother	Father	Offspring	Reference
Turtur orientalis ...	*Columba livia* ...	13 S ♂, 1 ♀	Whitman and Riddle (24)
Streptopelia risoria ...	,, ...	38 F ♂, no ♀[1]	,, ,, ,,
,, *alba-risoria*[2]	,, ...	11 ♂, no ♀	,, ,, ,,
,, *risoria* ...	*Zenaidura carolinensis*	16 S ♂, no ♀	,, ,, ,,
,, *alba-risoria*	*Stigmatopelia senegalensis*	17 F ♂, 1 ♂ or ♀, 9 F ♀	,, ,, ,,
,, *alba* and hybrids[2]	*Ectopistes migratorius*	10 S ♂, no ♀	,, ,, ,,
Gallus domesticus ...	*Phasianus colchicus* ...	>100 S ♂, 1 ? ♂	Lewis Jones (in litt.)
Phasianus reevesi ...	,, *torquatus* / ,, *versicolor*	161 S ♂, 6 S ♀	Smith and Haig-Thomas (25)
Tetrao urogallus ...	*Tetrao tetrix*	40 ♂, 8 ♀	Suchetet, cit. Guyer (26)

Besides these crosses many have been made, giving smaller numbers, or less aberrant sex-ratios. They are described by the authorities cited

[1] One male begot a few living young, most were sterile.

[2] *Alba* and *risoria* yield fertile hybrids with normal sex-ratio. It therefore seems legitimate to include crosses of such hybrids along with crosses of pure species.

above, and Phillips(27). With regard to unisexual sterility the evidence is not clear. Whitman and Riddle(24) report one case (*Columba livia* ♀ × *Turtur orientalis* ♂) which gave two fertile males and one sterile female with rudimentary ovaries, and four cases where the males were fertile, and the females not known to be so, though not apparently proved sterile. The only possible exception is the cross of *Turtur orientalis* ♀ × *T. turtur* ♂, which gave 7 males and 14 females, all fertile. This may be compared with some of Harrison's cases which gave a moderate excess of females.

In Diptera the male is heterozygous. The data for the only recorded cross are given below, from Sturtevant(28).

Drosophila melanogaster ♀ × *D. simulans* ♂ gave 2 ♂, 3552 ♀, the reciprocal 588 ♂, 171 ♀.

Drosophila melanogaster XXY ♀ × *D. simulans* ♂ gave 59 ♂, 128 ♀.

All these hybrids were sterile. The males produced from *XXY* ♀'s were shown genetically to contain a *simulans X* like those of the reciprocal cross. These latter all die in some families, but all or almost all survive in others, the difference perhaps depending on the *simulans* parent. Thus, though one cross often gives an excess of males, there is a far greater excess of females in the reciprocal, the two recorded males being perhaps non-disjunctional exceptions.

The data with regard to mammals, where again the male is heterozygous, are given in Table III.

TABLE III.

Mammalia.

Mother	Father	Offspring	Reference
Cavia porcellus ...	*Cavia rufescens* ...	14 S ♂, 23 F ♀	Detlefsen (29)
Bos indicus ...	*Bibos frontalis* ...	19 S ♂, F ♀'s	Kuhn[1]
,, ,, ...	,, *sondaicus* ...	1 S ♂, F ♀'s	,,
,, *taurus* ...	,, *grunniens* ...	S ♂'s, F ♀'s	,,
,, ,, ...	*Bison americanus* ...	6 S ♂, 39 F ♀	Boyd (30)
,, ,, ...	,, *bonasus* ...	1 S ♂, 3 F ♀	Iwanow (31)

Here the males are always sterile, and sometimes rare. This sterility and paucity may persist after one or more generations of back-crossing. Thus in the guinea-pig cross the F_1 females with *porcellus* males gave 31 S ♂, 52 F ♀, and it was only in the next generation that a few of the males proved fertile. Similarly 19 yak-cow male hybrids containing $\frac{1}{8}$, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, and $\frac{7}{8}$ cow "blood" were all sterile, and three out of four males containing $\frac{1}{4}$ bison blood were sterile. Mammalian crosses sometimes give small excesses of males, not exceeding 30 %. Buffon (33)

[1] Quoted by Detlefsen (29) and Ackermann (32).

states that he obtained 7 males and 2 females from *Ovis aries* ♀ × *Capra hircus* ♂, but this has never been confirmed.

In Anoplura the method of sex-determination is unknown. Keilin and Nuttall(34) found that *Pediculus corporis* ♀ × *P. capitis* ♂ gave 310 ♂, 12 ☿, 107 ♀, whilst the reciprocal cross gave 242 ♂, 187 ♀. The normal sex rates for *P. corporis* is 144 ♂ : 100 ♀. The increased excess of males suggests that sex-determination is here perhaps on avian and lepidopteran lines, the female being heterozygous.

In Cladocera there seems to be no obvious cytological difference between the sexes. *Daphnia obtusa* ♀ × *D. pulex* ♂ was found by Agar(35) to give a great excess of sexual broods and males (all sterile) among the descendants by parthenogenesis of the single original female hybrid. As these disturbances did not occur in the first generation they are not really comparable with the other cases cited.

Thus, with the exception of Goldschmidt's intersexual male families the rule always holds as regards sterility, while in the rare cases where an excess of the heterozygous sex is produced the reciprocal cross always gives a greater excess of the homozygotes.

As pointed out by Sturtevant(28) the excess of homozygotes may be due to two distinct processes, a killing-off of the heterozygotes, or their transformation into members of the normally homozygous sex. In *Drosophila* the missing males die as larvae, on the other hand both Goldschmidt and Harrison have shown that in certain moth hybrids partial or complete transformation occurs. If the generalization of this paper is more than a mere coincidence it must be shown how these two effects, and also sterility, may be explained as due to the same cause.

Goldschmidt and Harrison have shown that many of their results can be explained by difference of intensity of the sex factors carried by the *Z* or *X* chromosomes in the two parental species. In *Drosophila* at least the other chromosomes play a part as well. In the pure races these factors are balanced by the cytoplasm or *W* chromosome, but in the hybrids there is a lack of balance. This will be most serious in the heterozygous sex, since in the homozygotes the effect of the two *Z* or *X* chromosomes will be the average of the parental values. The heterozygotes will tend to be pushed either towards the homozygous sex or towards an exaggeration of their own sex. Either of these effects in moderation may be expected to cause sterility, as pointed out by Harrison. The former may cause gynandromorphism, sex-reversal, or death when pushed further, the latter only death. Thus where both

reciprocal crosses yield males only, as in *Fumea*, we may suppose that in one case some of the males are transformed females as in *Lymantria*, whilst in the other the zygotes with an exaggerated tendency to maleness have died. This hypothesis may be compared with the demonstration by Bridges(36) that in *Drosophila melanogaster* both supermales with one *X* chromosome and 3 sets of autosomes and superfemales with 3 *X*'s and 2 sets of autosomes are sterile and not very viable.

But since in some cases the heterozygotes are transformed, in others killed off, alteration of sex-potential must have different effects in different animals. That this should be so is intelligible when we consider the great difference between the effects of castration or parabiosis in different groups. In Lepidoptera these conditions have little or no effect on somatic development, in mammals a great deal. The case here is by no means parallel, since the somatic cells are affected directly and not through an internal secretion, but the analogy shows that we need not expect the same effect from the same cause in different groups.

Although the explanation in terms of sex factors is attractive we have no satisfactory evidence of their existence. If sex is due simply to a double dose of a factor in the *X* chromosome (or sex-linked factor group) we should expect this factor occasionally to mutate like its neighbours. This would lead, if the factor were lost in mammals or Diptera, to the production of males with two *X* chromosomes and two sets of sex-linked factors, which would now exhibit partial and not complete sex-linkage. But such a condition has never been observed.

Moreover, upsets of the sex-ratio similar to those found in species crosses have been recorded in which factors which are certainly not sex factors are involved. Examples from Drosophila are given in Table IV.

The missing males are not transformed, but die as embryos. The characters concerned are all sex-linked recessives to the normal, "glazed" and "rugose" being multiple allelomorphs. They appear in the normal

TABLE IV.

Mother	Father	Offspring	Offspring of reciprocal cross	Observer
Fused *melanogaster*	Normal *melanogaster*	No ♂, 823 *F* ♀	1 ♂ : 1 ♀	Lynch (37)
Fused *XXY melanogaster* ...	,, ,,	9 ♂, 744 *F* ♀	—	,,
Rudimentary ,, ...	,, ,,	10 ♂, 923 *F* ♀	1 ♂ : 1 ♀	Lynch (37) and Bridges (38)
Rudimentary *XXY melanogaster*	,, ,,	93 ♂, 647 *F* ♀	—	Lynch (37)
Rugose *virilis*	Glazed *virilis* ...	No ♂, *S* ♀'s	Nil	Metz and Bridges (39)

sex-ratio when the mother is a wild type heterozygote, but in each case the recessive female is almost wholly sterile. However "rudimentary" females have given 7 ♀ and 13 ♂ offspring with rudimentary males, so the upset of the sex-ratio is conditioned by crossing. The analogy with species crosses is striking, and may throw light on them. Two autosomal recessives in *melanogaster*, "morula" and "dwarf," behave similarly, except that with morula and dwarf males the recessive females have given 2 ♀ and 7 ♀ respectively, with no males. Finally according to Doncaster(40) colour-blind men have an excess of daughters by normal women. Although the data here are not so satisfactory, there is no sterility in the recessives.

Entia non sunt multiplicanda praeter necessitatem, and if ordinary factors, either sex-linked, like "rudimentary," or autosomal like "morula," can cause the disappearance of the heterozygous sex in crosses, we have no right to postulate sex factors for this purpose. A possible explanation of the phenomena under discussion is then as follows. In the course of the evolution of a species factorial differences arise between it and its parent species. They are perpetuated, probably by natural selection. Some of these factors, like "rudimentary," cause the death (or transformation) of the heterozygous sex when the new form is crossed with the ancestral. How this happens is quite obscure, but such factors do exist, whereas sex factors, though an attractive hypothesis, are nothing more. Moreover Bridges' (36) work on triploidy shows that sex may be determined by other groups of factors than those which normally determine it. It seems possible then, that sex is normally determined, not by a specific factor, but by the simultaneous activity of a fairly large group of factors, each of which has, or may have, other effects. The loss of any one member of this group will not cause a change of sex, though it may cause partial sterility. If sex were determined by a single factor it is very difficult to see what advantage there could be in its being linked with other factors. If on the other hand a number of factors determine it, it is essential that they should be linked. If in any animals sex is determined by one factor, there is probably no sex-linkage or chromosome difference between the sexes. As soon as another factor becomes necessary, complete linkage between the two must appear in the heterozygous sex, and the same mechanism which prevents them from crossing over may be expected to hinder or prevent crossing over of all factors in that sex.

I shall not attempt here to discuss the phenomena observed in the F_2 of the crosses considered. Their variability is partly explained by

the fact that the fertile F_1 may either be all homozygotes, or in part transformed heterozygotes, partly by failures in reduction.

It is worth noticing that other disturbing influences do not affect the heterozygous sex more than the homozygous. Thus late fertilization turns XX frog zygotes into males, and the blood of their brothers converts XX mammalian embryos into freemartins. On the other hand the distinction between homozygous and heterozygous sex is more fundamental than that between male and female in determining the intensity of partial linkage between factors. Obviously sex-linked factors must be completely linked in the heterozygous sex, but linkage between autosomal factors is also always stronger in that sex. In *Drosophila melanogaster*, *simulans* and *virilis* linkage is always complete in the heterozygous male, in Bombyx, as shown by Tanaka(41), in the heterozygous female. Nabours(42) in *Apotettix* and Haldane(43) in *Paratettix* found linkage much stronger in the heterozygous male. And Dunn(44) showed that in the rat and mouse linkage is slightly stronger in the heterozygous male. If these facts are anything more than a coincidence they may be due to a greater difficulty of fusion of chromosome pairs in the heterozygous sex, and this in turn may be a contributory cause of its sterility. A possible evolutionary explanation of this stronger linkage has been suggested above.

I wish to record my thanks to the Rev. E. Lewis Jones for his information concerning pheasant-poultry hybrids.

Summary.

When in the F_1 offspring of a cross between two animal species or races one sex is absent, rare, or sterile, that sex is always the heterozygous sex.

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STUDIES IN INHERITANCE IN THE HYBRID *PHILOSAMIA* (*ATTACUS*) *RICINI* (BOISD.) ♂ × *PHILOSAMIA CYNTHIA* (DRURY) ♀.

By ONERA A. MERRITT HAWKES.

(With One Diagram and Three Graphs.)

CONTENTS.

PART II. ON PUPAL CHARACTERISTICS.

SECTION I. ON THE INHERITANCE OF COCOON COLOUR.

THE only pupal character studied was cocoon colour. The parents differed greatly, *ricini* having a pure white and *cynthia* a red-brown cocoon.

The F_1 cocoons were all intermediate in colour, being fawn and pale brown. In F_2 there was no complete segregation but there was a much greater range of colours than in F_1, the colour varying from the characteristic cynthian red-brown to a cocoon which was very light, creamy, but never quite white. In the succeeding generations the same range of colour was continually reproduced but white cocoons never appeared. The colours of the cocoons were not correlated with any other characteristic of larva or imago. As there was no complete segregation, and as the effect of moisture on the colour very much complicated any deductions (4, 5), this part of the study was temporarily abandoned.

[1] Part I, "On Larval Characters," was published in this Journal, Vol. VII. 1918, pp. 135—154.

Part III. On Imaginal Characteristics.

Section I. On the Inheritance of Colour.

P. cynthia and *P. ricini* differ strikingly in the colour of the large medium expanses of the wings, *ricini* having this part a uniform vandyke brown, and *cynthia*, a mottled yellow. The colour in both cases is due to the long narrow scales which cover the wings. Underneath these there is another layer of short scales which do not in the least affect the apparent colour of the wings.

The colour of *ricini* is mainly due to scales which vary from palest fawn to deep brown, but a few pale grey scales are also present. The different coloured scales are however arranged in such a way, that, macroscopically, an effect of even coloration is produced. The darkest scales shade from a deep brown at the tip to a much lighter brown at the base.

The colour of *cynthia* is produced by the presence of scales of two very distinct colours, a bright yellow, and a brown which is deeper in tone than the deepest brown scales of *ricini*. In these brown scales there is little or no shading from the tip to the base. This is, however, a variable character, and one difficult to determine with complete satisfaction. I do not know whether the brown colour in the scales of the two species differs in degree only, or whether there is an actual chemical difference. The two colours of *cynthia* are not distributed regularly, but scales of the two respective colours are massed in groups, so that a mottled appearance is produced.

The difference in colour between the two species is therefore due to two factors, (1) anatomical, the arrangement of the scales, and (2) chemical, the colours of the scales.

F_1 generation consisted of 143 almost uniformly coloured specimens having the vandyke brown colour of the *ricini* parent, from which they could not be distinguished by macroscopical examination. Neither could these F_1 specimens be mistaken for any of the geographical varieties of *ricini* which I have so far examined.

Microscopical examination showed however that this generation, F_1, differed from its *ricini* parent in the presence of a small number of yellow scales in the brown areas under consideration and an increase of yellow in the various positions where yellow scales are normally present in both *ricini* and *cynthia*. This addition of yellow scales is so small and so evenly distributed that there is no perceptible variation

from the vandyke brown of *ricini*, and there is no indication whatever of the mottling of *cynthia*. These few yellow scales, inherited from *cynthia*, *do not disappear* in any of the *ricini*-like specimens produced in the succeeding generations. In some specimens in F_2 to F_5, although the vandyke brown remained characteristically ricinian, there is a distinct intensification of the yellow in the areas which are yellowish in both species.

Cynthia has not shown its parentage only by the presence of a few yellow scales, but among the characteristically ricinian brown scales are a few of the very dark brown from *cynthia*.

Macroscopical examination suggested complete dominance of *ricini* over *cynthia*, but microscopical examination proves that the dominance is incomplete, apparent, not real, owing to the presence of a few of both the coloured scales of *cynthia*.

This type of dominance is similar in appearance, though not necessarily in genetic constitution, to the inheritance of colour in pigeons, where, although black is dominant over white, a number of white feathers remain in F_1.

The method of inheritance of scale colour should also be compared with the inheritance of the dark spots of the larvae, in which it was found that although the condition of spotting in the larva of *cynthia* was completely dominant in most individuals over the spotless condition of the larva of *ricini*, there was a proportion of F_1 larvae which had not the full number of cynthian spots, so that, in their case also, the dominance was incomplete (6).

In F_2 there was a segregation of colour, not however into two, but into four groups.

1. Moths like *ricini* to be known as *DK* (dark).
2. Moths like *ricini*, but much darker, to be known as *DKK* (very dark).
3. Moths like *cynthia*, to be known as *LI* (light).
4. Moths like *cynthia* but having a faded appearance, to be known as *LII* (very light).

This generation consisted of 296 *DK*, 129 *DKK*, and 56 *LI* and *LII* moths. The light moths are only approximately one-half the expected number for the recessive, being 56 out of a total of 481. These numbers can only be regarded as an approximation to the truth as there are certainly intermediates between the main types.

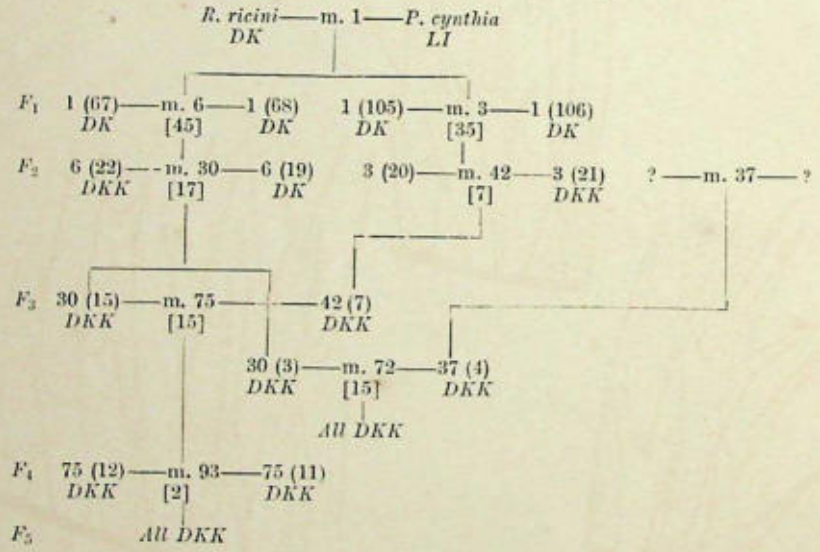
The very dark (*DKK*) moths are not produced only by this particular cross, but similar very dark specimens have been found by W. Watson (20)

and O. Strecher (14) in other Saturnid crosses in which *cynthia* has been one of the parents. One of these hybrids is figured by Packard (Vol. XII, Part I, Plate XCIII). Mr Watson did not attempt to trace the history of these very dark moths, but as a large collector, he was impressed by their appearance.

The microscopical study elucidates the method of inheritance. The brown scales of *ricini* (plus the few grey), are nearly dominant over the very deep brown plus the yellow scales of *cynthia*, and the method of even distribution of colour over the method of massed colouring. In the process of segregation, the approximately ricinian colour and the cynthian colour segregate, but in addition, the very dark (*DKK*) scales of *cynthia* segregate to form a *new* moth, and the pale brown and grey scales of

TABLE I.

The inheritance of the very dark (DKK) moths.



m. 6 = mating 6.

1 (67) = The 67th individual of mating 1.

The number of imagines in a family is placed in square brackets under the name of the family.

ricini are added to a cynthian type to form a *second new* moth, the faded type (*LII*). The yellow scales however do not segregate and no yellow moth appears.

There was no sex linkage with any of the characteristics studied, nor was there linkage between the colour of the imago and the spotted or

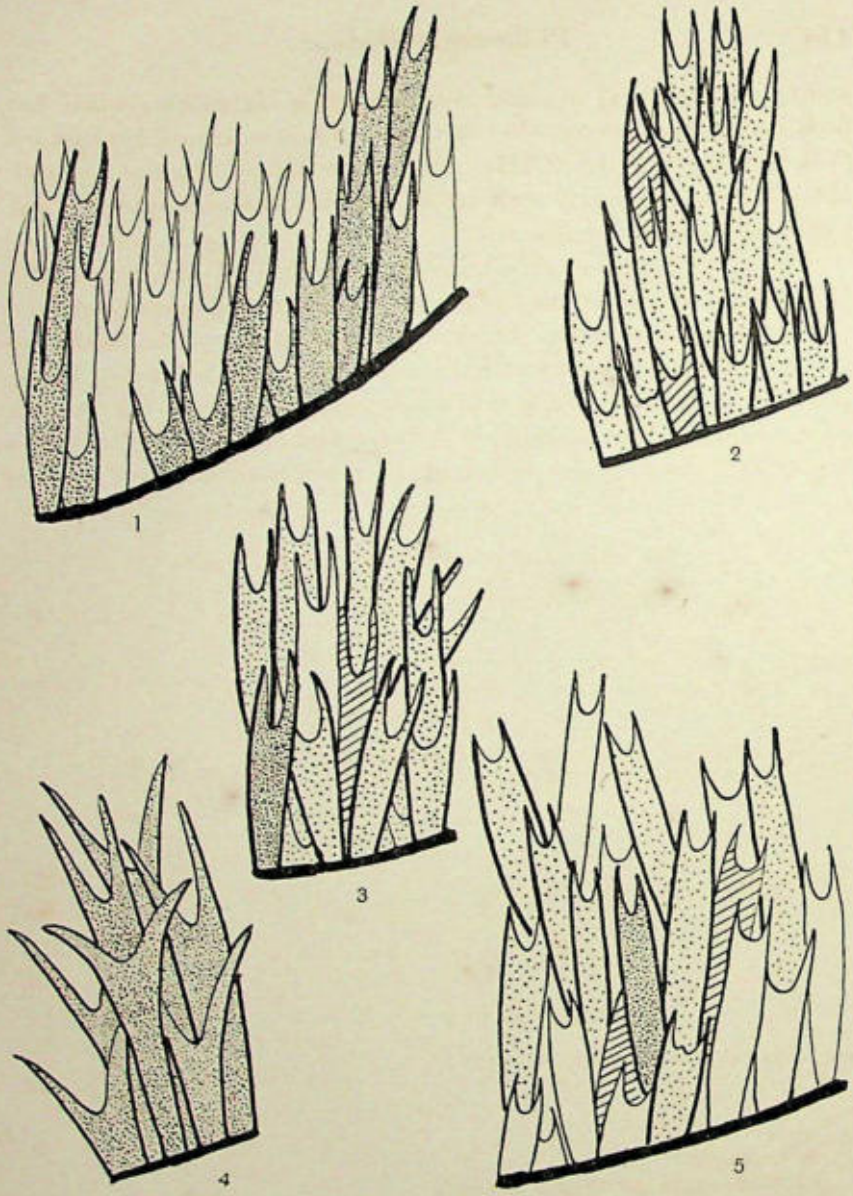


Diagram I. Five camera lucida drawings to illustrate the inheritance of colour: yellow scales are white: scales typical of *ricini*, ranging in colour from fawn to brown, are coarsely dotted: the very dark brown scales typical of *cynthia* are finely dotted: the grey scales of *ricini* are lined.

1. *P. cynthia*, showing the massing of the yellow and dark brown scales.
2. *P. ricini*, showing the irregular distribution of the various shades of brown scales and the few grey scales.
3. The scales in F_1 showing the various shades of brown, one yellow and one very dark brown scale.
4. The very dark (*DKK*) scaled wing which appeared in F_2 and later generations (mating 75).
5. The very light (faded) wing (*LII*) which appeared in F_2 and later generations; there is here the massing characteristic of *cynthia* combined with the lighter brown and grey scales of *ricini* (mating 79).

plain condition of the larvae. Eventually families were produced in which cynthian colour was combined with either cynthian or ricinian type of larva, that is, a recessive colour in the imago was combined with either a dominant or a recessive colour in the larva.

There was a very large proportion of males among the *LI* and *LII* moths of F_2, viz. 210 ♂ to 100 ♀ as compared with 147 ♂ to 100 ♀ for the whole generation.

The heterozygous parents were then studied in F_3, F_4, and F_5 and it was found that the *LI* and *LII* moths were near their theoretical number for the recessive, viz. 14 *LI* and *LII* to 49 *DK* and that the distribution of the sexes was the same among both *LI* and *DK* moths. There is no apparent reason why the proportion of the *LI* forms should be different in the later generations, but there does seem to have been some fundamental sex upset in the first generation (see Section IV, The Sex-ratio).

The LI and LII moths.

The *LI* moths which appeared in F_2 varied considerably in colour, most being indistinguishable from *cynthia*, but a few having a faded appearance (*LII*). These faded (*LII*) moths were more numerous in later generations, but in no generation were they characterised by anatomical or physiological degeneracy.

Microscopical examination showed that some of the F_2 moths which were most *cynthia*-like had a number of ricinian brown scales among the cynthian dark scales, while others could not even be distinguished microscopically from the *cynthia* parent. The recessive form is sometimes incompletely recessive just as the dominant form is incompletely dominant.

The nature and cause of the faded (*LII*) condition are interesting. It is found to be due to—

1. A large number of the brown scales are such as are found in *ricini*, only a few or none being the dark brown unshaded scales characteristic of *cynthia*. As the chemical difference between these two browns is unknown, there is the possibility that these apparently ricinian scales are really poorly coloured cynthian scales.

2. There are a greatly increased number of the grey scales which occur in small quantities in *ricini*.

3. There is a reduction in the proportion of the yellow scales. A few are less bright in colour or shaded from bright yellow at the tip to pale yellow at the base, but the majority are as bright a yellow as those found in *cynthia* itself.

The faded (*LII*) moth appears to be a segregate, due to a redistribution of colour, a parallel case to the very dark (*DKK*) segregate. This faded moth is probably approximately constant as it has reproduced itself for three generations. As it appeared in F_2 as well as in F_6, it cannot possibly be regarded as due to the effects of inbreeding.

Only one mating (m. 24) between light parents was made in F_2, the male, 10 (36), was a true *cynthia* (*LI*) and the female, 4 (44), was faded (*LII*). The progeny were all cynthian, one of them being faded.

In F_3 two matings (m. 79 and m. 62) were made between cynthian parents and both produced only *LI* and *LII* progeny.

Mating 79 had forty-five progeny which were both *LI* and *LII*. From these forty-five moths nine successful matings were made and from their progeny four hundred pupae were reared, mice however ate more than half and ultimately one hundred and twenty-six imagines, all *LI* and *LII* emerged.

Mating 98 (F_5) was between parents, 81 (21) and 83 (17) which were so cynthian in appearance that the presence of a large number of grey scales was only perceived on microscopical examination. Out of a large number of pupae only one escaped disease, and became a moth which both macroscopically and microscopically could not be distinguished from *cynthia*. This moth represented the sixth inbred generation, but no further breeding was done as disease had become too prevalent. The light moths had now bred true for four generations.

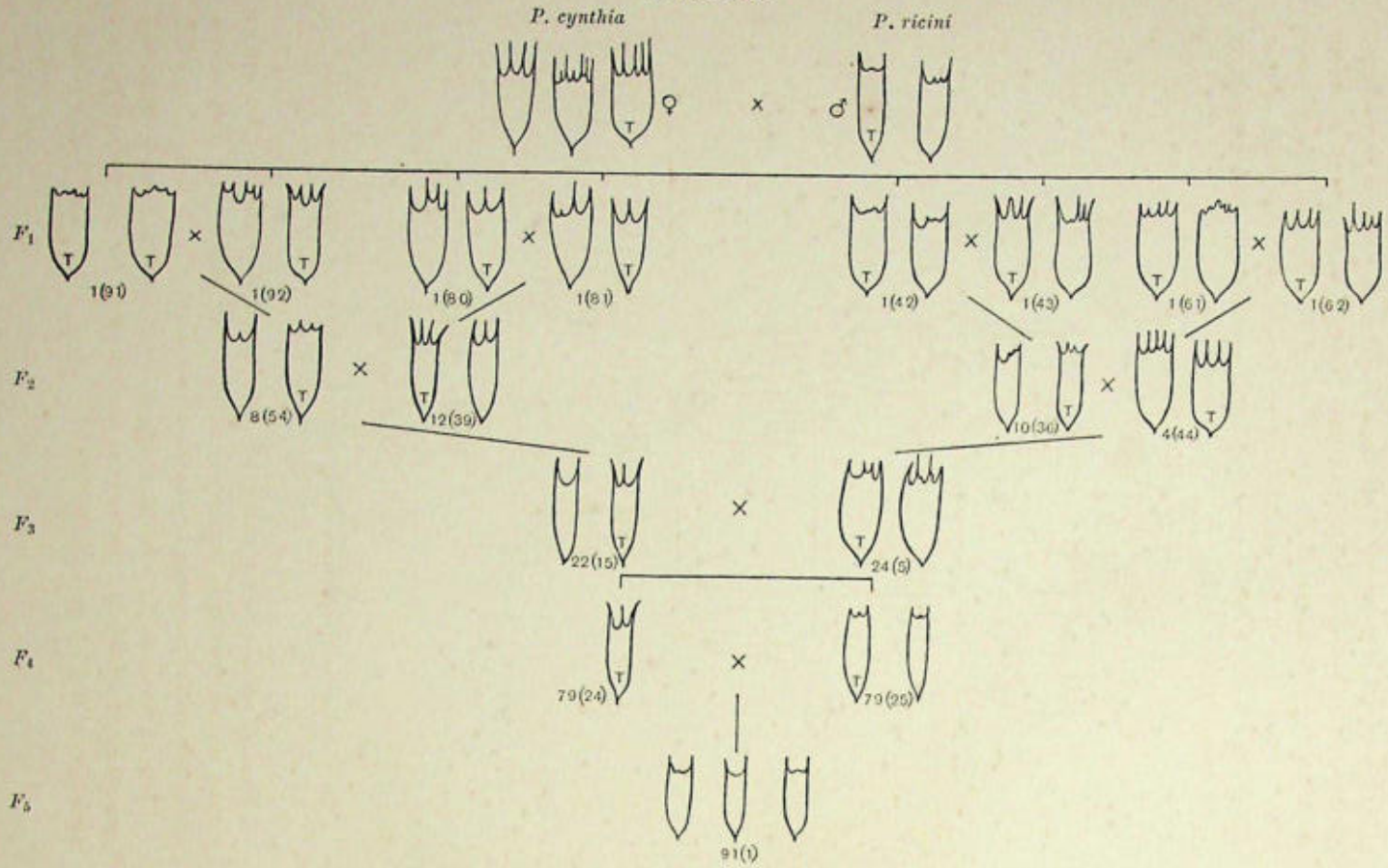
The DKK moths.

The *DKK* moths have no yellow scales, no grey scales, and only a few of the ricinian scales (the lighter brown). This type bred true in several families for two generations. I did not have enough matings with *DK* moths to be sure of its relation to that form. No mating was made with a *LI* moth.

Section II. The Inheritance of Scale Shape.

A study was made of the scales which occur on the large uniformly coloured outer half of both hind and fore wings, excluding those on the veins. This gave a considerable area in which the scales were uniform. But, to make the enquiry more accurate, a special small portion of this area was chosen for examination. This limited area was just beyond the outer angle of the lunule on the anterior right wing. It was necessary to choose an area between veins as the scales along the veins had their own special characteristics.

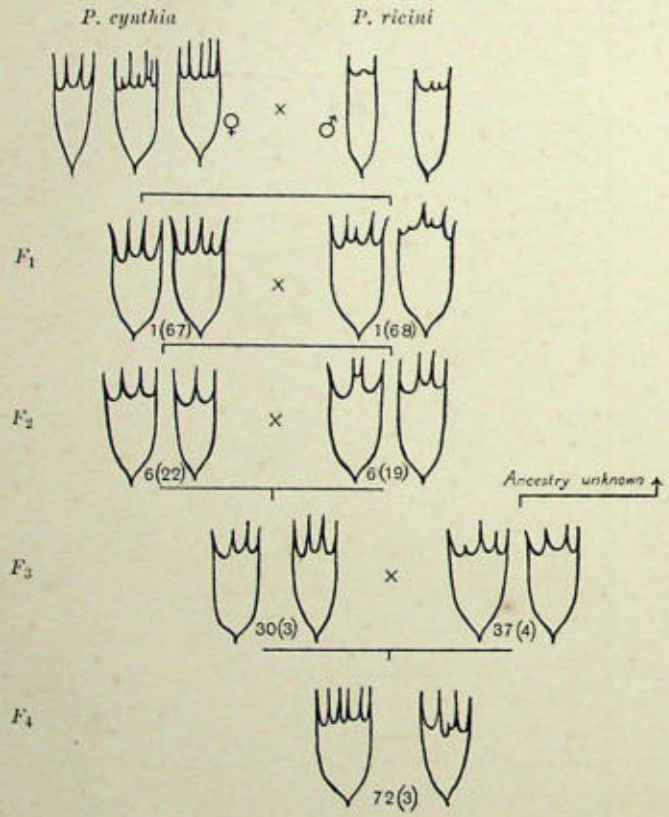
TABLE II.



The inheritance of scale shape, showing the reappearance of a moth with ricinian scales in F_5.

The results here recorded are those found in five inbred generations, the respective parents of the successive generations having been chosen in pursuit of certain characters already described. No mating was made with a knowledge of the condition of the scales of the parents, so that the results here recorded are those due to practically random matings in an inbred family.

TABLE III.



The inheritance of scale shape, showing the reappearance of scales of a distinctly cynthian shape in F_4.

Except on the veins, there are two types of scales on the wing; surface scales, to which the colour of the wing is due, and deep scales which are entirely hidden by the surface scales.

The surface scales are the same in both species, long, narrow and two-pronged. They do not lie flat and do not appear very regularly arranged even in a perfect specimen.

The deep scales, which lie evenly in regular lines, differ in shape in the two species and it is their inheritance which has been studied.

The total length of the deep scales is approximately the same in both species, but they have a number of differences (Table III).

1. *Comparative breadth.* The scale of *cynthia* is 50% wider than that of *ricini*.

2. *The number of the prongs and their length in proportion to the total length of the scale.* *Cynthia* has four, five, and six prongs which are approximately one-third of the total length of the scale, whereas *ricini* has two prongs (rarely a third) and frequently indications of a third and fourth. The two constant prongs of *ricini* are one-fifth of the total length of the scale.

3. *Shape of scale.* The sides of practically all *ricini* scales are parallel until the base is almost reached, but a number of the scales of *cynthia* tend to be cone-shaped.

4. *The scales of both species vary*, but those of *cynthia* more than those of *ricini*.

F_1.

In F_1 the majority of the scales are, in general appearance, much more like *cynthia* than *ricini*, but amongst them are found a very few scales which are exactly like typical *ricini* scales.

1. *Comparative breadth.* The majority of the scales are intermediate in breadth between those of *cynthia* and *ricini* but nearer the former (Table III).

2. *The number of prongs and their length in proportion to the total scale length.* The majority have four prongs but a large number have five. The length of the prongs is nearer to that of *ricini* than *cynthia* but varies greatly, some prongs being almost as long as those of *cynthia*, whilst others have prongs almost as small as the minute, incipient prongs which occur in the middle of some *ricini* scales (Table III).

3. *Shape of scale.* The sides may be parallel or converging.

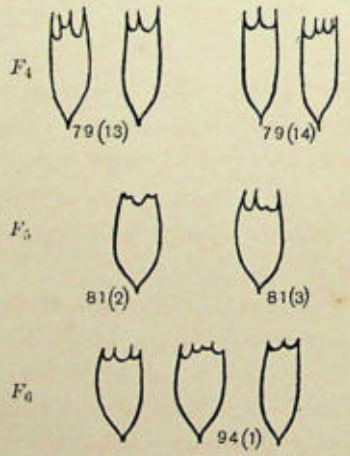
There is no typical F_1 scale, but certain individuals have characteristic scales; thus 1 (91) has scales with exceedingly short prongs (Table II, F_1), 1 (42) has a scale very suggestive of *ricini*, 1 (61) has a fairly regularly four and five-pronged scale. No F_1 moth could be mistaken for either of its parents as a result of an examination of the scales alone.

On the whole, *cynthia* has influenced the scales of F_1 more than *ricini*.

F_2.

In this generation there is greater variation than in F_1, but there is no segregation into the original types. One family (4) has some individuals 4 (44) whose scales differ very little from those of *cynthia*, but there is no individual characterised by *ricini*-like scales, although individual *ricini* scales are found 11 (46). But, in this generation there is segregation of the separate characters which make up the scales of the original parents. Thus, whilst in F_1 practically all the scales are intermediate in breadth, in F_2 there are scales as wide as those of *cynthia* and others as narrow as those of *ricini* 10 (36) (Table II, F_2), 11 (46). Again, some scales are long and parallel like *ricini* 12 (39) whilst others have a definite cone-shape 11 (11). Some have the one-third prongs of *cynthia* 4 (26) whilst others have the one-fifth prongs of *ricini* 11 (11). There appears to be a segregation of separate scale characters with a wide and irregular re-assortment.

TABLE IV.



The inheritance of the barrel-shaped scales, the shape of which is due to a re-assortment of the several factors which make up a scale.

As in F_1 certain individuals have distinctly characteristic scales, thus 10 (36 or 37) have four very short and irregular prongs on a narrow, almost parallel sided scale, whilst 11 (35) and 11 (11) have two pronged, cone-shaped scales.

F_3.

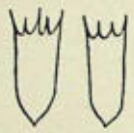
The scales of this generation are, on the whole, the same as those of F_2 but two new forms have appeared, 24 (1), in which the sides of the scale rapidly converge, and 24 (2) which is barrel-shaped (Table IV).

F_4.

Three families (79, 75, 72) in this generation show more homogeneity than any family in the earlier generations.

In mating 79, the offspring have a large number of the scales very suggestive of *ricini*, having the width, parallel sides and two prongs characteristic of that ancestor. In some individuals there is a tendency to a barrel-shape. In others the *ricini*-shape is combined with three or four prongs which may be long 79 (24) (Table II, F_4) but never so long as *cynthia*, or very short 79 (25) (Table II, F_4).

TABLE V.



Deep scales of *P. cynthia advena*.

In the matings 75 and 72, the majority of the scales are very similar to those of *cynthia*, broad, four, five, and six-pronged and the sides slightly converging. Mating 75 differs rather more from *cynthia* than mating 72, as many of the scales are too cone-shaped. In both families there are individuals in which the number of prongs is reduced, but even then the scale would be recognised as cynthian.

The remaining families in this generation are similar to those in the earlier generations.

F_5.

Nearly all the families of this generation were descended from mating 79 of F_4 (of which the scales were ricinian in character) and they have the same type of scale as in mating 79, except two of the families (90 and 91) in which the scales are almost purely ricinian, indeed there are even a larger proportion of "typical" ricini scales than in *ricini* itself, that is, there are only a few of the minute, intermediate incipient prongs which occur in *ricini*. But these scales are somewhat smaller than in *ricini*. These families all consist of small moths and it may be that the smaller scale is correlated with the smaller moth. I have not been able to find out whether the number of rows of scales on a wing is constant ; but if they are, a smaller descendant of a larger moth would have necessarily scales reduced in size. If the scales remained the same size there would have to be a reduction in the number of rows, or much overlapping.

In this generation again individuals have characteristic scales.

F_2.

This generation consisted of very few imagines. One family (94) showed that one type of scale (Table IV) with its barrel-shape and three or four short prongs might be inherited as an entity. By a re-assortment of factors, a new scale has arisen which is approximately stable for one generation. There is no barrel-shape in the original parents, but it appears in a few moths in F_1. It seems to result from a combination of the factor for wide scale with a poor development of the prongs.

From the above facts, one must suppose the shape of the scales is not due to one, but to a number of factors which in this crossing showed no linkage, but tended to behave independently; hence the large number of shapes which have arisen, each of which may be analysed into the following factors:

1. Total length of scale.
2. Number of prongs.
3. Relation of length of prong to total length of scale.
4. Direction of sides of scale, parallel or converging.

These factors may however re-combine to produce a scale which is inherited, just as the colours of the scales have re-combined to make a new coloured moth which breeds true.

A point of considerable interest, is that from the random mating of five generations there reappeared scales of one of the original parents (Table II, F_5).

The condition of the scales of *P. cynthia advena* is one of the most surprising finds of this scale study. This moth as seen by the naked eye, can only with difficulty be distinguished from *P. cynthia* (Ning-po), but the difference in the scales is considerable. The advena scale (Table V) most commonly has four prongs, and may have five, but never has six. The prongs are one-fourth or one-fifth the total length of the scale instead of the one-third characteristic of *cynthia*. The *advena* scale is also narrower. The scales are also more homogeneous than in the Ning-po moth. This change has presumably taken place since the moth was introduced to the United States from China in 1861, a space of 60 years but possibly 180 generations. There is no evidence that there has been any interbreeding, but a definite anatomical change has taken place for which no cause can be suggested, nor do I know how many years after the introduction this change took place or whether it occurs equally in moths from the various parts of the United States.

There is no proof of linkage between the colour and the shape of the

scales, although the *ricini* scale reappeared in a light family and the *cynthia* scale in a dark family.

It will be noticed on Diagram I (p. 115), which shows the inheritance of colour, that the long top scales are different in shape in families 75 and 79, and that they differ in shape not only from each other but from the original parents. As the scales of the original parents are the same the new shape cannot be accounted for as the reappearance of any known factor. Families 75 and 79 both belong to F_4, so that the longer prongs of the one and the shorter prongs of the other cannot both be accounted for by the supposedly bad results of inbreeding. They may be new factors so characteristic of hybrids.

Section III. The Inheritance of Size.

Cynthia and *ricini* differed so much in size that I hoped their offspring might throw some light upon the still obscure subject of size inheritance.

Progress in the study of inheritance in these breeding experiments was retarded somewhat by the necessity of breeding from the moths

TABLE VI.

Parents ♂ original *ricini* 49	Parents ♀ *cynthia* 59	Average size of progeny ♂	Average size of progeny ♀	Largest progeny ♂	Largest progeny ♀	Smallest progeny ♂	Smallest progeny ♀	Number of imagines ♂	Number of imagines ♀
Average size of parents									
F_1									
Matings 2—13									
51·1	51·5	50·52	51·3	55	57	43	41	46	64
48	*48·5*								
F_2									
Matings 15—52									
49·17	50·1	49·54	50·81	56	59	38	42	284	196
47·2	*47*								
F_3									
Matings 60—79									
48·3	49·49	47·66	49·49	56	57	37	41	74	47
44·1	*46·6*								
F_4									
Matings 80—92									
47·83	47·68	48·28	50·46	56	56	42	40	73	50
46	*46·4*								
F_5									
		45·45	46·09	58	54	33	36	105	64

The numbers give the wing length from the base to the middle of the eye spot in mm. The figures in italics in the first column are the sizes of the smallest parents used. The arrow points from parent to progeny.

very soon after emergence, for I was thus prevented from choosing the largest and smallest of each family. The individuals of each family emerge, in this climate, at intervals extending over some weeks. The males appear first, next both sexes, and finally females only, so that, unless one has a very large number of families, the largest and smallest specimens from which one would desire to breed may have to go unmated, for suitable mates may be already dead or may not yet have emerged.

The measurement taken as a criterion of size was the distance from the base of the wing to the middle of the eye spot. The difficulty of dealing with the edge of the wing, which was frequently broken after mating, was thus avoided. Wing measure is here used in the study of size, just as beaks were used in ducks (15, 16) and ears in rabbits (13), etc.

The original parents differed greatly in size. The male, *ricini*, being 49 mm. and the female, *cynthia*, 59 mm., that is, the female was nearly 20 % larger than the male.

The male was one of a family of 14 imagines reared by Mr Watson of Manchester from eggs laid by a wild, presumably pure *ricini* of Assam. This family consisted of twelve males, their average size being 50·71 mm. and two females of 52 and 53 mm. respectively. The maximum of the males was 54 mm. and the minimum 48 mm.

These numbers are of course quite inadequate but unfortunately the number of specimens of wild *ricini* in England is very small, but I here give measurements of those which I have been able to examine.

Number and sex	Locality	Size	Collection	Measurements taken by
1 ♂	Unknown	45 mm.	Hope Museum	Commander Walker
1 ♂	Sylhet	50 mm.	,,	,,
1 ♂	Java	49·5 mm.	,,	,,
1 ♂	Gowhatty	43 mm.	Tring Museum	Dr Jordan
1 ♂	,,	43 mm.	,,	,,
1 ♂	Sikkim	43·5 mm.	,,	,,
1 ♀	,,	47 mm.	,,	,,
1 ♂	Assam	56·5 mm.	,,	,,
1 ♂	Unknown	42 mm.	South Kensington	Mr West
1 ♂	Bengal	45·75 mm.	,,	,,
1 ♂	,,	45·75 mm.	,,	,,
1 ♂	India	46·75 mm.	,,	,,
1 ♂	N. India	44 mm.	,,	,,
1 ♀	India	47·5 mm.	,,	,,
1 ♂	Assam	47 mm.	,,	,,
1 ♀	,,	46·25 mm.	,,	,,

The average of the above males (leaving out the exceptionally large one from Tring Museum) is 45·4 mm. and the average of the very few females is 46·76 mm. These averages are smaller than those of the family bred by Mr Watson, but they do confirm the very small amount

of sex difference, a point on which *ricini* unexpectedly differs considerably from *cynthia* and most members of the Saturnids.

The Eri silk worm bred at Pusa and other places in India for silk producing purpose is called *P. ricini*, but there is no doubt that this domesticated form is a mongrel rather than a true hybrid.

Mr Bainbrigge Fletcher, entomologist at Pusa, has very kindly helped me with information concerning the size of the moths at his station: he sent me measurements of 25 males and 25 females, the average of the former was 53·7 mm. (min. 50, max. 57) and for the latter the average was 54·18 mm. (min. 50·5, max. 58·5). He also sent me 41 moths from which I obtained the following measurements: average of males 55·8 mm. (min. 52, max. 60); female average 57 mm. (min. 50, max. 60). Both these sets of figures show that there is little difference in the size of the sexes of the Eri moth, the females being about 1 mm. bigger than the males. The Eri mongrel evidently retains the sexual size character of its wild *ricini* progenitor.

The female parent *cynthia* was one of a family of 24 (16 male, 8 females) also reared by Mr Watson, of which the average male size was 55·87 mm. (min. 53, max. 59) and the female average 61·24 mm. (min. 56·5, max. 64·5).

The following table gives the measurements of the specimens of *cynthia* at Tring Museum. The measures were made by Dr Jordan.

	Number and sex	Average	Maximum	Minimum	Locality
	2 ♂	52 mm.	54 mm.	50 mm.	Kiangsi
	3 ♀	57 mm.	60 mm.	54 mm.	,,
	5 ♂	53·2 mm.	57·5 mm.	52 mm.	Kiukiang
	6 ♀	59·4 mm.	64 mm.	51·5 mm.	,,
	3 ♂	57·3 mm.	60 mm.	55 mm.	Sikkim, India
	3 ♀	62·5 mm.	68·5 mm.	57 mm.	,,
	3 ♂	54·1 mm.	58 mm.	49·5 mm.	Randakeit, N.W. India
	7 ♂	53 mm.	57 mm.	52·3 mm.	Bhutan, India
	2 ♂	56 mm.	56 mm.	56 mm.	Khasia, Assam
	3 ♀	62 mm.	64·5 mm.	62 mm.	,,
Totals	22 ♂	53·9 mm.	57·3 mm.	52·3 mm.	
	15 ♀	60·06 mm.	64·2 mm.	58·5 mm.	
Specimens of *cynthia advena* from the U.S.A.:					
	24 ♂	57·6 mm.	62·5 mm.	53 mm.	Brooklyn
	20 ♀	60·6 mm.	68 mm.	53·5 mm.	,,

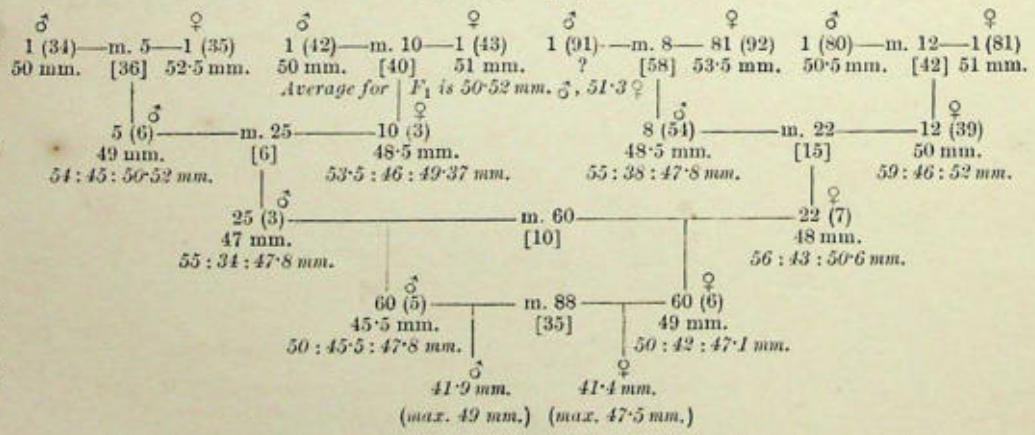
The numbers of the American *cynthia* have been given separately, as P. Packard (14) (p. 243) writes: "Since the date of the introduction into this country (1861) this insect has undergone a considerable change of colour and wing form, quite marked when compared with specimens from China. It is larger, deeper in colour and the wings are much broader

and more rounded, much less excavated below the apex." The size of the museum specimens corresponds with that of the one family reared by Mr Watson. It is clear that there is a considerable size sex difference of the *cynthias* of China, India and the U.S.A., the female in these specimens being from 6 % to 12 % bigger than the male.

The numbers of the pure *ricini* are so small that much more information will be needed, but the results obtained by these breeding experiments are worth stating for when the full details concerning the sex size of *ricini* are known they can be used to interpret the results given here.

Table VI gives the measurements of the five generations. The F_1 moths are not intermediate in size between the two parents, but are approximately the size of *ricini*. The large sexual size difference of *cynthia* has disappeared, the male and female being relatively the same size as in the pure *ricini*. The sex size difference, which is just as

TABLE VII.



This table shows the decrease in size of the moths with continual selection of smaller parents. Figures in normal type are the actual size of the moths, figures in italic are the maximum, the minimum and the average for the family. The number of imagines in a family is placed in square brackets under the name of the family.

characteristic and just as important as any other secondary sexual character, such as colour, wing-shape, etc., does not reappear even in the fifth generation, so that one must suppose it has permanently disappeared. The hybridisation has apparently caused a break-up of the sex complex of *cynthia*.

In these species there is no sex colour difference. The difference in the size of the antennae is excessively little, but the difference in the

falcation of the anterior wings is quite clear and remains just as clear in F_2 as in F_1 and as clear in the small specimens as in the large ones. As regards size the crossing has affected the female more than the male.

