New Series.—Vol. XI., No. 3—issued December, 1917. [Price Three Shillings and Sixpence, net.]

Journal

OF THE

MARINE BIOLOGICAL ASSOCIATION

OF

THE UNITED KINGDOM.



THE PLYMOUTH LABORATORY.

PLYMOUTH:

PRINTED FOR THE MARINE BIOLOGICAL ASSOCIATION BY W. BRENDON & SON, LTD., and PUBLISHED BY THE ASSOCIATION AT ITS OFFICES ON THE CITADEL HILL.

SENT FREE BY POST TO ALL MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION : ANNUAL SUBSCRIPTION FOR MEMBERSHIP, ONE GUINEA.

Agents in London :- Messrs. DULAU & Co., LTD., 37 Soho Square. W. 1.

PATRON.

HIS MAJESTY THE KING.

OFFICERS AND COUNCIL.

President.

Sir E. RAY LANKESTER, K.C.B., LL.D., F.R.S.

Vice-Presidents.

The Duke of BEDFORD, K.G. The Earl of DUCIE, F.R.S. The Earl of STRADBROKE, C.V.O., C.B. Lord MONTAGU OF BEAULIEU. Lord WALSINGHAM, F.R.S.

The Right Hon. A. J. BALFOUR, M.P., F.R.S.

The Right Hon. AUSTEN CHAMBER-LAIN, M.P. W. ASTOR, Esq., M.P. G. A. BOULENGER, Esq., F.R.S. A. R. STEEL-MAITLAND, Esq., M.P. Rev. Canon NORMAN, D.C.L., F.R.S. EDWIN WATERHOUSE, Esq.

COUNCIL.

Elected Members.

Prof. W. M. BAYLISS, D.Sc., F.R.S. E. T. BROWNE, Esq. L. W. BYRNE, Esq. W. C. DE MORGAN, Esq. Prof. H. J. FLEURE, D.Sc. E. S. GOODRICH, Esq., D.Sc., F.R.S. E. W. L. HOLT, Esq.

Prof. E. W. MACBRIDE, D.Sc., F.R.S. H. G. MAURICE, Esq., C.B. Dr. P. CHALMERS MITCHELL, F.R.S. C. C. MORLEY, Esq. F. A. Potts, Esq. C. TATE REGAN, Esq., F.R.S. Prof. D'ARCY W. THOMPSON, C.B., F.R.S.

Governors.

G. P. BIDDER, Esq., Sc.D.

- L. Towgood, Esq. R. (Prime Warden of the Fishmongers' Company).
- The Earl of PORTSMOUTH (Fishmongers' Company).
- Τ. T. GREG, Esq. (Fishmongers' Company).

The Hon. NATHANIEL CHARLES ROTHS-CHILD (Fishmongers' Company).

GEORGE EVANS, Esq. (Fishmongers' Company).

Prof. G. C. BOURNE, D.Sc., F.R.S. (Oxford University).

A. E. SHIPLEY, Esq., D.Sc., F.R.S. (Cambridge University).

Prof. W. A. HERDMAN, D.Sc., F.R.S. (British Association).

Chairman of Council.

A. E. SHIPLEY, Esq., D.Sc., F.R.S.

Hon. Treasurer.

GEORGE EVANS, Esq., 1 Wood Street, London, E.C. 2.

Hon. Secretary.

E. J. ALLEN, Esq., D.Sc., F.R.S., The Laboratory, Citadel Hill, Plymouth.

PERMANENT STAFF.

Director-E. J. Allen, Esq., D.Sc., F.R.S. Naturalists-L. R. CRAWSHAY, Esq., M.A. E. W. NELSON, Esq. J. H. ORTON, Esq., D.Sc. R. S. CLARK, Esq., M.A., B.Sc. Miss M. V. LEBOUR, D.Sc. Assistant Naturalist—E. FORD, Esq., A.R.C.Sc. Temporary Assistant Naturalist—Miss_G. E. WEBB.

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,

							L'AGE
SECTION I. ALBINO IMPERFECT EYE							274
Cross A. Albino Female AC × Red Male R.2. P	late I	. *					275.
Cross B. Albino Female AC × Black Male K. A	۱.						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 B.	1		Sala			3	987
Hypotheses I and II							288
Constitution of Blacks VI. Cross C				•	•	•	200
Cross-matings		•				• •	201
Constitution of Reds		•		•			205
Albinos		•	•	•		•	917
Fynonimonta with the Oniginal Stack	•	•	•	•	•	•	317
The Deat White Erre	•		•	•	•	•	324
Ine 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	Albin	o No-	white	or Co	olourle	ess	
eyes							336
Constitution of the Colourless eye			. 14				338
SECTION V. ONE-SIDED NO-WHITES			10.3		1900		339
SUMMARY							341
GENERAL CONSIDERATIONS			-				348
EXPLANATION OF PLATES			1.74	-			350
							000

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 NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

T

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 $\mathbf{B}+\mathbf{R}+\mathbf{A}$ means a blackeyed animal, carrying the factors for red and albino, $\mathbf{B}+\mathbf{N}$ 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 extraretinal pigment are both absent we employ the term "colourless."

ommatidia arranged in regular rows, each ommatidium being surrounded by pigmented retinular cells, the pigment being black in the normal eve, 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 eve 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 broodbowl 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 blackeyed, 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 allelomorphic 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 $\begin{array}{c} C \ R \\ C \ R \end{array}$ and of the albino female $\begin{array}{c} c \ B \\ c \ R \end{array}$ 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. $Black \times Black$.

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 × C c B R

gives gametes CB

c B

c R

which with chance meetings would give zygotes :---

C B	$\begin{array}{c} C B \\ C R \end{array}$	C B	CB
C B		c B	cR
C R	C R	CR	CR
C B	C R	cB	cR
c B	c B	c B	c B
C B	CR	c B	c R
c R	c R	c R	c R
C B	C R	c B	c R

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

1	with	constitution	CCBB
2	,,	",	CcBB
2	,,	,,	C'C B R
4	,,	,,	CcBR

* 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."

276

112 2-

3 Red-eyed, viz. :--

1	with	constitution	C	C	R	R
2	,,	"	С	с	R	R

4 Albinos, viz. :--

1	with	constitution	с	с	BB
1	,,	,,	с	с	RR
2	,,	,,	c	с	BR

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 \times 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-eved, 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. $Black \times Red$.

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 redeyed 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.

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

^{*} 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.

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 $\begin{array}{c} c & B \\ c & R \end{array}$ and of the hybrid black male $\begin{array}{c} C & B \\ C & R \end{array}$, 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 $(\mathbf{B}+A)$;

- 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. $(\mathbf{B}+R+A)$; 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 (**B**+R+ 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 $(\mathbf{B}+A)$; 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 (**B**+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, (**B**+A); 115 young, 78 Black, 37 Albino;

(2) with female VI.B.2.e. (**R**+A); (19 young, 11 Black, 8 Albino);

 (3) with female IV.X. (**R**+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, $(\mathbf{B} +$

R+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, $(\mathbf{B}+A)$; (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, $(\mathbf{B}+A)$; 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, $(\mathbf{B}+A)$;

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, $(\mathbf{R}+A)$; 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, $(\mathbf{B}+A)$; 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, $(\mathbf{R}+A)$; 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, $(\mathbf{B}+A)$; (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, $(\mathbf{B} + \mathbf{A})$

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.1. 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; $(\mathbf{R}+A)$; 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, $(\mathbf{B}+\mathbf{R}+\mathbf{A})$; (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, $(\mathbf{R}+A)$;
 - 154 young, 127 Red, 27 Albino;
- (3) with a female (from Brood 1 of III.C.),

IV.X. Female, Red carrying Albino.

Matings :—(1) with male J of the same brood, $(\mathbf{B}+\mathbf{R}+$

- 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, $(\mathbf{R}+\mathbf{A})$;

(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, $(\mathbf{R}+A)$; (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.

⁽**A**+B); 56 young, 29 Black, 27 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 indviduals 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 $_{C}^{C}$, that of the female $_{c}^{c} B$. 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)×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 "allwhite" 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 allwhite perfect-eyed male will be ${C \atop C}$, that of the albino female carrying black and red ${c \atop B}$. 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 ${}^{c}_{c}{}^{B}_{R}$ as already seen on p. 276, that of the hybrid black male with which it was mated is ${}^{C}_{c}{}^{B}_{R}$. The gametes are therefore for the male C B and C R, for the female c B and c R. The F₁ 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 :—

	$\begin{array}{c} \text{VI.A. } \mathbb{Q} \times \ \mathfrak{Z} \ \text{II.A.} \\ \text{CcB} \times \ \text{CcBR} \end{array}$					
Female gametes :— Male ,,	С В, С В,	C, C R,	с В, с В,	c c R		
F ₂ Zygotes	C B C B	C C B	c B C B	c C B		
	C B C R	C C R	c B CR	e C R		
	C B c B	C c B	c B c B	c c B		
	C B c R	c c R	c B c R	c 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 ${}_{CR}^{CR}$, and if it is mated with the albino female carrying black and red we shall have :—

$$\begin{array}{c} C R & c B \\ C R \times c R \end{array}$$

The gametes for the male will therefore be C R only, for the fema'e 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. $\mathfrak{Q} \times \mathfrak{F}$ II.A. C c B R \times C c B R

NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

289

U

Female Gametes C B, C R, c B, c RMale,, $F_2Zygotes$

C B C B	C B C R	C B c B	C B c R
C R C R	CR	CR	CR
c B	c B	c B	c B
C B	C R	c B	c R
C B	CR	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 F_2 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; (CCBB);

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 blackeyed animals, viz. :--

one	norma	al pure bl	ack,	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 l 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, $(\mathbf{B}+R+A)$; 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, $(\mathbf{A} + \mathbf{B} + \mathbf{R})$:

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 $(\mathbf{B}+\mathbf{A})$;

18 young, all Black.

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

(2) with female VI.A.1.1. Eggs laid, but female died before they were hatched.

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

Matings :—(1) with female 1 of the same brood $(\mathbf{B}+A, R)$

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, $(\mathbf{B}+\mathbf{R}+$

- 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 $(\mathbf{B} + \mathbf{R} +$

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, $(\mathbf{B}+\mathbf{R}+$

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.3.1. 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, $(\mathbf{B}+A)$; (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, $(\mathbf{B}+\mathbf{R})$; (46 young, 41 Black, 5 Red).

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

VI.A.3.0. 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, $(\mathbf{B} + \mathbf{R} + \mathbf{A})$;

(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 $(\mathbf{B}+\mathbf{R}+$

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 $(\mathbf{R}+A)$;

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 $(\mathbf{R} + A)$; 42 young, all Black;
 - (2) with male n of the same brood, $(\mathbf{R}+A)$; 49 young, all Black.

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

Matings :—(1) with male b of the same brood $(\mathbf{B} + \mathbf{R} + \mathbf{A})$;

- (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 $(\mathbf{R}+\mathbf{A})$; 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 $(\mathbf{B} + \mathbf{R} + \mathbf{A})$;

(27 young, 20 Black, 7 Albino) (Plate IV, Fig. 14).

VI.C.1.I. 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 $(\mathbf{B}+\mathbf{R}+\mathbf{A})$;

(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 $(\mathbf{B}+$

R+A); 8 young, 7 Black, 1 Albino;

 (2) with female 1 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 $(\mathbf{B} + \mathbf{R} + \mathbf{A})$;

(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 $(\mathbf{A}+\mathbf{R})$ 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 (\mathbf{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.2.1. 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, $(\mathbf{B}+R+A)$; (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, $(\mathbf{B}+\mathbf{R})$; 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).

.15 Dlack, 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.3.1. 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 \mathbf{R} ; by \mathbf{R} +A; by \mathbf{A} +R, 222 young all Black.

Black by **B**; by \mathbf{B} +A; by \mathbf{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 $(\mathbf{B}+\mathbf{R})$: tested with Red: 5 Black, 3 Red.

- (1) crossed with female VI.A.1.l. $(\mathbf{B}+R+A)$; 45 Black, 11 Red;
- (2) crossed with female VI.C.1.d. $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: 30 Black, 12 Red.

VI.A.1.b. Male $(\mathbf{B}+\mathbf{R})$: tested with Red: 5 Black, 10 Red.

- (1) crossed with female VI.A.1.g. $(\mathbf{B}+R+A)$; 23 Black, 4 Red;
- (2) crossed with female VI.A.1.f. (B+R+A); 17
 Black, 8 Red.

VI.A.1.d. Male $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: tested with Red: 3 Black, 7 Red.

(1) crossed with female VI.A.3.q. $(\mathbf{B}+R+A)$; 10 Black, 2 Red, 4 Albino.

VI.A.1.e. Male $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: tested with Red : 11 Black, 7 Red.

(1) crossed with female VI.C.1.h. $(\mathbf{B}+\mathbf{R})$; 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 $(\mathbf{B}+\mathbf{R}+\mathbf{A})$; tested with Red: 5 Black, 5 Red. (1) crossed with male b $(\mathbf{B}+\mathbf{R})$, see above.

VI.A.1.1. Female $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: tested with Red : 39 Black, 34 Red. (1) crossed with male a $(\mathbf{B}+\mathbf{R})$, see above.

VI.A.2.c. Female $(\mathbf{B}+\mathbf{R})$: tested with Red carrying Albino : 16 Black, 11 Red.

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

VI.A.3.c. Male $(\mathbf{B}+\mathbf{R}+\mathbf{A})$.

- (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 $(\mathbf{B}+\mathbf{R})$.

- crossed with female VI.A.3.n. (B+R+A); 41 Black, 5 Red;
- (2) crossed with female VI.C.1.d. $(\mathbf{B}+R+A)$; 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).

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

*VI.A.3.m. Female $(\mathbf{B}+\mathbf{R}+\mathbf{A})$.

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

*VI.A.3.p. Female $(\mathbf{B}+\mathbf{R}+\mathbf{A})$.

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

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

(1) crossed with VI.A.1.d. $(\mathbf{B}+\mathbf{R}+\mathbf{A})$; see above.

*VI.A.3.r. Female $(\mathbf{B}+R+A)$.

(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).

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

VI.C.1.c. Male $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: tested with Red: 33 Black, 20 Red.

 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. $(\mathbf{B}+\mathbf{R})$; 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. $(\mathbf{B}+R+A)$; see above.

*VI.C.1.g. Female (\mathbf{B} +R+A).

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

VI.C.1.h. Female $(\mathbf{B}+\mathbf{R})$: 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.1.1. Female $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: 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).

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

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

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

VI.C.2.e. Male $(\mathbf{B}+\mathbf{R}+\mathbf{A})$.

- crossed with female VI.C.2.k. (B+R+A); 7 Black, 1 Albino;
 - (2) crossed with female VI.C.2.1. (B+R+A); 15
 Black, 3 Red, 9 Albino.

X

NEW SERIES.-VOL. XI. NO. 3 DECEMBER, 1917.

VI.C.2.f. Female $(\mathbf{B} + \mathbf{R} + \mathbf{A})$.

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

*VI.C.2.g. Female (\mathbf{B} +R+A).

(1) crossed with male VI.C.2.b. $(\mathbf{B}+R+A)$; see above.

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

- 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.2.1. Female (**B**+R+A).

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

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

 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. $(\mathbf{B}+\mathbf{R})$; 13 Black, 5 Red.

