

The Loss of the Eye-pigment in *Gammarus chevreuxi*. A Mendelian Study.

By

E. J. Allen, D.Sc., F.R.S.,

Director of the Plymouth Laboratory,

AND

E. W. Sexton, F.L.S.

With Plates I to VII at the end.

CONTENTS,

	PAGE
SECTION I. ALBINO IMPERFECT EYE	274
Cross A. Albino Female AC × Red Male R.2. Plate I	275
Cross B. Albino Female AC × Black Male K. A.	278
Constitution of Blacks II, III, IV and V	278
" Reds II, III, IV and V	284
" F ₂ Albinos	286
SECTION II. ALL-WHITE PERFECT EYE	287
Cross C. Albino Female AB × White Male R.1.	287
Hypotheses I and II	288
Constitution of Blacks VI, Cross C	291
Cross-matings " " "	303
Constitution of Reds " " "	307
" Albinos " " "	317
Experiments with the Original Stock	324
The Part-White Eye	325
SECTION III. NO-WHITE EYE. VII	326
SECTION IV. COLOURLESS EYE	330
Cross between Coloured No-white and Albino	330
Independent Origin of Coloured No-white and Albino No-white or Colourless eyes	336
Constitution of the Colourless eye	338
SECTION V. ONE-SIDED NO-WHITES	339
SUMMARY	341
GENERAL CONSIDERATIONS	348
EXPLANATION OF PLATES	350

In a paper by Sexton and Wing (Journ. M.B.A., Vol. XI, No. 1, pp. 18-50) a mutation occurring in the Amphipod *Gammarus chevreuxi* Sexton, was described and figured (Pl. I, Fig. 3) in which the usual black

pigment of the eye was replaced by a bright red pigment.* It was shown that these red eyes behaved as a pure recessive in accordance with Mendel's law, the hybrid between red-eyed and pure black-eyed animals being black. Certain other mutations which had just occurred were also described and figured in that paper, and it is to a study of these and of others that have since appeared that the present paper is due.

Our thanks are due to Miss A. R. Clark, who has given valuable help in the care of the broods and in the examination of the young animals for eye-colour.

The system employed for designating the different broods and the individual animals in each brood is as follows: The two original Albino females from which the experiments started are called AB and AC. The five broods obtained from AC are numbered I to V, the one brood from AB is numbered VI. Each animal which came to maturity in each of these broods is designated by a capital letter, A, B, C, etc. Each brood derived from one of these females is numbered by an arabic numeral, and each animal in the brood is denoted by a small letter, a, b, c, etc. Thus I.E.3.a. means the first individual (a) in the third brood (3), of female E from brood I of the original female AC. (See Plate I.)

In the plates the colour developed in the eye of each animal is shown by the large circles, and the constitution of the animal in regard to the factors for eye-colour, when known, by the character and position of the small circles. The V-shaped mark indicates that the presence or absence of the factor usually represented in the position where the mark stands has not been proved.

In the text the colours are represented by capital letters. A means albino, B black, R red and N no-white. The first letter in a formula in black type gives the visible colour of the eye, the remaining letters the constitutional factors which are carried. Thus **B**+R+A means a black-eyed animal, carrying the factors for red and albino, **B**+N means a black-eyed animal carrying the factor for no-white. **BN** and **RN** mean black and red no-white respectively.

SECTION I. THE ALBINO † IMPERFECT EYE.

The shape of the normal eye of *Gammarus chevreuxi* is reniform, with the margin entire. (Plate VII. Fig. 2.) The eye is raised above the surface of the cephalon, and much rounded, and is composed of numerous

* It may be mentioned here that no second case of a red-eyed *Gammarus* arising independently has occurred up to the present time (September, 1917), all the red-eyed animals used in the experiments being descendants of the original stock.

† The term "Albino" is here used to designate those animals in which the eye possesses no coloured retinal pigment, but in which the chalk-white extra-retinal pigment is present. For eyes in which the coloured retinal pigment and the chalk-white extra-retinal pigment are both absent we employ the term "colourless."

ommatidia arranged in regular rows, each ommatidium being surrounded by pigmented reticular cells, the pigment being black in the normal eye, red in the mutation. On the surface and around the upper portion of the ommatidia, a chalky white extra-retinal pigment is found, the "accessory pigment," which gives the reticulated appearance to the ommateum. In the albino eye only this extra-retinal pigment is developed. (Plate VII. Fig. 4.) The ommateum is much altered, is reduced considerably in size, and is very variable in shape, even the eyes of the same animal often differing widely in form, and in the size, shape, number and arrangement of the ommatidia. The surface of the eye is flat, not convex as in the type, with a few ommatidia sparsely scattered, generally around the margin, and with some occasionally lying beyond it. Especially portions of the extra-retinal chalk-white pigment tend to become detached, causing white spots to appear in more or less definite positions on the head. A more detailed study of these spots is still in progress.

The Albino eye appeared in the F_2 generation from a mating of Pure Black with Pure Red. The young (F_1) of this mating all had normal black eyes. The 15 which survived to maturity were kept together in one bowl to breed, each female when ovigerous being removed to a separate bowl until her young were hatched, and then returned to the brood-bowl to mate again. The forty-second brood (F_2) obtained from this family consisted of 7 Black-eyed young, 1 Red-eyed and 4 with neither black nor red pigment, the Albino eye just described. The total number of young recorded from all the broods was 745, of which 559 were black-eyed, 182 red-eyed and 4 albino-eyed. The four albinos reached maturity, one male and three females, but only two females survived to produce offspring, the AB and AC (Plate II) of the following experiments.

All the albino-eyed animals used in the experiments are descendants of these, and there has been no other case observed of an independent origin of this mutation. The stock from which these two females came was kept for a further period of eighteen months, and no more albino eyes occurred in it.

Cross A.

CROSS BETWEEN THE ALBINO FEMALE AC AND A PURE
RED MALE R.2. (Plate I.)

One of these females (AC) was mated with a male from Pure Red stock (R.2), the resulting offspring being 3 black and 6 red-eyed young. This at once suggests that colour is dominant to absence of colour, and that the albino eye, in which only white accessory pigment appeared, contained the factors for both black and red retinal pigment.

Following Bateson and Punnett we may assume a colour factor C, which with its absence c forms an allelomorph pair. In the absence of C the factors for black and red in the retinal pigment do not produce any visible effect. The constitution of the pure red male would then be $\begin{matrix} C R \\ C R \end{matrix}$ and of the albino female $\begin{matrix} c B \\ c R \end{matrix}$ where B and R are the factors for black and red respectively.

The mating of these should give in F_1 :—

C c B R, a black carrying the factor for "red" and also the factor for "albino";*

C c R R, a pure red carrying the factor for "albino."

F.1. Generation. Black × Black.

The three black-eyed young of this F_1 generation were 2 females and 1 male (Pl. I : I.A.B.C.). The male was mated with the females in turn and three broods were obtained from each. The total number of young was 119, of which 61 were black-eyed, 28 red-eyed, and 30 albino-eyed.

Theoretically the cross

$$C c B R \times C c B R$$

gives gametes CB

CR

cB

cR

which with chance meetings would give zygotes :—

CB	CB	CB	CB
CB	CR	cB	cR
CR	CR	CR	CR
CB	CR	cB	cR
cB	cB	cB	cB
CB	CR	cB	cR
cR	cR	cR	cR
CB	CR	cB	cR

That is out of every 16 young there are 9 Black-eyed, viz. :—

1 with constitution C C B B

2 " " C c B B

2 " " C c B R

4 " " C c B R

* We shall for convenience refer to the factor c, which on the hypothesis represents the absence of the colour factor C, as the "albino factor."

3 Red-eyed, viz. :—

1	with constitution	C C R R
2	„ „	C c R R

4 Albinos, viz. :—

1	with constitution	c c B B
1	„ „	c c R R
2	„ „	c c B R

For 119 specimens the numbers should be according to theory
67 black, 22 red, 30 albino,
whilst those found by experiment were 61 black, 28 red, 30 albino,
a sufficiently close agreement.

F.1. Generation. Red × Red.

The six red-eyed young of the F_1 generation were 4 females and 2 males (Plate I : I.D.E.F.G.H.J.). The males were mated with the females and 875 young were obtained, including a brood of 17 not examined within 48 hours of extrusion.*

According to theory the parents all had the constitution CcRR, and these mated together should give :—

3 Red-eyed, viz. :—

1	with constitution	C C R R
2	„ „	C c R R

1 Albino „ „ c c R R

Experiment gave 658 red-eyed and 217 albino,† theory requires 656 red-eyed and 219 albino.

F.1. Generation. Black × Red.

A cross between a red-eyed female and black-eyed male of the F_1 generation (Pl. I : I.B. and D.) gave in three broods 9 black-eyed, 15 red-eyed and 8 albino. Theory requires the proportions 3 black, 3 red, 2 albino, which for 32 young would be 12 black, 12 red, 8 albino.

* Unless the young are examined and removed soon after they are extruded a certain number are lost through being eaten by the parents and the more delicate ones tend to disappear first. The albinos seem to be more delicate than the reds, and the reds than the blacks, so that unless the broods are counted within a short time the proportions of the different coloured eyes are liable to error. THE FIGURES GIVEN IN THE PRESENT PAPER INCLUDE ONLY SUCH BROODS AS WERE COUNTED WITHIN FORTY-EIGHT HOURS OF THE TIME OF EXTRUSION, UNLESS THE CONTRARY IS DEFINITELY STATED.

† Of these 589 red-eyed and 191 albinos came from the mating of one pair. (I.F. × I.E. Plate I, see p. 336).

Cross B.

CROSS BETWEEN THE ALBINO FEMALE AC. AND BLACK HYBRID MALE K.A.
(i.e. a black carrying red). (Plates I and II.)

The albino female that was used in Cross A was also crossed with a black hybrid male, the son of a pure black father by a pure red mother. The result was 7 black and 2 red offspring in the first brood.

If the constitution of the albino female is $\begin{smallmatrix} c & B \\ c & R \end{smallmatrix}$ and of the hybrid black male $\begin{smallmatrix} C & B \\ C & R \end{smallmatrix}$, the result of the cross should be 3 blacks (one pure and two hybrid) and 1 red, all of them carrying the factor for albino.

Three further broods were obtained from this cross, the total numbers for all four broods being 75 black, 15 red, a proportion 5 : 1 instead of 3 : 1, but three of the broods were not counted until some days after extrusion, which probably accounts for the small proportion of reds.

F.1. GENERATION. BLACKS.

Of the 75 black-eyed young, 49 reached sexual maturity, 27 being males and 22 females. Of these it was possible to test 33 from Broods II, III and IV by mating them together or with mates of known constitution, and 21 proved to be hybrids, i.e. carried both the factors B and R, whilst 12 were pure black. All without exception had albinos amongst their immediate offspring, or transmitted the character to their descendants, showing that both parents possessed the factor c. (Plate I : Broods II, III, IV, V.)

The following list gives the constitution of each individual animal and the different matings made to prove that constitution ; these constitutions are shown in detail on Plates I and II.

II.A. Male, *Black carrying Red and Albino* (Plate II).

Matings :—(1) with female D of the same brood (**B**+A) ;
88 young, 65 Black, 23 Albino ;

(2) with female VI.A (**B**+R+A) ; 79 young,
49 Black, 15 Red, 15 Albino ;

(3) with a female (**B**+R) (from a mating Pure
Black with Pure Red) ; 26 young, 18
Black, 8 Red.

II.C. Male, *Black carrying Red and Albino* (Plate II).

Matings :—(1) with female VI.C. (**B**+R+A) ; 115 young,
74 Black, 15 Red, 26 Albino ;

(2) with Red No-white female from No-white
Stock (previously mated with male
VI.A.t.) ; 34 young, 18 Black, 16 Red.

II.D. Female, *Black carrying Albino only* (Plate II).

Matings :—(1) with male A of the same brood (89 young, 66 Black, 23 Albino).*

III.A. Male, *Black carrying Red and Albino* (Plate I).

Mating: (1) with female K of the same brood ($\mathbf{B}+\mathbf{R}+\mathbf{A}$); 61 young, 30 Black, 14 Red, 17 Albino.

III.B. Male, *Black carrying Albino only* (proof obtained by mating the offspring).

Matings :—(1) with female L of the same brood ($\mathbf{B}+\mathbf{A}$); 33 young, 20 Black, 13 Albino.

The first brood of this pair were mated together, and also with Red mates; the resulting young numbered 153, 115 Black and 38 Albino (see Pl. III, Fig. 3, for an example). Black young of the first brood of these were mated together, and gave 19 Black, 3 Albino; mated with Reds they gave 52 young, all Black.

According to these matings both male B and female L are Blacks carrying the Albino factor only.

III.C. Male, *Black carrying Albino only* (probably).

Matings :—(1) with female M of the same brood ($\mathbf{B}+\mathbf{A}$, Red factor not known); 78 young, 57 Black, 21 Albino.

One of this pair is certainly a ($\mathbf{B}+\mathbf{A}$), the constitution of the other is not known.

III.D. Male, *Black carrying Albino only*.

Matings :—(1) with female N of the same brood, ($\mathbf{B}+\mathbf{A}$); 115 young, 78 Black, 37 Albino;

(2) with female VI.B.2.e. ($\mathbf{R}+\mathbf{A}$); (19 young, 11 Black, 8 Albino);

(3) with female IV.X. ($\mathbf{R}+\mathbf{A}$); 429 young, 329 Black, 100 Albino.

III.E. Male, *Black carrying Albino*. Red not proved.

Matings :—(1) with female O of the same brood, ($\mathbf{B}+\mathbf{R}+\mathbf{A}$); 5 young, 4 Black, 1 Albino.

III.F. Male, *Black carrying Albino only* (probably).

Matings :—(1) with female P of the same brood; 69 young, 53 Black, 16 Albino.

One of this pair is certainly a ($\mathbf{B}+\mathbf{A}$), the constitution of the other is not known.

* Figures between brackets are also given under the other member of the pair and must therefore not be included in the totals.

III.G. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female R of the same brood, (**R**+A) ;
2 young, 1 Black, 1 Red ;
(2) with female O of the same brood, (**B**+
R+A) ; 33 young, 22 Black, 2 Red,
9 Albino.

III.H. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female Q of the same brood, (**B**+
R+A) ; 111 young, 66 Black, 26 Red,
19 Albino.

III.J. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female (from wild stock, referred to
on p. 329) Black no-white ; 92 young, all
Black ;
(2) with female 14.b. (of the same stock as
male R.1. on Plate II, see p. 324), Pure
Red ; 14 young, 5 Black, 9 Red.

One black-eyed male from mating (1) was mated with an albino female. The first brood of 6 young consisted of 2 black and 4 albino. Hence III.J. must carry albino.

III.K. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male A of the same brood, (**B**+R+
A) ; (61 young, 30 Black, 14 Red, 17
Albino).

III.L. Female, *Black carrying Albino only*.

- Matings :—(1) with male B, (**B**+A) ; (33 young, 20
Black, 13 Albino).

Proof of male B and this female was obtained by mating broods (see under "Male III.B").

III.M. Female, *Black carrying Albino*. Red not known.

- Matings :—(1) with male C of the same brood (see note
to that animal) ; (78 young, 57 Black,
21 Albino).

III.N. Female, *Black carrying Albino*.

- Matings :—(1) with male D of the same brood, (**B**+A) ;
(115 young, 78 Black, 37 Albino) ;
(2) with male VI.A.3 u, (**R**+A) ; (42 young,
32 Black, 10 Albino).

III.O. Female, *Black carrying Albino*.

- Matings :—(1) with male E of the same brood, (**B**+**A**) ;
 (5 young, 4 Black, 1 Albino) ;
 (2) with male G of the same brood, (**B**+**R**+
A) ; (33 young, 22 Black, 2 Red, 9
 Albino).

III.P. Female, *Black carrying Albino*. Red factor not proved.

- Matings :—(1) with male F of the same brood (**B**+**A**) ;
 (69 young, 53 Black, 16 Albino).

III.Q. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male H of the same brood, (**B**+**R**+
A) ; (111 young, 66 Black, 26 Red, 19
 Albino) ;
 (2) with a male from the same brood, (**B**+
R+**A**) ; 19 young, 10 Black, 6 Red, 3
 Albino.

The one remaining Black-eyed animal, a male, died without mating.

IV.A. Male, *Black carrying Red and Albino* (Plate I).

- Matings :—(1) with female N of the same brood, (**B**+**A**) ;
 6 young, 2 Black, 4 Albino ;
 (2) with female T of the same brood, (**B**+**R**+
A) ; 108 young, 64 Black, 21 Red, 23
 Albino.

IV.B. Male, *Black carrying Albino*. Red not known.

- Matings :—(1) with female O of the same brood, (**B**+**A**) ;
 91 young, 70 Black, 21 Albino.

IV.C. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female P of the same brood, (**B**+**R**+
A) ; 61 young, 38 Black, 9 Red, 14
 Albino.

IV.D. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female Q of the same brood, (**B**+
R+**A**) ; 40 young, 22 Black, 8 Red, 10
 Albino.

IV.E. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female R of the same brood, (**B**+
R+**A**) ; 49 young, 28 Black, 7 Red, 14
 Albino ;
 (2) with female Y of the same brood, (**R**+**A**) ;
 19 young, 10 Black, 5 Red, 4 Albino.

- IV.F. Male, *Black carrying Albino*. Red not known.
 Matings :—(1) with female S of the same brood, (**B**+**A**) ;
 57 young, 40 Black, 17 Albino.
- IV.G. Male, *Black carrying Red and Albino*.
 Matings :—(1) with female T of the same brood, (**B**+
R+**A**) ; 61 young, 33 Black, 15 Red,
 13 Albino.
- IV.H. Male, *Black carrying Albino only*.
 Matings :—(1) with female U of the same brood, (**B**+**A**,
 Red not proved) ; 72 young, 54 Black,
 18 Albino.
- IV.J. Male, *Black carrying Red and Albino*.
 Matings :—(1) with female X of the same brood, (**R**+**A**) ;
 12 young, 3 Black, 4 Red, 5 Albino ;
 (2) with female VI.A.3.q. (**B**+**R**+**A**) ; (33
 young, 19 Black, 7 Red, 7 Albino).
- IV.K. Male, *Black carrying Red and Albino*.
 Matings :—(1) with female V of the same brood, (**B**+**A**) ;
 80 young, 63 Black, 17 Albino ;
 (2) with female VI.B.1.g. (Pure Red) ; (9
 young, 2 Black, 7 Red).
- IV.L. Male, *Black carrying Red (and Albino)*.
 Matings :—(1) with female Y of the same brood, (**R**+**A**) ;
 2 young, 1 Black, 1 Red.
- IV.M. Male, *Black*. Constitution not known.
- IV.N. Female, *Black carrying Albino only*.
 Matings :—(1) with a Black male of the same brood ;
 5 young, all Black.
 (8 young were produced from the
 matings of this brood with Pure Red,
 7 Black, 1 Albino.)
 (2) with male A of the same brood, (**B**+**R**+
A) ; (6 young, 2 Black, 4 Albino).
- IV.O. Female, *Black carrying Albino only*.
 Matings :—(1) with male B of the same brood (**B**+**A**,
 Red not known) ; (91 young, 70 Black,
 21 Albino) ;
 (2) with a Black male of the same brood, (**B**+
R+**A**) ; 32 young, 26 Black, 6 Albino ;
 (3) with male VI.A.1.m, (Pure Red) ; (39
 young, all Black).

IV.P. Female, *Black carrying Red and Albino.*

Matings :—(1) with male C of the same brood, (**B**+**R**+**A**); (61 young, 38 Black, 9 Red, 14 Albino).

IV.Q. Female, *Black carrying Red and Albino.*

Matings :—(1) with male D of the same brood, (**B**+**R**+**A**); (40 young, 22 Black, 8 Red, 10 Albino).

IV.R. Female, *Black carrying Red and Albino.*

Matings :—(1) with male E of the same brood, (**B**+**R**+**A**); (49 young, 28 Black, 7 Red, 14 Albino).

IV.S. Female, *Black carrying Albino only.*

Matings :—(1) with male F of the same brood, (**B**+**A**, Red not known); (57 young, 40 Black, 17 Albino);

(2) with a Black male of the same brood, (**B**+**R**+**A**); 14 young, 11 Black, 3 Albino;

(3) with male VI.B.1.d (**R**+**A**); (18 young, 13 Black, 5 Albino).

IV.T. Female, *Black carrying Red and Albino.*

Matings :—(1) with male G of the same brood, (**B**+**R**+**A**); (61 young, 33 Black, 15 Red, 13 Albino);

(2) with male A of the same brood, (**B**+**R**+**A**); (108 young, 64 Black, 21 Red, 23 Albino).

IV.U. Female, *Black carrying Albino.* Red not proved.

Matings :—(1) with male H of the same brood, (**B**+**A**); (72 young, 54 Black, 18 Albino).

IV.V. Female, *Black carrying Albino only.*

Matings :—(1) with male K of the same brood, (**B**+**R**+**A**); (80 young, 63 Black, 17 Red);

(2) with a Black male of the same brood, either J., K. or M.; 6 young, 3 Black, 3 Albino.

(3) with male VI.A.3.t, (**R**+**A**); (12 young, 10 Black, 2 Albino).

Brood V. This brood was unhealthy, only a few surviving to mate; the Blacks were not tried for the Red factor.

V.A. Male, *Black carrying Albino*. Red not known.

Matings :—(1) with female D of the same brood, (**B**+**A** only, probably); 17 young, 12 Black, 5 Albino.

V.B. Male, *Black carrying Albino*. Red not known.

Matings :—(1) with female E of the same brood, (**B**+**A** only, probably); 8 young, 6 Black, 2 Albino.

V.C. Male, *Black*. Constitution unknown.

V.D. Female, *Black carrying Albino only* (probably).

Matings :—(1) with a male of the same brood; 5 young, 4 Black, 1 Albino;

(2) with male A of the same brood; (17 young, 12 Black, 5 Albino).

V.E. Female, *Black carrying Albino only* (probably).

Matings :—(1) with a Black male of the same brood; 3 young, all Albino;

(2) with male B of the same brood; (8 young, 6 Black, 2 Albino).

V.F. Female, *Black*. Constitution unknown.

V.G. Female, " " "

V.H. Female, " " "

V.J.

F.I. GENERATION. REDS.

Of the 15 Red, 4 males and 6 females reached maturity. (Plate I.) Mated in the same brood they all gave some albino offspring, showing that they contained the factor c.

The following list shows the matings made to prove their constitutions:—

II.B. Male, *Red carrying Albino* (Plate II).

Matings :—(1) with female VI.B; (**R**+**A**); 101 young, 76 Red, 25 Albino;

(2) with female 14.a. from the original stock of all-white male R.1. (see p. 324);

29 young, all Red (one of these was mated with female VI.C.3.s.);

(3) with female 14.b. from same brood as 14.a.; 30 young, all Red (see p. 324);

(4) with female VI.A.2.k.; (**A**+**B**+**R**); (146 young, 33 Black, 44 Red, 69 Albino);

(5) with female VI.A.1.p.; (**R**+**A**); 90 young, 66 Red, 24 Albino (Plate IV, Fig. 12).

III.R. Female, *Red carrying Albino* (Plate I).

- Matings :—(1) with either male E or male F of the same brood, (**B**+**A**); (6 young, 3 Black, 3 Albino);
- (2) with male G of the same brood, (**B**+**R**+**A**); (2 young, 1 Black, 1 Red).

IV.W. Male, *Red carrying Albino* (Plate I).