The Eri worm, which is a mixture of *ricini* and *cynthia* as well as other bombycine moths, has been inbred for hundreds of generations and has a female which is about 1 mm. greater than the male, the same difference which has been found in the hybrid here studied. It is as yet impossible to state whether there is a blending of the differences of the two females, or whether *ricini* is dominant, even to the fifth generation, or, as in the commercial Eri, to many hundreds of generations.

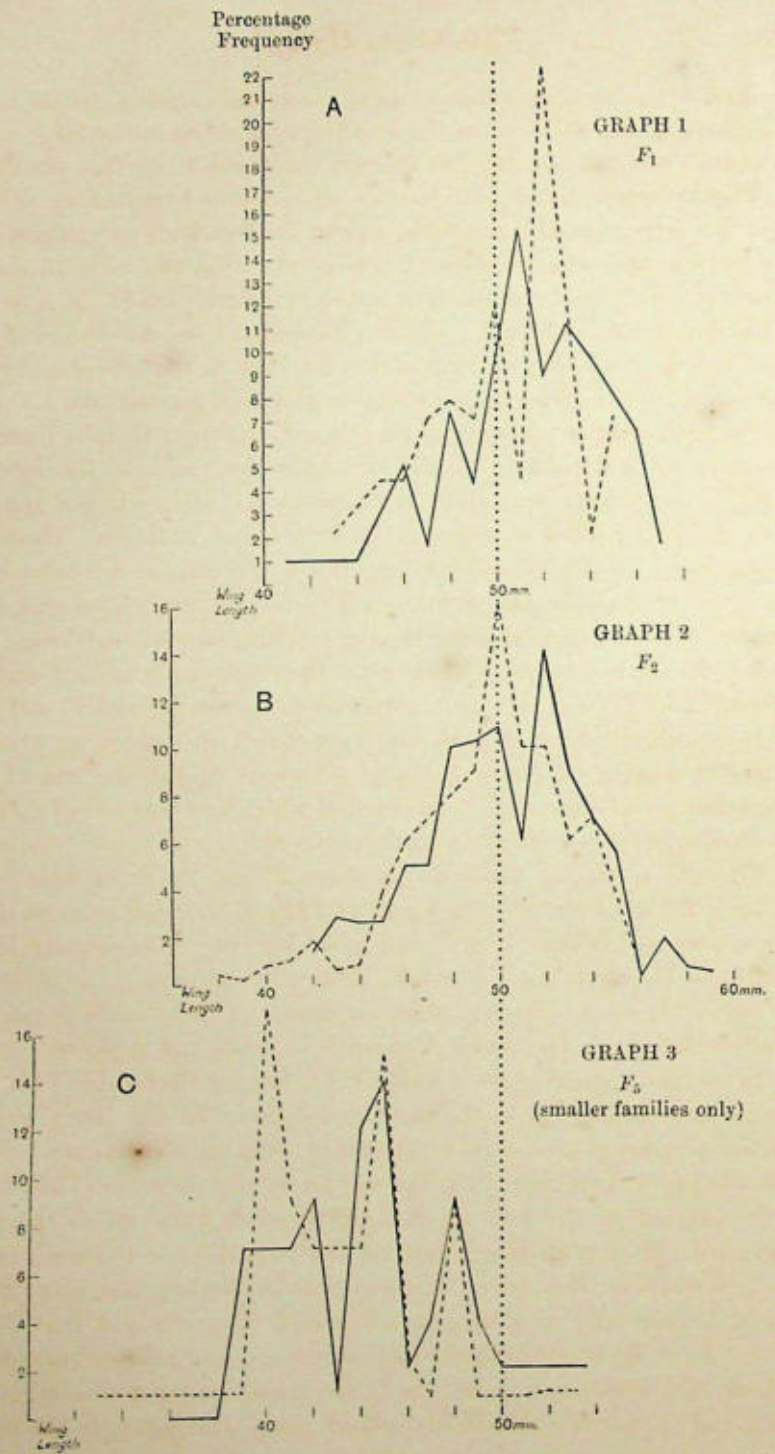
F_2 shows greater variation in size than F_1 (compare Graphs 1 and 2) but it is not sufficient to be called segregation, such as occurred so clearly in the second generation of Punnett's (17, 18) fowls, but appears more like the partial segregation Phillips found in ducks. Thus the largest female is 59 mm. and the largest male 56 mm., that is, about the size of the original female parent, but if there had been real segregation one would have expected some sign of reaching towards 64·5 mm., the largest size of the sorority. Neither are the results intermediate such as Harrison found in his *autumnata-filgrammaria* cross in both F_1 and F_2.

It is difficult to deal with the very small specimens, as a small departure from good environmental conditions upsets the size of the wings, but no specimen has been counted which was not perfect and did not show signs of normal reproductive activity.

There is a striking difference between F_1 and the small families in F_2. (See Table VI and Graphs 1 and 3). The differences between these generations is, I believe, due to deliberate breeding from selected small moths and in only a small degree to artificial conditions.

Table VII shows how the constant choice of the smaller forms has resulted in a small type which however was fertile and vigorous.

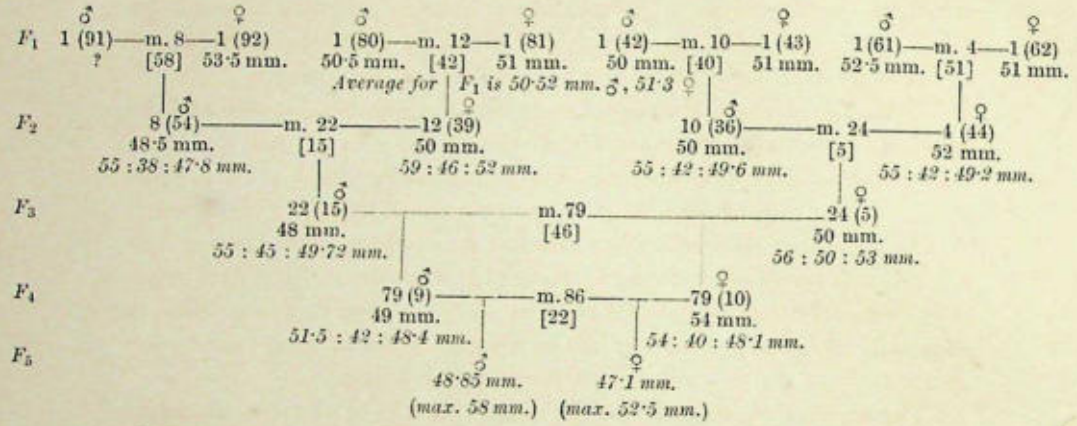
In contrast to mating 88 of Table VII is mating 86 of Table VIII, the two matings belonging to the same generation. In the latter family, parents of average size were constantly chosen, and the average of the ultimate progeny in generation five was practically the same (47·97 mm.) as the average of the four families (49·6) in F_2 from which they are descended. Mating 86 also produced the largest male (58 mm.) in all the generations. This table suggests that inbreeding has been detrimental to size only to a very small extent. Punnett and Bailey (18) state: " In so far as our limited experience goes, close inbreeding appears to lead to a diminution in weight "; the same tendency to reduce size was found by Sumner (19) in his inbred mice. But King, as the result



Graphs 1, 2, 3, showing the distribution of size in F_1, F_2, F_5 the much greater variation in F_2 than in F_1 and the great reduction of the mean size of the small families in F_5. Male, the dotted lines. Female, the solid lines.

of her very extensive work with rats writes: "The evidence does not warrant the conclusion that inbreeding, per se, has altered the form of the growth graph to any appreciable extent" (8—12).

TABLE VIII.



This table shows the small amount of decrease in size in five inbred generations when no attempt was made to breed from the smaller specimens. Figures in normal type are the actual size of the moths, figures in italic are the maximum, the minimum, and the average of the family.

TABLE IX.

Matings	Eggs laid	Eggs hatched	Imagines	Percentage of eggs becoming imagines
		F_2		
m. 2	250	200	53	21·2
m. 3	160	150	35	21·8
m. 4	250	230	52	20·8
m. 5	150	147	36	24
m. 6	160	140	44	27·5
m. 7	200	195	32	16
m. 8	250	230	58	23·2
m. 9	160	155	42	26·2
m. 10	200	195	39	19·5
m. 11	230	225	47	20·8
m. 12	180	165	42	23·3
		F_5		
m. 81	100	86	23	23
m. 87	25	18	4	16
m. 88	150	75	35	23

Table to show the percentages of eggs becoming imagines in F_2 and F_5, the percentages being considered as a criteria of vitality.

A further point of interest and importance is, that the small family (m. 88) and the large family (m. 86) had in common six out of eight of their ancestors in F_1, and also had in common two of their four ancestors

in F_2. The two ancestors, parents of mating 4 for m. 86 and parents of mating 5 for m. 88, which these two groups did not have in common, were in both cases above the average size (compare Tables VI, VII, VIII). Further, in F_2 there is a distinct difference between the ancestors which the small and large groups did *not* have in common, those of the small family (m. 88) being 49 mm. and 48·5 mm. respectively and those of the large family (m. 86) being 50 and 52 mm. respectively.

Table IX gives the number of eggs laid, the number hatched and the resultant number of imagines for all the families in F_2 and the three families of small moths in F_3 which were not badly attacked by disease. If the vitality is represented by the percentage of imagines produced, it will be seen that inbreeding has affected it only to a small degree, if at all. Similar results were found by King (12) who states: "the data given ...show clearly that, despite all theories to the contrary, it is possible to maintain a high degree of fertility in a mammal for at least twenty-five generations of the closest possible form of inbreeding."

The number of eggs laid by the smaller moths is less than that laid by the larger, but this is a necessity as the eggs remained the same size as in the original parents, whilst the body decreased in size. I am here dealing with the size inheritance of the moths only, for the majority of the worms were just as large as those produced in F_1. The statement as to the size of the eggs and the worms is based upon general observations and not on careful measurements.

An effort was made from the beginning to breed from the smaller moths, i.e. moths under 50 mm. in size. Of such matings, one was made in F_2, five in F_3, three in F_4, and seven in F_5. In all the generations the smaller parents produced, on the average, a smaller progeny than was produced by the larger parents, the differences were small—but—the accumulated differences of five generations produced small families.

Among the smaller matings, three had the male larger than the female, but the measurements of the progeny give no indication that the results are different from those in matings, where, as is usual, the female is larger than the male.

McDowell writes: "A law may be stated, the second generation of a size cross will show a greater diversity than does the first generation or the parental lines. The interpretation of multiple factors can be applied to all the facts."

This statement does not appear true here, for the large females, and the large of both sexes expected in F_2, failed to appear.

Further work will show what the reciprocal cross will produce.

Section IV. On the Sex-ratio.

The study of hybrids during the last decade has shown that crossing frequently produces a sex-ratio which is different from that of the pure races to which the parents belonged and King (8—12) states that this new ratio "almost invariably shows an excess of males."

TABLE X.

	Imagines		Pupae		Total		
	♂	♀	♂	♀	♂	♀	Ratio
F_1	46	64	0	0	46	64	0·718 : 1
F_2	284	196	26	19	310	215	1·44 : 1
F_3	74	47	31	19	105	66	1·58 : 1
F_4	73	50	27	19	100	69	1·45 : 1
F_5	105	66	19	12	124	78	1·58 : 1
Total	582	423	103	69	685	492	

The sex-ratios in five inbred generations.

The present hybrid is of interest as in the F_1 generation there is an excess of females, and further the succeeding generations, F_2, F_3, F_4, F_5, reversed the original ratio and produced an excess of males. This excess not only characterised the generations as a whole, but also 42 of the individual families out of the 47 bred. In the remaining families there was practical equality in three and an excess of females (50 %) in two. This shows that, whatever the cause of the excessive male rate, it is characteristic of, and distributed with considerable evenness throughout, the group. The reciprocal cross has not yet been made.

An excess of females is known in only a few crosses—the crosses of Doncaster (1), two moth hybrids of Harrison, crosses of Goodale (2) and this hybrid.

This cross, unlike so many insect crosses, has not produced any moths which are sexually intermediate.

H. E. Crampton tells me that data from both wild and pedigreed *Philosamia cynthia* and *cynthia advena* show that the numbers of the sexes tend to be equal. No record of the ratio of the impure Indian commercial *ricini* has been obtained. The presumably wild race which I have used as one of the original parents has never been bred in sufficient quantities for the sex-ratio to be determined. The few moths of both these species which emerged from the cocoons sent to Mr Watson show a great excess of males, *cynthia* 16 and 7, and *ricini* 12 and 2.

The 110 imagines reared, were from 180 eggs laid by a *cynthia* fertilised by a *ricini* at Manchester, but these eggs were only part of the

total number laid. Unfortunately, no records could be obtained from the entomologists who reared the remainder of the eggs. There is the possibility of course, that these eggs were not an average of the whole batch, for it may be that male and female eggs are not distributed evenly, but more of one sex than the other may be laid at the beginning or end of the batch, or there may be a variation with the age of the moth or with the duration of copulation.

The reversal of the sex-ratio is here constant and complete. Huxley's (7) suggestion of "swing back" does not apply to this hybrid as the ratio persists for four generations and has an approximate mathematical steadiness.

There is, however, one unknown quantity, viz., the sex of the dead larvae (the sex of the dead pupae was determined). But there is no evidence suggesting a selective death rate in the larvae, which acts lethally in F_1 on the males and then in the succeeding generations acts lethally on the females.

Harrison (3, 4) found that inbreeding had "a very profound effect in weakening the male sex determiners in *P. pomonaria*, *P. lapponaria* and *Zonosoma alicularia*. King seems to have found this true to a small degree in her six inbred generations of rats, but the results are very different in these five inbred generations where the excess of males is large and nearly constant. These inbred moths were either brother × sister or cousin × cousin matings. In inbred generations such as these the relation of sister to brother and cousin to cousin represents a far nearer genetic relationship in the later generations than in the first.

The moths always copulated as long as they desired, a period varying from 3 to 78 hours. Copulation invariably took place when the males were less than three days old, generally within a couple of hours after emergence. The females mated from shortly after emergence to about five days old. In a very few matings a week-old female was used, hence the excessive male rate could not be due to the retardation of fertilisation.

Two positive results only can be given:

1. Continued inbreeding to the fifth generation did not modify the sex-ratio of the F_1 generation in which an excess of males first appeared.

2. Whether the matings were cousin × cousin or brother × sister, the ratio remained the same.

There are at present no data that can account for the reversal of the sex-ratio, or for either the excess female rate in F_1, or the equally abnormal male rate in the succeeding four generations.

Section V. On the Inheritance of the White Hairs on the Abdomen.

The bodies of the *ricini* and *cynthia* differ very much in the degree of development and arrangement of the long white hairs on the abdomen.

Each segment of the abdomen of *ricini* has a transverse line of white hairs which extends across the dorsal side of the abdomen and a short distance down on each side. The hairs are long enough to extend backwards over the line of origin of the hairs on the succeeding segment, so that the whole abdomen has a white and woolly appearance. The abdomen of *cynthia* is covered with yellow-brown hairs, among which there are tufts of white hairs, the tufts being in the position of the tubercles of the larvae, four sets of tufts on each segment, as well as a median dorsal tuft. The hairs have the appearance of being somewhat erected.

When the cross is made, there is no regularity of inheritance of the condition of the white hairs. There is, in every generation, every variation between a ricinian and a cynthian abdomen, but the extremes are rare. The ricinian abdomen is apparently due to the lateral coalescence of the separate tufts of *cynthia*. I have not made a study of the exact anatomical relations of the brown and white hairs.

Elaborate analyses were made in regard to the bands or tufts on the successive segments and in relation to sex, colour, etc., but no definite results were obtained.

There is a certain regularity in the occurrence of the intermediate conditions—the tufts coalesce on the first segment before doing so on the second, and on the second before the third, and so on; further, there is a union of the median dorsal tuft with the upper lateral before the latter unites with the median lateral, thus reproducing the condition of *ricini*.

The actual parents used showed the two conditions clearly, but the specimens examined in the museums showed a considerable variation in both species, so that the intermediate results obtained may not be so much due to the hybridization as to the variations inherent in the parent species, but here again a larger knowledge is needed of the two species.

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A PECULIAR MODE OF INHERITANCE AND ITS CYTOLOGICAL EXPLANATION.

By Ö. WINGE.

(Report from the Genetic Laboratory of the Royal Veterinary and Agricultural College, Copenhagen.)

(With Plate XI.)

In *Drosophila* and other organisms hitherto examined in which sex-linked inheritance is found, it is the absolute rule that it has not been possible to show any factor in the unpaired *Y*-chromosome (or *W*-chromosome), whereas the *X*-chromosomes (or *Z*-chromosomes) contain many factors which are inherited sex-linked.

Goldschmidt[1], it is true, assumed that a female deciding factor in the *W*-chromosome is possibly found in *Lymantria dispar* which might serve as an explanation of the appearance of intersexual individuals in his interesting experiments. This, however, is not necessarily the case since the possibility exists that it is a question of plasmatic inheritance. Nor did Seiler succeed in showing any cytological difference in *Lymantria dispar* as to the male and female chromosomes. Thus this question may be set aside.

If we look upon a skeleton-like sketch of the sex-chromosomes, e.g. in *Drosophila melanogaster* (Text-fig. 1), we find that while the *X*-chromosomes are transferred from generation to generation in zigzag from

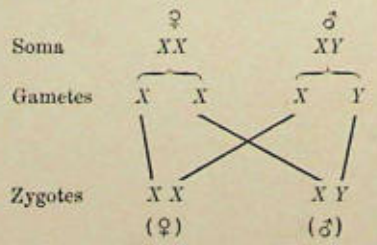


Fig. 1.

[1] "Untersuchungen über Intersexualität," *Zeitschr. f. ind. Abst. und Vererb.-lehre*, Vol. XXIII. 1920, p. 1.

one sex to the other, the *Y*-chromosomes are normally bound to the male individuals. Provided the *Y*-chromosomes contain a dominant factor, this will come out in a corresponding character, inherited from father to son, generation after generation, i.e. inheritance is literally sex-limited.

As to the hitherto examined cases of so-called sex-limited inheritance, the many investigations seem to show that the factors which form the basis of the characters in question do not have their seat in a *Y*-chromosome (or *W*-chromosome). The secondary sexual characters are, so far, not inherited in sex-limited fashion, but have their seat in chromosomes which are found in individuals of both sexes, although the characters phenotypically only appear in one of the sexes, while they are latent in the other sex.

The question of a literal sex-limited inheritance, even if it does not allow of definition, would only arise if a character could be shown following the chromosomes, which generation after generation are transferred from father to son, grandson, etc., or from mother to daughter, granddaughter, etc.

The investigations of the inheritable conditions of the cyprinodont *Lebistes reticulatus* made at the Carlsberg Laboratory, of which Dr Johs. Schmidt has given a detailed account [1], have given an exceedingly good instance of this hitherto quite unknown mode of inheritance, and the cytological investigations which I have made in order to explain the phenomenon have now been finished and are published in the present paper.

In order briefly to recapitulate the conditions of inheritance in *Lebistes reticulatus*, as they are accounted for by Dr Johs. Schmidt in his above-mentioned work, it appears that the male and female *Lebistes reticulatus* have a different appearance, the female being considerably larger than the male and of a plain greyish green colour, while the male, according to the race to which it belongs, is adorned in different ways, sometimes with red or yellow spots on the side, sometimes with a black spot on the dorsal fin, sometimes with vertical side stripes, sometimes with a round, sometimes with an elongated caudal fin. The difference in pigmentation and colouring in the males belonging to different races is very great, whereas the females, as mentioned above, virtually look alike. If a male with a black spot on the dorsal fin is crossed with a female of a race in which the males have no such spot, all the F_1 male offspring will resemble the father (i.e. have

[1] "The genetic behaviour of a secondary sexual character," *Comptes-rendus des trav. du Laboratoire Carlsberg*, Vol. XIV. No. 8, 1920.

a spot on the dorsal fin), and when attempting to segregate the material into F_2, all the F_2 males will also have a dorsal fin spot. Back-crossing of F_1 males with females of an unspotted form only gives males with dorsal fin spot, whereas F_1 females crossed with males of an unspotted form will get sons quite without dorsal fin spot. In other words it is exclusively the male that decides the looks of his sons, while the female does not in any way influence the pigmentation or colouring of her sons. No apparent segregation takes places, but an incessant imitation of the appearance of the father, of course always subject to more insignificant variations which, it is supposed, are mainly of a purely phenotypical nature.

These experiments were carried through to a great extent with about 1500 individuals and in several generations (5—6), so as to give an absolute guarantee as to the results. Furthermore, this holds good not only of a single "race" or "variety" but the same applies to several races of *Lebistes reticulatus*.

It was a natural assumption that we had to do with factors having their seat in chromosomes which were exclusively inherited through the male individuals. It is probable that a disposition in the *Y*-chromosome was shown here, and in the hope of solving the question cytologically I made the necessary fixations of both male and female individuals of the races in question of *Lebistes reticulatus*.

The Cytological Conditions of Lebistes reticulatus.

Lebistes reticulatus is not a pleasant object for an investigation of the chromosome conditions, as the chromosomes are exceedingly small in this fish. On the whole fishes seem to a small degree to have been made the object of cytological investigations. Experience has taught me that the young genital organs both of the male and the female are the organs best adapted for the studying of the chromosomes. Consequently I have mainly examined such organs. The individuals in question of *Lebistes* were decapitated, the genital organs prepared and for some hours fixed in Carnoy's liquid; after the necessary treatment and cutting on the microtome they were stained with Delafield's Hematoxylin.

Spermatogenesis. At an age of three months the males are fertile, provided they have been cultivated under favourable conditions in an aquarium placed in a light room at about 25 degrees. As has been accounted for by Erich Philippi[1] as regards some kindred species, and by

[1] "Fortpflanzungsgeschichte der viviparen Teleosteer *Glaridichthys januarius*, etc." *Zool. Jahrbücher*, Vol. XXVII. Heft 1, 1908.

Dr Johs. Schmidt (l.c.), the copulation and fertilisation take place in a very peculiar manner. Through the transformed anal fin (gonopodium) the male during the act of copulation discharges some roundish projectiles ("Spermatozeugmen"), consisting of thousands of spermatozoa, the heads of which form the cap of the projectile, while the tails are lying towards the middle of the ball. The male discharges these "Spermatozeugmen" like shot towards the genital ducts of the female. The spermatozoa, chemotactically affected by the secretion of the oviduct, are set free, and in large quantities they ciliate into the folds of the oviduct in order to fertilise the mature eggs. Some spermatozoa, however, remain in the oviduct where they are able to keep alive for several months, and when the female a month after the fertilisation has cast her young—generally in a number of 10—50—these spermatozoa can fertilise the eggs which have matured in the meanwhile. During this time the spermatozoa are lying ready by thousands in the folds of the oviduct. After the copulation they are seen lying in the ovary with their heads as near the immature eggs as possible. Off each egg they are seen lying as a shoal, their tails arranged in the form of a convoluted cord, as shown in the microphoto, Plate XI, fig. 5.

I do not intend to try to give a detailed account of the finer cytological conditions in *Lebistes reticulatus*, but only to point out the most striking features, and to account for the peculiar mode of inheritance of the male secondary sexual characters.

In the testis of a fertile male all stages of development are generally found, from the large newly developed mother-cells to spermatocysts with mature spermatozoa. The division of the nucleus generally takes place synchronally in a spermatocyst; however it occurs—especially at a later stage of development—that the contents of a spermatocyst, as regards stage of development, are divided into two parts of which one part is further divided, whereas the other part remains in a resting stage. Sometimes it is found that there is some difference as to the stage of development in the different spermatogonies of a spermatocyst. The chromosomes become very evident; however, it is not possible to ascertain their number, as they are not lying in a single layer, but so close together that it is impossible to count them. At the reduction division in the primary spermatocytes a very clear picture appears, making it possible with absolute certainty to state that the haploid chromosome number is 23. Figs. 1, 2 on Plate XI show some nuclei in which 23 chromosomes may be counted. The chromosomes are placed with great regularity, as 13 chromosomes nearly always are found on the circum-

ference, and 10 within the circumference. The chromosomes are very much alike. I myself have partly found, partly induced others to control the existence of this number so many times, that I venture to state with absolute certainty that neither more nor fewer chromosomes are found in the material which has been at my disposal.

After the reduction division the daughter nuclei remain together as seen on Plate XI, fig. 3, no secondary spermatocytes being formed, and are simultaneously dividing homoeotypically. After this division spermatocytes with four nuclear plates, Plate XI, fig. 4, and later on groups of four spermatids may be observed.

A very characteristic feature is the absolute lack of stages which may be called synapsis and diakinesis. At most a faint deposit of chromatine may be observed as a compensation for the synapsis.

The spermatids are comparatively quickly transformed into spermatozoa, the nucleus being elongated and forming the arrow-shaped split head. The spermatozoa quite fill up the cavity of the spermatocyst. Subsequently they gradually move towards the wall of the spermatocyst where they gather in large groups, each having a cell of the wall (Sertoli-cell) of the spermatocyst as a centre. At a certain stage the spermatozoa are seen lying towards the wall of the spermatocyst which is formed by one layer of cells, forming a polygonal shoal off each cell in the cellular wall. Gradually the spaces between the polygonal groups are also filled up, all the contents of the spermatocyst contracting into a globular or ellipsoid body, exclusively consisting of spermatozoa whose tails project into the middle of the ball, almost filling it, while the circumference is formed by the heads. The heads are placed very close together, and as generally all the spermatozoa do not succeed in finding a place in the circumference, a new layer of heads—as a second row—is formed. Thus the "Spermatozeugmen" are completed and glide towards the emunctory where they often gather in comparatively great quantities, gradually to be discharged—probably one at a time—during the act of copulation.

Oogenesis. On the whole the female *Lebistes reticulatus* become later mature than the males, and when fertilised they bring forth a little brood—generally about 5—10. Almost every month they will bring forth another brood, provided the conditions are favourable—as is described in detail in Johs. Schmidt's treatise (l.c.), the number of young gradually increasing; at the same time the females continue to grow considerably for many months.

The oogonies are placed—just as mentioned by Philippi (l.c.) when speaking about *Glaridichthys januarius*—partly one by one in the epithe-

lium of the cavity of the ovary, partly below the epithelium. Here the ovocytes are not formed one by one, a whole group being formed by synchronal divisions from a mother-cell, so that often more than half a dozen are found in the same group. When following these synchronal divisions of the oogonies there is a chance, although a very small one, of finding the stages of the divisions of the nuclei, rendering a counting of the chromosomes possible. Before succeeding in finding some oogonies in the proper stage of division and at the same time cut in the proper position, I have had to undertake a considerable work in vain. A great number was, it is true, observed under division, in most cases at a stage of metaphase, but very often several ovaries may be examined without finding any stages of division at all in the oogonies. It is a matter of course that consequently only a small number of the nuclei under division were placed so favourably that it was possible to count the chromosomes. Sometimes the spindle of the nucleus was cut obliquely and distributed on two sections which necessarily renders the counting of the chromosomes less accurate, as one or more chromosomes may be cut through or removed by the microtome knife, sometimes the incision plane was not parallel with the plane of division of the nucleus, which also renders the counting difficult. After many efforts I succeeded in finding some nuclei in the metaphase which seen from the pole were favourably placed. These nuclei appeared to contain a similar number of chromosomes as the male, i.e. 46. It must, however, be observed that this absolute number is not given with as great certainty as that with which the number 23 is given as regards the spermatocytes of the male. Only in a single one 46 chromosomes were counted with sufficient certainty (Plate XI, fig. 6). Fig. 7 on Plate XI seems to show only 45 chromosomes. It is quite out of the question that a higher number than 46 may be found.

As furthermore 23 pairs of gemini are found in diakinesis (Plate XI, fig. 8) there can be no doubt that also the female has 46 chromosomes.

The further development of the oogonies is of no interest for our object. The ovocytes which are finally formed are growing considerably, a great yolk being formed. Not until the fertilisation it is supposed that the reduction division, the egestion of the polar bodies, takes place, although I have not succeeded in finding this stage represented in the material at my disposal. The egg with the embryo remains in the follicle until it is full grown and the birth takes place.

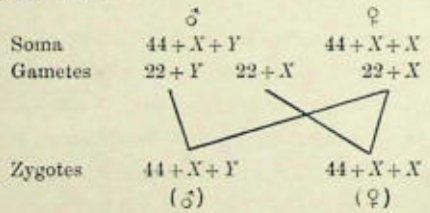
During a lapse of time of about 20 minutes to an hour and a half all the young have usually been bred and are often still provided with so

much yolk that they have sufficient food for some days. Besides they immediately start snatching small particles in the water.

As 46 chromosomes are found in the metaphase in the nuclei of the somatic cells of the female, the number of chromosomes in the two sexes is the same.

Conformity between the Mode of Inheritance and the Chromosome Conditions.

As the number of chromosomes in the two sexes is the same, it may without doubt be supposed that the chromosome conditions so far correspond to those found in *Drosophila*, the total number of chromosomes, however, being considerably larger. The result of the fertilisation is seen from the following sketch :



The *Y*-chromosome is, as will be seen, connected solely with the male individuals, and the factors this chromosome contains will not be found in the female individuals, but in all the young of male sex, and be visible, provided none of the factors in the autosomes predominate over the factors inherited through the *Y*-chromosome. It seems that the factors of the *Y*-chromosome fully dominate those of the autosomes, for, as already stated, the young of male sex always resemble the father so much that there seems to be no Mendelian segregation whatever which has influence upon their pattern and colouring.

This mode of inheritance has not yet been observed elsewhere, since inheritable characters, exclusively inherited through the male line, have not yet—as mentioned above—been shown elsewhere.

The ideas "sex-limited" and "sex-linked" inheritance will from now on be more difficult to separate. According to Morgan's definition the sex-linked characters depend on such factors as have their seat in the sex chromosomes. Our case belongs to this group. On the other hand one cannot think of characters being inherited sex-limited to a greater extent than the secondary sexual characters in *Lebistes*. I propose the term *one-sided* inheritance for our case—especially *one-sided masculine inheritance*. This term should then be used for the factors which have

their seat in the sex chromosomes only found in the one sex (*Y*- or *W*-chromosomes), whereas sex-linked inheritance concerns such factors as have their seat in the sex chromosomes found in both sexes (*X*- or *Z*-chromosomes). *Sex-limited* inheritance should probably, even though the indication is very unsatisfactory, continue to be employed as regards the factors for the secondary sexual characters found in the autosomes.

Whether the *Y*-chromosome itself also is sex-deciding is uncertain. Experiences gained from the *Drosophila* researches have proved that one must indeed take care not to state anything certain on this subject. The appearance of *Lebistes* individuals with differing chromosome conditions will probably be able to decide this question.

Finally it may be mentioned that at the Carlsberg Laboratory two forms of *Lebistes* are cultivated which differ from the other "races" in regard to inheritance of the secondary sexual characters of the male. The result of the experiments with these forms will be published in a later paper, as these experiments have not as yet been finished; but this much is known for certain, that it is a question both of one-sided masculine inheritance as well as of sex-linked inheritance. And the demonstration of both modes of inheritance in *Lebistes* does to a great extent support my view given in this treatise as to the chromosome conditions of this form.

CARLSBERG LABORATORY,
COPENHAGEN.
December 1, 1921.

EXPLANATION OF PLATE XI.

Figs. 1—2. Primary spermatocytes in heterotypic metaphase. 23 chromosomes. Obj. 1·5 mm. Oc. 18.

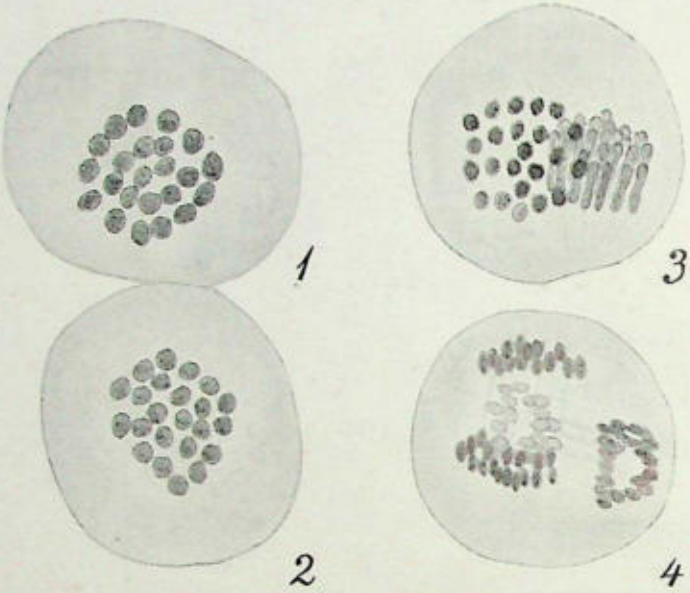
Fig. 3. Spermatocyte in homoeotypic division. No formation of secondary spermatocytes. Obj. 1·5 mm. Oc. 18.

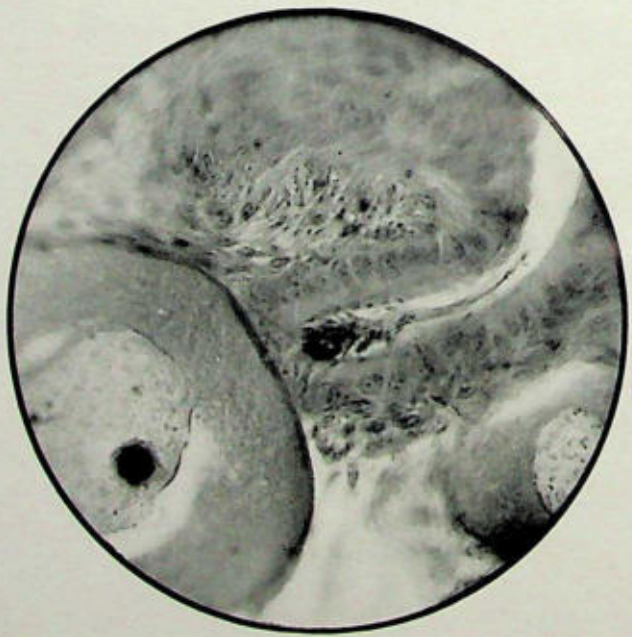
Fig. 4. Anaphase of homoeotypic division. Obj. 1·5 mm. Oc. 18.

Fig. 5. A shoal of spermatozoa off an egg in a fold of the ovary. Microphoto, unretouched.

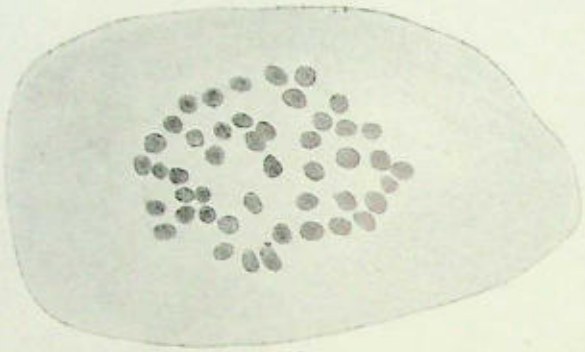
Figs. 6—7. Nuclear plates from oogonia, showing respectively 46 and apparently only 45 chromosomes. Obj. 1·5 mm. Oc. 18.

Fig. 8 *a*, *b*, *c*. Diakinesis in nucleus of a primary ovocyte. 3 sections. 23 pairs of gemini. Obj. 2 mm. Oc. 18.



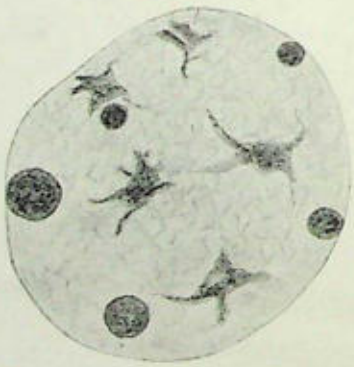


5

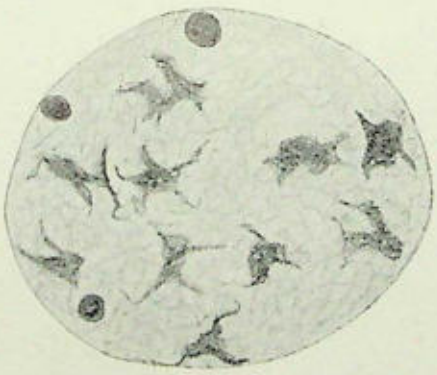


6

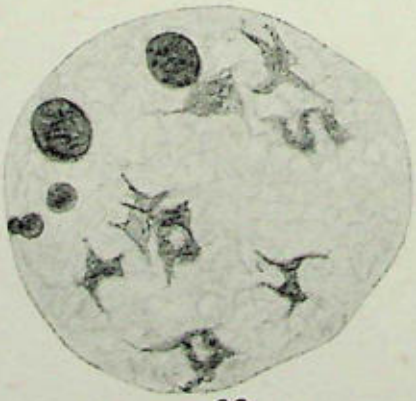
7



8a



8b



8c

ONE-SIDED MASCULINE AND SEX-LINKED INHERITANCE IN *LEBISTES RETICULATUS*.

By Ö. WINGE.

(*Report from the Genetic Laboratory of the Royal Veterinary and Agricultural College, Copenhagen.*)

(With Plates XII, XIII.)

From Schmidt's work (1920) on the inheritance of secondary male sex-characters in *Lebistes* we meet with the peculiar condition of an apparent absence of segregation for such characters; for all male offspring, notwithstanding the origin of the mother, always present the same appearance as the male parent[1].

It was impossible in any of the species mentioned in Schmidt's work to ascertain any influence whatever of the mother on the secondary sex-characters of the male offspring. This, however, did not exclude the possibility that other species behaved otherwise.

The one-sided mode of inheritance might be supposed to depend on a male sex-chromosome—as the *Y*-chromosome of *Drosophila*—constantly being transferred from father to son, without ever entering the female individuals, and that this sex-chromosome contained the factors for the said secondary male sex-characters.

This supposition induced me to make a cytological investigation of *Lebistes*. It appeared that both the male and the female had the same number of chromosomes, i.e. 46 in the somatic cells and 23 in the sexual cells; consequently the number of chromosomes of the female is probably $44 + X + X$, while that of the male is $44 + X + Y$.

However, I have not succeeded in laying down any morphological or other differences in the chromosomes, which render it possible to distinguish the sex-chromosomes from the autosomes. Thus it was a mere hypothesis to suppose that both the *Y*-chromosomes and the *X*-chromosomes existed in *Lebistes*, so that further proofs were demanded, to make out the correctness of this hypothesis.

[1] See also the present number of this Journal, p. 137.

Although a morphologically traceable *Y*-chromosome is not found, I was on the other hand obliged to take it for granted that the only explanation of the one-sided male inheritance was that such a *Y*-chromosome existed, and that it was the bearer of the one-sided inherited factors. The very fact that it was a question of *male* inheritance must be said to support the supposition to a far higher degree than a one-sided *female* inheritance; for in the latter case it was necessary to reckon with the possibility of plasmatic inheritance. As is well known, several cases of inheritance have been shown within the vegetable kingdom, which it seems possible to explain only by the supposition that in some cases plastids transfer the inheritable characters, while in other cases this is done by cytoplasm (see in this respect my treatise of 1919).

One-sided *female* inheritance could not with the same obviousness be indicative of the existence of a *W*-chromosome. It was necessary to take into consideration the possibility of cytoplasmic inheritance. The female cytoplasm, it is true, is transferred to both sexes; thus a one-sided female inheritance through the cytoplasm might, on a superficial view, seem out of the question. But where at the same time it was a question of *female sex-limited inheritance*—i.e. provided only female individuals phenotypically *showed* the said qualities—as only the males of the *Lebistes* phenotypically show the inherited secondary sex-characters—it might, in spite of everything that might be indicative that a female *W*-chromosome was the bearer of the said factors, virtually be a question of a cytoplasmic inheritance, that acts like a one-sided female inheritance. It is true, that this is mere supposition, but there would appear to be no very strong objections against it.

As mentioned in my last work, Punnett, Onslow and Goldschmidt thought it necessary to seek the explanation of certain conditions of inheritance in the presence of factors in the corresponding *W*-chromosome, i.e. what I call one-sided female inheritance, but it has not yet been shown with certainty whether the supposition is correct. Although I do not doubt for a single moment that a one-sided inheritance transferred through the *W*-chromosome must be found, I have desired in the foregoing to point out the difficulties in distinguishing the one-sided female inheritance through the chromosomes from the cytoplasmic one.

But although the existence of a *Y*-chromosome in *Lebistes*, on account of the conditions of inheritance, seems to be almost certain, it would of course be a great support for the correctness of the supposition, if it were possible to show the existence also of the *X*-chromosomes. For if the diploid chromosome number is 46 both in the male and in the

female, and if a *Y*-chromosome is found, *X*-chromosomes must also be found and thus a sex-linked inheritance is taking place, provided these *X*-chromosomes contain factors.

The present paper will prove that such *X*-chromosomes occur.

On theoretical considerations Castle (1909) long ago advanced the idea that secondary male sex-characters might accompany the *Y*-chromosome, a supposition of which the correctness has hitherto not been proved in other organisms.

In *Drosophila melanogaster* the *Y*-chromosome is empty, although it must be supposed to be of certain importance, as the males produced by "non-disjunction" are sterile if the *Y*-chromosome is wanting. One might say that the *Y*-chromosome in this case contains a "normal factor" necessary to the fertility of the males; so that this factor may be contrasted with the recessive, sex-linked, lethal factors, that have a killing effect on the males.

Although the *Y*-chromosome of *Drosophila* evidently has a physiological effect, it does not contain any factors in the sense that the males are morphologically marked hereby, as is the case with many of the other factors. And as on the whole no allelomorph to this possible "normal factor" has been shown in the *Y*-chromosome of *Drosophila*, it is only in a very improper sense that a factor is found. The factor content of the *Y*-chromosome in *Drosophila* must in reality be said to be of a doubtful nature.

In *Lebistes* on the other hand different values of the *Y*-chromosome have, as we know, been shown, since the *Y*-chromosome of each race has its special effect; and this brings it about that the secondary male sex-characters of each single race are inherited through the male line.

As yet it has not been possible to state whether the *Y*-factors in the different races are placed in the same locus in the chromosomes, i.e. whether they are allelomorphs. In case individuals with two *Y*-chromosomes were found, crossing-over might perhaps be possible, thereby proving whether they were absolutely linked real allelomorphs. Nor is it possible to say whether the *Lebistes* factors are dominant or recessive; for whether they are one or other their effect will presumably appear as long as no corresponding *Y*-chromosome is found. Their effect is so far epistatic in that no factors have as yet been found in the autosomes or the *X*-chromosomes that might conceal their effect.

As before mentioned, it is characteristic that the *X*-chromosome and *Y*-chromosome in the spermatocytes during the reduction division do not act otherwise than the autosomes, and cannot be distinguished from the

latter; I therefore take it for granted that the *X*-chromosome of the male individual in all respects acts like the partner of the *Y*-chromosome. That crossing-over between these two chromosomes may even take place —a phenomenon of extreme interest—will be treated in the last section of this treatise, although I reserve myself to undertake more elaborate investigations in a later work.

After these more general observations I may pass on to submit the special part of my investigations.

Effects of the Factors in X- and Y-chromosomes.

In order to facilitate the understanding of the crossing experiments undertaken by me, I shall submit the main results of these experiments at once; afterwards I shall mention the experiments themselves which form the basis of the results.

As mentioned before, *Lebistes reticulatus* has 46 chromosomes in the somatic cells of both sexes, the female having $44 + X + X$, while the male has $44 + X + Y$. No attention will be paid to the 44 autosomes here, for it is only the sex-chromosomes that play an essential part in the inheritance of the secondary male characters, i.e. only the sex-chromosomes contain the essential factors for the colour patterns, which are here taken into consideration.

In the different *Lebistes* races the *X*-chromosomes, as also the *Y*-chromosomes, are of different value, i.e. contain different characteristic colour factors. The *Y*-chromosome always contains factors for some colour pattern or other, while the *X*-chromosome only in certain races contains such factors, being empty in other races.

Where only the *Y*-chromosome in a given race contains factors, the above-mentioned one-sided male inheritance will be found dependent on the *Y*-chromosome being inherited only through the male line. If on the other hand the *X*-chromosomes also contain colour factors, the mode of inheritance on crossing is found to be a combination of the usual sex-linked inheritance and one-sided masculine inheritance.

Even if female individuals contain colour factors in their *X*-chromosomes, they remain phenotypically uncoloured, as only the males are coloured. This recalls de Meijere's account of *Papilio memnon* (1910), and Fryer's case of *Papilio polytes* (1913), in both of which the males always have the same appearance, while the females may be of different phenotype according to their genotypical content. That it is the opposite sex, the females, which in *Lebistes* are always phenotypically alike, is

evidently attributable to the fact that it is the female which here is the homogametic sex, while it is the male in the butterflies.

The two *X*-chromosomes of a *Lebistes* female may be alike or may differ as to their factor content. Thus we have homozygotic and heterozygotic females; the latter form two kinds of eggs in equal numbers.

A male *Lebistes* is always heterozygotic, as it is heterogametic, its *X*- and *Y*-chromosomes not containing the same factors. Thus the male *Lebistes* constantly forms two kinds of spermatozoa, of which one—the one with *Y*—is male determining, while the other—with *X*—is female determining.

In the male *Lebistes* containing a colour factor both in the *X*-chromosome, and in the *Y*-chromosome, the corresponding characters are phenotypically visible at the same time. The effects of the two factors are combined, leading to a sort of compromise between them. Thus it is possible in each male individual to see what factors it contains, whereas the females phenotypically are indistinguishable.

As only the males show the characters, we have *sex-limited* inheritance as a further complication; this badly designated conception is, as far as inheritance is concerned, of minor importance, as it is only a question of phenotypical differences between the male and female.

On the last 3 rows of Plate XIII I have reproduced in skeleton form the single effects of the factors[1] found in the *Lebistes* races with which I am engaged in this work, as also some instances of the combined effects of the same factors.

We shall here go over the said factors, or—more correctly—the "effects of the chromosomes" on the compound characters. They are called *X* and *Y* according as the factors are contained in an *X*- or *Y*-chromosome, and as index a letter is added to indicate in shortened form the most characteristic colour effect of the factor.

Of *the X-chromosomes* only two will be mentioned:

X_o does not involve any colour pattern of the males (see Plate XIII).

X_s (*sulfureus*) (see Plate XIII).

(1) Sulphur yellow colour in the dorsal fin and a dark dot that only at times is visible in the said fin.

(2) Sulphur yellow colour in the tail and in the caudal fin.

(3) Red colour in the lower edge of the caudal fin.

[1] That they are not single factors but complex ones is a matter which will be dealt with later.

Of *the Y-chromosomes* we shall mention four types:

Y_r (*ruber*) involves (see Plate XIII)

(1) Red colour proximally in the upper edge of the caudal fin.

(2) Large oblong red side-spot, lying for the most part below and behind the dorsal fin.

(3) Dark side-dot in the tail at the base of the caudal fin.

Y_i (*iridescens*) involves (see Plate XIII)

(1) A characteristic mother-of-pearl sheen on the body.

(2) 2—3 red smaller side-spots.

(3) Black side-dot on the tail near the caudal fin.

(4) Black side-dot on the body.

Y_m (*maculatus*) involves (see Plate XIII)

(1) Large black spot in the dorsal fin.

(2) Large red side-spot below and in front of the dorsal fin.

(3) Black dot at the gat (sometimes invisible).

Y_f (*ferrugineus*) involves (see Plate XIII)

(1) Black rust-coloured part in the proximal part of the caudal fin.

(2) Black side-dot in the tail near the caudal fin.

The said effects of the factors must be understood in the sense that I have only mentioned the constant "positive" effects. I have, for example, stated that Y_m involves a black spot in the dorsal fin, while it is not stated—what in itself might be justified—that Y_i involves the uncoloured dorsal fin. Besides the colour patterns dealt with above, other less conspicuous differences might be included. Thus, there are cases in which a little red side-spot occurs more or less constantly on the front of the breast, and so on. Doubtless the phenotypical variation plays a part as regards these less constant patterns, but it is not impossible that the autosomes may contain important factors. We need not busy ourselves with this question here. The colour patterns beyond the said characteristics are under all circumstances of such small extent that they do not in any way conceal the factor effects described.

The races of *Lebistes* that have been used for the crossing experiments mentioned in this treatise have the following formulae:

The "*Magdeburg Race*" ... ... (Plate XIII, figs. 23—25)	$X_s X_s$	$X_s Y_r$
The "*Spot Race*" ... ... (Plate XIII, fig. 30)	$X_o X_o$	$X_o Y_m$
The "*Old Race*" ... ... (Plate XII, fig. 13)	$X_o X_o$	$X_o Y_i$

The names of the races refer to the designations which they have received during the daily work in the Laboratory. When comparing the pictures of the coloured tables with the above descriptions of the effects of the factors, one will easily obtain a notion of the peculiarities of the single races.

In addition to the above-mentioned three races, the effect of the *Y*-chromosome has been described above in a fourth race, i.e. the *Y*-chromosome of the so-called "*Hamburg Race*." As the conditions of inheritance of this race have not as yet been used in the experiments treated here, I shall confine myself to the above mention of the factor effect of the *Y*-chromosome and to the illustration on Plate XIII.

The Crossing Experiments.

As will be seen from the preceding, it only holds good of a single one of the above-mentioned races—the "*Magdeburg Race*"—that the *X*-chromosome (X_s) contains a factor for the colour pattern of the males, i.e. the factor (the complex factor) *s*. In the "*Spot Race*" and the "*Old Race*" on the other hand the *X*-chromosomes (X_o) are empty, as is also the case with the *Y*-chromosome of *Drosophila*.

Although I have determined the presence of colour factors in *X* for other *Lebistes* races, the work is not yet sufficiently complete for publication; and, therefore, I shall confine myself to the crosses I have made with the "*Madgeburg Race*" in order to show the combined sex-linked and one-sided masculine inheritance.

A general description of the "*Magdeburg Race*" is as follows:

The female individuals, as with all the *Lebistes* forms, are dark greyish green, semi-transparent, without any colour pattern, and with nearly colourless fins. The males are characteristic in the body and the tail having a vivid red and yellow pattern. Especially conspicuous is a large oblong side-spot below the dorsal fin and extending somewhat behind it. On the breast may be found a little black and a little red spot, the black one usually above the red one. The dorsal fin is of a vivid yellow colour and sometimes also has a little black spot. The lower edge of the tail has the same vivid yellow colour as the dorsal fin, and there is a dark side-spot on the tail near the caudal fin. The form of the caudal fin is not quite round, but has a tendency to be prolonged above and below, the prolongation however not being flagelliform. The prolongation tendency often shows itself in the hindmost edge becoming more

or less vertical instead of rounded. The caudal fin has a red and yellow pattern, of which a vivid red patch at the top, proceeding from the root of the fin, is especially noticeable, while another somewhat similar patch is seen below.

It has already been stated, that the factors for the colour pattern of the "*Magdeburg Race*" are placed partly in the *X*-chromosome, partly in the *Y*-chromosome. I would refer here to the illustration of the three "*Madgeburg*" males in figs. 23—25 of Plate XIII, and to the figures on the same Plate representing the single effect of Y_r and X_s, as also the combined effect of $Y_r + X_s$, which thus is a skeleton-like produced "*Magdeburg*" male.