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

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

VI.C.3.e. Female $(\mathbf{B}+\mathbf{R}+\mathbf{A})$: tested with Reds; 27 Black, 14 Red.

(1) crossed with male VI.A.3.d. $(\mathbf{B}+\mathbf{R})$; 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)	$C C R \times C C R$
Male Gametes :	C R and C
Female "	C R and C
Zygotes	C R C R
	C R C
	CRC
	CC

that is one CCRR, two CCR, one CC

,, ,, 3 reds and 1 albino.

(2) Male Gametes Female ,,

Zygotes

	$\begin{array}{c} C c R \times \\ C R, C, \\ C R, C, \\ C R, C, \end{array}$	СсR сR, с сR, с	
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)	$\mathrm{C}\mathrm{C}\mathrm{R} imes\mathrm{C}\mathrm{c}\mathrm{R}$				
Male Gametes	CR and C				
Female ,,	CR, C, cR, c				
Zygotes	CR	C	c R	c	
	CR	C R	C R	C R	
	ĊR	C	c R	с	
	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 c R c B c B all-whites of the same hypothetical constitution as the c R, c B, c R, c R,

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

(1)		$C C R R \times C$	CRR	
Gametes all C R				
Zygotes all CCI	RR.			
That is, all red.				
(2)		$C c R R \times C$	c R R	
Male Gametes	CR,	c R		
Female "	CR,	c R		
Zygotes	CCF	RR, CcRR,	CcRR, c	e c R R
That is, 3 reds an	nd 1 albin	no.		
(3)		$CCRR \times C$	c R R	
Male Gametes	CR			
Female "	C R	and c R		
Zygotes	CCI	RR 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.2.1. (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, $(\mathbf{R}+A)$; 48 young, 36 Red, 12 Albino;

E, J. ALLEN AND E. W. SEXTON.

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, $(\mathbf{R}+A)$; 16 young, 10 Red, 6 Albino.

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

Matings :—(1) with male u of the same brood, $(\mathbf{R}+A)$; (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. $(\mathbf{B}+\mathbf{R}+\mathbf{A})$; (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, $(\mathbf{B} + \mathbf{R} + \mathbf{A})$;

(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, $(\mathbf{B}+\mathbf{R})$;

(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, $(\mathbf{R}+A)$; 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 $(\mathbf{R}+A)$; 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, $(\mathbf{B}+\mathbf{R})$;

(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, $(\mathbf{R}+A)$; 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, $(\mathbf{R}+A)$; 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, $(\mathbf{R}+A)$; (21 young, 17 Red, 4 Albino).

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

Matings :—(1) with male d of the same brood, $(\mathbf{R}+A)$; (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, $(\mathbf{R}+A)$; 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, $(\mathbf{R}+A)$; 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, $(\mathbf{R}+A)$;

(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, $(\mathbf{R}+A)$; (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, $(\mathbf{R}+A)$;

- (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, $(\mathbf{R}+A)$; (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.2.1. Female, Red carrying Albino.

Matings :—(1) with male VI.C.2.p. $(\mathbf{A}+\mathbf{R})$; (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, $(\mathbf{R}+A)$; (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. $(\mathbf{A}+\mathbf{R})$; (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 ; E. J. ALLEN AND E. W. SEXTON.

Matings:—(2) with male VI.A.2.a. $(\mathbf{B}+\mathbf{R}+\mathbf{A})$; (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, $(\mathbf{R} + A)$;

(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 \mathbf{R} ; \mathbf{R} +A; and \mathbf{A} +R; 709 young, all Red. Red carrying Albino by \mathbf{R} +A; and \mathbf{A} +R; 883 Red, 582 Albino. Red and \mathbf{R} +A by Black; 258, all Black. Red and \mathbf{R} +A by \mathbf{B} +R; 135 Black, 115 Red.

Red carrying Albino by \mathbf{B} +A and \mathbf{A} +B; 141 Black, 44 Albino. Red carrying Albino by \mathbf{B} +R+A and \mathbf{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 $C \\ C$ 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 nowhite); 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, (\mathbf{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, $(\mathbf{B}+R+A)$;

(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.2.1. Female, Albino carrying Black and Red.

Matings :—(1) with male VI.A.3.t. $(\mathbf{R}+A)$; (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);

E. J. ALLEN AND E. W. SEXTON.

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. $(\mathbf{R}+A)$; 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 $(\mathbf{A}+\mathbf{R})$;

(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, $(\mathbf{A}+\mathbf{R})$;

(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.

NEW SERIES.-VOL. XI. NO. 3.

3. DECEMBER, 1917.

Y

- 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. $(\mathbf{R}+A)$; 31 young, 19 Red, 12 Albino.

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

Matings :--(1) with male VI.B.3.c. $(\mathbf{R}+A)$; 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 1 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, $(\mathbf{R} + \mathbf{A})$;
 - (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 F_2 Generation.

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

E. J. ALLEN AND E. W. SEXTON.

Reds.		Constitution.		Number.
	Pure Red	CCRR		1
	Red carrying Albino	C c R R		2
Albin	008.		·	
	Albino carrying Black	ссВВ		1
	Albino carrying Red	c c R R		1
	Albino carrying Black and Red	ссBR		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 coatcolour 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 "allwhite" 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 redeyed 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 partwhite, 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.

E. J. ALLEN AND E. W. SEXTON.

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 $(\mathbf{B}+\mathbf{R})$ 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 (\mathbf{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 eves; in five other cases (four black and one red) it was entirely absent from the eve of one side only, being normal in the other eve. 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 Feb ruary 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 eves 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 eves 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-eved, half-grown animals, with normal extraretinal 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 :----

WWccBR×wwCCRR

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 $W \le C c B R$ WwCcRR Black with the white normal but carrying red, albino and no-white. carrying albino and no-white.

Red with the white normal

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 :---

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

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

WCB, WCR, WcB, WcR, wCB, wCR, wcB, wcR Zygotes :—

W C B W C B	$\begin{smallmatrix} W & C & R \\ W & C & B \end{smallmatrix}$	$\begin{array}{c} W \ c \ B \\ W \ C \ B \end{array}$	$\begin{smallmatrix} W & c & R \\ W & C & B \end{smallmatrix}$	$\begin{smallmatrix} w & C & B \\ W & C & B \end{smallmatrix}$	$\begin{smallmatrix} w & C & R \\ W & C & B \end{smallmatrix}$	w c B W C B	w c R W C B
$\begin{array}{c} W C B \\ W C R \end{array}$	$\begin{smallmatrix} W & C & R \\ W & C & R \end{smallmatrix}$	W c B W C R	$\begin{array}{c} W \ c \ R \\ W \ C \ R \end{array}$	$\begin{smallmatrix} w & C & B \\ W & C & R \end{smallmatrix}$	$\begin{smallmatrix} w & C & R \\ W & C & R \end{smallmatrix}$	$\begin{smallmatrix} w & c & B \\ W & C & R \end{smallmatrix}$	$\begin{smallmatrix} w & c & R \\ W & C & R \end{smallmatrix}$
$\begin{array}{c} W \ C \ B \\ W \ c \ B \end{array}$	$\begin{array}{c} W \ C \ R \\ W \ c \ B \end{array}$	$\begin{array}{c} W \ c \ B \\ W \ c \ B \end{array}$	$\begin{array}{c} W \ c \ R \\ W \ c \ B \end{array}$	w C B W c B	$\begin{smallmatrix} w & C & R \\ W & c & B \end{smallmatrix}$	w c B W c B	w c R W c B
W C B W c R	$\begin{array}{c} W \ C \ R \\ W \ c \ R \end{array}$	$\begin{array}{c} W \ c \ B \\ W \ c \ R \end{array}$	$\begin{smallmatrix} W & c & R \\ W & c & R \end{smallmatrix}$	$\begin{smallmatrix} w & C & B \\ W & c & R \end{smallmatrix}$	$\begin{smallmatrix} w & C & R \\ W & c & R \end{smallmatrix}$	w c B W c R	w c R W c R
W C B w C B	W C R w C B	W c B w C B	W c R w C B	w C B w C B No- white	w C R w C B No- white	w c B w C B No- white	w c R w C B No- white
WCB wCR	W C R w C R	W c B w C R	W c R w C R	w C B w C R No- white	w C R w C R No- white	w c B w C R No- white	w c R w C R No- white
WCB wcB	WCR wcB	W c B w c B	W c R w c B	w C B w c B No- white	w C R w c B No- white	w c B w c B Albino No- white	w c R w c B Albino No- white
WCB wcR	WCR wcR	W c B w c R	W c R w c R	w C B w c R No- white	w C R w c R No- white	w c B w c R Albino No- white	w c R w c R Albino No- white

E. J. ALLEN AND E. W. SEXTON.

That is, out of every 64 anim	hals there should be :
16 "No-whites," of which 4 are Albino and therefore colourle	1 carrying Black 1 ,, Red ss 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	$\begin{array}{c} 1 \text{ Pure Red} \\ 2 \text{ Red carrying Albino} \end{array}$
48 with White, of which 27 are Black	1 Pure 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	$, \begin{cases} 1 \text{ Pure Red} \\ 2 \text{ Red carrying Albino} \\ 2 \ ,, \ ,, \ No-white \\ 4 \ ,, \ ,, \ Albino and No-white \end{cases}$
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 blackeyed 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 $(\mathbf{A}+\mathbf{B}+\mathbf{R}\times\mathbf{RN})$.

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 $(\mathbf{A} + \mathbf{B} \times \mathbf{RN})$.

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 blackeyed 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 $(\mathbf{A} + \mathbf{R} \times \mathbf{RN})$.

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

F.1. Generation from $\mathbf{A} + \mathbf{B} + \mathbf{R} \times \mathbf{RN}$.

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 :—

E. J. ALLEN AND E. W. SEXTON.

	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,	(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×**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× \mathbf{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-

	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, H.D.1.j.1.) of Albino carrying black and red crossed with Red No-white. See Parent Generation 1 (\mathbf{A} +B+R× \mathbf{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

	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 $A + B \times RN$.

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 $\mathbf{A} + \mathbf{R} \times \mathbf{RN}$.

The young belonging to this generation were mated together and produced 220 young, classified as follows :—

	Red.	Red No-white.	Albino.	Albino (Colcurless) No-white.
Theory	124	41	41	14
Experiment	127	38	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-eved 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 eve 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 eves 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 nowhite.

In Brood 22, two Red-eyed had hardly any white pigment in the eyes, and one Albino had the left eye Colourless.

NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

z

E. J. ALLEN AND E. W. SEXTON.

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 Redeyed 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 (AN+R) (Plate VII, Fig. 6) (whose parents are shown on Plate I, viz. I.E.3.1. \Im and I.E.3.0. \Im , and whose ancestry is discussed on p. 336), the colourless character having originated independently, was mated with a Red No-white male **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 (=**RN**+AN) and 35 Colourless (**AN**+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 Nowhite male with a Colourless female, 24 young were obtained, \mathbf{RN} + AN 14 and \mathbf{AN} +R 10. The first mating from the next generation F_3 (\mathbf{RN} +AN× \mathbf{RN} +AN) produced 14 \mathbf{RN} +AN and 3 \mathbf{AN} +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 $\mathbf{B}+\mathbf{R}+\mathbf{A}$ 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 (\mathbf{R} +N).

These young were mated together and gave a total of 490, 365 Redeyed, 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 L oft eye no-white, i.e. Colourless. Parentage, Albino male carrying Black (\mathbf{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 $(\mathbf{R}+N)$ with Red $(\mathbf{R}+N)$, 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} +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	
$\mathbf{B} \times \mathbf{B} + \mathbf{R}$	146	
$\mathbf{B} \times \mathbf{B} + \mathbf{A}$	87	
$\mathbf{B} \times \mathbf{B} + \mathbf{R} + \mathbf{A}$	17	
$\mathbf{B} \times \mathbf{R}$	618	
$\mathbf{B} \times \mathbf{R} + \mathbf{A}$	126	
B × A +B	18	
$\mathbf{B} \times \mathbf{A} + \mathbf{R}$	79	
$\mathbf{B} + \mathbf{R} \times \mathbf{B} + \mathbf{A}$	46	
$\mathbf{B} + \mathbf{A} imes \mathbf{R}$	251	
B (half no-white) \times BN	15	
BN × B +R+A	92	
$\mathbf{A} + \mathbf{B} imes \mathbf{R}$	87	
A+B×RN	158	Total, 2015.

Red, offspring all normal-eyed Red in appearance, in agreement with theory.

$\mathbf{R} imes \mathbf{R}$	1525	
$\mathbf{R} \times \mathbf{R} + \mathbf{A}$	679	
$\mathbf{R} \times \mathbf{A} + \mathbf{R}$	259	
$\mathbf{R} \times \mathbf{RN}$	24	
$\mathbf{RN} \times \mathbf{A} + \mathbf{R}$	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.
LOSS OF EYE-PIGMENT IN GAMMARUS.

Albino, offspring all the usual-eyed Albino in appearance, in agreement with theory.

Number of y	oung, Albino-e	eyed.
$\mathbf{A} + (?) \times \mathbf{A} + (?)$	1157	
$\mathbf{A} + \mathbf{R} \times \mathbf{A} + \mathbf{R}$	225	
$\mathbf{A} + \mathbf{R} \times \mathbf{A} + (?)$	330	
$\mathbf{A} + \mathbf{R} \times \mathbf{A} + \mathbf{B} + \mathbf{R}$	103	
$\mathbf{A} + \mathbf{R} imes \mathbf{AN}$	126	
$\mathbf{A} + (?)$ (half no-white) $\times \mathbf{AN}$	271 Te	otal. 2212.

2. Matings giving normal-eyed offspring of two colours in the proportion 3:1.

Black.	В	Number of yo	oung. Red-eved
$\mathbf{B} + \mathbf{R} imes \mathbf{B} + \mathbf{R}$	Experiment	735	249
	Theory	738	246
$\mathbf{B} + \mathbf{R} \times \mathbf{B} + \mathbf{R} + \mathbf{A}$	Experiment	300	90
	Theory	292	97
\mathbf{B} +R×A+B+R	Experiment	7	2
	Theory	7	2
$\mathbf{B} \! + \! \mathbf{R} \! \times \! \mathbf{A}(?)$	Experiment	13	7
	Theory	15	5 Total, 1403.
	Bl	ack-eyed.	Albino-eyed.
$\mathbf{B} + \mathbf{A} \times \mathbf{B} + \mathbf{A}$	Experiment	468	156
	Theory	468	156
$\mathbf{B} + \mathbf{A} \times \mathbf{B} + \mathbf{R} + \mathbf{A}$	Experiment	144	59
	Theory	153	51
$\mathbf{B}{+}\mathbf{A}{\times}\mathbf{R}{+}\mathbf{A}$	Experiment	481	158
	Theory	480	160 Total, 1466.
Red.	R	ed-eved.	Albino-eved.
$\mathbf{R} + \mathbf{A} imes \mathbf{R} + \mathbf{A}$	Experiment	1408	471
	Theory	1408	470 Total, 1879.