- Matings :—(1) with female Aa, of the same brood, (**R**+**A**); 72 young, 54 Red, 18 Albino;
- (2) with female Z of the same brood, (**R**+**A**); 154 young, 127 Red, 27 Albino;
- (3) with a female (from Brood 1 of III.C.), (**A**+**B**); 56 young, 29 Black, 27 Albino.

IV.X. Female, *Red carrying Albino*.

- Matings :—(1) with male J of the same brood, (**B**+**R**+**A**); (12 young, 3 Black, 4 Red, 5 Albino);
- (2) with male VI.A.1.e., (**B**+**R**+**A**); (111 young, 42 Black, 42 Red, 27 Albino);
- (3) with male III.D, (**B**+**A**); (429 young, 329 Black, 100 Albino).

IV.Y. Female, *Red carrying Albino*.

- Matings :—(1) with male L of the same brood, (**B**+**R**+**A**); (2 young, 1 Black, 1 Red);
- (2) with male E of the same brood, (**B**+**R**+**A**); (19 young, 10 Black, 5 Red, 4 Albino);
- (3) with a male (Brood 1 of III.B.); (**A**+**B**); (16 young, 12 Black, 4 Albino).

IV.Z. Female, *Red carrying Albino*.

- Matings :—(1) with male W of the same brood, (**R**+**A**); (154 young, 127 Black, 27 Albino);
- (2) with a male (Brood 1 of III.B.), (**A**+**B**); (65 young, 31 Black, 34 Albino) (Plate III, Fig. 3).

IV. Aa. Female, *Red carrying Albino*.

- Matings :—(1) with male W of the same brood, (**R**+**A**); (72 young, 54 Red, 18 Albino).

V.K. Male, *Red*. Constitution not proved.

V.L. Male, *Red carrying Albino*, mated with female M; 8 young, 6 Red, 2 Albino.

V.M. Female, *Red carrying Albino*.

F.2. GENERATION. ALBINOS.

In the F_2 generation the most interesting feature for study is the constitution of the albino offspring: These were mated together successfully in fifteen instances, and without exception gave albino young, the total number of young examined and recorded being 140. (For an example see Plate III, Fig. 1.) One of these young, in addition to having no black or red retinal pigment, also lacked the white accessory pigment and was quite colourless. This specimen is again referred to on p. 339.2. In addition to these separate matings, the albino young of III were put together in a jar to breed, producing 15 young, all Albino. Two others were mated with albinos from VI, and had 138 young, all Albino.

The albinos may carry either (1) pure black, (2) pure red or (3) both black and red. Amongst the F_2 offspring belonging to this section the constitution has been proved in the following cases:—

(1) *Albino carrying pure black.*

One male (II.D.1.k.) mated with a red no-white gave 38 young, all black-eyed.

One male (Brood 1 of III.B.) mated with a red female from the same stock (carrying albino) gave 12 black and 4 albino.

One male (Brood 1 of III.B.) mated in the same way gave 31 black and 34 albino (Plate III, Fig. 3).

One female (Brood 1 of III.C.) mated with a red male (IV.W.) from the same stock (carrying albino) gave 29 black and 27 albino.

(2) *Albino carrying red.*

One female (from a brood of female I.G.) mated with a pure red male of the same brood gave 12 all red young (Plate III, Fig. 4).

Another similar female (from the same brood as above) mated with a male of the same brood (red carrying the factor for albino) gave 7 red and 10 albino young (Plate III, Fig. 5).

(3) *Albino carrying black and red.*

One male (II.D.1.j.) mated with a red no-white gave 42 black and 38 red young (Plate III, Fig. 6).

The original albino female AC was like this.

SECTION II. THE ALL-WHITE PERFECT EYE.

In the former paper (p. 45 and Fig. 8) a second form of white eye, i.e. one of perfect form but with no black or red retinal pigment, and with only the extra-retinal chalk-like white accessory pigment, was described and figured. This occurred in the pure red stock and the details of the origin of the only two individuals of the kind that were seen are given in the paper referred to. Only one individual, a male, survived to produce offspring. The stock has not since produced any more of them.

Cross C.

CROSS BETWEEN ALBINO IMPERFECT-EYED FEMALE AB. AND "ALL-WHITE" PERFECT-EYED MALE R.1. (Plate VII, Figs. 4 and 7; Plate II.)

The male just referred to was mated with an albino imperfect-eyed female (AB) from the degenerate-eyed stock described on p. 275. There resulted 2 black and 3 red-eyed offspring all normal eyed as regards form, and the male died in moulting without mating again (Plate II). The fact that two parents, neither of which showed any coloured pigment, produced all coloured-eyed offspring seemed to make this case specially interesting and some pains have been taken to investigate it thoroughly. Since the male came from pure red stock, and some black-eyed offspring were obtained it seems clear that the black came from the female which must, since both black and red offspring were produced, have contained the red factor also. This female was therefore an albino carrying both black and red, like the sister from the same brood whose offspring we have already studied in **Cross A**.

There seem to be two possible ways of regarding this case, in which two albino parents produced coloured offspring. Following Bateson and Punnett we may endeavour to explain it by supposing that the factor for red has been lost in the perfect-eyed male, whilst a "colour factor," which must be present if colour is to appear, has been retained in the male, but is absent in the female. If we represent the colour factor by C and its absence by c, the constitution of the male would be $\frac{C}{c}$, that of the female $\frac{c}{c} \frac{B}{R}$. On the other hand, it may be that the absence of colour in the male is a somatic and not a germinal character, and is not inherited at all. Breeding experiments carried on to the fourth generation have shown that this second supposition is the true one, and that the "all-white" male from the pure red stock behaves, as regards its offspring, exactly as if it were a pure red.

Of the offspring of the cross between the "all-white" perfect-eyed male and the albino imperfect-eyed female, three only survived until they were mature, 2 black-eyed and 1 red-eyed, all being females. Of the F_1 offspring of the cross between the imperfect albino and the hybrid black already dealt with (**Cross B**) there were four survivors of the first brood (II), one black female, one red and two black males, as already described. At this stage of the investigation it was important to increase as quickly and with as little risk as possible the stock of albino-eyed animals. This could be most easily done by crossing the two broods, which soon gave us large numbers of albino-eyed offspring. This crossing of the two broods has somewhat complicated the analysis necessary for the determination of the germinal constitution of the perfect-eyed "all-white" male, but the result nevertheless appears to be definite and not without interest.

The following matings were made, the offspring of **Cross C** being designated VI, those of **Cross B** being II (Plate II) :—

(1) VI.A. (Black female) \times II.A. (Black male). The offspring were black, red and albino, hence both male and female were hybrids, carrying factors for black, red and albino.

(2) VI.C. (Black female) \times II.C. (Black male). Again the offspring were black, red and albino, and both male and female therefore hybrids.

(3) VI.B. (Red female) \times II.B. (Red male). Offspring red and albino.

(1) and (2) being quite similar crosses their offspring may be added together. In three broods from each, examined immediately the young were extruded, there were 91 black, 26 red and 37 albino, a total of 154 young.

In the cross of the two reds (3), out of 101 young there were 76 red and 25 albino.

We must now proceed to consider the analysis of these matings according to the two hypotheses for the constitution of the perfect-eyed "all-white" male already mentioned, in order to determine which, if either, of the two hypotheses is correct.

Taking first the cross between the two blacks, we have :—

HYPOTHESIS I. On the first hypothesis the constitution of the all-white perfect-eyed male will be $\begin{matrix} C \\ C \end{matrix}$, that of the albino female carrying black and red $\begin{matrix} c B \\ c R \end{matrix}$. The gametes for the male will therefore be C only, for the female c B and c R. The F_1 zygotes resulting from the mating of these two will be C c B and C c R, giving black and red-eyed animals in equal numbers.

The constitution of the albino imperfect-eyed female is $\begin{smallmatrix} c & B \\ c & R \end{smallmatrix}$ as already seen on p. 276, that of the hybrid black male with which it was mated is $\begin{smallmatrix} C & B \\ C & R \end{smallmatrix}$. The gametes are therefore for the male $C B$ and $C R$, for the female $c B$ and $c R$. The F_1 zygotes resulting from the mating of these two will be one $C c B B$, a black carrying albino, two $C c B R$, blacks carrying red and albino, and one $C c R R$, a red carrying albino.

If we now cross an F_1 black from the first of the above matings with an F_1 hybrid black from the second, we have:—

VI.A. ♀ × ♂ II.A.

$CcB \times CcBR$

Female gametes:— $C B$, C , $c B$, c
 Male „ $C B$, $C R$, $c B$, $c R$
 F_2 Zygotes

$C B$	C	$c B$	c
$C B$	$C B$	$C B$	$C B$
$C B$	C	$c B$	c
$C R$	$C R$	$C R$	$C R$
$C B$	C	$c B$	c
$c B$	$c B$	$c B$	$c B$
$C B$	c	$c B$	c
$c R$	$c R$	$c R$	$c R$

That is 9 black, 3 red and 4 albino.

HYPOTHESIS II. On the second hypothesis the all-white perfect-eyed male is constitutionally a pure red, but the non-appearance of the red is a pathological condition which is not inheritable. Its constitution may then be represented as $\begin{smallmatrix} C & R \\ C & R \end{smallmatrix}$, and if it is mated with the albino female carrying black and red we shall have:—

$C R$ $c B$
 $C R \times c R$

The gametes for the male will therefore be $C R$ only, for the female $c B$ and $c R$.

The F_1 zygotes resulting from the mating of these two will be $C c B R$ and $C c R R$, giving black and red-eyed animals in equal numbers.

If one of these F_1 black-eyed animals (VI) is mated with a black from brood II, carrying red, we shall have:—

VI.A. ♀ × ♂ II.A.

$CcBR \times CcBR$

Female Gametes C B, C R, c B, c R

Male " the same as the female.

F₂Zygotes

C B	C B	C B	C B
C B	C R	c B	c R
C R	C R	C R	C R
C B	C R	c B	c R
c B	c B	c B	c B
C B	C R	c B	c R
c R	c R	c R	c R
C B	C R	c B	c R

That is 9 Black, 3 red and 4 albinos.

It will be seen therefore that according to either theory the visible result should be exactly the same in the F₂ generation, viz. :—

9 *Black*, 3 *Red*, 4 *Albino*. The experimental result was

91 black, 26 red, 37 albino and theory requires

87 " 29 " 38 " which is a good agreement.

The germinal constitution will however be different according to which hypothesis is true. We will consider the different colour classes separately.

Under *Hypothesis I* there would be six different kinds of black-eyed animals, which in every sixteen animals would occur on the average as follows :—

one normal pure black, without the albino factor ; (C C B B) ;

two " " " with " " " (C c B B) ;

one pure black, with one dose of black only instead of two, and without the albino factor ; (C C B) ;

two " " with one dose of black and with the albino factor ; (C c B) ;

one black carrying red, without the albino factor ; (C C B R) ;

two " " " with " " " (C c B R).

Under *Hypothesis II* there would be only four different kinds of black-eyed animals, viz. :—

one normal pure black, without the albino factor ; (C C B B) ;

two " " " with " " " (C c B B) ;

two black carrying red, without " " " (C C B R) ;

four " " " with " " " (C c B R).

The difference between the results given by the two hypotheses is that under II there are no blacks with one dose of black only, their place being taken by additional hybrid blacks.

One means of testing the hypotheses, therefore, will be to find out

by further breeding experiments whether or not the F_2 offspring contain blacks with one dose of black. If a one-dose black be mated with another one-dose black the offspring will be all black, if mated with a two-dose black they will be all black, but if mated with a hybrid black (black carrying red) the offspring will contain some red, as we have seen in considering the cross VI.A. \times II.A.

If we mate together the blacks of the F_2 generation we obtain in F_3 some broods which contain red-eyed animals, others which contain only blacks. The parents of the broods containing red eyes will either be two hybrids, or a hybrid and a one-dose black, if the latter exists. If we cross-mate the parents of a number of such broods, in as many different ways as possible, we ought eventually to bring two one-dose blacks together, in which case we should get all black offspring.

A second test will be as follows. If a one-dose black be mated with a red it will, according to theory, give blacks and reds in equal numbers, behaving in exactly the same way as a hybrid black. If therefore we take blacks which give red offspring when mated with red, and mate them together, we ought, if the one-dose black exists, to obtain some broods which give all black as the result of two one-dose blacks coming together.

By mating together blacks tested with reds in this way, and blacks tested with other blacks and giving red in their broods, we have a further opportunity of bringing together two one-dose blacks (if they exist).

These tests have been applied, but we have not been able to find any one-dose blacks, all those tried proving ordinary hybrid blacks, giving both red and black offspring. (See list of cross-matings, p. 303.)

CROSS C. F.2. GENERATION. BLACKS.

The following lists show (1) the constitutions of all the blacks of these broods which have been tested (see Plate II, VI.A and VI.C); and (2) the results of the cross-matings made with blacks which had given some red offspring when mated with either red or black mates:—

(1) The Black-eyed young, showing their constitution and the matings by which they were proved.

VI.A.1.a. Male, *Black carrying the factor for Red only* (Plate IV, Figs. 2, 4 and 5).

- Matings:—(1) with female from Pure Red Stock; 8 young, 5 Black, 3 Red;
- (2) with female I of its own brood, (**B**+**R**+**A**); 61 young, 49 Black, 12 Red;
- (3) with female of VI.C.1.d. (**B**+**R**+**A**); 42 young, 30 Black, 12 Red.

VI.A.1.b. Male, *Black carrying Red only.*

- Matings :—(1) with female from Pure Red Stock ; 15 young, 5 Black, 10 Red ;
 (2) with female g of its own brood (**B+R+A**) ; 27 young, 23 Black, 4 Red ;
 (3) with female f of its own brood, (**B+R+A**) ; 25 young, 17 Black, 8 Red.

VI.A.1.c. Male, *Pure Black* (Plate IV, Figs. 7 and 8).

- Matings :—(1) with female from Pure Red Stock, 16 young, all Black ;
 (2) with female q of its own brood, (**R+A**) ; 45 young, all Black.

VI.A.1.d. Male, *Black carrying Red and Albino.*

- Matings :—(1) with female from Pure Red Stock ; 10 young, 3 Black, 7 Red.
 (2) (3) (4) (5) with four other females, which it ate ;
 (6) with female VI.B.2.u. (**A+R**) ; 24 young, 1 Black, 3 Red, 20 Albino * ;
 (7) with female VI.A.3.q. (**B+R+A**) ; 16 young, 10 Black, 2 Red, 4 Albino.

VI.A.1.e. Male, *Black carrying Red and Albino.*

- Matings :—(1) with female from Pure Red Stock ; 18 young, 11 Black, 7 Red ;
 (2) with female VI.C.1.h. (**B+R**) ; 88 young, 60 Black, 28 Red ;
 (3) with female IV.X. (**R+A**) ; 111 young, 42 Black, 42 Red, 27 Albino.

VI.A.1.f. Female, *Black carrying Red and Albino.*

- Matings :—(1) with male from Pure Red Stock ; 12 young, 4 Black, 8 Red ;
 (2) with male VI.C.1.m. (**R+A**) ; 71 young, 31 Black, 18 Red, 22 Albino ;
 (3) with male b of its own brood ; (25 young, 17 Black, 8 Red) ;
 (4) with male VI.A.3.c. (**B+R+A**) ; 5 young, 2 Black, 1 Red, 2 Albino.

* Compare footnote p. 344. The exceptional numbers were specially noted at the time the brood was extruded, and there is no doubt as to the accuracy of the record.

VI.A.1.g. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male from Pure Red Stock ; 10 young,
5 Black, 5 Red ;
(2) with male b, of its own brood ; (27 young,
23 Black, 4 Red) ;
(3) with male VI.C.1.m. (**R**+A) ; 22 young, 10
Black, 8 Red, 4 Albino.

VI.A.1.h. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male from Pure Red Stock ; 7 young,
3 Black, 4 Red ;
(2) with male o of its own brood, Pure Red ;
31 young, 17 Black, 14 Red.

That the female carried the factor for Albino was proved by mating the young of the first brood, when Black, Red, and Albino eyes appeared in the offspring (207 young, 89 Black, 106 Red, 12 Albino). One Red male was also mated with female VI.C.3.e. and one Red male with female VI.B.1.f. and a Black female with male VI.B.2.t.

VI.A.1.j. Female, *Black carrying Red, albinism not known*.

- Mating :—(1) with male from Pure Red Stock ; 19 young,
7 Black, 12 Red ;

VI.A.1.k. Female, *Black carrying Red only*.

- Mating :—(1) with male from Pure Red Stock ; 17 young,
8 Black, 9 Red.

Of the young of this brood 11 survived to maturity ; from their matings in the bowl 77 young have been obtained, 38 Black, 39 Red, but no albino-eyed young have appeared.

VI.A.1.l. Female, *Black carrying Red and Albino* (Plate IV, Figs. 1, 2 and 3).

- Matings :—(1) with male from Pure Red Stock ; 73
young, 39 Black, 34 Red ;
(2) with male a of its own brood ; (61 young,
49 Black, 12 Red) ;
(3) with male VI.C.1.o. (**R**+A) ; 82 young, 37
Black, 24 Red, 21 Albino (and 21 others
not examined).

Three other black-eyed young were hatched, two died, immature, and the third, a female, which reached maturity was eaten by its mate.

VI.A.2.a. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female k of its own brood, (**A+B+R**);
7 young, 2 Black, 1 Red, 4 Albino ;
(2) with female VI.B.3.e. (Pure Red) ; 20
young, 8 Black, 12 Red.

VI.A.2.b. Male, *Black, factors carried not known*.

- Mating :—(1) with Red female VI.B.3.g. ; 5 young, all Black.
Both male and female died before mating again ; constitution
therefore of both unknown.

VI.A.2.c. Female, *Black carrying Red only*.

- Matings :—(1) with male VI.A.3.h. (**B+A**) ; 46 young,
all Black ;
(2) with male VI.B.2.d. (**R+A**) ; 27 young,
16 Black, 11 Red ;
(3) with male VI.A.3.d. (**B+R**) ; 43 young,
29 Black, 14 Red.

VI.A.2.d. Female, *Black carrying Albino*.

- Mating :—(1) with male VI.A.3.aa. (**A+R**) ; 18 young,
8 Black, 10 Albino.

VI.A.2.e. Female, *Black carrying Albino*.

- Mating :—(1) with male VI.A.3.aa. (**A+R**) ; 29 young ;
13 Black, 16 Albino.

VI.A.2.f. Female, *Black carrying Albino*.

- Mating :—(1) with male VI.A.3.aa. (**A+R**) ; 30 young,
12 Black, 18 Albino.

11 others ; 9 died immature ; one male and one female which
reached maturity, died without mating.

VI.A.3.a. Male, *Black, Red not known. No Albino*.

- Matings :—(1) with female k of the same brood (**B+A**) ;
18 young, all Black.

(Chance matings amongst these 18
black young gave 29 young, all black.)

- (2) with female VI.A.1.l. Eggs laid, but
female died before they were hatched.

VI.A.3.b. Male, *Black carrying Albino*.

- Matings :—(1) with female l of the same brood (**B+A, R**
not proved) ; 4 young, all Black ;
(2) with female bb. of the same brood (**A+B+R**) ; 14 young, 2 Black, 12 Albino ;
(3) with female I.D.2.d. (**A+B+R**)* ; 7 young,
3 Black, 4 Albino.

* This constitution was proved after Plate I was printed.

VI.A.3.c. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female m of the same brood, (**B**+**R**+**A**) ; 28 young, 18 Black, 6 Red, 4 Albino ;
 (2) with female VI.A.1.f. (**B**+**R**+**A**) ; (5 young, 2 Black, 1 Red, 2 Albino) ;
 (3) with female VI.C.1.d. (**B**+**R**+**A**) ; 71 young, 36 Black, 15 Red, 20 Albino ;
 (4) with female VI.C.3.d. (**B**+**R**) ; 11 young, 9 Black, 2 Red.

VI.A.3.d. Male, *Black carrying Red only*.

- Matings :—(1) with female n of the same brood (**B**+**R**+**A**) ; 46 young, 41 Black, 5 Red ;
 (2) with female VI.C.1.d. (**B**+**R**+**A**) ; 115 young, 91 Black, 24 Red ;
 (3) with female VI.A.2.c. (**B**+**R**) ; (43 young, 29 Black, 14 Red) ;
 (4) with female VI.C.3.e. (**B**+**R**+**A**) ; 56 young, 46 Black, 10 Red.

VI.A.3.e. Male, *Pure Black*.

- Matings :—(1) with female o of same brood, (**B**+**A**, **R** not proved) ; 9 young, all Black ;
 (2), (3), (4), (5) with 4 other females, which it ate ;
 (6) with female VI.B.2.v. (**A**+**R**) ; 19 young, all Black.

VI.A.3.f. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female p of its own brood, (**B**+**R**+**A**) ; 13 young, 6 Black, 2 Red, 5 Albino.

VI.A.3.g. Male, *Black carrying Albino*.

- Matings :—(1) with female q of its own brood, (**B**+**R**+**A**) ; 55 young, 35 Black, 20 Albino ;
 (2) with female III Q. (**B**+**R**+**A**) ; 37 young, 27 Black, 10 Albino.

VI.A.3.h. Male, *Black carrying Albino*.

- Matings :—(1) with female VI.A.2.c. (**B**+**R**) ; (46 young, all Black) ;
 (2) with female VI.B.2.v. (**A**+**R**) ; 92 young, 52 Black, 40 Albino.

VI.A.3.j. Male, *Black*. Constitution not known.

- Matings :—(1) with female s of the same brood ; 1 young Black.

VI.A.3.k. Female, *Black carrying Albino*.

- Matings :—(1) with a Black male of the same brood ; 6 young, 5 Black, 1 Albino ;
 (2) with male a of the same brood ; (18 young, all Black) ;
 (3) with male VI.C.1.p. (**R**+**A**) ; 38 young, 27 Black, 11 Albino.

VI.A.3.l. Female, *Black carrying Albino*. Red not proved.

- Matings :—(1) with a Black male of the same brood ; 5 young, all Black ;
 (2) with male b of the same brood, (**B**+**A**) ; (4 young, all Black).

Only one young survived to maturity, and was mated with a Red female carrying albino ; 19 offspring were produced, 8 Black and 11 Albino.

VI.A.3.m. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a Black male of the same brood, 1 young, Black ;
 (2) with male c of the same brood, (**B**+**R**+**A**) ; (28 young, 18 Black, 6 Red, 4 Albino).

VI.A.3.n. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male d of the same brood, (**B**+**R**) ; (46 young, 41 Black, 5 Red).

From the matings of these, 73 young were produced, 69 Black, 2 Red and 2 Albino.

VI.A.3.o. Female, *Black carrying Albino*. Red factor not proved.

- Matings :—(1) with a Black male of the same brood ; 5 young, 4 Black, 1 Albino ;
 (2) with male e of the same brood, (Pure Black) ; (9 young, all Black).

As these young all died before reaching maturity, it was not possible to test the brood for Reds.

VI.A.3.p. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a black male of the same brood ; 6 young, 3 Black, 3 Albino ;
 (2) with male f of the same brood, (**B**+**R**+**A**) ; (13 young, 6 Black, 2 Red, 5 Albino).

VI.A.3.q. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male g of the same brood, (**B**+**A**) ;
 (55 young, 35 Black, 20 Albino) ;
 (2) with male IV.J. (**B**+**R**+**A**) ; 33 young, 19
 Black, 7 Red, 7 Albino ;
 (3) with male VI.A.1.d. (**B**+**R**+**A**) ; (16
 young, 10 Black, 2 Red, 4 Albino).