The crossing experiments I have made with the "*Magdeburg Race*" were commenced as early as 1917, but as other work was then considered to be of greater importance, the recording and drawing of the different types of the young individuals were partly neglected. During the last year I have again thoroughly gone into the material, so that I have realised that beside the one-sided masculine inheritance, sex-linked inheritance is also taking place. This is so much more to be regretted, since the *Lebistes* females of late years have suffered from a rather limited propagation ability, so that only rarely have I had such large hatches as in former years. Twenty young in one hatch is at present highly satisfactory, while double the number in former years was general. The birth-rate has also decreased, as the females now seldom bring forth one hatch of young per month as was formerly the case.

The crossings made are the following:

I. "*Spot Race*" ♀ 149 × "*Magdeburg Race*" ♂ 114
$X_o X_o$ | $X_s Y_r$

♀♀ | ♂♂

F_1 Theoretically: All $X_o X_s$ | All $X_o Y_r$

Found: Of which
174 used in Exp. IV
175 „ „ V
176 „ „ VI
| 44 $X_o Y_r$ All[1] as in Plate XIII, figs. 26—28 [of which some used for Exp. XIV]

♀♀ | ♂♂

F_2 Theoretically: 1 $X_o X_o$: 1 $X_o X_s$ | 1 $X_o Y_r$: 1 $X_s Y_r$

Found: | 7 $X_o Y_r$ + 7 $X_s Y_r$

[1] Besides a deviating male, the only individual in all the experiments mentioned in this treatise that did not fall in with what was expected. It will be made the object of a closer examination later.

II. "*Magdeburg Race*" ♀ 244 × "*Spot Race*" ♂ 189
$X_s X_s$ | $X_o Y_m$

♀♀ ♂♂

F_1 Theoretically: All $X_s X_o$ All $X_s Y_m$
Found: 1[1] $X_s Y_m$, depicted in Plate XII, fig. 2 [used as ♂ 334 in Exp. XIII]

III. "*Magdeburg*" ♀ 188 × "*Spot Race*" ♂ 189
$X_s X_s$ | $X_o Y_m$

♀♀ ♂♂

F_1 Theoretically: All $X_s X_o$ All $X_s Y_m$
Found: Of which ♀ 258 used for F_2, ♀ 335 „ Exp. VII, ♀ 337 „ „ VIII, Others „ „ IX — 2[2] $X_s Y_m$ Used as ♂ 259 in Exps. XI, XII and for F_2; ♂ 280 in Exp. X

♀♀ ♂♂

F_2 Theoretically: 1 $X_s X_s$: 1 $X_o X_s$ 1 $X_s Y_m$: 1 $X_o Y_m$
Found: [Of F_1 ♀ 258 × F_1 ♂ 259] 3 $X_s Y_m$ + 1 $X_o Y_m$

The above-mentioned F_1 individuals have—as will be seen—the following formulae:

F_1 All F_1 ♀♀ $X_o X_s$
♂♂ of "*Spot Race*" × "*Magdeburg*" : $X_o Y_r$
"*Magdeburg*" × "*Spot Race*" : $X_s Y_m$

The appearance of the above-mentioned 47 F_1 males agrees with what was theoretically expected, as they all have received the factors characteristic of the *Y*-chromosome of the paternal race. That the nature of the offspring from the F_1 parent of both sexes is consistent with the theory will appear partly from the appearance of the F_2 individuals, and partly from the following crossings.

As will be seen, the two types of F_1 males, which are produced by the reciprocal crosses, contain quite different colour factors, namely $X_o Y_r$ and $X_s Y_m$ respectively, while the F_1 females all have the formula $X_o X_s$.

Re-crossing of F_1 ♀ ♀ $X_s X_o$ with the "Magdeburg" father $X_s Y_r$.

IV. ♀ 174 [from Exp. I] × ♂ 114
$X_s X_o$ | $X_s Y_r$

♀♀ ♂♂

Theoretically: 1 $X_s X_s$: 1 $X_o X_s$ 1 $X_s Y_r$: 1 $X_o Y_r$
Found: 4 $X_s Y_r$ + 4 $X_o Y_r$

[1] Several individuals of the same appearance have not been entered.
[2] Several individuals of the same appearance have not been entered.

V. ♀ 175 [from Exp. I] × ♂ 114
$X_s X_o$ | $X_s Y_r$

	♀♀	♂♂
Theoretically:	1 $X_s X_s$: 1 $X_r X_s$	1 $X_s Y_o$: 1 $X_o Y_r$
Found:		1 $X_s Y_r$ + 1 $X_o Y_r$

VI. ♀ 176 [from Exp. I] × ♂ 114
$X_s X_o$ | $X_s Y_r$

	♀♀	♂♂
Theoretically:	1 $X_s X_s$: 1 $X_o X_s$	1 $X_s Y_r$: $X_o Y_r$
Found:		2 $X_s Y_r$ + 2 $X_o Y_r$

The three F_1 females (Experiments IV—VI) thus by re-crossing with the father have given two kinds of sons in equal number, in all $7\ X_s Y_r : 7\ X_o Y_r$ as expected. Despite the very small number an equal number of the two types has by chance fallen in each of the three crossings.

Other Crossing Experiments with F_1 ♀♀ $X_s X_o$.

VII. ♀ 335 [from Exp. III] × "*Old Race*" ♂ 336
$X_s X_o$ | $X_o Y_i$

	♀♀	♂♂
Theoretically:	1 $X_s X_o$: 1 $X_o X_o$	1 $X_s Y_i$: 1 $X_o Y_i$
Found:		7 $X_s Y_i$ + 5 $X_o Y_i$

Individuals from this cross will be found figured on the lower half of Plate XII, where female 335 and male 336 are seen reproduced with 9[1] of the sons, viz. 5 with $X_s Y_i$ and 4 with $X_o Y_i$.

VIII. ♀ 337 [from Exp. III] × "*Spot Race*" ♂ 338
$X_s X_o$ | $X_o Y_m$

	♀♀	♂♂
Theoretically:	1 $X_s X_o$: 1 $X_o X_o$	1 $X_s Y_m$: 1 $X_o Y_m$
Found:		9 $X_s Y_m$ + 5 $X_o Y_m$ [of which ♂ 379 $X_o Y_m$ used for Exp. XVIII]

Individuals concerned in this cross will be found represented on Plate XIII. Figs. 29 and 30 represent the parents; while 3 $X_o Y_m$ sons are shewn in figs. 31, 34, 36, and 3 $X_s Y_m$ sons in figs. 32, 33, 35.

IX. F_1 ♀♀ [several individuals of Exp. III] × "*Old Race*" ♂ 340
$X_s X_o$ | $X_o Y_i$

	♀♀	♂♂
Theoretically:	1 $X_s X_o$: 1 $X_o X_o$	1 $X_s Y_i$: 1 $X_o Y_i$
Found:		11 $X_s Y_i$ + 14 $X_o Y_i$

[1] On account of lack of space only a few individuals from the different experiments are figured.

It will be seen from the above experiments that F_1 females ex "*Magdeburg*" × "*Spot Race*," together with the reciprocal, accord with the theory in having the formula $X_s X_o$; for half of their male offspring show yellow in the dorsal fin, on the lower edge of the tail, and in the caudal fin, together with red on the lower edge of the caudal, all of which is due to the chromosome X_s, while the other half lack these colours, as their X-chromosome, X_o, does not contain any colour factor. In accordance with the theoretically expected relation 1 : 1, we find that the offspring of F_1 females, $X_o X_s$ in the above-mentioned experiments, were 39 males with X_o and 44 with X_s. When we include the offspring of the $X_o X_s$ females mentioned below, the theoretical expectation of equality is exactly attained, as altogether we have 50 individuals with X_o and 50 with X_s.

Crossing Experiments with F_1 ♂♂ $X_s Y_m$ (from "Magdeburg" × "Spot Race").

X. "*Spot Race*" ♀ 279 × ♂ 280 [from Exp. III]
$X_o X_o$ | $X_s Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_s$	All $X_o Y_m$
Found:		11 $X_o Y_m$

XI. "*Spot Race*" ♀ 260 × ♂ 259 [from Exp. III]
$X_o X_o$ | $X_s Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_s$	All $X_o Y_m$
Found:		13 $X_o Y_m$

XII. "*Spot Race*" ♀ 341 × ♂ 259 [from Exp. III]
$X_o X_o$ | $X_s Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_s$ [Of which ♀ 353 used in Exp. XVII.]	All $X_o Y_m$
Found:		3 $X_o Y_m$ [Of which used ♂ 364 in Exp. XIX, ♂ 365 ,, XX]

XIII. "*Spot Race*" ♀ 333 × ♂ 334 [from Exp. II]
$X_o X_o$ | $X_s Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_s$	All $X_o Y_m$
Found:	[Of which used ♀ 350 in Exp. XV, ♀ 351 ,, XVI]	36 $X_o Y_m$

(See moreover experiment III, F_2)

Individuals from this experiment are reproduced at the top of Plate XII. In figs. 1 and 2 female 333 and male 334 are seen, and in figs. 3—11 are shewn 9 out of the 36 sons of similar appearance. These all have the character of the pure "*Spot Race*" ($X_o Y_m$), as the sex-linked inheritance involves that none of the sons receives the X_s character, while this character on the other hand is transferred cryptomerically to all the daughters.

Experiments X—XIII show very clearly the combined sex-linked and one-sided masculine inheritance in *Lebistes*. While none of the F_1 males used ($X_s Y_m$) transfers the X_s-colours of the "*Magdeburg Race*" to their sons—63 in number—all the sons have received the one-sided masculine inherited Y_m-chromosome and consequently the black spot in the dorsal fin and so on.

Crossing Experiments with F_1 ♂ ♂ $X_o Y_r$ (from "Spot Race" × "Magdeburg Race").

XIV. "*Spot Race*" ♀ 200 ($X_o X_o$) × Several F_1 ♂ ♂ [from Exp. I] ($X_o Y_r$)

	♀♀	♂♂
Theoretically:	All $X_o X_o$	All $X_o Y_r$
Found:		8 $X_o Y_r$

Crossing Experiments with segregated $X_o X_s$.

XV. ♀ 350 [from Exp. XIII] ($X_o X_s$) × "*Spot Race*" ♂ 354 ($X_o Y_m$)

	♀♀	♂♂
Theoretically:	1 $X_o X_o$: 1 $X_s X_o$	1 $X_o Y_m$: $X_s Y_m$
Found:		1 $X_o Y_m$

XVI. ♂ 351 [from Exp. XIII] ($X_o X_s$) × "*Spot Race*" ♂ 355 ($X_o Y_m$)

	♀♀	♂♂
Theoretically:	1 $X_o X_o$: 1 $X_s X_o$	1 $X_o Y_m$: 1 $X_s Y_m$
Found:		10 $X_o Y_m$ + 5 $X_s Y_m$

XVII. ♀ 353 [from Exp. XII] ($X_o X_s$) × "*Spot Race*" ♂ 357 ($X_o Y_m$)

	♀♀	♂♂
Theoretically:	1 $X_o X_o$: 1 $X_s X_o$	1 $X_o Y_m$: 1 $X_s Y_m$
Found:		1 $X_s Y_m$

Crossing Experiments with segregated $X_o Y_m$ ♂ ♂.

XVIII. "*Spot Race*" ♀ 377 × ♂ 379 [from Exp. VIII]
$X_o X_o$ | $X_o Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_o$	All $X_o Y_m$
Found:		6 $X_o Y_m$

XIX. "*Spot Race*" ♀ 360 × 364 [from Exp. XII]
$X_o X_o$ | $X_o Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_o$	All $X_o Y_m$
Found:		3 $X_o Y_m$

XX. "*Spot Race*" ♀ 361 × ♂ 365 [from Exp. XII]
$X_o X_o$ | $X_o Y_m$

	♀♀	♂♂
Theoretically:	All $X_o X_o$	All $X_o Y_m$
Found:		2 $X_o Y_m$

Finally, male 383, which originated in Experiment IV, and which, from its appearance, had the formula $X_s Y_r$ was crossed with a female of another race. The six males thus produced all had the red colour pattern proximally in the upper edge of the caudal fin, and the other peculiarities accompanying Y_r, while they all lacked the red and yellow patterns accompanying X_s, as was expected.

Crossing-over between the X- and Y-chromosome.

From the above experiments we cannot decide whether each single colour character depends on one, or more genes. As long as the chromosomes retain their integrity, it is impossible to decide whether a whole series of factors in the chromosome, or only a single one, is responsible for the hereditary phenomena.

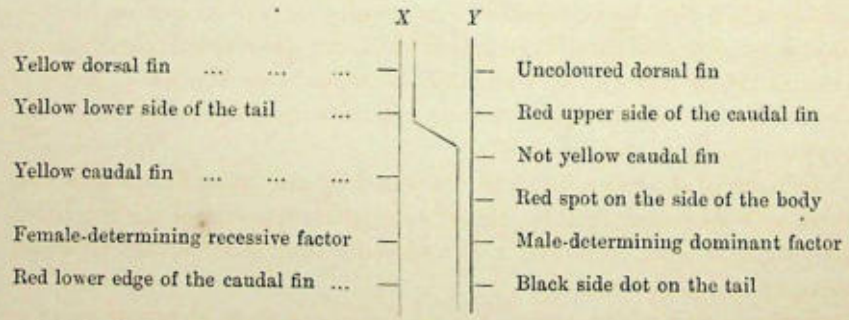
However, I have in my experiments a few highly interesting cases which admit of no doubt that the colour characters in a chromosome are due to more than a single gene, since I have substantiated crossing-over between the *X*- and *Y*-chromosome in *Lebistes* males.

In Experiment I it was found that when crossing a pure "*Spot Race*" female 140 ($X_o X_o$) with a pure "*Magdeburg*" male ($X_s Y_r$) 44 males were produced, all of which looked alike (cf. Plate XIII, figs. 26—28). Characteristic of all these F_1 males ($X_o Y_r$) was (1) red colour

proximally in the upper edge of the caudal fin, (2) a long red side-spot placed below and behind the dorsal fin, (3) a dark side-dot in the tail near the caudal fin, sometimes displaced into the caudal fin, and (4) a colourless dorsal fin, i.e. they all showed the characters due to the factors in the *Y*-chromosomes. None of them had the yellow colour on the dorsal fin, on the lower side of the tail and on the caudal fin, nor the red colour on the lower edge of the caudal fin, which accompanies the X_s-chromosome of the "*Magdeburg Race*." All this is in accordance with the fact that the *X*-chromosome alone was transferred to all the daughters of male 114 ($X_o X_s$).

In addition to the 44 males another male individual was, however, found (mentioned in foot-note p. 152) which was of quite special interest, as it had the yellow dorsal fin and the yellow colour on the lower side of the tail which follow the X_s-chromosome, while it lacked completely the red and yellow colours in the caudal fin, which was consequently uncoloured.

As I have found a somewhat similar instance in another of my cultures, I entertain the view that the said individual is brought about by crossing-over between the X_s- and the Y_r-chromosome, as shown diagrammatically in the following sketch of the chromosomes:



This is the only way in which the origin of the individual can be explained.

I am sorry to say that the individual in question was not submitted to any genetic analysis, for it occurred at such an early stage of the experiments—being born in October 1917—that I did not fully realize its significance at that time, as I was engaged in other investigations. Therefore, the individual was only registered, while I myself drew it with colours in June 1918 together with its 44 brothers. On the drawing of the individual, which I recollect very well, I noted: "Very anomalous specimen; notwithstanding fully developed."

In itself it is not strange that a crossing-over may take place between chromosomes which are morphologically alike, and which evidently conjugate like the autosomes previous to the reduction division; and perhaps it is correct to suppose that, at any rate here in *Lebistes*, there is no other principal difference between the *X*- and *Y*-chromosomes than that the latter contains a dominating factor for the male sex, while the former contains the allelomorphic factor for the female sex.

The case is of considerable interest, as it suggests *that a crossing-over between an X- and a Y-chromosome may take place, and the hitherto sharp limit between the X- and Y-chromosomes has been done away with.* I suppose that all investigators of heredity will realize the highly important consequences in respect of the theory of heredity entailed by this fact.

I expect before long to be able to give the decisive proof of the crossing-over by the experiments I am now undertaking, experiments which already are fairly advanced.

DISCUSSION.

As will appear from the experiments, the mode of inheritance of the secondary sex-characters in *Lebistes* is clearly either one-sided masculine, namely when the *X*-chromosomes are empty, or a combination of one-sided masculine and sex-linked inheritance, viz. when the *X*-chromosome contains colour factors. To this must be added that the whole mode of inheritance is sex-limited to the male individuals, as the factors are found cryptomerically in the females.

In none of the races hitherto examined by me, were *Y*-chromosomes found without colour factors; therefore it is the opposite of the condition in *Drosophila* where it is the *Y*-chromosome that lacks factors affecting the morphological structure.

Since an exchange between *X*- and *Y*-chromosomes, as briefly pointed out, may take place, it is probably only a matter of time when it will be possible to find in Nature—or to produce experimentally—*Lebistes* males without colour factors in the *Y* chromosome. There is a possibility that the sex-determining factor is extremely closely linked to some colour factor or other, so that crossing-over only takes place very seldom. That the sex-determining factors should be identical with some of the colour factors is, it is true, improbable, as males of different *Lebistes* races have different colour factors, but notwithstanding they all evidently contain a dominating male sex factor. But as regards the sex factors it may also be a question of multiple allelomorphs.

The allelomorph conditions are as yet an open question as far as *Lebistes* is concerned. Although the factors for colour pattern found in the X-chromosomes act like allelomorphs in the above-mentioned experiments, it is certainly only on account of the relative rareness of the crossings-over, or of the insufficiency of the material, that this appears to be the case. At any rate the above-mentioned cross-over male has shown that the X_s character and the Y_r character are divisible unities.

I cannot finish this work without conveying my warmest thanks to Dr Johs. Schmidt, Director of the Physiological Department of the Carlsberg Laboratory, who entrusted me with the *Lebistes* material for further investigation when I left the Laboratory in the spring of 1921. He also provided room for the *Lebistes* cultures, until my own laboratory was able to contain the necessary aquaria. I also thank Mr J. Clausen, M.A., who with great care has assisted me of late years, and the commissionaire of the Laboratory, Mr N. R. Poulsen, who has had charge of the feeding of the fishes.

Résumé.

1. It is shown that in a race of *Lebistes reticulatus* sex-linked inheritance of the secondary male sex-characters occurs in connection with the one-sided masculine inheritance found in the *Lebistes* races hitherto examined.

2. This result agrees with the previous demonstration of 46 chromosomes in both sexes of *Lebistes*, the female having presumably $44+X+X$ chromosomes, and the male $44+X+Y$. The factors found in the X-chromosomes show sex-linked inheritance, those in the Y-chromosomes show one-sided masculine inheritance.

3. Two kinds of X-chromosomes are described differing as to their genetic content, of which one is empty (X_o), while the other (X_s) contains characteristic factors for secondary male sex-characters. The colour effects of the chromosomes are depicted and described.

4. Four Y-chromosomes differing as to their genetic content are described (Y_r, Y_i, Y_m, Y_f) that severally contain characteristic factors for secondary male sex-characters. The colour effect of the four Y-chromosomes are described and depicted.

5. If both the X- and Y-chromosome in a *Lebistes* male involve factors for colour pattern, the colour effects in the individual are added

up; consequently it is possible by direct observation to judge of the genotype of each male.

6. In the females the factors are always found cryptomerically, therefore all females look alike. In this respect inheritance in *Lebistes* is further sex-limited.

7. Crossing-over between the *X*- and the *Y*-chromosome in a male individual has been noted, by which colour factors are exchanged, and the sharp separation between the *X*- and *Y*-chromosomes has thus been removed. The above described secondary male sex-characters in *Lebistes* are not a consequence of single factors, but of a series of linked factors.

COPENHAGEN, 17 *May* 1922.

EXPLANATION OF PLATES.

PLATE XII.

Fig. 1. ♀ 333 ("Spot Race") = $X_o X_o$.
Fig. 2. ♂ 334 (from Exp. III) = $X_s Y_m$.
Figs. 3—11. Nine sons ex ♀ 333 × ♂ 334. All of composition $X_o Y_m$.
Fig. 12. ♀ 335 (From Exp. III) = $X_o X_s$.
Fig. 13. ♂ 336 ("Old Race") = $X_o Y_t$.
Figs. 14—22. Nine sons ex ♀ 335 × ♂ 336. Nos. 14, 16, 18, 21, and 22 are $X_s Y_t$ in composition; Nos. 15, 17, 19, and 20 are $X_o Y_t$.

PLATE XIII.

Figs. 23—25. Three ♂ ♂ of the "Magdeburg Race" = $X_s Y_r$.
Figs. 26—28. Three ♂ ♂ ex ♀ 140 ("Spot Race" = $X_o X_o$) × ♂ 114 ("Magdeburg Race" = $X_s Y_r$). All of composition $X_o Y_r$.
Fig. 29. ♀ 337 (from Exp. III) = $X_s X_o$.
Fig. 30. ♂ 338 ("Spot Race") = $X_o Y_m$.
Figs. 31—36. Six sons ex ♀ 337 × ♂ 338. Nos. 31, 34, and 36 are $X_o Y_m$; Nos. 32, 33, and 35 are $X_s Y_m$.

The remaining nine figures at the bottom of Plate XIII represent schematically the effects produced by the various factors in the *X* and *Y* chromosomes, both singly and in combination. For explanation, see text, pp. 149—150.

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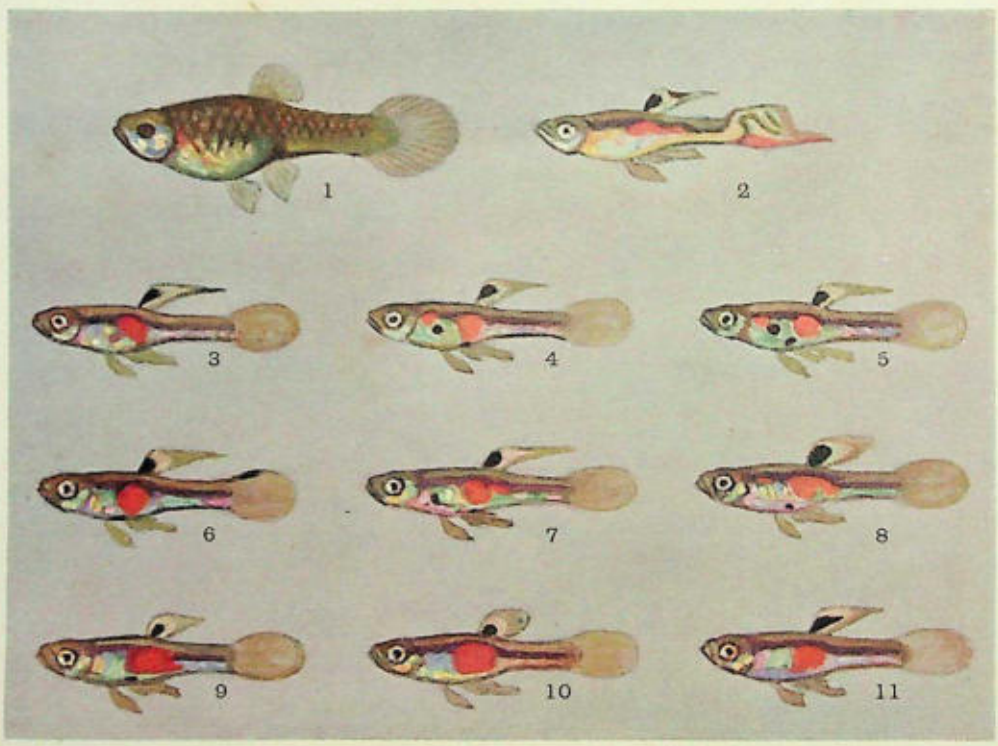
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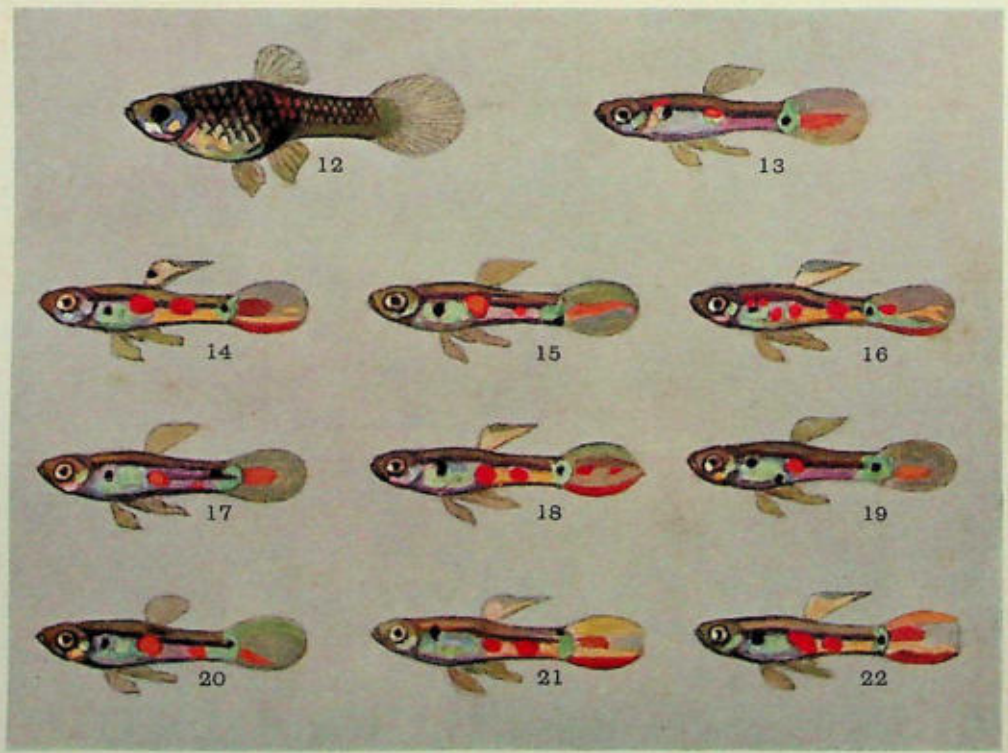
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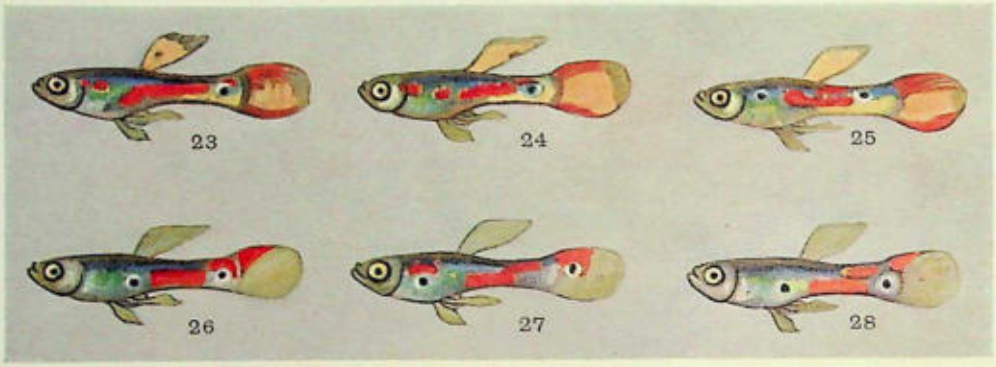
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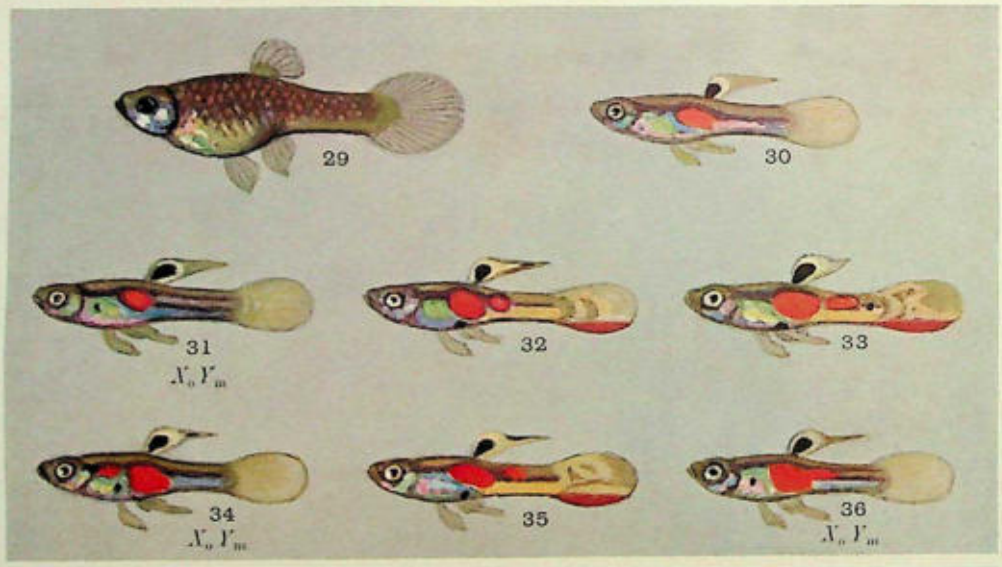
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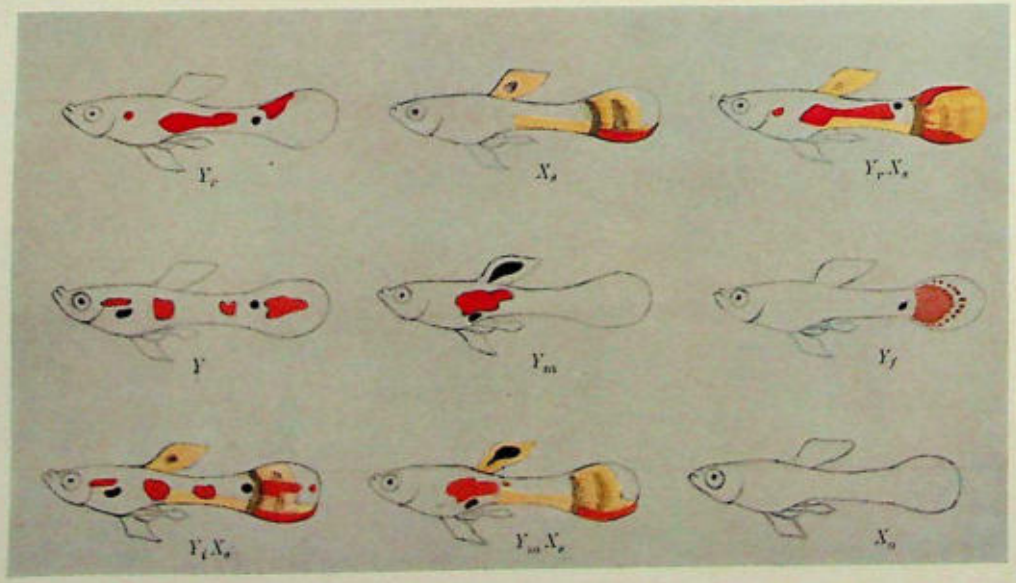
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SEX-LINKAGE IN THE SILKWORM[1].

By Y. TANAKA,

Department of Agriculture, University of Kyushu, Japan.

(With Plate XIV.)

When I was working at Fukushima in the summer of 1916, I happened to find three lots[2] of F_1 silkworms (Ex. *Okusa* (Japanese bivoltine) ♀ × *Giallo puro indigeno* (Italian univoltine) ♂) in which a number of animals with translucent skin were found mixed with more numerous normals. These translucent silkworms were all females, while the normals consisted of both sexes. By mating these translucent females with their normal brothers I got some males showing the same translucency. This form of translucency proved to be sex-linked, following the same system of descent as that well known in *Abraxas*. At first I did not know from which parent the linked factor came, but later I found some translucent females in a pure breed of *Giallo puro indigeno*, which possessed the sex-linked character. Hence it is evident that the linked factor is introduced by the Italian parent, but not by the Japanese. I started my experiments with these materials and am still continuing them with the addition of a considerable number of translucent silkworms from various sources.

Having examined the translucent larvae which belong to thirty-seven different races and strains, I have found that there are at least eight translucent factors, any one of which, when homozygous, is able to make the skin translucent. Among these multiple translucent factors, one is sex-linked, while the others are all independently transmitted so far as the sex is concerned.

A brief account on the subject was given in a Japanese sericultural journal (1917), and further results were mentioned in one of my books (1919), both in Japanese. Except these, there has been, so far as I am aware, no literature published concerning sex-linkage in the silkworm.

[1] These experiments were done at Fukushima Branch of Imperial Sericultural Institute, Japan, by kind permission of Dr T. Kagayama, the Director of the Institute.

[2] A "lot" means the whole group of the offspring from a pair of parents.

I. Morphological Characters of Translucent Silkworms.

The normal silkworms are provided with the skin opaque white in ground colour, the opacity perhaps owing to white granules contained in the epidermal cells. The skin of translucent silkworms is, on the contrary, more or less destitute of the opaqueness, allowing some internal organs and tissues, e.g. muscles, fatty tissues, tracheas and the dorsal vessel, to be seen from outside to a certain extent.

The translucency is, however, not necessarily uniform in degree but differs in different races. In some races, it is highly developed and more approaches to transparency, while in others it is difficult to distinguish from opaque without sufficient caution. The character attains its highest development only in the last instar of the larval life, though it is distinguishable in much younger instars. When a larva gets full-grown and evacuates all green contents of the stomach preparing for spinning, the body becomes translucent even in normal silkworms, and becomes very difficult to distinguish from the translucent type. In moths, the character is, as a rule, hardly distinguishable except in certain races in which it is still conspicuous in the adult form.

The sex-linked translucent silkworm belongs to the type in which the character is not highly developed, but this is not the characteristic of the sex-linked strain alone, since some non-sex-linked silkworms show an appearance quite like it, so that you cannot guess at all by mere inspection whether a silkworm belongs to the sex-linked strain or not.

In my previous paper (1916), I stated that a translucent factor[1] is recessive to its normal allelomorph. This holds true for all translucent factors which have been examined since 1916, no matter whether they are sex-linked or not.

II. Crossing between Sex-linked Translucent and Normal.

1. *Sex-linked Translucent* ♀ × *Normal* ♂. (Table I.)

F_1.

Number of the lots	Normal	Translucent
15	4405	0

In nine lots out of fifteen, the sexes were discriminated, the result follows: 1374 females, 1354 males, total 2728.

F_2. Number of the lots, 17.

	Normal	Translucent	Totals
Females ...	1362	1301	2663
Males ...	2510	0	2510
Totals ...	3872	1301	5173

[1] The factor was called "oily" at that time.

2. *Normal* ♀ × *Sex-linked Translucent* ♂. (Table II.)

F_1. Number of the lots, 9.

	Normal	Translucent	Totals
Females ...	0	774	774
Males ...	782	1 (exception)	783
Totals ...	782	775	1557

F_2. Number of the lots, 15.

	Normal	Translucent	Totals
Females ...	610	456	1066
Males ...	524	453	977
Totals ...	1134	909	2043

3. *Theoretical Analysis.*

The above results evidently show that the linkage in the silkworm is of the *Abraxas* type. The exceptional translucent male might be due to the non-disjunction of chromosomes such as found by Bridges (1913). As is shown later, two more exceptional males were met with in my experiments, but the number is, of course, too small to discuss the frequency of their occurrence.

As to the manner of representing the sex-factors, opinions are divergent. Morgan and his colleagues give a summary of the alternatives in their book (1915). After discussing the question, they come to the conclusion that the symbols should be used for the sex *chromosomes* instead of sex *factors*, i.e. *X*, *Y* for *Drosophila* type, and *W*, *Z* for *Abraxas* type. But this does not apply, without making an additional assumption, to an animal as the silkworm in which no sex chromosome has, as yet, been discovered.

For the present, I do not find any objection to adopting the old symbols given by Bateson (1909), and in assuming that the female is here of the genetic constitution *Ff*, the male *ff*, and that the linkage exists between *F* and a sex-linked factor. Under this assumption, I will represent the sex-linked translucency by o^s and its normal allelomorph by O^s, therefore, the sex-linked translucent female by Ffo^so^s, sex-linked translucent male by ffo^so^s, normal female by FfO^so^s, and normal male by ffO^sO^s.

In crossing $Ffo^so^s \times ffO^sO^s$, F_1 should be all normal, and F_2 should consist of normal females, normal males and translucent females in proportion of 1:2:1. The crossing $FfO^so^s \times ffo^so^s$ should, on the other hand, give rise to normal males and translucent females in equal numbers in F_1, and four possible combinations in equal numbers in F_2. These expectations are fairly realised in the experiments.

III. Crossing between Sex-linked Translucent and Non-sex-linked Translucent.

The results of the crossing of this sort are naturally more complex than those described on pp. 164–165.

1. *Sex-linked Translucent* ♀ × *Non-sex-linked Translucent* ♂.
(Table III.)

F_1.

Number of the lots	Normal	Translucent
8	2011	0

In five lots out of eight, the sexes were discriminated, the result follows: females 542, males 528, total 1070.

F_2. Number of the lots, 14.

	Normal	Translucent	Totals
Females ...	787	988	1775
Males ...	1350	499	1849
Totals ...	2137	1487	3624

F_3. Five lots, which were produced by mating F_2 normal males and females, gave the following results.

(*a*) Two lots consisted of all normal individuals.

Female	Male	Total
214	175	389

(*b*) One lot produced four phenotypes in the same proportion as in the preceding generation.

	Normal	Translucent	Totals
Females ...	44	100	144
Males... ...	119	36	155
Totals ...	163	136	299

(*c*) One lot produced normal as many as three times of translucent.

	Normal	Translucent	Totals
Females ...	69	22	91
Males ...	51	17	68
Totals ...	120	39	159

(*d*) One lot produced four phenotypes in equal numbers.

	Normal	Translucent	Totals
Females ...	77	56	133
Males ...	65	65	130
Totals ...	142	121	263

2. *Theoretical Analysis.*

As already mentioned, there are, at least, seven multiple non-sex-linked factors for translucent character, which I will represent by letters o^1, o^2, o^3 etc. The results of experiments concerning these non-sex-linked translucent factors only, will be reported in a separate paper. For the present time, I will denote one of the non-sex-linked factors generally by o and its normal allelomorph by O, so that an individual homozygous either for o^s or o, or for both, will develop the translucent character.

The parents used in above experiments were Ffo^so^sOO and ffO^sO^soo, and F_1 generation consisted of FfO^so^sOo (normal female) and ffO^so^sOo (normal male). In F_2 nine genotypes are expected, i.e.

Females		Males	
1 FfO^so^sOO	normal	1 ffO^sO^sOO	normal
2 FfO^so^sOo	,,	2 ffO^sO^sOo	,,
1 Ffo^so^sOO	translucent	1 ffO^so^sOO	,,
2 Ffo^so^sOo	,,	2 ffO^so^sOo	,,
1 FfO^so^soo	,,	1 ffO^sO^soo	translucent
1 Ffo^so^soo	,,	1 ffO^so^soo	,,

Accordingly the F_2 ratio should be theoretically 3 normal females : 5 translucent females : 6 normal males : 2 translucent males. It is evident that there are 9 normal to 7 translucent all together, and 1 female to 1 male. The experimental results are compared with the theoretical expectations as follows :

	Actual figures	Expectation	σ[1]	Deviations
Normal	787	679·5	±23·5	+107·5
Translucent ...	988	1132·5	±27·9	−144·5
Normal	1350	1359·0	±29·2	− 9·0
Translucent ..	499	453·0	±19·9	+ 46·0
Totals	3624	3624·0		

The above comparison shows that the deviations of actual figures from theoretical numbers fall within three times of σ in males, while those in females far exceed that limit. We can consider two possible causes of the somewhat remarkable discrepancy of actual figures in females. One of them is differential viability in normal and translucent females. In some strains, I have found that the translucent silkworms were notably less vigorous, slower in growth and more liable to disease than the normals, while in other strains, no sensible difference was found between the normal and translucent types. In the former case, translucent females were, as a rule, weaker than males of the same category. If this is the case also with the sex-linked translucent, although

[1] Standard error.

no definite evidence for this has yet been discovered, the deficiency of translucent females and excess of normal females in the experiments would be largely accounted for.

The other possible cause is the differential development of the translucent character in both sexes. If it is assumed that the translucent character is less developed in females so that some translucent females might be taken for normal females, the discrepancy would be fairly well explained. The fact that the deficiency in translucent females and the excess in normal females are nearly the same in absolute values not only in the above case, but in almost all cases described in this paper, seems to make this supposition plausible. This point has, however, not yet been studied morphologically.

Notwithstanding somewhat remarkable deviation, there is scarcely any doubt that 3 : 5 : 6 : 2 ratio is realised in the F_2 generation in above experiments: no other adequate explanation can be suggested.

From the genetical constitutions of F_2 individuals above given, we can easily understand why four different F_3 ratios were obtained; therefore I shall not go further into this point.

3. *Non-sex-linked Translucent* ♀ × *Sex-linked Translucent* ♂. (Table IV.)

F_1. Number of the lots, 6.

	Normal	Translucent	Total
Females ...	0	452	452
Males ...	616	0	616
Totals ...	616	452	1068

F_2. Number of lots, 9.

	Normal	Translucent	Totals
Females ...	569	600	1169
Males ...	529	605	1134
Totals ...	1098	1205	2303

4. *Theoretical Analysis.*

The genetical constitutions of the parents must have been *FfO^{s}o^{s}oo* and *ffo^{s}o^{s}OO*, and F_1 individuals *Ffo^{s}o^{s}Oo* (translucent females) and *ffO^{s}o^{s}Oo* (normal males), which should give rise to the following F_2 genotypes:

Females		Males	
1 *FfO^{s}o^{s}OO*	normal	1 *ffO^{s}o^{s}OO*	normal
2 *FfO^{s}o^{s}Oo*	,,	2 *ffO^{s}o^{s}Oo*	,,
1 *FfO^{s}o^{s}oo*	translucent	1 *ffO^{s}o^{s}oo*	translucent
1 *Ffo^{s}o^{s}OO*	,,	1 *ffo^{s}o^{s}OO*	,,
2 *Ffo^{s}o^{s}Oo*	,,	2 *ffo^{s}o^{s}Oo*	,,
1 *Ffo^{s}o^{s}oo*	,,	1 *ffo^{s}o^{s}oo*	,,

That is 3 normal females : 5 translucent females : 3 normal males : 5 translucent males. The experimental results are rather far from the above expectation as shown below:

	Actual figures	Expectation	σ	Deviation
Normal females ..	569	432	±18·8	+137
Translucent females ...	600	720	±22·3	−120
Normal males ...	529	432	±18·8	+ 97
Translucent males ...	605	720	±22·3	−115
Totals ...	2303	2304		

Here we meet again a deficiency of translucent and an excess of normal, the absolute values of deviation being practically the same. The discrepancy may be accounted for if differential viability is assumed to exist between translucent and normal silkworms as suggested on p. 167.

5. *F_1 Sex-linked Translucent ♀ × Homozygous Non-sex-linked Translucent ♂*. (Table V.)

As already stated, F_1 offspring from the crossing between non-sex-linked translucent females and sex-linked translucent males consists of two phenotypes, normal male and translucent female. These F_1 translucent females were mated with non-sex-linked translucent males which belong to a different strain from that to which the female translucent parents belonged.

F_1. Number of the lots, 4.

	Normal	Translucent
Females ...	700	0
Males ...	705	0
Totals ...	1405	0

F_2. Number of the lots, 8.

	Normal	Translucent	Totals
Females ...	598	596	1194
Males ...	932	359	1291
Totals ...	1530	955	2485

6. *Theoretical Analysis.*

In the above experiments, two distinct non-sex-linked factors are concerned, which I will represent by symbols o^a and o^b, their normal allelomorphs being O^a and O^b respectively. The parents are $Ffo^so^sO^aO^ao^bO^b$ and $ffO^sO^sO^aO^ao^bo^b$ genetically, and F_1 individuals are of following genotypes:

I. $FfO^sO^sO^aO^aO^bo^b$ normal female
II. $FfO^sO^sO^ao^aO^bo^b$ „
III. $ffO^sO^sO^aO^aO^bo^b$ normal male
IV. $ffO^sO^sO^ao^aO^bo^b$ „

These males and females will, when mated at random, give rise to the following F_2 ratios:

	Normal Females		Translucent Females		Normal Males		Translucent Males	Totals
I × III I × IV II × III	3	:	5	:	6	:	2	16
II × IV ...	9	:	23	:	18	:	14	64

From the experimental results, it will be easily seen that 3 : 5 : 6 : 2 ratio was realised, admitting the already discussed deficiency of translucent females.

7. *Non-sex-linked Translucent* ♀ × *Normal* ♂, *Heterozygous for Sex-linked Factor.* A. (Table VI.)

F_1 normal males obtained from the crossing non-sex-linked translucent females × sex-linked translucent males are, of course, heterozygous for the sex-linked factor. They were mated to homozygous non-sex-linked translucent females, which belong to a different strain from that to which the translucent females used in the first crossing belonged.

F_1. Number of the lots, 6.

	Normal	Translucent	Totals
Females ...	601	495	1096
Males ...	1173	2 (exceptions)	1175
Totals ...	1774	497	2271

F_2. Two F_2 lots were obtained by mating F_1 normal males and females.

	Normal	Translucent	Totals
Females ...	119	145	264
Males ...	234	63	297
Totals ...	353	208	561

Another two F_2 lots were obtained by mating F_2 normal males to their translucent sisters.

	Normal	Translucent	Totals
Females ...	90	128	218
Males ...	77	124	201
Totals ...	167	252	419

B. (Table VII.)

This crossing is similar to that given under A, except that the male parents were not actually taken from F_1 generation, but, as the result showed, they were heterozygous for the sex-linked factor.

F_1. Number of the lots, 9.

	Normal	Translucent	Totals
Females ...	499	423	922
Males ...	907	0	907
Totals ...	1406	423	1829

F_2. Two lots, produced by F_1 normal males and females, gave the following results:

	Normal	Translucent	Totals
Females ...	188	53	241
Males ...	170	56	226
Totals ...	358	109	467

8. *Theoretical Analysis.*

The genetical constitutions of individuals in the above experiments are as follows:

Parents. $FfO^sO^sO^aO^aO^bO^b \times ffO^sO^sO^aO^aO^bO^b$.

F_1

I.	$FfO^sO^sO^aO^aO^bO^b$	normal female
II.	$FfO^sO^sO^aO^aO^bO^b$	„
III.	$Ff\mathrm{O}^s\mathrm{O}^sO^aO^aO^bO^b$	translucent female
IV.	$Ff\mathrm{O}^s\mathrm{O}^sO^aO^aO^bO^b$	„
V.	$ffO^sO^sO^aO^aO^bO^b$	normal male
VI.	$ffO^sO^sO^aO^aO^bO^b$	„
VII.	$ffO^sO^sO^aO^aO^bO^b$	„
VIII.	$ff\mathrm{O}^s\mathrm{O}^sO^aO^aO^bO^b$	„

That is, normal females, normal males and translucent females are expected in the ratio 1 : 2 : 1 in F_1, which is fairly realised.

By mating F_1 normal females and males, we should obtain the following F_2 ratios:

	Normal Females		Translucent Females		Normal Males		Translucent Males	Totals
I × V, I × VI, II × V ...	3	:	1	:	3	:	1	8
I × VII, I × VIII, II × VII ...	3	:	5	:	6	:	2	16
II × VI ...	9	:	7	:	9	:	7	32
II × VIII ...	9	:	23	:	18	:	14	64

In A experiments the 3 : 5 : 6 : 2 ratio was realised.

By mating F_1 translucent females and normal males, the following ratios are to be expected:

	Normal Females		Translucent Females		Normal Males		Translucent Males	Totals
III × V III × VI IV × V	... 3	:	1	:	3	:	1	8
III × VII III × VIII IV × VII	... 3	:	5	:	3	:	5	16
IV × VI	... 9	:	7	:	9	:	7	32
IV × VIII	... 9	:	23	:	9	:	23	64

In the experiments, 3 : 5 : 3 : 5 ratio was obtained.

In the *B* experiments, F_1 exactly corresponds to that of *A* experiments and F_2 ratio is 3 : 1 : 3 : 1, which can be easily analysed from the statements above given.

IV. Summary.

1. The translucent factor found in an Italian race, *Giallo puro indigeno*, is sex-linked.

2. The linkage in the silkworm belongs to the *Abraxas* type.

3. Besides the sex-linked translucent, there are some other multiple translucent factors which are inherited independently of sex. When sex-linked and non-sex-linked translucent strains are crossed together, very peculiar F_2 ratios are obtained.

4. The number of translucent silkworms, especially females, are, as a rule, below theoretical expectations. The actual cause of this is not yet clear.

EXPLANATION OF PLATE XIV.

1. Normal-skinned silkworm from *Giallo puro indigeno*.
2. Sex-linked translucent silkworm from *Giallo puro indigeno*.
3. Sex-linked translucent silkworm from a hybrid generation.

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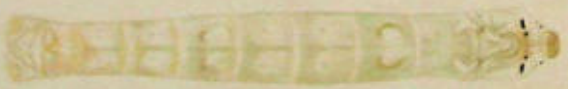
3 

TABLES.

s. l. t. = sex-linked translucent. *n.* = normal. *n. s. l. t.* = non-sex-linked translucent.

TABLE I.