3. Matings giving normal-eyed offspring of two colours in the proportion 1:1.

Black.	BI	Numbe	r of young. Red-eved
$\mathbf{B} + \mathbf{R} imes \mathbf{R}$	Experiment	403	410
	Theory	406	406
$\mathbf{B}\!+\!\mathbf{R}\!\times\!\mathbf{R}\!+\!\mathbf{A}$	Experiment	44	48
	Theory	46	46
$\mathbf{B} + \mathbf{R} \times \mathbf{RN}$	Experiment	50	57
	Theory	53	53
$\mathbf{B} + \mathbf{R} \times \mathbf{A} + \mathbf{R}$	Experiment	71	95
	Theory	83	83

LIBRARY M.B.A. PLYMOUTH

E. J. ALLEN AND E. W. SEXTON.

and the system of the second	Store and Strates	Number of	young.	
Black.	Bl	ack eyed.	Red-eyed	
$\mathbf{B} + \mathbf{R} + \mathbf{A} \times \mathbf{R}$	Experiment	180	165	
	Theory	172	172	
B +R+A× RN	Experiment	18	16	
	Theory	17	17	
$\mathbf{A} + \mathbf{B} + \mathbf{R} \times \mathbf{R}$	Experiment	87	72	
	Theory	79	79	
A+B+R×RN	Experiment	31	31	
	Theory	31	31	Total, 1778.
	Bla	ack-eyed.	Albino-ey	ed.
B +A× A +R	Experiment	103	106	
	Theory	104	104	
B +A× A +B+R	Experiment	5	16	
	Theory	10	10	
$\mathbf{B} + \mathbf{A} \times \mathbf{A} + (?)$	Experiment	24	25	
	Theory	24	25	
$\mathbf{A} + \mathbf{B} \times \mathbf{B} + \mathbf{R} + \mathbf{A}$	Experiment	8	6	
	Theory	7	7	
A+B×R+A	Experiment	76	77	
	Theory	76	77	Total, 446.
Red.	R	ed-eyed.	Albino-eye	ed.
\mathbf{R} +A× \mathbf{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. Number of young.

· · · · · · · · · · · · · · · · · · ·					
		Black-eyed.	Red-eyed.	Albino-eyed.	
\mathbf{B} +R+A× \mathbf{B} +R+A	Experiment	542	189	241	
	Theory	547	182	243	

5. Matings giving normal-eyed offspring of three colours in the proportion 3:1:4.

\mathbf{B} +R+A× \mathbf{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.

$\mathbf{A} + \mathbf{B} + \mathbf{R} \times \mathbf{R} + \mathbf{A}$	Experin	ment		84		92	1	47
	Theory			81		81	1	62
\mathbf{B} +R+A× \mathbf{A} +R	Experin	nent		31		8		34*
	Theory			18		18		26
* These totals are mad	e up as follow	's :			Black.	Red.	Albino.	
VI.A.1.d. 3 ×	VI.B.2.u. 9				1	3	20	
VI.C.2.k. 9 ×	VI.C.2.u. 8				17	1	3	
VI.C. 3.e. 9 ×	VI.B. 2. t. 8		. 45		13	4	11	
					31	8	34	

It will be seen that two of these families gave unexpected numbers.

LOSS OF EYE-PIGMENT IN GAMMARUS.

7. Matings giving normal-eyed offspring of three colours in the proportion 3:3:2.

		Number of young.			
		Black-eyed.	Red-eyed.	Albino-eyed.	
\mathbf{B} +R+A× \mathbf{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 "nowhite" 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 (\mathbf{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.
$\mathbf{RN} imes \mathbf{RN}$	61
RN × AN +R	177

Albino, offspring all Albino no-white in appearance, in agreement with theory.

Albino no-whites (i.e. Colourless). 489

AN×AN

E. J. ALLEN AND E. W. SEXTON.

2. Matings giving No-white offspring of 2 kinds in the proportion 3:1.

	Re	Number ed 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.			
- Charles and the second second	Bla	ck no-whites.	R	ed no-whites,
$\mathbf{BN} + \mathbf{R} \times \mathbf{RN}$	Experiment	47		42
	Theory	44		44
		Red.		Albino.
$\mathbf{RN} + \mathbf{AN} \times \mathbf{AN} + \mathbf{R}$	Experiment	14		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.

Black	Number of young.			
Diack.		Black.	Black no-whites.	
$\mathbf{B} + \mathbf{N} imes \mathbf{B} + \mathbf{N}$	Experiment	24	7	
ga crises en esitebre de	Theory	23	8	
Red.		Red.	Red no-whites.	
\mathbf{R} +N× \mathbf{R} +N	Experiment	440	149	
	Theory	441	147	
Albino.		Albino.	Albino no-whites.	
\mathbf{A} +R+N× \mathbf{A} +R+N	Experiment	45	10	
	Theory	41	14	
\mathbf{A} +N× \mathbf{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.

\mathbf{R} +A+N× \mathbf{R} +A+N	Normal Red.	Red No-white.	Normal Albino.	Colourless (Albino No- white).
Experiment	473	149	147	51
Theory	461	153	153	51
$\mathbf{B} + \mathbf{R} + \mathbf{N} \times \mathbf{B} + \mathbf{R} + \mathbf{N}$	Normal Red.	Black No-white.	Normal Red.	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.]

LOSS OF EYE-PIGMENT IN GAMMARUS.

(c) Those which give normal and no-white eyes in two colours in the proportions 3:1:3:1.

B +R+N	$N \times R + N$	Normal Black.	Black No-white,	Normal Red.	Red No-white.
199	Experiment	45	4	24	10
	Theory	31	10	31	10
$\mathbf{B} + \mathbf{R} + A$	$\mathbf{x} \times \mathbf{R} + \mathbf{N}$				
	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.

\mathbf{B} +R+A+N $\times \mathbf{R}$ +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.

\mathbf{B} +R+A+N× \mathbf{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.

RINVRNIP	Fynaminant	Normal Black.	Black No-white,
D +N×DN+V	Theory	20 16	12 16
DINDU		Normal Red.	Red No-white.
$\mathbf{R} + \mathbf{N} \times \mathbf{RN}$	Experiment	11	15
	Theory	13	13

(b) Those which give normal and no-white eyes in two colours in the proportions 3:3:1:1.

		Normal Black.	Black No-white.	Normal Red.	Red No-white.
\mathbf{B} +R+N× \mathbf{BN} +R	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 albinoand 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. $AN \times AN$).

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 "nowhite" 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

LOSS OF EYE-PIGMENT IN GAMMARUS.

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 nowhite 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-eved 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-eved 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 nowhites, 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.

E. J. ALLEN AND E. W. SEXTON.

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 extraretinal 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-eved.

The male $(\mathbf{A}+B)$ is from the first brood of III.B. (p. 279, Plate I); the female (\mathbf{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 $(\mathbf{A}+B)$ is from the same brood as the male of Fig. 2 (pp. 279 and 286), the female $(\mathbf{R}+A)$ IV.Z. (p. 285, Plate I).

FIG. 4.—Mating of Albino carrying the factor for Red with Pure Red; offspring all Redeyed.

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 $(\mathbf{R}+A)$ and the female $(\mathbf{A}+R)$ 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 Nowhite, and half Red-eyed, carrying the factors for Albino and No-white.

The male $(\mathbf{A}+\mathbf{B}+\mathbf{R})$ is II.D.1.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 $(\mathbf{B} + R + A)$ (also in Figs. 2 and 3) is VI.A.1.l. (p. 293, Plate II); the male (\mathbf{R}) came from the Pure Red Stock.

- FIG. 2.—Mating of Black carrying the factors for Rcd 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 Albinoeyed animals.

The same female $(\mathbf{B}+\mathbf{R}+\mathbf{A})$ as in the two previous figures mated with the male $(\mathbf{R}+\mathbf{A})$ 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 $(\mathbf{B} + R)$ as in Fig. 2, mated with a female (\mathbf{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 Redeyed.

The same male $(\mathbf{B}+R)$ as in Figs. 2 and 4, mated with the female $(\mathbf{B}+R+A)$ 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 $(\mathbf{B}+R+A)$ as in Fig. 5; the male $(\mathbf{R}+A)$ 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 jactor for Albino; offspring all Black-eyed.

Both animals from the one brood; the same male (**B**) as in Fig. 7; the female (\mathbf{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 $(\mathbf{R} + A)$ 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 Redeyed.

Both animals from the one brood; the same female $(\mathbf{R}+A)$ as in Figs. 8 and 9; the male (\mathbf{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 $(\mathbf{B}+A)$ VI.C.1.k. (p. 298, Plate II); the male \mathbf{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 Albinoeyed.

Both animals from the one brood; the male $(\mathbf{B}+\mathbf{R}+\mathbf{A})$ VI.C.1.b. (p. 297, Plate II); the female $(\mathbf{B}+\mathbf{A})$ 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 $(\mathbf{B}+R+A)$ was used in the previous figure; the female $(\mathbf{B}+R+A)$ 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 $(\mathbf{A}+B)$ VI.A.1.r. (p. 318, Plate II); the female (\mathbf{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 $(\mathbf{A} + B)$ from the previous experiment—Fig. 16; the female (\mathbf{RN}) VII.C.3.a. (p. 333) is an F₃ 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 brccd; some of the F_4 generation are also shown.





E.J.A. and E.W.S. del.







Journ. Mar. Biol. Assoc. XI 3.

PLATE VI.



JOURN. MAR. BIOL. ASSOC. XI. 3.

PLATE VII.



E. W. Sexton del.

GAMMARUS CHEVREUXI.

LOSS OF EYE-PIGMENT IN GAMMARUS.

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 E₁ and F₂ 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 Nowhite; 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. ($\mathbf{B}+\mathbf{R}+\mathbf{A}$ with \mathbf{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. ×7.

FIG. 2.—Normal Black Eye. B. ×58.

FIG. 3.—Normal Red Eye. R. ×58.

- FIG. 4.—Normal Albino Eye. A. from Female AB. (See p. 287.) Figured November 16th, 1915. ×58.
- FIG. 5.-Red No-white. RN. ×58.
- FIG. 6.—Colourless (Albino No-white. AN+R. See p. 339 for ancestry). ×58.
- FIG. 7.—All-white perfect Eye. (See p. 287.) ×58.

NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

2 A

Heredity in Plants, Animals, and Man.

Being the Presidential Address delivered before the Plymouth Institution, October 12th, 1916.

By

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

Director of the Plymouth Laboratory.

[Reprinted from the Transactions of the Plymouth Institution.]

With Diagrams 1-11 in the Text.

OF the many branches of biological enquiry which have occupied the attention of naturalists during the last twenty years the one which has perhaps yielded the most striking results, from a theoretical point of view, has been the study of heredity in plants and animals—the study of the laws according to which the characters of parents are transmitted to their descendants.

The practical achievements of the farmer, the gardener, and the animal breeder in obtaining and fixing innumerable varieties of cultivated plants and domesticated animals had made everyone familiar with the general facts that variations occur, and that these variations sometimes are and sometimes are not transmitted from parent to offspring. Common observation of the men, women, and children with whom we come in contact shows us that human beings also exhibit similar phenomena. Amongst a family of children several quite distinct types of feature, of build, of colour of hair or eye are found, and it is often quite plain from which parent, or from the family of which parent, a particular characteristic has been derived. The same thing is sometimes clearly true of mental and moral traits.

Charles Darwin, especially in his work "On the Variations of Animals and Plants under Domestication," brought together a great collection of facts bearing on this subject, which formed the basis upon which his theory of natural selection was built up. Around the question of the cause or origin of such variations much discussion has centred. Darwin himself was inclined to favour the view generally associated with the

HEREDITY IN PLANTS, ANIMAL'S, AND MAN.

name of Lamarck, that variations were brought about by the direct action of the environment—of the conditions under which the life of the animal or plant was carried on—and that variations originating in this way were capable of being inherited. Changes of structure brought about by the use or disuse of organs were considered of particular importance in this connection. Especially when the environmental conditions had remained the same for many generations did the characters produced by them become, it was thought, permanently fixed in the species as part of its hereditary constitution. This view was strongly attacked by Weismann, who held that variations produced by external conditions, and especially by use and disuse of parts, were not hereditary, and the characters of the germ plasm as received from the parents were transmitted to the offspring without change. Weismann's view has been considered the more probable by the majority of biologists since he wrote, though by a minority it has always been subjected to vigorous criticism.

With the question of the causes that give rise to variations capable of being inherited, it is not however my intention to deal to-night. Accept ing the fact, which cannot be disputed, that such variations do occur, and recognising that characters of the parent sometimes do and sometimes do not appear in the offspring, when parents with different characters are mated together, we shall consider the system or law in accordance with which the hereditary transmission of characters takes place.

What is now recognised as the epoch-making pioneer work in this subject was carried out by Gregor Mendel, Abbot of Brünn, a small town in Austria, and published by him in the Proceedings of the local natural history society at Brünn in 1865. This work unfortunately escaped attention for many years, and it was not until 1900 that the importance of Mendel's paper was recognised by de Vries, Correns and Tschermak, who all three about the same time brought it into notice. The work has since been repeated and extended by Bateson, Punnett and many other workers in this country, on the Continent, and in America, and to-day there is a very extensive literature dealing with heredity on Mendelian principles in plants, animals, and man.

Mendel chose the common garden pea for the purposes of his experiments, a plant which exists in a number of well-marked varieties, capable of being crossed easily one with the other. The nature of his experiments and the character of the results which he obtained will perhaps be made clear by the description of a simple example. There is one variety of the pea plant that produces seeds, which when the pods are fully ripe and dry are of a uniform yellow colour. Another variety, on the other hand, produces peas which when they are ripe and dry are green.

It will be well known to you that in order to produce a ripe seed, which

shall be capable of germination and growth, the union is necessary of two elements which occur in the flower. These elements are the ovule, which lies at the base of the flower, and the pollen, which generally takes the form of a fine dust or powder, and is formed by the stamens. The pollen is the male element, the ovule the female element; both are single cells, and together with the corresponding elements in animals they are called by the general name of *gametes*. The union of the ovule and pollen, which results in the formation of the ripe seed, is known as fertilisation. The general term applied to the ripe seed, the adult plant or the adult animal, which results from the union of the male and female gametes, is *zygote*— that which is yoked together. Two gametes or germ cells unite to form a zygote.

If plants of the variety which produces yellow peas are fertilised with the pollen from their own flowers or from flowers of the same variety, the seeds produced will all be yellow in colour, exactly resembling the parents. The variety breeds true to colour, and for however many generations the breeding is continued the colour remains the same, provided both parents in every case belong to the same variety.

Similarly the green-coloured variety, when the flowers are fertilised with their own pollen or with that from similar plants, produces pods which contain only green-coloured peas.

What Mendel did was to cross one of these varieties with the other. The ovules of a plant normally producing yellow-coloured peas were fertilised with pollen from a plant which produced green-coloured peas, or *vice versâ*. In this way a hybrid between the two varieties was obtained.

The hybrid peas resulting from this cross are all yellow in colour, and the result is the same whichever way the cross is made. The yellow -colour is therefore said to be *dominant* to green, and green is said to be *recessive*.

This is illustrated in Diagram 1, in which the black discs represent vellow peas, the rings represent green peas.

The hybrid yellow seeds were then sown, and the resulting plants produced flowers. These flowers were allowed to fertilise themselves that is to say, the ovules were fertilised with pollen from the same flower, so that hybrid was mated with hybrid. The pods produced by these plants were found to contain both yellow and green peas. The recessive form—the green—therefore, which was lost in the first hybrid generation, appears again in the second generation.

As the result of a large number of experiments Mendel found that the proportion of yellow to green seeds amongst the offspring of the hybrids was 3:1, there were three times as many yellow as green.