VI.A.3.r. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a Black male of the same brood ; 7
 young, 4 Black, 3 Albino ;
 (2) with male VI.C.3.a. (**B**+**R**+**A**) ; 8 young,
 3 Black, 2 Red, 3 Albino.

VI.A.3.s. Female, *Black*. Constitution not proved.

- Matings :—(1) with a Black male of the same brood ; 4
 young, all Black ;
 (2) with male j of the same brood ; (1 young,
 Black).

VI.C.1.a. Male, *Black carrying Albino*.

- Matings :—(1) with a female from Pure Red Stock ; 66
 young, all Black ;
 (2) with an Albino female I.D.2.d. ; 49 young,
 24 Black, 25 Albino.

VI.C.1.b. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female f of the same brood (**B**+**R**+
A) ; 74 young, 41 Black, 15 Red, 18
 Albino (Plate IV, Fig. 15) ;
 (2) with female k of the same brood (**B**+**A**) ;
 27 young, 20 Black, 7 Albino (Plate IV,
 Fig. 14).

VI.C.1.c. Male, *Black carrying Red and Albino*.

- Matings :—(1) with a female from Pure Red Stock ; 53
 young, 33 Black, 20 Red ;
 (2) with female l of the same brood (**B**+**R**+
A) ; 17 young, 12 Black, 3 Red, 2 Albino.

VI.C.1.d. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male n of the same brood (**R**+**A**) ;
 96 young, 37 Black, 35 Red, 24 Albino ;
 (2) with male o of the same brood, (**R**+**A**) ;
 39 young, 12 Black, 16 Red, 11 Albino
 (Plate IV, Fig. 6) ;

- Matings :—(3) with male VI.A.1.a. (**B**+**R**) ; (42 young, 30 Black, 12 Red) (Plate IV, Fig. 5) ;
 (4) with male VI.A.3.d. (**B**+**R**) ; (80 young, 62 Black, 18 Red) ;
 (5) with male VI.A.3.c. (**B**+**R**+**A**) ; (71 young, 36 Black, 15 Red, 20 Albino).

VI.C.1.e. Female, *Pure Black*.

- Matings :—(1) with male o of the same brood (**R**+**A**) ; 42 young, all Black ;
 (2) with male n of the same brood, (**R**+**A**) ; 49 young, all Black.

VI.C.1.f. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male b of the same brood (**B**+**R**+**A**) ; (74 young, 41 Black, 15 Red, 18 Albino) (Plate IV, Fig. 15) ;
 (2) with male p of the same brood (**R**+**A**) ; 78 young, 32 Black, 23 Red, 23 Albino (and 11 others not examined).

VI.C.1.g. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a male of the same brood (either b or c), (**B**+**R**+**A**) ; 17 young, 8 Black, 5 Red, 4 Albino.

VI.C.1.h. Female, *Black carrying Red only*.

- Matings :—(1) with male p of the same brood (**R**+**A**) ; 40 young, 16 Black, 24 Red ;
 (2) with male VI.A.1.e. (**B**+**R**+**A**) ; (88 young, 60 Black, 28 Red) ;
 (3) with male VI.C.3.b. (**B**+**R**+**A**) ; 12 young, 8 Black, 4 Red.

VI.C.1.j. Female, *Black carrying Red only*.

- Matings :—(1) with a male from Pure Red Stock ; 58 young, 25 Black, 33 Red.

These broods were mated together on reaching maturity ; 64 young were produced, Black and Red, no Albinos.

VI.C.1.k. Female, *Black carrying Albino only*.

- Matings :—(1) with a male from Pure Red Stock ; 82 young, all Black (Plate IV, Fig. 13) ;
 (2) with male b of the same brood (**B**+**R**+**A**) ; (27 young, 20 Black, 7 Albino) (Plate IV, Fig. 14).

VI.C.1.1. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a male from Pure Red Stock ; 40 young, 18 Black, 22 Red ;
 (2) with male c of the same brood (**B**+**R**+**A**) ;
 (17 young, 12 Black, 3 Red, 2 Albino).

VI.C.2.a. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female f of the same brood (**B**+**R**+**A**) ; 18 young, 7 Black, 2 Red, 7 Albino,
 (and 2 others eaten).

VI.C.2.b. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female g of the same brood (**B**+**R**+**A**) ; 21 young, 10 Black, 4 Red, 7 Albino.

VI.C.2.c. Male, *Black carrying Albino only*.

- Matings :—(1) with female h of the same brood, Black carrying Albino only probably ; 8 young, 6 Black, 2 Albino ;
 (2) with female VI.B.3.f. (**R**+**A**) ; 6 young, 5 Black, 1 Albino.

VI.C.2.d. Male, *Pure Black*.

- Matings :—(1) with female j of the same brood ; 67 young, all Black ;
 (2) with female VI.B.2.g. (Pure Red) ; 23 young, all Black ;
 (3) with female VI.B.2.v. (**A**+**R**) ; 21 young, all Black.

VI.C.2.e. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female k of the same brood (**B**+**R**+**A**) ; 8 young, 7 Black, 1 Albino ;
 (2) with female l of the same brood (**B**+**R**+**A**) ; 27 young, 15 Black, 3 Red, 9 Albino.

VI.C.2.f. Female, *Black carrying Red and Albino*.

- Matings :—(1) with either male b or male e of the same brood (**B**+**R**+**A**) ; 12 young, 4 Black, 1 Red, 7 Albino ;
 (2) with male a of the same brood (**B**+**R**+**A**) ;
 (18 young, 7 Black, 2 Reds, 7 Albino and 2 others eaten).

VI.C.2.g. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a male of the same brood (probably male d Pure Black); 6 young, all Black;
 (2) with male b of the same brood (**B+R+A**);
 (21 young, 10 Black, 4 Red, 7 Albino).

VI.C.2.h. Female, *Black carrying Albino only* (probably).

- Matings :—(1) with a male of the same brood (probably male d, Pure Black); 8 young, all Black;
 (2) with male c of the same brood (**B+A**);
 (8 young, 6 Black, 2 Albino).

Only three of this brood came to maturity, 1 male and 2 Black females. The male mated with one female and had 4 young, 2 Black and 2 Albino. The females were mated with Red males, and gave (1) 2 Black and (2) 25 Black and 4 Albino; no Reds.

VI.C.2.j. Female, probably *Pure Black* (other factors not proved).

- Matings :—(1) with a Black male of the same brood;
 7 young, all Black;
 (2) with male d of the same brood, (Pure Black); (67 young, all Black).

Of these young, only two males survived to maturity; mated with Albino females (**A+R**) they gave 10 young, all Black.

VI.C.2.k. Female, *Black carrying Red and Albino*.

- Matings :—(1) with male b or e of the same brood (**B+R+A**); 13 young, 7 Black, 2 Red, 4 Albino;
 (2) with male e of the same brood; (**B+R+A**);
 (8 young, 7 Black, 1 Albino);
 (3) with male u of the same brood (**A+R**);
 21 young, 17 Black, 1 Red, 3 Albino.

VI.C.2.l. Female, *Black carrying Red and Albino*.

- Matings :—(1) with a Black male of the same brood;
 4 young, 2 Black, 2 Albino;
 (2) with male e of the same brood, (**B+R+A**);
 (27 young, 15 Black, 3 Red, 9 Albino).

The remaining one, a male, died before its constitution was proved.

VI.C.3.a. Male, *Black carrying Red and Albino*.

- Matings :—(1) with female VI.A.3.r. (**B+R+A**); (8 young, 3 Black, 2 Red, 3 Albino).

VI.C.3.b. Male, *Black carrying Red and Albino.*

- Matings :—(1) with female VI.B.2.e. (**R**+**A**) ; 38 young,
15 Black, 12 Red, 11 Albino ;
(2) with female VI.C.1.h. (**B**+**R**) ; (12 young,
8 Black, 4 Red) ;
(3) with female g of the same brood, (**B**+**R**) ;
18 young, 13 Black, 5 Red.

VI.C.3.c. Male, *Black carrying Albino only.*

- Matings :—(1) with female VI.A.3.w. (**R**+**A**) ; (17 young,
15 Black, 2 Albino).

VI.C.3.d. Female, *Black carrying Red only.*

- Matings :—(1) with male n of the same brood (Red,
albinism not known) ; 16 young, 13
Black, 3 Red ;
(2) with male VI.A.3.t. (**R**+**A**) ; (25 young,
12 Black, 13 Red) ;
(3) with male VI.A.3.c. (**B**+**R**+**A**) ; (11
young, 9 Black, 2 Red).

VI.C.3.e. Female, *Black carrying Red and Albino.*

- Matings :—(1) with a male, Pure Red (from the same
stock as R.1 on Plate II, see page 324) ;
7 young, 5 Black, 2 Red ;
(2) with male VI.B.2.t. (**A**+**R**) ; 28 young,
13 Black, 4 Red, 11 Albino ;
(3) with a male from Brood 1 of female
VI.A.1.h. (Pure Red) ; 34 young, 22
Black, 12 Red ;
(4) with male VI.A.3.d. (**B**+**R**) ; (56 young,
46 Black, 10 Red).

VI.C.3.f. Female, *Black carrying Albino only.*

- Matings :—(1) with male VI.B.3.b. (**R**+**A**) ; 25 young,
21 Black, 4 Albino.

VI.C.3.g. Female, *Black carrying Red only.*

- Matings :—(1) with male VI.C.2.u. (**A**+**R**) ; (28 young,
13 Black, 15 Red) ;
(2) with male b of the same brood
(**B**+**R**+**A**) ; (18 young, 13 Black, 5
Red).

VI.C.3.h. Female, *Pure Black.*

- Matings :—(1) with male VI.A.2.g. (**A**+**R**) ; (29 young,
all Black).

VI.C.3.j. Female, *Black carrying Albino only*.

- Matings :—(1) with male p of the same brood (**A**+**R**) ;
31 young, 14 Black, 17 Albino ;
(2) with a male (from Brood 1 of male
VI.C.2.p.) (**A**+**R**) ; 9 young, 4 Black,
5 Albino.

VI.C.3.k. Female, *Black carrying Albino*. Red not known.

- Matings :—(1) with a Black male of the same brood ;
6 young, 3 Black, 3 Albino.

This brood died before reaching maturity, and could not therefore be tested for Reds.

- (2) with male VI.A.2.j. Died.

VI.C.3.l. Female, *Black*. Constitution not proved.

- Matings :—(1) with Red male I.E.1.a. ; 2 young, Black.
These died without mating.

To sum up, 69 animals were tested, 28 males and 41 females ; 58 of these gave conclusive results, while six others are marked "doubtful," either because the number of offspring obtained was not considered quite sufficient, or because the animal after being proved for one factor, red or albino, died before the presence or absence of the second factor could be definitely established. The remaining five gave no definite results.

The proportions should be, according to Hypothesis II, 1 : 2 : 2 : 4, which for 64 would be 7 : 14 : 14 : 28.

The actual figures counting the "doubtfuls" are 7 : 17 : 10 : 30. They were divided as follows :—

Pure Blacks, 5, three males and two females, 2 others, male and female, "doubtful," i.e. showing neither the red nor the albino factor in their young nor in the matings obtained from these.

Black carrying Albino only, 14, six males and eight females, 3 others, females, "doubtful," i.e. no proof of the red factor.

Black carrying Red only, 9, three males and six females, 1 other, female, "doubtful," i.e. no proof of the albino factor.

Black carrying Red and Albino, 30, thirteen males and seventeen females.

In all, 3,137 young were obtained from these matings, 32 of which were not examined for eye-colour.

The matings *Black* by **R** ; by **R**+**A** ; by **A**+**R**, 222 young all Black.

Black by **B** ; by **B**+**A** ; by **B**+**R**+**A**, 121 all Black.

Black carrying Albino, by **R** ; 148 all Black : by **R**+**A** ; 53 Black and 16 Albino : by **A**+**R**, 103 Black, 106 Albino.

Black carrying Albino, by **B+R+A**, 92 Black, 45 Albino : by **A+B+R**, 29 Black, 41 Albino : by **B+A**, 15 Black, 8 Albino : by **B+R**, 51 all Black.

Black carrying Red, by **R**, and **R+A**, 95 Black, 105 Red.

Black carrying Red, by **B+R**, 29 Black, 14 Red : by **B+R+A**, 387 Black, 114 Red.

Black carrying Red and Albino, by **R**, 168 Black, 147 Red : by **R+A**, 216 Black, 178 Red, 143 Albino : by **A+R**, 31 Black, 8 Red, 34 Albino.

Black carrying Red and Albino, by **B+R+A**, 205 Black, 72 Red, 104 Albino : by **A+B+R**, 2 Black, 1 Red, 4 Albino.

[In the F_3 generation proceeded with for proof 450 young (F_4) were produced, 272 Black, 147 Red and 31 Albino.]

(2) **List of the cross-matings** made with the black-eyed animals which had given some red offspring when mated with reds or other blacks :—

VI.A.1.a. Male (**B+R**) : tested with Red : 5 Black, 3 Red.

(1) crossed with female VI.A.1.l. (**B+R+A**) ;
45 Black, 11 Red ;

(2) crossed with female VI.C.1.d. (**B+R+A**) ;
30 Black, 12 Red.

VI.A.1.b. Male (**B+R**) : tested with Red : 5 Black, 10 Red.

(1) crossed with female VI.A.1.g. (**B+R+A**) ;
23 Black, 4 Red ;

(2) crossed with female VI.A.1.f. (**B+R+A**) ; 17
Black, 8 Red.

VI.A.1.d. Male (**B+R+A**) : tested with Red : 3 Black, 7 Red.

(1) crossed with female VI.A.3.q. (**B+R+A**) ;
10 Black, 2 Red, 4 Albino.

VI.A.1.e. Male (**B+R+A**) : tested with Red : 11 Black, 7 Red.

(1) crossed with female VI.C.1.h. (**B+R**) ; 60 Black,
28 Red.

VI.A.1.f. Female (**B+R+A**) : tested with Red : 4 Black, 8 Red.

(1) crossed with male b, see above ;

(2) crossed with male VI.A.3.c. (**B+R+A**) ; 2
Black, 1 Red, 2 Albino.

VI.A.1.g. Female (**B+R+A**); tested with Red: 5 Black, 5 Red.

(1) crossed with male b (**B+R**), see above.

VI.A.1.l. Female (**B+R+A**): tested with Red: 39 Black, 34 Red.

(1) crossed with male a (**B+R**), see above.

VI.A.2.c. Female (**B+R**): tested with Red carrying Albino: 16 Black, 11 Red.

(1) crossed with male VI.A.3.d. (**B+R**); 29 Black, 14 Red.

VI.A.3.c. Male (**B+R+A**).

(1) crossed with female VI.A.3.m. (**B+R+A**); 18 Black, 6 Red, 4 Albino;

(2) crossed with female VI.A.1.f. (**B+R+A**); see above;

(3) crossed with female VI.C.1.d. (**B+R+A**); 36 Black, 15 Red, 20 Albino;

(4) crossed with female VI.C.3.d. (**B+R**); 9 Black, 2 Red.

VI.A.3.d. Male (**B+R**).

(1) crossed with female VI.A.3.n. (**B+R+A**); 41 Black, 5 Red;

(2) crossed with female VI.C.1.d. (**B+R+A**); 91 Black, 24 Red;

(3) crossed with female VI.A.2.c. (**B+R**); see above;

(4) crossed with female VI.C.3.e. (**B+R+A**); 46 Black, 10 Red.

*VI.A.3.f. Male (**B+R+A**).

(1) crossed with female VI.A.3.p. (**B+R+A**); 6 Black, 2 Red, 5 Albino.

*VI.A.3.m. Female (**B+R+A**).

(1) crossed with male VI.A.3.c. (**B+R+A**); see above.

*VI.A.3.p. Female (**B+R+A**).

(1) crossed with male VI.A.3.f. (**B+R+A**); see above.

*VI.A.3.q. Female (**B+R+A**): tested with a male (**B+R+A**); 19 Black, 7 Red, 7 Albino.

(1) crossed with VI.A.1.d. (**B+R+A**); see above.

*VI.A.3.r. Female (**B+R+A**).

(1) crossed with male VI.C.3.a. (**B+R+A**); 3 Black, 2 Red, 3 Albino.

*VI.C.1.b. Male (**B+R+A**).

- (1) crossed with female VI.C.1.f. (**B+R+A**); 41
Black, 15 Red, 18 Albino.

VI.C.1.c. Male (**B+R+A**): tested with Red: 33 Black, 20 Red.

- (1) crossed with female VI.C.1.l. (**B+R+A**); 12
Black, 3 Red, 2 Albino.

VI.C.1.d. Female (**B+R+A**): tested with Reds carrying Albino; 49
Black, 51 Red, 35 Albino.

- (1) crossed with male VI.A.1.a. (**B+R**); see above;
(2) crossed with male VI.A.3.d. (**B+R**); see
above;
(3) crossed with male VI.A.3.c. (**B+R+A**); see
above.

VI.C.1.f. Female (**B+R+A**): tested with Red carrying Albino; 32
Black, 23 Red, 23 Albino.

- (1) crossed with male VI.C.1.b. (**B+R+A**); see
above.

*VI.C.1.g. Female (**B+R+A**).

- (1) crossed with male from VI.C.1. (**B+R+A**);
8 Black, 5 Red, 4 Albino.

VI.C.1.h. Female (**B+R**): tested with Red: 16 Black, 24 Red.

- (1) crossed with male VI.A.1.e. (**B+R+A**); see
above.
(2) crossed with male VI.C.3.b. (**B+R+A**); 8
Black, 4 Red.

VI.C.1.l. Female (**B+R+A**): tested with Red: 18 Black, 22 Red.

- (1) crossed with male VI.C.1.c.; see above.

*VI.C.2.a. Male (**B+R+A**).

- (1) crossed with female VI.C.2.f. (**B+R+A**); 7
Black, 2 Red, 7 Albino.

*VI.C.2.b. Male (**B+R+A**).

- (1) crossed with female VI.C.2.g. (**B+R+A**); 10
Black, 4 Red, 7 Albino.

VI.C.2.e. Male (**B+R+A**).

- (1) crossed with female VI.C.2.k. (**B+R+A**); 7
Black, 1 Albino;
(2) crossed with female VI.C.2.l. (**B+R+A**); 15
Black, 3 Red, 9 Albino.

VI.C.2.f. Female (**B+R+A**).

- (1) crossed with a male from VI.C.2. (**B+R+A**);
4 Black, 1 Red, 7 Albino;
- (2) crossed with male VI.C.2.a. (**B+R+A**); see
above.

*VI.C.2.g. Female (**B+R+A**).

- (1) crossed with male VI.C.2.b. (**B+R+A**); see
above.

VI.C.2.k. Female (**B+R+A**): tested with Albino carrying Red; 17
Black, 1 Red, 3 Albino.

- (1) crossed with male from VI.C.2. (**B+R+A**);
7 Black, 2 Red, 4 Albino;
- (2) crossed with male VI.C.2.e. (**B+R+A**); see
above.

*VI.C.2.l. Female (**B+R+A**).

- (1) crossed with male VI.C.2.e. (**B+R+A**); see
above.

*VI.C.3.a. Male (**B+R+A**).

- (1) crossed with female VI.A.3.r. (**B+R+A**); see
above.

VI.C.3.b. Male (**B+R+A**): tested with Red carrying Albino; 15 Black,
12 Red, 11 Albino.

- (1) crossed with female VI.C.1.h. (**B+R**); see
above;
- (2) crossed with female VI.C.3.g. (**B+R**); 13
Black, 5 Red.

VI.C.3.d. Female (**B+R**): tested with Reds: 25 Black, 16 Red.

- (1) crossed with male VI.A.3.c. (**B+R+A**); see
above.

VI.C.3.e. Female (**B+R+A**): tested with Reds; 27 Black, 14 Red.

- (1) crossed with male VI.A.3.d. (**B+R**); see above.

VI.C.3.g. Female (**B+R**): tested with Albino carrying Red; 13 Black,
15 Red.

- (1) crossed with male VI.C.3.b. (**B+R+A**); see
above.

* The animals marked with an asterisk had not been previously tested.

In each of the above instances *some red young were produced*, showing that the parents were all blacks carrying red and not one-dose blacks.

These tests therefore are in favour of *Hypothesis II* being the correct one.

CROSS C. F. 2. GENERATION. REDS.

Turning now to the Red F_2 , according to *Hypothesis I* these are of two kinds, one with only one dose of red and no factor for albino (C C R), and two with only one dose of red and with the factor for albino (C c R).

There are three possible ways in which these reds could be mated together and these matings would give the following:—

(1)	C C R × C C R
Male Gametes:—	C R and C
Female „	C R and C
Zygotes	C R C R
	C R C
	C R C
	C C

that is one C C R R, two C C R, one C C
 „ „ 3 reds and 1 albino.

(2)	C c R × C c R
Male Gametes	C R, C, c R, c
Female „	C R, C, c R, c
Zygotes	

C R	C	c R	c
C R	C R	C R	C R
C R	C	c R	c
C	C	C	C
C R	C	c R	c
c R	c R	c R	c R
C R	C	c R	c
c	c	c	c

That is 9 reds and 7 albinos.

(3)	C C R × C c R
Male Gametes	C R and C
Female „	C R, C, c R, c
Zygotes	

C R	C	c R	c
C R	C R	C R	C R
C R	C	c R	c
C	C	C	C

That is 6 reds and 2 albinos.

It will be seen that in each case, that is to say, *in whatever way the*

reds in this generation are mated, there would be albinos in the offspring. Further, in each case, in addition to the usual imperfect-eyed albinos cR cB cB all-whites of the same hypothetical constitution as the cR , cB , cR , original "all-white" male from red stock $\frac{C}{C}$ should occur, and if these resemble the original parent they will have perfectly formed eyes.

According to *Hypothesis II* the Reds can also be mated in three different ways. The results would be:—

$$(1) \quad CCR R \times CCR R$$

Gametes all CR

Zygotes all $CCR R$.

That is, all red.

$$(2) \quad CcR R \times CcR R$$

Male Gametes CR , cR

Female ,, CR , cR

Zygotes $CCR R$, $CcR R$, $CcR R$, $ccR R$

That is, 3 reds and 1 albino.

$$(3) \quad CCR R \times CcR R$$

Male Gametes CR

Female ,, CR and cR

Zygotes $CCR R$ and $CcR R$

That is, all red.

In two of the instances therefore the offspring would be all red-eyed. In one instance there would be albinos in the brood.

Experiment has shown that when reds of the F_2 generation are mated together *some broods consist entirely of red-eyed young*, whilst others consist of reds and albinos. Further, the albinos when they occurred were of the usual imperfect-eyed type. Hypothesis II is therefore in agreement with the experimental facts, whilst Hypothesis I is not.

The following list shows the Red-eyed young and the matings made to prove their constitution.

VI.A.1.m. Male, *Pure Red* (Plate II).

- Matings:—(1) with female p of its own brood, ($R+A$);
72 young, all Red (Plate IV, Fig. 11);
(2) with female q of its own brood, ($R+A$);
32 young, all Red (Plate IV, Fig. 10);
(3) with female IV.O ($B+A$); 39 young, all
Black;
(4), (5) mated with 2 Albino females: ate
them.

VI.A.1.n. Male, *Red carrying Albino*.

- Matings :—(1) with female q of its own brood, (**R**+A);
63 young, 52 Red, 11 Albino (Plate IV,
Fig. 9);
(2) with female VI.B. (**R**+A); 69 young,
50 Red, 19 Albino.

VI.A.1.o. Male, *Pure Red*.

- Matings :—(1) with female h of its own brood (**B**+**R**+A);
(31 young, 17 Black, 14 Red);
(2) with female p of its own brood, (**R**+A);
40 young, all Red.