P	F_1			F_2		Totals
				O^s	o^s	
s. l. t. ♀ × *Kinshiryu, n.* ♂	—*A*ª 1—9 '17	O^s 488	*A*ª 1—5 '18 ♀	133	109	469
			*A*ª 1—5 '18 ♂	227	0	
			A*ª* 1—6 '18 ♀	110	105	418
			A*ª* 1—6 '18 ♂	203	0	
			*A*ª 1—7 '18 ♀	94	83	334
			*A*ª 1—7 '18 ♂	157	0	
		o^s 0				
Giallo puro indigeno t. ♀ × *n.* ♂	*A*ª 1—10 '17	O^s 13				
		o^s 0				
	*A*ª 1—11 '18	O^s 158	♀ 78			
			♂ 80			
		o^s 0				
s. l. t. ♀ × *Daikakuryu, n.* ♂	*A*ᶜ 1— 9 '17	O^s 363	*A*ª 1—12 '18 ♀	74	62	265
		o^s 0	♂	129	0	
	*A*ᶜ 1—10 '17	O^s 346	*A*ª 1—13 '18 ♀	128	103	465
		o^s 0	♂	234	0	
	*A*ᶜ 1—11 '17	O^s 443	*A*ª 1—14 '18 ♀	106	98	402
		o_s 0	♂	198	0	
s. l. t. ♀ × *Chiyozuru, n.* ♂	—*A*ᶜ 1—22 '17	O^s 33	♀ 16			
		o^s 0	♂ 17			
Giallo puro indigeno, t. ♀ × *Shinshina, No. 4, n.* ♂	—*A*ᵇ 1—52 '18	O^s 460	♀ 226			
		o^s 0	♂ 234			
			*A*ᶜ 1—12 '18 ♀	88	84	340
			♂	168	0	
			*A*ᶜ 1—13 '18 ♀	41	48	168
			♂	79	0	
Giallo puro indigeno, t. ♀ × *Chiyozuru, n.* ♂	—*A*ᵇ 1—53 '18	O^s 24				
		o^s 0				
Giallo puro indigeno, t. ♀ × *n.* ♂	*A*ª 1—76 '19	O^s 124	♀ 61			
		o^s 0	♂ 63			
			—*A*ª 1—52 '20 ♀	85	105	378
			♂	188	0	
	*A*ª 1—77 '19	O^s 280	♀ 140			
		o^s 0	♂ 140			
	*A*ª 1—78 '19	O^s 482	♀ 255			
		o^s 0	♂ 227			
			*A*ᵇ 1—41 '19 ♀	10	9	39
			♂	20	0	
			*A*ᵇ 1—42 '19 ♀	47	38	177
			♂	92	0	
			*A*ᵇ 1—43 '19 ♀	3	2	15
			♂	10	0	
			*A*ª 1—55 '20 ♀	112	100	408
			♂	196	0	
	*A*ª 1—79 '19	O^s 348	♀ 175			
		o^s 0	♂ 173			
			*A*ª 1—56 '20 ♀	98	110	401
			♂	193	0	
			*A*ª 1—57 '20 ♀	70	77	273
			♂	126	0	
Giallo puro indigeno, t. ♀ × *Chiyozuru, n.* ♂	—*A*ª 1—80 '19	O^s 452	♀ 236			
		o^s 0	♂ 216			
			*A*ᵇ 1—110 '19 ♀	69	59	238
			♂	110	0	
			*A*ᵇ 1—126 '19 ♀	94	99	373
			♂	180	0	
Giallo puro indigeno, t. ♀ × *Chiyozuru, n.* ♂ *and Shinshina, No. 4, n.* ♂	—*A*ª 1—81 '19	O^s 391	♀ 187			
		o^s 0	♂ 204			

TABLE II.

P	F_1			F_2			
					O^s	g^s	Totals
Araya, *n.* ♀ × *s. l. t.* ♂ — A^b 1—2 '17	O^s 162	♀	0	A^c 1—1 '17	♀	108	71	362
		♂	162		♂	96	87	
	o^s 179	♀	179	A^c 1—2 '17	♀	120	66	343
		♂	0		♂	83	74	
				A^c 1—3 '17	♀	47	37	167
					♂	49	34	
				A^c 1—4 '17	♀	24	17	74
					♂	18	15	
				A^c 1—5 '17	♀	90	61	310
					♂	81	78	
Chiyozuru, *n.* ♀ × *s. l. t.* ♂ — A^b 1—3 '17	O^s 98	♀	0	A^c 1—18 '17	♀	8	2	21
		♂	98		♂	8	3	
	o^s 91	♀	90	A^c 1—23 '17	♀	22	26	101
		♂	1		♂	36	17	
				A^c 1—24 '17	♀	31	21	93
					♂	18	23	
				A^c 1—25 '17	♀	8	7	32
					♂	11	6	
P^a 92, *n.* ♀ × *s. l. t.* ♂ — A^b 1—82 '19	O^s 4	♀	0					
		♂	4					
	o^s 5	♀	5					
		♂	0					
— A^b 1—75 '19	O^s 6	♀	0					
		♂	6					
	o^s 5	♀	5					
		♂	0					
Chiyozuru, *n.* ♀ × *s. l. t.* ♀ — A^b 1—118 '19	O^s 94	♀	0					
		♂	94					
	O^s 79	♀	79					
		♂	0					
Shinshina, No. 4, *n.* ♀ × *s. l. t.* ♂ — A^b 1—120 '19	O^s 98	♀	0	A^c 1—112 '19	♀	39	36	118
		♂	98		♂	20	23	
	o^s 107	♀	107	A^c 1—113 '19	♀	81	68	283
		♂	0		♂	72	62	
				A^c 1—114 '19	♀	32	44	139
					♂	32	31	
Chiyozuru, *n.* ♀ × *s. l. t.* ♂ — A^c 1—105 '19	O^s 19	♀	0					
		♂	19					
	o^s 37	♀	37					
		♂	0					
P^a 201—1, *n.* ♀ × *s. l. t.* ♂ — A^a 1—101 '20	O^s 223	♀	0					
		♂	223					
	o^s 203	♀	203					
		♂	0					
Marke, *n.* ♀ × *s. l. t.* ♂ — A^b 1—51 '20	O^s 78	♀	0					
		♂	78					
	o^s 69	♀	69					
		♂	0					

TABLE III*a*.

P	F_1			F_2					F_3		Totals
									O	o	
s. l. t. ♀ × *n. s. l. t.* ♂	A^c 1—6 '17	♀♂ 294 / *o* 0	—	A^a 1—4 '18	♀				61	62	232
					♂				82	27	
	A^c 1—7 '17	♀♂ 374 / *o* 0									
	A^c 1—8 '17	♀♂ 273 / *o* 0									
s. l. t. ♀ × *n. s. l. t.* ♂	A^c 1—5 '18	♀♂ 189 / *o* 0	♀ ♂ 104 85	A^a 1—5 '19	♀				78	71	307
					♂				131	27	
				A^a 1—6 '19	♀				90	90	348
					♂				125	43	
				A^a 1—7 '19	♀				68	78	299
					♂				107	46	
				A^a 1—8 '19	♀				49	55	229
					♂				93	32	
	A^c 1—6 '18	♀♂ 137 / *o* 0	♀ ♂ 67 70	A^a 1—9 '19	♀				48	72	250
					♂				84	46	
				A^a 1—10 '19	♀				82	91	335
					♂				116	46	
s. l. t. ♂ × *Kynshiryu*, *n. s. l. t.* ♂	— A^b 1—69 '19	♀♂ 111 / *o* 0	♀ ♂ 56 55								
s. l. t. ♀ × *R*9 *n. s. l. t.* ♂	— A^b 1—91 '19	♀♂ 311 / *o* 0	♀ ♂ 145 166	A^c 1—149 '19	♀				21	33	104
					♂				37	13	
				A^c 1—150 '19	♀				31	52	155
					♂				43	29	
				A^a 1—105 '20	♀				34	61	240
					♂				108	37	
				A^a 1—106 '20	♀				28	58	186
					♂				72	28	
s. l. t. ♀ × *Racconigi*, *n. s. l. t.* ♂	— A^b 1—154 '19	♀♂ 322 / *o* 0	♀ ♂ 170 152	A^c 1—134 '19	♀				65	95	313
					♂				115	38	
				A^c 1—135 '19	♀				45	61	236
					♂				97	33	
				A^c 1—147 '19	♀				87	109	390
					♂				140	54	

TABLE III *b*.

P	F_1			F_2					F_3		Totals
									O	o	
s. l. t. ♀ × *n. s. l. t.* ♂	A^c 1—6 '17	♀♂ 394 / *o* 0	A^a 1—2 '18	♀♂ 222 / *o* 96	♀♂ 106 116 / ♀♂ 69 27	A^b 1—1 '18	♀		44	100	299
							♂		119	36	
						A^b 1—2 '18	♀		77	56	263
							♂		65	65	
						A^b 1—3 '18	♀		109	0	198
							♂		89	0	
			A^a 1—4 '18	♀♂ 143 / *o* 89	♀♂ 61 82 / ♀♂ 62 27	A^b 1—4 '18	♀		105	0	191
							♂		86	0	
						A^b 1—5 '18	♀		69	22	159
							♂		51	17	

TABLE IV.

P	F_1				F_2		
					O	o	Totals
Racconigi, *n. s. l. t.* ♀ × *s. l. t.* ♂	A^c 1—7 '18	O 98	♀ 0	A^a 1—11 '19 ♀	71	34	219
			♂ 98	♂	71	43	
		o 95	♀ 95	A^a 1—13 '19 ♀	59	67	256
			♂ 0	♂	63	67	
	A^c 1—8 '18	O 58	♀ 0	A^a 1—14 '19 ♀	62	81	284
			♂ 58	♂	63	78	
		o 58	♀ 58	A^a 1—15 '19 ♀	45	45	176
			♂ 0	♂	40	46	
n. s. l. t. ♀ *s. l. t.* ♂	A^c 1—9 '18	O 125	♀ 0	A^a 1—16 '19 ♀	84	64	288
			♂ 125	♂	76	64	
		o 101	♀ 101	A^a 1—17 '19 ♀	72	87	326
			♂ 0	♂	66	102	
				A^a 1—18 '19 ♀	74	104	342
				♂	66	98	
	A^c 1—10 '18	O 150	♀ 0	A^a 1—19 '19 ♀	66	55	229
			♂ 150	♂	51	57	
		o 135	♀ 135	A^a 1—20 '19 ♀	36	63	182
			♂ 0	♂	33	50	
Aojiku, *n. s. l. t.* ♀ × *s. l. t.* ♂	A^a 1—61 '19	O 185	♀ 0				
			♂ 185				
		o 60	♀ 60				
			♂ 0				

TABLE V.

P	F_1				F_2		
					O	o	Totals
Hetero. *s. l. t.* ♀ × *Aojiku*, *n. s. l. t.* ♂	A^a 1—111 '19	O 465	♀ 223	A^b 1—131 '19 ♀	66	83	346
			♂ 242	♂	156	41	
		o 0		A^b 1—132 '19 ♀	79	68	288
				♂	103	38	
Hetero. *s. l. t.* ♀ × *Aojiku*, *n. s. l. t.* ♂	A^a 1—113 '19	O 359	♀ 173	A^b 1—133 '19 ♀	71	79	301
			♂ 186	♂	113	38	
		o 0		A^b 1—134 '19 ♀	42	60	225
				♂	88	35	
Hetero. *s. l. t.* ♀ × *Aojiku*, *n. s. l. t* ♂	A^a 1—115 '19	O 254	♀ 139	A^b 1—135 '19 ♀	81	52	269
			♂ 115	♂	81	55	
		o 0		A^b 1—136 '19 ♀	65	92	324
				♂	115	52	
				A^b 1—137 '19 ♀	105	68	345
				♂	112	60	
Hetero. *s. l. t.* ♀ × *Aojiku* *n. s. l. t.* ♂	A^a 1—117 '19	O 327	♀ 165	A^b 1—60 '19 ♀	89	94	387
			♂ 162	♂	164	40	
		o 0					

TABLE VI.

P		F_1				F_2 O	F_2 o	Totals
Aojiku, *n. s. l. t.* ♀ × Hetero. *n.* ♂	— A^a 1—112 '19	O 308	♀ 113	A^b 1—124 '19	♀♂	67	84	310
					♂♀	128	31	
				A^b 1—125 '19	♀♂	52	61	251
					♂♀	106	32	
			♂ 195	A^b 1—122 '19	♀♂	63	83	295
					♂♀	59	90	
		o 106	♀ 106	A^b 1—123 '19	♀♂	27	45	124
			♂ 0		♂♀	18	34	
Aojiku, *n. s. l. t.* ♀ × Hetero. *n.* ♂	— A^a 1—114 '19	O 316	♀ 108					
			♂ 208					
		o 77	♀ 77					
			♂ 0					
Aojiku, *n. s. l. t.* ♀ × Hetero. *n.* ♂	— A^a 1—116 '19	O 325	♀ 85					
			♂ 240					
		o 95	♀ 93					
			♂ 2					
Aojiku, *n. s. l. t.* ♀ × Hetero. *n.* ♂	— A^a 1—118 '19	O 275	♀ 101					
			♂ 174					
		o 92	♀♂ 92					
			♂♀ 0					
	A^a 1—119 '19	O 333	♀ 121					
			♂ 212					
		o 74	♀ 74					
			♂ 0					
	A^a 1—120 '19	O 217	♀ 73					
			♂ 144					
		o 53	♀♂ 53					
			♂♀ 0					

TABLE VII.

P		F_1			F_2			
						O	*o*	Totals
n. s. l. t. ♀ × Hetero. *n.* ♂	A^b 1—14 '17	*O* 161	♀	71	A^c 1—34 '17 ♀	106	33	267
			♂	90	♂	95	33	
		o 41	♀	41	A^c 1—35 '17 ♀	82	20	200
			♂	0	♂	75	23	
	A^b 1—15 '17	*O* 219	♀	75				
			♂	144				
		o 57	♀	57				
			♂	0				
n. s. l. t. ♀ × Hetero. *n.* ♂	A^c 1—12 '17	*O* 125	♀	43				
			♂	82				
		o 35	♀	35				
			♂	0				
	A^c 1—13 '17	*O* 178	♀	64				
			♂	114				
		o 77	♀	77				
			♂	0				
	A^c 1—14 '17	*O* 35	♀	15				
			♂	20				
		o 14	♀	14				
			♂	0				
	A^c 1—15 '17	*O* 141	♀	49				
			♂	92				
		o 49	♀	49				
			♂	0				
	A^c 1—16 '17	*O* 164	♀	56				
			♂	108				
		o 34	♀	34				
			♂	0				
n. s. l. t. ♀ × Hetero. *n.* ♂	A^c 1—58 '17	*O* 198	♀	64				
			♂	134				
		o 56	♀	56				
			♂	0				
	A^c 1—59 '17	*O* 185	♀	62				
			♂	123				
		o 60	♀	60				
			♂	0				

THE INHERITANCE OF FUR TYPES AND HAIR CHARACTERS IN RABBITS.

By REDCLIFFE N. SALAMAN, M.A., M.D.

(With Twenty-four Text-figures.)

THE investigation, the results of which are now recorded, concerning the hair shapes in the coats of rabbits, was begun in the spring of 1907, repeated in 1908, and again in 1919. The long delay between the inception of the work and its publication is due to the fact that in 1908 it was apparent to the author that there was evidenced by the material a phenomenon which suggested the occurrence of a local differentiation of hair types taking place under certain conditions in the pelt of an animal heterozygous for the same, a condition which, at that time, he ventured to call somatic segregation. The suggestion was not favoured by those most competent to advise and the author was urged to repeat and extend his observations. This was done, nevertheless, the pressure of other work and military service during the period of the war not only delayed the publication of the results but has effectually prevented a more extended research in this direction.

The inheritance of the shape of hairs was suggested by a preliminary work which the author undertook on human material collected by Professor C. G. Seligman including the hair of crossbreds chiefly between Europeans, Papuans and Malays. The investigation yielded very suggestive results but was hampered by the paucity of the material. It therefore occurred to the writer that a parallel phenomenon might be found in the furs of animals. The extensive series of pelts which Major C. C. Hurst[1] had recently exhibited in relation to his work, the Inheritance of Characters in Rabbits, appeared to form just the desired basis. Major Hurst responded to the request for the use of his rabbit skins with the utmost generosity and has ever since placed them freely at the writer's disposal.

The method employed for examining the hair shapes has been to isolate a pencil of hair in the mid-dorsal line and to sever it with scissors

[1] Hurst, C. C., "Experimental Studies in Heredity in Rabbits." *Linnean Soc. Journ. Zool.* 1905, Vol. xxix. p. 233.

as close to the skin as possible. The proximal end was then dipped in soft paraffin and when that was firm the distal end was steeped. A silk ligature was tied round the pencil ¼″ from the basal end and the soft paraffin removed in xylol. The hair was then transferred to absolute alcohol, again to xylol, and then through the paraffins and cut on a rocker microtome.

To obtain thin and perfect transverse sections is not easy. The diameter of the small hairs at their base is about 12 m., or twice that of a human red blood corpuscle, and their substance is very brittle. Moreover there is in such a pencil no supporting matrix to sustain the minute and delicate transverse sections of the individual hairs, nor are they very readily retained on the slide. It was found that the chief element in obtaining successful specimens was to maintain an exquisitely sharp razor. In practice the razor was stropped after every few sections, and its edge controlled under the microscope. Drawings were made with the camera lucida. Exclusive of the series of moulting rabbits, hair was examined from 90 skins, in all cases twice, and in some instances three or four times. In several instances hair was also examined from the shoulders, flanks and hindquarters, but no difference, except in the special cases to be mentioned later, was observed between the hair shapes from these different parts of the pelt of the same animal.

The Rabbit's Pelt. The coats of rabbits may be short, as in the wild rabbit, the "Flemish Giant," the "Belgian Hare" and many other breeds, or it may be long, as in the Angora breeds. The pelts may be of varying colours, and these colours, as in the "Dutch" or "English" pattern fancies, may be obtained in both long and short-haired animals.

In general, the hairs of the rabbit's coat are of two kinds. Very fine delicate hairs of a more or less uniform diameter, and Contour-hairs, which are stout and flat and vary in shape at different levels, terminating, as do the small ones, in a whip end.

The hairs arise from follicles in which a very definite grouping can be observed; in the short-haired coats the follicles in the skin are grouped in islets in which a Central-contour hair is surrounded by three groups of follicles, each containing six or seven small hairs (Fig. 3). The individual hair follicles, as well as the compound group and the islets, are wrapped strongly round with fibrous bands, and they give rise to a very characteristic picture.

At the skin level, only one Contour-hair has been observed in each islet, but within each group of follicles, at least one of the smaller hairs is of slightly greater diameter than its fellows, and if such hair be traced

distally it will be seen ultimately to expand and take on the character of a Contour-hair (Fig. 3).

The relation of the number of Contour to Small-hairs varies with the distance from the skin at which the hair is examined, increasing distally, till at about 1″ from the proximal end the Contours may almost equal the small single hairs in number. The change which takes place in these small hairs, which become transformed to Contour-hairs, manifests itself at a level of about $\frac{1}{4}$″ from the skin and consists in an exaggeration of a flattening of the cross section which had begun about $\frac{1}{8}$″ lower down, till the section becomes definitely rectangular and oblong, passing from that to a bean shape, then to that either of a dumb-bell or a sausage finally narrowing down to a whip-lash end (Fig. 1). In addition to this change of shape, there occurs a reduplication of the medulla, which originally single in the simple hairs becomes subdivided so that at its extreme width it may be as many as thirteen-chambered. The Primary Contour-hairs start with 3–4 chambered medullas in the short-coated animals and, like those already described, increase the numbers of their medullary chambers *pari passu* with their increase of diameter (Fig. 4).

Apart from certain peculiarities, which will be dealt with in detail later, the sections of the small and big hairs at different levels may be represented as in Fig. 1. At a level $\frac{1}{2}$″ distally from the skin, the smaller hairs have for the most part become flattened and a certain proportion of them have acquired two or three medullary chambers, whilst the original Contour-hairs are becoming more sausage-shaped and have increased their medullary chambers to at least five in number, from thence onwards it is increasingly difficult to distinguish the metamorphosed Small-hairs from the original Contour ones. Those Small-hairs which do not take on the Secondary Contour type have, however, become flattened towards the middle of their course and thinning down towards their proximal ends are found in section as more or less circular solid chitinous bodies which represent the section of their terminal whip ends. The Contour-hair, whether primary or secondary, generally assumes at its widest part an outspoken dumb-bell shape and the medullary cavities increase up to a maximum of about 15 chambers. At 1″ from the skin no sections of Small-hairs of the open circular or ovid type are to be seen, and the larger Contour-hairs become narrower, their dumb-bell lateral extremities more pronounced till finally they narrow down, losing gradually their medullary cavities, or terminate, like the smaller hairs, in solid whip ends.

The changes described have been followed in the wild rabbit as well as in the domesticated short-haired varieties. In the Angoras a similar process takes place. In the type of pelt, which later will be described as the "*A*" type, the changes are identical with those in the short-coated ones, except that they begin at a higher level. In the "*B*" type, on the other hand, the Contour-hairs persist as single medullated fibres or at most acquire two or three medullary cavities (Fig. 2). The Small-hairs become somewhat enlarged, but are still furnished with only one medullary cavity, thus differing from the Secondary Contour-hairs already described, and neither they nor the Contour-hairs become much flattened or indeed assume any of the extreme shapes figured in Fig. 1, retaining rather those features which characterised the type at the skin level. At the termination of the individual hairs, both small and big, however, a slight flattening may be observed as the solid whip end is approached.

The explanation of the changes in shape which occur in both Small and Contour-hairs presents some difficulty, for whilst the varying change of shape can be readily followed at different levels of the hair, yet in both sections of skin, and of hair at skin level, one can observe but slight trace of the flattening of the Small-hairs or an increase of their medullary cavities, nor does one find, except very occasionally, amongst the Contour-hair sections immediately outside the skin other than simple bean-shaped ones with 2, 3, or at the most 4, medullary cavities, and then it might be presumed that a hair has become misplaced and has been cut at a higher level than its fellows.

If the hair is a non-living structure excreted by a follicle by which its shape is solely determined, it is difficult to understand how the hair can assume the bizarre dumb-bell and sausage forms which the majority ultimately do, without finding some evidence in the shape of the follicles themselves which corresponds with that of the issuing hair, but neither in the adult rabbit nor in the young of various ages whose hair was examined at skin level every week for 18 weeks, is the evidence forthcoming entirely convincing.

Serial sections of portions from a couple of adult skins have been cut and in one only was a single dumb-bell section found, and but few Contour-hairs with a transverse section of the bean shape with 3 to 4 medullary cavities. The smaller hair groups in their compound follicles were all simple. Skin sections in rabbits of 3, 4, 5 and 6 days old exhibit a greater simplicity of follicular grouping than in the adult.

In the 3, 4, and 5 day old animals, none but single medullated hairs

were seen in the skin, but in the 6th day animal several Contour-hairs with 2 and 3 medullas occur. On the other hand, in an 8 weeks old animal, although well developed Contour-hairs exist in the coat which towards their distal ends spread out into the characteristic sausage and dumb-bell shapes already described, not one follicle was found with more than a single medullated fibre in it, although 250 sections of the skin were searched. It would seem, therefore, that the formation of the Contour-hair in the follicle takes place with extreme rapidity and that when the first coat is formed no fresh hairs are thrown out for some time. After the 8th week a moult begins and in the series of 4 rabbits whose hair was examined weekly between the 4th and the 22nd week of life, sausage and dumb-bell sections of Contour-hairs were met with between the 9th and 14th week at skin level. It was, however, surprising how relatively few such sections were actually met with, a fact which lends further support to the idea that the extrusion of the Contour-hair from the follicle must be a very rapid process.

The evidence is at present perhaps insufficient to decide as to whether the highly variable shape of an individual hair throughout its length is controlled entirely by the follicle, or whether it is dependent on changes outside it. But the latter hypothesis is inconsistent with the view that the hair is an inert and virtually dead structure excreted by the follicle and, so far, there does not seem to be any adequate evidence on which to challenge this view.

In respect to moulting, in the four young Flemish Giants observed, the shifting of the hair began about the 8th week and ended about the 16th. The change of hair was gradual, occurring on different parts of the pelt in varying intensity. After the 16th week moulting slowed down, but in those domestic rabbits examined it appeared that at no time of the year was moulting entirely quiescent.

The distinction between mature and immature hair is not easy to define, but it may be stated at once that in the very young coat there are fewer Secondary Contour-hairs than in the adult. Indeed in the new-born rabbit the skin sections display no Contour-hairs of the multi-medullated type met with later. The sections of the Small-hairs are generally round and the medullary cavity is always much larger than in the adult.

When it is remembered that the difference of area between the cross section of a Contour-hair at its widest and the same at its proximal end in the skin is as much as 10 : 1, and in the case of the Secondary Contour-hairs even greater, and further, that in an "*A*" type pelt about

half the whole hair covering assumes the Contour characters, it will be obvious that a moult which occurred simultaneously all over the body, and in which all the hairs were thrown up from the follicles at the same stage, would excite a tremendous disturbance in the skin at one critical moment. Indeed under such conditions the volume occupied by the hairs in the cutis would have increased some five-fold and would produce an almost impossible congestion. It may therefore be not improbable that the prolonged and disseminate method of moulting observed in the rabbit has some definite relation to the type of the hair covering.

The "*B*" type of pelt in its moult would not involve its owner in any such like discomfort under similar conditions.

It would be of interest to know whether the slackness and elasticity of the rabbit skin is related to the extreme variability of the transverse section of the hair, as compared with other animals, and more particularly whether there is in this respect any difference in the living between long-coated rabbits of the "*A*" and "*B*" types respectively.

Types of Pelt. The examination of Hurst's collection of pedigree skins has disclosed the existence of two distinct types of fur in the rabbit, which for convenience may be described as the "*A*" and "*B*" types.

"A" type of Pelt. This type is characterised by the following:

(*a*) The relation between Contour and Small-hairs at the skin level is in the neighbourhood of 1 : 20.

(*b*) The Contour-hair at its basal end is bean-shaped in section (Fig. 1). As one proceeds distally along the hair the shape passes gradually to kidney, thence to sausage, and finally to an outspoken dumb-bell shape, when it attains its maximum diameter, which may be as much as ten times that at its base. From that point the width of the hair becomes reduced, the section begins to lose its dumb-bell ends and becomes flattened, the medullary cavities coalesce and gradually it passes into a somewhat compressed ribbon with rounded angles and ends in a very fine whip point (Fig. 4).

(*c*) The Contour-hairs may leave the follicle with from 1 to 4 medullary cavities, but in general the 4 medullary stage is not reached till the hair is about $\frac{1}{16}$" from the skin level, and the cavities increase in number till in the dumb-bell shaped portion of the hair they may be from 12–15 in number, from thence they decrease and finally become obliterated.

(*d*) The Small-hairs on leaving the follicles may be round, oval or square in shape (Fig. 6). All these forms may occur together, but a pelt may be pure for either round or square, probably never for oval.

(*e*) The Small-hairs are themselves of two kinds. More than half remain simple, single, medullated fibres throughout their length, the remainder, after a course of $\frac{1}{4}$ to $\frac{1}{2}$ an inch in the adult, take on the characteristics of the fully developed multi-medullated Contour-hairs and become "Secondary Contour-hairs" (Figs. 3 and 4) indistinguishable, except at their proximal ends, from the Primaries.

The "*A*" type of pelt is found on all the short-coated rabbits examined, including the wild rabbit (Fig. 6). (The pelt of the wild hare is also of the "*A*" type.) It is also found in some, possibly the majority, of the long-coated or Angora rabbits. In such long-coated animals the types of individual hairs in the pelt are just the same as in the short-coated ones, the only difference being that the changes both in the Primary and in the Secondary Contour-hairs take place at a somewhat greater distance from the skin level (Figs. 8 and 9).

The "B" type of Pelt differs from the "*A*" type in the following manner:

(*a*) The relation between Contour and simple Small-hairs at the skin level is from 1 : 50 to 1 : 70. In a very good example in other respects of this type (No. 23 Hurst's series) the ratio is but 1 : 30. It is of interest to note that in this case the maternal parent was heterozygous in respect to "*A*" and "*B*."

(*b*) The Contour-hair at its basal end is either circular or almost so and retains this shape throughout its length, except towards the distal end where it flattens somewhat, becoming slightly bean-shaped before it ends as a whip point (Fig. 2).

(*c*) The Contour-hairs are furnished for the most part with a single medullary cavity but hairs with two or three may be occasionally met with at the skin level. Close to the distal end a very occasional hair, about 1 in 200, has been observed to be of a flattened kidney-shape, and to contain as many as six medullas. Still rarer, and possibly not occurring more frequently than 1 in 1000 hairs, is a more or less dumb-bell shaped section (see Fig. 2*a*).

(*d*) The Small-hairs are in general of smaller diameter than in the "*A*" type and at the skin level their transverse section is more or less circular.

(*e*) About one half of the Small-hairs enlarge circularly but rarely

reach the same size as the Primary Contour-hairs or acquire more than one medullary cavity (Fig. 2).

Figs. 11 represent the "*B*" type at skin level.

The "*B*" type of pelt differs from the "*A*" type not only in the manner described but also in its general appearance and to the touch. Owing to the lesser number of both kinds of Contour-hairs and to the lesser degree of flattening, the fur is softer and has less gloss or surface, a character which in the "*A*" type is due to the ribbonlike flattening of the Contour-hairs. The absence of this feature, in addition to the lesser diameter of the hair fibres, renders the "*B*" type of pelt more silky than the "*A*" type to the touch.

The "*B*" type of pelt is found exclusively in the long-coated rabbit and is always made up of hairs of circular or widely ovoid shape and never with the square type of Small-hair. It may be carried by a short-coated parent of "*A*" type whose hair shapes are mixed.

Seeing that the two types of pelt "*A*" and "*B*" are distinct and differ in several characters, it becomes of interest to observe in what manner, if at all, either is inherited—whether as a unit character or otherwise. The evidence is derived from the examination of Hurst's series of skins, the genealogical relationships of which are shown in Figs. 22–24, and as these were derived from rabbits bred without any reference to the "*A*" or "*B*" type of pelts, or the shape of hair sections in general, it is unfortunately scanty and insufficient. It is possible, however, to draw the following conclusions:

1. Type "*A*" is dominant to type "*B*," whether the "*A*" is a short or a long coat. The evidence for which is: (*a*) The "*B*" type can be carried by short-coated parents heterozygous for long coat and will segregate out therefrom. See Fig. 22, matings 8×12 and 5×12. (*b*) The "*B*" type occurs as a result of the mating of a rabbit with a long-coated "*A*" pelt presumably heterozygous for "*B*" with a son of the same whose father was homozygous for an "*A*" type of short coat. See Fig. 23 (p. 206), mating 3×10. (*c*) The "*B*" type occurs as an F_2 from a mating in which one of the original parents is an Angora "*A*" type and the other a short-coated "*A*" type. See Fig. 22, mating 8×10. (*d*) The two Angora parents Nos. 2 and 3 of Hurst's were mated, but of the offspring one skin was alone preserved, the coat of which is of the "*B*" type. The parent No. 3, both from its behaviour in other matings and from the character of its own hair sections, is clearly heterozygous for "*A*" and "*B*," which strengthens the inference that the "*B*" type is recessive.

2. The "*B*" type can only be found in long-coated rabbits.

3. It may be associated with any colour and with the Dutch pattern. Of the twelve "*B*" coated animals in Hurst's collection, six are white, two are black, two are grey, and two are black Dutch.

The heterozygous forms may be met with in either long or short-coated animals. If in the latter there is no distinctive sign in the hair shapes which betrays the presence of the recessive "*B*" type, "*A*" is completely dominant. On the other hand, if the Small-hairs are uniformly square as in No. 4, Fig. 7, then there is good reason to believe, as will be seen later, that such a short-coated animal does not carry the "*B*" type at all.

The Angora heterozygous for "*A*" and "*B*" types of pelt may be recognised by the examination of the cross section of its hairs at skin level. In such sections (Figs. 8 and 9) there may be found, besides those Contour-hairs typical of "*A*," perhaps 5 % of those peculiar to "*B*," whilst of the Small-hairs a very considerable portion will be more or less circular as is common in the "*B*" type. If however an animal is exhibiting the Dutch pattern besides being heterozygous for "*A*" and "*B*," then characteristic changes may take place which will be described later.

Unfortunately no mating was made between two "*B*" type Angoras.

The "*B*" type is not peculiar to Hurst's series, nor is it probable that it arose spontaneously in his stocks, for the writer has found two examples of it amongst the stock of a fancier which was presumably unrelated to that of Hurst's.

The Shapes of the Transverse Sections of the Small-hairs.

So far we have dealt with types of fur involving several characters in both the Small and Contour-hairs. It remains now to deal with the occurrence of various types of hair shapes and their inheritance. The part of the hair considered is that most proximally situated on a level with the skin.

Three types of sections are to be distinguished: (*a*) square, (*b*) round, and (*c*) oval.

The square type of Small-hair sections was found in one of Hurst's original Belgian Hare parents, No. 4 (Fig. 7). The type is characterised by the rectangular shape of the sections, indeed as the sides are more or less equal, the majority of the hairs are definitely square in outline. The outstanding feature is the sharp angularity of the sections to which the hair scales, here more strongly developed than elsewhere, lend emphasis.

The square section has been found pure in short coats only. In the long-haired pelts, only a small minority of the hairs are ever square except in the case of Dutch coats to be described.

The square type is recessive to both round and oval, although in the dominant form it is always possible to distinguish a few square sections (Fig. 5).

A pelt in which all the Small-hairs were pure "squares" was found in the F_2 generation in one instance only, viz. No. 31 (Fig. 22). It was derived from the grand parental mating of an animal heterozygous for oval and square section shapes with another homozygous for round respectively. When the two Belgian parents Nos. 1 and 4 (Figs. 5 and 7) were mated, one of the three offspring possessed a pure square typed section, the remaining two were like the No. 3 parent, mixed.

The round type of Small-hair is found in both long and short-coated rabbits: it is very closely associated with the "*B*" type of long coat. It is not always easy to distinguish this type in short coats from the next, or oval type, but in long coats when it is present, the almost perfectly round section of the Small-hair is readily recognised.

When the round and square types are mated, the F_1 is oval, Fig. 10, though a few rounds and a few squares may be still found. In the F_2 generation the round type, unmixed with others, has been found in the long but not in the short coats in pure form.

The oval type of Small-hair section is an elliptical one in which the long axis is almost one and a half times the length of the short axis (Figs. 6 and 10). It is to be found equally in both long and short coats. A few examples occur where the oval type is quite pure but in most cases diligent search will discover not only some circular types, but also some squares (Fig. 9). This indeed is to be expected, seeing that the oval type is certainly dominant to both round and square.

It is worthy of note that whilst in the wild rabbit the oval type is the predominant one, yet in all of the four wild rabbits examined, both rounds and squares in varying degree were observed.

A point of considerable interest is the relation of the "*B*" type of pelt to the three kinds of hair section just described. Of 12 "*B*" type skins in the series examined, 11 possess Small-hairs which are all rounds—using this term to include forms which, whilst not quite circular, are yet not so ellipsoidal as to be included under the term oval. In the twelfth skin, No. 33, however, there are to be found about 10 % of squared forms and the same quantity of ovals. The shape of the Contour-hairs in this

pelt is normal but it is noteworthy that the relation of Contour to Small is down to about 1 : 40.

Inasmuch as square is recessive to round and oval, and the "*B*" type is correlated with round hair sections, it is not probable that this type of coat, though itself recessive, should ever be carried by an animal pure to square-shaped hair section.

There would seem to be, therefore, a very close relation between the "*B*" type of pelt and the roundness of the Small-hair sections. It may be that in the presence of the "*B*" type, the dominance of the round, rather than the oval form of Small-hairs, is assured.

The Dutch Pattern and its Relation to Hair Shapes.

It will be remembered that in Hurst's experiments there appeared in the F_2 generation rabbits with well developed Dutch markings, although neither of the original parents showed any trace of such character. Indeed they were known to be pure bred for many generations, each to its own type, viz. White Angora and Belgian Hare. Hurst showed that the pattern factor had been smuggled in by one of the Angora parents, viz. No. 3. In the F_1 derived from the cross between No. 3 and the square-haired Belgian Hare No. 4, it was noticed that four out of five of the F_1 family had small patches of white on the shoulders. The extent of the patch varied from a single pencil of white hairs on one shoulder to patches four square inches in extent on both shoulders.

It occurred to the writer that it might be of interest to examine the shape of the transverse sections of the hair in the white shoulder patches in these F_1 animals. The Contour-hairs exhibited no difference, and the remarks that follow refer to the Small-hairs only. The result, indeed, was rather surprising, for whereas the dark hairs in one, No. 9, of this series was almost completely and regularly oval, the white area was to a considerable extent covered with square-shaped hairs. In a brother, No. 10, in whom the white patches reached their largest expansion, there was no appreciable difference, the square-sectioned hairs forming about 10 % of the whole both in the dark and the white areas. In a third, No. 8, whose white patch consisted of a mere tuft of hair on the left shoulder, it was found extremely difficult to determine whether a change in shape had taken place or no, for the hair on this patch was undergoing a rapid moult quite independently of the remainder of the coat. The impression conveyed, however, was that there was no differentiation towards squareness of section at the extreme base of the hairs. It was, however, clear that in the F_1 series some differentiation of hair character

was taking place and that this differentiation was not present in all, nor did its degree vary directly with that of the white patching. The F_2 series yielded more definite results. In Fig. 24 is shown the breeding of the Dutch marked rabbits of Hurst's series. There were fifteen fully marked Dutch, including No. 51, which was a pure bred Dutch, and seven "marked" rabbits including Nos. 62 and 63 offspring of No. 50, and a Silver Fawn No. 47, and No. 82 the offspring of another Silver Fawn by No. 51. Nos. 46, 47 and 51 were introduced from without.

Four of the Dutch were long-coated and two of them, No. 200 and No. 41, were of the pure "*B*" type, neither of which showed the slightest difference between the structure of the hairs in the white as opposed to the dark areas. Rabbits Nos. 103, 113, 116 and 121 were small and immature, and although some showed certain evidence of differentiation, such evidence derived from the consideration of the infantile coat cannot be regarded as of definite value in considering the changes apparent in the adult. The same in a lesser degree applies to rabbits Nos. 92 and 95, both but three-quarters grown, and the section of whose hair shows a very considerable majority of them to be still immature. Of the remaining members of the series, Nos. 54, 40 and 94, all displayed striking differences between the character of their hair shapes in the white and black areas of their coats.

It will be best to consider these separately in some detail. No. 54 is an Angora Dutch, the dark hairs, Fig. 14, are nearly all rounded with small medullas and thick cortices, though a few small square forms occur. The Contour-hairs are thick, rounded and contain one or two medullary cavities; the impression conveyed by an examination at this level is that the pelt is of a "*B*" type (compare Figs. 2 and 11). Moreover, the ratio of Contour to Small-hairs is 1:50, the characteristic "*B*" ratio. If, however, the dark hair be examined at stages progressively distal from the skin, the character of the hairs soon alters: the Contour-hairs become more numerous and gradually take on all the "*A*" type characters, whilst the Small-hairs become flattened in the manner already described as common to the "*A*" type. In fact, what has occurred would appear to be a reversal of the usual dominance of the "*A*" over the "*B*" type in an animal heterozygous for "*A*" and "*B*." And that this has shown itself in the lower part of the hair, and that a gradual restoration of the dominance has taken place in the more distal portion. The white area of the coat is covered by hair of an outspoken "*A*" type, see Fig. 15. Here the ratio of Contour to Small is 1:20, the normal "*A*" ratio. A further outstanding difference is that the Small-

hairs of the white are sharply square in section and for the most part the medullas are big and square and the cortex much reduced. Whilst the area of the individual fibre is much greater than the corresponding hairs of the dark area, the character of the Contour-hairs for the most part is that of the "*A*" type, though some sections are reminiscent of those seen in "*B*" type pelts, and the dark haired portions of the same coat.

Besides the differentiation of "*A*" and "*B*" types there is here a further differentiation of round and square shaped Small-hairs, so that the "squares" occur in the white and the "rounds" in the dark areas of the skin. In addition, the Small-hairs of the white area are modified in size and structure as compared with the white hairs of the white-coated and Himalayan rabbit, whether long or short.

No. 40 is a short-coated Dutch. Here there is no question of a differentiation affecting "*A*" and "*B*" type as this pelt, like that of all short-coated rabbits, is unquestionably of the "*A*" type throughout. However, the Small-hairs of the dark and white areas contrast very forcibly. In the dark area, Fig. 16, the sections are, for the greater part, rounded and oval, with medium to small-sized medullas, whilst in the white area the hairs are all square in section, of large area, with big square medullary cavities and thin cortices. It will be noticed that a few square forms are to be seen in the dark area, which would seem to show that the animal is in fact heterozygous for both rounded and squared section hairs and that a more or less complete differentiation of the two takes place in the two areas of the coat.

No. 94, Figs. 20, 21, presents a very similar picture to that of No. 40. The differentiation between round and square typed sections in the dark and white areas respectively is as definite, whilst the larger size of the white hairs with their large square medullas is rather more evident.

Before passing to any discussion of the facts, attention must be drawn to No. 51, Figs. 18 and 19, a pure bred Dutch rabbit introduced from without. Repeated examination showed no distinction to exist between the hair of the white and dark areas. In both, square and oval forms are equally mixed but the latter, whether in the dark or white areas, are neither larger than the round, nor are they furnished with the big square medullary cavities which have been described in the preceding examples.

A daughter, No. 82, of this Dutch out of a Silver Fawn 46 (Fig. 23) was heavily marked with white on the shoulders, but here, as in its father, no differentiant was observed. Further, in the adults Nos. 62

and 63 (Fig. 23), the offspring of another pure bred Silver Fawn and of a "*B*" type Angora white derived from the same stock as the original Angora parents of Hurst carrying the Dutch factor from its mother, No. 3, the hairs in the white areas showed no distinction of any kind from those in the dark.

The differentiation which has been observed is obviously dependent for its exhibition in any animal on the co-existence in the same of at least one factor for the Dutch pattern, or perhaps more correctly, the absence of one or both factors for self pattern. But it is clear that if this differentiation is due to a factor which we may call "*D*," that this latter is not identical with that for Dutch pattern, nor is it carried by all Dutch rabbits. In the F_1 family it was seen that not all the "marked" members evidenced this differentiation, whilst in the F_2 series it was only present in 3 out of 10 (excluding the immature).

It is practically certain that the factor came in with the White Angora No. 3, for whilst No. 10 shows no differentiation itself, yet when mated to No. 3 (Fig. 24) one of the two offspring shows the differentiation in its most characteristic form. Without discussing whether the differentiation should more properly be considered as due to an inhibitor of normal development rather than the presence of a differentiating factor we may call "*D*." There is evidence which suggests that the new and disturbing gene probably acts as a dominant when occurring in conjunction with that for "Dutch" pattern. Thus from the mating 51 × 3 (Fig. 24) a strongly differentiated offspring arose which could not have happened had absence of the differentiating factor been dominant over its presence, for No. 51 is the outside Dutch in which no differentiation was observed either in its own pelt or in any of the four offspring derived from the two other matings shown in Fig. 24 in which it participated.

It is unfortunate that the chief male F_1 parent that has been used is No. 10 because this animal, as has been already observed, although the most marked with white of all the F_1 series, is yet quite undifferentiated as regards hair shapes. Three matings were made, 7 × 10, 8 × 10, and 9 × 10 (Fig. 23). The first two matings produced ten young, of which four were Dutch, none of which were differentiated; the latter mating produced seven young (Fig. 21) of which only one was Dutch and was differentiated. These facts all tend to strengthen the view that No. 10 is itself free from the factor "*D*" and that No. 9 contains it, and that the factor "*D*" is, in the presence of the Dutch pattern, a dominant character.

Two of the Dutch rabbits were Angoras of the "*B*" type of pelt, and in neither was there any differentiation, whilst it is possible that a complete incompatibility exists between the factors for the "*B*" type pelt and that for differentiation of hair shapes, on the other hand the "*B*" type has no true square forms which might be segregated to any particular part of its pelt. It is clearly impossible, in view of the inadequacy of the numbers, to do more than speculate on the possible characters of a differentiating factor such as has been suggested.

The outstanding differences of shape, medulla and cortex which exist between the hairs of the white and dark areas in the three cases already described, suggest that something more is involved than a separation or sorting out of hair types in the phenotype, that the process is much more in the nature of a modification than a somatic segregation. This view is further borne out by the changes that were found in No. 54 where apparently there was a differentiation highly suggestive of a real segregation which condemned the "*B*" character pelt and the round hairs to the dark skin areas, and the "*A*" type and square hairs to the white ones. Yet when the dark hairs were examined along their length serially, it was found that no separation of "*A*" and "*B*" types had in reality occurred, but that a structural modification of the proximal ends of the hair had been effected, giving rise to the appearance of a "*B*" type pelt. If the dark hairs alone be considered, it could be said that in this case the normal dominance of "*A*" over "*B*" had been partially suspended during the latter part of the hairs growth, but in view of the fact that the white hairs are also much modified, it would seem more reasonable to regard the change as due to some factor which, in the presence of that which produces Dutch, can effect a structural modification of the hair of the white area and, if the factor for the "*B*" type pelt be present as well as that for the "*A*," that of the dark hairs also.

Onslow[1] has shown that recessive white coloration is due to the absence of the enzyme unit of the pigment-producing system, as opposed to dominant whites which are due to an inhibitor.

It would have been of interest had it been possible to establish any relationship between the phenomena here described and that of colour. The white hair of "*A*" and "*B*" type are different in structure (Figs. 8 and 11) yet both are recessive. A short-haired albino, also recessive, was found to be different from either, being indeed identical with the normal

[1] Onslow, H., "A contribution to our knowledge of the Chemistry of Coat Colour in Animals and of Dominant and Recessive Whiteness," *Proc. Roy. Soc.* Series B, Vol. LXXXIX. p. 36, 1915–1917.

short-coated type seen in Fig. 10. The Himalayan, another recessive form of white, is similar to the last.

Three coats, two black and one tortoiseshell, of the "English" breed of rabbits were examined, but no difference whatever was found between the shape and structure of the hairs of the black and white areas, both in all three being similar in all respects to that shown in Fig. 10. The "English" pattern is a dominant form of white and its behaviour was identical with that of the recessive whites, excepting only the three Dutch rabbits which have been described. There is therefore no reason to associate differentiation of structure with either recessive or dominant form of albinism.

The three differentiated Dutch pelts belong two to one sex and one to the other. Two are full black "Dutch" and one dilute, so that there is no suggestion of an association of hair structure differentiation either with colour or sex.

Attention has already been drawn to the fact that all hairs in "*A*" type pelts become flattened towards their distal parts, the section becoming definitely rectangular between one quarter and one half an inch from the skin level, see Figs. 1 and 2. This flattening is distinct in degree, but possibly not in kind, from that observed in the white areas of the differentiated Dutch rabbits. The distinction is that in the latter the hair section is more or less completely square, whilst the flattened one is rectangular with the shorter side about half that of the larger. Again, in the former the angles are sharp, and in the latter, rounded. On the other hand, the open medullary cavity and the thin cortex are common to them both. The normal flattening occurs equally in dark and colourless hairs, but the change which has been observed in the three Dutch rabbits might perhaps be considered an aberrant phase of the normal process which affects the white haired areas only. Whether this suggestion is a valid one or not, it still fails to account for the delayed dominance of the "*A*" over the "*B*" type in the dark areas of the skin of the No. 54 Dutch.

The new facts adduced in this paper as regards hair type and differentiation of hair shapes may be summarized:

1. There are two distinct types of fur in the rabbit, designated in this paper as "*A*" and "*B*" types.

2. "*A*" is common to the wild and all short-coated rabbits, and in addition it is found in some Angoras.

3. There is no correlation between either of the two types and coat

colour or other distinctive patterns recognized by the fancier or with sex.

4. "*B*" is a type exclusively found in some long-coated rabbits.

5. There are three shapes common to the transverse sections of the Small-hair at the skin level, square, round and oval.

6. The square type is recessive and can occur pure, the round type is dominant to the square and was found pure only in relation to "*B*" type pelts; the oval is the form most in evidence in the wild rabbit, and is the normal dominant form in short coats.

7. In certain rabbits exhibiting the Dutch marking transverse sections of the Small-hairs in the white areas are found to be of a square shape, and that in the dark of a round or oval. This condition is to be found on both short and long-coated Dutch marked animals.

8. In one instance where the Dutch pattern was developed in an animal, heterozygous for square and round hair section, as well as "*A*" and "*B*" pelt types, a differentiation took place so that the white area presented entirely different hair characters from that existing in the dark portion.

9. The differentiating factor, whether heterozygous or otherwise, is able to influence the hair shapes much more completely in an animal which is pure for the Dutch pattern factor than in one which is heterozygous and which only exhibits the presence of the factor by the "marking" on the shoulder.

10. The suggestion is made that the extreme looseness and elasticity of the ordinary rabbit pelt in life is associated with the physiological requirements of the hair follicles, which at certain recurrent phases of the coat's growth, must accommodate hairs the transverse area of which is as much as tenfold that of the same when fully grown.

It would have given great pleasure to the writer to invite Major Hurst to allow his name to be associated with his, in the production of this paper, but inasmuch as the former is entirely innocent of the unexpected findings and their interpretation, it was not felt to be just to put forward a request, the granting of which, whilst it would have assured the writer much moral support, would have burdened Major Hurst with an unmerited responsibility. The indebtedness of the writer to Major Hurst for the free use of the material employed is indeed great, and his most grateful thanks are here recorded.

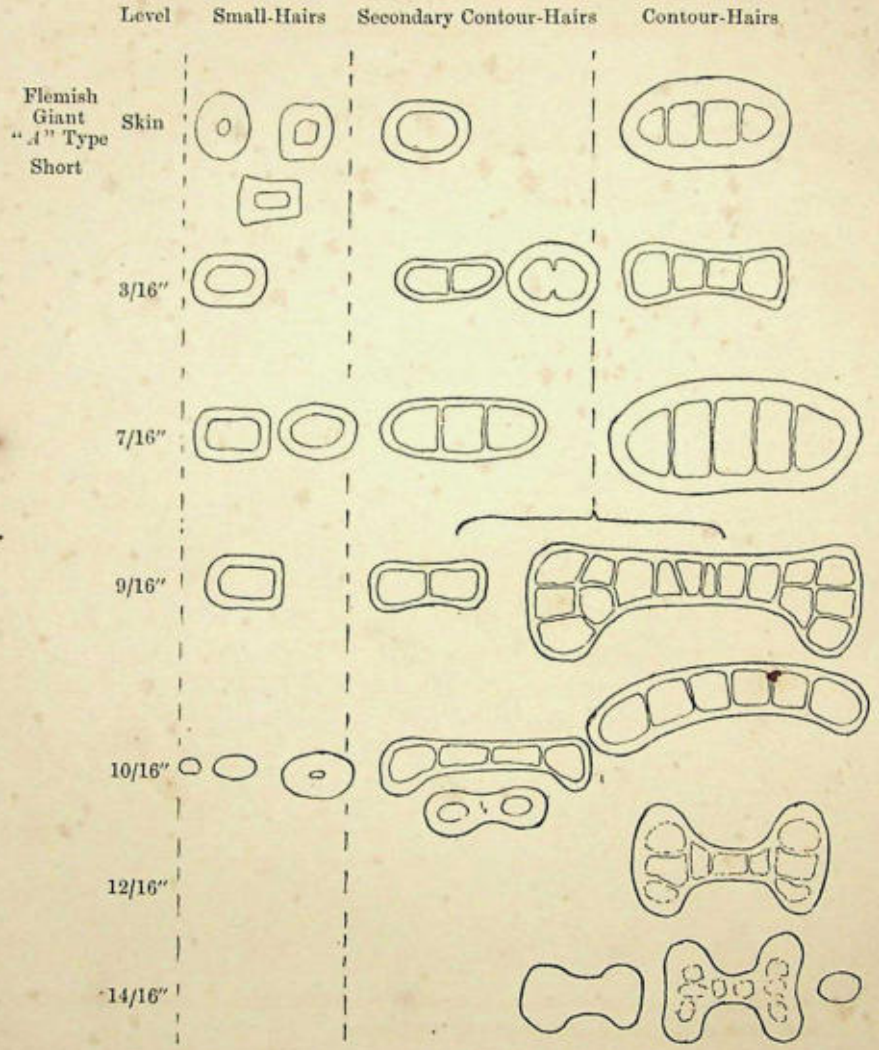


Fig. 1. Transverse sections at successive levels of Small, Primary, and Secondary Contour-hairs in the normal "A" type short-coated rabbit.