HEREDITY IN PLANTS, ANIMALS, AND MAN.

The seeds from this generation were collected and separately sown. The plants from the green seeds, when self-fertilised, produced all green seeds, and when these were again sown plants producing all green seeds again resulted. The pure recessive green variety had, therefore, com-



pletely segregated, or separated out from the hybrid, and the pure strain was completely recovered.

The yellow seeds, on the other hand, behaved differently. Two kinds of plants were produced, one kind which on self-fertilisation gave all yellow seeds, the other kind which gave both green and yellow, the two colours being in the proportion of three yellow to one green. There were twice as many plants which gave both green and yellow seeds as there were plants which gave only yellow. Peas from the kind which produced only yellow peas, when sown, produced plants which again gave all yellows, and this continued in succeeding generations. The pure dominant yellow variety, like the green recessive, had completely separated out and was re-established.

What happens will be clear from the diagram.

The fact that one of a pair of characters is dominant and the other recessive is not, however, a primary or essential feature of the scheme of Mendelian inheritance. When one character is dominant the hybrid has the appearance of the parent which bore that character, but in other cases the hybrid appears quite different from either parent. This is well illustrated by the case of the Andalusian Fowl figured in Diagram 2. The Blue Andalusian is a variety well known to the poultry fancier. It was known that the strain was not pure, and that when bred together the birds gave not only blues, but also some blacks and some splashed whites—a white with splashes of dark colour on the feathers. After the rediscovery of Mendel's work this case was investigated by Bateson and Punnett, who found that the blue bird was really a hybrid between the black and the splashed white. Both the blacks and the splashed whites are pure strains; blacks bred together give all blacks, whites bred together give all whites. When black is bred with white the birds obtained are all blue. The



blue birds bred together give blacks, blues and splashed whites in the proportions of one black, two blues, one splashed white.

When the blues of this second generation are bred together they give offspring in the same proportions : one black, two blues, one splashed white.

The diagram showing these relations should be compared with that representing the yellow and green peas. It will be seen that the scheme of inheritance is really exactly the same in the two cases, the apparent difference being due to the fact that whereas the hybrid pea takes on the character of the dominant yellow parent, the hybrid Andalusian has an appearance intermediate between the two parents.

That the yellow hybrid pea has a different constitution from its yellow parent, although its appearance is the same, is shown when hybrid plants are self-fertilised or bred together. As we have seen, the offspring are one pure yellow, two hybrid yellow, and one pure green. A further means of testing the hybrid character of this yellow pea is to fertilise the plant grown from it with pollen from a pure recessive plant grown from a green pea. Hybrid yellow crossed with green gives green and yellow peas in equal numbers.

Similarly a blue Andalusian mated with a splashed white gives blue hybrids and splashed whites in equal numbers, or a blue crossed with a black gives blues and blacks in equal numbers.

What I have described so far are the experimental facts, which have been repeatedly confirmed on these and many other plants and animals, and can be seen for himself by anyone who will take the trouble to carry out the necessary experimental work, taking all precautions to prevent false crossings by insects or false matings.

Mendel himself experimented also on a number of other characters in peas, and found that they followed the same scheme. Tall plants were dominant to dwarfs, and when the first tall hybrids were self-fertilised they gave tall and dwarf plants in the proportion of 3:1. Coloured flowers were dominant to white, but the whites reappeared again in the next generation.

In order to explain his results Mendel put forward a simple theory, the correctness of which all subsequent work has tended to confirm. Before attempting to explain this theory I must ask you to regard plants and animals from a point of view somewhat different from that which we usually take—from the point of view of the race or species rather than from that of the individual life. The plant withers, the flower fades, the creature dies, but still the race continues,

"So careful of the type she seems, So careless of the single life."

How is this continuity of the race preserved ? That is the fundamental question which the physiology of heredity must seek to answer. What we know is that the germ cell, the germ plasm as Weismann called it, passes on uninterruptedly from generation to generation, increasing in bulk by the absorption of nourishment, dividing and subdividing, but apparently only seldom or extremely slowly undergoing any essential modification of its structure. The permanent, essential feature for the species is this germ plasm ; the body of the individual plant or animal is an elaborate but purely temporary home for its protection and nourishment. As Samuel Butler puts it in his quaint way "a hen is merely an egg's way of producing another egg." "The germ plasm, according to this view," says Darbishire "is immortal; the excrescence, the body, is mortal."

It is in the gametes or germ cells—the ovule and the pollen of the plant and the corresponding structures of the animal—that the germ plasm is carried on. In the higher plants and animals this transmission is generally, though not always, complicated by the introduction of the phenomenon of sex, the union of the germ cells from two individuals of the species, or at least of germ cells of two different kinds.

In formulating his theory to account for the scheme of the hereditary transmission of characters which has been described, Mendel directed his attention primarily to the germ cells. Every gamete, that is to say every ovule and every grain of pollen, must contain something by means of which each character of the offspring is determined. What this something is, whether a material particle, a definite chemical substance, or some special arrangement of the molecules, we have no idea. For want of a better name it is usual to call it a "factor." Thus we should say that each ovule and each pollen grain of the green pea contains a "factor" for green colour ; each ovule and each pollen grain of the pure yellow pea contains a "factor" for yellow colour. When he had to deal with two alternative characters in a plant, such as green and yellow colour, Mendel assumed that any particular gamete was able to contain the factor for only one of these characters. In the same gamete the two characters are mutually exclusive. Each gamete *must* be pure for one or other of the factors. In the zygote, the individual produced by the union of two gametes, on the other hand, the factors for the two characters can both have place.

Let us see how this conception can be applied to the case of the yellow and green peas. In Diagram 3 the factor for yellow colour is represented



by \mathbf{Y} , that for green colour by \mathbf{G} . The pure yellow peas never produce anything but yellow; we may therefore represent their constitution by $\begin{bmatrix} \mathbf{Y} \\ \mathbf{Y} \end{bmatrix}$, one factor having been derived from each parent. Similarly, pure green will be $\begin{bmatrix} \mathbf{G} \\ \mathbf{G} \end{bmatrix}$. These will produce gametes \mathbf{Y} male, \mathbf{Y} female, in the one case, \mathbf{G} male, \mathbf{G} female, in the other, and no other kinds are possible.

If we cross the two, the only possible combination is $\begin{bmatrix} \mathbf{Y} \\ \mathbf{G} \end{bmatrix}$, which will represent the constitution of the 1st Hybrid generation. What Mendel's

theory lays down is that when gametes are formed by these hybrids with the constitution $\begin{bmatrix} \mathbf{Y} \\ \mathbf{G} \end{bmatrix}$, only one of the factors can enter into the same gamete, so that we have gametes of two kinds, the first containing the **Y** factor only, the second containing the **G** factor only.

If the gametes from a male and a female individual of these hybrids are now allowed to unite together they can do so in four different ways, and in four ways only. Amongst a large number coming together by chance equal numbers of each combination will result.

The combinations are :---



We have therefore in the second hybrid generation (F.2.)

1 Y Y 2 Y G 1 G G

that is 1 pure yellow, 2 hybrid yellow, 1 pure green.

This result agrees exactly with the facts as determined by experiment. Mendel's theory of the purity of the gametes is, therefore, in this case in complete accord with the facts.

We may test it further by seeing the result of crossing a hybrid yellow pea with a pure green pea, as illustrated in Diagram 4.



The hybrid yellow contains the factors for both yellow and green, its constitution being $\begin{bmatrix} \mathbf{Y} \\ \mathbf{G} \end{bmatrix}$, and it produces gametes \mathbf{Y} and \mathbf{G} in equal numbers.

E. J. ALLEN.

The constitution of the green pea is $\begin{bmatrix} \mathbf{G} \\ \mathbf{G} \end{bmatrix}$, and it produces gametes of one kind only, namely **G**. If we unite equal numbers of **Y** and **G** with **G** only, we get equal numbers of $\begin{bmatrix} \mathbf{Y} \\ \mathbf{G} \end{bmatrix}$ and $\begin{bmatrix} \mathbf{G} \\ \mathbf{G} \end{bmatrix}$, that is equal numbers of the yellow hybrid and of the pure green. This result is again in accordance with experiment.

So far we have considered in each case only one pair of alternative characters. There are of course often a number of such pairs existing at the same time, each pair of which behaves in accordance with Mendel's law. This gives us a result which perhaps appears at first sight to be more complex than it really is. Diagram 5 (p. 364) represents a case studied by Mendel in peas, in which two pairs of characters are involved. First we have the two colours, yellow and green, which have already been considered. At the same time, some of the peas are round in shape, whilst others are very much wrinkled, the wrinkling being really dependent upon the character of the starch grains which constitute the bulk of the pea. In the diagram yellow is represented by a broad black line, green by a broad white line, wrinkled by a broken line.

If we cross-fertilise flowers from a plant bearing pure yellow, wrinkled peas with those of one bearing green round ones, we get in the first hybrid generation yellow round peas. Yellow is dominant to green, as we already know, and round is dominant to wrinkled, which is recessive.

Plants grown from such double hybrid peas were allowed to selffertilise and four kinds of peas were produced : yellow round, yellow wrinkled, green round, and green wrinkled. Mendel's figures for this cross are shown below, the figures required by theory being placed underneath them :—

			Yellow round.	Yellow wrinkled.		Green round.	W	Green vrinkled.
Mendel's	Exper	iment	315	101		108		32
Theory			313	104		104		35
			9	: 3	:	3	:	1

The combination which contained two dominants, yellow and round, was most numerously represented, that containing two recessives, green and wrinkled, was least numerous.

The theoretical analysis of the case is as follows :-----

Let **Y**=yellow, **G**=green, **R**=round, **W**=wrinkled.

HEREDITY IN PLANTS, ANIMALS, AND MAN.

The constitution of the original parents will be

	Y W Y W	G R G R
	Yellow wrinkled.	Green round.
Gametes :	YW.	GR.
The Hybrid mu	st therefore be	Y W G B

The Gametes from this hybrid are :-

Females		Y	W,	Y	R,	G	R,	G	W.
Males		Y	W,	Y	R,	G	R,	G	W.

The second (F.2.) generation will therefore give (see Diagram 5) :--

YW	YR	GR	GW
YW	YW	YW	YW
Yellow	Yellow	Yellow	Yellow
wrinkled.	round.	round.	wrinkled.
ΥW	YR	GR	GW
YR	YR	YR	YR
Yellow	Yellow	Yellow	Yellow
round.	round.	round.	round.
ΥW	YR	GR	G W
GR	GR	GR	GR
Yellow	Yellow	Green	Green
round.	round.	round.	round.
YW	YR	GR	GW
GW	GW	GW	GW
Yellow	Yellow	Green	Green
wrinkled.	round.	round.	wrinkled.

That is 9 Yellow round, 3 Yellow wrinkled. 3 Green round, 1 Green wrinkled.

It will be seen by an examination of Diagram 5 that the yellow rounds of the second hybrid generation have not all the same constitution. Some of them carry a factor for green, which being recessive does not appear in the visible result of the experiment; some carry a factor for

E. J. ALLEN.

wrinkled, which also is recessive. That these factors are actually present can be proved by continuing the experiment to the next generation. Similarly the yellow wrinkled and the green rounds are not all the same.



In the case of the green wrinkled, on the other hand—the double recessive—one constitution only occurs, and these peas would all breed true for however many generations the breeding were continued.

From what has been said already you will I hope have got a clear idea of the simple law, first enunciated by Mendel, which often governs the hereditary transmission of characters from parent to offspring. I propose now to communicate to you some results of the study of a particular instance of Mendelian inheritance, which has been worked out during the last two or three years in connection with the Marine Biological Laboratory. One paper, describing the earlier portions of the work, has been published already in the Journal of the Marine Biological Association, bearing the title "Experiments on the Mendelian Inheritance of Eyecolour in the Amphipod *Gammarus chevreuxi*, by E. W. Sexton and M. B. Wing." I have now in preparation a further paper (see page 273 of this Journal) dealing with the later investigations, the experimental work connected with which has been carried out by Mrs. Sexton.*

* SEXTON, E. W., and WING, M. B. Experiments on the Mendelian Inheritance of Eyecolour in the Amphipod Gammarus chevreuxi. Journ. Mar. Biol. Assoc., XI, p. 18, 1916. ALLEN, E. J., and SEXTON, E. W. The Loss of the Eye-pigment in Gammarus : chevreuxi. Journ. Mar. Biol. Assoc., XI, p. 273. 1917.

Gammarus chevreuxi is a small shrimp-like animal, belonging to the Crustacean order, Amphipoda. It is about $\frac{1}{2}$ inch long, and lives in great abundance in the brackish-water ditches at Chelson Meadow, just above Laira Bridge. It has never been found anywhere else. A drawing of the animal is shown on Plate VII, Fig. 1, which accompanies the preceding paper by Allen and Sexton in this number of the Journal.

The animals are kept alive easily in glass finger-bowls and feed freely on dead leaves, especially on elm leaves. The eggs are carried by the female in a brood pouch until they are hatched. As soon as one batch of eggs is hatched and the young liberated from the pouch, another batch is laid. A batch may contain as many as 50 eggs, so that a large number of young can be obtained altogether from one pair of animals. The eggs take 14 days to hatch at a temperature of about 60° F. The young grow rapidly and reach maturity in about 36 days at summer temperatures. Hence from 5 to 6 generations can be obtained in the course of a year, a fact which makes the animal specially suitable for the study of the problems of heredity.

The eye of *Gammarus*, like that of all crustaceans and insects, is of the compound type. It is made up of a considerable number of single elements, the ommatidia, each provided with a simple lens and receiving a nerve-fibre from the optic nerve.

In the normal animal each ommatidium is surrounded by 5 pigment cells, which lie deeply in the tissue of the eye, and are filled with pigment of a jet-black colour. Just below the surface of the cuticle or skin and surrounding the black pigment there is a quantity of milk-white or rather chalk-white pigment. This gives the whole eye, when looked at directly in the living animal, a honeycombed appearance, the white pigment forming a kind of network in which the round, black ommatidia are enmeshed. (See Plate VII, Fig. 2, of preceding paper.)

Whilst the habits and development of this animal were being studied, there appeared amongst the descendants of a pair of normal black-eyed *Gammarus* brought in from Chelson Meadow in June, 1912, in the third generation, that is amongst the grandchildren, a small number of young ones which had bright red eyes. The usual black pigment was replaced by red pigment, the network of chalk-white remaining as in the ordinary eyes. (Plate VII, Fig. 3, of preceding paper.) From this family a race of red-eyed animals was established, which has been used in these experiments. It is only in this one family that red eyes have ever appeared, and although very many thousands of specimens from the natural habitat have been examined, and many thousands more have been bred from pure black-eyed parents, no other case of the sudden appearance of a red eye has been met with. Sudden and unexpected changes in a character of a pure race have been known by naturalists, as well as by practical breeders, to occur from time to time in both animals and plants, and are called in popular language "sports." Sometimes, no doubt, these sports are due to the reappearance of a latent or hidden character, which existed in the ancestry of the organism; at other times the so-called sports may be due to a sudden change in the constitution of the individual or of the germ cell from which it sprang, so that the character may be said to originate in the particular individual, instead of being inherited from its ancestors. To new characters which originate suddenly in this way the name mutation has been given. The red eye of *Gammarus* may be described as a mutation, appearing in the third generation of a wild animal which had been subjected to the artificial conditions of captivity.