VI.A.1.p. Female, *Red carrying Albino*.

- Matings :—(1) with male m of its own brood; (72 young,
all Red) (Plate IV, Fig. 11);
(2) with male II.B. (**R**+A); (90 young, 66
Red, 24 Albino) (Plate IV, Fig. 12);
(3) with male o of its own brood; (40 young,
all Red);
(4) with male VI.B.1.b. (**R**+A); 17 young,
16 Red, 1 Albino.

VI.A.1.q. Female, *Red carrying Albino*.

- Matings :—(1) with male n of the same brood; (63 young,
52 Red, 11 Albino) (Plate IV, Fig. 9);
(2) with male m of the same brood; (32
young, all Red) (Plate IV, Fig. 10);
(3) with male c of the same brood, (Pure
Black); (45 young, all Black) (Plate IV,
Fig. 8).

Brood 2 of VI.A.

The 4 Red hatched died immature.

VI.A.3.t. Male, *Red carrying Albino*.

- Matings :—(1) with female VI.A.2.l. (**A**+**B**+**R**); 6
young, 1 Red, 5 Albino;
(2) with female VI.B.3.g.; ate it;
(3) with female IV.V. (**B**+A); 12 young, 10
Black, 2 Albino;
(4) with female VI.C.3.d. (**B**+**R**); 25 young,
12 Black, 13 Red.

VI.A.3.u. Male, *Red carrying Albino*.

- Matings :—(1) with female w of the same brood, (**R**+A);
48 young, 36 Red, 12 Albino;

- Matings:—(2) with female x of the same brood, (Pure Red); 10 young, all Red;
 (3) with female III.N. (**B**+**A**); 42 young, 32 Black, 10 Albino.

VI.A.3.v. Male, *Red carrying Albino*.

- Matings:—(1) with female x of the same brood, (Pure Red); 28 young, all Red;
 (2) with female w of the same brood, (**R**+**A**); 16 young, 10 Red, 6 Albino.

VI.A.3.w. Female, *Red carrying Albino*.

- Matings:—(1) with male u of the same brood, (**R**+**A**); (48 young, 36 Red, 12 Albino);
 (2) with male v of the same brood, (**R**+**A**); (16 young, 10 Red, 6 Albino);
 (3) with male VI.C.3.c. (**B**+**A**); 17 young, 15 Black, 2 Albino.

VI.A.3.x. Female, *Pure Red*.

- Matings:—(1) with male u of the same brood, (**R**+**A**); (10 young, all Red);
 (2) with male v of the same brood, (**R**+**A**); (28 young, all Red);
 (3) with male VI.C.2.r. (**A**+**B**+**R**); 34 young, 22 Black, 12 Red.

VI.C.1.m. Male, *Red carrying Albino*.

- Matings:—(1) with female VI.A.1.f. (**B**+**R**+**A**); (71 young, 31 Black, 18 Red, 22 Albino);
 (2) with female VI.A.1.g. (**B**+**R**+**A**); (22 young, 10 Black, 8 Red, 4 Albino).

VI.C.1.n. Male, *Red carrying Albino*.

- Matings:—(1) with female d of the same brood, (**B**+**R**+**A**); (96 young, 37 Black, 35 Red, 24 Albino);
 (2) with female e of the same brood, (Pure Black); (49 young, all Black).

VI.C.1.o. Male, *Red carrying Albino* (Plate IV, Figs. 3 and 6).

- Matings:—(1) with female e of the same brood, (Pure Black); (42 young, all Black);
 (2) with female d of the same brood, (**B**+**R**+**A**); (39 young, 12 Black, 16 Red, 11 Albino);
 (3) with female VI.A.1.l. (**B**+**R**+**A**); (82 young, 37 Black, 24 Red, 21 Albino).

VI.C.1.p. Male, *Red carrying Albino*.

- Matings :—(1) with female h of the same brood, (**B**+**R**) ;
 (40 young, 16 Black, 24 Red) ;
 (2) with female f of the same brood, (**B**+**R**+**A**) ; (78 young, 32 Black, 23 Red, 23 Albino) ;
 (3) with female VI.A.3.k. (**B**+**A**) ; (38 young, 27 Black, 11 Albino).

VI.C.2.m. Male, *Red carrying Albino*.

- Matings :—(1) with female n of the same brood, (**R**+**A**) ;
 5 young, 2 Red, 3 Albino.

VI.C.2.n. Female, *Red carrying Albino*.

- Matings :—(1) with male m of the same brood ; (5 young, 2 Red, 3 Albino) ;
 (2) eaten by mate.

VI.C.2.o. Female, constitution unknown.

- Matings :—(1) with male m of the same brood (**R**+**A**) ;
 eleven batches of eggs were laid, but no young were hatched ; female died.

VI.C.3.m. Male, *Red carrying Albino*.

- Matings :—(1) with female o of the same brood, (Pure Red) ; 48 young, all Red ;
 (2) with female r of the same brood, (**A**+**R**) ;
 381 young, 181 Red, 200 Albino.

VI.C.3.n. Male, *Red. Albinism not known*.

- Matings :—(1) with female d of the same brood, (**B**+**R**) ;
 (16 young, 13 Black, 3 Red).

These young all died immature, and it was therefore not possible to test the brood for albinism.

VI.C.3.o. Female, *Pure Red*.

- Matings :—(1) with male m of the same brood, (**R**+**A**) ;
 (48 young, all Red) ;
 (2) with male q of the same brood, (**A**+**R**) ;
 36 young, all Red.

VI.B.1.a. Male, *Pure Red*.

- Matings :—(1) with female f of the same brood, (**R**+**A**) ;
 29 young, all Red ;
 (2) with female j of the same brood, (Pure Red) ; 37 young, all Red ;
 (3), (4) with a Black female and an Albino female, both of which it ate.

VI.B.1.b. Male, *Red carrying Albino*.

- Matings :—(1) with female g of the same brood, (Pure Red) ; 49 young, all Red ;
 (2) with female VI.A.1.p. (**R**+A) (17 young, 16 Red, 1 Albino).

VI.B.1.c. Male, *Red carrying Albino*.

- Matings :—(1) with female h of the same brood, (**R**+A) ; 21 young, 17 Red, 4 Albino ;
 (2) with female g of the same brood, (Pure Red) ; 11 young, all Red.

VI.B.1.d. Male, *Red carrying Albino*.

- Matings :—(1) with female j of the same brood, (Pure Red) ; 55 young, all Red ;
 (2) with female f of the same brood, (**R**+A) ; 51 young, 37 Red, 14 Albino ;
 (3) with female IV.S. (**B**+A) ; 18 young, 13 Black, 5 Albino.

VI.B.1.e. Male, *Red. Albinism not known*.

- Matings :—(1) with female from the same stock as R.1. male (see Plate II and p. 324), (Pure Red) ; 16 young, all Red.

Only two of these survived to maturity, and were mated with Albino females ; 33 young were produced, 19 Black, and 14 Red, no albinos.

VI.B.1.f. Female, *Red carrying Albino*.

- Matings :—(1) with male a of the same brood, (Pure Red) ; (29 young, all Red) ;
 (2) with male d of the same brood, (**R**+A) ; (51 young, 37 Red, 14 Albino) ;
 (3) with a male (from Brood 1 of VI.A.1. female h), (**R**+A) ; 27 young, 15 Red, 12 Albino ;
 (4) with male e of same brood ; ate it.

VI.B.1.g. Female, *Pure Red*.

- Matings :—(1) with male b of the same brood, (**R**+A) ; (49 young, all Red) ;
 (2) with male c of the same brood, (**R**+A) ; (11 young, all Red) ;
 (3) with male IV.K. (**B**+**R**+A) ; 9 young, 2 Black, 7 Red.

VI.B.1.h. Female, *Red carrying Albino*.

- Matings :—(1) with male c of the same brood, (**R**+A) ; (21 young, 17 Red, 4 Albino).

VI.B.1.j. Female, *Pure Red*.

- Matings :—(1) with male d of the same brood, (**R**+**A**) ;
 (55 young, all Red) ;
 (2) with male a of the same brood, (Pure
 Red) ; (37 young, all Red).

VI.B.1.k. Female, *Red*. Albinism not known.

- Matings :—(1) with male m of the same brood, (**A**+**R**) ;
 four months in the bowl, six matings, no
 young hatched, female died.

VI.B.1.l. Male, *Red*. Albinism not known.

Put with a female from the same
 stock as R.1. male (Plate II), no mating.

VI.B.2.a. Male, *Red carrying Albino*.

- Matings :—(1) with female f of the same brood, (**R**+**A**) ;
 8 young, all Red ;
 (2) with female p of the same brood, (Red,
 albinism not known) ; 2 young, Red ;
 (3) with female e of the same brood, (**R**+**A**) ;
 8 young, 6 Red, 2 Albino ;
 (4) with female v of the same brood, (**A**+**R**) ;
 38 young, 35 Red, 3 Albino ;
 (5) with female u of same brood, (**A**+**R**) ;
 48 young, 24 Red, 24 Albino (Plate IV,
 Fig. 18).

VI.B.2.b. Male, *Red carrying Albino*.

- Matings :—(1) with female g of the same brood, (Pure
 Red) ; 87 young, all Red ;
 (2) with female w of the same brood, (**A**+**R**) ;
 222 young, 118 Red, 104 Albino.

VI.B.2.c. Male, *Red carrying Albino*.

- Matings :—(1) with female h of the same brood, (**R**+**A**) ;
 11 young, 7 Red, 4 Albino ;
 (2) with female g of the same brood, (Pure
 Red) ; 21 young, all Red.

VI.B.2.d. Male, *Red carrying Albino*.

- Matings :—(1) with female r of the same brood ; 7 young,
 all Red ;
 (2) with female e of the same brood, (**R**+**A**) ;
 25 young, 21 Red, 4 Albino ;
 (3) with female VI.A.2.c. (**B**+**R**) ; (27 young,
 16 Black, 11 Red).

VI.B.2.e. Female, *Red carrying Albino*.

- Matings :—(1) with male a of the same brood, (**R**+**A**) ;
 (8 young, 6 Red, 2 Albino) ;
 (2) with male d of the same brood, (**R**+**A**) ;
 (25 young, 21 Red, 4 Albino) ;
 (3) with male III.D. (**B**+**A**) ; 19 young, 11
 Black, 8 Albino ;
 (4) with male VI.C.3.b. (**B**+**R**+**A**) ; (38
 young, 15 Black, 12 Red, 11 Albino) ;
 (5) with male VI.B.1.m. (**A**+**R**) ; (87 young,
 50 Red, 37 Albino).

VI.B.2.f. Female, *Red carrying Albino*.

- Matings :—(1) with male a of the same brood, (**R**+**A**) ;
 (8 young, all Red) ;
 (2) with male VI.C.2.q. (**A**+**B**+**R**) ; (20
 young, 6 Black, 5 Red, 9 Albino).

VI.B.2.g. Female, *Pure Red*.

- Matings :—(1) with male b of the same brood, (**R**+**A**) ;
 (87 young, all Red) ;
 (2) with male c of the same brood, (**R**+**A**) ;
 (21 young, all Red) ;
 (3) with male VI.C.2.d. (Pure Black) ; (23
 young, all Black) ;
 (4) with male from Brood 1 of male III.B.
 (**A**+**B**) ; 54 young, all Black.

VI.B.2.h. Female, *Red carrying Albino*.

- Matings :—(1) with male c of the same brood, (**R**+**A**) ;
 (11 young, 7 Red, 4 Albino).

VI.B.2.j. Female, *Pure Red*.

- Matings :—(1) with male VI.A.2.g. (**A**+**R**) ; (26 young,
 all Red).

VI.B.2.k. Female, *Red carrying Albino*.

- Matings :—(1) with male VI.A.2.j. (**A**+**R**) ; (38 young,
 22 Red, 16 Albino) ;
 (2) with male VI.A.2.h. (**A**+**B**+**R**) ; (16
 young, 6 Black, 2 Red, 8 Albino).

VI.B.2.l. Female, *Red carrying Albino*.

- Matings :—(1) with male VI.C.2.p. (**A**+**R**) ; (6 young,
 3 Red, 3 Albino) ;
 (2) with male VI.C.2.u. (**A**+**R**) ; (1 young,
 Albino).

VI.B.2.m. Female, *Red carrying Albino*.

Matings :—(1) with male VI.C.2.s. (**A+B+R**) ; (9 young, 3 Black, 2 Red, 4 Albino).

VI.B.2.n. Female, *Pure Red*.

Matings :—(1) with male VI.A.3.z. (**A+B+R**) ; (15 young, 10 Black, 5 Red).

VI.B.2.o. Female, *Pure Red*.

Matings :—(1) with male VI.A.3.aa. (**A+R**) ; (12 young, all Red).

VI.B.2.p. Female, *Red*. Albinism not known.

Matings :—(1) with male a of the same brood, (**R+A**) ; (2 young, Red).

VI.B.2.q. Female, *Red*. Albinism not known.

Matings :—(1) with male VI.A.3.y. (**A+B**) ; (1 young, Black).

VI.B.2.r. Female, *Red*. Albinism not known.

Matings :—(1) with male d of the same brood, (**R+A**) ; (7 young, all Red).

One male, mated with female v, and 5 females which reached maturity and mated, were eaten by their mates. One died immature.

VI.B.3.a. Male, *Red carrying Albino*.

Matings :—(1) with female VI.C.3.u. (**A+B+R**) ; (47 young, 15 Black, 13 Red, 19 Albino) ;
(2) with female VI.A.2.m. (**A+B+R**) ; 33 young, 6 Black, 14 Red, 13 Albino.

VI.B.3.b. Male, *Red carrying Albino*.

Matings :—(1) with female VI.C.3.w. (**A+R**) ; (31 young, 19 Red, 12 Albino) ;
(2) with female VI.C.3.f. (**B+A**) ; (25 young, 21 Black, 4 Albino).

VI.B.3.c. Male, *Red carrying Albino*.

Matings :—(1) with female VI.C.3.x. (**A+B+R**) ; (19 young, 7 Black, 4 Red, 8 Albino).

VI.B.3.d. Male, *Red*. Not proved.

Matings :—(1) with Albino female VI.C.3.t. ;
(2) with Red female of the same brood ;
(3) with Albino female I.G.1.c. ; all of which it ate ;
(4) with Albino female VI.A.2.m. Died.

VI.B.3.e. Female, *Pure Red*.

Matings :—(1) with a Red male of the same brood ; 2 young, Red ;

- Matings :—(2) with male VI.A.2.a. (**B**+**R**+**A**) ; (20 young, 8 Black, 12 Red) ;
 (3) with male VI.C.2.u. (**A**+**R**) ; (24 young, all Red).

VI.B.3.f. Female, *Red carrying Albino*.

- Matings :—(1) with male VI.C.2.c. (**B**+**A**) ; (6 young, 5 Black, 1 Albino).

VI.B.3.g. Female. *Red. Not proved*.

- Matings :—(1) with Black male VI.A.2.b. ; (5 young, Black) ;
 (2) with a Red male VI.A.3.t. ; was eaten.

4 others, females, reached maturity, mated and died ; one died immature.

VI.B.4.a. Male, *Red carrying Albino*.

- Matings :—(1) with Black female (from Brood 1 of female IV.N.) ; 8 young, 7 Black, 1 Albino ;
 (2) with female c of the same brood, (**R**+**A**) ; 22 young, 17 Red, 5 Albino.

VI.B.4.b. Male, *Red carrying Albino*.

- Matings :—(1) with female d of the same brood, (Pure Red) ; 13 young, Red ;
 (2) with female g of the same brood, (**A**+**R**) ; 132 young, 71 Red, 61 Albino.

VI.B.4.c. Female, *Red carrying Albino*.

- Matings :—(1) with male a of the same brood, (**R**+**A**) ; (22 young, 17 Red, 5 Albino).

VI.B.4.d. Female, *Pure Red*.

- Matings :—(1) with a Red male of the same brood ; 1 young, Red ;
 (2) with male b of the same brood ; (13 young, Red) ;
 (3) with a Red male (from Brood 3 of female III.Q) ; 51 young, all Red.

VI.B.4.e. Female, *Red*. Constitution unknown.

In all, 3,443 young were produced. The numbers from the different matings are as follows :—

Red by **R** ; **R**+**A** ; and **A**+**R** ; 709 young, all Red.

Red carrying Albino by **R**+**A** ; and **A**+**R** ; 883 Red, 582 Albino.

Red and **R**+**A** by Black ; 258, all Black.

Red and **R**+**A** by **B**+**R** ; 135 Black, 115 Red.

Red carrying Albino by **B**+**A** and **A**+**B** ; 141 Black, 44 Albino.

Red carrying Albino by **B**+**R**+**A** and **A**+**B**+**R** ; 217 Black, 177 Red, 182 Albino.

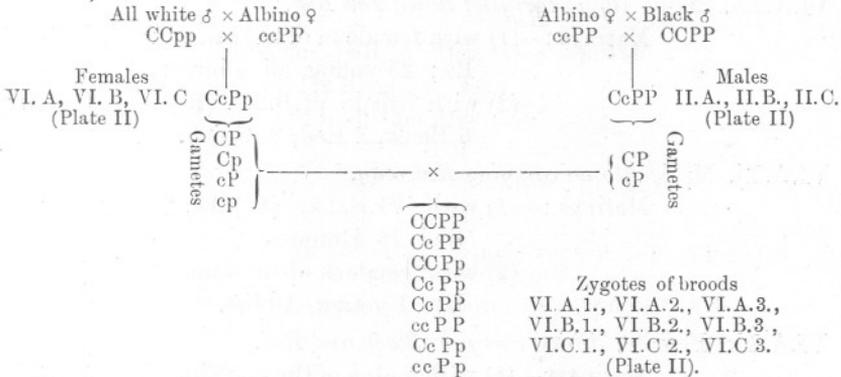
To sum up, 60 red-eyed animals were tested, 49 gave definite results, 36 proving to be Red with the albino factor, and 13 Pure Red. Theory demands 36.6 Red with albino, 12.2 Pure Red.

These results are in full agreement with *Hypothesis II* and not in agreement with *Hypothesis I*.

CROSS C. F.2. GENERATION. ALBINOS.

A final test of the two hypotheses would be obtained by testing the F_3 albinos got by crossing F_2 coloured parents. Amongst these F_3 albinos animals with the constitution $\begin{matrix} C \\ C \end{matrix}$ like the original all-white male parent should occur if *Hypothesis I* were true. If therefore we make many crosses amongst the albinos of this generation we ought to find some pairs which would give all coloured offspring. If these are not produced it will be an additional proof that *Hypothesis II* is the right one. We have made 18 matings of this character, and they yielded a total of 588 young, all of them albino.*

* In all the animals referred to in this paper as "albino," the eyes had the irregular, degenerate form figured on Plate VII, Fig. 4. If we take the view that, in the absence of red and black pigment, the regular form is in itself sufficient to distinguish the "all white" eye (Plate VII, Fig. 7) from the imperfectly shaped "albino" eye, the following statement, the form of which we owe to Prof. R. C. Punnett, who has been good enough to read this paper in proof, puts the argument against our Hypothesis I in a brief form. The letter P must be understood to represent the factor for either red or black pigment, p the absence of such a factor. Hypothesis I. That two complementary colour factors are concerned, of which the "albino" female contains one, viz. P, and the "all white" male the other, viz. C.



Mated among themselves the chances of Pp zygotes coming together are 16 in 64, i.e. 1 in 4, and in such cases "all-white" eyes should appear in ratio 1 : 3. Amongst the blacks 109 such matings have been made, amongst the reds 40, and amongst the albinos 27, making a total of 176 such matings, and no "all-white" eyes of perfect form appeared. Hence Hypothesis I is not valid here.

The Albinos of VI.A. may be taken as a fairly accurate record of the proportions found, most of them, 13 out of 15, having survived to maturity. Of these 3 carried Black only, 3 Red only, and 7 carried both Black and Red.

VI.A.1.r. Male, *Albino carrying Black only.*

- Matings :—(1) with female VII.C.3.a. (Plate V) (Red no-white); 36 young, all Black (Plate IV, Fig. 17);
 (2) with female VI.A. (its female parent) (**B+R+A**); 1 young, Black;
 (3) with female from the Pure Red Stock; 23 young, all Black (Plate IV, Fig. 16).

VI.A.1.s. Male, *Albino carrying Black only.*

- Matings :—(1) with female VII.C.3.b. (Plate V) (Red no-white); 57 young, all Black.

VI.A.1.t. Male, *Albino carrying Black and Red.*

- Matings :—(1) with female from No-white Stock (Red no-white); 34 young, 17 Black, 17 Red;
 (2) with female VI.C. (**B+R+A**); 14 young, 8 Black, 6 Albino.

VI.A.2.g. Male, *Albino carrying Red only.*

- Matings :—(1) with female VI.B.2.j. (Pure Red); 26 young, all Red;
 (2) with female VI.C.3.h. (Pure Black); 29 young, all Black.

VI.A.2.h. Male, *Albino carrying Black and Red.*

- Matings :—(1) with female m of the same brood, (**A+B+R**); 25 young, all Albino;
 (2) with female VI.B.2.k. (**R+A**); 16 young, 6 Black, 2 Red, 8 Albino.

VI.A.2.j. Male, *Albino carrying Red only.*

- Matings :—(1) with VI.B.2.k. (**R+A**); 38 young, 22 Red, 16 Albino;
 (2) with female m of the same brood, (**A+B+R**); 1 young, Albino.

VI.A.2.k. Female, *Albino carrying Black and Red.*

- Matings :—(1) with male a of the same brood, (**B+R+A**); (7 young, 2 Black, 1 Red, 4 Albino);
 (2) with male VI.A.3.aa. (**A+R**); 42 young, all Albino;

Matings :—(3) with male II.B. (**R**+**A**) ; 146 young, 33 Black, 44 Red, 69 Albino.

VI.A.2.l. Female, *Albino carrying Black and Red*.

Matings :—(1) with male VI.A.3.t. (**R**+**A**) ; (6 young, 1 Red, 5 Albino).

The female died after extruding this brood ; the proof of her constitution was obtained by mating the young, when mature, together and with mates of proved constitution. The red one was a male, the albinos were one male and four females. The Albino male and one female mated ; 9 young, all Albino. The female was then mated with the Red male, and gave in 38 young, 13 Black, 8 Red, 17 Albino. (The albino male mated with a Pure Red female had 31 young, all Red.)

VI.A.2.m. Female, *Albino carrying Black and Red*.

Matings :—(1) with an Albino male of the same brood ; 5 young, all Albino ;
 (2) with male h of the same brood, (**A**+**B**+**R**) ; (25 young, all Albino) ;
 (3) with male j of the same brood, (**A**+**R**) ; (1 young, Albino) ;
 (4) with male VI.B.3.d. ; no results ;
 (5) with male VI.B.3.a. (**R**+**A**) ; (33 young, 6 Black, 14 Red, 13 Albino).

VI.A.3.y. Male *Albino carrying Black only*.

Matings :—(1) with female VI.B.2.q. (Red, albinism not known) ; 1 young, Black ;
 (2) with female I.E.2.f. (**R**+**A**) ; 15 young, 3 Black, 12 Albino.

VI.A.3.z. Male, *Albino carrying Black and Red*.

Matings :—(1) with female VI.B.2.n. (Pure Red) ; 15 young, 10 Black, 5 Red.

VI.A.3.aa. Male, *Albino carrying Red only*.