Above the half inch level from the skin it is impossible to distinguish with any degree of accuracy the Primary from the Secondary Contour-hairs.

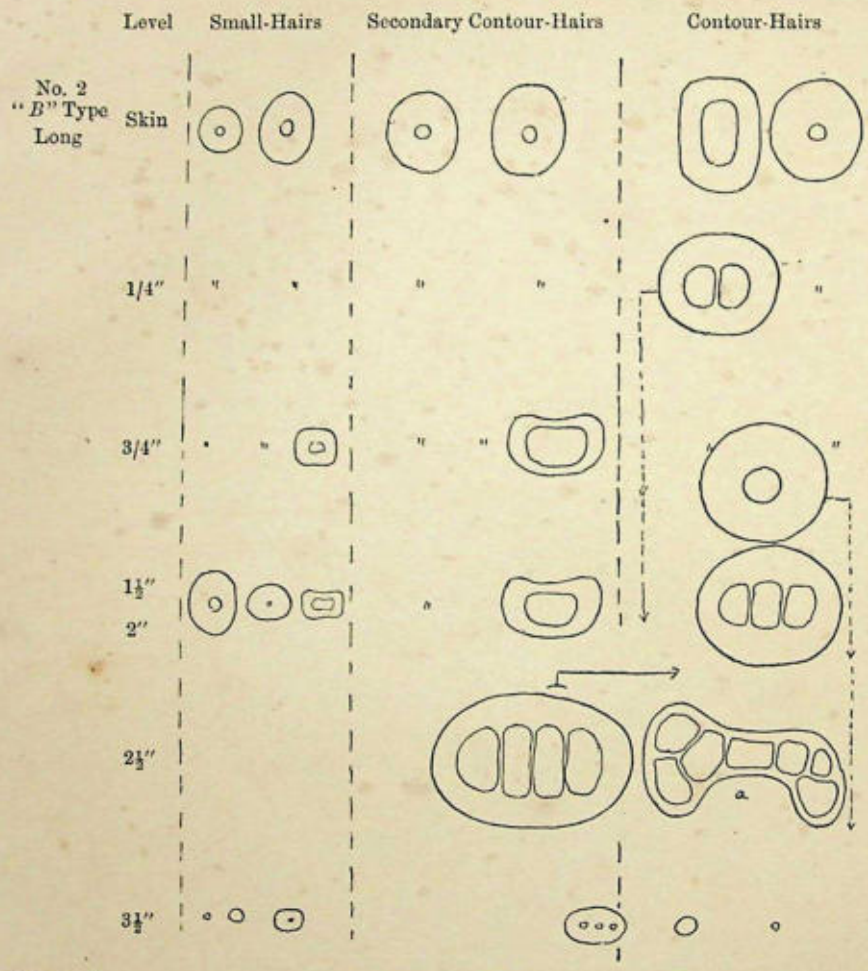


Fig. 2. Transverse sections at successive levels of the Small, Primary, and Secondary Contour-hairs in the long-coated Rabbit of "*B*" type.

The Secondary Contour-hairs probably retain their simple character throughout, differing from the Small-hairs in size only.

The section (*a*) is an abnormal one which, common in the "*A*" type, was found but once in the "*B*" type pelts. It may possibly be an impurity.

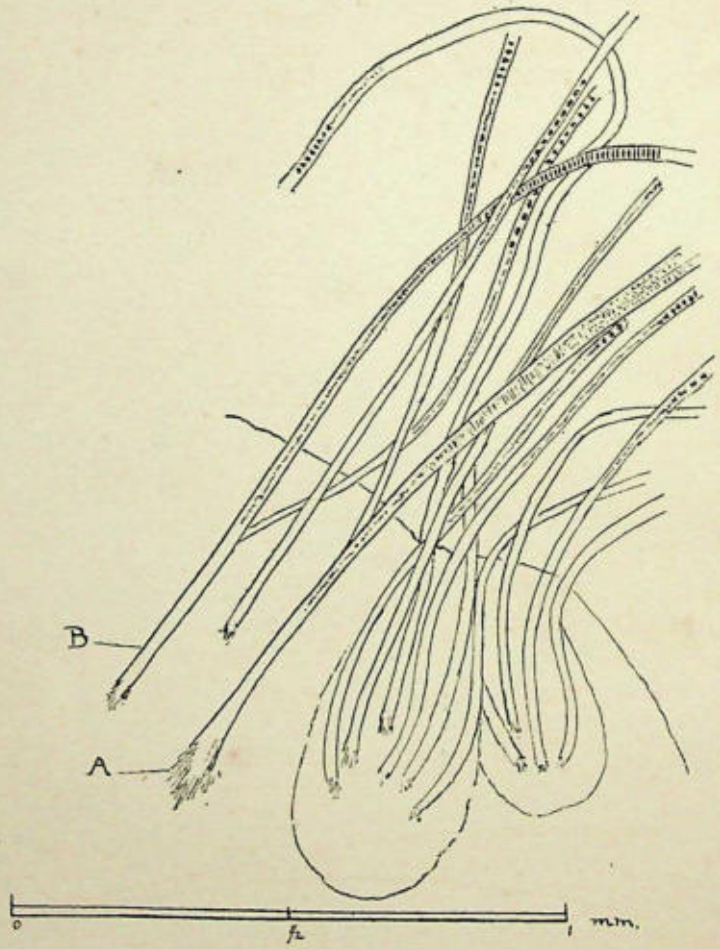


Fig. 3. A teased out hair follicle from the coat of a short-coated rabbit of the Flemish breed.

A = Primary Contour-hair. B = Secondary Contour-hair.

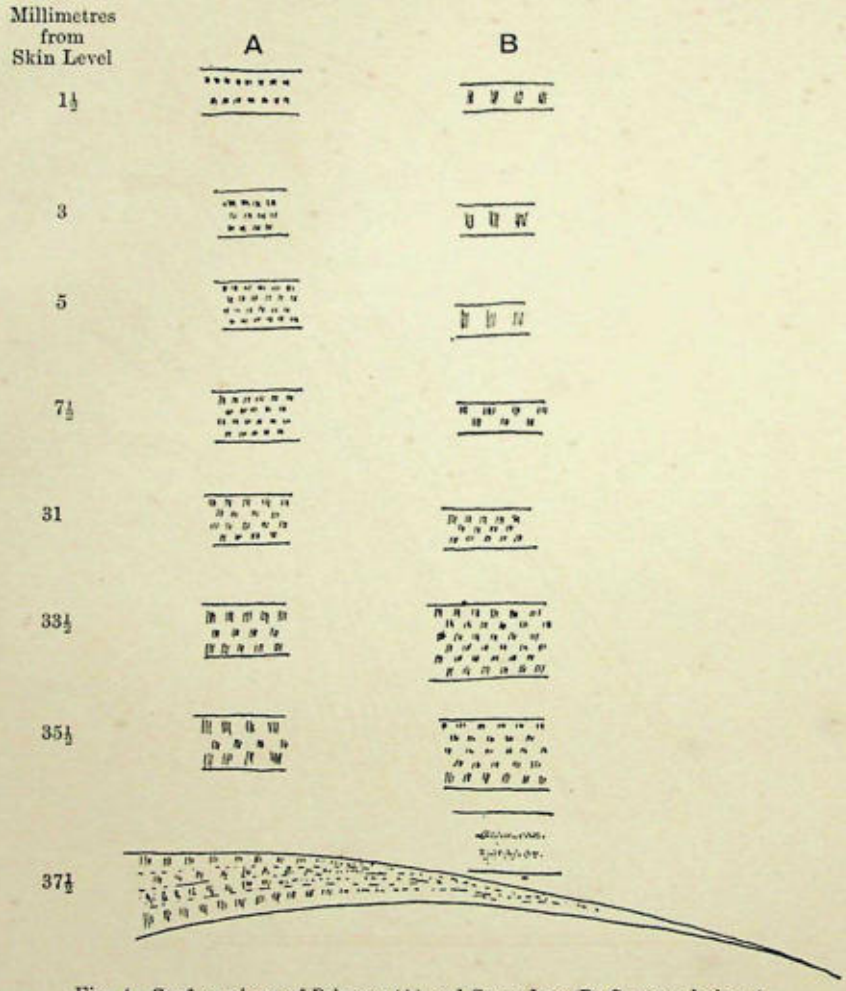
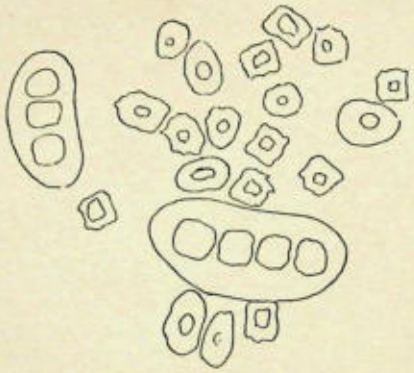


Fig. 4. Surface views of Primary (A) and Secondary (B) Contour-hairs at successive distances, measured in millimetres from the skin level.



1

Fig. 5. Transverse section of hair, at the level of the skin, from the coat of Belgian Hare, No. 1 of Hurst's series.

The Small-hairs are mixed, oval and square. The Fur Type is "*A*."

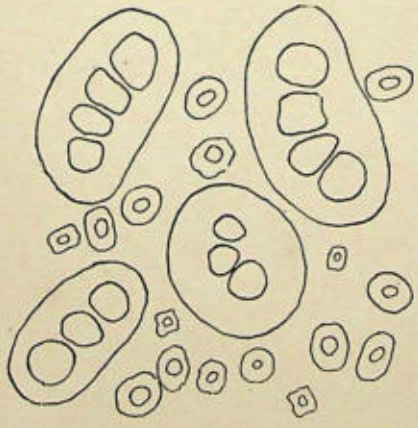
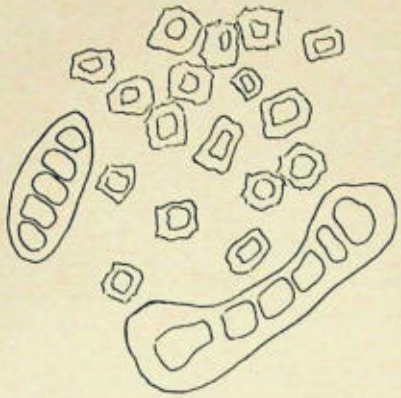


Fig. 6. Transverse section of hair, at the level of the skin, from the coat of a Wild Rabbit.

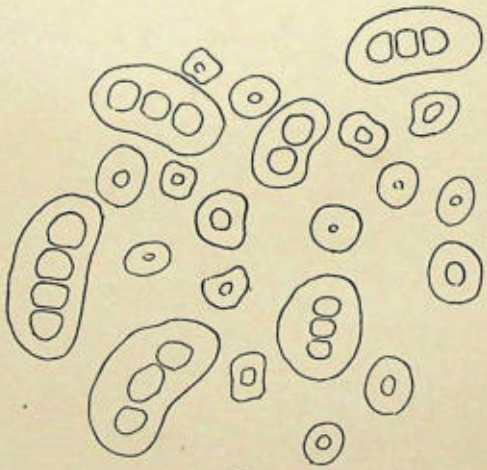
The Small-hairs are of all three types, round, oval and square. The Contour-hairs are in general those peculiar to the "*A*" type pelt, but the central one with 3 medullary chambers is suggestive of the "*B*" type.



4

Fig. 7. Transverse section of hair, at the level of the skin, from the coat of Belgian Hare, No. 4 of Hurst's series.

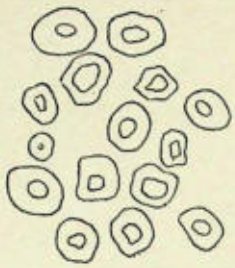
The Small-hairs are uniformly rectangular or "square." The Fur Type is "*A*."



3

Fig. 8. Transverse section of hair, at the level of the skin, from the coat of White Angora Rabbit, No. 3 of Hurst's series.

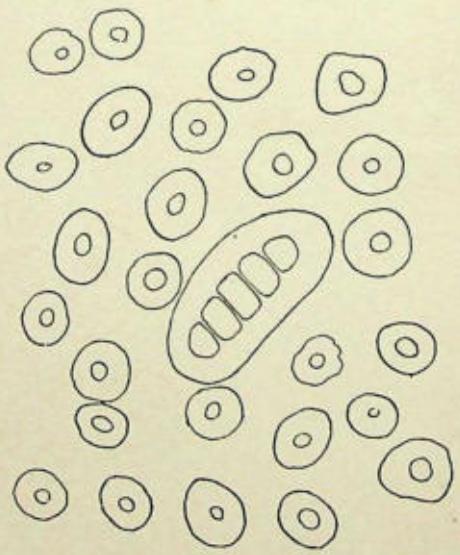
The Small-hairs are oval and round. Fur is of the "*A*" type, but one Contour-hair, more rounded than the others, is suggestive of the "*B*" type, for which this animal is heterozygous.



3*a*.

Fig. 9. Transverse section of hair, at the level of the skin, from the coat of the Rabbit, No 3 of Hurst's series.

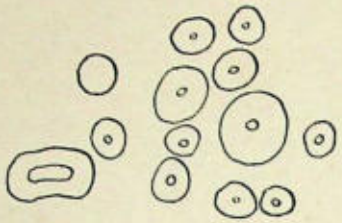
In this group certain "squarish" forms occur. Compare Fig. 8.



7

Fig. 10. Transverse section of hair, at the level of the skin, from the coat of Rabbit, No. 7 of Hurst's series.

The Fur Type is "*A*," the Small-hairs are of the typical oval type found in the great majority of all breeds of short-coated Rabbits.



2

Fig. 11. Transverse section of hair, at the level of the skin, from the coat of the White Angora Rabbit, No. 2 of Hurst's series.

The section illustrates the typical "*B*" type of pelt, with its round, Small-hairs and simple Contour-hairs.

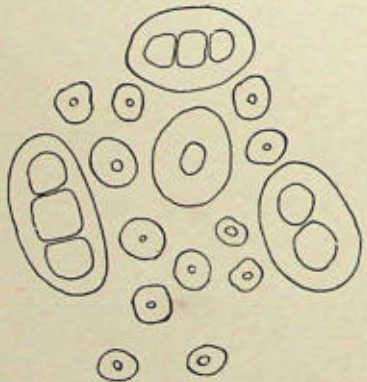


Fig. 12. 53 *D*.

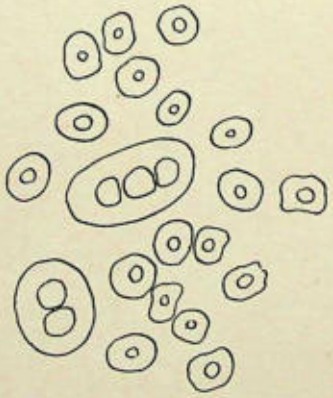


Fig. 13. 53 *W*.

Figs. 12 and 13. Transverse sections of hair, at the level of the skin, from the coat of the Dutch Angora Rabbit, No. 53 of Hurst's series. Fig. 12 from the dark, Fig. 13 from the white area. The type is "*A*," possibly heterozygous for "*B*." There is no differentiation of hair shapes or fur types.

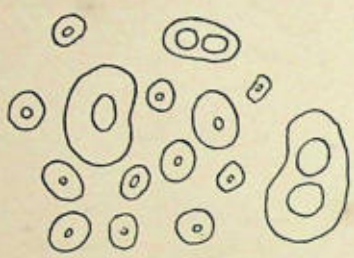


Fig. 14. 54 *D*.

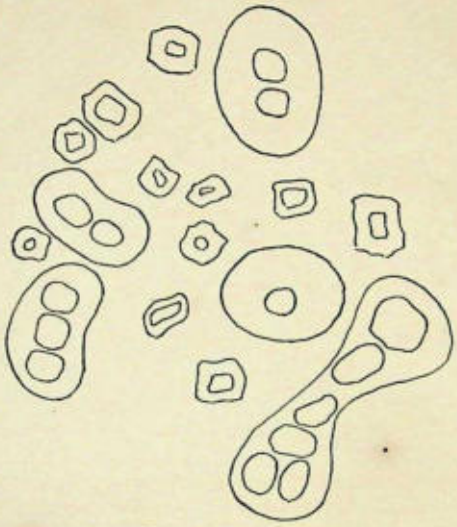


Fig. 15. 54 *W*.

Figs. 14 and 15. Transverse sections of hairs, at the level of the skin, from the coat of the Dutch Angora Rabbit, No. 54 of Hurst's series. Fig. 14 from the dark, Fig. 15 from the light area. There is a differentiation both as regards Fur Type and hair section, the dark hairs being round and the fur of "*B*" type, the white square and the fur of "*A*" type.

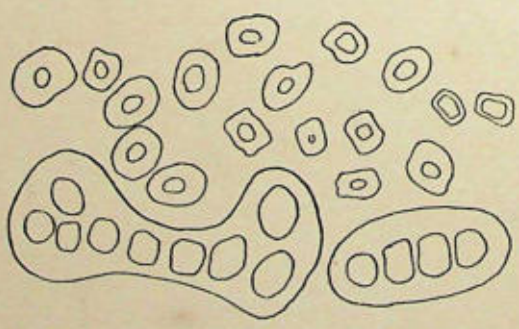


Fig. 16. 40 *D*.

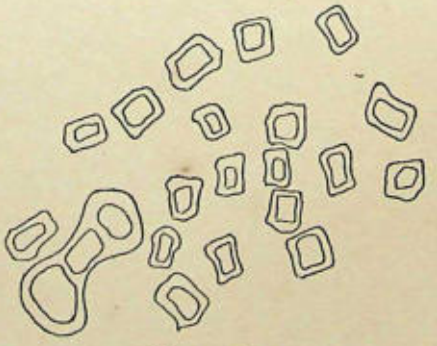


Fig. 17. 40 *W*.

Figs. 16 and 17. Transverse sections of hairs, at the level of the skin, from the coat of the Dutch short-coated Rabbit, No. 40 of Hurst's series. Fig. 16 from the dark, Fig. 17 from the white area.

There is differentiation as to hair section, the oval types being predominant in the dark area, whilst the light contains only square forms with large medullas. There is no differentiation of Fur Type, which is all "*A*."

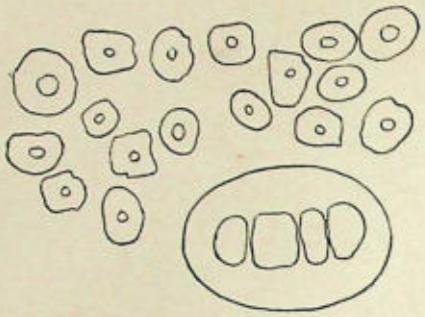


Fig. 18. 51 *D*.

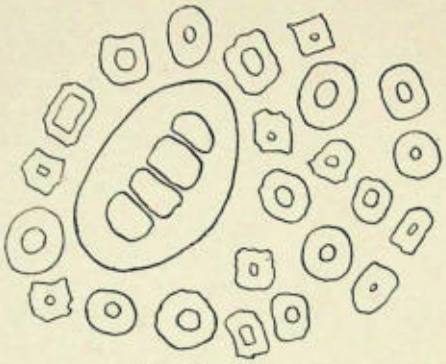


Fig. 19. 51 *W*.

Figs. 18 and 19. Transverse sections of hair, at the skin level of the coat, of the Dutch Angora Rabbit, No. 51 of Hurst's series. Fig. 18 from the dark, Fig. 19 from the white area.

There is neither differentiation of fur type nor hair section in this case.

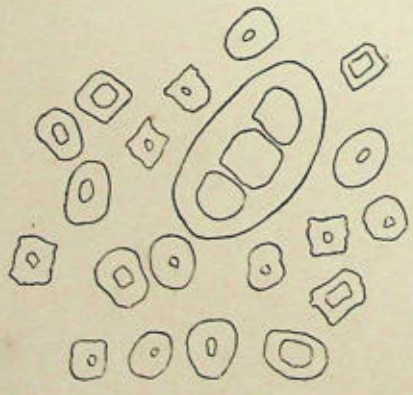


Fig. 20. 94 *D*.

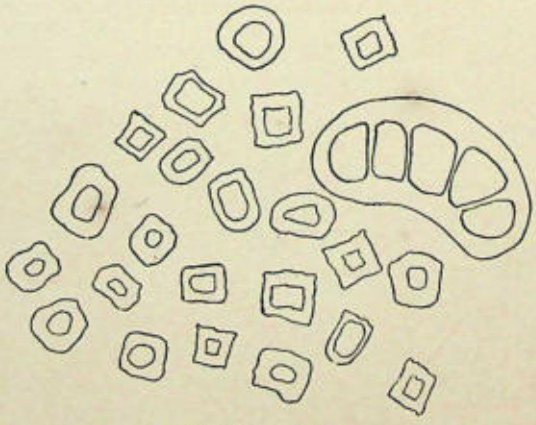


Fig. 21. 94 *W*.

Figs. 20 and 21. Transverse sections of hair, at the skin level, of the coat of the Dutch short-coated Rabbit, No. 94 of Hurst's series. Fig. 20 from the dark, Fig. 21 from the white area.

There is a differentiation of hair shape in this case, the dark hairs being predominantly oval, the white almost exclusively square. There is no differentiation of Fur Type, which is "*A*."

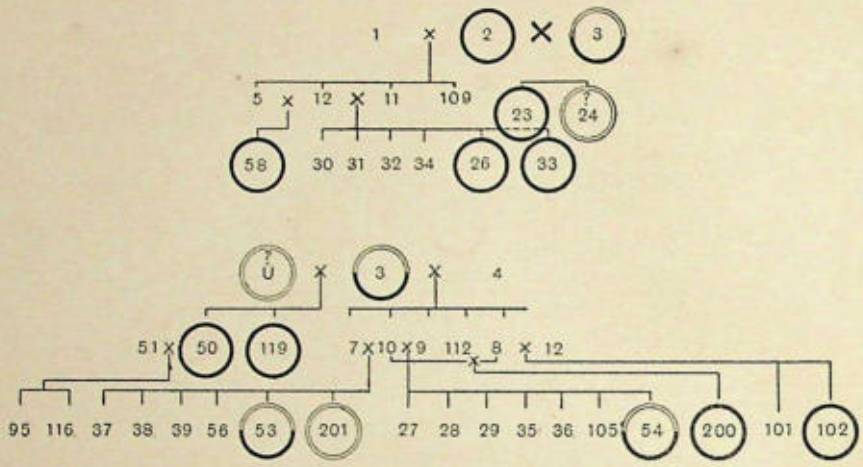


Fig. 22. A chart showing the pedigree of the "*A*" and "*B*" type Angora Rabbits of Hurst's series.

The Angora-coated rabbits are shown as circles with a double contour; the short-coated ones as plain numbers.

The "*B*" type coats are shown as solid contours, the "*A*" types as open double contours, and those "*A*" types known to be heterozygous for "*B*" as open above and solid below. No. 24 marked with a (?) was not available for examination.

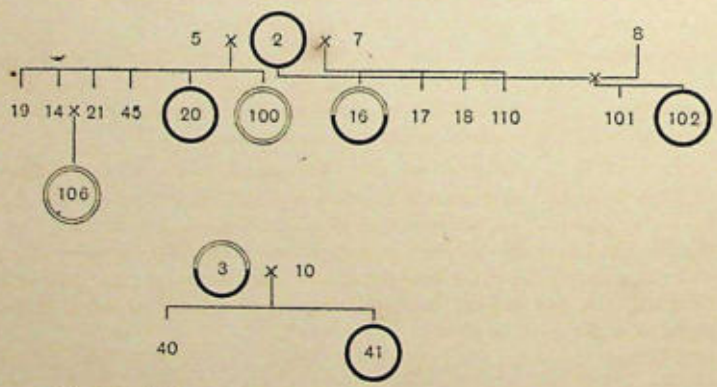


Fig. 23. A chart showing the matings of the parental forms Nos. 2 and 3 with various members of the F_1 series.

The symbols are as in Fig. 22.

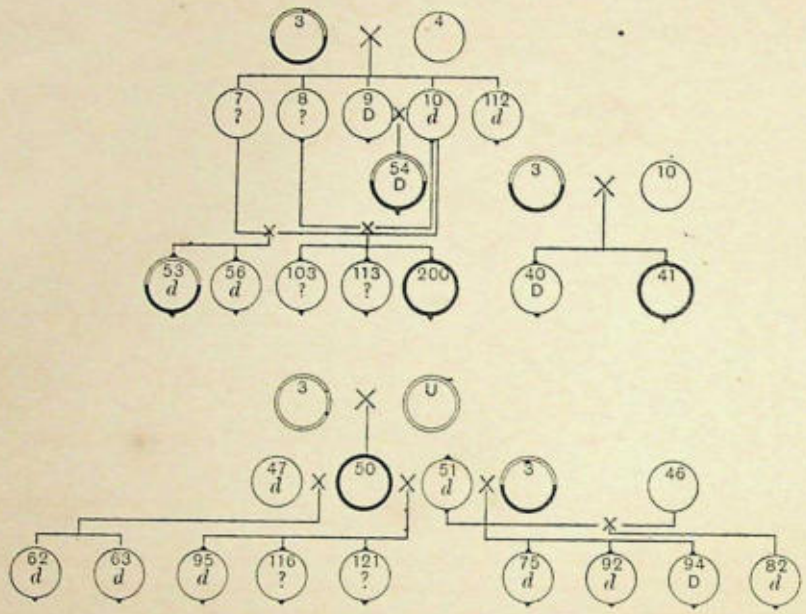


Fig. 24. A chart showing the pedigree of the Dutch and "marked" rabbits of Hurst's series.

The Angora-coated animals are shown with double or solid contours as in Fig. 22. The single contours represent rabbits with short coats.

A black triangle at both poles of the circle indicates a rabbit homozygous for the Dutch pattern and fully marked, whilst a triangle at the lower pole only, indicates a rabbit which is heterozygous for the Dutch pattern but which may, however, be "marked" with white on the shoulders.

The letter "*D*" at the centre of the circle indicates a rabbit which is differentiated as to its hair characters in the dark and light areas respectively. The letter "*d*" indicates complete absence of such differentiation, and the sign ? that its absence is not definitely proved either because of the absence of any white area as in No. 7 or because of the immaturity of the coat as in Nos. 103, 113, 116 and 121 or, finally because of a localized moult in progress, as in No. 8.

THE MALE TORTOISESHELL CAT

By RUTH C. BAMBER, M.Sc. (Mrs BISBEE).

In 1920 Professor Doncaster published a paper in the *Journal of Genetics*(1) in which he suggested that the occasional male tortoiseshell cats which unexpectedly appear, may perhaps be explained in the same way as the freemartins amongst cattle.

Female tortoiseshell cats are common: they are apparently the heterozygous female progeny of parents carrying the factors for black and yellow respectively. The corresponding male progeny of such parents are yellow, but that they are heterozygous is beyond doubt as shewn by their behaviour in breeding: very rarely, however, they are tortoiseshell.

The tortoiseshell colouration is not a sex-linked character in the usual meaning of the term. The factor for yellow is apparently sex-linked in the male but not in the female. The cross yellow male × black female gives tortoiseshell females and black males; whereas the reciprocal cross, yellow female × black male gives yellow males and tortoiseshell females; also a tortoiseshell female crossed with a black male gives tortoiseshell females, yellow males, and black males and females. From this it appears that the yellow males and tortoiseshell females are both heterozygous, but in the male yellow is dominant to black whereas in the female it is incompletely dominant.

Nevertheless, occasionally a tortoiseshell male appears, and, to account for these exceptions, several suggestions have been put forward along the lines of failure of sex-linkage, non-disjunction, etc.(2).

Last year Professor Doncaster suggested an explanation along entirely different lines. He had previously(3) recorded the fact that male tortoiseshell cats are usually sterile, and he conceived the idea that these males are possibly females which have been turned during development to the male condition, in the same way as the freemartin.

In cattle, when a male and a female are born as twins, the female, called a freemartin, is often imperfect sexually, shewing varying degrees of maleness and femaleness in different cases. F. R. Lillie(4) has shewn, beyond question, that the freemartin is a female which during develop-

ment has been intimately associated with a developing male due to confluence of blood vessels in their fused chorions. He suggested that this fusion of blood vessels allows hormones from the male embryo to pass into the female embryo, and so to inhibit the development of femaleness.

Professor Doncaster suggested that a similar confluence of blood vessels may occur in cats and may account for the tortoiseshell males, these having been turned even further towards the male condition than is the case in the most male freemartins, but usually not far enough to be fertile males.

Simultaneously with the publication of this suggestion he began an examination of all pregnant female cats available. He had examined fourteen when he died, and I have continued his observations up to the present time. Altogether, seventy cats have been examined, giving a total of two hundred and fifty-three kittens, and so far no case of confluence of blood vessels has been found. There have been two cases which could not be reported on with certainty. In one there was a slight attachment of the chorions of two adjacent embryos, but unfortunately it was impossible to settle definitely by injection whether or not the blood vessels were confluent, for by an accident the kittens were moved in my absence and the two had separated. The area of attachment was carefully examined under the microscope and shewed no break anywhere. It is almost certain that this was a case of simple adhesion and not of fusion. In the second case two nearly full time embryos were so tightly packed in the uterus that one was pushed under the placenta of the other, carrying the two chorions before it. The chorions were here so closely adherent that, as the specimens were not fresh, but had been preserved in formalin, it was impossible to say with certainty that there was no fusion. However, several similar cases have been found in fresh specimens where there was certainly no fusion, so that it is probable that in the formalin specimens it was again a case of simple adhesion.

There seems to be no reason however why this adhesion should not occasionally be carried a stage further, giving fusion and thus confluence of blood vessels. It can only be said that at present we have no record of such confluence. Lillie, discussing the probability of confluence occurring in other groups than cattle, remarks that "the highly localized" type of placenta found in carnivores makes it unlikely that confluence occurs in that group. But the chorion is very vascular quite outside the placental region, and fusion of the chorions apart from the actual placentas could conceivably give a large degree of confluence of the two embryonic blood streams. There seems no reason however why the

placentas themselves should not sometimes fuse, for they are by no means always in the typical central position on the chorions, being very often nearer to one end than the other. Sometimes the placenta even forms a cap over one end of the chorion, particularly where it is pressed against the distal end of the uterus. If pressure induces this condition fusion of the placentas of adjacent embryos is not at all unlikely. However it has certainly not been found, and at present the parallel between the tortoiseshell tom cat and the freemartin remains an open question until further observations throw more light on the subject.

It seems possible however that the tortoiseshell male may still be a case of sex reversal quite apart from confluence of embryonic blood streams. Recent work by Riddle on pigeons(5), and by Goldschmidt(6) and Harrison(7) on moths has brought to light the fact that, apart from any possible connection between male and female embryos through fusion of foetal membranes, certain fertilized eggs, apparently predestined by their chromosome content to develop into one sex, can be made to develop more or less completely into the opposite sex. It has also been shewn that animals are not quite so sharply separated into males and females as has been commonly believed, but that there are degrees of maleness and femaleness.

Riddle has shewn that in pigeons "generic crosses produce from their 'stronger' germs—those of spring and early summer—nearly all males. If however the birds of such a generic cross be made to 'overwork at egg production'—i.e. if their eggs are taken from them as soon as laid, and given to other birds for incubation—then the same parents which in spring threw all or nearly all male offspring may be made to produce all or nearly all female offspring in late summer and autumn." Riddle's evidence against selective maturation seems sound, and one is almost forced to the conclusion that some eggs, which normally would have developed into one sex, have been induced by special circumstances to develop into the opposite sex.

Moreover amongst the females Riddle finds a series ranging from those which, though females anatomically, are distinctly male in instincts and relative weights, to those which are excessively female, even to the extent of retaining both ovaries in the adult, whereas only one is normally present. When judged by weight the males gave a similar series, but apparently were too pugilistic to give evidence in regard to instinct.

It seems clear that not only may a "predestined" male become a female, or *vice versa*, but also that there are varying degrees of maleness and femaleness.

Now in the light of these facts it seems possible to account theoretically for the tortoiseshell male cat, even apart from confluence of embryonic blood streams. There is no evidence, so far as I know, to suggest that the cause—whatever it may be—which is able to reverse the sex of the embryo completely or partially in birds and in moths cannot also work in mammals. If by this agency a fertilized egg which would normally develop into a tortoiseshell female, be turned from its original "intention" and transformed into a male, then the unexpected tortoiseshell male cat would be produced, just as he might be by hormones due to confluence of blood vessels during development. Also it is equally conceivable, on either hypothesis, that he might be sterile—as is known to be often the case—due to the interference not having been quite strong enough to overcome entirely the original female tendency.

If the tortoiseshell males be comparable to some of the animals in Riddle's series, whose sex has been reversed (or less closely to Goldschmidt's intersexes), one would expect to find a tendency to produce unisexual families in those strains in which they occur. I have not been able to obtain very full information on this point, but the following facts seem significant. Of the four or five tortoiseshell males whose records are available, one was produced by the cross black female × yellow male, and this black female had previously, by different sires, produced only male kittens. By this sire she produced one tortoiseshell male, one tortoiseshell female, and a black kitten of unknown sex. Two other tortoiseshell males are recorded[1] from the mating tortoiseshell female × yellow male and in each case every kitten in the litter was tortoiseshell: it follows therefore that in each case every kitten except the recorded tortoiseshell male was a female. If the records of these last two males are to be trusted, they could not, of course, possibly have arisen due to confluence of blood vessels, as in neither case was there a male in the family with which they could have been united during development. The three records given above provide dangerously scanty evidence, but so far as it goes that evidence supports the hypothesis here suggested that the tortoiseshell males are due to some cause within the fertilized egg, tending to reverse the sex of certain individuals, and so to produce, in extreme cases, unisexual families, as in Riddle's pigeons and Goldschmidt's and Harrison's moths[2].

There are however two separate possibilities to be kept in view. Is

[1] *Fur and Feather*, May 10, 1912.

[2] I find that Professor Dakin, thinking along separate lines, has concluded that possibly the tortoiseshell male may be comparable to Goldschmidt's intersexes.

the tortoiseshell male necessarily always a female turned more or less completely towards the male condition, or may he be sometimes a male which has been turned slightly towards the female condition—enough in most cases to make him sterile, but never enough to mask his essential maleness?

The answer to these questions seems to depend on the exact Mendelian constitution of a yellow male, a tortoiseshell male and a tortoiseshell female.

There is no evidence that a tortoiseshell male is different from a yellow male in his Mendelian factors. There is, however, very little evidence to shew how a tortoiseshell male transmits factors to his offspring. Fertile tortoiseshell males are very rare, and when they do occur they are nearly always mated with tortoiseshell females in the hope of obtaining other tortoiseshell males. This mating does not test the constitution of the male. There is only one doubtful record of the mating of a tortoiseshell male with a black female, which is of course the one required, and this gave the same result as the cross yellow male × black female. If ever I am fortunate enough to find a fertile tortoiseshell male I hope to test the matter more thoroughly. At present the very slender evidence from breeding suggests that the yellow male and the tortoiseshell male behave alike in the transmission of factors to their progeny. In origin they are also the same, with one exception. Tortoiseshell males are recorded from the cross black male × tortoiseshell female and from yellow male × tortoiseshell female: yellow males are also produced from these matings. There is however one record of a tortoiseshell male from the cross yellow male × black female. A yellow male could not have been produced from this mating apart from a breaking down of sex-linked inheritance, and it has been suggested(8) that this breaking down is the cause of the tortoiseshell male. In regard to the tortoiseshell female it seems almost certain that she has the same constitution as the yellow male as far as the factor for yellow is concerned (both arise from the cross, yellow female × black male), but whether the complete dominance of yellow over black in the male, and its incomplete dominance in the female is due to some other sex-linked colour factor, or whether it is due to the different physiological conditions of the two sexes seems uncertain. If the female possesses some colour factor not present in the male, then one is forced to conclude that if the tortoiseshell male is the result of sex reversal at all he can only be a female turned to the male condition and never the reverse. But may it not be possible that the tortoiseshell colour of the female and the yellow colour of the male are

simply the result of different reactions of the same Mendelian factors to the different physiology of the two sexes? The male physiology may be favourable to the dominance of yellow over black, and the female physiology not so favourable. If this be possible, then a tortoiseshell male may equally well be a male with a very slight female tendency, or a female turned almost entirely to the male condition. In either case he would be a "not very male male," and this may account both for his characteristically female colouration and for his usual sterility[1].

In other cases where a character usually found in one sex appears in the opposite sex the animals shewing this abnormality have also been shewn to be sterile[2], e.g. birds and moths; and it is tempting to suggest that these more normal cases of the apparent breaking down of sex-linkage are also in reality examples of sex reversal. The unexpected black female cats which occasionally appear from the cross yellow male × black female may also be accounted for in the same way.

The cause underlying this reversal of sex has deliberately not been discussed here; but quite apart from any theory, the fact itself has been unmistakeably demonstrated by Riddle in pigeons and by Goldschmidt and Harrison in moths, and it is here suggested that the tortoiseshell male cat is another example of the same phenomenon. Whether the reversal in this case must always be from female to male, or whether it can be in either direction, is not clear until further evidence throws more light on the subject.

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1. Doncaster, L. "The Tortoiseshell Tom Cat. A Suggestion." *Journal of Genetics*, Vol. ix. 1920.
2. A fuller discussion of the inheritance amongst cats of the colours yellow, black and tortoiseshell, will be found in the following papers:
   i. Doncaster, L. "On the Inheritance of tortoiseshell and related colours in Cats." *Proc. Camb. Phil. Soc.* Vol. xiii. p. 35, 1904.

[1] If the colour be a matter of sex physiology then by castrating a very young yellow male and grafting ovaries it might be possible to bring up the black to some extent later. Similarly by grafting a functional testis into a newly born tortoiseshell male it might be possible to inhibit the development of black in future coats. There is not very much hope of success in these experiments, for after birth it seems late to attempt to alter such a well-fixed character as coat colour. Still, birds from which ovaries have been removed develop male plumage, and castrated deer cease to grow their horns. Administration of extracts of the endocrine glands and transfusion of blood might also give interesting results. I hope to attack the problem along these lines in the near future.

[2] See Literature cited 3 i and ii.

ii. DONCASTER, L. "Sex-limited Inheritance in Cats." *Science*, N.S. Vol. XXXVI. p. 144, 1912.

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v. LITTLE, C. C. "A Preliminary Note on the Occurrence of a Sex-limited Character in Cats." *Science*, N. S. Vol. XXXV. p. 784, 1912.

vi. ——. "Colour Inheritance in Cats, with special reference to the colours black, yellow, and tortoiseshell." *Journal of Genetics*, Vol. VIII. p. 279, 1919.

vii. ——. "Is the Fertile Tortoiseshell Tom Cat a Modified Female?" *Journal of Genetics*, Vol. X. p. 301, 1920.

viii. WHITING, P. W. "The Tortoiseshell Cat." *Amer. Nat.* Vol. XLIX. p. 518, 1915.

ix. ——. "Inheritance of Coat-Colour in Cats." *Journ. Exp. Zool.* Vol. XXV. p. 539, 1918.

x. WRIGHT, S. "Colour Inheritance in Mammals. X. The Cat." *Journ. Heredity*, Vol. IX. p. 139, 1918.

3[1]. i. DONCASTER, L. "A possible connection between Abnormal Sex-limited Transmission and Sterility." *Proc. Camb. Phil. Soc.* Vol. XVII. p. 307, 1914.

ii. ——, and CUTLER, D. W. "On the Sterility of the Tortoiseshell Tom Cat[2]." *Journal of Genetics*, Vol. V. p. 65, 1915.

4. LILLIE, F. R. "The Free-Martin; A Study of the Action of Sex-hormones in the Foetal Life of Cattle." *Journ. Exp. Zool.* Vol. XXIII. 1917, p. 371.

5. RIDDLE, O. "Sex Control and known Correlations in Pigeons." *American Naturalist*, Vol. L. 1916, p. 385.

[1] Little's theory of non-disjunction has not yet, to my knowledge, been tested experimentally: it remains therefore as a fascinating possibility. There are however several difficulties. As Little himself points out, it does not account for the production of a tortoiseshell male from the mating black male × tortoiseshell female, as reported by Doncaster. Little suggests that the breeders' records may have been at fault; and that of course is possible. If records are to be trusted at all however, another difficulty seems to arise in the case of the black female, referred to elsewhere in the present paper. When crossed with a yellow male she produced a tortoiseshell male, a tortoiseshell female and a black of unknown sex: previously, mated with many different males, she had produced male offspring only. This would not be expected on the theory of non-disjunction; unless, indeed, the females referred to by Little, "with peculiar gametic conditions," prove to be males.

[2] I have had the opportunity of dissecting Professor Doncaster's tortoiseshell tom cat. Anatomically he was typically male; but microscopic examination of the testis shewed the left remaining one to be like the right one previously described by Professor Doncaster: there was a large amount of interstitial tissue, and well-developed seminiferous tubules but no spermatozoa.

6. i. Goldschmidt, R. "Experimental Intersexuality and the Sex-problem." *American Naturalist*, Vol. L. 1916, p. 705. (A short account in English.)

ii. ——. "Mechanismus und Physiologie der Geschlechtsbestimmung." Berlin, 1920. (Full account in German.)

7. Harrison, J. W. H. "Studies in the Hybrid Bistoninae. IV. Concerning the Sex and related problems." *Journal of Genetics*, Vol. IX. 1919, p. 1.

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VOLUME XII DECEMBER, 1922 No. 3

POSTAXIAL POLYDACTYLISM IN SIX GENERATIONS OF A NORWEGIAN FAMILY.

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(With one Text-figure and Plates XV to XX.)

Introduction.

THE material forming the basis for this investigation was kindly given to me by Professor K. Bonnevie, Christiania, to whom I am also greatly indebted for the valuable help rendered me during the work. I wish also to give my thanks to Dr Thue and Dr Heyerdahl of "Rigshospitalets Röntgenavdeling," Christiania, for providing me with the radiographs necessary.

At the time the work was started the material consisted of radiographs of the hands of a polydactylous young man (1.1321, Pl. XVI, fig. 6) and the information obtained from him concerning the distribution of the abnormality in his family. The case seemed interesting because of the peculiar and high development of the polydactylism in this boy and also because of the great number of polydactylous individuals present in the family. Later it was found that an account of the case had been published by W. Magnus (1909) containing short descriptions of some of the members of what is below described as line 1 of the family.

During the investigation great stress has been laid upon a personal examination of as many members of the family as possible in order to get an indication of the variability of the character in question; second-hand information is in this respect very unsatisfactory, the descriptions always being vague and uncertain. I have succeeded in getting radiographs and in part photographs of hands as well as of feet from no less than 23 members of the family now living, 15 of whom were polydactylous; further, two polydactylous individuals, who would not allow themselves to be radiographed, have been examined and photographed. It was found that the polydactylism in question is subject to much variation and also that in certain cases it is associated with brachydactylism caused by the shortening of the metacarpal and metatarsal bones.

The distribution of the abnormality within the family studied is shown in the pedigree (Pl. XV) which has been constructed from information supplied by members of the family, the relationship itself being corrected and confirmed through the church registers. The polydactylism has been traced back through six generations, the radiographs obtained covering four generations. The two branches of the family which in the pedigree are marked as line 1 and line 3 contain the individuals which have been most thoroughly studied, most of the living members having been personally examined and radiographed.

The members of the family are numbered in the pedigree after the method used at "Universitetets Institut for Arvelighetsforskning," Christiania. The ancestress of the family is given the number 1; each of her children is numbered according to his order of birth in his fraternity, getting the numbers 1.1, 1.2, 1.3, etc. to 1.10; the offspring of 1.1 is 1.11, 1.12, etc. of 1.3, 1.31, 1.32, etc. The advantage of this method is that new members of the family can always be entered without renumbering those already present; it also at once shows the relationship between different members.

Description of the abnormality studied.

The abnormality met with in this family is no clearcut case of multiple fingers and toes. As mentioned above the polydactylism in question is in several cases combined with a shortening of the metacarpal and metatarsal bones, this brachydactylism also in a few cases appearing in hands and feet with 5 fingers and toes. The variation in the development of the polydactylism itself is considerable and two different types seem to be present; it has also been found that a certain relation exists between the type of polydactylism and the appearance of the brachydactylism.

As a matter of convenience I shall describe the polydactylism and the brachydactylism separately, although very little can be said with certainty as to their genetical or anatomical connection.

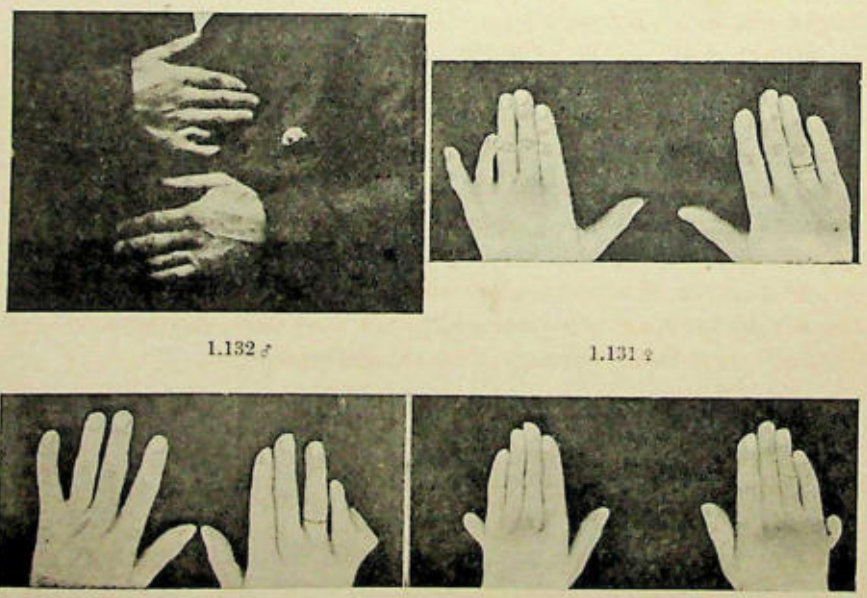
The Polydactylism.

At first the most prominent feature of this material seemed to be the uniformity in the development of the polydactylism, the affected individuals originally met with all belonging to what is below described as type *A*. Later on, however, this appearance of uniformity proved to be misleading, the polydactylism in reality exhibiting a great deal of variation.

Common to all cases examined is the postaxial development of the supernumerary digits, which were always found at the ulnar and the fibular side of hands and feet. Mostly both hands and both feet carry six fingers and toes, in other cases the polydactylism is restricted to one hand and both feet, or one hand and one foot, or only the hands and so on. If the affection is unilateral it may occur on either side with equal frequency.

The development of the extra digits, however, varies to a high degree from a small wart-like appendage to a fully developed finger or toe provided with a metacarpal, phalanges, and nail. A closer examination of this variation suggested that one is probably dealing with two different types of polydactylism, although there is some intergradation between them.

The two types, described below as type *A* and type *B*, differ in several respects but the main thing is that in one case, type *A*, we find what is probably a duplication of one finger, most frequently the fifth one, with an equally strong development of both parts, whereas in the other case, type *B*, the sixth finger is represented by a small appendage loosely attached to the ulnar border of the hand. Examples of the two types are shown in text-fig. 1, exhibiting hands from different members of the



1.132 ♂ 1.131 ♀

1.134 ♀ 1.1344 ♂

Text-fig. 1. Hands from different members of the family studied.

family. This classification has been used by different authors, for instance by Bateson (1894), Lewis (1912) and Plate (1913) as a convenient method of description. The following investigation seems to indicate that a genetic difference between the two types really exists.

Type A covers the most highly developed cases of polydactylism in the family. The hands of the woman 1.13 (Pl. XVI, fig. 1) whose progeny is represented by line 1, give a typical example of this kind of polydactylism. The radiographs give the impression that an extra finger has been inserted between the fourth and fifth fingers on both hands. It is, however, in cases like this difficult or impossible to tell which of the fingers is to be regarded as the extra one; to my mind we are most probably dealing with a bifurcation of the fifth finger, in which case both parts must be regarded as co-ordinate organs. What I think must be regarded as clear evidence of a bifurcation of the fifth finger is found in the right hand of 1.1321 (Pl. XVI, fig. 6) where a dichotomously branched first phalanx carries two fingers, each of which consists of two terminal phalanges; the left hand of the small child 1.13251, shown in Pl. XX, also points to the possibility that a bifurcation has taken place, only in this case the fourth finger is the affected one; in all other cases of this type the bones of the two most ulnar fingers are separate but the hypothesis of bifurcation is strongly supported by the development of the abnormality in the feet; a glance at the radiographs Pl. XVIII shows the frequent occurrence of a dichotomously branched fifth metatarsal. This apparent branching of the fifth finger or toe may be interpreted as in reality due to a fusion of two originally separate bones, but I can see no reason why this fusion should always happen between the fingers and toes at the ulnar and fibular border of the hand and foot.

Plate XVI, figs. 1 to 9, show the range of variation within this type. One is at once struck with the completeness and equality of the two external digits whenever a *left* hand is affected. The appearance is as if the fifth finger were represented by two equally developed straight fingers, the inner of the two having only a short metacarpal. The length of this incomplete metacarpal varies slightly, but otherwise all the affected left hands are extraordinarily alike, with the exception of the left hand of 1.135 where the bifurcation is limited to the third phalanx of the fifth digit; but even here the equality is maintained; unfortunately the man would not allow the photographs of his hands to be published. The affected *right* hands, on the contrary, show a great deal of variation. The incomplete metacarpal of this hand is liable to much more variation; sometimes only a small head is present as in 1.134,

fig. 5, whereas in other cases the development of this metacarpal is more like that found in the left hand. In one case, 1.1321 [Pl. XVI, fig. 6], the radiograph shows a right hand carrying seven fingers, the seventh one being very small but provided with three phalanges. A conspicuous feature also in most of the right hands of this type is the crookedness of the finger at the ulnar border of the hand compared with that of the left hand. This crookedness is plainly shown in the right hands of 1.134 and 1.1321; it seems to be connected with the degree of bifurcation as it is always most pronounced in hands showing a low development of the incomplete metacarpal. In this connexion I may recall the observation of Bond (1920) that in fowls heterozygous for extra toe the development of these toes is commonly more complete on the left side.

As pointed out before in spite of this variability the hands of this type show a great deal of uniformity. In all cases the two ulnar fingers are strongly and equally developed; further a more or less defective additional metacarpal bone is always present; later on it will be shown that the postaxially situated metacarpal in hands of this type is always shorter than a normal fifth metacarpal.—The fifth and sixth fingers are more or less united and cannot be moved separately.—Some of the feet of the individuals belonging to this type are seen in Pl. XVIII, figs. 17–24. The same bifurcation of the fifth digit as met with in the hands is present here. The doubling may be more complete, giving six fully developed metatarsals as in 1.131 and 1.134. More often the fifth metatarsal is forked and each branch carries three phalanges; these two variations may be met with in the same individual (see 1.134, fig. 20). In a few cases the reduplication is limited to the phalanges only, the fifth metatarsal not being affected at all.