The red-eye is transmitted from parent to offspring, and it behaves quite in a typical Mendelian way, red eye-colour being recessive (like the green pea), and black eye-colour dominant (like the yellow pea). For use in the hybridisation experiments a pure black stock, obtained from Chelson, was kept and thoroughly tested. The stock was maintained for over three years, the offspring and descendants being all examined at different seasons of the year, and in no single case has one with red eyes been found amongst them. Numbers of pairs of red-eyed animals, also, have been bred together, each pair being kept in a separate vessel. The young have all been examined for eye-colour, and the experiment has been continued to the fifth generation and beyond, well over a thousand young having been recorded. A black-eyed animal was never once found amongst them. Both the wild, black-eyed *Gammarus*, therefore, and the red-eyed variety, which arose in the Laboratory, breed perfectly true to type.

Red-eyed animals were mated with pure black, the cross being made in both ways, red female with black male, black female with red male. In the early experiments 3,779 young ones were examined and recorded. Without exception the eyes were black. Clearly, therefore, black is dominant and red recessive.

The black-eyed hybrids obtained from the cross between black and red were mated together. They produced altogether 4,393 young, of which 3,327 were black-eyed and 1,066 were red-eyed. (See Diagram 6.1.) This is a very close approximation to the 3:1 ratio. There are 32 reds too few on a total of 1,066 reds. This may be due merely to chance, or it may be due to the fact ascertained during the course of the experiments that the red-eyed animals are not quite as vigorous and healthy as the black-eyed. The deficiency in the number of reds may therefore mean that more red than black failed to survive whilst the eggs were developing in the brood-pouch of the mother.

HEREDITY	IN	PLANTS,	ANIMALS,	AND	MAN
----------	----	---------	----------	-----	-----

BLACK	CARRYING RED	\times BI	ACK CAI	RRYII	NG RED.		
			Blacks.		Red.		
	Experiment		3,327		1,066		
	Theory .		3,294		1,098		
			3	:	1		
BLACK	CARRYING RED	\times RF	ED.				
			Blacks.		Reds.		
	Experiment		2,176		2,079		
	Theory .	10.10	2,128		2,128		
	v		1	:	1		
BLACK	CARRYING RED	AND A	$_{\rm LBINO}$ \times	BLA	CK CAR	RYIN	G ALBINO.
			Blacks.		Reds.		
	Experiment		144		59		
	Theory .		153		51		
			3	:	1		
BLACK	CARRYING RED	AND A	$_{ m ALBINO}$ $ imes$	REI	D CARRY	ING	ALBINO.
			Blacks.		Reds.		Albinos.
	Experiment		235		169		144
	Theory .		205		205		137
			3	:	3	:	2
BLACK	CARRYING RED) AND	$_{ m ALBINO}$ $ imes$	BL	ACK CAL	RRYI	NG RED AN
		А	LBINO.				
			Blacks.		Reds.		Albinos.
	Experiment		542		189		241
	Theory .		547		182		243
			9	:	3	:	4
RED CA	RRYING ALBING	\times R	ED CARRY	ING	ALBINO.		
			Reds.		Albinos		
	Experiment		1,408		471		
	Theory .		1,409		470		
			. 3	:	1		
			1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1				

Hybrid blacks were mated with red-eyed recessive animals. (Diagram 6. 2.) 4,255 young were obtained and examined as soon as extruded from the brood-pouch. 2,176 were black-eyed, and 2,079 were red-eyed, which is very close to the equality which Mendel's theory demands. There is again a slight deficiency of red-eyes, namely 49.

This cross of the hybrid with the recessive, which we have already studied in the yellow and green peas, is a specially important one to anyone investigating problems of inheritance, because its result enables us to distinguish the pure dominant from the hybrid which in appearance resembles it. We have seen that the pure black mated with red gives all black offspring. If, therefore, when a black and a red are mated together we get some red-eyes amongst the children, we know that it is a hybrid black that we are dealing with.

One other mating of these two varieties remains to be considered. When hybrid blacks are mated with pure blacks, the dominant asserts itself completely, and all the offspring are black-eyed. The total number of young obtained in our earlier experiments from crosses of this kind was 379—all with black eyes.

In one family, belonging to the first generation of hybrids got by crossing the red-eyed *Gammarus* with the pure black-eyed one, a second sport



A Black disc with white centre represents a black-eyed animal. A Black disc with white cross represents a red-eyed animal. A Black ring represents an albino-eyed animal. $\delta = male, \quad \varphi = female.$

or mutation appeared. The brood in which this mutation occurred consisted of 7 black-eyed young, 1 red-eyed and 4 in which neither black nor red pigment could be seen, and only the network of chalk-white pigment was left. (Plate VII, Fig. 4, of preceding paper.) The eye was also very irregular in shape and altogether of a degenerate character, the number of ommatidia being very few. These degenerate eyes, with only white pigment, we shall speak of as "albino" eyes.

In order to determine the constitution of these degenerate albino eyes, and to find out whether or not the condition was hereditary, one of the animals, a female, was mated first with a pure red male, and then with a known hybrid black one.

The result of these matings is shown on Diagram 7, and will probably

HEREDITY IN PLANTS, ANIMALS, AND MAN.

surprise you. Albino-eyed female mated with pure red-eyed male gave 6 red-eyed and 3 black-eyed young. Albino-eyed female mated with hybrid black gave in four broods 75 black-eyed and 15 red-eyed young.*

In the grandchildren from both crosses, however, you will see that the albino-eyed form reappears.

From this it follows :--

- that the factor for albino eye is transmitted from parent to offspring, but that colour is dominant and albino recessive, for when albino is mated with coloured eye no albinos occur in the first generation of offspring;
- (2) that the original albino-eyed female must have contained the factor for black, since black offspring were produced when it was mated with pure red, which we know from the previous work contains no black;
- (3) that the albino-eyed female must contain the factor for red, and this for two reasons : in the first place, if it had contained black only we should have got only black offspring when it was mated with red, for we know that black is dominant to red; in the second place, and again because black is dominant to red, if the albino had contained black only, when mated with the black hybrid we should have had only black offspring, whereas we obtained 75 blackeyed and 15 red-eyed. We know that when the hybrid, containing red and black, is mated with another hybrid of the same kind the resulting offspring should be 3 black to 1 red.

We must now look more closely at the grandchildren of the original albino-eyed female, which were all obtained by mating together her immediate offspring of the F.1 generation. When two blacks were mated together in F.1 two kinds of broods resulted, some in which only black and albino-eyed young occurred, others in which black, red, and albino were present. When two F.1 reds were mated together the broods contained red-eyed and albino-eyed young. (See Diagram 7.)

This resembles closely what is found in coat colour in animals such as rabbits, mice, and rats, which has been worked out by Bateson, Punnett, and others. To explain the phenomena these authors assume that in order that the colour in the coat of an animal may be visible it is necessary that at least two factors should be present, one factor representing the colour itself—say black or brown, as the case may be—and a second factor which must be present in order that the colour may show itself. In the absence of this latter factor, which they call the colour factor, the

* In the diagram one brood only is shown from this mating, consisting of 7 black-eyed and 2 red-eyed young.

NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

2 B

E. J. ALLEN.

animal will be white, though it may still retain the power of transmitting a particular colour to its offspring. The black or brown factor is present in the animal's constitution, but in the absence of the colour factor the black or brown does not appear.

Pure BLACK .		·	•	•	C B C B
Pure RED	·		•		C R C R
BLACK CARRYING R	ED (HY	BRID	BLACI	x).	C B C R
ALBINO CARRYING	BLACK	·	•	•	c B c B
ALBINO CARRYING	RED				c R c R
ALBINO CARRYING	BLACK A	ND R	ED	•	c B c R
BLACK CARRYING A	LBINO	·	•		CB cB
RED CARRYING ALB	INO .	·	·		CR cR
BLACK CARRYING R	ED AND	ALBI	NO		CB cR
BLACK NO-WHITE					W C B W C B
RED NO-WHITE .		•	·	•	W C R W C R

DIAGRAM 8.

Eye-colour of Gammarus. Constitutions of some of the different kinds. ${\bf C}$ represents the factor for colour, ${\bf c}$ the absence of this factor. ${\bf B}$ represents the factor for black, ${\bf R}$ that for red.

w represents the factor for absence of white pigment.

Animals of the first nine constitutions shown on the diagram all possess the white pigment, and this might have been indicated by adding $\frac{\mathbf{W}}{\mathbf{W}}$ to the formula in each case.

A similar hypothesis will explain the present case. Diagram 8 shows the constitutions on this hypothesis of some of the varieties of Gammarus

HEREDITY IN PLANTS, ANIMALS, AND MAN.

which have been obtained in the experiments. The colour factor is indicated by \mathbf{C} , the absence of this factor by \mathbf{c} . \mathbf{C} is dominant to \mathbf{c} . \mathbf{B} and \mathbf{R} represent the factors for black and red-eye respectively.

Just as we worked out on Mendel's theory the result to be expected from the crossing of yellow-wrinkled and green-round peas, so in this case we can work out the result from mating together animals with any two of these various constitutions. This has been done for all possible combinations, and the results of the experiments are in good agreement with theoretical expectations, as may be seen from a study of Diagram 6, which gives the numbers actually obtained from several of these matings, as well as those which the theory requires.

The black-eyed children of the original albino-eyed female mated to the hybrid male, all of which carry the factor for albino, or, to put it more accurately, lack one colour factor, can be crossed in three different ways :—

- (1) Pure black \times Pure black.
- (2) Pure black \times Hybrid black (Black carrying red).
- (3) Hybrid black \times Hybrid black.

If we work out the theory for these crosses, just as we worked it out for the peas, we find that altogether amongst the offspring, that is amongst the grandchildren of the original parents, there will be animals of nine different constitutions of eye-colour (compare Diagram 8), namely :—

4 kinds of black-eyed animals	. Pure black.
	Black carrying albino.
	Black carrying red.
	Black carrying both red and albino.
2 kinds of red-eyed animals .	. Pure red.
	Red carrying albino.
3 kinds of albino-eyed animals	. Albino carrying black.
	Albino carrying red.
	Albino carrying black and red.

In the actual experiments we have been able to prove that animals of all these nine kinds occur, and the numbers also in which they are found are in sufficiently good agreement with the theoretical expectation to satisfy us of the correctness of the theory.

In Diagram 9 the actual results of a number of matings in which the albinos take part are shown, as these results are specially interesting.
E. J. ALLEN.

Mated together the albinos give all albino offspring, whatever their constitution, since neither parent contains the colour factor, which we have indicated by great \mathbf{C} , which enables the colour to appear.



Mated with pure red, albinos give three kinds of broods :---

- All black-eyed young. In this case the albino contains the factor for pure black, which is dominant to red.
- (2) All red-eved young. In this case the albino contains pure red.
- (3) Black-eyed and red-eyed young in equal numbers. The albino is then hybrid as regards colour, containing factors for both black and red.

There is still another sport or mutation which has occurred in the eye of *Gammarus*. This is the entire absence of the chalk-white pigment which lies near the surface between the ommatidia. (Plate VII, Fig. 5, of preceding paper.) These we call "no-white" eyes.

Animals with eyes like this may be either black-eyed or red-eyed, and the black-eyed ones may be either pure black or hybrid black containing red. By cross-breeding we have obtained all three kinds.

The character "no-white" is transmitted to the offspring in strict accordance with Mendel's law, the presence of white pigment being dominant and its absence recessive. If an animal therefore which possesses the white pigment is mated with one which does not possess it the offspring in the first generation all have the white pigment—their eyes are quite normal. If males and females of this first generation are mated together, in their offspring—in the grandchildren of the original pair— "no-whites" reappear.

HEREDITY IN PLANTS, ANIMALS, AND MAN.

At this stage of the investigation a very interesting question arose. What would be the result of crossing the "no-whites" with albinos, and mating together their offspring ?

We may represent the factor for white pigment by \mathbf{W} , and its absence by \mathbf{w} . These two factors behave as an alternative pair, according to Mendel's law. The constitutions of the black and the red "no-whites"

will then be w C B and w C R w C R.

If we cross these with albinos and work out the theory, as in the case of the peas, we find that in the first generation we get all normal-eyed offspring, the "no-whites" provide the colour factor, the albinos provide the white.

The result of such a cross obtained in an actual experiment is shown in the Diagram 9 (the second brood shown on the diagram). The young are all normal-eyed blacks. They, however, differ in constitution from any black-eyed animals previously obtained, for they carry not only the factors for black and red but also the factors for both "albino" and "no-white," and are capable of transmitting all four factors to their children.

When these animals are mated together, according to the theory, which we can work out in the usual way, there should be, out of every 64 offspring, 48 with white pigment present, and 16 with no white pigment. Of these 16 with no white pigment 4 should be ALSO ALBINO, that is to say they should, according to the theory, show neither white, nor black, nor red pigment. The eyes should be quite colourless.

Animals with quite colourless eyes we had never seen when the theory for this cross was first worked out. Would they be produced when an actual experiment was made? A pair of these black-eyed hybrids was mated. The first brood hatched was a small one, but our pleasure was naturally great when we found that it consisted of 2 with normal black eyes, 1 black with no white, and 2 quite colourless, with no eye-pigment visible at all. Since then other broods have been obtained, and there is no doubt that the facts agree with the theoretical analysis.

Looked at from a general point of view the cross of the "no-white" with the albino-eye is of great interest, and is particularly instructive. We here took the two most degenerate and abnormal types of eye that were known, and mated together the animals which carried them. In the first generation the offspring have all perfectly normal characters and are indistinguishable, as far as their own visible structures are concerned, from the perfect wild creatures. The factors lacking in one parent were supplied by the other parent and perfect children resulted. The

E. J. ALLEN.

defects, however, persist in a latent condition in the germ plasm of these children, and if they are mated with those of like constitution the defective characters all reappear in the grandchildren. The factors may even combine in such a way that some of these grandchildren are more defective than the defective ancestors from which they sprang. They unite the defects which were borne separately by the two grandparents. This no doubt explains some of the ill-effects which result from too close inbreeding. We should remember, too, that if here defects have been united, in other cases it would be equally possible that the excellences of different ancestors should be combined in some of their descendants.

With Gammarus, however, what we have actually observed has been a degeneration of the eye, taking place step by step as one factor after another has been lost. Bateson, in his presidential address to the British Association in Australia in 1914, emphasised the fact that most, though perhaps not all, the Mendelian cases studied up to the present can be explained rather by the loss of factors than by the introduction of new factors. Since that address was delivered there has been, shall we say, in the air-for no one has ventured. I believe, to declare himself a complete adherent to it—a theory of a kind of inverted evolution, starting with a highly complex primitive protoplasm or germ plasm, which by the loss of factor after factor has given rise to the endless varieties of plants and animals that we know. These factors are conceived of as being for the most part restraining or inhibiting factors, whose loss, one by one, in the course of ages has allowed the full powers and glories hidden in the primitive plasm to unfold themselves—a process which still goes on. What the final excellence or final catastrophe is to be, when all the bonds are broken and all the restraints are lost, no one, as far as I know, has ventured to suggest. When, however, we take into consideration the whole range of facts upon which our conceptions of organic evolution are based we find little to support such a view.