Matings :—(1) with female VI.B.2.o. (Pure Red) ; 12 young, all Red ;
 (2) with female VI.A.2.k. (**A**+**B**+**R**) ; (42 young, all Albino) ;
 (3) with female VI.A.2.d. (**B**+**A**) ; (18 young, 8 Black, 10 Albino) ;
 (4) with female VI.A.2.e. (**B**+**A**) ; (29 young, 13 Black, 16 Albino) ;

Matings :—(5) with female VI.A.2.f. (**B**+**A**) ; (30 young, 12 Black, 18 Albino).

VI.A.3.bb. Female, *Albino carrying Black and Red*.

Matings :—(1) with male I.E.2.a. (**R**+**A**) ; 12 young, 3 Black, 2 Red, 7 Albino ;
(2) with male b of the same brood (**B**+**A**) ; (14 young, 2 Black, 12 Albino).

VI.C.1.q. Male, *Albino carrying Red only*.

Mating :—(1) with female I.E.2.d. (Red) ; 13 young, all Red.

VI.C.2.p. Male, *Albino carrying Red only*.

Matings :—(1) with female VI.B.2.l. (**R**+**A**) ; 6 young, 3 Red, 3 Albino.

Five of these young came to maturity, Red, one male and one female, and Albino, two males and one female ; these were mated together to see if the Albinos carried the Black factor ; 203 young were produced, 116 Red, and 87 Albino ; no Black appeared. (One of the Albino males was mated with female VI.C.3.j.)

VI.C.2.q. Male, *Albino carrying Black and Red*.

Matings :—(1) with female VI.B.2.f. (**R**+**A**) ; 20 young, 6 Black, 5 Red, 9 Albino.

VI.C.2.r. Male, *Albino carrying Black and Red*.

Matings :—(1) with female I.G.1.c. (**A**) ; 49 young, all Albino ;
(2) with female VI.A.3.x. (Pure Red) ; (34 young, 22 Black, 12 Red).

VI.C.2.s. Male, *Albino carrying Black and Red*.

Matings :—(1) with female VI.B.2.m. (**R**+**A**) ; 9 young, 3 Black, 2 Red, 4 Albino.

VI.C.2.t. Male, *Albino carrying Black and Red*.

Matings :—(1) with two Red females which it ate ;
(2) with female I.E.2.e. (Pure Red) ; 27 young, 15 Black, 12 Red.

VI.C.2.u. Male, *Albino carrying Red only*.

Matings :—(1) with Red female which it ate ;
(2) with female k of the same brood, (**B**+**R**+**A**) ; (21 young, 17 Black, 1 Red, 3 Albino) ;
(3) with female VI.B.2.l. (**R**+**A**) ; 1 young, Albino ;

- Matings :—(4) with female VI.B.3.e. (Pure Red); 24 young, all Red ;
 (5) with female VI.C.3.g. (**B**+**R**); 28 young, 13 Black, 15 Red.

One other reached maturity, a female, which died before its constitution could be tested.

VI.C.3.p. Male, *Albino carrying Red only*.

- Matings :—(1) with female r of the same brood, (**A**+**R**); 11 young, all Albino ;
 (2) with female j of the same brood, (**B**+**A**); (31 young, 14 Black, 17 Albino);
 (3) with female VI.B.2.j. (Pure Red); 17 young, all Red).

VI.C.3.q. Male, *Albino carrying Red only*.

- Matings :—(1) with female u of the same brood, (**A**+**B**+**R**); 11 young, all Albino ;
 (2) with Albino female v of the same brood (constitution unknown); 30 young, all Albino ;
 (3) with female t of the same brood, (**A**) 14 young, all Albino ;
 (4) with female o of the same brood, (Pure Red); (36 young, all Red).

VI.C.3.r. Female, *Albino carrying Red only*.

- Matings :—(1) with male p of the same brood (**A**+**R**); (11 young, all Albino);
 (2) with male m of the same brood, (**R**+**A**); 381 young, 181 Red, 200 Albino.

VI.C.3.s. Female, *Albino carrying Red only*.

- Matings :—(1) with a male descended from the same stock as R.1. (see male II.B. p. 284) (Pure Red); 5 young, all Red.

VI.C.3.t. Female, *Albino*. Constitution unknown.

- Matings :—(1) with male q of the same brood, (**A**+**R**); (14 young, all Albino);
 (2) with Red male VI.B.3.d.; eaten.

VI.C.3.u. Female, *Albino carrying Black and Red*.

- Matings :—(1) with male q of the same brood (**A**+**R**); (11 young, all Albino);
 (2) with male VI.B.3.a. (**R**+**A**); 47 young, 15 Black, 13 Red, 19 Albino.

VI.C.3.v. Female, *Albino*. Constitution unknown.

Matings :—(1) with male q of the same brood, (**A**+**R**) ;
(30 young, all Albino).

All the young died without mating.

VI.C.3.w. Female, *Albino carrying Red only*.

Matings :—(1) with male VI.B.3.b. (**R**+**A**) ; 31 young,
19 Red, 12 Albino.

VI.C.3.x. Female, *Albino carrying Black and Red*.

Matings :—(1) with male VI.B.3.c. (**R**+**A**) ; 19 young,
7 Black, 4 Red, 8 Albino.

VI.B.1.m. Male, *Albino carrying Red*.

Matings :—(1) with female k of the same brood ; no
results ;
(2) with female VI.B.2.e. (**R**+**A**) ; 87 young,
50 Red, 37 Albino.

VI.B.2.s. Male, *Albino*.

Matings :—(1) with Albino female w of the same brood ;
38 young, all Albino.

VI.B.2.t. Male, *Albino carrying Red*.

Matings :—(1) with Albino female u of the same brood ;
70 young, all Albino ;
(2) with a female I.E.2.e. (Pure Red) ; 50
young, all Red ;
(3) with female VI.C.3.e. (**B**+**R**+**A**) ; (28
young, 13 Black, 4 Red, 11 Albino) ;
(4) with a female of brood l of female VI.A.1.h
(**B**+**R**) ; 23 young, 7 Black, 16 Red ;
(5) with a female (from a mating in the first
brood from male II.D.1.k.) (Colourless) ;
90 young, all Albino.

VI.B.2.u. Female, *Albino carrying Red*.

Matings :—(1) with male t of the same brood ; 70 young,
all Albino ;
(2) with male a of the same brood, (**R**+**A**) ;
(48 young, 24 Red, 24 Albino) (Plate
IV, Fig. 18).
(3) with male VI.A.1.d. (**B**+**R**+**A**) ; (24
young, 1 Black, 3 Red, 20 Albino).

VI.B.2.v. Female, *Albino carrying Red*.

Matings :—(1) with male from Pure Red Stock ; 49 young,
all Red ;

- Matings :—(2) with male a of the same brood, (**R**+A); (38 young, 35 Red, 3 Albino);
- (3) with a Red male of the same brood which it ate;
- (4) with male VI.A.3.h. (**B**+A); (92 young, 52 Black, 40 Albino);
- (5) with male VI.A.3.e. (Pure Black); (19 young, all Black);
- (6) with male VI.C.2.d. (Pure Black); (21 young, all Black);
- (7) with a Black male from a brood of VI.C.2.d × j.; 2 young, Black.

VI.B.2.w. Female, *Albino carrying Red*.

- Matings :—(1) with male s of the same brood; (38 young, all Albino);
- (2) with male b of the same brood (**R**+A), (222 young, 118 Red, 104 Albino).

VI.B.3.h. Female, *Albino*.

- Matings :—(1) with an Albino male I.C.2.d.; one brood, all Albino; two survived and mated, producing 228 young, all Albino.

VI.B.4.f. Female, *Albino*.

- Matings :—(1) with an Albino male (from Brood 3 of male VI.C.2.r.); eggs laid; female eaten.

VI.B.4.g. Female, *Albino carrying Red*.

- Matings :—(1) with an Albino male, a, from Brood 2 of male VI.C.1.b.;
- (2) with male b of same brood (**R**+A): (132 young, 71 Red, 61 Albino).

Classes in F₂ Generation.

According to *Hypothesis II*, which has proved to be in agreement with the facts so far ascertained, there should be in the F₂ generation, resulting from the mating of two blacks both carrying red and albino, the following different kinds in the proportions shown :—

<i>Blacks.</i>	Constitution.	Number.
Pure Black	C C B B	1
Black carrying Albino	C c B B	2
Black carrying Red	C C B R	2
Black carrying Red and Albino	C c B R	4

<i>Reds.</i>	Constitution.	Number.
Pure Red	C C R R	1
Red carrying Albino	C c R R	2
<i>Albinos.</i>		
Albino carrying Black	c c B B	1
Albino carrying Red	c c R R	1
Albino carrying Black and Red	c c B R	2

As a result of breeding tests, made either within the generation, or by crossing with known pure reds, all these classes have been proved to exist amongst the offspring of this generation, the actual numbers obtained for the blacks, reds and albinos being given on pp. 302, 317 and 318 respectively.

The results recorded in this section afford further proof of the fact set out in Section I that the imperfect albino eye behaves in inheritance in accordance with the theory formulated by Bateson and Punnett for coat-colour in mice, etc., which assumes in addition to the factors for the individual colours the existence of a factor (C), which must be present if the colour characters are to become visible.

Experiments with the Original Stock (p. 287).

The fact that the absence of coloured retinal pigment in the "all-white" perfect-eyed animals derived from red stock is a somatic character and not hereditary receives some slight support from further breeding experiments which were carried out with the original stock from which the animals came. These experiments give no indication that the abnormality is latent in the stock.

The two all-white specimens had occurred in two succeeding broods from a pair of red-eyed animals (see former paper, p. 45), all the other offspring of which were normal red-eyed animals. Two of these red-eyed offspring survived and 3 young (which reached maturity) were obtained by mating them together. These three were one male and two females, and their eyes, though distinctly red, were much paler in colour than usual, and in other ways not quite normal. The male mated with both the females. Altogether 21 young were obtained, all with normal bright red eyes, and from their matings 17 similar young were produced in the next generation. The 2 females were also mated with the male II.B. (p. 284), a red carrying albino. One female (14.a.) had 29 normal red-eyed young, and the other (14.b.) had 30. Two pairs of these young were mated together; the one pair had a brood of 17 red, and 5 albino all of the usual imperfect form, and the other pair had

39 red-eyed young in three broods. The experiment was not carried further.

The "Part-white" Eye.

The "Part-white" animals referred to in the former paper, p. 43 (Fig. 7), were also investigated, as it appeared probable that the abnormality might be related to that of the "All-white" perfect eye.

In the "part-whites," the eye was of perfect form, the chalk-white accessory pigment was always present, and most of the ommatidia were normal, with black or red retinal pigment developed; some of the ommatidia, however, were quite colourless, thus giving the effect of a patch of white on the eye.

The brood in which the "part-whites" first appeared consisted of 21 young, 13 black and 8 red. Of the red, 4 survived to maturity, 2 being part-white, male and female. The left eye of this male was figured (Fig. 7 in former paper), in the right eye two or three ommatidia were colourless, and on the inner side two ommatidia were separated from the ommateum, one pigmented and one unpigmented. The other "part-white," a female, had a cluster of 9 colourless ommatidia in the right eye and 5 in the left. These two mated several times, but no eggs were laid, and the female died. The male was then mated with a normal red-eyed female and had 30 young, all normal red-eyed animals. These died before reaching maturity.

The male was then mated with a Pure Black female, also a part-white, with a large patch of white on the upper side of the ommateum of the left side, and a small patch in the same position on the right side. This female came from wild stock brought in on July 14, 1915, and left to breed till February 11, 1916. When examined on that date, 60 young were found, 59 normal black-eyed, and the "part-white" female just mentioned.

The result of the mating was a brood of 22 young, all black-eyed. They were left to mate together and on October 3, 1916, 44 young were found, 22 black and 22 red, all normal-eyed.

These young were left to mate together and on February 22nd, 1917, the pots were examined. There were then present 73 young, 36 black and 37 red, all normal-eyed.

It seems certain therefore that the "part-white" character is not inherited.

SECTION III. THE NO-WHITE EYE

(Plate V).

As was mentioned in the former paper (p. 21), a mutation occurred in which the superficial chalk-white, extra-retinal pigment that forms a reticulation in which the ommatidia lie was entirely absent. This was called the "no-white" eye, and a black one was figured (Plate I, Fig. 6). A red one is figured in Plate VII, Fig. 5, of this paper.

The chalk-white extra-retinal pigment is much less resistant to alcohol and formalin than the black or red retinal pigment, quickly disappearing when placed in either of these liquids. It may be noted here, also, that the red retinal pigment is more easily dissolved by alcohol than the black, the latter being practically insoluble.

Animals occur in which the white pigment is present in the eye on one side and absent in that of the other. For details of experiments with these see p. 340.

ORIGIN OF EXPERIMENTAL STOCK.

The "no-whites" with which most of the experiments have been made had the following history:—

A pure black male from Chelson Meadows, which had been tested by mating with two wild females and with two other red females, and had given normal results, was mated with a pure red female (a descendant of the fourth brood of Female A of the former paper, p. 22) and had a large family (Family K, in former paper, p. 31). Of this family 24 survived, 5 males and 19 females, all normal-eyed hybrid blacks; the young from their matings are now called "VII." At least 6 of these females when mated with males from the same family gave some "no-white" young, both black and red. Details are given in the former paper, p. 44.

PROOF THAT "NO-WHITE," i.e. THE ABSENCE OF WHITE PIGMENT, BEHAVES AS A MENDELIAN RECESSIVE TO THE PRESENCE OF WHITE PIGMENT.

One of the red "no-whites" from K family (VII, D.) was mated with a black male from the ordinary hybrid stock (Plate V, Fig. 2). There were 29 young, 12 black and 17 red, all normal-eyed, showing that the presence of white pigment is dominant, and its absence in the "no-white" eye is recessive.

An F_2 brood got by mating together two of the red young ones from the first brood (male e and female g) gave 3 "no-whites" to 13 normal, showing that the abnormality behaved in a Mendelian way and both the red-eyed animals carried the factor for no-white. In other broods, which

were not examined immediately on extrusion, (1) red mated with red (male e and female f) gave 11 normal reds and 2 no-white reds; (2) red mated with red (male e with females f and g) gave 12 normal reds and 5 no-white reds; (3) two black females, 3 red females, and 2 red males belonging to this F_2 generation from the second brood (VII.D.2), left together in the same bowl gave

7 normal blacks, 4 no-white blacks.
11 ,, reds 3 ,, ,, reds.

The proportions are here however not significant, as red may have mated with red, as well as red with black.

Two other experiments give direct evidence of the dominance of normal white pigment over its absence in no-white eyes.

(1) A Red male (VII.E.) with both eyes no-white (**RN**), from K family was mated with a Black carrying the factor for red (**B+R**), and there resulted a brood of 14, all normal-eyed, 7 black (**B+R+N**) and 7 red (**R+N**). When the young ones were mated together, "no-whites" both red and black appeared in the next generation.

(2) A Black male (III.J.) carrying the factors for Red and Albino was mated with a Black no-white female (pp. 280, 329) and had 92 young in four broods, all normal black-eyed.

That these no-white animals behave as simple recessives is illustrated by further matings which will now be described.

A brood resulting from the mating together of two of the hybrid blacks (**B+R**) of K family (Plate V, Fig. 1) consisted of 9 normal black-eyed young, 1 normal red-eyed and 5 black no-whites (VII). Three of these survived to maturity, 2 normal black-eyed females and one black no-white male. The male A mated with each female (B and C) in turn. With female C there were 26 young in three broods, 18 black and 8 red. The blacks consisted of 9 normal blacks, and 9 with no-white on both sides. The 8 red were 2 normal and 6 no-white on both sides.

From this it follows that both the male A and the female C were hybrids as regards red and black.

The male when mated with female B gave 42 young in four broods, all with black eyes, 25 being normal-eyed and 17 being no-whites. Female B is therefore pure black as regards retinal colour.

Both female C and female B in these matings behave as though they were hybrids for the character "no-white." Their no-white offspring when mated together give all no-white young. Thus a male and a female Black no-white (in brood B.1.) gave 3 black no-whites, a similar pair (in brood B.2.) gave 10 black no-whites. A male and a female, both Red no-whites (in brood C.2.) mated together gave 11 red no-whites.

A Black no-white male mated with a Red no-white female in the same brood (C.2.) gave 13 black no-white young. (This Black no-white therefore did not contain the factor for red.)

Brood C.1.b.1., the offspring of a black no-white male (b) with a red female (c) both from brood C.1., gave 1 normal black, 3 no-white blacks, and 2 no-white reds, which is explained by supposing that the black no-white male carries red, and the red female carries the factor for "no-white."

Other illustrations are the following:—

(1) The Red no-white male VII.E. (already used in Experiment (1) referred to on p. 327, where it was mated with a hybrid black female) was mated with a Red no-white female VII.F. of his own stock (Plate V, Fig. 3) and had 26 young in three broods, all red no-whites.

(2) The Red no-white female VII.F. was then mated with the Black no-white male (VII.A., see Fig. 1, Pl. V) and had two broods, with 63 in all, 34 being Black no-whites and 29 Red no-whites. This confirms the hybrid (**B+R**) character of the no-white male, which had already been shown in Fig. 1.

(3) A Black male (**BN.**) and a Red female (**RN.**), both no-whites, out of the same brood from K stock (VII. G and H), gave in one brood 26 young, 13 Black no-whites and 13 Red no-whites.

FURTHER INSTANCES OF "NO-WHITE" EYES ARISING.

In the case of the animals already described with which most of the experiments on the inheritance of no-white eyes were made, the mutation appeared in the hybrid stock. Another instance of a similar origin also occurred and was referred to in the former paper, p. 44. In the A family 7 animals out of 93 surviving produced some no-whites amongst their young. Altogether there were 277 of these young, and of these 126 showed some abnormality in the white extra-retinal pigment. In five cases (four black and one red) it was entirely absent in both eyes; in five other cases (four black and one red) it was entirely absent from the eye of one side only, being normal in the other eye. In the other 116 the white pigment was very much reduced in amount and the reticulation was much broken up. In extreme cases there were only a few bars of white remaining. This gradual disappearance of the white pigment is an interesting feature, and might with advantage be studied further by means of definite breeding experiments. Other instances of a similar kind will be mentioned later.

No-white eyes have also originated independently of those described

above, from wild stock which had not been crossed with red-eyed animals.

From a number of animals brought in from Chelson Meadow on February 11, 1915, certain pairs already mated in the open were put in separate finger-bowls. In the descendants of two of these pairs, no-white eyes have occurred. The pairs and their offspring will be considered separately.

(1) Pair V. In this pair the female had the white pigment very much reduced, the reticulation was perfect but the lines of white were very thin and thread-like. She was mated with a normal-eyed male, and had a fairly large brood which was not examined when young. Of this brood four reached maturity, three males and one female. One of the males mated with the female. The eyes of this male were examined and the white reticulation though perfect was so thin that it required microscopical examination with a 1-inch power to trace it. The eyes of the female were not examined, the male having devoured her after the extrusion of the brood. The brood numbered 13; 5 had a white reticulation which could just be seen under a hand-lens; 6 had eyes like the male parent, in which the reticulation could only be seen with a microscope; 2 had no reticulation and were typical no-whites. All the individuals of this brood were left together in the same finger-bowl, where they remained for some months. At the end of the time 6 very small young were found, all the other animals having died as the conditions in the bowl had become unhealthy. Of the 6 young ones, three had no-white eyes on both sides, one had no-white on the left side and very faintly marked reticulation on the right. The other two were quite normal in appearance. One of the no-whites, a female, was mated with male III.J. (p. 280).

For the mating of the one-sided no-white female see p. 340.

The male referred to above, with very thin white reticulation in the eye, was also mated with a normal red-eyed female. There were 47 black-eyed young, in 45 of these the white reticulation was very much reduced, varying from complete but very thin lines to a few scattered flecks of white, and in many cases more reduced in the eye of one side than in that of the other. In the other two of the 47 young ones the white was completely absent from the eyes of both sides. This result is unexpected because the reduction of the white pigment appears to be dominant over normal white pigment, whereas the absence of white pigment has in other cases always behaved as a recessive.

(2) Pair IV. The parents had normal black eyes, and gave 66 young, all normal. These young were left together for six months, and the vessel in which they were living then contained 28 survivors, three large

ones, 1 male and 2 females, and 25 young. The white pigment in the eyes of both the large females was very much reduced. Twenty-three of the young were black-eyed, half-grown animals, with normal extra-retinal pigment and 2 very small ones, just extruded, one of which had no-white eyes.

(3) A number of the animals brought in on February 11, 1915, were examined and all had normal eyes. They were kept together in one large bell jar, which was not examined until April 5, 1916. The bell-jar then contained 20 animals, all having black eyes with the white normal, excepting in one instance. This was a young animal and there was so little white pigment in the eyes that it required examination with the microscope (1 inch) to detect it.

For another instance of the independent origin of no-white eyes see p. 336.

SECTION IV. THE COLOURLESS EYE.

CROSS BETWEEN COLOURED NO-WHITE AND ALBINO

(Plate VI).

The "albino" eye shows neither black nor red retinal pigment, and is irregular and imperfect in shape, the ommatidia being few in number and unequal in size. The "coloured no-white" eye lacks only the white extra-retinal pigment, the black or red pigment, as well as the shape of the eye, the number, the size, and the arrangement of the ommatidia being normal. When animals with eyes of these two kinds are mated together what is lacking in one is compensated by its presence in the other, and the offspring ought to be quite normal in appearance, since the three defects, lack of coloured pigment, lack of white pigment, and imperfect form are all recessives.

The theoretical analysis is as follows for the case of the albino carrying black and red crossed with a red no-white:—

If W represents the factor for the presence of white pigment and w that for its absence, the other letters being used as before:—

$$W W c c B R \times w w C C R R$$

Albino carrying	Black and Red	Red no-white
Male Gametes	W c B and W c R	
Female Gametes	w C R	
F ₁ Zygotes	W w C c B R	W w C c R R
Black with the white normal but carrying red, albino and no-white.		Red with the white normal carrying albino and no-white.

Similarly if we cross an albino carrying black with a red no-white, we should get all black-eyed offspring, the animals having the same constitution as the above, viz. black with the white normal, carrying red, albino and no-white.

If we cross an albino carrying red with a red no-white, we should get all red-eyed offspring with the white normal, but carrying albino and no-white.

For the next generation, if we mate together two of the black hybrids we should get :—

$$W w C c B R \times W w C c B R$$

Black with the white normal, carrying red, albino and no-white. The gametes are (male and female being the same) :—

W C B, W C R, W c B, W c R, w C B, w C R, w c B, w c R

Zygotes :—

W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
W C B	W C B	W C B	W C B	W C B	W C B	W C B	W C B
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
W C R	W C R	W C R	W C R	W C R	W C R	W C R	W C R
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
W c B	W c B	W c B	W c B	W c B	W c B	W c B	W c B
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
W c R	W c R	W c R	W c R	W c R	W c R	W c R	W c R
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
w C B	w C B	w C B	w C B	w C B	w C B	w C B	w C B
				No-white	No-white	No-white	No-white
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
w C R	w C R	w C R	w C R	w C R	w C R	w C R	w C R
				No-white	No-white	No-white	No-white
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
w c B	w c B	w c B	w c B	w c B	w c B	w c B	w c B
				No-white	No-white	Albino	Albino
						No-white	No-white
W C B	W C R	W c B	W c R	w C B	w C R	w c B	w c R
w c R	w c R	w c R	w c R	w c R	w c R	w c R	w c R
				No-white	No-white	Albino	Albino
						No-white	No-white

That is, out of every 64 animals there should be :—

16 "No-whites," of which	}	1 carrying Black
4 are Albino		1 " Red
and therefore colourless		2 " Black and Red
9 are Black	}	1 Pure Black
		2 Black carrying Albino
		2 Black carrying Red
		4 Black carrying Red and Albino
3 are Red	}	1 Pure Red
		2 Red-carrying Albino
48 with White, of which	}	1 Pure Black
27 are Black		2 Black carrying Albino
		2 " " No-white
		4 " " Albino and No-white
		2 " " Red
		4 " " Red and Albino
		4 " " Red and No-white
		8 " " Red, Albino and No-white
9 are Red	}	1 Pure Red
		2 Red carrying Albino
		2 " " No-white
		4 " " Albino and No-white
12 are Albino	}	1 Albino carrying Black
		2 " " Black and No-white
		2 " " Black and Red
		4 " " Black, Red and No-white
		1 " " Red
		2 " " Red and No-white

This may be summarised as follows :—

27 Black-eyed, 9 Black no-white, 9 Red-eyed, 3 Red no-white, 12 Albino-eyed, 4 Albino no-white or Colourless.

From the above it will be seen that four of the no-whites out of each 64 offspring should be also albinos, that is to say, they should show neither white, black nor red pigment, and should therefore be quite colourless. At the time the analysis was made no animals having a quite colourless eye had been seen, and it was a great satisfaction to us to find

that the first brood of grandchildren got by mating together two black-eyed children of the cross albino by red no-white, consisted of two normal black-eyed animals, one black no-white, and two quite colourless. Since then a number of others with colourless eyes have been bred. The full details of the experiments made may now be given.