Type B. During the further investigation of the distribution of the abnormality within this family a different anatomical type was discovered. The hands of individuals belonging to this type are supplied with small postaxially attached appendages having no bony connection with the hand. In cases like this it is very easy to remove the superfluous limb and I regret to say that only one case still exists in which an amputation of the extra finger has not taken place. The hands of this individual (1.1344) are represented in Pl. XVII, fig. 13 and can also be seen in text-fig. 1.

The supernumerary fingers are in this boy very small but are equally developed and have the appearance of normal fingers; in the radiographs these appendages are shown to contain several small bones, from their shape probably representing a small metacarpal with its epiphysis and

three phalanges; it seems that even in this case a bifurcation of the fifth digit has taken place but one part of the bifurcated limb has been left behind in the further development of the hand. In another case, that of 1.312, the left hand carried an extra finger like that just described, whereas the extra finger of the right hand of the same man was represented by a small warty knob without nail. The daughter of this man had on both hands warty appendages without nails or bones. In both cases the extra fingers have been removed and the radiographs (Pl. XVII, figs. 14 and 16) show no sign of the abnormality. The cases of 1.3111 and 1.3114 (Pl. XVII, fig. 15, and Pl. XVIII, fig. 17) are perhaps to be regarded as the extreme of this type, the polydactylism being restricted to the feet only (Pl. XIX, figs. 26 and 27). As will be shown later, in hands of this type a shortening of the metacarpals like that met with in hands of type *A* is never found.

The muscular equipment seems in *B*-type hands always badly developed; the extra fingers of 1.1344 (see text-fig. 1 and Pl. XVII, fig. 13) are for instance seen to hang limply from the side of the hand and cannot be moved at all, either separately or in connection with the fifth finger.

Strangely enough polydactylous feet of individuals having *B*-type hands show no sign of a diminution in the development of the abnormality; these feet are like those found in *A*-type individuals. This is illustrated in Pl. XIX, figs. 30–32, the feet of 1.3123 even exhibiting the highest degree of bifurcation met with in the family. But as found in *A*-type individuals the development of the abnormality varies; thus in 1.1344 (Pl. XIX, fig. 29) the right foot is polydactylous owing to the bifurcation of the fourth toe instead of the usual fifth one.—Highly developed polydactylism in feet combined with a slightly pronounced polydactylism in hands is however a feature not seldom met with in individuals of the *B*-type.

A case illustrating this was sent to "Universitetets Institut for Arvelighetsforskning" from "Rigshospitalet," Christiana, and is shown in Plate XIX, figs. 31 and 32. The radiographs here exhibited represent hands and feet of a six year-old girl having no connection with the family here described. As will be seen each foot carries six toes all supplied with metatarsals and phalanges whereas the hands show a pronounced *B*-type, the superfluous limb being represented by a small knob containing no skeleton. Another case showing the same difference between hands and feet is that of Fackenheim (1888). He figures hands carrying small postaxially developed appendages, whereas the feet of the

same individuals are seen to be supplied with six completely developed toes.

There is one case in the family here described which is so complex and exceptional that it is not possible to decide whether the hands should be classed as of the *A*- or *B*-type. The radiographs appear in Pl. XVII, fig. 12. At birth the boy had six fingers on his hands, but an external digit was at once amputated from each. The hospital journal states that both the fingers removed had "nails and two phalanges." That of the left side is said to have articulated with the metacarpal; whereas that of the right had no bony connexion with the hand, as would be the case in the *B*-type. The radiographs show the present condition at the age of 14. Of the five metacarpals represented, the central two of the palm have a common base, and digit IV is displaced centralwards so that it appears to be too short. Digit V however is somewhat longer than the normal. The boy's feet show no abnormality except for a shortening of V in the left foot. Without more evidence as to how much was removed it is impossible to say to what type the left hand belonged, though the right was almost certainly of the *B*-type. It may be worth mentioning in this connection that two of his brothers have *B*-type polydactylous hands, and his mother, though decidedly belonging to the *A*-type, shows some deviation towards the *B*-type.

The hands of this woman (1.134) are shown in Pl. XVI, fig. 5; her right hand is polydactylous of the *A*-type but the radiograph shows that the extra metacarpal is only represented by a small roundish bone between the metacarpal IV and V; the ulnar branch of the doubled fifth finger has been pushed more towards the border of the hand, giving the impression that if this pushing outwards had been carried further a type like the *B*-type would have resulted. A development in the same direction is shown in the right hand of 1.1425 (Pl. XVI, fig. 8); this hand has, like that just described, a small extra bone between the metacarpals IV and V; the sixth finger of this hand had been represented by a small postaxially attached warty appendage removed just after birth; a similar appendage is characteristic of *B*-type hands, but a bone between the metacarpals is never present.

The Brachydactylism.

In *A*-type individuals of this family the shortness of the fifth and sixth fingers is conspicuous, as can be seen in the radiographs of Pl. XVI. This brachydactylism seems to be due to a shortening of the ulnar metacarpal, but in some cases also some of the phalanges look shortened. To

settle the question whether a special shortening of the ulnar finger is really present or if we are only dealing with normal fluctuating variation it was necessary to undertake a comparison with sufficient material of normal hands. Such material was obtained from Pfitzner's measurements of the hand bones of 301 normal-handed skeletons (1892, 1893). Based on this material the coefficient of correlation has been worked out for the fourth and fifth metacarpals and for each of the phalanges of the fourth and fifth digits respectively.

The values obtained are seen in Table I. As can be seen evidently a strong correlation exists for the different parts of the fourth and fifth fingers, the correlation-coefficient being particularly high for the metacarpals IV and V and for the phalanges IV and V; a somewhat weaker correlation exists for the two distal phalanges.

TABLE I.

Coefficient of correlation for length of different finger bones based on Pfitzner's material.

Coefficient of correlation for length of	n	r p.e.
Metacarpal IV and V ...	293	0·97 ± 0·003
Phalanx IV 1 and V 1 ...	302	0·92 ± 0·009
,, IV 2 and V 2 ...	301	0·83 ± 0·018
,, IV 3 and V 3 ...	298	0·71 ± 0·023

Table II gives the length of the first phalanges and the metacarpals of the fourth and the fifth fingers of the right and left hands measured from the radiographs representing the polydactylous as well as the normal hands of the members of the family studied. In polydactylous hands of the *A*-type the measurements of the phalanges and metacarpals are taken from the more ulnar of the doubled finger; it has however been found that, as far as the phalanges go, it makes no difference if one chooses the inner finger to measure from. In *B*-type hands the bones of the well-developed fifth finger are measured. The measuring has been made in the way given by Braune and Fischer (1887), also used by Pfitzner, the metacarpals being measured from the centre of their basal plane to the top of their heads and the phalanges along their chief axis.

When Pfitzner's measurements of the metacarpals IV and V from 293 normal-handed individuals are arranged in a correlation table we get the result seen in Table III. The numbers of each class represent Pfitzner's measurements; they all fall along a main axis. Into the table made up in this way are then plotted the values obtained by measuring

the radiographs of the family concerned; the measures from *A*-type hands are represented by black spots, those from *B*-type hands by semi-black circles and those from five-fingered hands by open rings.

TABLE II.

Length in mm. of the metacarpals IV and V and the phalanges IV 1 and V 1 of members of the family, measured from radiographs.

Line 1.

		Length of metacarpal				Length of phalanx			
		IV in mm.		V in mm.		IV 1 in mm.		V 1 in mm.	
Individual	Age	Right	Left	Right	Left	Right	Left	Right	Left
1.13 ♀	76	59	60	48	49	38	38	28	29
1.131 ♀	53	65	62	58	50	39	40	33	31
1.132 ♂	50	66	67	55	56	42	41	31	32
1.133 ♀	47	56	55	51	51	38	38	30	29
1.134 ♀	45	73	74	56	65	42	42	31	36
1.1321 ♂	24	70	71	58	59	42	42	32	32
1.1324 ♀	20	58	55	50	46	35	33	30	26
1.1325 ♀	18	62	60	47	50	37	37	30	30
1.1326 ♂	17	69	70	58	59	43	44	31	31
1.1327 ♂	15	58	58	53	53	37	38	30	30
1.1328 ♀	11	49	47	45	43	33	32	26	26
1.1331 ♀	17	55	54	50	50	40	39	30	30
1.1344 ♂	10	48	48	42	43	31	31	26	26
Line 3.									
1.312 ♂	45	—	—	—	—	40	41	34	35
1.3111 ♂	18	67	67	60	60	43	44	37	37
1.3113 ♀	12	55	56	52	51	39	38	32	31
1.3114 ♀	10	51	52	47	48	33	33	27	28
1.3123 ♀	18	63	—	56	—	40	40	34	34
1.3125 ♂	15	—	53	—	49	39	39	30	30
1.3126 ♀	13	—	53	—	49	37	37	30	29

From this table a few striking facts are revealed. First, it shows that all *A*-type hands fall outside the limits of extreme variation in normal hands forming a group of their own, parallel to the "swarm" of normal measures; the conspicuous shortness of the fifth and sixth fingers in these hands therefore has at least one of its causes in a shortening of the metacarpals. Secondly, one sees that the semi-black circles fall within the classes represented in Pfitzner's material, showing that in the cases of *B*-type hands measured no shortening of the fifth metacarpal is present; unfortunately I have not been able to get measures from more than three hands of this type owing to the indistinctness of some of the radiographs. Finally, with one exception, the five-fingered hands represented by open rings also fall along the same main axis as the hands from Pfitzner's material. This last category includes the

normal hands of three individuals belonging to the *A*-type, those individuals having one normal and one polydactylous hand; further two individuals having normal hands but polydactylous feet; and finally eight individuals showing no sign of polydactylism in either hands or feet. In all these cases the result is the same: A five-fingered hand from the family studied is normal both in regard to polydactylism and brachydactylism. As mentioned, one exception from this rule exists; this case is found in the left hand of a woman (1.134) belonging to line 1 of the family; it is of importance because it is the only case observed where the brachydactylism found in the hands of this family is not associated with polydactylism; it must, however, be remembered that the right hand of the same woman is polydactylous of the *A*-type.

Table IV in the same way shows the correlation existing for the first phalanges of the fifth and fourth fingers from Pfitzner's material. The distribution within this table of the measures from the first phalanges of the family concerned clearly shows that no shortening whatever is present in this bone.

Correlation tables based upon Pfitzner's material have also been constructed for the second and the third phalanges of the fourth and the fifth digits. These tables have not been reproduced as they give the same result as shown in Table IV; on plotting the values obtained from the digits of the family studied into these tables it became apparent that neither of the two terminal phalanges of the fifth digit are shortened; it is true that in a few cases the second phalanx of the fifth digit shows small deviations from the extreme limits of variation; but considering the smaller correlation here present these deviations are probably of no significance.

The examination of the relation between the different bones of the finger at the ulnar border of the hand to those of the fourth finger therefore lead to the conclusion that the brachydactylism found in several individuals of this family is due to a shortening of the metacarpals, the phalanges being found to be normal. It was further shown that the brachydactylism, with one exception, is restricted to hands which are also polydactylous of the *A*-type.

A similar examination of the metatarsals of the feet was undertaken. Using Pfitzner's measurements from the bones of 293 normal feet a correlation table was constructed for the metatarsals IV and V, and the working out of the correlation coefficient gave the value $r = 0{\cdot}93 \pm 0{\cdot}008$. Unfortunately the radiographs were not fit for measuring and only from 17 feet approximate measures were obtained. Among those there were

TABLE III.

Table of correlation for the metacarpals IV and V based upon Pfitzner's material and measurements from the hands of the family here studied.

Metacarpal IV.

Metacarpal V.

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
41																															
42				◐																											
43			○	◐																											
44			1																												
45			1	4	○	1																									
46				2	1	4	2				●																				
47						6	○ 3	2	1									●													
48							6	○ 8	4						●																
49								6	○○ 7	2						●															
50								1	7	○ 8	○ 11	3	1	○		●		●													
51									9	6	○ 15	○○ 8	4		1																
52									1	4	○ 14	11	7	3																	
53										1	2	8	8	○○ 4	1																
54											2	1	6	9	8	1	1														
55													2	4	12	7	2					●									
56													1	2	4	9	2	1	◐ 1				●						●		
57														1	1	4	2	1	1												
58																1		1	1		○				●	●					
59																		1	1		○					●	●				
60																				1			○○								
61																															
62																						1									
63																					1										
64																															
65																														○	

● A-TYPE POLYDACTYLOUS HANDS ◐ B-TYPE POLYDACTYLOUS HANDS. ○ NORMAL HANDS.

TABLE IV.

Table of correlation for the phalanges IV 1 and V 1 based upon Pfitzner's material and measurements from the hands of the family here studied.

Finger IV.

Finger V.	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
21																							
22																							
23			1																				
24			1																				
25																							
26				●○	○	●○	1																
27						○	1	3	1														
28						○		3	6	4	●2	1											
29								1	5	○11	●○6	3											
30								○	1	●●○4	○○18	○○○5	○1										
31											○13	22	15	2	●●3	●	●						
32												○4	24	●20	●●○10	1							
33												○	2	25	16	○7	1	2					
34													○○○	2	8	17	4	1					
35														◐1		5	5	1	2				
36															○	2	2	1		1			
37																○	○		2				
38																				1	1		
39																							
40																							

● A-TYPE POLYDACTYLOUS HANDS. ◐ B-TYPE POLYDACTYLOUS HANDS. ○ NORMAL HANDS.

8 feet having a bifurcated fifth metatarsal developed in a way corresponding to the polydactylous hands of the *A*-type; their metatarsals, like the corresponding metacarpals, all proved to be shortened, their measures falling outside the "swarm" of normal feet in the table. Measures were also obtained from the metatarsals of 8 feet showing no sign of polydactylism and the length of these metatarsals was found to be normal. Finally one case exists (1.1343 Pl. XVIII, fig. 24) in which a five-toed foot shows a conspicuous shortening of the fifth toe and here a shortening of the fifth metatarsal was found to be present; as mentioned above, the hands of this boy are of a peculiar type, and it is also of interest to find that his mother has the one exceptional five-fingered hand with a shortened fifth metacarpal.

Discussion of the type of heredity followed.

Hereditary polydactylism in man has been said to behave as a dominant character and the present case forms no exception from this rule. In the family pedigree (Pl. XV) the abnormality can be traced through six successive generations. As can be seen the character is, without any exception, transmitted from one of the parents to their children, without ever passing through a normal. As previously mentioned, two branches of the family, in the pedigree represented by lines 1 and 3, have been most thoroughly examined and the following discussion is chiefly based upon the material given in these lines.

Intermarriage within the family has never, to my knowledge, occurred and there exists no case of marriage between two polydactylous individuals; all affected members of the family, therefore, must be regarded as heterozygotes for the character in question, this being supported by the fact that in no case are all the children of a marriage abnormal. On this basis and provided that the polydactylism in question is due to one Mendelian factor one would expect half of the children of a polydactylous individual to show the character.

TABLE V.

Numbers of affected and normal individuals from the family studied.

	Normals	Polydactylous
From generation, II one family	1	9
From line 1, including four generations and six families	8	17
From line 3, including three generations and five families	14	8
Totals ...	23	34

The actual ratio between affected and normal individuals is shown in Table V and is found to differ greatly from this expectation. The

table gives the result that among 57 children from 12 marriages in which one of the parents has supernumerary fingers there are 34 polydactylous and 23 normal individuals. This ratio, 34 : 23, already is out of accordance with the 1 : 1 expectation; considering, however, the small numbers we are here dealing with this aberration might be without significance, if the different occurrence in numbers and types of the abnormality within the two lines of the family did not indicate that another interpretation is possible. A glance at the table shows that line 1 gives a conspicuous excess of polydactylous individuals, the ratio being 17 polydactylous to 8 normal ones, and if each family of the line is considered separately it is seen that an excess of abnormal individuals is always present. In line 3, on the contrary, an excess of normal individuals is found, there being among 22 individuals 8 polydactylous and 14 normal ones.

Even if we bear in mind that these numbers from a genetical point of view are too small for any definite conclusions I think the difference is too large to be considered as quite accidental. Moreover, the distribution of the types of the abnormality, previously described as types *A* and *B*, points to the same conclusion that a real genetical difference exists between the two lines. The *A*-type polydactylism which covers all the most pronounced cases of the abnormality, has only been met in line 1; within this line with its great excess of polydactylous individuals most of the cases are of the *A*-type, only occasionally *B*-type individuals being found; thus in one case a woman (1·134) having herself an *A*-type hand has children showing the *B*-type of the abnormality; the ancestress of the family (1) is also reported to have *A*-type as well as *B*-type polydactylous children. The polydactylous individuals of line 3, however, all exhibit the *B*-type of the abnormality. A consideration of the distribution of these two types within the family therefore leads to the conclusion that an *A*-type individual gives an excess of polydactylous children over the normal ones, whereas a *B*-type individual never has been found to give more than a 1 : 1 ratio of polydactylous to normal individuals among his children. Further it is found that *A*-type individuals can have children showing *A*-type as well as *B*-type polydactylism, whereas a *B*-type individual never was found to have *A*-type individuals in his offspring.

There are a few cases met with in literature in which the polydactyles are in excess of the normal individuals: these cases are of great interest also because in them the abnormality is of a high-grade type.

The first of these cases is that of Carlisle (1814). The polydactylism there described seems to resemble the A-type polydactylism met with

in line 1 of our family. The abnormality is said to be confined to the fifth digit and the extra fingers and toes are all completely formed and provided with nails and three perfect phalanges. One must remember that in those pre-radiographic times a small metacarpal like those very often found among the *A*-type individuals of our family would probably escape detection. The great excess of abnormal individuals is very striking, there being from 3 marriages with 23 children 19 polydactylous and 4 normal ones. There is a possibility that one woman is a homozygote for the abnormality as she is reported to have had 11 polydactylous children and no normal ones; but even if this family is omitted we get from 2 marriages 12 children whereof 8 were polydactylous ones.

Smith and Norwell (1894) describe a case of polydactylism, where among 27 individuals from 5 marriages there are 20 polydactylous and 7 normal ones. The description of the polydactylism, which is here combined with syndactylism, is rather incomplete; but it seems to have been a strong malformation also affecting the metacarpals of the hand.

A third case showing a great excess of polydactylous individuals compared with the normal ones is that of Nylander (1904), the ratio being 23 polydactylous to 14 normal ones. The type of polydactylism, it must be admitted, is very different from the one here described, as in it the pollex is the digit affected; all the same I have brought it in here because of the ratio mentioned, and also because the polydactylism is of a high grade, the splitting always affecting the metacarpal as well as the phalanges of the thumb.

Such great excess of polydactylous individuals compared to the number of normal ones seems to indicate that in cases of strongly pronounced polydactylism in man probably cumulative factors are at work. This assumption is supported by the experimental work of Castle (1906) on polydactylism in guinea-pigs. Castle started his work with a polydactylous race of guinea-pigs showing the abnormality to a varying degree; the extra toe character was greatly developed by selection, wherewith a strongly polydactylous race was established. The result was, at that time, regarded by Castle as a proof of the inconstancy of Mendelian unit characters and an imperfect segregation of gametes but later (1911) he himself says of it: "An alternative is possible, viz. that the development of the fourth toe depends upon the inheritance of several independent factors, and that the more of these there are present, the better will the structure be developed."

Cases of more incomplete polydactylism, like the one here described

as *B*-type polydactylism, are often met with in literature and in these cases an excess of abnormal individuals never seems to be present; on the contrary very often the normal individuals are in the majority. Bonnevie (1919) describes a family showing a postaxial asymmetrically developed polydactylism; the extra finger is fixed at the base of the fifth finger and the metacarpals in the cases investigated show no abnormalities. One branch of this family approximately shows the expected 1:1 ratio of a one-factor Mendelian character, the offspring of 6 heterozygotes being 16 normal to 11 polydactylous individuals. Another branch of the same family, however, exhibits a very small amount of polydactylous individuals, 17 out of 53 children; within this branch we also meet with two cases of polydactylism being transmitted through five-fingered conductors; those deviations from the expectation are explained as being due to the imperfection of dominance of the polydactylism in question. A similar shortness in the amount of abnormal individuals is found in line 3 of the family here studied, but whether this is due to an incompleteness of the dominance of the character is not settled; as yet no case of a transmission of the character through apparently unaffected parents has been found. As in all other such cases in which imperfection of dominance has been appealed to, the cause of this imperfection remains to be explained.

These reflections, then, lead to the conclusion that in the case under consideration the *A*-type polydactylism, most probably is due to the operation of cumulative factors, whereas the *B*-type is produced by one Mendelian factor possibly sometimes in connection with factors suppressing its development.

A further point of interest in this family is the appearance of a form for brachydactylism being caused by the shortening of the metacarpal and metatarsal bones at the external border of the hands and feet. The brachydactylism in question has only been found within the members of line 1 of the family studied, and only in individuals having at the same time *A*-type polydactylous hands or feet; possibly therefore it may be regarded as a concomitant of the strongly pronounced bifurcation of the fifth finger.

Against this interpretation, however, we have the fact that one woman (1.134, Pl. XVI, fig. 5) has a five-fingered left hand in which the fifth metacarpal is slightly but decidedly shortened. Further, in her son (1.1343) a very remarkable and conspicuous shortness of the fifth toe of his left foot can be seen (Pl. XVIII, fig. 24), the toe in question showing no sign of bifurcation.

The possibility therefore exists that this brachydactylism, occurring among *A*-type individuals of the family, is due to a hereditary factor different from that causing the polydactylism; this factor must here be supposed to be linked to one of the factors for polydactylism as the abnormality is always connected with the *A*-type polydactylism and has never been found in individuals having normal numbers of fingers and toes. More data, however, are required to settle these questions.

A case of combined brachydactylism and polydactylism has recently been reported from "Universitetets Institut for Arvelighetsforskning," Christiania. To the institute was forwarded a foetus, born three weeks before term, having six fingers on each hand and six toes on each foot, both hands and feet at the same time showing a conspicuous shortness. The case was anatomically examined by W. Bjerknes (1922). The brachydactylism affects all fingers and is, as shown by the radiographs (Pl. XX, fig. 37) due to a deficiency in the development of the terminal phalanges; a small rudiment of a second phalanx is present in some digits but there is no sign of a third phalanx in any finger, whereas at this stage of normal development second as well as third phalanges ought to be present. The radiographs from the hands of 1.13251 (Pl. XX, figs. 33 and 34) show the difference existing. Further, from the musculature the conclusion is drawn that the fifth as well as the sixth finger has a certain power of independent movement, a condition not met with in the family here described.

Cases of brachydactylism caused by the shortening of the metacarpals and metatarsals have been reported, for instance by Joachimsthal (1900), Wagner (1903–4) and Hochheimer (1903–4), but as far as I know only one case has been described, that of Mathew (1908), showing this kind of brachydactylism combined with polydactylism. Mathew describes a family in which some of the members have shortened metacarpals, 3, 4 and 5 exhibiting at the same time a bifurcation there exclusively confined to the ring finger. From the description of the affected individuals it is not clear whether all the polydactylous individuals were also brachydactylous. The bifurcation is restricted to the two terminal phalanges. The case therefore does not really agree with the malformation here described.

The case of Morand (1770) may be mentioned in this connection; from the pictures the polydactylism seems to be very strong and in several points similar to the *A*-type polydactylism here described; the left hand shows 6 completely developed metacarpals articulating to the carpal; but in this case no sign of shortening is present; on the

contrary it is pointed out that the fifth digit is rather longer than it would have been in the normal hand. A shortening of the affected bones, therefore, does not follow as a necessity of the strongly developed polydactylism.

Descriptions of Members of Pedigree.

As mentioned above the polydactylism in this family has been traced backwards through six generations. The knowledge of the two first generations, living about 1800, is derived from members of the family now living and very little can be said as to the degree and development of the malformation in these long-dead individuals.

First Generation.

1. ♀, *E. P.* (living about 1800) is the first polydactylous individual known in the family. The information concerning her is very scanty. One of the members of the family (1.134) tells me that her great-grandmother's hands were said to be like her own; even if little importance can be paid to this it does indicate that the hands of this woman were of the *A*-type, this being confirmed by her having children whose hands are partly of the *A*-type, partly of the *B*-type. It is said that she had 10 children, all but one polydactylous. From the church register it was, however, found that she had 11 children; she married twice and had by her first marriage 7 children, 3 sons and 4 daughters, and by her second marriage 4 children, all sons. If some of the children from both marriages were polydactylous as indicated by the 9 polydactylous children, this would confirm the story that she was the polydactylous one of the parents, as otherwise one has to suppose both husbands polydactylous. It has, however, been impossible to obtain any information concerning the children of the second marriage and their progeny.

Second Generation.

The descriptions of the second generation contain all the information I have been able to get concerning the children of the woman just described. As mentioned she was said to have had 9 polydactylous children but only concerning a few of these do closer details exist.

1.1 ♂, *P. E. F.* (b. 1805) is the ancestor of line 1 of the family. According to his daughter (1.13) his right hand carried six fingers; concerning his left hand or his feet nothing is remembered. He married a woman from another parish; she had normal hands and feet. They had 4 children, 3 polydactylous and 1 normal one. His wife married a second time and had by her second marriage a normal son.

1.2 ♀, *G. E. F.* (b. 1807) has been put down in the pedigree as being polydactylous in spite of the fact that no particulars exist concerning her hands or feet. The fact that she has a polydactylous son makes it, however, very probable that she herself is one of the nine polydactylous brothers and sisters, as there is no case known in this family in which normal parents have polydactylous children. She had by her marriage 11 children, one of whom is known to have had six fingers, whereas nothing is known about the others.

1.3 ♀, *A. E. F.* (b. 1809) had according to her grandson (1.312) six fingers but whether both or only one hand was affected he does not remember. Concerning her feet nothing is known. She had by her marriage 6 children, 3 polydactylous and 3 normal ones.

1.5 ♂, *O. E. F.* (b. 1812) was a well-known person in this parish. Information from different sources all agree that he had six fingers on his right hand. The extra finger was according to the descriptions loosely attached to the outside of the hand; it was said that he generally carried it inside his clenched fist; from the description there can be no doubt of the type of the malformation; he must have had a *B*-type hand. He had 5 children, one of whom is known as being polydactylous of the *B*-type.

Third Generation.

With this generation my own observations begin. One polydactylous woman belonging to this generation is still alive and her hands and feet have been radiographed; from her also most of the information concerning the preceding generations was obtained.

1.11 ♂, *H. P. F.* (1840) had according to his sister six fingers on his right hand and six toes on each foot. His sister is confident that his right hand was like her own, having two equally developed shortened fingers in the place of the minimus. If this is to be relied upon he must belong to the *A*-type individuals. He went to America and died, having no children.

1.12 ♀ (b. 1841) had normal hands and feet. She was married but had no children.

1.13 ♀ *H. V.* (b. 1844) is the first person in the family from whom radiographs are obtained. Her hands (Pl. XVI, fig. 1) are previously mentioned as a typical example of the *A*-type polydactylism. The radiographs show all the features characteristic of this type. There are two nearly equally developed digits present at the ulnar side of the hand, the inner one of the two having an incomplete metacarpal between those of the fourth and fifth digits, the shortness of the two fingers is striking. As mentioned,

A-type individuals generally have the outer of the two fingers on their right hand crooked; this is not very conspicuous in this case, but, compared to the left hand a greater angle between the first and second phalanges can be seen. The symmetry in the development of the anomaly is in this case beautifully demonstrated; both feet (Pl. XVIII, fig. 17) carry six toes, the two fibular ones being carried by the dichotomously branched fifth metatarsals. In her marriage with a normal man this woman had 5 children, 4 of whom exhibit the same type of polydactylism as their mother.

1.14 ♂, *P. P. F.* (b. 1847) had like his sister (according to her) six fingers on each hand and six toes on each foot. He went to America where he died 25 years old.

1.21 ♂, *C. M. H.* (b. 1847) is remembered by different individuals living in the same parish as having six fingers; but more particulars could not be given and nothing therefore can be said as to the type of the malformation.

The information concerning the family 1.31—1.36 is all obtained from the son of 1.31; I have not been able to examine any of these individuals, some of them are dead and some of them gone to America.

1.31 ♂, *H. H.* (b. 1847) had, according to his son, normal hands, but six toes on each foot. He had by his marriage with a normal woman 2 sons, both polydactylous.

1.32 ♀, *T. H.* had normal hands and feet. She married a normal man. They had no children.

1.33 ♀, *M. H.* had six fingers on each hand. Her nephew cannot remember the type of the polydactylism and nothing is known about her feet. She went to America and married there. She has 3 children, all normal, and their offspring is normal too.

1.34 ♂, *E. H.* went to America when young and nothing is known about him.

1.35 ♂, *C. H.* had six fingers on each hand, according to his nephew developed in the same way as his own (1.312); normal feet. He died quite young as a medical student.

1.36 ♀, *M. H.* normal hands and feet. Went to America. Unmarried.

1.54 ♂, *J. L.* (b. 1885) had, according to people in his neighbourhood, six fingers on each hand, the extra fingers were amputated when he was about 30 years old. The descriptions make it very probable that he belonged to the *B*-type. He had by his marriage 2 normal sons and all his brothers and his one sister were normal.

Fourth Generation.

The individuals 1.131–1.135 are the children of the *A*-type polydactylous woman described as 1.13. Every one of them has been radiographed and photographed.

1.131 ♀, *B. O.* (b. 1867) has a normal right hand whereas the left hand shows a polydactylism like that of her mother (Pl. XVI, fig. 2). Her right foot (Pl. XVIII, fig. 22) is enormously broad owing to the complete development of the abnormality, the splitting of the fifth metatarsal nearly reaches the tarsus so as to form a bone with a broad basis and two branches each carrying its toe. Her left foot (Pl. XVIII, fig. 18) is like that of her mother, having a dichotomously branched metatarsal, each branch carrying a toe. The abnormality revealed is a decided *A*-type polydactylism. She had by her marriage to a normal man one child, a daughter, having six fingers on each hand and six toes on each foot.

1.132 ♂, *A. V.* (b. 1870) is like his sister and mother an *A*-type individual. Both hands (Pl. XVI, fig. 3) carry six fingers developed in a way strikingly like that of his mother, the only difference being the stronger development of the left hand's fifth metacarpal. His right foot (Pl. XVIII, fig. 19) is like that of his mother, having the characteristic dichotomously split fifth metatarsal bone. The left foot is normal. He has by his marriage 9 children, 5 of whom are polydactylous.

1.133 ♀, *J. B.* (b. 1873) has hands and feet with five fingers and toes (Pl. XVI, fig. 4). The fifth finger, especially that of her left hand, looks shortened, and it was at first believed that this was a case of brachydactylism in an individual not showing polydactylism. This apparent shortness however proved to be due to a slight shortening of the second phalanx; this shortening is not so considerable that any significance can be ascribed to it. She has by her marriage two normal children.

1.134 ♀, *A. S. N.* (b. 1876) shows in her right hand a polydactylism somewhat different from the preceding ones, even if its general appearance is that of an *A*-type hand. The extreme ulnar finger of this hand (Pl. XVI, fig. 5) is crooked to a much higher degree than that of her mother; further the fifth metacarpal is only represented by a small roundish bone of epiphysial character at the base of the finger. The shortening of the outer metacarpal in this hand also is more pronounced than usual, as seen in the correlation table, where the measures from this hand fall far to the right of the normal swarm. The left hand of this woman is apparently normal but measurement of the bones revealed a shortening of the fifth metacarpal. This is the only case found where a five-fingered hand shows the brachydactylism characteristic of this family.

Her feet (Pl. XVIII, fig. 20) are exactly like those of her sister (1.131). By her marriage to a normal man she has 5 children, 3 polydactylous and 2 normal ones.

1.135 ♂, *H. V.* (b. 1882) is like his brother and two sisters polydactylous, showing the *A*-type of the abnormality in a somewhat modified condition. He was not to be persuaded to be radiographed; a photograph of his hands was taken under the condition that it was not to be published. His right hand is strikingly like that of his sister just described (1.134), the outer finger being perhaps even more crooked than hers. His left hand has a doubled fifth finger but from its outer appearance it looks as if only the third phalanx is affected; this part of the digit is very broad and is provided with two nails. His feet are according to himself normal.

The last two cases of this generation represent two brothers belonging to line 3 of the pedigree. They are both polydactylous of the *B*-type.

1.311 ♂, *C. H.* (1869–1917) had six fingers on each hand; the extra fingers were removed at an adult age. Among his 4 children there are 2 polydactylous ones.

1.312 ♂, *C. H.* (b. 1875) had according to his own information six fingers on each hand. His left hand possessed a small extra finger loosely attached to the hand like that of 1.1344 (Pl. XVII, fig. 13); this finger had a nail and he thinks two phalanges. The extra finger of the right hand was represented by a small warty appendage without nail or phalanges. The radiographs from his hands (Pl. XVII, fig. 14) show that there is no sign left of this polydactylism and no shortening of the fingers is present. His feet are normal.

Fifth Generation.

The polydactylous individuals from the first family of this generation (1.1321–1.328) are all *A*-type individuals.

1.1321 ♂, *R. V.* (b. 1896) exhibits the strongest polydactylism yet found during this investigation. His right hand carries seven fingers (Pl. XVI, fig. 6); the type is somewhat modified, the first phalanx being very broad and dichotomously branched, each branch carrying two terminal phalanges; in addition to these two fingers a small dorsally situated finger is seen consisting of three slender phalanges; the extra metacarpal is represented by a roundish bone articulating to the inner side of the broadened first phalanx of the fifth digit. The left hand is typically like that of his father and grandmother. No radiographs from his feet have been obtained but according to his mother each foot has six toes.

1.1322 ♂, *E. V.* (b. 1897) died immediately after birth. According to his mother he had six fingers on each hand. Concerning his feet nothing is known.

1.1323 ♂-♂ (b. 1899). Twin boys who died immediately after birth. According to their mother they had normal hands and feet.

1.1324 ♀, *H. V.* (b. 1900) has six fingers on her left hand and six toes on each foot. Her right hand from the outer appearance is quite normal; the radiograph (Pl. XVI, fig. 7) however indicates a shortening of the second phalanx of the fifth digit; this shortening proved to be very slight compared with the second phalanx of the fourth finger and is perhaps of little significance; the radiograph also shows a small pisiform bone at the head of the fifth metacarpal not met with in normal hands. Her left hand is *A*-type polydactylous like that of her father and brother. In her feet (Pl. XVIII, fig. 21) the bifurcation is restricted to the phalanges, the first phalanx of the fifth toe on each foot being dichotomously branched.

1.1325 ♀, *A. V.* (b. 1902) is an *A*-type individual of especial interest as her right hand (Pl. XVI, fig. 8) shows a variation of the abnormality which points in the direction of the *B*-type; this hand had according to the description of her mother a sixth finger which was removed just after birth; this finger was situated not between the fourth and fifth finger but at the ulnar border of the hand as an easily removable appendage. The great space between the fourth and the fifth finger therefore must be due to the extra metacarpal head between the metacarpals IV and V; this feature as well as the shortening of the ulnar metacarpal marks the hand as belonging to the *A*-type whereas the loosely attached appendage indicates the *B*-type. Her left hand is of the *A*-type, as in all the other polydactylous members of her family. Her right foot (Pl. XVIII, fig. 22) has a bifurcated fifth toe like that of her sister, the bifurcation being restricted to the phalanges, whereas her left foot possesses six well developed toes supplied with metatarsals and phalanges. Her son, born 1922, is a pronounced *A*-type individual.

1.1326 ♂, *S. V.* (b. 1903) is a typical *A*-type individual with hands and feet strikingly like those of his father (see Pl. XVIII, fig. 9 and Pl. XVIII, fig. 23) only in this case the right foot shows the stronger development of the abnormality whereas in the case of his father the left foot is the more polydactylous.

1.1327 ♂, *G. V.* (b. 1905) has, as seen from the radiographs, normal hands (Pl. XVII, fig. 10). His feet are, according to his mother and sister, normal.

1.1328 ♀, *I. V.* (b. 1909) also has normal hands and feet (Pl. XVII, fig. 11).

The individuals of the next family covering the numbers 1.1341–1.1344 are cousins of the ones just described; the anomaly here met with is as will be seen more irregular.

1.1341 ♂, *E. N.* (b. 1900) was born at the Hospital for Women in Christiania and the medical journal states that the boy had six fingers on each hand and six toes on each foot, giving no further description of the structures. The extra fingers were removed a few years ago. No radiographs have been taken but from external appearance it is evident that no shortening of the metacarpal had taken place. Both feet have according to himself six toes.

1.1342 ♀-♀, (b. 1902). Twin girls. Like their brother they were born at the Hospital for Women. The medical journal says that two placentas were present, showing the twins were from two ova; it also states that both girls had normal hands and feet.

1.1343 ♂, *H. N.* (b. 1907) was born with six fingers on each hand the extra ones being amputated just after birth. The details are discussed in the text, p. 227. The 5-toed feet are shown Pl. XVIII, fig. 24.

1.1344 ♂, *H. N.* (b. 1909) gives a beautiful demonstration of a *B*-type individual. Both hands are exactly alike (Pl. XVII, fig. 13), the extra finger on both having the appearance of a small appendage at the ulnar border of the hand; the little extra finger is supplied with nail and the radiograph shows several small bones probably consisting of a small metacarpal with its epiphysis and three phalanges. His right foot (Pl. V, fig. 25) carries six toes owing to the reduplication of the fourth toe.

The following family (1.3121–1.3127) consists of 7 brothers and sisters and among them all but one are normal individuals.

1.3121 ♀, *M. H.* (b. 1900) according to her father with normal hands and feet.

1.3122 ♀, *K. H.* (b. 1901) with normal hands and feet.

1.3123 ♀, *H. H.* (b. 1902) belongs to the *B*-type individuals. When born she had, according to her father, a sixth finger on each hand developed as a warty appendage attached to the ulnar border of the hand, this appendage having neither nail nor skeleton; they were removed at once. Otherwise her hands as seen from the radiograph (Pl. XVII, fig. 16) are quite normal and the measurements show no shortenings whatever. Her feet (Pl. XIX, fig. 28) on the contrary have the most pronounced bifurcation of the fifth toes among all individuals in this family; there

are six fully developed toes present in each foot, all of them furnished with six complete metatarsal bones.

1.3124 to 1.3127 are all normal. Two of them are seen in the radiographs.

The following individuals 1.3111–1.3114 are cousins of the preceding ones and the abnormality when present is of the *B*-type.

1.3111 ♂, *H. H.* (b. 1904) with normal hands (Pl. XVII, fig. 15) but six toes on each foot (Pl. XIX, fig. 26). The *right foot* has six fully developed metatarsal bones each carrying a toe. The *left foot* carries an extra toe interpolated between the fourth and fifth ones—the extra toe being provided with a short metatarsal bone.

1.3112 ♂, *N. H.* (1908) died as a child. No information has been obtained.

1.3113 ♀, *A. H.* with normal hands and feet.

1.3114 ♀, *W. H.* has normal hands, her left foot (Pl. XIX, fig. 27) has six toes developed in the same way as in that of her brother.

Sixth Generation.

1.13251 (b. 1922) is a typical *A*-type individual. The radiographs (Pl. XX, fig. 33) were taken when the child was only seven days old and are because of this of peculiar interest. The left hand carries six fingers and here the dichotomously branched fourth metacarpal seems to justify the hypothesis that the polydactylism in question is due to a duplication of one of the fingers, the bifurcated finger this time being the fourth one; anyhow, if this branched metacarpal has been produced by a fusing of separate bones, this process must have taken place early in foetal life. Concerning the length of the fingers nothing can be said at this stage; a shortening seems as yet not to be present, but it will be of great interest to follow the further development of this hand. The right hand exhibits a doubled fifth finger and an additional roundish bone between the metacarpals IV and V like that found in the right hand of the mother (Pl. XVI, fig. 8). Both feet have six toes, in the right foot six completely developed metatarsals being present, whereas the left has five metatarsals, the fifth being dichotomously branched. The total absence of the second phalanges in these feet may be mentioned, this probably being due to a belated development of these bones, since a brachyphalangy of this kind has never been found in any other members of the family.

The figures are all described in the text. Observe that in each case the rights and lefts are as shown by the letters R and L at foot, the right being on the reader's left.

Full-sized prints of all the photographs will be deposited for reference at the Royal College of Surgeons, London.

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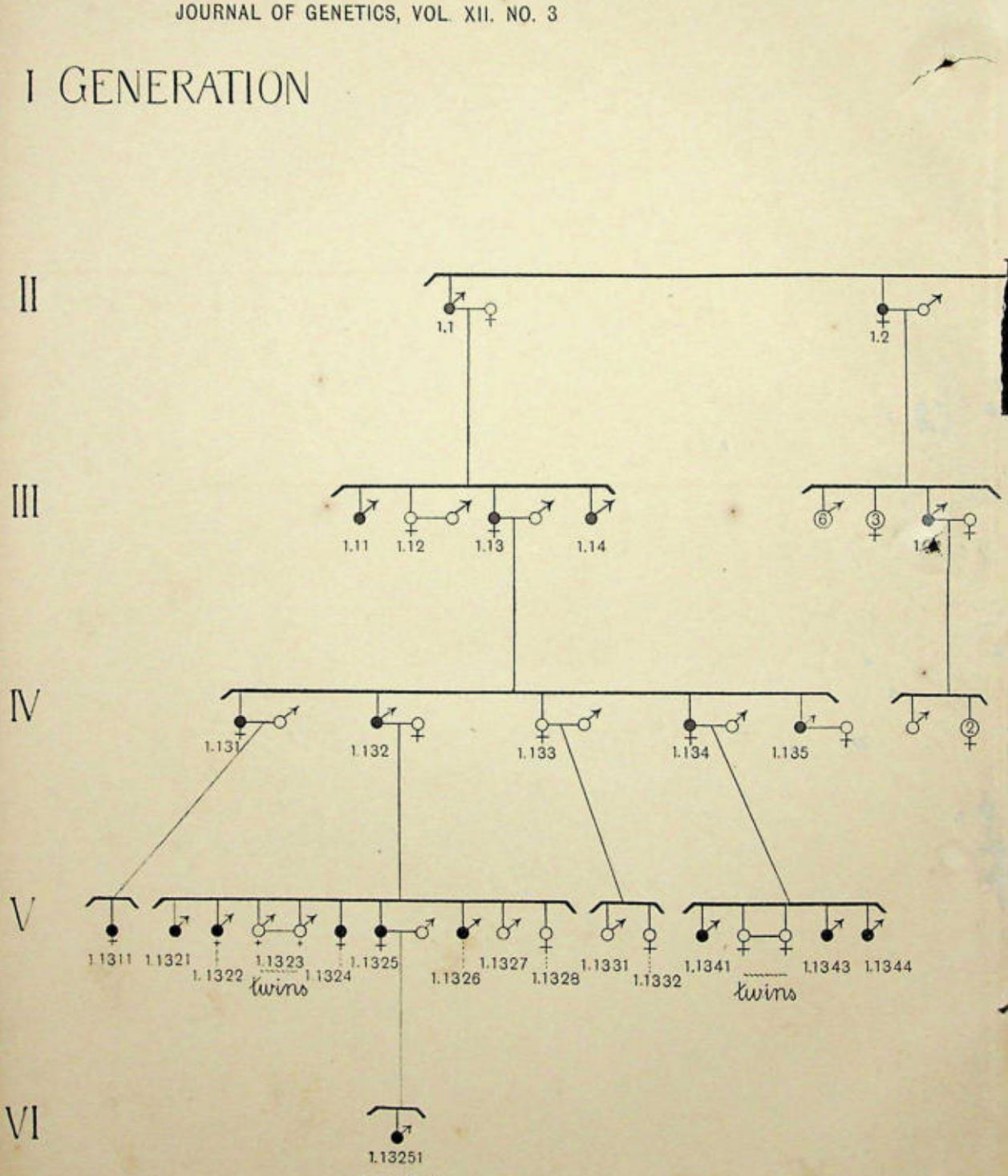
I GENERATION
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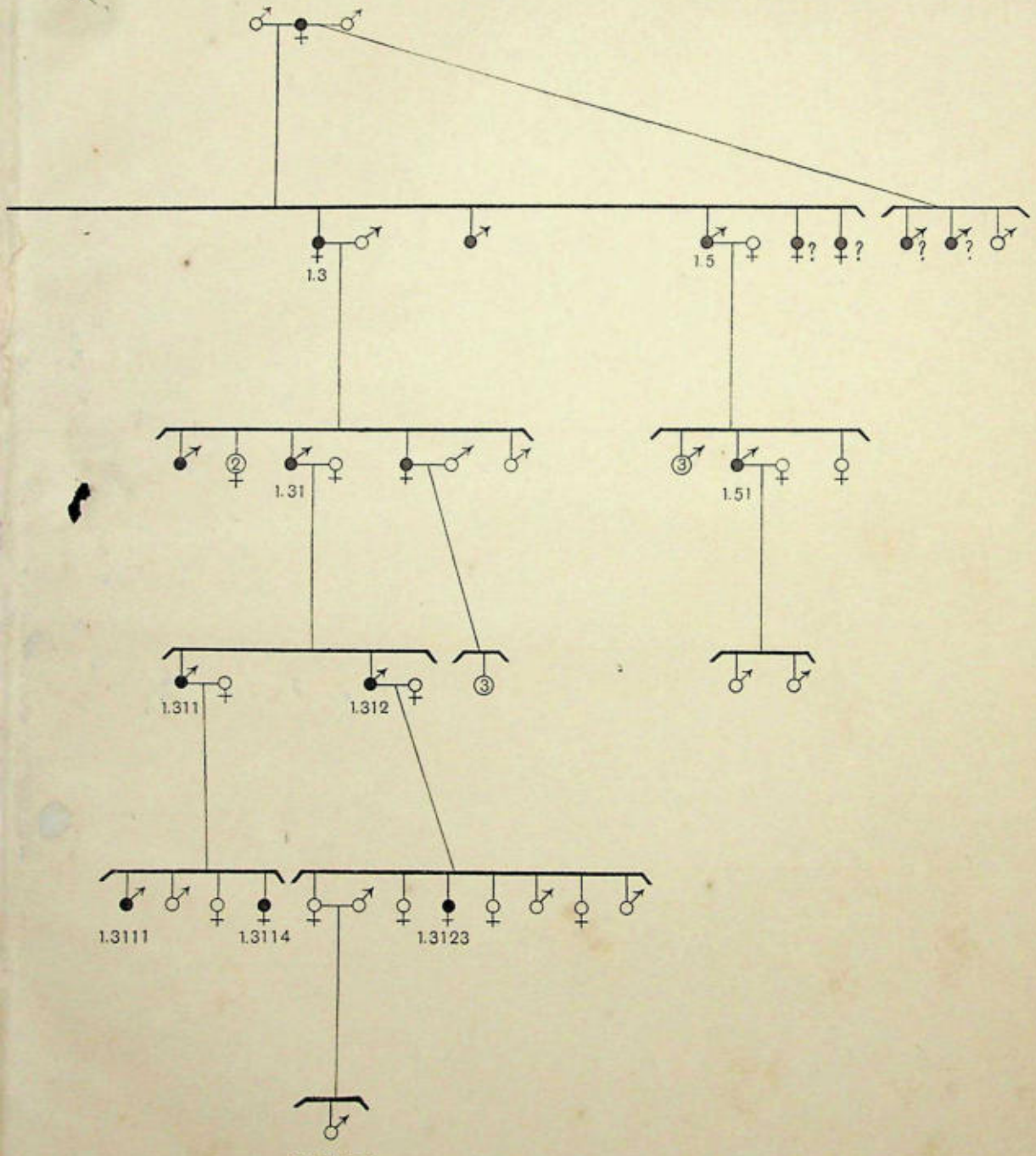
LINE 1



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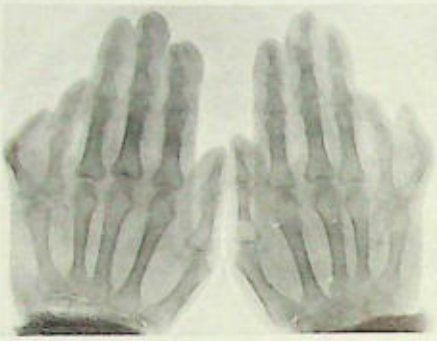


Fig. 1. 1.13 ♀ H. V.

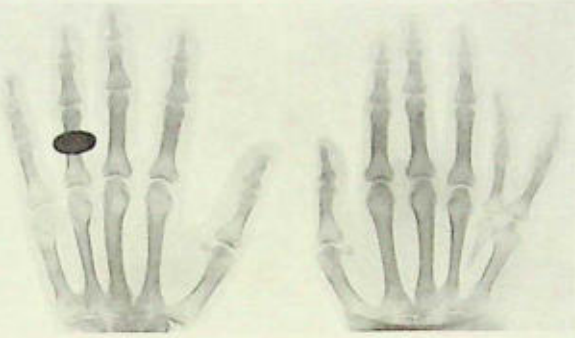


Fig. 2. 1.131 ♀ B. O.

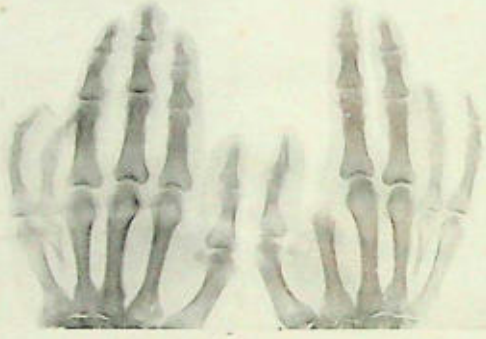


Fig. 3. 1.132 ♂ A. V.

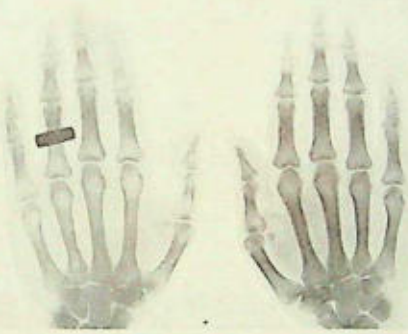


Fig. 4. 1.133 ♀ J. B.

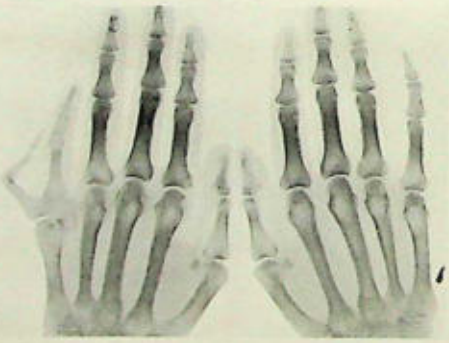


Fig. 5. 1.134 ♀ A. S. N.

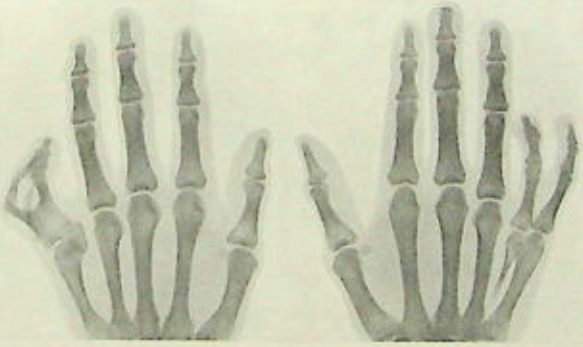


Fig. 6. 1.1321 ♂ R. V.