The cases of Mendelian inheritance which I have so far discussed have been of a simple character, following exactly the law which Mendel first laid down. Sometimes, however, the phenomena are more complicated. We saw that the albino-eye of *Gammarus* was always imperfect in shape. Absence of colour and imperfect form are here always united and remain united in inheritance. Characters which behave in this way are spoken of as linked characters, and the factors in the germ cells from which they originate are also said to be linked. There is often also a special connection between a particular character and the sex of the animals which transmit and inherit it. This is known as sex-linkage and is well illus-

HEREDITY IN PLANTS, ANIMALS, AND MAN.

trated by eve-colour in the American fruit fly Drosophila. The wild fly has red eyes, and a sport or mutant is known which has white eyes. If a white-eved male is mated with a red-eved female all the offspring are redeyed, and males and females occur in equal numbers. When these hybrids are mated together there result three red-eved flies and one with white eves-the usual Mendelian proportions. The white-eved flies, however, in this generation are all males, like the grandfather. If however we make the original cross in the opposite way, mating a red-eyed male with a white-eved female a different result is obtained. Instead of having all red-eved children, males and females in equal numbers, we have equal numbers of white-eved males and red-eved females. In the next generation also the result is different, for when one of these red-eved females is mated with a white-eved male the offspring are red-eved females, redeved males, white-eved females and white-eved males in equal numbers. It would carry us too far were I to attempt to give the explanation which has been put forward to account for this, so I shall content myself with stating the facts to show that the simple Mendelian law may at times seem to give highly complex results.

That knowledge gained by Mendelian investigations may be of great value to practical agriculture is shown by Prof. Biffen's work on the varieties of wheat. The wheats usually grown in England produce heavy crops, but the flour obtained from them is not satisfactory from a baker's point of view. A loaf made from this flour does not rise well when baked. In order to correct this it is usual to mix the English flour with flour from a so-called "hard" foreign wheat, which contains a larger proportion of gluten. English wheats, also, are very liable to a disease known as "rust," which is caused by the growth of a fungus on the plants. Prof. Biffen was able to show that good cropping power, hardness, and ability to resist rust are all characters which behave in a Mendelian way. By a long series of experiments in crossing different varieties of wheat he was able to produce a variety which possessed good cropping powers, the hard qualities of foreign wheat, and also a complete power of resisting rust. This wheat can be grown quite successfully in the English climate, and it has kept its special qualities unchanged for a number of years.

And now for a few minutes we will direct our attention to the question in connection with this subject of Mendelian heredity, which is perhaps of more interest to us than any other. In the human race does inheritance take place in accordance with Mendel's law? There is considerable evidence that certain characters do follow this law and that the same thing is true of certain diseased conditions.

The inheritance of eye-colour is a striking instance, which was investi-

E. J. ALLEN.

gated in this country by Hurst and in America by Davenport. Hurst examined the eyes of children in a Leicestershire village, and also the eyes of their parents and grandparents, where that was possible.

The iris, the part of the eye in which the colour is situated, owes its colour to two separate layers of pigment, a deep-seated layer which gives the effect of blue, and a layer near the surface which contains yellow and brown pigment. When the brown pigment of the surface layer is fully developed it hides completely the blue underneath it, and the eyes are dark brown in colour. If the brown pigment is entirely absent we get the true blue eye, and such an eye Hurst calls *simplex*. Eyes with both blue and brown pigment he calls *duplex*, and these duplex eyes are of two



kinds. First, those in which the brown completely covers the iris and hides the blue, the so-called self-coloured or whole-coloured eye, and second, eyes in which the brown pigment forms a ring round the black pupil in the centre of the eye, whilst the greater part of the blue layer can still be seen. Such duplex eyes are called "ringed." The details of distribution of eye-colour in two of the families examined by Hurst are shown in Diagram 10.

These and other results which were obtained showed that whole-coloured brown eyes were always dominant to ringed and also to blue. Ringed eyes were also dominant to blue. The blue simplex eyes were pure reces-

HEREDITY IN PLANTS, ANIMALS, AND MAN.

sives, and whenever father and mother both had such eyes all the children also had eyes of the same kind.

The dominant self-coloured and ringed eyes, on the other hand, might be either pure dominants, or hybrids containing the factor for recessive blue eyes. Several instances of these hybrids are seen in the diagram.

The next diagram (Diagram 11), which is extracted from a much larger pedigree illustrated by Bateson in his book on "Mendel's Principles of Heredity," shows a portion of the pedigree of a family living in a cluster



DIAGRAM 11.

The black discs represent the affected individuals, the rings those who did not suffer from the disease. In the exceptional case (black disc with white centre) both parents were affected. The arabic figures indicate numbers of unaffected children. Nine generations (I-IX) are illustrated.

 $\delta = \text{males}, \ \varphi = \text{females}.$

of villages in the south of France, in which many members have suffered from what is known as night-blindness, the affected persons being quite unable to see in a dim light. The pedigree commences with one Jean Nougaret, born in 1637, and has been followed through ten generations. In this family the disease has always behaved as a Mendelian dominant, though not a simple one, and it has always been inherited from an affected parent. Unaffected parents have never had affected descendants.

In another disease, hæmophilia, there is a curious relation with sex.

The symptom of the disease is that the blood refuses to clot, and hence there is great loss of blood from even a very slight wound, such as a scratch. The peculiarity about its inheritance is that only the male members of a family are affected, but the disease is usually transmitted through the females, who do not themselves develop it. An apparently healthy daughter belonging to such a family will transmit the affection to her sons, and her daughters will be capable of handing it on to their children.

If we pass from a consideration of man's physical nature and ask ourselves whether and to what extent the principles we have been discussing are applicable to his moral and intellectual qualities, we enter a field of speculation of the very highest interest. In his work on "Hereditary Genius," published in 1869, Francis Galton brought together and analysed a great mass of information which proved conclusively that excellence in many intellectual and moral qualities occurred in particular families with a frequency out of all proportion to that in which it was found in the general population. No one will, I think, dispute the fact that musical ability is inherited in certain families, and the same seems to be true of mathematical genius, though by no means all the nearly related members of the families possess the exceptional powers. Galton gives a list of 36 men who took the place of senior classic at Cambridge between 1824 and 1869. In this list of 36, the name Kennedy occurs four times, three of the men being brothers and the fourth a nephew of the others. The name Lushington occurs twice, the men being brothers, whilst a third brother was fourth classic of his year.

Mendel's law was unknown to Galton when this book was written, but a consideration of his data certainly suggests that some at least of the exceptional mental and moral attributes with which he deals may follow the general principles of inheritance which Mendel first made clear. The question is one which may well repay further investigation. And if the future should reveal to us with certainty the fundamental principles according to which human qualities, both physical and mental, are handed on from generation to generation, shall we not have reached a real landmark in the progress of the human race towards well-being ? It is not that one contemplates direct interference with the liberty of the individual, excepting perhaps in extreme cases of physical or mental disease, but we may, I believe, look forward to a gradual incorporation in the traditions and social usages of the people, of such knowledge as shall come to stand on a certain and indisputable scientific basis. The immense power of such traditions and customs on the life of the general population cannot be denied. Gradually, too, as the new facts become firmly established, religious teachers will lend their aid, and ethical

HEREDITY IN PLANTS, ANIMALS, AND MAN.

thinkers will submit that a high standard of morality demands that the welfare of unborn generations shall not be sacrificed. Man, it is true, is prone to follow desire rather than reason; but all these influences should not be without effect in producing a definite progressive improvement in the inborn qualities of the race. Such at least would seem to be the possibilities opened up by the detailed study of the laws of heredity.

Food from the Sea.

Being the Presidential Address delivered before the Plymouth Institution, October 14th, 1915.

By

E. J. Allen, D.Sc., F.R.S., Director of the Plymouth Laboratory.

[Reprinted from the Transactions of the Plymouth Institution.]

. . . PASSING now to the special subject of my address to-night, I will ask your attention in the first place to some general aspects of our Sea Fisheries as a source of national food supply and to the general scientific investigations which have been undertaken in the hope that the yield of the harvest of the sea may be still further increased. In the second place a more detailed account will be attempted of some particular researches bearing upon these matters, which happen to have formed during the past few years the subject of my own special work. If in the course of my remarks you may seem to be asked to follow me in excessive detail into some of the more remote corners of the problems which arise, my excuse must be that, even at the risk of upsetting the balance of the picture as a whole, it is probably possible to speak to more purpose and with a better prospect of stimulating others to fresh efforts. by describing researches with which I have been personally concerned, than by a more general and better proportioned, but necessarily more superficial treatment of the whole subject.

As a direct consequence of our geographical position, our immediate proximity to large areas of shallow sea, our extended coast-line, with its many fine harbours and serviceable fishing coves, lying at distances not too remote from the large centres of population, and of our well-developed railway systems, the sea fisheries of Great Britain have become of much greater relative importance as a source of food supply than has been the case in almost any other country of the world. The statistics for the year 1913, the last complete year for which normal figures are available, show that $1\frac{1}{4}$ million tons of fish were landed in England, Scotland and Ireland, having a value at the port of landing of some 15 million pounds. By way of comparison, and to give you some idea of the relative importance of the industry, similar figures for one or two other sources of our food supply may be of interest. In the same year 1913, $1\frac{1}{2}$ million tons of wheat were grown in the United Kingdom, as against the $1\frac{1}{4}$ million tons of fish landed, the wheat being valued somewhere about 13 million pounds, as against 15 million pounds for the fish. Imported wheat was $5\frac{1}{4}$ million tons, valued at 44 million pounds. Imported beef was valued at 16 million pounds, imported mutton at 11 million.

It should be added, however, that one-third of the total value of the fish landed is attributable to herrings, which were salted and exported chiefly to Germany and Russia, the sum received for these fish being 5 million pounds.

It is interesting to compare the value of fish landed in the United Kingdom with that of fish landed in other European countries. Of the total value of sea-fish landed in Europe in 1910, $47\frac{1}{2}$ per cent (very nearly one-half) stands to the credit of British fisheries, other countries showing France, 19 per cent; Norway, 10 per cent; Germany, 7 per cent; Holland, 7 per cent; Sweden, 3 per cent; Denmark, 3 per cent; Belgium, 1 per cent; Russia, 1 per cent.

From these figures you will see what a preponderating part our islands take in the total yield of the fisheries.

Now the two pressing questions which present themselves, from the practical point of view, are : Do we at present make the best possible use of the harvest of the fishing grounds ? And how can the yield of human food in the form of fish be increased ?

As a matter of fact from year to year, for many years past, the total quantity and the total value of the fish landed in this country have both shown a steady and continuous increase. Even since the year 1890, when the industry of steam-trawling was already in full swing, the total landings have doubled both in quantity and in value. This increase has been brought about entirely by increasing the number and the power of the fishing vessels and extending the areas over which they have worked. To-day the region worked by the steam-trawlers, which bring their fish in ice to the English market, extends northwards to the Barent's Sea. off the north coast of Russia-the so-called White Sea grounds-to Iceland and the Faroes, and southwards through the Bay of Biscay to the banks off the coast of Morocco, trawling being carried on to a depth of 200 fathoms or even more. Doubtless this process of increasing the power of fishing vessels and extending the area over which they fish will still continue. Trawlers have already made experimental voyages to the Banks of Newfoundland, and halibut from the Pacific Coast of Canada has been sent in a frozen state to the London market. This kind of development of the fisheries may well be left to the energy and enterprise of the fishing industry. The only useful help which the scientific expert might give, would be in making preliminary explorations of more distant grounds. Government has, however, never thought it right to provide public funds for work of this character, and it is probably better to leave it to the trade and the practical fishermen.

The subject with which fishery science is called upon to deal is rather, whether the best possible use is being made of the resources of food which the sea is capable of yielding in those waters in which fishing is already extensively and exhaustively carried on. British researches have dealt chiefly with the North Sea, the Irish Sea, the English Channel and the waters around the Irish coast. Are the methods of fishing now employed in these areas unnecessarily wasteful of fish life or could the total annual landings be made more valuable by a more rational regulation of the methods of capture ? Are there other means, analogous to the cultivation of the land, which might be adopted to improve the yield of the fishing grounds and to what extent could such means be profitably employed ?

It must be at once admitted that, except to a very limited extent, we are not at present in a position to give definite answers to these questions. We cannot assert with confidence that any attempted regulation of the fisheries upon a considerable scale has been followed by marked and definite improvement. In matters of cultivation also, excepting as regards some of the fisheries for shell-fish, such as oysters and mussels, we are unable to point with certainty to any success upon a large scale, when dealing with sea fish.

And the reasons for this comparative inability to obtain favourable practical results are not far to seek. In the first place, the sea is so vast and so powerful are its elemental forces, that control by human agency must always be immensely difficult. We should not forget, however, that the evidence is now almost conclusive that human agency has been powerful enough to exert a marked adverse influence upon many of the best and most productive fishing grounds, and if destruction can be wrought by man, it should not be beyond his power to do something to repair the damage he has caused.

In the second place, our knowledge of the many complex factors with which we have to deal is still very imperfect. It is, indeed, only very slowly approaching a point when proposals for practical measures can be made with any hope of foreseeing what the actual effect of those proposals would be. In this direction much further enquiry and study will be required. Notwithstanding all that has been done in the way of research during the last thirty or forty years the gaps in our knowledge on many of the most fundamental points are very great. Until more adequate means can be secured for carrying out actual experimental work at sea progress cannot possibly be rapid, and many of the problems cannot be studied in a satisfactory way.

Slowly, however, we are building up a true science of the fisheries. The direction and velocity of the currents, the differences in temperature and salinity of the water, and the variations in these factors from season to season and from year to year upon which the fluctuations in the abundance of fish must very largely depend, are being gradually worked out and understood. The effects of wind and weather and of the varying amount of sunshine falling on the water in different years are questions which are being studied. Then again, the natural history of the fishes themselves is the subject of much research ; their habits and food, when and where they spawn, the characters of the larval fishes and when and where their younger stages are to be found, all fall under this head.

Many of the results of investigations on these lines have already from time to time been described and discussed at the meetings of our institution, and for that reason I will not to-night dwell upon them, important -indeed, essential-as they are for an adequate understanding of the problems which have been put forward. It is to a more general aspect of the matter that I would especially refer-the question of how the primary or fundamental food supply of the sea is built up. Suppose that during the late summer or autumn we capture in the waters of Plymouth Sound, a mackerel. The body of that mackerel represents some 8 ounces of excellent human food. What is the ultimate source from which that food has been produced ? If we examine the stomach of the mackerel, we shall probably find it filled with small fishes, chiefly sprats and quite young herrings, with perhaps a certain number of those small, shrimp-like creatures which are known as Copepods. The young herrings and sprats have themselves fed largely upon Copepods of a similar kind. We conclude, therefore, that the body of the mackerel has been formed either directly, or indirectly, through the young herrings and sprats, from the organic substance contained in the bodies of the shrimplike Copepods. Then if we carry the problem a stage further back and enquire how the bodies of the Copepods have been built up, we find with the aid of a microscope that their food consists in large measure of minute plants, chiefly belonging to the class of diatoms.

We have here a particular and perhaps exceptionally simple and straightforward example of the general principle, applicable equally to land and sea animals, that the organic substance which constitutes their flesh is always derived either directly or indirectly from vegetable life. The amount of animal life, therefore, which a given area of sea or land can support, depends upon the amount of plant life on which the animal life can feed.