Parent Generation.

1. *Albino carrying black and red mated with Red No-white (A+B+R × RN).*

A mating of this kind is illustrated on Plate III, Fig. 6, where the male (II.D.1.j.) is Albino and the female "No-white" (from Family K, Plate V). Eighty young were obtained of which 42 were normal black-eyed animals and 38 normal red-eyed.

Another mating of this kind gave 34 young, 17 normal black-eyed and 17 typical red-eyed young.

2. *Albino carrying black mated with Red No-white (A+B × RN).*

The male II.D.1.k. (Plate II) was mated with a female red "No-white" from Family VII (Plate V) and gave 38 young, all being normal black-eyed animals. (Two of these 38 young which were mated together gave in the first brood 1 colourless young one, which is referred to as C.27, p. 338.)

From several matings of this kind including the one mentioned a total of 158 young was obtained, all normal black-eyed animals. One of these matings is illustrated in Plate IV, Fig. 17 (cf. p. 349).

3. *Albino carrying red mated with Red No-white (A+R × RN).*

From the matings of this kind there resulted 137 young; all typical red-eyed animals.

F.1. Generation from A+B+R × RN.

Three typical experiments are illustrated on Plate VI, Figs. 1, 2 and 3, the ancestry of the animals used being shown on Plate III, Fig. 6.

Black with Black.

Fig. 1 (Plate VI) shows the result of mating together two black offspring (Plate III, Fig. 6, II.D.1.j.2.) of Albino carrying black and red crossed with Red No-white (see Parent generation above, Section I). The first five broods given in the figure consisted of 80 young.

The numbers of each category required by the theory (see p. 332) for 80 young are given below, and those actually obtained are placed beneath them:—

	Normal Blacks.	Black No-whites.	Normal Reds.	Red No-whites.	Normal Albinos.	Colourless (Albino No- whites).
Theory	34	11	11	4	15	5
Experiment ..	38	11	10	3	14	4

Since the Plate was made further broods have been obtained from this pair and the figures now stand as follows, the total number of young being 417 :—

	Normal Blacks.	Black No-whites.	Normal Reds.	Red No-whites.	Normal Albinos.	Colourless (Albino No- whites).
Theory	176	58	58	20	78	26
Experiment ..	185	57	54	27	75	19

In addition to the family illustrated in Fig. 1 (Plate VI) a number of other matings have been made of blacks carrying red belonging to Parent Generation 1 ($\mathbf{A+B+R \times RN}$). Adding together all the figures for the young obtained from these matings we have a total of 663 distributed as follows :—

	Normal Black.	Black No-white.	Normal Red.	Red No-white.	Normal Albino.	Albino No- White (or Colourless).
Theory	278	92	92	30	123	41
Experiment ..	278	93	89	50	118	35

Red with Red.

Fig. 2 (Plate VI) shows the result of mating together two red offspring (Plate III, Fig. 6, II.D.1.j.2.) of Albino carrying black and red crossed with Red No-white. See Parent Generation 1 ($\mathbf{A+B+R \times RN}$).

Theory requires that out of 16 animals, 12 should show white pigment, 9 of them being red and 3 albinos, and 4 should show no-white, 3 of them being red and 1 colourless.

Fig. 2 shows the first 5 broods with a total of 84 young, and the numbers of each category required by theory for this number are given below, with the numbers actually obtained beneath them.

	Normal Reds.	Red No-whites.	Normal Albinos.	Colourless (Albino No-white).
Theory	47	16	16	5
Experiment	48	16	16	4

Since the plate was made further broods have been obtained and the total number of young is 141, distributed as follows :—

	Normal Reds.	Red No whites.	Normal Albinos.	Colourless (Albino No-white).
Theory	79	26	26	9
Experiment	79	26	24	12

In addition to the family illustrated in Fig. 2 (Plate VI) a number of other matings have been made of red with red belonging to this genera-

tion. Adding together all the figures for the young obtained from all the matings of this generation we have a total of 600 distributed as follows:—

	Normal Red.	Red No-white.	Normal Albino.	Colourless (Albino No-white).
Theory	338	112	112	38
Experiment	346	111	105	38

Black with Red.

Fig. 3 (Plate VI) shows the result of mating together a black and a red offspring (Plate III, Fig. 6, II.D.1.j.1.) of Albino carrying black and red crossed with Red No-white. See Parent Generation 1 (**A+B+R × RN**).

In this case theory requires that out of 32 young, 9 should be normal blacks, 9 normal reds, 3 black no-whites, 3 red no-whites, 6 normal albinos and 2 colourless (albino no-whites).

Fig. 3 shows the first 5 broods with a total of 100 young, the theoretical and experimental numbers for the categories being:—

	Normal Blacks.	Black No-whites.	Normal Reds.	Red No-whites.	Normal Albinos.	Colourless (Albino No- whites).
Theory	28	9	28	9	18	6
Experiment	28	15	30	4	20	3

Since the plate was made further broods have been obtained, and the total number of young is 491, distributed as follows:—

	Normal Blacks.	Black No-whites.	Normal Reds.	Red No-whites.	Normal Albinos.	Colourless (Albino No- whites).
Theory	138	46	138	46	92	30
Experiment	109	53	157	45	104	23

F.1. Generation from A+B × RN.

The young belonging to this generation were mated together and produced 434 young, classified as follows:—

	Normal Blacks.	Black No-whites.	Normal Reds.	Red No-whites.	Normal Albinos.	Colourless (Albino No- whites).
Theory	184	61	61	20	82	27
Experiment	164	60	66	27	94	23

F.1. Generation from A+R × RN.

The young belonging to this generation were mated together and produced 220 young, classified as follows:—

	Red.	Red No-white.	Albino.	Albino (Colourless) No-white.
Theory	124	41	41	14
Experiment	127	33	42	13

INDEPENDENT ORIGIN OF COLOURED NO-WHITE AND ALBINO NO-WHITE
OR COLOURLESS EYES.

In the last section colourless-eyed animals were described amongst the grandchildren of the cross Albino eye by No-white eye, and it was shown that these were to be expected according to theory. These animals always had the eye colourless on both sides of the head.

Instances of colourless eyes have also occurred in two families amongst the offspring of our original Albino female mated with a pure Red male (**Cross A**) (Plate I).

(1) The Red-eyed male (I.F.) mated with the Red female (I.E.) had a very large number of young, 780 in twenty-six broods, 589 red eyes and 191 albinos (Plate I). Amongst the reds there was a small number of individuals in which the white extra-retinal pigment had become reduced or entirely disappeared, giving rise to the typical Red No-white eye. In 24 animals the white had almost but not entirely disappeared from one or both eyes, only a few small specks of white being discovered with a 1-inch power, four on right side, eight on left side, and twelve on both sides. In 14 animals the eye on one side had no white pigment (12 on the right side, 2 on the left), that on the other was normal. In 5 animals the white pigment had completely disappeared from both eyes, the eyes being typical Red No-whites.

A similar state of things occurred amongst the Albinos. In seven animals the white pigment had entirely disappeared from the eye of one side (5 on the left side and 2 on the right side), and was present as usual in the eye of the other side. In one animal the white pigment was absent from both eyes, which therefore were quite colourless (see pp. 286 and 339.2).

The following are the details of the No-whites in the successive broods:—

In Brood 1, one Red-eyed animal had the right eye affected, there being only a fleck or two of white; when mature the eye was completely no-white. It died without offspring. Another had very thin reticulation in both eyes. (Several of the next generation had hardly any white pigment in their eyes.)

In Brood 2, one Red-eyed animal had the right eye completely no-white.

In Brood 3, one Albino-eyed animal had the right eye small, and the left eye no-white, i.e. Colourless. (From the mating of two albinos of this Brood 3, 12 young were produced, one of which was Colourless on the right side, and one was Colourless on both sides. In the next generation again, 10 young were obtained from the mating of two of the normal albinos, and one of these again showed the no-white strain, having the right eye Colourless.)

In Brood 4, the animals were all normal-eyed. One Albino, a female, was mated with the Red male from Brood 1, which had very thin white reticula-

tion in both eyes, and in their offspring the no-white strain appeared. (Out of 76 young produced by this pair 38 were Red-eyed, 29 with normal eyes, 3 with one eye normal and the other no-white, and 6 no-white on both sides; 38 Albinos, 22 of which were normal-eyed and 16 no-white, i.e. Colourless. Two of these young albinos have mated, and had 41 young, 33 normal Albino-eyed and 8 Colourless, which is the usual 3:1 ratio. The Colourless have also had offspring, 8 all Colourless.)

In Brood 5, one Red-eyed had the right eye practically no-white, with only a fleck or two of white pigment, left eye normal. (Examined again at maturity the right eye was found to have developed the normal white reticulation, cf. p. 340.4.) One Albino had the left eye Colourless. (In the first brood of 13 young of the next generation one Red-eyed had the left eye no-white, and very little white pigment in the right eye.)

In Brood 6, one Red-eyed animal had the right eye no-white, and one Albino had the left eye Colourless. (In the next generation one Red had the left eye no-white, and very little white pigment in the right eye.)

In Broods 7 and 8, which were not examined for some days after extrusion, the animals were all normal-eyed.

In Brood 9 three Red-eyed animals were affected, one with the right eye, one with the left eye, and one with both eyes no-white; and two Albinos, one having the right eye and one both eyes no-white.

In Brood 10, all the animals were normal-eyed.

In Brood 11, one Albino had the left eye no-white.

In Brood 12, two Reds had both eyes practically no-white.

In Brood 13, one Red had both eyes practically no-white.

In Brood 14, three Red-eyed were affected, two had the right eye and one had both eyes no-white.

A number of other Reds in Broods 10 to 14 showed a tendency for the white reticulation to break down.

In Brood 15 two Red-eyed had the right eye no-white, and one of the two had the reticulation much broken on the left side. Two others had the reticulation so much broken, one on the right and one on the left, as to be practically no-white, and in many others the reticulation was very thin. One Albino had the right eye affected, there being only one spot of the white pigment at the upper end of the eye.

In Brood 16, two of the Red-eyed had the left eye practically no-white.

In Brood 17, three Red-eyed were affected, one with the right eye, and two with the left practically no-white.

In Brood 18, one Red-eyed had the right eye no-white, and one Albino had the right eye no-white, and a very small eye on the left side.

In Brood 19, one Red-eyed was no-white on both sides.

In Brood 20, all the animals were normal-eyed.

In Brood 21, one Red-eyed had the right eye and one had the left eye no-white.

In Brood 22, two Red-eyed had hardly any white pigment in the eyes, and one Albino had the left eye Colourless.

In Brood 23 all the Red-eyed animals had the red pigment much reduced, giving a yellow appearance to the eyes, and two had the left eye practically no-white. This brood is breeding and has given so far, normal Reds, Red no-whites, one-sided Red no-whites and Albinos.

In Brood 24, the red pigment was greatly reduced, only 2 out of 19 Red-eyed showing a faint pink tinge, the others were of a pale yellow tint. Seven of them had hardly any white pigment, and in one of them the right eye was practically no-white. One Albino had the right eye very small.

In Brood 25, the coloured pigment in the Red-eyed animals was the normal bright red tint, one had very thin reticulation on the left side, one had the right eye no-white, and very thin reticulation in the left, one had the right eye no-white, with no red pigment in the centre of the eye, two had both eyes no-white.

The last Brood, 26, consisted of only three animals, Red-eyed, with the red pigment much reduced.

(2) The same Red-eyed male (I.F.) was mated with another Red-eyed female (I.G.) from the same brood as the last and had in 3 broods 46 red-eyed and 18 albino-eyed young (Plate I). The 3rd brood consisted of 25 red and 12 albino-eyed young. These were left together in one bowl, and 15 young were obtained from their chance matings, 4 red, 8 albino and 3 with colourless eyes on both sides.

Two of these colourless ones survived, a male and a female (Plate V, Fig. 5). For details of offspring, see p. 339.3.

CONSTITUTION OF THE COLOURLESS EYE.

That these colourless eyes, whether obtained by breeding together no-whites and albinos (see p. 330) or having an independent origin, behave as recessives to white and to colour is shown by the following results:—

1. (a) A female with both eyes Colourless (C.27, see p. 333), belonging to the F_2 generation from the mating Albino carrying black crossed with Red No-white, was mated with an Albino male (Plate II, VI.B.2.t.) and produced 108 young in 5 broods all with the usual albino eyes.

Two of these broods have reached maturity and from their matings 218 young have been obtained, 163 with the usual albino eyes, and 50 albino no-whites. Theory demands for this number 164 albinos and 54 albino no-whites (Colourless).

Some of the albino-eyed young of this second generation have just become mature, and when mated together gave 19 albino-eyed and 5 albino-no-whites (Colourless).

(b) From another mating of this kind, Colourless female with Albino male, one brood of 18 young resulted, all with normal albino eyes. These

mated together have given 106 young, 85 Albino-eyed and 21 Albino no-whites.

(c) The first F_3 brood from F_2 albinos ($\mathbf{A}+\mathbf{R}+\mathbf{N} \times \mathbf{A}+\mathbf{R}+\mathbf{N}$) from the family described on p. 336 numbered 55, 45 usual-eyed albinos and 10 albino no-whites, i.e. Colourless. Theory requires 41 albinos and 14 Colourless.

2. A female with both eyes Colourless ($\mathbf{AN}+\mathbf{R}$) (Plate VII, Fig. 6) (whose parents are shown on Plate I, viz. I.E.3.l. ♂ and I.E.3.o. ♀, and whose ancestry is discussed on p. 336), the colourless character having originated independently, was mated with a Red No-white male \mathbf{RN} descended from Family VII. The resulting broods are charted on Plate V, Fig. 4, there being 177 young, all with Red No-white eyes.

The offspring obtained by mating together individuals from the first brood of these young ones are shown on the plate. In the ten broods figured there were 124 young, 89 Red No-whites ($=\mathbf{RN}+\mathbf{AN}$) and 35 Colourless ($\mathbf{AN}+\mathbf{R}$). Altogether in this generation we have obtained

481 young, 359 Red No-whites and 122 Colourless. Theory requires
 361 " " " 120 "

From the mating of the first two F_2 young which matured, a Red No-white male with a Colourless female, 24 young were obtained, $\mathbf{RN}+\mathbf{AN}$ 14 and $\mathbf{AN}+\mathbf{R}$ 10. The first mating from the next generation F_3 ($\mathbf{RN}+\mathbf{AN} \times \mathbf{RN}+\mathbf{AN}$) produced 14 $\mathbf{RN}+\mathbf{AN}$ and 3 $\mathbf{AN}+\mathbf{R}$.

3. Of the three Colourless-eyed young referred to on p. 338, which arose independently, two survived, a male and a female. These two mated together and the three first broods are shown on Plate V, Fig. 5. Altogether they produced 85 young, all Colourless (F_1). The first brood of these has reached maturity, and mated together these have produced 386 young all with colourless eyes (F_2). The first two of these broods are shown on the Plate. Some of these F_2 broods have just reached maturity, and in chance matings within the brood have produced 10 young, all Colourless (F_3).

SECTION V. ONE-SIDED NO-WHITES. ANIMALS WITH ONE EYE NORMAL AND THE OTHER ABNORMAL.

A number of instances have occurred in which the eye on one side of the head was normal, whilst that on the other was either a coloured "no-white" eye or a colourless eye, i.e. an albino "no-white."

In most cases these animals died before maturity, so that up to the present, we have never had males and females mature at the same time, to breed together.

We have therefore mated the few one-sided no-whites which survived with normal-eyed animals and with typical no-whites. The details of the experiments are as follows:—

1. Red female, *No-white on the Left side*, the white reticulation rather broken on the Right side, mated with a Red no-white male (Plate VI, Fig. 4).

This female is descended from the **B+R+A** female, VI.A.1.h. (p. 293), which was mated with a Red male from Pure Red Stock, and gave a brood of 7 young, 3 Black and 4 Red, hatched on May 18, 1916. On examining the brood, August 18, 1916, two Black females and three Red males were found with 25 young (6 Black and 17 Red), 23 of which were normal-eyed, and two, a Red and a Black (see 4), were no-white on the Left side.

The Red one was again examined on reaching maturity and the Left eye was found unchanged, still no-white. It was mated with a Red no-white male (i.e. one practically normal eye, to three no-white eyes), and produced 20 young, all with normal Red eyes (**R+N**).

These young were mated together and gave a total of 490, 365 Red-eyed, and 125 Red no-whites. In each animal both eyes were of the same type. The results therefore are in full agreement with the Mendelian theory of the dominance of the white pigment, the numbers required by the theory being 367 Red-eyed to 122 Red no-white.

2. A Black female from Pure Black stock (p. 329) *with the Left eye no-white*, and very little white reticulation in the Right eye, mated with a No-white male from the same stock and had 15 young, all with normal Black eyes.

3. An Albino female *with the Left eye no-white*, i.e. Colourless. Parentage, Albino male carrying Black (**A+B**) from Brood 1 of III.B (p. 279) and Red female IV.Y (p. 285). The female was mated with an Albino male, the eyes of which were very small and the shape of the head abnormal on both sides; 271 young were produced, all with the usual Albino eyes and head shape normal. From 3 pairs of these young mated within the brood 122 offspring were obtained, 121 being normal albinos and 1 being colourless on the left side and normal albino on the right, exactly resembling the grandmother.

4. It may be interesting to add here the account of the young Black female referred to in paragraph 1, above, and of the same parentage as the Red female described.

When hatched the Left eye was no-white, and the Right eye had only one streak of white in it. It was examined again at maturity and it was

then found that the Right eye had developed the normal white reticulation, and the left eye had the upper half with the white reticulation, the lower half no-white. Mated with a Red no-white male, it had 64 offspring $\mathbf{B}+\mathbf{R}+\mathbf{N}$ 31 and $\mathbf{R}+\mathbf{N}$ 33, all with normal eyes.

Two pairs of these have produced young; the first pair, Black with Red, had 83 young, 45 Black, 4 Black no-white, 24 Red, 10 Red no-white; and the second pair, Red ($\mathbf{R}+\mathbf{N}$) with Red ($\mathbf{R}+\mathbf{N}$), gave 53 young, 39 Red, 14 Red no-white, none showing any variation from the normal types.

These Red F_2 young are now mature, and their matings Red no-white by Red no-white have given 13 Red no-white, and Red ($\mathbf{R}+\mathbf{N}$) by Red no-white have produced 26 young, 11 Red and 15 Red no-white.

SUMMARY.

Sections I and II. Amongst the stock of *Gammarus chevreuxi* which had been kept under Laboratory conditions for at least two years a small number of animals appeared in which the coloured retinal pigment was absent, whilst the white extra-retinal pigment remained. The experiments described in the present paper have shown that these eyes were of two different kinds.

Eyes of the first kind were derived from a stock which originated in a cross between Black-eyed and Red-eyed animals, and were degenerate and irregular in shape. Four animals of this kind appeared in one brood, and such eyes have since been seen only in direct descendants from these. Eyes of this kind were found to behave as simple Mendelian recessives to eyes showing coloured retinal pigment, whether that pigment was red or black, and they are referred to in this paper as "albino" eyes.

Eyes of the second kind were derived from a pure red-eyed stock, and were perfect in shape. The absence of coloured pigment has been shown not to be inherited, and the one animal of the kind experimented with, when mated with a female of the first kind, gave all coloured offspring. By a study of the descendants of these coloured offspring it has been shown that the parent animal behaves in inheritance exactly as if it were one with normal red eyes.

In the course of this investigation all possible crosses have been made between Black-eyed, Red-eyed and Albino-eyed animals. In this way 4 different kinds of black-eyed animals were produced, viz. pure black, black carrying albino, black carrying red, and black carrying red and albino; 2 different kinds of red-eyed animals, viz. pure red and red carrying albino; 3 different kinds of albinos, viz. albino carrying black, albino carrying red, and albino carrying black and red.

The figures given below show the number of offspring obtained in our experiments by mating together animals of the constitutions specified in each heading. These are summary figures, giving the totals for all crosses of each particular kind, and include many cases which are not referred to in the previous sections of the paper. The figures demanded by theory are placed below those given by our experiments. The total number of animals of which both eyes were examined for eye-colour to Sept. 8th, 1917, is 26,553.

The figures are arranged in the following order under the different eye-colours:—

1. The matings giving offspring all of one colour ;
2. Those giving offspring of two colours in the proportion 3 : 1 ;
3. Those giving offspring of two colours, half of one and half of the other ;
- 4.-7. Those giving offspring of three colours.

1. *Matings giving normal-eyed* offspring all of one colour.*

Black, offspring all normal-eyed Black in appearance, in agreement with theory.

	Number of young, Black-eyed.	
B × B	275	
B × B + R	146	
B × B + A	87	
B × B + R + A	17	
B × R	618	
B × R + A	126	
B × A + B	18	
B × A + R	79	
B + R × B + A	46	
B + A × R	251	
B (half no-white) × BN	15	
BN × B + R + A	92	
A + B × R	87	
A + B × RN	158	Total, 2015.

Red, offspring all normal-eyed Red in appearance, in agreement with theory.

	Number of young, Red-eyed.	
R × R	1525	
R × R + A	679	
R × A + R	259	
R × RN	24	
RN × A + R	137	
R (half no-white) × RN	20	Total, 2644.

* In this section the word "normal-eyed" is used in the sense that the chalk-white extra-retinal pigment is present.

Albino, offspring all the usual-eyed Albino in appearance, in agreement with theory.

	Number of young, Albino-eyed.	
$A+(?) \times A+(?)$	1157	
$A+R \times A+R$	225	
$A+R \times A+(?)$	330	
$A+R \times A+B+R$	103	
$A+R \times AN$	126	
$A+(?)(\text{half no-white}) \times AN$	271	Total, 2212.

2. *Matings giving normal-eyed offspring of two colours in the proportion 3 : 1.*

<i>Black.</i>		Number of young.		
		Black-eyed.	Red-eyed.	
$B+R \times B+R$	Experiment	735	249	
	Theory	738	246	
$B+R \times B+R+A$	Experiment	300	90	
	Theory	292	97	
$B+R \times A+B+R$	Experiment	7	2	
	Theory	7	2	
$B+R \times A(?)$	Experiment	13	7	
	Theory	15	5	Total, 1403.