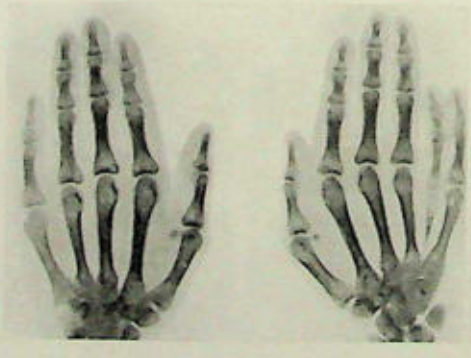


Fig. 7. 1.1324 ♀ H. V.

R L

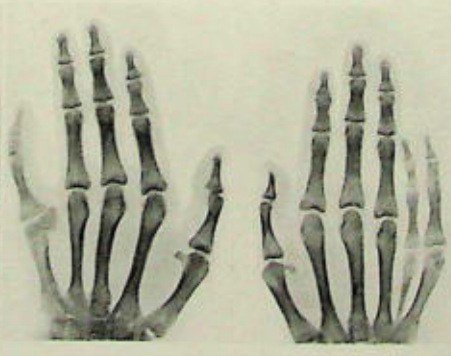


Fig. 8. 1.1325 ♀ A. V.

R L

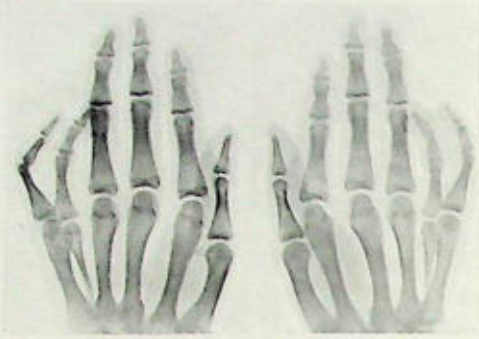


Fig. 9. 1.1326 ♂ S. V.

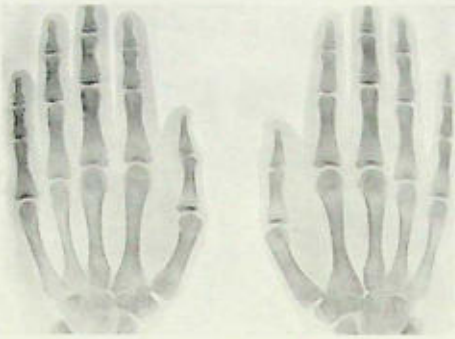


Fig. 10. 1.1327 ♂ G. V.

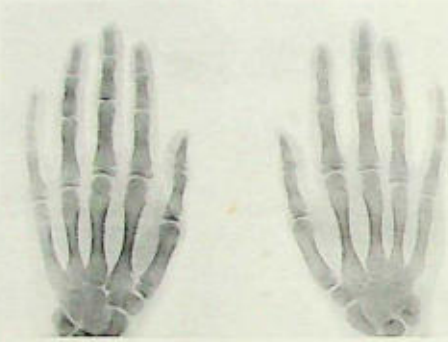


Fig. 11. 1.1328 ♀ I. V.

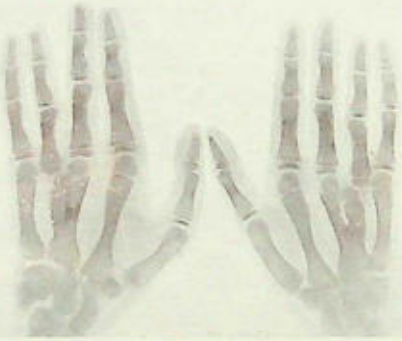


Fig. 12. 1.1343 ♂ H. N.

Fig. 13. 1.1344 ♂ H. N.

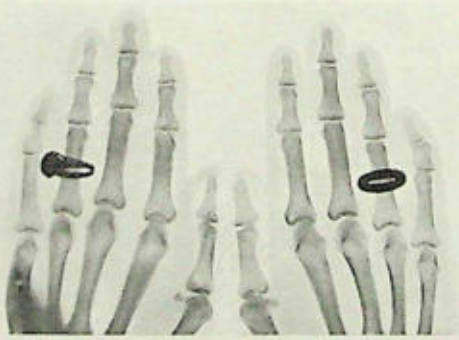


Fig. 14. 1.312 ♂ C. H.

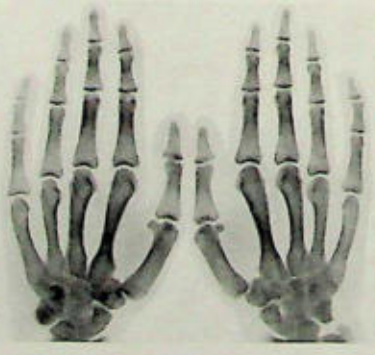


Fig. 15. 1.3111 ♂ H. H.

R L

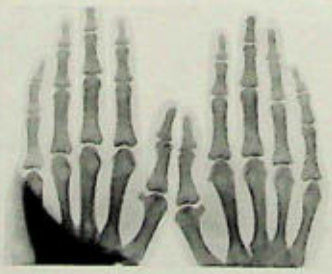


Fig. 16. 1.3123 ♀ H. H.

R L

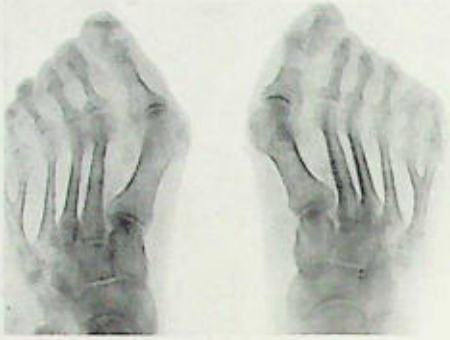


Fig. 17. 1.13 ♀ H. V.

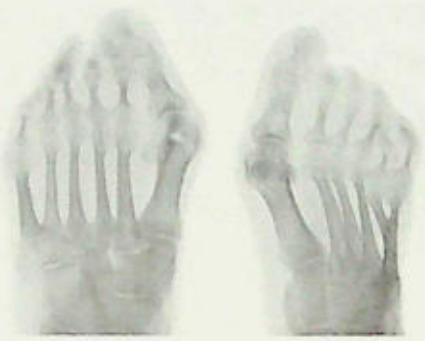


Fig. 18. 1.131 ♀ B. O.

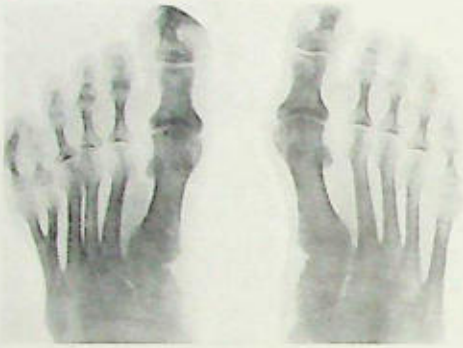


Fig. 19. 1.132 ♂ A. V.

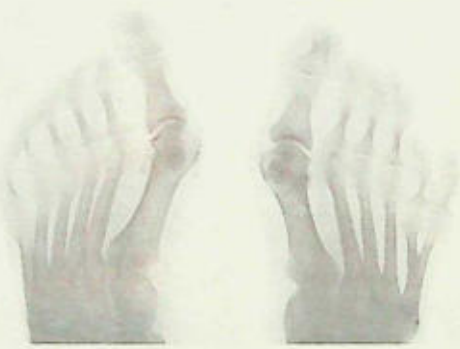


Fig. 20. 1.131 ♀ A. S. N.

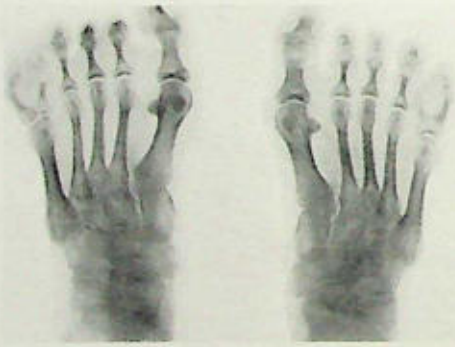


Fig. 21. 1.1324 ♀ H. V.

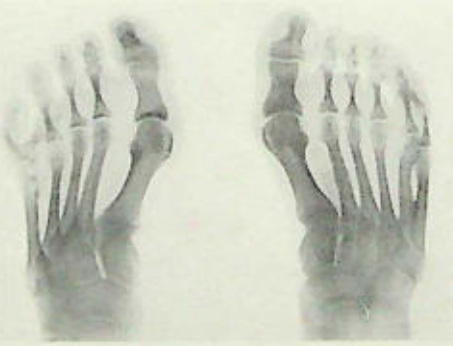


Fig. 22. 1.1325 ♀ A. V.

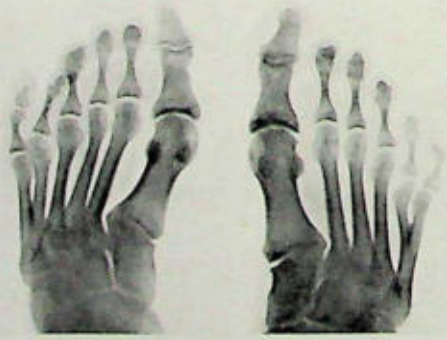


Fig. 23. 1.1326 ♂ A. V.

R L

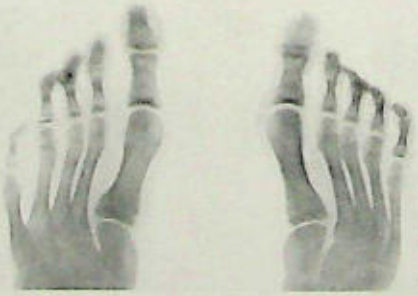


Fig. 24. 1.1343 ♂ H. N.

R L

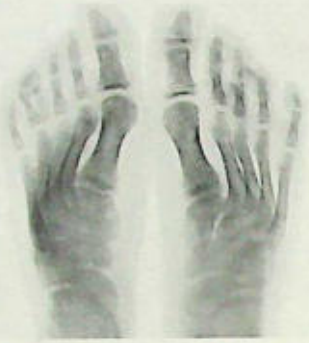


Fig. 25. 1.1344 ♂ H. N.

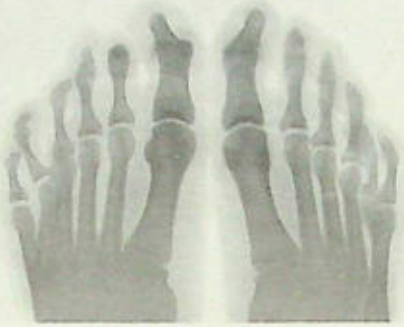


Fig. 26. 1.3111 ♂ H. H.

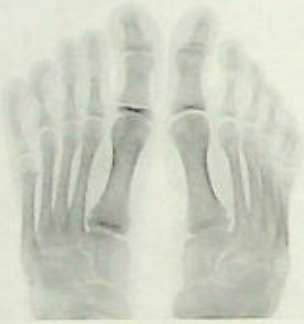


Fig. 27. 1.3114 ♀ W. H.

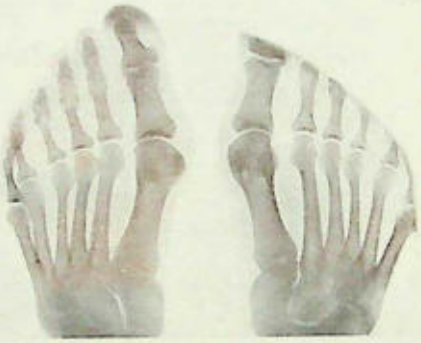


Fig. 28. 1.3123 ♀ H. H.

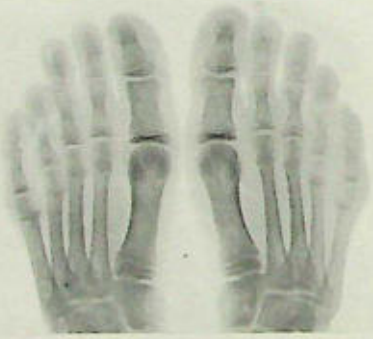


Fig. 29. 1.3125 ♂ T. H.

Fig. 30. 1.3126 ♀ T. H.

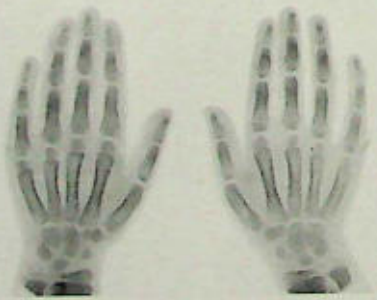


Fig. 31. ♀ L. T.

R L

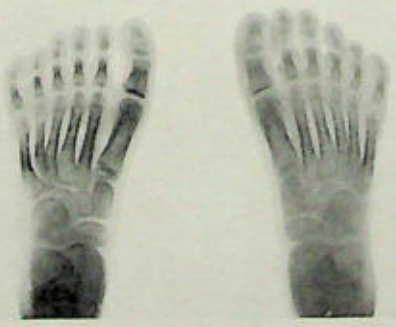


Fig. 32. ♀ L. T.

R L

Fig. 33. 1.13251 ♂ Left hand.

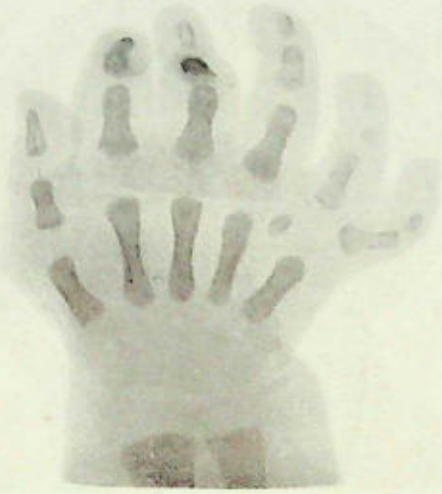


Fig. 34. 1.13251 ♂ Right hand.

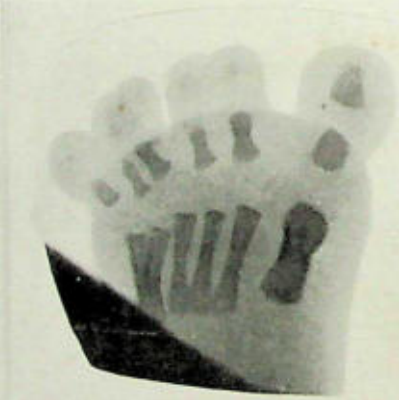


Fig. 35. 1.13251 ♂ Left foot.

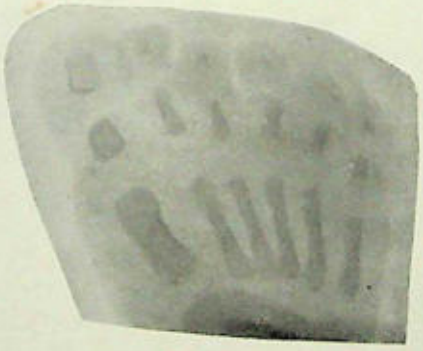


Fig. 36. 1.13251 ♂ Right foot.

Fig. 37. Foetus Right hand.

Fig. 38. Foetus Left foot.

DIALLEL CROSSINGS WITH THE DOMESTIC FOWL.

By JOHS. SCHMIDT, D.Sc.,
Director of the Carlsberg Physiological Laboratory, Copenhagen, Denmark.

In three previous papers (1919, 1; 1919, 2; 1921) I have described the results of diallel crossings with the common trout (*Salmo trutta* L.)[1]. The task being to classify or to value a certain number of individuals in regard to some *quantitative* character, i.e. a character which may be analysed by counting, measuring or weighing—the manner of proceeding in diallel crossing is as follows. Each female is paired with each male, care being taken that the offspring is raised under external conditions as uniform as possible. If there are a females and b males $a \times b$ different combinations will occur among the offspring of the diallel crossings. Within each offspring-combination the character in question is analysed —by counting, measuring, or weighing each individual—and then the average value of all individuals is determined. *It is with such average values*—determined by analysing a number of individuals, as great as possible; and developed under external conditions as uniform as possible —*that the method of diallel crossings operates.*

Already the first experiments showed the necessity of distinguishing clearly between the purely *personal* value of an individual—in the case under consideration the number of vertebrae that may be counted in the individual at hand—and the *generative* value, i.e. the value it imparts to its offspring. The generative value of an individual may differ widely from its personal value, so that from the latter few or no conclusions can be drawn with regard to the former. This particular fact is largely responsible for the difficulties which the work with quantitative characters entails, not only upon the student of genetics, but also upon the practical breeder. It is the generative value which both of them need to know, the geneticist when he has to classify the offspring-individuals from a crossing experiment, and the breeder when he has to select—

[1] "La valeur de l'individu à titre de générateur, appréciée suivant la méthode du Croisément diallèle" (*C.R. Laboratoire Carlsberg*, Copenhagen, 1919); "Diallel crossings with trout (*Salmo trutta* L.) (*Journal of Genetics*, IX. 1919); "The numerical significance of fused vertebrae" (*C.R. Laboratoire Carlsberg*, Copenhagen, 1921).

perhaps among a number of individuals personally very similar—those best fit to breed from.

A frequently occurring special case of diallel crossings is when $b = 1$, i.e. when a single male—let us call it x—is paired with a females. $1 \times a = a$ different offspring-combinations will then arise. Each of these will, provided a sufficiently large number of individuals be present, exhibit a full representation of all the different gametes possessed by the father x, which is common to all of them. The a offspring-combinations, therefore, differ only in those gametes coming from each of the a mothers. From this it follows that we are able to compare directly the average values of the a offspring-combinations, and to get thereby an expression of the differences between the generative values of the females, the common male x cancelling, so to speak, in such a comparison. These differences are thus independent of the father common to all offspring-combinations. After pairing a number of females with the same male we can therefore determine the differences between their generative values irrespective of the male, and similarly, we may, of course, determine the differences between a number of males, after having paired them with the same female. *This is the leading principle in the method of diallel crossings.*

When this method was described, in 1919, we did not know the way in which such quantitative characters are inherited, and the manner of proceeding had therefore necessarily to be entirely empirical[1]. In consequence of its principle the method, however, is *self-checking*. When pairing the same a females, which were paired with x, with other males (y, z, v), and calculating the differences between the values of the females in the same way as after the first pairing with male x, *the same differences were found in all cases.* In this way the *automatic checking of the method yielded experimental evidence of the rightness of the principle of diallel crossings.*

In our trout experiments we were dealing with heterozygous individuals the genetic structure of which was entirely unknown. Nevertheless it proved possible to determine the differences between the various individuals—in other words to classify them—with no less certainty than when classifying a number of Pure Lines. On that subject I refer to my previous papers (1919, 1 and 1919, 2).

With a character like "number of vertebrae" we have to do with so-called *integrated variates*, which are generally realised only as integral

[1] Since then I have been able to clear up the genetic behaviour of the number of vertebrae. A detailed report is expected to appear shortly.

numbers. The diallel crossings showed that not only the generative values, or the differences between them, may be any fraction, but further, that the *personal values may be fractions*. Certain "fusions" of two vertebrae in the trout thus had to be interpreted as "attempts" at realising fractional parts of a vertebra (1921). This would seem to mean that no fundamental difference exists between "integrated variates" and "class-variates."

When it was established that the method of diallel crossings could be applied to characters as different as the number of vertebrae in fishes and the length of petals in a species of *Nicotiana* (1919, 1) there was reason to believe that the method might be generally employed in the study of quantitative characters. It appeared to me, however, of importance to have the method tested for as many species as possible. After having tried various vertebrates I selected the domestic fowl which proved to be a useful subject. The experiments were made in 1919 and 1920 in the Carlsberg Laboratory, Copenhagen, and the character examined was again the number of vertebrae. This number proved to vary more than was expected. As a matter of fact, in our small stock we found a range of 6, the number of vertebrae varying from 39 to 44.

The countings were made by Mr Vilh. Ege, M.Sc., who has worked out a very reliable technique.

Two cocks (x and y) and five hens (a, b, d, e, f) were used in the experiment. Most of them were mongrels; y was a Faverolles cock and e a Plymouth Rock hen.

Table I shows the result of the diallel crossings. For each of the ten (2×5) offspring-samples the number of vertebrae in each individual chicken is shown graphically. The average numbers of vertebrae of the various offspring-combinations are given in Table II, the figures in each case being denoted by the symbols of the parents, thus:

$$\frac{x+a}{2} = 40{\cdot}53 \text{ etc.}$$

By means of the ten equations

$$\left(\frac{x+a}{2} = 40{\cdot}53,\ \frac{y+a}{2} = 41{\cdot}21 \text{ etc.}\right)$$

we are, in the manner described in my previous papers, able to calculate the generative values of the 7 parents and to compare them with their personal values. Several of the animals being, however, still alive, we do not know all the personal values as yet and we may therefore better postpone such a comparison until all the figures in question are available

(for the hens *e* and *f* the personal values are given in the foot-note on page 245).

TABLE I.

Diallel crossings of two cocks (x and y) with five hens (a, b, d, e, f). The graphs show the number of vertebrae in each individual of the offspring.

	Females	Male *x*	Male *y*
a	43		43
	42	0	42 00000000
	41	00000000000000000000	41 0000000000000
	40	000000000000000000	40 000
	39	0	39
b	43		43 0
	42		42 00000000000
	41	00000000000000000000000000000	41 00000000000
	40	0000	40
	39		39
d	43		43 0
	42	00000	42 00000000000
	41	0000000000000000000000000000000000000	41 0000000000
	40	0000000	40
	39		39
e	43		43
	42		42 000
	41	000000000000000000000000000	41 000000000000
	40	0000000000000000000000000	40
	39		39
f	43		43 000
	42	000000	42 000000000000000000000000000
	41	00000000000000000000000000000	41 000000000
	40	00	40 0
	39		39

TABLE II.

Average numbers of vertebrae in the ten offspring-combinations (first and second columns) and difference between the generative values of cocks y and x (third column).

		$\frac{y-x}{2}$
$\frac{x+a}{2}=40{\cdot}53$	$\frac{y+a}{2}=41{\cdot}21$	0·68
$\frac{x+b}{2}=40{\cdot}88$	$\frac{y+b}{2}=41{\cdot}57$	0·69
$\frac{x+d}{2}=40{\cdot}96$	$\frac{y+d}{2}=41{\cdot}59$	0·63
$\frac{x+e}{2}=40{\cdot}53$	$\frac{y+e}{2}=41{\cdot}20$	0·67
$\frac{x+f}{2}=41{\cdot}11$	$\frac{y+f}{2}=41{\cdot}78$	0·67

For the time being we shall therefore content ourselves with an examination of the applicability of the method to the present subject—number of vertebrae in the domestic fowl—in other words to examine whether the method already tested for other species also holds good in the present case.

As the two cocks x and y both enter into all 5 crossings, the differences between their generative values have been determined 5 times, each determination being made independently of the other.

In Table I the offspring-combinations of a vertical row have the same father (x and y) and those of a horizontal row have the same mother (a, b, d, e, f). Already an inspection of the graphs shows that cock y must have a greater generative value than cock x. Suppose the property of imparting a great number of vertebrae to its offspring is a valuable character, we are enabled by our experiment to classify cock y as being superior to cock x.

In Table II we find numerical expressions for the five determinations of $\frac{y-x}{2}$, that is to say of the differences between the generative values of y and x. It must be remembered that the determinations were made independently of each other, by means of five different hens.

We see that the five values for $\frac{y-x}{2}$ *vary between* 0·63 *and* 0·69. In spite of the number of offspring-individuals in some cases being but small, *these values agree so well that no reasonable doubt can exist that the principle of diallel crossings holds good here as in the previously examined cases.*

Provided that the character in question had been of practical importance itself, or if another character of practical importance, e.g. a great egg-laying capacity were associated with a high number of vertebrae, our valuation of the two cocks would have been of practical importance. Through a direct examination of the personal values of the two animals little or nothing could have been concluded in regard to their generative values[1].

Note added during printing. Cock y died on 14/3/1922, and on examination proved to possess 42 vertebrae, i.e. the same number as cock x which died in 1920. This yields a fresh instance of the fact that two personally identical individuals may differ widely in regard to the generative values. The difference between the generative values of cocks y and x, or rather, the half difference $\left(\frac{y-x}{2}\right)$, appears from Table II.

[1] I may mention here that hens e and f both proved to possess 40 vertebrae (personal values). From Table II it appears that they are far from being identical in regard to generative values. The difference between the latter amounts to no less than

$$1{\cdot}16 \left(\frac{f-e}{2} = 0{\cdot}58\right).$$

THE COLORATION OF THE TESTA OF THE POPPY SEED (*PAPAVER SOMNIFERUM L.*)

By H. MARTIN LEAKE, Sc.D., and B. RAM PERSHAD.

(*From the Agricultural Research Station, Department of Agriculture, United Provinces, India.*)

In Vol. x, part 1 of this Journal appeared an account of the inheritance of certain characters of the Opium poppy. Among the observations there recorded are included a few notes on the colour of the seed coat. Subsequent experiment has thrown further light on the inheritance of these characters and the results are here summarised. There appear to be three factors involved,

Straw Colour (*S*), Pink (*P*), Blue (*B*).

In the absence of *P* and *B*, the form *SS* is distinguishable from the form *Ss* by the darker colour. The difference, however, is not very marked and, as the result of the variation in the intensity displayed, the two form practically a complete series. Light straw coloured seed from three parents have given the following figures:

	White *ss*	Light straw *Ss*	Straw *SS*	*Ss* and *SS*
	220	526	222	748
Expectation	*244*	*488*	*244*	*732*

In the absence of *S* and *B*, the two forms *PP* and *Pp* are indistinguishable and, as has been noted in the paper referred to above, the *Pp* parent gives 3 pink (dominant) to 1 white (recessive) plants. We may note here that the pink colour is a bulk phenomenon not shown by the single seed which, on magnification, appears slate grey.

The association of the two factors, *S* and *P*, produces a brown colour with difficulty distinguishable from the pure *SSpp* form. Since, however, as has been noted, the association between the two factors *P* and *M*, the latter of which develops the eye colour of the petal, is complete, the observation of the petal colour affords an infallible method of determining whether the seed should be classified as straw or brown. In the present case this record was, unfortunately, not made, and a full analysis

of the seed colours is, consequently, not possible. The figures, however, are sufficiently indicative.

Of eleven families raised from brown seed

5 have given brown seeded plants only, indicating a constitution represented either by *SSPP* or by *SSPp*;

5 have given the following figures, indicating the constitution of the parent to be *SsPP*:

	Pink *ssPP*	Brown *SSPP* and *SsPP*
	468	1332
Expectation *1 : 3*	*450*	*1350*

while one family only has given results which indicate the constitution *SsPp*:

	White	Pink	Straw and Brown
	11	35	187
Expectation *1 : 3 : 12*	*14·5*	*43·5*	*174*

As has been noted, the blue colour only develops in the presence of the *P* factor, and, consequently, all blue seeded plants possess a coloured eye in the petal. The form *PPBb* gives blue and pink seeded plants in the proportion of 3 : 1; while the form *PpBb* gives 4 white seeded plants, having the petal white eyed, 9 blue seeded plants, and 3 pink seeded plants, both having the petal eye coloured. Evidence confirming the above was obtained by crossing the 358 single plant, and apparently pure, cultures of white seeded poppies with the pure *PPbb* form. Of these 358 cultures 344 have given an F_1 of only pink seeded plants, indicating for the white seeded parent a constitution *ppbb*, 13 have given an F_1 of only blue seeded plants, indicating for the white seeded parent a constitution *ppBB*, while 1 has given an F_1 of both blue and pink seeded plants, indicating for the white seeded parent a constitution *ppBb*.

In the presence of the factor *S*, giving straw colour, the factor *B* develops a series of colours, varying from grey to a deep purple, so completely graded that it is only possible to isolate the extremes of colour.

The relation between the *S* and *B* factors is determinable, in the simplest case, in material homozygous for the *P* factor.

The form *SSBB* has a deep purple seed and has been obtained in the pure condition; 5 families have given the following figures:

	Blue *ssBB*	Grey *SsBB*	Purple *SSBB*	(Grey-Purple *SsBB* and *SSBb*)
	368	1003	296	(1299)
Expectation	*417*	*834*	*417*	(*1251*)

indicating a probable constitution of *SsBB*; 1 family has given the following figures:

	Brown *SSbb*	Grey-Purple *SSBb* and *SSBB*
	85	270
Expectation	*89*	*267*

indicating a probable constitution of *SSBb*; while 12 families have given a range of colours summarised in the following figures:

		Pink	Blue	Brown	Grey	Purple	(Grey-Purple)
		363	123	141	1241	473	(1714)
Expectation	*8 : 1 : 1 : 8*	*463*	*123*	*123*	*1171*	*463*	(*1634*)
	7 : 1 : 1 : 7	*448*	*137*	*137*	*1171*	*448*	(*1619*)

indicating a probable constitution of *SsBb*. Linkage, however, occurs between the two factors *S* and *B*. It is the only such case that has been identified among the characters that have been studied in the opium poppy.

INHERITANCE IN *RICINUS COMMUNIS* L.

PART II.

By S. C. HARLAND, D.Sc. (Lond.).

In the first part of this paper[1] the writer demonstrated the existence of four Mendelian factors in the castor-oil plant. These factors are *B* (bloom), *S* (spines), *M* (mahogany), and *G* (green). Experiments on the interrelations of these four factors shewed that the following pairs of factors are independently inherited: *S* and *M*, *S* and *B*, *M* and *G*, and perhaps *G* and *B*. Factors *M* and *B* are repelled in the cross $Mb \times mB$.

A further series of crosses was made with the object of clearing up certain outstanding points, and the results of these crosses will now be given.

Relation between the factors M (mahogany) and B (bloom).

The back-cross F_1 (*MbmB*) by double recessive (*mbmb*).

Family	*MB*	*Mb*	*mB*	*mb*
RX 2—4 × *Gb* 10	3	30	28	3
RX 2—4 × *Gb* 18	6	38	33	0
RX 2—2 × *Gb* 3	11	98	88	9
RX 2—4 × *Gb* 14	1	27	22	1
RX 2—4 × *Tb* 18	2	24	26	1
RX 2—4 × *Tb* 19	10	77	69	4
Totals ...	33	294	266	18

By Morgan's method of calculation the percentage of cross-overs is 8·3, and on the chromosome hypothesis the factors *B* and *M* are located on the same chromosome 8·3 units apart.

Relation between the factors B (bloom) and G (green).

The results of a previous series of back-crosses $BGbg \times bgbg$ indicated that *B* and *G* were either independently inherited or very loosely

[1] *Journal of Genetics*, Vol. x. No. 3.

linked. The results from a further series of back-crosses are now available.

Family	*GB*	*Gb*	*gB*	*gb*
RX 2—3 × *RG* 3—1	5	3	2	4
RG 3—7 × *RX* 2—3	7	8	9	12
RG 3—4 × *RX* 2—3	18	13	20	9
RG 3—3 × *RX* 2—3	10	14	9	10
RG 3—5 × *RX* 2—3	14	4	9	6
RG 3—8 × *RX* 2—3	3	2	4	4
RG 3—9 × *RX* 2—3	8	9	15	12
RG 3—*j* × *RX* 2—3	10	4	6	6
RG 3—*k* × *RX*,2—3	17	20	27	13
Totals	92	77	101	76
Expected ...	*86·5*	*86·5*	*86·5*	*86·5*

In this series of crosses the number of cross-overs is 178, and the number of non-cross-overs 168, an excess of the former. It may be concluded that *G* and *B* are independently inherited.

Relation between the factors S and G.

The relation between *S* and *G* was investigated in the back-cross *SgsG* × *sgsg*. The following were the results:

Family	*SG*	*Sg*	*sG*	*sg*
1	8	4	4	6
2	33	15	4	10
3	18	17	14	14
4	17	9	9	13
Totals	76	45	31	43

The factors *S* and *G* entered the cross from different sides, the cross being *Sg* × *sG*. The results from the above back-crosses are such as would be expected if *S* and *G* entered the cross from the same side and were linked. The small number of plants grown does not enable us to decide whether the excess of *SG* and *sg* is due to some accidental cause, or whether we are dealing with a new phenomenon. It would be difficult to imagine any mechanism which could give rise to more than 50 per cent. crossing over.

In the original F_2 results the two types Rose and Tinged were not separated, so that it is not possible to trace the ratio of the four phenotypes *SG*, *Sg*, *sG*, and *sg* in this generation. In the two colour classes green and mahogany, however, the proportions of spiny and spineless were distinguished thus:

Green Spiny *nSG*	Green Spineless *nsG*
61	27
Mahogany Spiny *MSg*	**Mahogany Spineless** *Msg*
93	37

In both the above ratios there is an excess of the spineless form, and it would be justifiable to conclude that there is no repulsion between factors *S* and *G*. It is intended to study the linkage relation of *S* and *G* in a much larger series of back-crosses.

Relation between the factors M (mahogany) and G (green).

The F_2 results led to the conclusion that *M* and *G* were inherited independently, and this view is confirmed by the results of back-crosses of F_1 by double recessive, placed below.

Family	*MG*	*Mg*	*mG*	*mg*
1	7	12	10	5
2	9	5	8	7
3	15	11	15	12
4	56	36	39	34
5	26	17	14	28
Totals	113	81	86	86
Ratio	1·2	0·9	0·9	0·9

The only point arising out of these results is the excess of *MG*, which should form the subject of further experiment.

SUMMARY.

1. Factors *M* and *B* are linked, there being 8·3 per cent. cross-overs in the back-cross of F_1 by double recessive.

2. Factors *G* and *B* are independently inherited.

3. Factors *M* and *G* are independently inherited.

4. The relation between *S* and *G* is somewhat obscure, the percentage of cross-overs in the back-cross of F_1 by double recessive being considerably greater than the percentage of non-cross-overs.

INHERITANCE OF CERTAIN CHARACTERS IN THE COWPEA (*VIGNA SINENSIS*).

PART III. THE VERY SMALL-EYE PATTERN OF THE SEED-COAT.

By S. C. HARLAND, D.Sc. (Lond.).

The genetic constitution of certain types of seed-coat pattern in the cowpea has already been discussed in the first part[1] of this paper. Briefly the factorial composition of these is as follows:

Solid	... ...	DH_1H_2, DH_1h_2, or Dh_1H_2,
Watson	... ...	Dh_1h_2,
Holstein	... ...	dH_1H_2, dH_1h_2, or dh_1H_2,
Small-eye	...	dh_1h_2.

A cowpea with another type of seed-coat pattern was obtained from Vilmorin of Paris. The eye, or pigmented area was very limited in extent, being confined to a narrow belt of colour about 0·5 mm. broad round the hilum. This type was called Very Small-eye.

A cross of Small-eye by Very Small-eye gave the following results:

F_1.	Watson		
F_2.	Watson	Small-eye	Very Small-eye
	324	117	145
Expectation on 9 : 3 : 4 basis	*330*	*110*	*147*

Obviously the expectation on a 9 : 3 : 4 basis is practically realised. We may regard the cross as:

Small-eye × Very Small eye
dY Dy

giving in F_2:

$9DY$	$3dY$	$3Dy$	$1dy$
Watson	Small-eye	Very Small-eye	

The Small-eye pattern may be regarded as being due to a factor Y, dominant to its absence. The factor D has no effect on seed-coat pattern except in presence of Y, but as it is also the factor for Dark flower, the Very Small-eye forms carrying D may be distinguished from forms without D by the flower colour, which is typically Dark.

It would be interesting to work out the relation of the Solid and Holstein patterns to Very Small-eye, but unfortunately the present writer will have no opportunity of carrying out further experiments on *Vigna* for several years. For this reason the above admittedly incomplete series of experiments have been recorded in this short note.

[1] *Journal of Genetics*, Vol. VIII. No. 2.

ON A CASE OF PATCHING IN THE FLOWER COLOUR OF THE SWEET PEA (*LATHYRUS ODORATUS*).

By R. C. PUNNETT, F.R.S.

(With three Text-figures and Plate XXI.)

CONTENTS.

THE publication of Baur's striking researches on variegated Pelargoniums and other plants, and his enunciation of the chimaera hypothesis, have led to a growing interest in the genetics of variegated plants in general. Not only do the anomalies in their hereditary behaviour offer a standing challenge to the geneticist, but it is difficult for those who work with them to resist the conviction that they hold the clue to much that is puzzling in connection with the process of segregation. No excuse therefore is offered for adding to the literature an account

of a fresh case, even though it cannot at present be satisfactorily related to the existing corpus of genetical knowledge. Since it is one of some complexity, a description of the material will be followed by a brief outline of what appear to be the main genetical features before passing on to consider it in detail.

Material.

The wild purple type of flower, once met with among cultivated forms as "Purple Invincible," is closely related to the deep purple[1], and to the hooded forms of purple known as "Duke of Westminster" and "Duke of Sutherland." Earlier experiments on the genetics of these four forms shewed that their interrelations could be expressed in terms of two factors, viz. a factor for light wing (L) in the absence of which the wing is dark (l), and a factor for the notched erect standard (E) in the absence of which the standard is hooded (e). The experiments further shewed that, where the standard is erect, its colour is deeper and brighter than in the corresponding hooded form. Flowers with the erect standard are more markedly bicolor than the corresponding hooded forms. The four forms will be found illustrated on Pl. V, figs. 4, 5, 7 and 8 of Bateson's *Mendel's Principles of Heredity*[2].

Corresponding to each of these four normal purple forms is a recessive "red-purple" form. The difference between the normal and the red-purple is perhaps best appreciated in the case of the light-winged varieties, where there is a striking contrast between the blue wing of the normal, and the pink wings, slightly tinged with purple, of the corresponding red-purple. This is well shewn on Figs. 4 and 6 of the plate accompanying this paper, from which a good idea may be obtained of the difference in colour between a normal Duke of Westminster flower and its corresponding red-purple form. The red-purple forms of the deep purple (Ppw.) and Duke of Sutherland have the characteristic coppery appearance shewn on Pl. XXI, fig. 1. We may attribute the appearance of the red-purple colour to the lack of a factor J which is present in the normal purple. And here it should be stated that this factor brings about a change in the general appearance of the plant as well as in the colour of the flower. Red-purples are always smaller plants than normals, reaching on the average to

[1] Known as Ppw. (=purple with purple wings) in our earlier experiments. See *Rep. to Evol. Comm. Roy. Soc.* III. 1906, p. 31.

[2] Though this plate brings out the relative difference in the four forms, the actual colours are not well rendered. A better representation of "Duke of Westminster" is that shewn on Fig. 4 of the Plate at the end of this paper.

about two-thirds of the height of the latter. This diminution in height is accompanied by a corresponding diminution in the parts of the plant; the stems are thinner, the leaves are smaller, and flower stems shorter. The vegetative parts of the red-purple also present a different appearance to the eye, for the foliage is of a deeper green, and there is a greater development of anthocyan pigment, especially in the flower stems and pedicels, which give to the plant a characteristic "dusky" appearance.

Corresponding to the series of normal purples there is also a recessive "blue" series in the sweet pea. Lord Nelson, for example (Pl. XXI, fig. 3), is the blue form of Ppw., and there are blue forms corresponding to the other three members of the normal purple series. We may suppose that these blue forms each lack a factor D which is found in the normal purple. Corresponding to each of these "blue" forms there is a "red-blue" which bears the same relation to the blue that the red-purple bears to its equivalent normal purple form. In the blue series the colour assumed by the "red" form is a peculiar dusky violet, such as is shewn on Pl. XXI, fig. 2. We have therefore the following 16 colour varieties which, at one time or another, have figured in the present series of experiments.

Normal Series		Red Series	
Purple Invincible (P. I.)	ELDJ	Red P. I.	ELDj
Deep Purple (Ppw.)	ElDJ	Red Ppw.	ElDj
Duke of Westminster (D. W.)	eLDJ	Red D. W.[1]	eLDj
Duke of Sutherland (D. S.)	elDJ	Red D. S.	elDj
Blue bicolor	ELdJ	Violet bicolor	ELdj
Deep blue	EldJ	Deep Violet bicolor	Eldj
Blue hood	eLdJ	Violet Duke	eLdj
Lord Nelson (L. N.)	eldJ		eldj

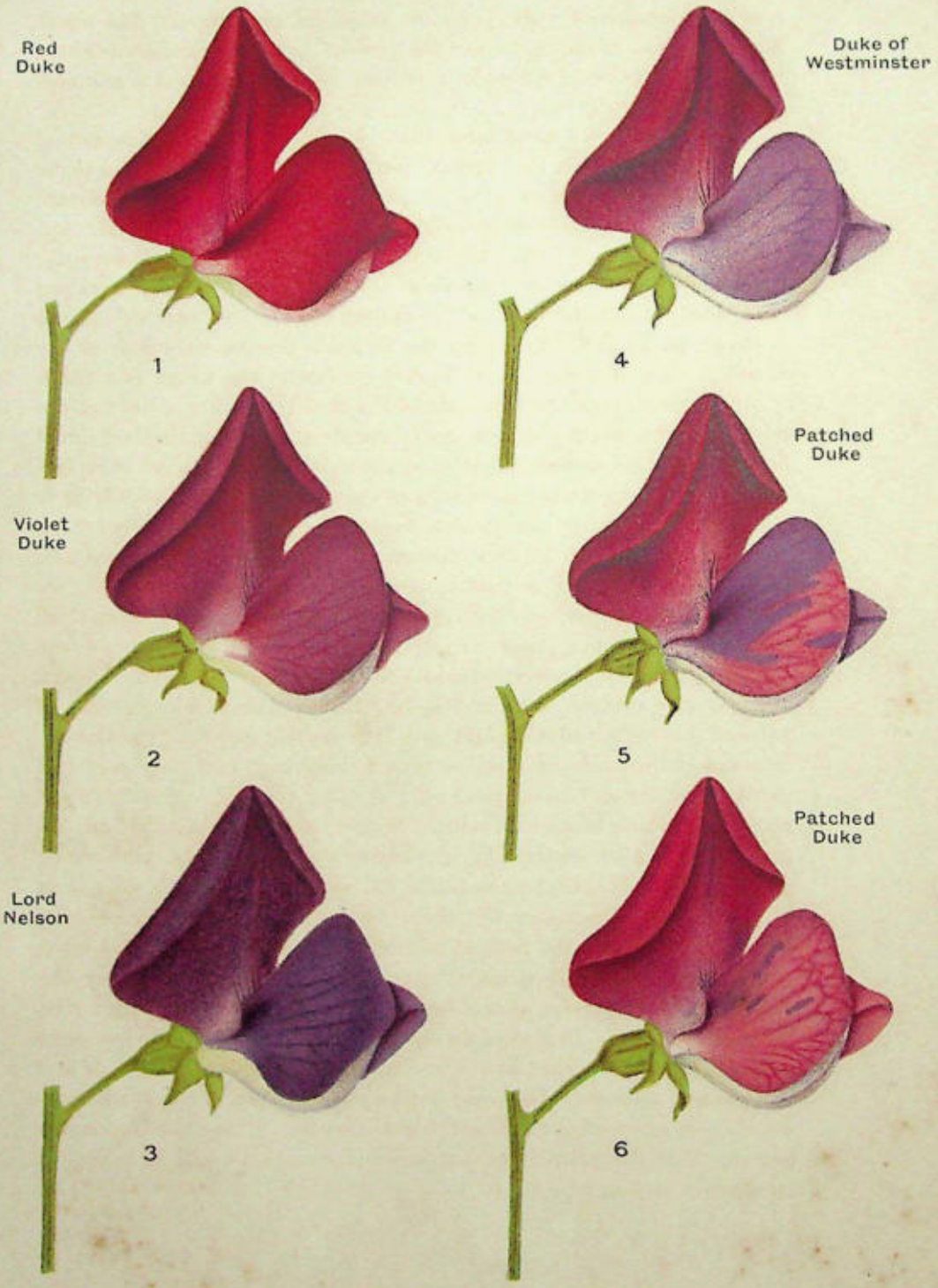
It should at once be stated that the "Red" series has nothing to do with red sweet peas in the accepted sense. They are all true purples in that they contain the factor B, upon the presence or absence of which depends the difference between a purple sweet pea and its corresponding true red, e.g. between Purple Invincible and Painted Lady, or between Picotee and Tinged White[2]. Thus a cross between Red Duke and Painted Lady gives Purple Invincible. Where the colour is deep, a visible difference may be exhibited among true reds between those containing and those lacking J. There is a "red" series also among true reds, but ordinarily it is not possible to differentiate the true

[1] The term "Red Duke" includes Red D. W. and Red D. S.

[2] *Reports to the Evolution Committee of the Royal Society*, III. 1906, p. 4; cf. also Bateson's *Mendel's Principles of Heredity*, 1909, Pl. III.

reds (J) from the red reds (j) by the colour of the flowers. The point, however, is not of importance in the present series of experiments since, with the exception of a couple of crosses, the material used was homozygous in B throughout.

Though, as will appear later, there is ample evidence for regarding the relation between the normal purple or blue, and its homologue in the red-purple series, as a simple Mendelian one, yet in certain families this relation does not obtain, but is complicated by the appearance of another form. These are plants in which the flowers are characterised by shewing a mosaic of the normal and the corresponding "red" shade of colour. A typical flower from one of these "patched" plants is shewn on Pl. XXI, fig. 5. In this instance the general colour of the flower is that of a normal D. W., but on one of the wings is a patch of the purplish pink characteristic of the Red D. W. The extent of the patching on a plant exhibits great variability among the individual flowers borne on a given plant. Usually most of the flowers shew but small patches of normal colour, such as the one figured on Pl. XXI, fig. 6. But there are nearly always flowers, more on some plants, fewer on others, which shew a greater amount of normal colour. One may be predominantly normal, as that figured on Pl. XXI, fig. 5, another may be red except for a blue wing, while another again may be patched all over, but with much more normal colour than the flower figured on Pl. XXI, fig. 6. Or the normal colour may be reduced to a minute speck which is only evident when looked for. Besides these various grades of patched flowers, a patched plant may bear normal and fully red flowers. Sometimes these are isolated, so that a flowering stem may bear two patched flowers and one normal one; at other times the plant may put up a shoot which bears only normal flowers, or again, one that has only red flowers. After examining hundreds of these patched plants, one gets the impression that in some the nature of the mosaic is finer than in others. In the former the great majority of the flowers are predominantly red, and the normal colour is present as small flecks, often very numerous, scattered about over the surface. In the latter the normal colour is present as blotches, fewer in number but of larger size, and it is in these that completely normal flowers are perhaps more common. No sharp line, however, can be drawn between the finer and the coarser mosaics. Moreover either can put up a shoot which is wholly normal, or wholly red, as the case may be. I have the impression however that the normal shoot is more often to be found in plants of the coarser mosaic type.


Red Duke
1
Violet Duke
2
Lord Nelson
3
Duke of Westminster
4
Patched Duke
5
Patched Duke
6

In general habit of growth the patched plant is intermediate between the red and the normal, tending however more towards the red, a point easily noted in families where all three kinds appear. When, however, a shoot bearing only normal flowers arises on a patched plant, the habit of that shoot is the habit of the normal flowered plant. With its normal purple flowers, more luxuriant habit, and brighter green colour, such a shoot offers a striking contrast to the rest of the plant.

Brief outline of the case.

In its main features the genetic behaviour of the normals, reds, and patched arising from patched plants may be summarized as follows:

(1) *Normals* give either

(*a*) Normals only.

(*b*) Normals and reds in the ratio 3 : 1.

(*c*) Normals, reds, and patched. In such families the proportions are irregular, but there is almost always a considerable excess of normals over the other two classes taken together.

(2) *Patched* give all three kinds in irregular proportions[1], but the reds and patched together are almost always considerably in excess of the normals.

(3) *Reds* give either

(*a*) Reds only[2].

(*b*) All three kinds. When this is the case the proportions are similar to those arising from patched plants, and I regard such reds as, in all probability, patched plants in which the patching is so reduced as to have escaped notice.

Such, in its barest outline, is the nature of the case. It will be found substantiated by the data given below, and is introduced here to enable the reader to grasp more clearly the fuller account that follows. Since the mode of origin of the red and of the patched forms has a bearing upon their interpretation, we may commence our analysis with what is known of it.

Earlier History.

In 1903 a cross was made between the two whites Emily Henderson (round pollen) and Blanche Burpee (long pollen). The F_1 plants, grown in 1904, were normal P. I. in appearance. In one of the F_2 families raised

[1] With one exception in which only reds occurred (cf. p. 272).

[2] Occasional normals or patched may appear in families which are almost entirely composed of reds. I am inclined to regard these as rogues due to insect agency.

in 1905 it was recorded that several of the purples had a reddish tinge, but beyond noting the fact no further attention was paid to it at the time. From a normal P. I. sister plant, 309[2]/05, was raised the family 305/06 (see Pedigree, p. 261). It consisted of purples, reds and whites. Of the 59 purples, 54 were normal, while the remaining 5 were patched. From one of the latter came Fam. 66/07 which consisted of 7 plants only. One of these is recorded as a red purple with a normal branch, and another as a Red Duke. No note was made of the rest. The Red Duke may have been a patched plant with a small amount of patching, for at that time so few red plants had been seen that we were not conversant with the material. The Red Duke, 66[1]/17, was used as pollen parent in a cross with 93[3]/07, a plant belonging to a pure Ppw. strain, and the three F_1 plants raised in the following year (40[1–3]/08) were recorded as being "reddish P. I."[1]

Here the matter rested for three years. At that period Mr Bateson and I were busy working at the problem of repulsion and coupling, and had neither time nor space to spare for other material. It was for this reason that nothing had been done with the Red P. I. story beyond the few observations recorded above. When, in 1911, it fell to my lot to continue the sweet pea work alone, I decided, among other things, to look into the case more fully. The only material existing consisted of the seeds of the 2 F_1 plants from the cross with Ppw. above mentioned. From these were reared the 2 F_2 families, 63/11 and 64/11, forming the starting point of the series of experiments tabulated in Tables I—IV and the accompanying pedigree.

Account of the Experiments.