When we push the enquiry further back we find, as you know, that the bulk of the plant substance consists, in addition to water, of compounds of the element carbon, which are known under the general name of organic compounds. This carbon is derived entirely from the carbonic acid gas present in the air or dissolved in the water, the gas being split up and the carbon assimilated by the plant in the presence of sunlight. The source of the energy by means of which all organic matter is built up is the light of the sun, whilst the great mass of the solid substance contained in the bodies of both animals and plants is derived ultimately from carbonic acid gas, obtained in the case of land plants from the air, in the case of sea plants from gas dissolved in the water. In addition to carbon and water the plant requires a number of other substances, chiefly inorganic salts, but the quantities of these which are necessary are comparatively small. In the case of land plants these salts are obtained from the soil, in the case of sea plants from the water in which they are dissolved.

It may be interesting here to compare the yield of organic substance derived from a given area of sea or fresh water with that from a similar area of land, to compare the harvest of the sea with the harvest of the land.

It has been calculated by Brandt, from the catches of fishermen in an enclosed harbour, that the annual yield was 89 lbs. of fish per acre. In Continental carp ponds, where the culture has been carefully carried on, 95 lbs. of fish per acre per year have been obtained.

Making a similar calculation for the North Sea from the statistics of fish landed, we get, as we should expect, a much lower annual yield, namely, 15 lbs. of fish per acre. The average value of this is only 1s. 6d. per acre per year.

Beds of shellfish give a very much higher yield, but they of course in reality, owing to the tidal currents which pass over them, draw their food supply from a much greater area of water than that of the sea-floor to which they are attached. Johnstone finds for the uncultivated mussel beds of Morecambe Bay, on the Lancashire coast, a yearly production of 86 cwts. (or nearly 10,000 lbs.) per acre, valued at £14 16s. per acre.

For comparison with these figures here is one taken from agricultural statistics. Young bullocks fed on cultivated land give an average annual yield of 73 lbs. of beef per acre.

Putting the figures side by side we have first the mussels from More-

FOOD FROM THE SEA.

cambe Bay, with a yearly production of 10,000 lbs. per acre; then in quite a different category :---

Fish from Carp Ponds	95 lbs.	per acre	per year.
Fish from the enclosed Harbour	89 lbs.	,,	,,
Beef from Young Bullocks .	73 lbs.	,,	,,
Fish from the North Sea	15 lbs.	,,	,,

It will be seen, therefore, that although the figures for the open sea are far below those for cultivated land, more restricted areas of water are capable of producing a considerably greater weight of crop. Especially the figures for the mussel beds seem to indicate that much larger returns from the sea might be possible, if sufficient knowledge of the complex conditions of marine life could be successfully obtained.

The possibilities of a still greater yield have recently been suggested by Prof. Benjamin Moore of Liverpool, from observations made in the Irish Sea. This author has calculated from measurements of the change in alkalinity of the water, that under the action of sunlight there is an annual production of two tons of dry organic matter per acre, which would be equivalent to at least *ten tons* of moist vegetable substance. This is a preliminary estimate to which it would be unwise to attribute too great exactitude at present, but it does seem to confirm the view that we are as yet a very long way indeed from making full use of the organic food substance which the seas around our coasts are capable of producing.

And this leads me to ask your attention in a little more detail, to the particular aspect of the conditions upon which marine life depends, to which my own researches have recently been directed.

The marine vegetation, which constitutes the fundamental food supply of the sea, may be divided into two principal groups. All round our shores we find attached to the sea-floor the green, red and brown seaweeds. These form a fringe in the shallow water around the coast, but do not extend to a greater depth than about 15 fathoms, owing to the fact that sufficient light to enable them to grow does not penetrate through the water below this depth. Many animals feed upon these seaweeds as they grow, and recent researches by Danish naturalists seem to show that when the weeds die and decay the organic fragments into which they break up constitute an important source of food for many other animals, which in their turn serve as food for fish.

Outside this coastal fringe, however, the plant life of the sea consists of minute organisms, microscopic in size, which float freely in the water, and live and grow in the upper layers from the surface to a depth of 100 or 200 fathoms, or even deeper. Amongst these microscopic plants

NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

2 c

one of the most important and prolific groups is that of the diatoms. These plants possess a delicate and often very elaborately constructed skeleton of silica, and contain a brown colouring matter, which like the green chlorophyl of land vegetation is able in the presence of sunlight to assimilate the carbon from carbonic acid gas.

It has formed an interesting subject of research to endeavour to ascertain as exactly as possible the conditions necessary for the growth of these diatoms, and to find out by means of experiments in the laboratory how the amount of growth may be increased. In order to carry out such experiments with exactitude and to obtain precise and definite results it is necessary to work with cultures of a diatom which are as nearly as possible pure, that is to say, cultures which contain no other living organisms excepting the single species of diatom upon which the experiments are being made. If two or more living organisms are present in the experimental cultures the results at once become complicated, since a second organism not only uses up the different constituents in the culture solution, but it also excretes waste products of its own, which become dissolved in the water and may affect either favourably or unfavourably the growth of the diatom which is being experimented upon.

The experiments had, therefore, to be conducted as nearly as it was possible under sterile conditions. The glass flasks in which the cultures⁻ were made, after being carefully cleaned, were baked in an oven, and all the culture solutions were boiled before being used.

The particular diatom upon which the experiments were made is one that is found in the Plankton, that is to say amongst the large number of microscopic organisms which float freely in the waters of the sea, and are drifted about at the mercy of wind and current. Such organisms are collected by dragging through the water a bag-shaped net, made of muslin or fine-meshed silk, which strains them out. This form of net is generally known as a tow-net. The organisms collect in a tin or bottle attached to the end of the net, and can be brought alive to the laboratory in a bottle of sea-water.

The species of diatom used in the experiments is called *Thalassiosira* gravida. Each diatom cell consists of two flat, cup-shaped valves, fitting one into the other and enclosing the protoplasmic substance of the cell. The whole cell of *Thalassiosira* looks something like a flat, shallow pillbox. A number of these cells are joined together by threads, which run from the middle of one cell to the middle of the next, so that long chains are formed. These chains of diatoms have much the appearance of a number of buttons strung on a thin wire, with a considerable interval between successive buttons. This chain formation is of some importance

in the experiments, because the length of the chains which are formed gives a good indication of the healthiness of the culture.

In order to obtain a pure culture of a Plankton diatom two methods may be used. The first—which, however, does not give very satisfactory or certain results in practice—is to pick out under the microscope, by means of a very fine glass pipette, a single cell or short chain of the diatom and put it in a flask containing a suitable culture solution.

The second method, which is the one I have more often used, is as follows : A glass flask, containing about 2 litres (say, half a gallon) of suitable culture solution, the nature of which I shall describe presently, is brought to the boil in order to kill off any animals or plants which may be present in it, and then allowed to cool. We then take some seawater containing a mixture of Plankton animals and plants, which have been collected with a fine silk net in the way already described, and add just one or two drops of it to the flask containing the half-gallon of cold culture solution. The flask is shaken up, and the living organisms, which were present in the two drops of sea-water, become evenly distributed through it. The water in the flask is then divided up, by pouring it into, say, forty or fifty tiny flasks, and these small flasks are put to stand in a north light and kept at an even temperature. After a week or ten days a brownish growth appears in many of the flasks, and if the experiment is successful, that is to say if our one or two drops of water containing the mixture of organisms has been sufficiently divided up, we shall find in perhaps two or three of our fifty small flasks a pure culture of one of the Plankton diatoms. A culture once obtained in this way can be kept as long as we wish, by continually inoculating new flasks of sterile culture solution, transplanting to one new flask after another as often as may be desired. I have kept cultures alive in this way for six or seven years.

Such cultures are, however, not quite perfect. They always contain in addition to the diatoms some bacteria, and these are very difficult to get rid of; indeed I have never really succeeded in entirely eliminating them. They may be greatly reduced by a process of differential poisoning. By adding to a series of culture flasks gradually increasing doses of chlorine gas, it is possible to hit off a strength of the poison which will kill most of the bacteria without killing the diatoms. In this way a culture of the diatom *Thalassiosira* was obtained in which there remained only one kind of micro-organism, or at least only one kind that could be detected in the ordinary way by growth on agar-agar plates. The experiments to be described were made chiefly with this culture. Its growth was very rapid and healthy under favourable conditions, and very long chains of diatoms were formed. Previous work dealing with the culture of diatoms had been done mainly by the French bacteriologist Miquel. Miquel himself investigated principally fresh-water diatoms, but he showed that the methods he employed could be used also for marine forms, his experiments in this direction having been made chiefly with shore and bottom species. My own work, in which during the earlier stages I received much assistance from my colleague, Mr. E. W. Nelson, has dealt mostly with the floating or Plankton diatoms, which are much more delicate organisms to deal with than the fresh-water or marine bottom forms.

Miquel showed that fresh-water diatoms could be most successfully grown when to the water there was added a very small quantity of certain inorganic salts, together with a small proportion of soluble organic matter, prepared by making an infusion or maceration of straw, bran or some other vegetable substance.

The inorganic salts, which Miquel considered necessary, were the following :----

Magnesium sulphate Sodium chloride Sodium sulphate Ammonium nitrate Potassium nitrate Sodium nitrate Potassium bromide Potassium iodide

Sodium phosphate Calcium chloride Ferric chloride

Of these salts the most important were found to be the nitrates, the phosphate and the iron salt, a result which agrees with what we know of the requirements of plant-life in general. These three substances, especially the nitrates and phosphate, are as is well known largely used by farmers as artificial manures.

In order to grow marine diatoms, Miquel added to sea-water the same salts which he had used for growing fresh-water diatoms. Our experiments have shown, however, that it is by no means necessary to add all these salts to sea-water in order to get good cultures. Quite as good results can be obtained by the addition only of Potassium nitrate, Sodium phosphate and Iron chloride, the two latter being made into solution with calcium chloride and hydrochloric acid, according to a special method described by Miquel.

If sea-water which has been obtained near the coast is used as the

basis for the culture medium it is not necessary to add an infusion of organic matter.

The actual quantities of inorganic salts added to the sea-water are really very small, those employed in our later experiments being in 100,000 parts of sea-water :---

40 parts of Potassium nitrate.
4 ,, ,, Sodium phosphate.
4 ,, ,, Calcium chloride.
2 ,, ,, Ferric chloride.

When the culture solution has been prepared it is first boiled in order to kill off any organisms it may contain, and a precipitate which forms is allowed to settle. The clear water is then poured off into small flasks, in which the experimental cultures are made, a second boiling being carried out before the flask is inoculated with the diatom culture. The diatoms grow best at a temperature of about 60° F., in a good north light. They must not be exposed to direct sunlight, as in the small flasks used this is found to kill them.

The culture solution just described has sea-water for its basis. Now sea-water is a very complex solution containing both inorganic and organic substances, and although it is true that the relative proportions of the predominating salts are remarkably constant everywhere in the sea, there are present in it also, often in very minute quantities, many other important substances which are subject to considerable variation from place to place and from time to time. These varying substances are in many cases just those which are of special importance to the living plant. They occur often in such minute traces that it is practically impossible to measure accurately by means of chemical analysis the quantities in which they are present.

In order, therefore, to study the effect on the growth of the diatoms of very small quantities of various substances a different method of procedure was adopted. Instead of using natural sea-water as the basis for the culture solutions, an artificial sea-water was built up by dissolving in pure distilled water the purest chemicals that could be obtained. The distilled water was made specially pure by distilling it a second time in all-glass apparatus, so that it did not come in contact with any metal such as tin or copper. Further, when being distilled for the second time, the water was boiled with bichromate of potash and sulphuric acid in order to destroy as far as possible any volatile organic matter what it might contain. By taking the right proportions of the pure chemicals and dissolving them in this doubly distilled water an artificial sea-water was made having as nearly as possible the composition of natural sea-water. It was, of course, also possible to make up artificial sea-waters of different compositions, one or other of the constituent salts being increased or diminished in amount, or omitted altogether.

What we may call the normal artificial sea-water, that is, the one with a composition as nearly as possible that of natural sea-water, had the following constitution :---

Sodium chloride .	A	. 10	28·13 g	rams p	per litre.
Potassium chloride			.77	,,	,,
Calcium chloride .			1.2	,,	,,
Magnesium chloride			2.55	,,	,,
Magnesium sulphate		nd.	3.5	,,	,,
Sodium bicarbonate			·11	,,	,,

To this there was added in some of the experiments a trace of Potassium iodide and Potassium bromide, but the results did not seem to be affected by this addition.

There is another substance which requires careful consideration when we are dealing with diatom cultures. The skeleton of a diatom is composed of Silica, so that to get a healthy growth that substance must be supplied. An Austrian botanist, Richter, has shown that when cultures are made in glass vessels, enough silica dissolves from the glass to supply the diatoms with all they require. In my experiments I found that the addition of silica in other forms to the culture solutions appeared to make no difference to the growth. We may therefore in what follows disregard the silica, remembering that all the needful supply of it could be obtained from the glass of the flasks in which the experiments were made.

Having made the artificial sea-water in the way described the essential constituents of Miquel's solutions—Potassium nitrate, Sodium phosphate and iron—were added. After boiling and cooling, the flasks containing the solution were inoculated by adding a small quantity of a culture of the diatom *Thalassiosira*, which was already growing in natural seawater. The flasks were then placed in a good light and the cultures given an opportunity to develop.

In the early experiments the results were very uncertain and difficult to understand. In most cases there was an entire failure of growth, but every now and then quite a good growth was obtained. It was noticed also that a good growth more frequently resulted when a flask which had failed was inoculated a second or a third time. It remained for a long time a puzzle why the cultures should generally fail but occasionally succeed, until it occurred to me that the quantity of natural sea-

FOOD FROM THE SEA.

water transferred to the artificial sea-water when the latter was being inoculated was not always quite the same, and that when a culture was inoculated two or three times a much larger quantity of natural seawater was introduced than when it was inoculated only once. Was it the addition of this increased quantity of natural sea-water that enabled the diatoms to grow in the purely artificial solutions ? Definite experiments were made to determine this point, and it soon appeared that the previous irregularity of the results could be accounted for in this way. It was found that if the inoculations were always made by adding only a very small quantity of the liquid from which the living culture was taken, say, by adding just one or two drops of culture to a flask containing 75 cubic centimetres of artificial sea-water, only a very slight growth, if any at all, took place. If, however, before the artificial water was inoculated in this way, and also before it was sterilized by boiling, as little as 1 part in 100 of natural sea-water was added to it, the diatoms grew well and excellent cultures were obtained. With 4 per cent of natural sea-water added to the purely artificial solution the cultures were quite as good as, if not better than the best that were got when natural sea-water was used entirely as the basis of the culture solution.

This result is somewhat remarkable because it seems to show the absolutely essential importance to the growth of the diatoms of an extraordinarily minute trace of some substance which exists in the natural sea-water. In the artificial water all the salts were included that occur in natural sea-water in any quantity above a mere trace—a trace so small that it is hardly capable of accurate measurement. Yet when this trace of substance is diluted down by adding 1 part of it to 100 parts of artificial sea-water, there is still enough of it introduced to make a vigorous and abundant growth possible where no growth at all was possible without it. This substance can hardly itself be regarded as a food substance. Its real action can only be conjectured, but we may think of it as a growth stimulant without the aid of which the plant is unable to build up its structure out of the real food substances.