		Black-eyed.	Albino-eyed.	
		Experiment	468	
$B+A \times B+A$	Theory	468	156	
	Experiment	144	59	
$B+A \times B+R+A$	Theory	153	51	
	Experiment	481	158	
$B+A \times R+A$	Theory	480	160	Total, 1466.

<i>Red.</i>		Red-eyed.	Albino-eyed.	
		Experiment	1408	
$R+A \times R+A$	Theory	1408	470	Total, 1879.

3. *Matings giving normal-eyed offspring of two colours in the proportion 1 : 1.*

<i>Black.</i>		Number of young.		
		Black-eyed.	Red-eyed.	
$B+R \times R$	Experiment	403	410	
	Theory	406	406	
$B+R \times R+A$	Experiment	44	48	
	Theory	46	46	
$B+R \times RN$	Experiment	50	57	
	Theory	53	53	
$B+R \times A+R$	Experiment	71	95	
	Theory	83	83	

<i>Black.</i>		Number of young.		
		Black-eyed.	Red-eyed.	
B+R+A×R	Experiment	180	165	
	Theory	172	172	
B+R+A×RN	Experiment	18	16	
	Theory	17	17	
A+B+R×R	Experiment	87	72	
	Theory	79	79	
A+B+R×RN	Experiment	31	31	
	Theory	31	31	Total, 1778.
B+A×A+R	Experiment	103	106	
	Theory	104	104	
B+A×A+B+R	Experiment	5	16	
	Theory	10	10	
B+A×A+(?)	Experiment	24	25	
	Theory	24	25	
A+B×B+R+A	Experiment	8	6	
	Theory	7	7	
A+B×R+A	Experiment	76	77	
	Theory	76	77	Total, 446.
<i>Red.</i>		Red-eyed.	Albino-eyed.	
	R+A×A+R	Experiment	601	554
	Theory	577	577	Total, 1155.

4. *Matings giving normal-eyed offspring of three colours in the proportion 9 : 3 : 4.*

B+R+A×B+R+A		Number of young.		
		Black-eyed.	Red-eyed.	Albino-eyed.
Experiment		542	189	241
Theory		547	182	243

5. *Matings giving normal-eyed offspring of three colours in the proportion 3 : 1 : 4.*

B+R+A×A+B+R	Experiment	11	4	16
	Theory	12	4	15

6. *Matings giving normal-eyed offspring of three colours in the proportion 1 : 1 : 2.*

A+B+R×R+A	Experiment	84	92	147
	Theory	81	81	162
B+R+A×A+R	Experiment	31	8	34*
	Theory	18	18	26

* These totals are made up as follows :—

	Black.	Red.	Albino.
VI. A. 1. d. ♂ × VI. B. 2. u. ♀	1	3	20
VI. C. 2. k. ♀ × VI. C. 2. u. ♂	17	1	3
VI. C. 3. e. ♀ × VI. B. 2. t. ♂	13	4	11
	31	8	34

It will be seen that two of these families gave unexpected numbers.

7. *Matings giving normal-eyed offspring of three colours in the proportion 3 : 3 : 2.*

		Number of young.		
		Black-eyed.	Red-eyed.	Albino-eyed.
B+R+A × R+A	Experiment	235	169	144
	Theory	205	205	137

It will be noticed that in both this and the preceding instance the proportion of total coloured (red and black combined) to albino is in good agreement with the Mendelian theory. In each case, however, the experiment gives a great excess of blacks over reds, whereas theory requires equality in each case. The numbers are fairly large and it is possible that this result may have some significance.

Section III. Animals occurred in which the chalk-white extra-retinal pigment of the eyes was absent. These we have called "no-whites." This mutation appeared independently in several different stocks, and there is evidence that it may be produced in a series of steps or stages, the white pigment being gradually reduced in amount. In some cases the two eyes of the same animal differ in respect to the presence or absence of white pigment, or in the amount of white pigment. The "no-white" eye behaves in inheritance as a simple Mendelian recessive to the presence of white.

The following numbers are derived from the experiments made with these animals, including also the experiments made with the Albino no-whites (**AN**) or Colourless, described in the next Section.

1. *Matings giving no-white-eyed offspring all of one colour.*

Black, offspring all Black no-white in appearance, in agreement with theory.

	Number of young, Black no-white.
BN × BN	13
BN × RN	13

Red, offspring all Red no-whites in appearance, in agreement with theory.

	Red no-whites.
RN × RN	61
RN × AN + R	177

Albino, offspring all Albino no-white in appearance, in agreement with theory.

	Albino no-whites (i.e. Colourless).
AN × AN	489

2. *Matings giving No-white offspring of 2 kinds in the proportion 3 : 1.*

		Number of young.	
		Red no-whites.	Albino no-whites.
RN+AN × RN+AN	Experiment	373	125
	Theory	373	125

3. *Matings giving No-white offspring of 2 kinds in the proportion 1 : 1.*

		Number of young.	
		Black no-whites.	Red no-whites.
BN+R × RN	Experiment	47	42
	Theory	44	44
RN+AN × AN+R	Experiment	Red. 14	Albino. 10
	Theory	12	12

4. *Matings of normal-eyed animals carrying the factor for No-white, the offspring of crosses between normal-eyed and no-whites.*

(a) Those which give normal and no-white eyes of one colour in the proportion of 3 normal to 1 no-white, i.e. 3 : 1.

<i>Black.</i>		Number of young.	
		Black.	Black no-whites.
B+N × B+N	Experiment	24	7
	Theory	23	8
<i>Red.</i>		Red.	Red no-whites.
R+N × R+N	Experiment	440	149
	Theory	441	147
<i>Albino.</i>		Albino.	Albino no-whites.
A+R+N × A+R+N	Experiment	45	10
	Theory	41	14
A+N × A+N	Experiment	246	72
	Theory	238	79

(b) Those which give normal and no-white eyes in two colours in the proportions 9 : 3 : 3 : 1.

R+A+N × R+A+N	Normal	Red	Normal	Colourless
	Red.	No-white.	Albino.	(Albino No-white).
Experiment	473	149	147	51
Theory	461	153	153	51
[B+R+N × B+R+N	Normal	Black	Normal	Red
	Red.	No-white.	Red.	No-white.
Experiment	73	24	18	6
Theory	67	23	23	7

Note.—This is the K family VII, referred to on p. 326 in which the No-white mutation arose independently.]

(c) Those which give normal and no-white eyes in two colours in the proportions 3 : 1 : 3 : 1.

$B+R+N \times R+N$	Normal Black.	Black No-white.	Normal Red.	Red No-white.
Experiment	45	4	24	10
Theory	31	10	31	10
$B+R+A \times R+N$				
Experiment	7	3	3	1
Theory	6	2	6	2

(d) Those which give normal and no-white eyes in three colours in the proportions 9 : 3 : 9 : 3 : 6 : 2.

$B+R+A+N \times R+A+N$	Normal Black.	Black No-white.	Normal Red.	Red No-white.	Normal Albino.	Colourless (Albino No-white).
Experiment	109	53	157	45	104	23
Theory	138	46	138	46	92	30

(e) Those which give normal and no-white eyes in three colours in the proportion 27 : 9 : 9 : 3 : 12 : 4.

$B+R+A+N \times B+R+A+N$	Normal Black.	Black No-white.	Normal Red.	Red No-white.	Normal Albino.	Colourless (Albino No-white).
Experiment	442	153	155	77	212	58
Theory	461	154	154	51	205	68

5. *Matings of animals, one normal-eyed carrying no-white, the other no-white.*

(a) Those which give normal and no-white eyes in one colour in the proportion 1 : 1.

$B+N \times BN+R$	Experiment	Normal Black.	Black No-white.
Theory		20	12
		16	16
$R+N \times RN$	Experiment	Normal Red.	Red No-white.
Theory		11	15
		13	13

(b) Those which give normal and no-white eyes in two colours in the proportions 3 : 3 : 1 : 1.

$B+R+N \times BN+R$	Normal Black.	Black No-white.	Normal Red.	Red No-white.
Experiment	26	21	3	10
Theory	22.5	22.5	7.5	7.5

Section IV. By breeding together "albinos" and "no-whites" a certain proportion of offspring are produced in which both the coloured retinal pigment and the white extra-retinal pigment are absent. The

eyes of these are quite colourless. The figures for these are given under Section III, Summary (pp. 346 and 347, b, d and e).

In addition to the colourless-eyed animals obtained by crossing albino- and no-whites, the colourless eye has arisen independently as a mutation.

Colourless-eyed animals mated together give all colourless-eyed offspring. The figures for these are given under Section III, Summary (p. 345. **AN** × **AN**).

GENERAL CONSIDERATIONS.

The phenomena described in the present paper show a progressive degeneration of the eye of *Gammarus*, taking place in a series of definite steps or stages, each of considerable magnitude. In the end we see the entire loss of the eye-pigment, together with a broken and irregular arrangement of the ommatidia and a great reduction in their number. We only need to imagine the continuation of this process for a few further steps, and we should reach the complete absence of eyes found in those blind genera of Amphipoda, which live in subterranean waters.

There is no direct proof that the change from the black eye-pigment of the wild animal to the red pigment, which occurred as a mutation in the eyes of the animals first used in the experiments, is due to the loss of a factor, but it seems not improbable that this may be the case. It is clear, at any rate, that these degenerative changes—the change from black pigment to red pigment, the entire loss of the coloured retinal pigment, the loss of the white extra-retinal pigment, and the degeneration in the form of the eye—all take place in exact conformity with Mendel's Law. The only feature which may at first sight seem to show a divergence from this law is the more gradual process of degeneration of the white extra-retinal pigment, which gives rise to what we call the "no-white" eyes described in Section III. This, however, may perhaps be capable of explanation by supposing that the loss of the pigment takes place in a series of steps, instead of in one single step.

The experiments recorded throw little or no light on the question of the conditions under which mutations arise or of the causes which give rise to mutations. The mutation of red eye-pigment has arisen once only in the whole course of the work and then after the animals had been kept under Laboratory conditions for only 2 generations.

The complete loss of the inter-retinal coloured pigment, giving rise to the "albino" eye, was first seen in one brood belonging to a particular family as described on p. 275, the female parent being from stock which had been living under laboratory conditions for over 3 years, and the male parent also from stock which had been in the laboratory for several generations. Out of 733 offspring of the same family, 4 with albino eyes

occurred, all in one brood, two of which survived to produce offspring. All the animals used in the experiments were descendants of these two and the mutation has never occurred again.

The loss of the white, extra-retinal pigment, on the other hand, has originated apparently independently on several occasions. It is discussed in detail on p. 336. There seem to be some grounds for concluding that the loss of this pigment occurs when animals have been allowed to remain together for long periods and to interbreed promiscuously under somewhat unfavourable conditions as regards the quantity of water in which they are kept and the amount of food available. The loss of this pigment too, as already mentioned, seems sometimes to occur rather gradually and not suddenly as in the case of the change from black to red or the loss of the red.

Quite colourless eyes have arisen independently from albinos by the loss of the white extra-retinal pigment, just in the same way that no-white eyes have arisen from normal red and black eyes. Cases of this kind have been discussed on pp. 336-338.

A point of general interest which is somewhat strikingly illustrated by experiments described in this paper is the way in which the offspring of two abnormal, in this case degenerate, parents may themselves be quite normal in their characters, but are nevertheless capable of transmitting the abnormalities to their children. Such a case is that described on p. 333 (paragraph 2), where an Albino male (i.e. a male whose eye contained only the white extra-retinal pigment but neither black nor red inter-retinal pigment) was mated with a female Red No-white (i.e. one whose eyes contained only red inter-retinal pigment) with the result that all the young were black-eyed animals, normal in form and colour and indistinguishable on inspection from their wild ancestors (Plate VII, Figs. 4 and 5; Plate IV, Fig. 17). When, however, these or black-eyed animals of similar constitution are mated together the essential difference between them and the wild form comes out at once, all the abnormalities of the grandparents being reproduced in the grandchildren, and these abnormalities may even be combined in such a way that some of the grandchildren are more abnormal than the grandparents from whom they sprang. In the particular case mentioned the offspring consist, on the average, of 27 normal blacks, 9 black no-whites, 9 normal reds, 3 red no-whites, 12 normal albinos and 4 colourless (albino no-whites). (Cf. Plate VI, Fig. 1.)

Other results of a similar kind are recorded on p. 333 and the following pages.

EXPLANATION OF PLATES.

Plate I.

FIG. 1.—Explanation of the signs employed in the diagrams.

Normal Black, i.e. with both the black retinal and the white extra-retinal pigments present.

Black no-white, with the black retinal pigment present, the white pigment absent.

Red normal, with both the red retinal and the white extra-retinal pigments present.

Red no-white, with the red retinal pigment present, the white pigment absent.

Normal Albino, with the white pigment present, the coloured retinal pigment absent.

Albino no-white or *Colourless*, with both the coloured retinal and the white extra-retinal pigments absent.

A black spot attached outside the large circles indicates that the animal carries the factor for Black. Similarly, a red spot indicates that the factor for Red is carried, a small black circle the factor for Albino, and a small red circle the factor for No-white.

The small V-shaped sign outside the large circles means that it has not been determined whether the factor usually indicated in the position where the sign is placed is present or absent.

FIG. 2.—The matings of the Albino female A.C. (Albino carrying the factors for Black and Red) with a Red male and a Black male.

Cross A. (p. 275) with the male R.2 from Pure Red Stock.

One brood, I, and the young from their inter-matings.

Cross B. (p. 278) with the male K.A. Black carrying the factor for Red from Family K (p. 326 and Plate V).

Four broods, II, III, IV and V.

Many of the young died before reaching maturity. The constitution of those which survived to be tested is shown when known.

Plate II.

Cross C. The mating of the Albino female A.B. (Albino, carrying the factors for Black and Red), with the All-White male R.I.; the brood resulting from this mating is designated VI.

Cross B. The mating of the Albino female A.C. (from the same brood and of the same constitution as A.B.) with the male K.A. from the family K, shown on Plate V, Fig. 1, Black carrying the factor for Red; the brood from this mating is designated II. The number of the offspring resulting from the cross-mating of Brood VI, with Brood II, together with the sex, and constitution when known, of the surviving animals, are shown below. Animals to which no letter is attached could not be tested for constitution.

II.D 1, 2, 3, 4, are broods from the mating of two animals of Brood II. The number of young is shown, and the sex of those which reached maturity, but not the constitution, as, except in two or three instances, they were not tested for the factors carried.

Plate III.

FIG. 1.—*Mating of Albino with Albino*; offspring all Albino-eyed.

The male (h) and the female (l) are both from the second brood of II.D. (p. 279, Plate II).

FIG. 2.—*Mating of Albino carrying the factor for Black with Pure Red*; offspring all Black-eyed.

The male (**A+B**) is from the first brood of III.B. (p. 279, Plate I); the female (**R**) is VI.B.2.g. (p. 314, Plate II).

FIG. 3.—*Mating of Albino carrying the factor for Black with Red carrying the factor for Albino*; half the offspring Black-eyed, half Albino-eyed.

The male (**A**+**B**) is from the same brood as the male of Fig. 2 (pp. 279 and 286), the female (**R**+**A**) IV.Z. (p. 285, Plate I).

FIG. 4.—*Mating of Albino carrying the factor for Red with Pure Red*; offspring all Red-eyed.

The male (**R**) and the female (**A**+**R**) are both from a brood of the female I.G. of Cross A (p. 286).

FIG. 5.—*Mating of Albino carrying the factor for Red with Red carrying the factor for Albino*; half the offspring Red-eyed, and half Albino-eyed.

Both the male (**R**+**A**) and the female (**A**+**R**) are from the same brood as the pair of Fig. 4 (p. 286).

FIG. 6.—*Mating of Albino carrying the factors for Black and Red with Red No-white*; half the offspring, Black-eyed, carrying the factors for Red, Albino and No-white, and half Red-eyed, carrying the factors for Albino and No-white.

The male (**A**+**B**+**R**) is II.D.I.j. on Plate II (p. 333); the female is a Red no-white from Family K (Plate V, Fig. 1).

Some of this brood came to maturity, but died before their constitution could be proved; their sex is shown in the diagram, but no distinctive letters have been given them.

Plate IV.

FIG. 1.—*Mating of Black carrying the factors for Red and Albino with Pure Red*; half the offspring Black-eyed, half Red-eyed.

The female (**B**+**R**+**A**) (also in Figs. 2 and 3) is VI.A.1.l. (p. 293, Plate II); the male (**R**) came from the Pure Red Stock.

FIG. 2.—*Mating of Black carrying the factors for Red and Albino with Black carrying the factor for Red only*; offspring in the proportion of 3 Black-eyed to 1 Red-eyed.

Both animals from the one brood; the same female (**B**+**R**+**A**) as in Fig. 1 mated with the male (**B**+**R**) VI.A.1.a. (p. 291, Plate II).

FIG. 3.—*Mating of Black carrying the factors for Red and Albino with Red carrying the factor for Albino*; offspring should consist of Black-eyed, Red-eyed and Albino-eyed animals.

The same female (**B**+**R**+**A**) as in the two previous figures mated with the male (**R**+**A**) VI.C.1.o. (p. 310, Plate II).

FIG. 4.—*Mating of Black carrying the factor for Red only with Pure Red*; half the offspring Black-eyed, and half Red-eyed.

The same male (**B**+**R**) as in Fig. 2, mated with a female (**R**) from the Pure Red Stock.

FIG. 5.—*Mating of Black carrying the factor for Red only with Black carrying the factors for Red and Albino*; offspring in the proportion of 3 Black-eyed to 1 Red-eyed.

The same male (**B**+**R**) as in Figs. 2 and 4, mated with the female (**B**+**R**+**A**) VI.C.1.d. (p. 297, Plate II).

FIG. 6.—*Mating of Black carrying the factors for Red and Albino with Red carrying the factor for Albino*; offspring should consist of Black-eyed, Red-eyed and Albino-eyed animals.

Both animals from the one brood; the same female (**B**+**R**+**A**) as in Fig. 5; the male (**R**+**A**) as in Fig. 3.

FIG. 7.—*Mating of Pure Black with Pure Red*; offspring all Black-eyed.

The male (**B**) VI.A.1.c. (p. 292, Plate II); the female (**R**) from the Pure Red Stock.

- FIG. 8.—*Mating of Pure Black with Red carrying the factor for Albino*; offspring all Black-eyed.
Both animals from the one brood; the same male (**B**) as in Fig. 7; the female (**R**+**A**) VI.A.1.q. (p. 309, Plate II).
- FIG. 9.—*Mating of Red carrying the factor for Albino with Red carrying the factor for Albino*; offspring in the proportion of 3 Red-eyed to 1 Albino-eyed.
Both animals from the one brood; the male (**R**+**A**) VI.A.1.n. (p. 309, Plate II); the female (**R**+**A**) VI.A.1.q. (also in Figs. 8 and 10).
- FIG. 10.—*Mating of Red carrying the factor for Albino with Pure Red*; offspring all Red-eyed.
Both animals from the one brood; the same female (**R**+**A**) as in Figs. 8 and 9; the male (**R**) VI.A.1.m. (p. 308, Plate II).
- FIG. 11.—*Mating of Red carrying the factor for Albino with Pure Red*; offspring all Red-eyed.
Both animals from the one brood; the same male (**R**) as in Fig. 10; the female (**R**+**A**) VI.A.1.p. (p. 309, Plate II) (also in Fig. 12).
- FIG. 12.—*Mating of Red carrying the factor for Albino with Red carrying the factor for Albino*; offspring in the proportion of 3 Red-eyed to 1 Albino-eyed.
The male (**R**+**A**) is II.B. (p. 284, Plate II); the female (**R**+**A**) VI.A.1.p. (also in Fig. 11).
- FIG. 13.—*Mating of Black carrying the factor for Albino only with Pure Red*; offspring all Black-eyed.
The female (**B**+**A**) VI.C.1.k. (p. 298, Plate II); the male **R** from the Pure Red Stock.
- FIG. 14.—*Mating of Black carrying the factors for Red and Albino with Black carrying the factor for Albino only*; offspring in the proportion of 3 Black-eyed to 1 Albino-eyed.
Both animals from the one brood; the male (**B**+**R**+**A**) VI.C.1.b. (p. 297, Plate II); the female (**B**+**A**) VI.C.1.k. was used in the previous figure.
- FIG. 15.—*Mating of Black carrying the factors for Red and Albino with Black carrying the factors for Red and Albino*; offspring in the proportion of 9 Black-eyed to 3 Red-eyed to 4 Albino-eyed.
Both animals from the one brood; the male (**B**+**R**+**A**) was used in the previous figure; the female (**B**+**R**+**A**) VI.C.1.f. (p. 298, Plate II).
- FIG. 16.—*Mating of Albino carrying the factor for Black only with Pure Red*; offspring all Black-eyed.
The male (**A**+**B**) VI.A.1.r. (p. 318, Plate II); the female (**R**) from the Pure Red Stock.
- FIG. 17.—*Mating of Albino carrying the factor for Black only with Red No-white*; offspring all normal Black-eyed.
The same male (**A**+**B**) from the previous experiment—Fig. 16; the female (**RN**) VII.C.3.a. (p. 333) is an F_3 from the Family VII figured on Plate V.
- FIG. 18.—*Mating of Albino carrying the factor for Red only with Red carrying the factor for Albino*; half the offspring Red-eyed and half Albino-eyed.
Both animals from the one brood; the male (**R**+**A**) VI.B.2.a. (p. 313, Plate II); the female (**A**+**R**) VI.B.2.u. (p. 322, Plate II).

Plate V.

- FIG. 1.—*The origin of K. Family, in which the No-White Mutation first occurred.*

Parent Generation, Pure Black mated with Pure Red. F_1 Generation, 24 survivors, all Black carrying the factor for Red. The No-whites appeared in some of the broods of the F_2 generation. One of these broods is figured here, with the offspring (F_3) resulting from the inter-mating in the brood; some of the F_4 generation are also shown.

Fig. 1.

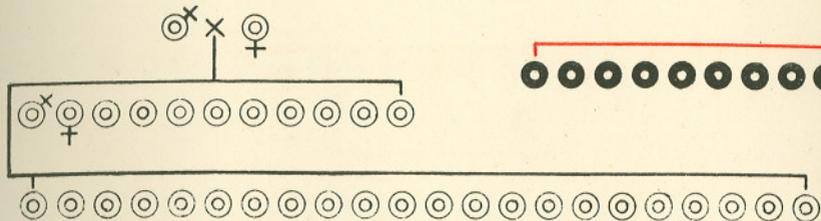


Fig. 2.

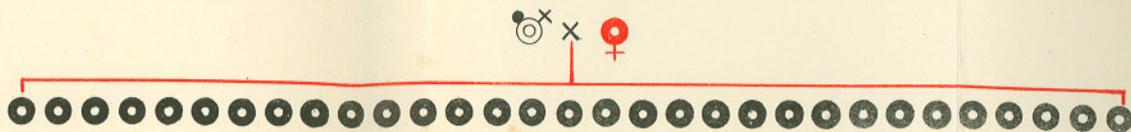


Fig. 3.

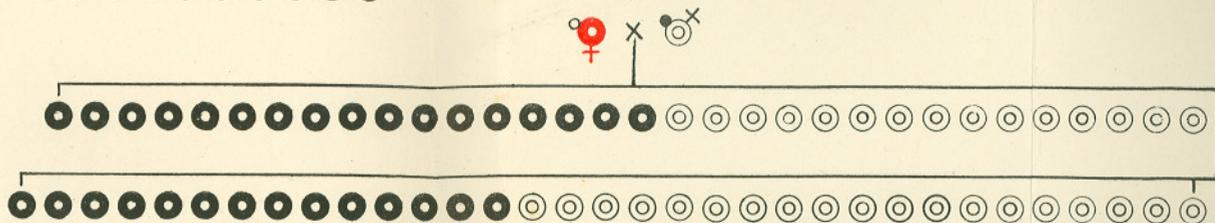


Fig. 5.