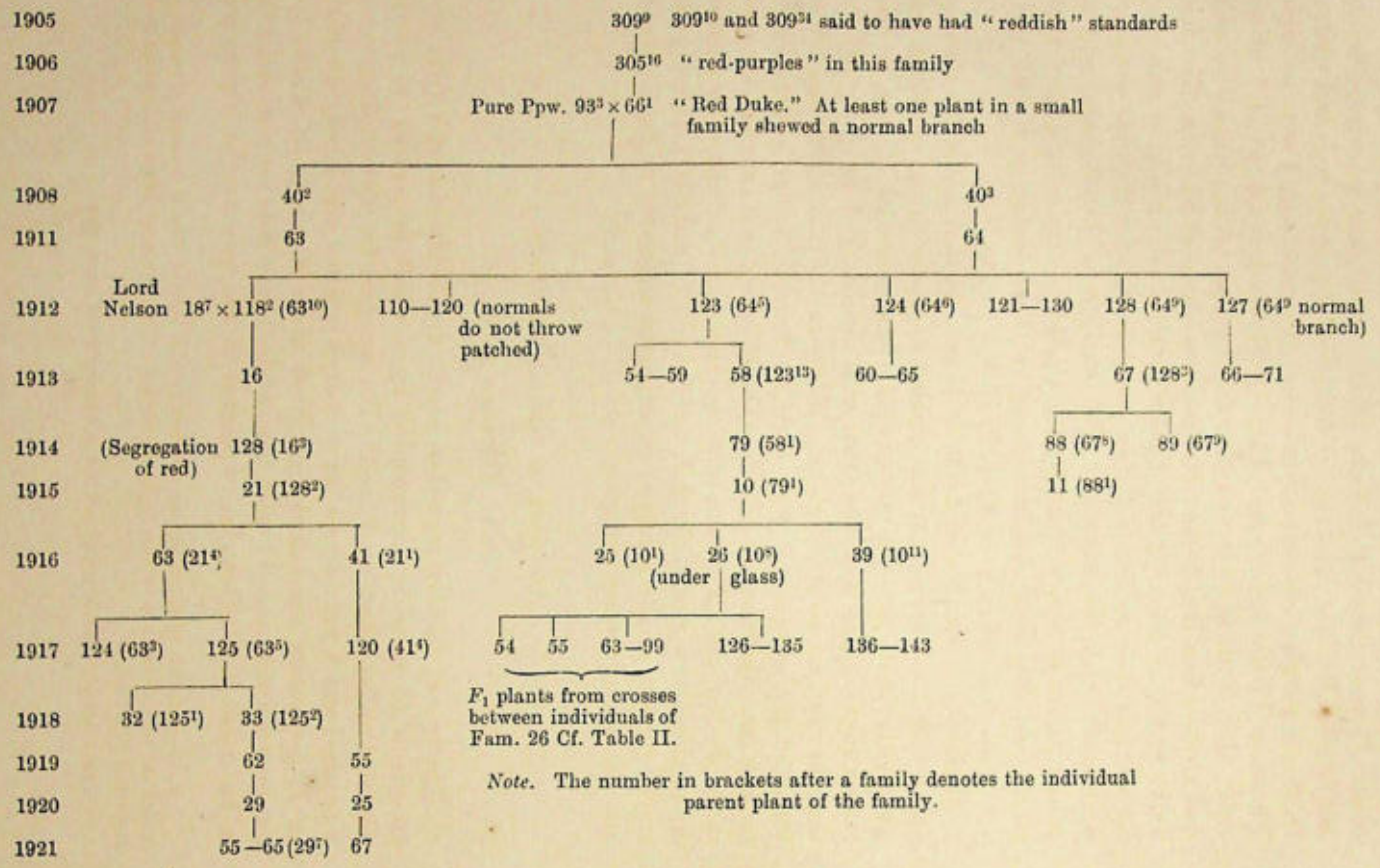
A. *The main series.*

The two F_2 families proved to be not dissimilar. In each there was an excess of normals accompanied by a small proportion of plants recorded as "patched" and "red." The numbers for 63 were 76 normal, 3 patched and 4 red: for 64, 40 normal, 4 patched and 3 red. In 1912 an F_3 generation was raised from 20 of these F_2 plants (cf. Table I)[2]. Of the 9 normals tested 7 bred true, while 2 gave only normals and reds in the ratio 3:1. This clearly pointed to the existence of a pure red

[1] My recollection of the meaning attached to this term is that it denoted a purple in which the wings were not so blue as in the normal. They were far removed however from the "red P. I." itself.

[2] These families will be found set out in tabular form on p. 273.

Pedigree.



Note. The number in brackets after a family denotes the individual parent plant of the family.

behaving as a simple recessive to the normal. Of the five patched plants tested all gave normals, patched, and reds. In 4 families the patched and reds, taken together, were in excess of the normals, a relation which later experiments shewed to be generally true. In one family (124/12) the normals were considerably in excess, an aberrant result which is referred to later on p. 271. Of the six plants classed as reds, five behaved similarly to patched plants, giving all three classes with the reds and patched in excess. Genetically these reds were evidently of the same nature as the patched. One of them, viz. $64^9/11$, was a red bearing a normal branch, and for this reason should perhaps have been more appropriately classed as a patched. The seeds of the normal branch were harvested separately from those of the rest of the plant, and in 1912 were sown as No. 127, the remainder as No. 128. Each sowing gave a similar result. This point will however be gone into in more detail later on. One red plant ($63^{10}/11$) gave a family consisting only of reds viz. 118/12. Of these one plant, $118^2/12$, was used for crossing with Lord Nelson and provided the basis of a set of experiments which will be dealt with below (p. 263). From individuals of the F_2 family, 64/11, the main series of experiments was carried on until the F_5 generation was reached in 1917, when it was brought to an end with families 126–143. The details can be readily gathered from a study of Table I in conjunction with the pedigree. The data so obtained serve to demonstrate the existence of the six different kinds of plants already set out on p. 259.

B. *Data from crosses inside the "red" families.*

In 1916 the seeds of a patched plant, $10^8/15$, were sown and raised in pots under glass. They gave a small family 26/16 consisting of 2 normals, 8 patched, and one red. During their flowering period in the greenhouse various crosses were made between these different plants. Of the successful fertilisations the nature and results are set out on Table II. Where patched plants were concerned note was made as to whether the particular flower used in each instance was normal, patched or red. The results will be discussed below (p. 266) in considering the question whether the different kinds of flower on a patched plant differ in their genetic behaviour.

In 1917 the seeds of 10 of the 11 plants of Family 26 were sown in the open. Neither of the two normals proved to breed true. There was however a marked difference in the proportion of normals that they produced. This proportion was very much higher in the case of 26^4

(cf. 129/17) than of 26¹ (cf. 126/17). To this point we shall return later. The patched plants behaved as expected, while the red (26²/16), though giving but six plants, bred true (127/17). That 26² was a true-breeding red is confirmed by the results of the F_2 generation raised from it when crossed by its two normal sister plants. Ten families of this breeding were grown in 1918, and, as Table I shews, nine of them exhibited a clean segregation between normal and red. The appearance of patched plants in the remaining family, 47/18, is doubtless to be traced to the normal parent, 26¹/16, which had been shewn to throw all three classes.

In 1918 and 1919, the seeds of a number of the F_1 plants were sown, and the results are recorded in Table II. We need only say here that they are consistent with the data obtained in the main series of experiments.

C. *Data from crosses with unrelated normals.*

The Red Duke, devoid of patches, made an undoubted appearance in 1911. One such plant in the F_2 family, 63/11, was grown on in the following year to produce a small family consisting only of reds (118/2). A cross was made between one of these reds (a red D. S.) and Lord Nelson. From the F_1 D. S. plants was raised an F_2 generation shewing clean segregation of the red from the normal purples. Corresponding to D. S. were deep red Dukes such as that figured on Pl. XXI, fig. 1, while among the blues the red class was represented by the Violet Duke (Pl. XXI, fig. 2), a distinct colour hitherto unrecorded in the sweet pea. The close approximation to a 3 : 1 ratio indicated a case of simple segregation, red behaving as recessive to normal (cf. Table III, p. 281). No patching was seen on any plant belonging to the red class. A Red Duke (128²/14) saved from one of these F_2 families (cf. Pedigree) subsequently gave rise to the stock used in further crossing experiments. The details of these may be readily gathered from Table III in conjunction with the pedigree. The results in most cases indicate simple segregation as in the Nelson cross, but in three cases there is a record of a single patched plant, while in another cross (Red D. × E. H. round) no less than 12 patched plants appeared among 104 purples. This last case is certainly aberrant, but it is doubtful whether much stress can be laid on it. For the white parent (43¹/16) was a lineal descendant of the Emily Henderson strain used in the original cross of 1903, and it is not impossible that the patched character may have been introduced similarly in the two instances. Certainly we are not entitled to make

use of it as evidence of the failure of the purity of the Red Duke parent. And this is also the case for the 1918 cross, R. White × Helen Pierce[1], where a single patched plant occurred in a small family. There remain the two other exceptions. Ought we to regard them as real exceptions involving some process of segregation different from what we are accustomed to regard as normal, or should we look upon them as due to an accidental cross-fertilisation due to insect agency? For patched plants were growing in the garden alongside of these F_1 plants, and *Megachile* is always with us. It is not impossible that the single patched plant arising in F_2 from the cross Red Duke × M. H. hood may owe its origin to this cause. Fortunately, however, the circumstances are such as to allow of our arriving at a definite decision in the case of the last remaining exception, viz. that from the cross Red Duke × Helen Pierce. The F_1 plants were D. S., and in F_2 appeared the four colour varieties D. S., Nelson, Red Duke, and Violet Duke, together with their respective marbled forms. Now the single patched plant that made its appearance was *marbled*. The only marbled plants growing in the garden where these F_1 plants were setting seed were Helen Pierce: the only plants carrying marbling were certain F_1 plants derived from crosses with Helen Pierce. Helen Pierce has never produced a patched or a red plant; nor has such a thing occurred in the F_2 of any of the crosses with Helen Pierce. Hence the single patched plant in F_2 cannot be attributed to what we may term a red patched marbled gamete brought by *Megachile* from some other plant. We are forced to regard it as having arisen through some process of imperfect segregation in the parent plant. Moreover the strong evidence that exists for this particular plant must render us willing to admit that something of the nature of imperfect segregation may also underlie the other exception dealt with above.

Apart from these exceptional patched plants the result of the outcrosses with Red Duke clearly suggests a single factor difference between the red-purple and the normal purple classes. In a total of over 2000 F_2 plants a 3:1 ratio is closely approximated to.

D. *The Red Duke line.*

The Red strain isolated in family 118/12 was accidentally allowed to die out. Another strain was however established from an F_2 plant,

[1] A blue hooded marbled form. Marbling is recessive to self colour, and Helen Pierce behaves as a recessive to Lord Nelson.

$128^2/14$, which arose from the 1912 cross between Lord Nelson and 118^2. The subsequent history of this strain, which is shewn in the pedigree, presents a point of interest, in spite of the fact that all of the plants in it proved to be shy seeders. In 1916 the line was duplicated. Of the one branch (Ex. $21^1/15$) five generations have been grown to date. The total number of individuals only amounts to 35, but all have been clear reds with no indication of any patching. In the other branch however (Ex. $21^4/15$), which has been grown on for six generations, patched plants have occurred. Family 124 of 1917 consisted of 9 plants. On a single flower of one of these plants occurred a patch of purple which covered about one third of one of the wings. Unfortunately it was not found possible to save seed from any member of this family. No further indication of patching occurred in the line until 1920 when two patched plants made their appearance in a small family of seven (No. 29). Here the parent (62/19) was a Violet Duke, a fact of importance in helping us to decide upon the origin of these two patched plants. In 1919 there were numbers of patched plants growing in the garden. But all of these belonged to what we have termed the main series of experiments, all of the plants of which were homozygous in D. Had the two patched plants from 62/19 been due to insect agency they must have been red-purples—not violet. The evidence clearly points to their spontaneous origin from 62/19. It may be added that the patching in these two plants was pronounced and of a coarse type. One of them bore a full blue branch of which further mention will be made below.

SPECIAL POINTS.

A. *The genetical behaviour of the different kinds of flowers on patched plants.*

In any attempt to formulate views as to the nature of the patched plant, one is at once met with the question whether the mosaic arrangement of the colours indicates an irregular distribution of the corresponding genetic factors in the germinal tissue. Do normal flowers on patched plants tend to produce a higher proportion of normals than do patched flowers? The facts that may contribute to a decision fall into two groups, and are as follows:—

(1) In four cases where a patched plant has put up a normal branch, the seeds of that branch have been harvested separately from those of the rest of the plant. These plants are:

		N.	P.	R.	N.	P.	R.
$64^2/11$	normal branch ...	2	9	10	—	—	—
	red branches ...	—	—	—	13	19	36
$66^2/17$	normal branch ...	6	1	3	—	—	—
	patched branches...	—	—	—	6	4	25
$97^1/17$	normal branch ...	1	4	4	—	—	—
	patched branches...	—	—	—	—	3	2
$29^7/20$	normal branch ...	3	10	15	—	—	—
	patched branches...	—	—	—	1	8	3
Totals ...		12	56		20	100	

I.e. normal branches give ... 17·6 °/₀ normals
red and patched branches give 16·6 °/₀ ,,

The data afford no ground for supposing that normal branches of a patched plant exhibits any constant genetical difference from the rest of the plant.

(2) Crosses were made in 1916 between normal and patched members of the same family (26), in which the nature of the flower used from the patched plant was recorded. The two sister normal plants used, viz. $26^1/16$ and $26^4/16$, were subsequently shewn to give a markedly different result on selfing, and must therefore be considered separately. The data, which are given in full in Table II, may, for our present purpose, be summarized as follows:

(α) Crosses between 26^1 (a normal which gave 10 N.: 6 R. + P.) and different sorts of flowers from various sister patched plants.

	N.	P.+R.
Normal flowers gave ...	10	7
Patched ,, ,, ...	28	14
Red... ,, ,, ...	5	6

(β) Crosses between 26^4 (a normal which gave 17 N.: 1 P.) and different sorts of flowers from various sister patched plants.

	N.	P.+R.
Normal flowers gave ...	2	1
Patched ,, ,, ...	13	5
Red ,, ,, ...	7	0

These figures shew that the three sorts of flowers tend to behave in the same way. In spite of irregularities there is no indication of any excess of normals when normal flowers were used as compared with patched; nor again when patched flowers were used as compared with red. In other words, there are no grounds for supposing that the normal, patched, and red flowers on a patched plant differ genetically from one another.

B. *The genetical behaviour of earlier and later ripened seed.*

It is conceivable that in the cell divisions of a mosaic plant a process may occur whereby the more distal parts of the germinal layer may come to differ genetically from the more proximal. The possibility was tested in the case of one plant, 29⁷/20, by saving separately the seed of each flowering stem on the normal branch (cf. p. 265). The pods set well, but the final result is meagre owing to the numerous casualties from the drought of 1921. Such as it is, it is set out in Fig. 1, and offers no suggestion of any regular genetical differentiation with the age of the stem.

Some further observations bearing on the point are given in Table I. From three large normals in Fam. 40/20 the ripe seeds were taken at intervals, the first gathering being made some three weeks earlier than the second. In the case of one plant (40⁹) five gatherings were made, the last being in October. Only fully ripe seeds were taken, some of those ripening between the successive gatherings being naturally shed and

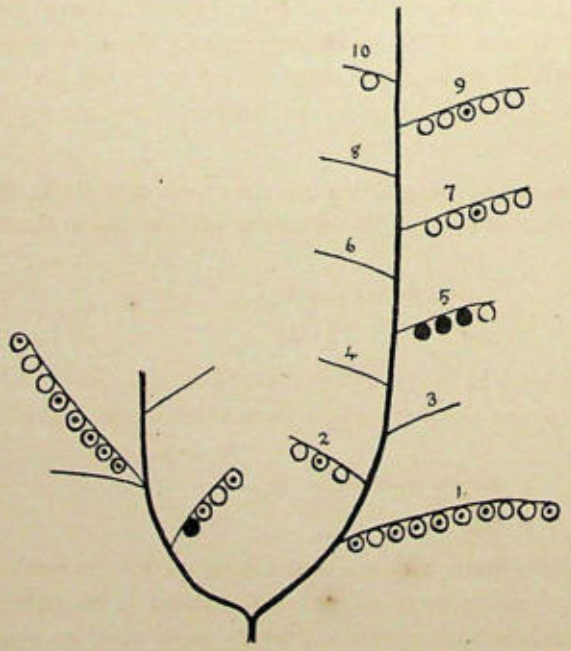


Fig. 1. Diagram of 29⁷/20. On the left a patched branch; on the right a normal-flowered branch. Seeds giving rise to normal flowered plants shewn black; seeds giving rise to patched plants shewn as ⊙; seeds giving rise to red plants shewn ○. The order in which the seeds are shewn on the flowering stem is imaginary.

lost. The data may be regarded as rough samples indicating the nature of the germ plasm at different stages in the history of the plant. It cannot however be said that they reveal any indication of definite change in the nature of the germ plasm in the later, as compared with the earlier stages of its growth.

C. *On the proportions of red, patched, and normal plants produced by individuals of the three kinds.*

Although the data are too scanty for adequate statistical treatment they offer nevertheless some interesting points for discussion. The first question which it is natural to ask is whether there is any evidence of regularity in the proportions of the three kinds of plants, reds, patched, and normals, when they occur together in mixed families. This may be attempted on the data given in Table I. Not all of these data are suitable for treatment in this connection, for many of the families are unfortunately too small to allow of our attaching much meaning to the proportions in which the three sorts occur. For this reason we shall consider only families containing 20 or more plants. Again, the records refer in large measure to plants which were small and imperfectly developed owing to adverse conditions. In extreme cases the individual had to be classified on a single flower, and often on but a few. Though there is no mistaking a normal, it is, under these circumstances not possible to be certain that a plant classified as a red should not more properly have been placed in the patched class. For the history of some plants that were kept under critical observation shewed that an individual may sometimes start as a red, and later on come to have a fair proportion of patched flowers, or even a normal branch. Moreover, as is evident from Table I, a plant classified as a red may, in its breeding behaviour, be indistinguishable from a patched. Doubtless many plants classified as reds ought really to be regarded as patched plants in which the flecks of normal colour are very much reduced. No parallel difficulty arises in the case of the normals, for I have never seen a normal with flecks of red. While red and patched grade insensibly into one another, the distinction between patched and normal is always unmistakeable. In the following paragraphs therefore I have taken account only of two groups of plants, viz. reds and patched taken together, and normals.

For the construction of Fig. 2 there were available 56 parents which arose in mixed families and gave all three kinds among their progeny[1]. Of these 20 were normals (Fig. 2, A), 20 were patched

[1] These families are all marked by an asterisk in Table I.

(Fig. 2, B), and the remaining 16 were reds (Fig. 2, C). In each of these 56 families the percentage of reds and patched taken together was calculated, and these percentages are plotted in Fig. 2. Here the percentage in each family is shewn separately, and grouped according as the parent was (A) normal, (B) patched, or (C) red. With the exception of one aberrant family (No. 111/19), all the families produced by

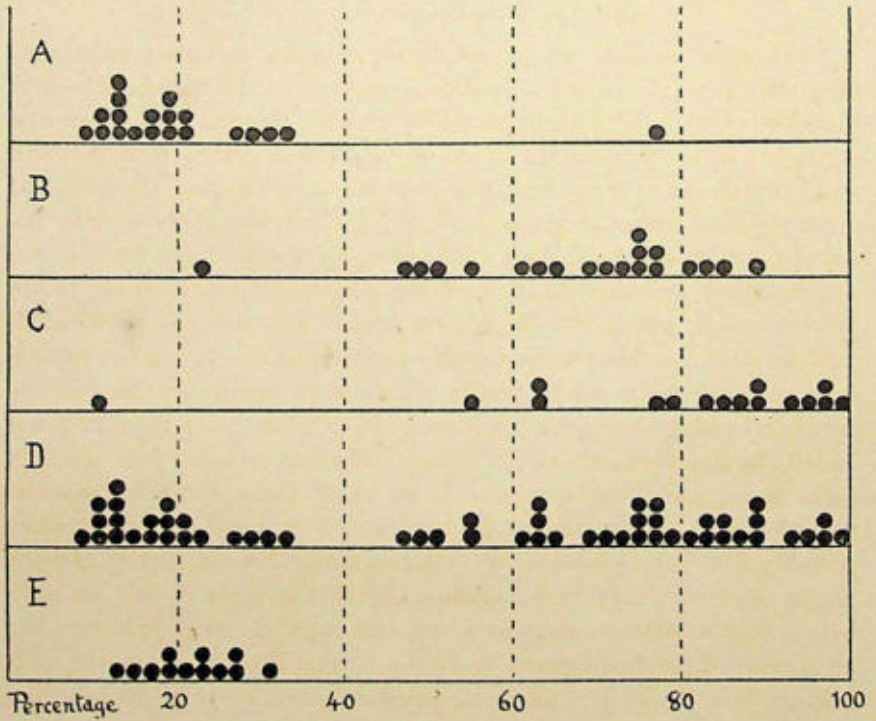


Fig. 2. Shewing percentage of reds and red-patched, as opposed to normals, in families from (A) normals, (B) red-patched, and (C) red parents. D is combined from A, B, and C, and shews families in which the three kinds of plants appeared, irrespective of their parentage. E shews percentage of reds where only normals and reds occurred. The data are derived from Table I. Only families containing 20 or more plants have been made use of.

normals agree in having a low percentage of reds and patched, varying from 10–33 %. The total number of reds and patched in the 20 families was 199, and of normals 876; so that the average percentage of normals is 18·5 %. This is distinctly below the 25 % characteristic of a simple recessive relation, such as occurs in families where normals and reds alone are found. Sixteen such families are shewn in Table IV, and the percentage of reds in those with 20 or more individuals is also plotted

in Fig. 2, E. Though the proportion of reds and patched in A is lower than that of reds in E, the range of variation is not widely dissimilar in the two cases.

When however we turn to families derived from patched we find a very much wider range of variation (Fig. 2, B). But except for one aberrant family (124/12) the proportion of reds and patched hardly drops below 50 %, while it may rise to almost 90 %. Out of a total of 855 plants in these 20 families 574 are red or patched, i.e. 67 %. The range of variation is here very considerable.

There remain the 16 families from red parents. Some of these may be closely matched by families derived from patched plants. In others however the proportion of patched and normals is very low, and it is not impossible that in such cases we may be dealing with rogues, due to *Megachile*, in families of pure reds. Taken as they stand however the families from reds (Fig. 2, C) resemble those from patched in their wide range of variation, though, on the whole, the proportion of reds and patched is higher. The 16 families comprised 708 plants, among which were 109 normals, giving an average of 77 % of reds and patched.

A point which seems to emerge from this necessarily inadequate analysis is that the patched plants can hardly be regarded as all constituted alike genetically. The proportion of normals produced even by sister plants (cf. 57 and 58 of 1913) differs too widely, and to these differences attach even greater weight when it is remembered that there is no evidence of a genetical difference being associated with a preponderance of normal coloration in the mosaic (cf. p. 266). On the other hand we must not lose sight of the possibility that the germinal layer may also be constituted as a mosaic, and that the germinal mosaic may be independent of the epidermal mosaic which is rendered visible through colour difference. An unusually high proportion of normals from a patched might conceivably be due to the higher prolificness of a branch in the germinal mosaic in which the factors making for normal were preponderant. A difference in the proportion of normals produced by two plants might depend upon the manner in which this mosaic happened to develope. In some plants a "normal" germinal covering of the flowering shoots might, through accidents of growth, preponderate more than in others. Such patched plants would throw a higher, and even a considerably higher proportion of normal offspring, than other patched plants in which, through accidents of growth, the greater part of the germinal layer consisted of the portion lacking in the factors for normal. Yet all may have started as similar zygotes. The point might

be tested by harvesting separately the separate branches of a number of patched plants. The data on p. 266 are obviously too few for testing the point.

The great range of variation for the patched and red plants, as brought out in Fig. 2, B and C, obviously points to a gametic output which differs quantitatively in different plants. For the normals the range of variation (Fig. 2, A) is much smaller, and not very markedly different from that shewn by plants where the relation between normal and red is that of ordinary dominant and recessive (Fig. 2, E). Nevertheless there is other evidence to shew that the normals which give rise to normals, patched, and reds, must often differ quantitatively in their gametic output.

In the series of crosses made between the various members of Fam. 26/16 (see Table II, p. 280) two different normals were made use of, viz. 26^1 and 26^4. The selfing of these two plants (see Table I) resulted in a very much higher proportion of normals from the latter. The inference that the normal output of gametes was higher in 26^4 is borne out by the behaviour of these two normals on crossing. Crossed with 26^2, a pure red, 26^1 gave 16 normals, 2 patched, and 6 reds, while 26^4 gave 9 normals and 2 reds. Crossed with various patched plants in the same family 26^1 produced 43 normals, 24 patched, and 3 reds, while 26^4 gave 22 normals, 4 patched and 2 reds. Whether selfed, crossed with red, or crossed with patched, 26^4 consistently gave a much higher proportion of normals than did 26^1.

There remains, in connection with the data represented on Fig. 2, the question of the three aberrant plants, one of which occurred in each of the three groups A, B, and C. The exception in A is a family with an unusually high proportion of reds and patched (111/19) from a normal parent. A conceivable explanation is that the parent was genetically a patched. Patched plants often throw up one, or even more, normal branches. It is not impossible that a small plant, such as the parent of this family was, may shew only normal flowers. Such a plant would be genetically a patched, putting up one or more normal branches, as any patched may do, but failing to develope flowering stems from the non-normal part of the mosaic. On the other hand the exception in B, where a patched plant (64^6/11) produced a family (124/12) with a great excess of normals, is harder to account for. I can only suggest that it may be an extreme instance of preponderance on the part of the normal portion of the germinal mosaic in the region of the flowering stems. Of the authenticity of the last exception (139/17) in which a red gave a high

proportion of normals I am doubtful. For in 1916 the seeds of some plants were collected by my gardener, and among them was 39^{18}, the parent of the family in question. I detected one certain error of labelling among the seed so taken, and for this reason I have never been satisfied that the present aberrant result may not also be due to some mistake.

D. *The formation of "pure" gametes by plants giving mixed families.*

That the patched plant must be regarded as producing some "pure" normal, and some "pure" red gametes is evident from a study of Table I. For example 39/16 contained 7 normals out of a total of 32 plants. Of these 7 normals 5 were grown on in the following year. Two of them, viz. 39^{3} and 39^{19}, gave families consisting respectively of 29 (137/17) and 61 (138/17) normals. The numbers are in each case sufficiently large to make it fairly certain that we are dealing with true-breeding normals in each case. Other examples of the origin of such normals are to be found among the crosses undertaken in 1916 among the members of Fam. 26. Thus Fam. 90/19 arose from a normal (63^{6}) that was produced by fertilising a patched plant with a normal (cf. Table II). Since it produced only normals to the number of 84 we are justified in regarding it as a true-breeding normal, and in supposing that the gamete from the patched parent (26^{6}) was a normal one. So also a patched plant gives rise to "pure" red gametes, for from such plants may be derived true breeding recessive reds such as $26^{2}/16$. From patched plants too may come normals which give normals and recessive reds only. 60/13 and 65/13 are examples of this. Moreover there is the peculiar case of 41 + 42/18. The parent of this family was a patched plant ($96^{2}/17$) derived from the fertilisation of a purple flower on a patched plant ($26^{11}/16$) by the pollen of a pure red ($26^{2}/16$). It was a patched plant with a pure red branch. The seed from the red branch was sown separately and gave 25 reds; that from the patched portion gave 5 reds. All of the plants were unfortunately small and failed to set seed satisfactorily, so that the matter could not be followed up. Nevertheless we have here an undoubted case of a patched plant from which only reds were recorded. It is conceivable that some of these reds, under more favourable conditions of growth, would have developed into patched plants to give a family similar to 34/13. Still we can hardly help inferring that $96^{2}/17$ was producing a high proportion of "pure" red gametes.

In connection with the proportion of normal gametes produced by normals occurring in families with a large excess of normals, the F_2

families from the 1908 cross between Ppw. and Red Duke are of interest. The details are set out separately in tabular form below:

Fam. 63/11, Ex. 40²/08, a normal which on selfing gave

N., 76 : P., 3 : R., 4.

11 F_2 plants tested by growing on to F_3, viz.:

	Normals							Patched		Reds	
1911 nos.	63^2	63^3	63^4	63^5	63^6	63^{11}	63^{12}	63^7	63^9	63^8	63^{10}
1912 nos.	110	111	112	113	114	119	120	115	117	116	118
Result N.	15	25	10	30	23	40	32	7	4	3	—
P.	—	—	—	—	—	—	—	5	2	2	—
R.	—	—	2	—	—	—	12	12	6	19	12

In this family out of 7 F_2 normals tested, 5 bred true, while 2 gave only normals and reds. None of the normals tested produced a patched plant. This may have been an accident, but in any case it is evident that we must suppose such plants to have been producing a high proportion of normal gametes.

Fam. 64/11 Ex. 40³/08, a normal which on selfing gave

N., 40 : P., 3 : R., 4.

9 F_2 plants tested by growing on to F_3, viz.:

	Normals		Patched				Reds		
1911 nos.	64^2	64^3	64^6	64^7	64^9	64^{11}	64^5	64^8	64^{10}
1912 nos.	121	122	124	125	{127}{128}	130	123	126	129
Result N.	30	39	32	6	15	5	8	3	8
P.	—	—	4	11	28	13	18	6	13
R.	—	—	6	8	46	8	13	12	1

The interesting point is that of the 9 F_2 normals tested in these 2 F_2 families where patched occurred, 7 bred true, while 2 gave only normals and reds. None of these normals produced a patched plant This may have been an accident, but in any case it is evident that we must suppose such plants to have been producing a high proportion of normal "gametes." As shewn in Table V some of the normals arising in mixed families breed true, but the proportion here indicated—viz. 4 out of 20—is very much smaller than in the case of the 2 F_2 families referred to above. The facts suggest that true breeding normals are much more likely to occur in mixed families where the proportion of normals is unusually high, than in families where it is markedly lower.

Discussion.

The case of the patched sweet pea naturally challenges comparison with the other cases in which the genetics of mosaic flower colour have been investigated, notably in *Antirrhinum*, *Primula*, and *Mirabilis*. In maize, too, a case of somewhat similar nature was described some years ago by Emerson, where the patch-work affected the colour of the pericarp. As these various cases all present peculiar features it will be convenient to consider them separately.

Gregory's[1] work suggests that the flaked *Primula* breeds true, but this is based more upon the behaviour of the flaked forms on crossing, than upon the offspring of flaked plants themselves. He does not, however, give any records of self-coloured flowers arising from flaked plants. Certainly a close parallel cannot be instituted between the Primula and the sweet pea, and Gregory was able to symbolise his results on a simple factorial scheme.

Emerson[2] shewed that in maize the variegated throws some reds, but no non-reds, while the proportion of reds thrown by the variegated depends upon the amount of red in the variegated grains. The reds so formed behaved as heterozygotes between self-red (dominant) and variegated (recessive), and in later generations homozygous self-reds were established. Though the amount of colour in some of the variegateds was much less than in others, no completely uncoloured head was produced.

The much discussed case of de Vries' striped Antirrhinums[3] presents many features in common with Emerson's maize. Here again the striped throw a variable, though relatively small proportion of self-red, while the self-reds so produced behave as heterozygotes between self and striped. It is true that de Vries did not obtain a homozygous red, but this was evidently due to his not having tested the offspring of the self-reds which sprang from the striped[4]. As with the maize, no

[1] *Journal of Genetics*, Vol. I. 1911, p. 121.

[2] *Amer. Nat.* Vol. XLVIII. p. 191.

[3] *Die Mutationstheorie*, Vol. I. 1901, p. 494; Vol. II. 1903, p. 351. *Species and Varieties*, 1905, p. 315.

[4] In some experiments with a striped strain of *Antirrhinum* I have recently produced homozygous reds in a manner analogous to that in which Emerson produced his homozygous red maize. Some reds arising from a self-fertilised red branch on a striped plant proved to be heterozygous, striped being recessive to self-colour. On self-fertilisation such reds produced striped, heterozygous reds, and homozygous reds in the expected proportions. I hope later to publish a fuller account of these and other experiments with the striped Antirrhinum.

completely uncoloured individual appeared during the course of the experiments. A further point of resemblance between these two cases is that the variegated maize appears to behave as a simple dominant to white, and, except for the production of a few reds, the striped Antirrhinum appears to behave similarly towards the colourless form[1]. The schemes of inheritance for *Antirrhinum* and for maize appear to be similar, though presenting points of difference from that for *Lathyrus*.

There remains the case of *Mirabilis*. Miss Marryat came to the conclusion that "though flaked forms occasionally throw self-coloured individuals, this phenomenon is so irregular that its significance is quite uncertain[2]." In the following year Correns[3] published his interesting account of the behaviour of the striped forms in this species. He found that *striata* plants did not, as a rule, breed true, but gave a small percentage ("0 bis 10 und mehr") of *rosea* plants with self-coloured flowers. When, as at times happened, *rosea* branches appeared on *striata* plants, such branches, on self-fertilisation, behaved as *striata* branches, though the proportion of *rosea* plants produced tended to be rather higher[4]. The *rosea* plants, which sprang from seed, turned out on testing, to be of 3 kinds, viz.

(*a*) those which bred true,

(*b*) those giving *striata* as recessive,

(*c*) those giving *gilva*[5] as recessive.

[1] Cf. *Die Mutationstheorie*, Vol. II. p. 352.

[2] *Reports to the Evolution Committee of the Royal Society*, v. 1909, p. 49.

[3] *Ber. d. Deut. Bot. Gesell.* Vol. XXVIII. 1910.

[4] There appears to be some misconception of this case in the accounts given by Bateson and by Baur, for both of these authors state that the majority of the plants raised by selfing the red branches are reds.

"When a plant bears both striped branches and unstriped branches, each type produces offspring which in the great majority resemble itself." *Mendel's Principles of Heredity*, 3rd Imp. 1913, p. 312.

"Alle gestreiften Pflanzen bilden einzelne rotblühende Äste, die weiterhin bei Selbstbefruchtung aufmendeln in 3/4 rot : 1/4 gestreift....." *Einführung in die Experimentelle Vererbungslehre*, 3 u. 4 Aufl. 1919, p. 302.

Correns however is explicit in his statement as to the genetical similarity between striped and red branches on the same plant.

"Die *rosea*-Äste geben (als F_1) eine Nachkommenschaft, die ebenfalls aus *striata*- und *rosea*-Pflanzen besteht. Auch das Zahlenverhältnis ist oft annähernd das gleiche wie bei den *striata*-Ästen. Zuweilen kommen aber doch relativ mehr *rosea*-Pflanzen vor, gelegentlich entschieden mehr als bei der Nachkommenschaft der *striata*-Äste desselben Individuums." (*Loc. cit.* p. 426.)

Moreover the scheme he gives on p. 427 is in accordance with his statement.

[5] I.e. the pale yellow form without any red flaking.

According to Correns class (*c*) was very rare. Further, Correns states that occasional *gilva* plants were produced from self-fertilised *striata* (*loc. cit.* p. 426), and that these bred true to *gilva* (*loc. cit.* p. 429). Owing probably to their rarity, Correns lays no stress upon these *gilva* plants, and omits them in the scheme of inheritance that he has drawn up on p. 427. Nevertheless the recognition of their existence allows us to institute a close parallel between the *Mirabilis* and the *Lathyrus* cases. In either case the general scheme of inheritance is the same. In either case we must suppose the variegated plants to be giving off three kinds of gamete, viz. *rosea*, *striata*, and *gilva* in *Mirabilis*; purple, patched, and red in *Lathyrus*. In *Lathyrus* the patched gametes are more numerous than the purple, and much more numerous than the red gametes: in *Mirabilis* the *striata* gametes are much more numerous than the *rosea* gametes, and very much more numerous than the *gilva* gametes. The most noticeable difference between the two cases would appear to be the higher proportion of "flaked" gametes, as opposed to the "pure" ones, that is produced by the flaked *Mirabilis*[1]. But in either case the flaked plant produces also two kinds of "pure" gametes, and the relation between these two is the simple Mendelian relation with which we are so familiar.

Although some stress has been laid upon the points of difference between the *Primula*, *Antirrhinum* and maize cases on the one hand, and those of *Mirabilis* and *Lathyrus* on the other, it is yet possible that they may be all fundamentally of the same nature. For as we pass through the series *Lathyrus*, *Mirabilis*, *Antirrhinum*, maize, *Primula*, translating it, so far as we can, into terms of "pure" and "mosaic" gametes, we cannot but notice the gradual increase in the proportion of "mosaic" gametes, with its accompanying diminution in that of the "pure" ones. Further, those of the "pure" gametes corresponding to the recessive form are not only fewer to begin with, but decrease more rapidly than those corresponding to the dominant form. In a crude way the idea of such a conjectural series is illustrated in Fig. 3. Whether *Primula* properly belongs here must depend upon future work with flaked

[1] The statement that in *Mirabilis* one of the classes of *rosea* throws *striata* as a recessive would at first sight appear to constitute a difference from the *Lathyrus* case. For the purple sweet pea that throws patched, throws also a small proportion of reds. I am inclined to regard the difference as more apparent than real, and to suppose that, if a considerable number of offspring were bred from such *rosea* plants, a very small proportion of *gilva* would appear. At present we have no means of testing the probability of this conjecture since Correns does not give the actual numbers of plants bred in his experiments.

forms. If it is rightly placed in the series we should look for occasional self-coloured forms from self-fertilisation of the "flakes"; also, very rarely, for a white.

But whether *Primula*, *Antirrhinum*, and maize fall into such a series or not, it is clear that in *Lathyrus* and *Mirabilis* we have two cases where, in a given strain, a pair of colour characters may either shew a simple Mendelian relation, or else form a mosaic. The most interesting thing about such a mosaic is the nature of its germ cells. Must we suppose that "mosaic" germ cells are formed besides "pure" ones that give ordinary Mendelian phenomena? Or is it possible that only "pure" gametes are formed, and that the "mosaic" is a special manifestation of the heterozygous condition. On this latter view it is

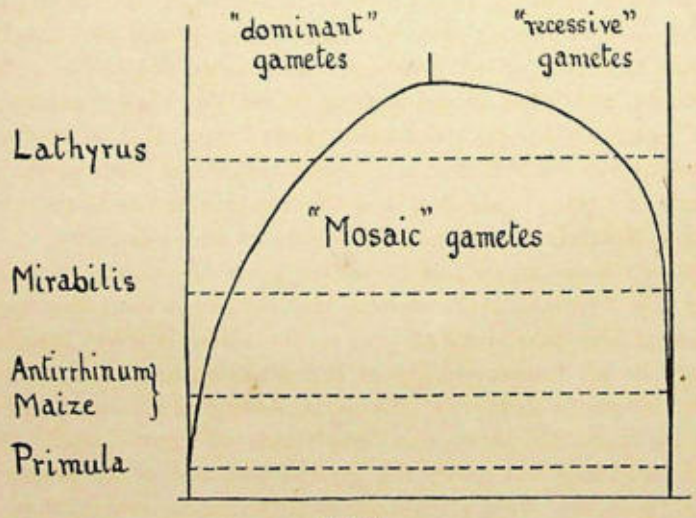


Fig. 3.

clear that the case is one of great complexity. For if we are to interpret it in terms of factors which are located in chromosomes, and segregate at the reduction division, we must explain, not only the difference between the normal and the mosaic heterozygotes, and the fact that either can throw all three kinds, but also the widely variable proportions in which the three kinds appear in different families. Though an interpretation must probably be sought along some such lines if this case is to be reconciled with the widely accepted chromosome theory of heredity, it seems unlikely that this reconciliation will prove to be a simple task.

On the other hand one cannot help being struck by a general similarity between these cases of flaking in flower colour, and certain

cases where the leaf is variegated[1]. Here, as has been pointed out by Baur and others, we must suppose that the hereditary factors, whether in the form of plastids, or of some other cytoplasmic enclosure, are extra-nuclear, and distributed in segregation independently of the reduction division. Indeed, while considering these cases of variegation, Bateson has suggested that even in normal Mendelian heredity, segregation may possibly be regarded as brought about on similar lines, i.e. as "a phenomenon capable of occurring at *any* cell-division, and not merely in gameto-genesis[2]." The nature of the resultant mosaic, whether coarse or fine, regular or irregular, would depend upon the number of cytoplasmic enclosures which go to make up the "factor," upon the way in which the surrounding protoplasmic medium affected their separation during cell-division, and upon various other circumstances. Ordinary Mendelian heredity would on this view be but a special case, due to the regularity and fineness of the heterozygous mosaic. Whether such a view will prove to be more than a suggestion, and whether it could be extended from plants to animals, further work alone can decide.

EXPLANATION OF PLATE XXI.

Fig. 1. Red D. S.
Fig. 2. Violet D. S.
Fig. 3. Blue (Lord Nelson).
Fig. 4. Normal D. W.
Fig. 5. Patched D. W.
Fig. 6. Red D. W., with a few small flecks of purple on wing (i.e. lightly patched).

For the coloured drawings of the flowers from which the Plate was made I am greatly indebted to the skill and kindness of the Hon. Mrs H. Onslow.

[1] For a recent discussion of such cases, see Winge, Ö., "On the Non-Mendelian Inheritance in Variegated Plants." *Comptes Rendus des Travaux du Laboratoire Carlsberg*, Vol. xiv. 1919.

[2] *Mendel's Principles of Heredity*, 3rd Imp. 1913, p. 313.

TABLE I.

	Parent normal					Parent patched					Parent red				
			N.	P.	R.			N.	P.	R.			N.	P.	R.
1912	110	63^{2}	15+	—	—	115*	63^{7}	7	5	12	116*	63^{8}	3	2	19
	111	63^{3}	25+	—	—	117	63^{9}	4	2	6	118	63^{10}	—	—	12
	112	63^{4}	10	—	2	124*	64^{6}	32	4	6	123*	64^{5}	8	18	13
	113	63^{5}	30+	—	—	125*	64^{7}	6	11	8	126*	64^{8}	3	6	12
	114	63^{6}	23+	—	—	127*, 128	64^{9}	15	28	46	129*	64^{10}	8	13	1
	119	63^{11}	40+	—	—	130*	64^{11}	5	13	3					
	120	63^{12}	32	—	12										
	121	64^{2}	30+	—	—										
	122	64^{3}	39+	—	—										
1913	59*	123^{14}	17	4	3	57*	123^{5}	36	25	8	54*	123^{1}	13	32	11
	60	124^{4}	16	—	4	58*	123^{13}	6	22	9	68*	128^{4}	4	9	13
	62	124^{7}	12	—	—	67*	128^{3}	9	15	13	70*	128^{10}	9	13	3
	63*	124^{9}	35	2	7	71*	128^{11}	9	20	6	34*	118	—	10	27
	64*	124^{10}	47	6	7										
	65	124^{11}	17	—	3										
	66	128^{2}	50+	—	—										
	69*	128^{9}	18	4	3										
1914	76	57^{1}	3	—	1	78	57^{3}	1	1	2	84	67^{3}	6	2	5
	86	67^{6}	10	—	2	79*	58^{1}	10	4	6	88	67^{8}	7	6	5
						81	67^{1}	4	—	1	90	67^{10}	1	—	5
						82	67^{2}	2	—	2					
						85	67^{5}	3	2	2					
						87	67^{7}	1	1	6					
						89	67^{9}	7	—	3					
1915						10	79^{1}	7	7	1					
						11	88^{1}	—	3	3					
1916						25	10^{1}	—	4	—					
						26	10^{8}	2	8	1					
						39*	10^{11}	7	21	4					
1917	126	26^{1}	10	2	4	128	26^{3}	11	1	4	127	26^{2}	—	—	6
	129	26^{4}	17	1	—	130	26^{6}	4	(?)	7	139*	39^{18}	32	—	4
	136*	39^{2}	42	3	3	131	26^{7}	2	6	11	140*	39^{21}	9	6	5
	137	39^{3}	29	—	—	132	26^{8}	2	3	—	142*	39^{26}	1	5	41
	138	39^{10}	61	—	—	133	26^{9}	4	3	3					
	141*	39^{23}	43	3	4	134*	26^{10}	10	10	9					
	143	39^{31}	6	—	1	135*	26^{11}	20	20	6					
1918	35	54^{1}	20	—	4	39*, 40	66^{2}	13	38	7	46*	72^{1}	2	—	119
	36	54^{2}	21	—	6	41, 42	96^{2}	—	—	30	50*	81^{1}	3	1	46
	37	54^{4}	37	—	11	43, 44	97^{1}	1	6	7	51*	81^{2}	6	—	55
	38	55^{2}	15	—	7	49*	92^{5}	24	38	2					
	45	70^{2}	19	—	6										
	47*	72^{3}	40	12	6										
	48	74^{2}	66	—	26										
	52	78^{2}	19	—	3										
	53	79^{3}	66	—	22										
	54	79^{5}	40	—	10										

(*continued over page*)

* Families used in compilation of Fig. 2.

TABLE I—*continued.*

	Parent normal					Parent patched					Parent red				
			N.	P.	R.			N.	P.	R.			N.	P.	R
1919	88*	63^{2}	16	2	2	83	39^{6}	9	1	4	92	65^{4}	—	—	27
	89	63^{5}	8	—	—	84	39^{17}	3	1	1	95*	66^{4}	3	5	96
	90	63^{6}	84	—	—	85	39^{19}	1	1	—	100*	82^{6}	5	27	17
	91	64^{1}	7	1	—	96	67^{2}	—	1	1	102	89^{3}	—	—	5
	93*	65^{5}	25	5	2						103	90^{3}	—	—	4
	94*	66^{3}	27	2	2										
	97	68^{2}	6	1	1										
	98*	76^{3}	47	10	2										
	99*	82^{1}	57	8	—										
	101*	82^{8}	25	13	—										
	104	91^{1}	13	5	—										
	106*	94^{1}	59	9	—										
	107	94^{3}	24	—	—										
	108	94^{4}	11	2	1										
	109	94^{5}	20	—	—										
	110	94^{7}	6	—	—										
	111*	98^{4}	5	15	2										
	112*	98^{1}	25	3	2										
	113*	98^{6}	30	3	2										
	114	99^{1}	8	4	—										
	115*	99^{4}	25	3	—										
1920						40*	106^{1}	31	32	2					
						41*	111^{5}	32	45	11					
						86*	111^{1}	5	22	8					
1921	101*	$40^{2}(a)$	47	1	6	55–65*	29^{7}	4	18	18					
	102*	,, (*b*)	30	1	8										
	103*	$40^{5}(a)$	12	2	1										
	104*	,, (*b*)	12	—	2										
	105*	$40^{9}(a)$	48	3	6										
	106*	,, (*b*)	47	—	7										
	107*	,, (*c*)	57	—	4										
	108*	,, (*d*)	26	1	2										
	109*	,, (*c*)	14	1	—										

* Families used in compilation of Fig. 2.

TABLE II.

1917 No.	Cross (1916 plants)	Nature of Cross	Result: Normal	Result: Patched	Result: Red
63	$26^{6} \times 26^{1}$	$P \times N$	5	1	—
65	,,	$P(p)^{*} \times N$	2	2	1
66	,,	$P(p) \times N$	2	2	1
67	,,	$P(r) \times N$	—	3	—
69	$26^{10} \times 26^{1}$	$P \times N$	1	—	—
75	$26^{3} \times 26^{1}$	,,	1	—	—
80	$26^{7} \times 26^{1}$	,,	7	3	—
82	$26^{7} \times 26^{4}$	,,	5	1	2
84	$26^{9} \times 26^{1}$	,,	1	—	—
85	,,	,,	2	1	—
86	,,	,,	1	—	—
87	$26^{10} \times 26^{1}$	,,	1	1	—
91	,,	,,	3	1	—
92	,,	,,	2	3	—
93	,,	,,	2	1	1
94	$26^{11} \times 26^{4}$	$P(r) \times N$	7	—	—
95	$26^{11} \times 26^{1}$	$P \times N$	2	1	—
98	,,	$P(p) \times N$	6	2	—
99	,,	$P(r) \times N$	4	—	—
64	$26^{1} \times 26^{6}$	$N \times P(r)$	1	3	—
68	$26^{4} \times 26^{6}$	$N \times P(p)$	2	1	—
76	$26^{4} \times 26^{7}$	$N \times P$	5	1	—
77	,,	,,	3	1	—
54	$26^{1} \times 26^{2}$	$N \times R$	5	—	—
55	,,	,,	1	1	2
70	,,	,,	2	—	1
71	,,	,,	3	1	2
78	$26^{4} \times 26^{2}$	,,	3	—	2
79	,,	,,	6	—	—
72	$26^{2} \times 26^{1}$	$R \times N$	2	—	1
74	,,	,,	3	—	—
81	$26^{7} \times 26^{2}$	$P \times R$	3	—	4
89	,,	$P(r) \times R$	—	—	3
90	,,	,,	—	—	3
96	$26^{11} \times 26^{2}$	$P(p) \times R$	—	2	1
97	,,	,,	—	1	—

* (*p*) denotes a normal purple flower, and (*r*) a red flower on a patched plant. In other cases the flower used was a patched one.

TABLE III.

Nature of Cross	Parents	No. of F_1 plants	F_2 Results: Normal	Red. Pur.	Patched	Remarks
Lord Nelson × Red Duke ...	$18^7/12 \times 118^2/12$	4	248	74	—	—
Red Duke × D. W. Cupid ...	$26^2/16 \times 24^1/16$	3	57	27	—	—
Red Duke × M. H. hood ...	$26^2/16 \times 22^5/16$	5	60	15	1	+18 reds
Red Duke × Ppw. rd.	$41^4/16 \times 50^1/16$ $41^5/16 \times 50^2/16$	3	21	9	—	—
Red Duke × E. H. rd. ...	$41^2/16 \times 43^1/16$ $41^4/16 \times 43^1/16$	3	74	18	12	+reds and whites
Red Duke × Robert Sydenham	$63^5/16 \times$ R. S.	7	111	41	—	—
Red Duke × Helen Pierce ...	$120^1/17 \times 100^1/17$ $120^5/17 \times 100^1/17$ $120^6/17 \times 100^1/17$	7	433	134	1	—
Helen Pierce × Red Duke (Cupid) ...	$29^1/18 \times 78^1/18$	1	86	16	—	$78^1/18$ was F_2 plant ex Red D. × D. W. cupid. (See above.)
R. White × Helen Pierce (ex Red Duke) ...	$27^3/18 \times 29^5/18$	1	22	5	1	$27^3/18$ was F_2 plant ex Red D. × E. H. rd. (See above.)
		34	1112	339	15	
119/13* +5 offspring	—	6	457	163	—	
	Totals ...	40	1569	502	15	
	Expectation ...		*1564·5*	*521·5*		

* An F_2 family which doubtless arose from the union of a normal purple cretin gamete with a Red P. I. gamete through insect agency in 1911.

TABLE IV.

Normals giving normals and reds only.

		N.	R.
1912	112	10	2
	120	32	12
1913	60	16	4
	65	17	3
1914	76	3	1
	86	10	2
1917	143	6	1
1918	35	20	4
	36	21	6
	37	37	11
	38	15	7
	45	19	6
	48	66	26
	52	19	3
	53	66	22
	54	40	10
Totals ...		397	120
Expectation		*388*	*129*

TABLE V.

Families produced by normals arising in mixed families.

		N.	P.	R.
1913	59	17	4	3
	60	16	—	4
	62	12	—	—
	63	35	2	7
	64	47	6	7
	65	17	—	3
	66	50+	—	—
	69	18	4	3
1914	76	3	—	1
	86	10	—	2
1917	126	10	2	4
	129	17	1	—
	136	42	3	3
	137	29	—	—
	138	61	—	—
	141	43	3	4
	143	6	—	1
1921	101+	77	2	14
	103+	24	2	3
	105+	192	5	19

Hence out of 20 normals arising in mixed families 4 produced only normals. (Numbers however too small for certainty in 62/13.) Therefore patched plants must produce a fair proportion of normal gametes.

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