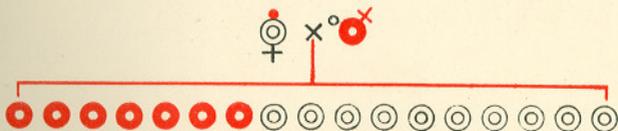


Fig. 4.

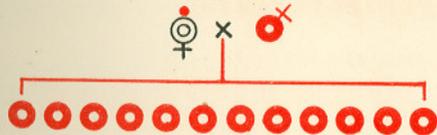
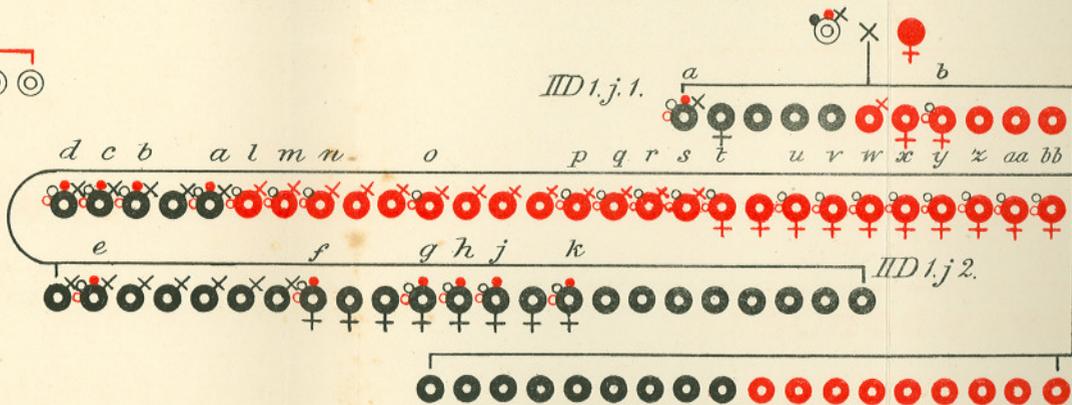
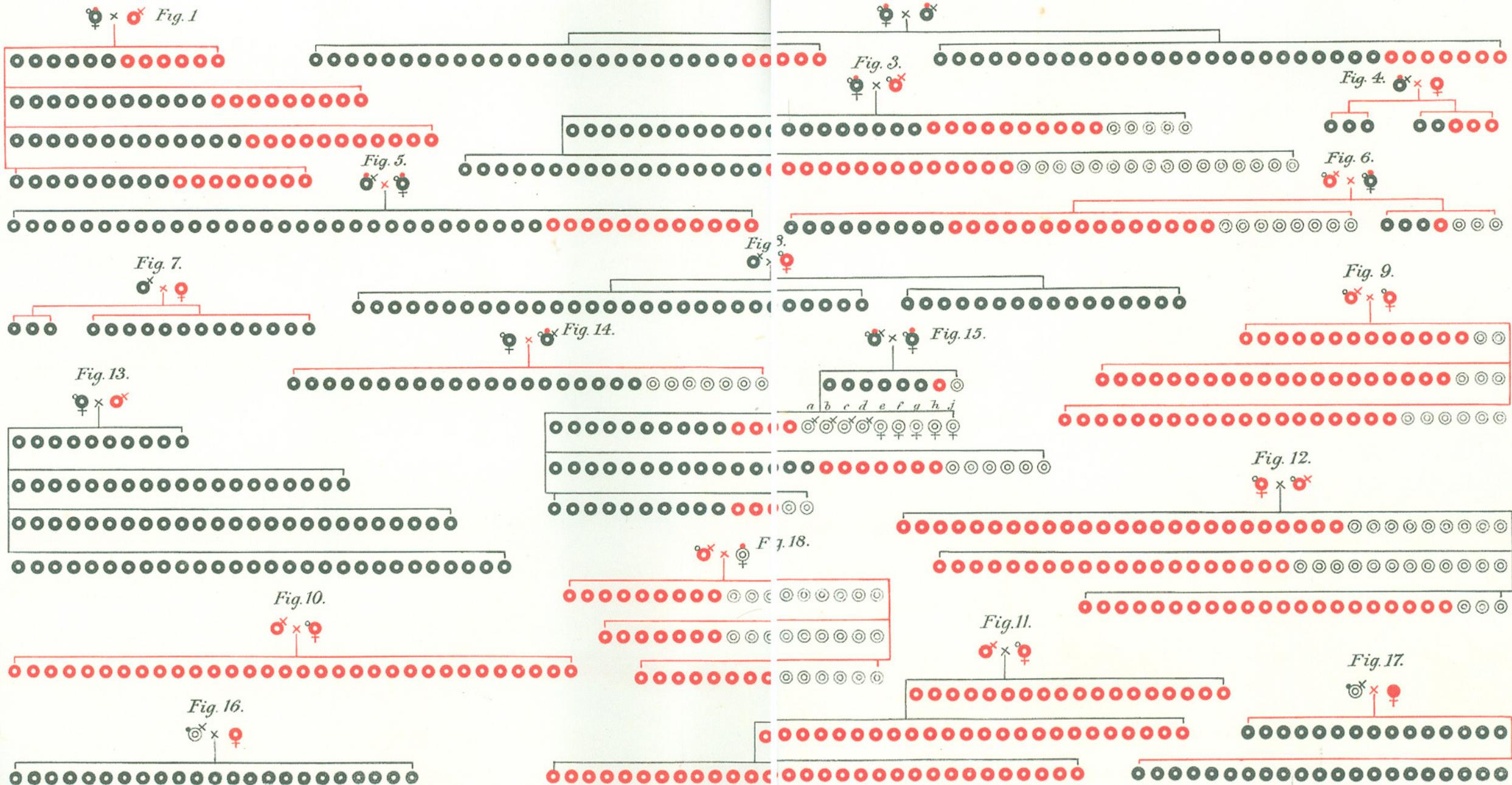
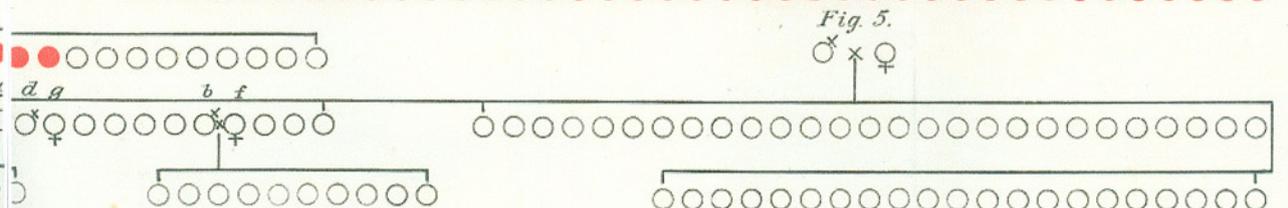
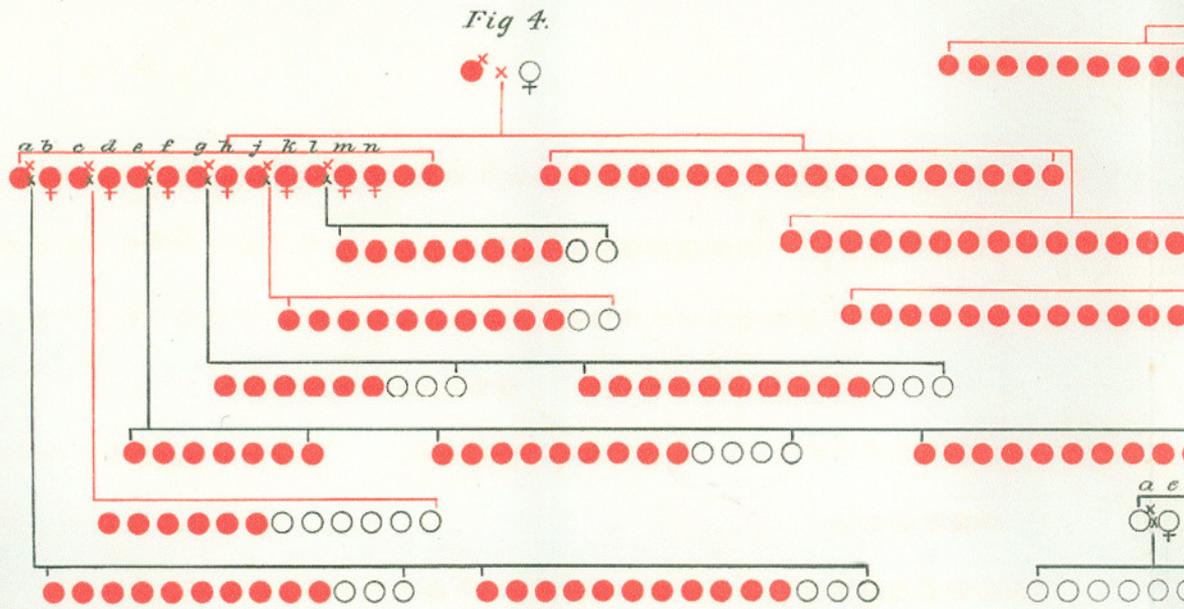
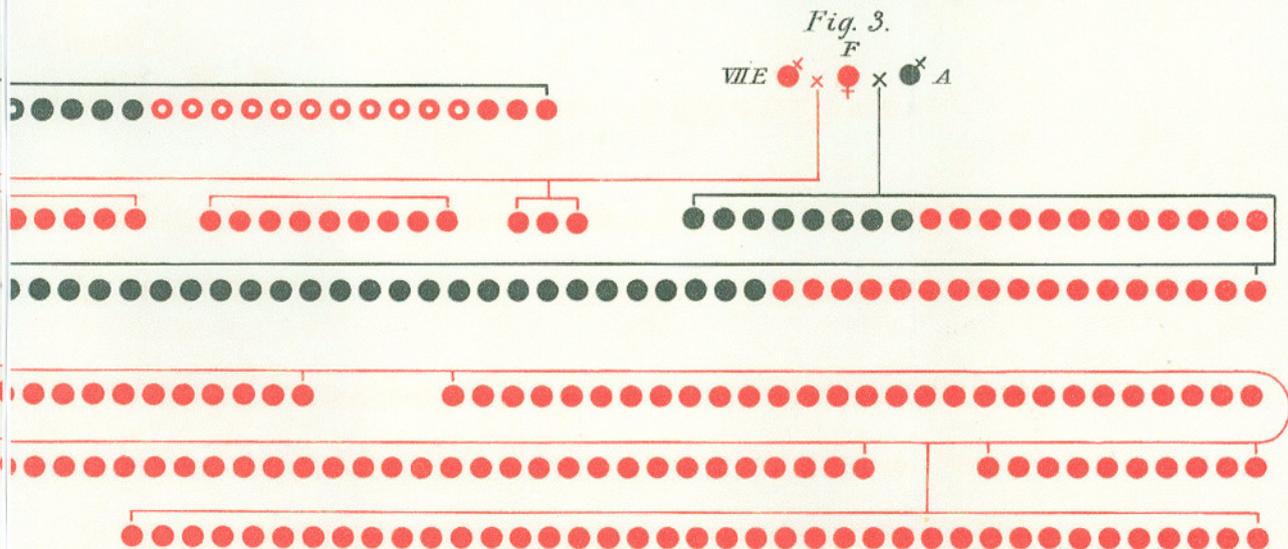
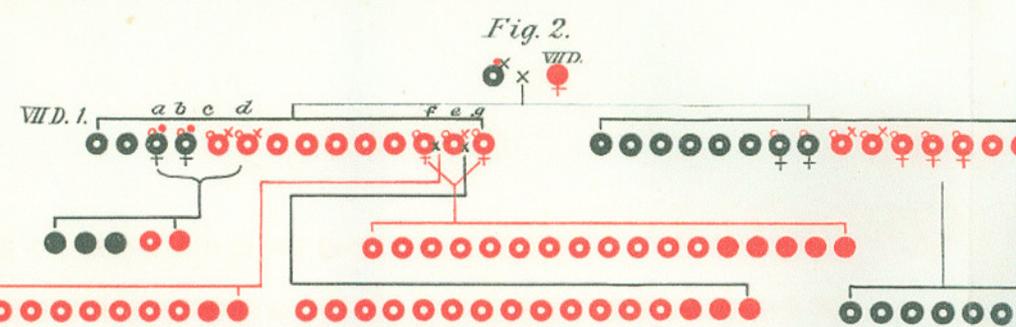
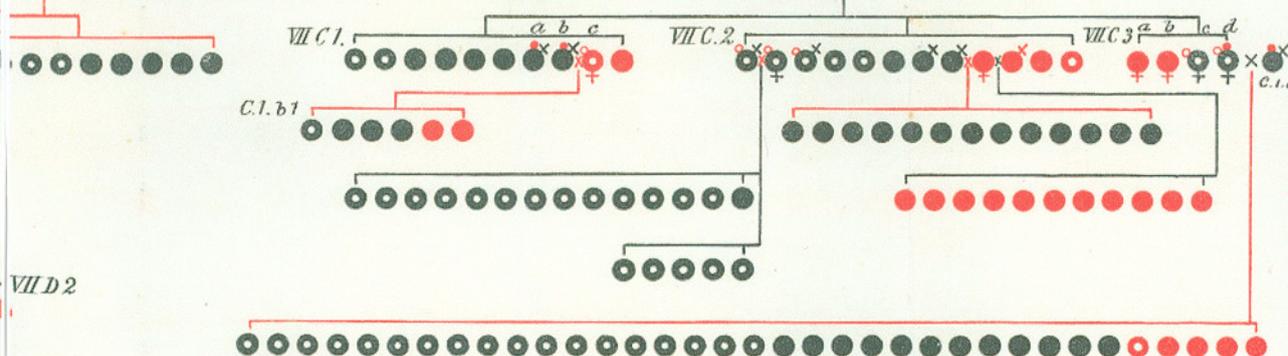
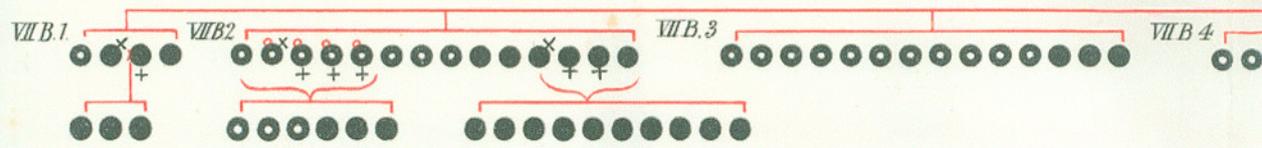
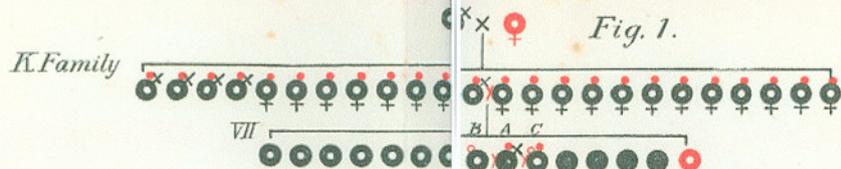


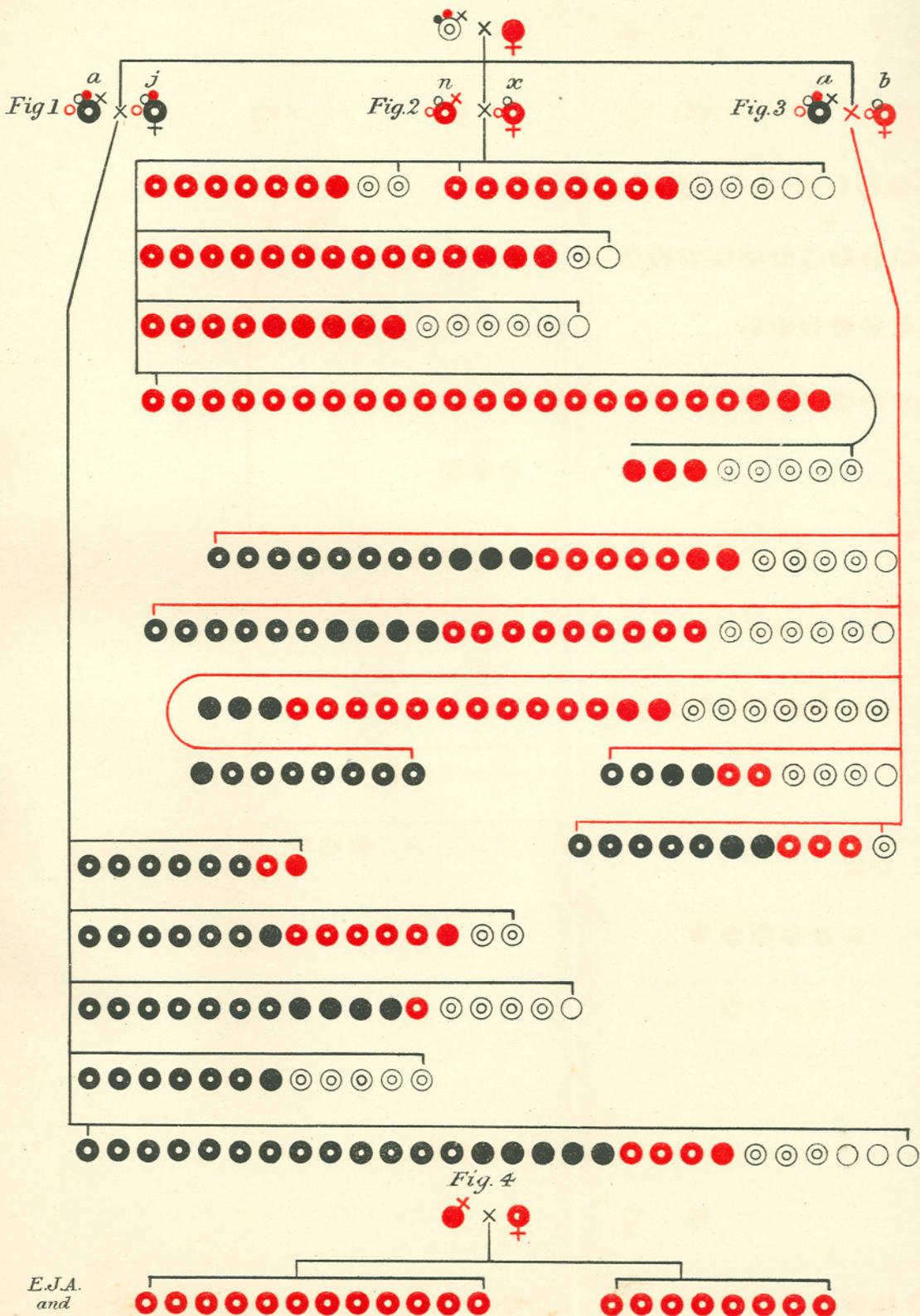
Fig. 6.





1.A.
2
3.

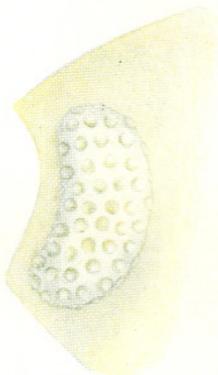




E.J.A.
and
E.W.S.
del.



1



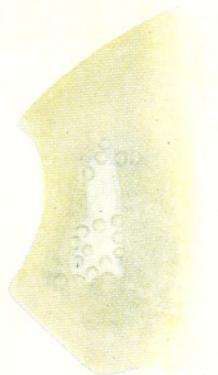
7

All-White.



6

Colourless.



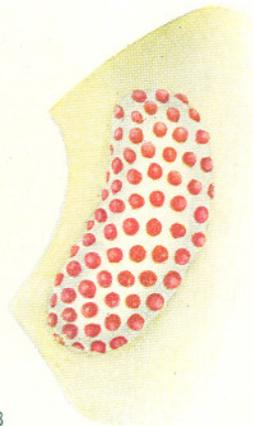
4

Normal Albino.



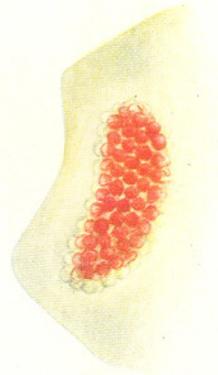
2

Normal Black.



3

Normal Red.



5

Red No-White.

E. W. Sexton del.

GAMMARUS CHEVREUXI.

As the young in this figure (and in Fig. 2) were not all examined immediately on extrusion, the proportions given of normal-eyed to no-white-eyed cannot be regarded as exact.

- FIG. 2.—*Mating of a normal Black carrying the factor for Red with a Red No-white female* (VII.D) from a K Family brood not figured; with their F_1 and F_2 offspring (p. 326).
- FIG. 3.—*Matings of Red and Black No-whites*; Red male (**RN**) VII.E; with Red female (**RN**) VII.F; the same Red female with Black male (**BN+R**) VII.A. of Fig. 1 (p. 328). VII.E. and VII.F. are from broods from K Family which are not figured.
- FIG. 4.—*Mating of Red No-white with Albino No-white*; F_1 offspring all Red No-white; F_2 offspring in the proportion of 3 Red No-white to 1 Albino No-white. The figure shows the first ten F_2 broods from the inter-mating of the first F_1 brood. (See also p. 339.)
- FIG. 5.—*Mating of Albino No-white or Colourless with Albino No-white*; offspring all Albino No-white.

For details of this mating, see pp. 338 and 339.

Plate VI.

Albino carrying the factors for Black and Red crossed with Red No-white (see also Plate III, Fig. 6, p. 333); the Black offspring carry the factors for Red, Albino and No-white; the Red offspring the factors for Albino and No-white.

- FIG. 1.—*Mating of two of the Black offspring from the second brood of the above cross*; male a and female j (p. 333).
- FIG. 2.—*Mating of two of the Red offspring from the second brood*; male n and female x (p. 334).
- FIG. 3.—*Mating of Black and Red offspring from the first brood of the above cross*; male a and female b (p. 335).
- FIG. 4.—*Mating of a Red half No-white with Red No-white*; all the offspring normal Red-eyed (p. 340).

The male is a red no-white descended from K Family.

The female is an F_2 from the first mating of VI.A.1.h. (**B+R+A** with **R**) (p. 293). Out of 25 young of the F_2 generation, two, a Red and a Black, were partly no-white when hatched. The Red one, figured here, had the Left eye no-white, the Right eye with the white reticulation present but thin; this did not alter throughout its life. The Black one, when hatched, had the Left eye no-white, and only one streak of white in the Right eye. Two months later, it reached maturity, a female, and it was then found the Right eye had developed the perfect white reticulation all over, and the Left eye had also developed it over the upper half of its surface.

Plate VII.

All the figures from living specimens.

- FIG. 1.—*Gammarus chevreuxi* Sexton. Male. From a wild specimen. $\times 7$.
- FIG. 2.—Normal Black Eye. **B**. $\times 58$.
- FIG. 3.—Normal Red Eye. **R**. $\times 58$.
- FIG. 4.—Normal Albino Eye. **A**. from Female AB. (See p. 287.)
Figured November 16th, 1915. $\times 58$.
- FIG. 5.—Red No-white. **RN**. $\times 58$.
- FIG. 6.—Colourless (Albino No-white. **AN+R**. See p. 339 for ancestry). $\times 58$.
- FIG. 7.—All-white perfect Eye. (See p. 287.) $\times 58$.