In the course of further experiments it was shown that, provided this small quantity of natural sea-water were present, the composition of the artificial sea-water could be altered to an extraordinary extent without much if any effect being produced on the culture. In the first place the density of the artificial water could be changed within very wide limits without affecting the cultures appreciably. The solution might be diluted to one-half the normal strength or even below, or it might be concentrated so as to increase the density by as much as 50 per cent.

All the Potassium chloride might be omitted or the amount of Potas-

sium chloride might be doubled. Similarly the Magnesium sulphate could be omitted or doubled without detriment. In the case of the Calcium chloride, also, the amount of permissible variation was very great, though not quite so great as with the Potassium chloride and Magnesium sulphate. These results were a little surprising, as it had generally been assumed that the Plankton diatoms were particularly sensitive to changes in the composition of the medium in which they live. It is clear, however, that provided all the essential substances are present, in some cases even excessively minute quantities being sufficient, the composition of the medium can be very greatly altered without affecting the organisms.

Incidentally, the facts which I have been describing would appear to have an important bearing upon all theoretical questions concerning the relation of the organism to its environment. If such a minute change in the environment as is involved in the addition of 1 per cent of natural sea-water to the artificial solutions can make all the difference between reproduction and no reproduction of the diatom, can we be said in the case of any organism whatever to have an adequate conception of what the effective environment really is ? Clearly we are very far indeed from appreciating or understanding how intricate and varied are the many factors upon which the life of even the simplest plant or animal depends.

But this is a digression. Let us return to the diatom cultures, and ask what is the chemical nature of the essential substance, a trace of which must be present in the artificial culture solution before the diatoms can flourish. Up to the present I have been unable to give any final or adequate answer to this question. Certain hints and suggestions have, however, been obtained which give us an indication of the lines upon which the answer to the question is to be sought. Some of the experiments which have given rise to these suggestions may be of interest to you.

To a flask containing some of the artificial sea-water, which had been treated with nitrate, phosphate and iron, a small fragment of the green seaweed Ulva was added and the liquid boiled for a few minutes. A slight infusion of seaweed in the artificial sea-water was thus made. The piece of Ulva was removed and the liquid allowed to cool. It was found that good cultures of the diatom could then be made in the solution. The slight infusion of vegetable matter therefore performed the same function as the 1 per cent of natural sea-water, which had been added in the previous successful experiments.

When, on the other hand, instead of making an infusion of the seaweed

FOOD FROM THE SEA.

as a whole, a piece of the seaweed was burnt and the resulting ash added to the artificial solution, the diatoms did not grow.

These two experiments together make it probable, though they do not completely prove the point, that it is an organic extract of the seaweed, and not some inorganic salt dissolved out of it, which has made the artificial solution a suitable medium for diatom growth.

In other experiments it was found that if instead of adding a small quantity of natural sea-water from the open sea, the same quantity of sea-water taken from the tanks of the Aquarium were added, the resulting diatom cultures were larger and more vigorous. The Aquarium water seems therefore to contain more of the substance whose nature we are trying to determine than the water from the open sea. Now in the Aquarium animal life is more concentrated than in the sea outside, and one chief difference between Aquarium water and that brought in from outside is that the former contains more of the waste products of animal life. The suggestion here again is that the substance we are seeking is an organic substance, a substance produced by some living organism—in this case a waste product of the living fish.

It must, however, be one of the more stable organic substances, for it was found that if some of the Aquarium water was evaporated to dryness and the remaining salt heated to a comparatively low temperature, say, to 200° C., and then again dissolved in distilled water, the solution thus obtained was practically as effective as natural sea-water in promoting diatom growth. The effective substance therefore can be dried and heated to at least 200° C. without being destroyed. When, however, the heating was carried further, until a dull red glow was produced, the substance was destroyed or so altered that it ceased to stimulate growth.

Again we have the suggestion that the growth stimulant is probably an organic substance rather than a mineral salt. Further than this it has not up to the present been possible to carry the matter. In addition to small quantites of many inorganic salts, traces of a number of organic substances have been tried, amongst them being asparagin, calcium succinate, calcium malate, theobromine, tyrosine, urea and uric acid, but in all cases the results were negative.

An observation recorded by my colleague Mr. L. R. Crawshay is of much interest in connection with this point. Mr. Crawshay was carrying out experiments in which he tried to keep alive in the Laboratory some Copepods belonging to the species *Calanus finmarchicus*, which he was feeding on the diatom *Nitzschia*. He found that in the vessels containing the animals the diatoms grew and multiplied rapidly. If, however, the diatoms were put into similar vessels in which no animals were present, and kept under precisely the same conditions, very much less growth took place. Here again it looks at if some substance excreted by the animals helped to produce a luxuriant growth of the plants. The analogy seems complete with what we are all familiar with on land, the beneficial effect of animal manure upon plant life. A particular interest, however, attaches to Crawshay's work, because he did not get the increased diatom growth with other species of Copepods which he tried, but only with *Calanus finmarchicus*.

The outstanding feature then of the experiments which I have been describing to you on the growth of marine plankton diatoms, is the essential importance for the vigorous growth of these plants of some specific substance which is present in exceedingly minute quantities in natural sea-water and without which energetic growth does not take place. This substance, which acts as a growth stimulant, is, we have reason to suspect, a somewhat stable organic compound produced by other living organisms.

And now perhaps you will pardon me if I appear to wander into subjects which may seem far removed from my immediate purpose, but I hope I may succeed in showing how intimately the most diverse branches of scientific enquiry are often interwoven one with the other, and what unexpected light may be thrown upon a problem by investigations which at first sight look very remote.

Much striking work has been done recently on the subject of animal nutrition. At Cambridge Dr. Hopkins has shown that young rats do not grow when fed on an artificial diet composed of pure protein, starch, cane sugar, lard and inorganic salts, although such a diet, which we might almost call an artificial milk, contains all the generally recognised constituents of a perfect food. If, however, quite a small quantity of natural milk is added to this artificial food the young rats thrive. A minute trace of some substance present in the natural milk makes all the difference between growth and no growth.

Amongst the natives in some parts of Eastern Asia a very troublesome disease known as beri-beri has been prevalent in recent years, and has caused considerable mortality. It has been shown that the disease is directly caused by a too exclusive diet of polished rice. In the process of polishing, the outer husk or skin of the rice is entirely removed, and with the removal of the husk some substance is taken away which is essential if the rice is to be a sufficient food. The disease is at once cured by putting the patients on a suitable mixed diet.

The disease is also produced in pigeons if they are fed entirely on polished rice, and some interesting results on the cure of birds suffering from it have been obtained by Drs. Cooper and Casmir Funk. These

FOOD FROM THE SEA.

investigators were able to extract from rice polishings a definite chemical substance, an organic compound of a highly complex character, which when added in exceedingly minute quantities to the diet of polished rice very rapidly cured the birds of the disease. To this substance, which is present in minute quantites in the husk of the rice, they gave the name of vitamine. They were able to isolate the same curative substance or vitamine from yeast, from milk and from bran. Another instance of a similar character concerns us more nearly in this country. In the preparation of fine white flour, from which our ordinary white bread is made, the outer layers of the wheat are entirely removed. It appears, however, that in these outer layers there is an active principle which is of essential importance to the value of the wheat as food material. In experiments carried out by Dr. Leonard Hill it was found that young rats and mice would not live when fed exclusively on white flour and water, whilst those fed on wholemeal flour did much better. Pigeons fed on a diet consisting only of pure white bread all died, but if to the white bread was added an extract of bran and sharps, that is an extract of the outer husks of the grain, the pigeons lived quite healthily. Here again we have to do with minute traces of the so-called vitamines, which are essential to healthy nutrition. In an ordinary mixed diet, such as is usually adopted in this country, the use of white bread made from refined flour is probably not very harmful, as the small quantity of vitamine required will be obtained from other constituents of the food. such as milk or fresh vegetables. Amongst some of the poorer classes of the population, where white bread is often the principal food, there is a distinct danger of malnutrition, especially in growing children.

It seems probable that scurvy, a disease so dreaded by the deep-sea sailors of former days and one which has proved so disastrous to our Arctic and Antarctic explorers, is due to the absence from the diet of accessory substances similar in their nature to vitamines. These substances are present in minute quantities in lime juice, fresh vegetables and fruit, the addition of which to the diet has a curative effect on the disease.

A connection between the study of the growth of marine diatoms and the study of the cause and cure of cancer may at first sight seem remote, but some recent work in connection with that disease certainly suggests that the two studies may be mutually helpful. In cancer we have a rapid and uncontrolled growth of certain tissues, and the work of H. C. Ross and others is directed to show that this rapid growth is due to the production in the body of the patient of minute quantities of certain complex organic substances, which act as growth stimulants and bring about the rapid and abnormal proliferation of the tissue cells. These growth stimulants have been termed *auxetics*, and it is not improbable that they resemble in their action, if not in their chemical constitution, the vitamines which cure the disease of beri-beri and the potent substance occurring in natural sea-water, the merest trace of which is capable of producing a luxuriant growth of diatoms in an artificial solution, which in its absence is unable to sustain growth at all.

A still closer parallel to what occurs in the case of the diatom cultures has recently been brought to light in connection with agricultural research. I refer to the investigations of Prof. Bottomley, of King's College, London, on certain substances derived from Sphagnum peat. Sphagnum peat consists of the partly decaved remains of the Sphagnum moss, which occurs so commonly in moorland bogs, as for example in much of the bogland of Dartmoor. Prof. Bottomley found that when Sphagnum peat was subjected to the action of certain bacteria obtained from soil, a kind of fermentation took place which resulted in the formation of a substance which, when fed to growing plants, stimulated and accelerated their growth to a quite surprising extent. This substance was soluble in water and was effective in very small quantities. Prof. Bottomley states that "Dr. Rosenheim, of King's College, found that seedlings of Primula malacoides potted up in loam, leaf-mould and sand, and treated twice with a water extract of only two-tenths (0.18 grams) of a gram of bacterised peat, were after six weeks' growth, double the size of similar untreated plants, and it was noted that flower production and root development were promoted equally with increase of foliage."

By using methods similar to those which had been employed in separating vitamine from rice polishings, Bottomley was able to separate the active substance from the bacterised peat and to test its effect upon the growth of wheat seedlings. Some seedlings were allowed to grow in a solution containing only pure food salts (nitrates, phosphates, and so on), whilst others were grown in the same solution to which one part in three millions of the active substance from bacterised peat had been added. During the first fortnight both sets of seedlings grew at about the same pace. After that those to which no active substance had been fed began to dwindle, and at the end of fifty days their weight had actually diminished by 8.4 per cent. Those seedlings, on the other hand, which had received the one part in three millions of active substance from the bacterised peat, continued to grow and at the end of the fifty days their weight had increased by 55 per cent of the original weight.

Bottomley's observations are of great practical interest, since they seem to explain in an intelligible way the beneficial effect upon crops of farmyard and organic manures. It is not sufficient to add to the soil

FOOD FROM THE SEA.

only artificial fertilizers, since without a supply of the necessary accessory organic substances, which act as growth stimulants, the crops are unable to make use of the food supply which these artificial fertilizers provide. The accessory substances are, however, produced in the minute quantities required when a certain proportion of organic manure is also employed.

But it is time for me to return to the conditions which prevail in the sea, although I hope that these digressions into animal nutrition, into the causes and cure of certain diseases, and into the treatment of agricultural crops have been of some service in throwing light upon the subject in hand. What is the source from which the sea obtains the food substances necessary for the growth of its plant life—the phosphates, nitrates and other inorganic salts and the organic substances of the nature of growth stimulants? There is clearly within the sea itself a continuous cycle of these plant foods, and we may to that extent regard the sea as a selfcontained whole. The plant makes use of the food substances dissolved in the water and is then itself eaten by some animal. The animal, either directly as the product of its own vital activity or indirectly through the action of putrefying bacteria when it dies, returns the plant foods to the sea.

In addition, however, to this food cycle within the sea itself, there is another source of supply, the importance of which is probably very great, though up to the present it has not been studied with all the attention it deserves. This source of supply is the material carried into the sea by drainage from the land, the great bulk of it being, of course, brought down by the rivers. The subject has recently been discussed in an important memoir by Prof. Gran of Christiania. It has long been known that life in the sea is specially abundant in the neighbourhood of the coasts and in regions which are under the influence of currents containing a great admixture of river water. The study of the distribution of the plankton, or floating life of the sea, has helped greatly in throwing light upon this question. The quantity of plankton in coastal waters is very much greater than that found in the open ocean far from land. The proportion has been estimated at 50:1.

Prof. Gran maintains that this can only be explained by supposing that the coastal waters are richer in nutritive or food substances, and these nutritive substances must have been supplied by drainage from the land. It has been found that the development of the plankton, especially of the plant plankton, commences in the inshore or coastal waters and from thence spreads out gradually into the ocean. All the great fishing areas are found in regions where coastal water predominates and where the admixture of river water is large. The North Sea, the most productive area of the British fisheries, receives the waters of the Rhine, the Elbe, the Thames, and many other rivers. The great cod fisheries off the coast of Norway take place in waters which are derived in large part from the Baltic current. The Bristol Channel and Irish Sea are other examples upon a smaller scale.

On the other hand, over the vast areas of the open ocean far from the coasts, where the influence of land drainage is not felt and where the quantity of minute life in the water is small, no important fisheries are carried on. As far as we seem to understand the conditions of the problem at present, it does not appear likely that any great fisheries can be developed in these open waters. Just as the desert areas of the land, notwithstanding the abundant energy of sunlight which falls upon them, are unable to support vegetation from lack of water, so it seems these great ocean wastes fail in making use of the sun's power for the production of organic life from lack of substances which only the land can supply. If this be a true view of the case, when, as will probably happen sooner or later, the fisheries of the coastal banks have reached the maximum extent of their capacity, we shall have to look for any further increase of the supply of fish for food purposes to an extended practice of fish culture, a method at present confined almost entirely to fresh-water fishes. The extension of fish culture to marine fishes, which are much more delicate and difficult to rear than those which live in fresh-water, is by no means an easy matter, and much further knowledge will be necessary before successful results can be obtained. The researches which I have described to you to-night were commenced largely with a view to obtaining information about some of the fundamental problems upon which any scientific practice of fish culture would need to be based. The investigation has at the present time reached only an early stage, but the results obtained are unexpected and not without interest. There seems reason to hope that a further extension of the work may be of some practical importance.

For a more detailed account of the researches referred to in this address see :--

ALLEN, E. J., and NELSON, E. W., On the Artificial Culture of Marine Plankton Organisms, Quart. Journ. Micr. Sci., Vol. 55, p. 361, 1910, and Journ. Mar. Biol. Assoc., VIII, p. 421, 1910.

ALLEN, E. J., On the Culture of the Plankton Diatom Thalassiosira gravida Cleve, in Artificial Sea-water, Journ. Mar. Biol. Assoc., X, p. 417, 1914.

The Age of Fishes and the Rate at which they Grow.

Being the Presidential Address delivered before the Devonshire Association for the Advancement of Science, Literature and Art at the Plymouth Meeting, 18th July, 1916.

By

E. J. Allen, D.Sc., F.R.S. Director of the Plumouth Laboratory.

[Reprinted from the Transactions of the Devonshire Association.]

With Figures 1-9 in the Text.

At a time like the present, when the Empire we have inherited stands facing a crisis of its fate, when indeed the whole structure of civilization as we know it has seemed to sway, when that which generations of earnest thinkers have dreamt of as the progress of the race recoils before the forces it has itself unchained, it is difficult to restrain a feeling of incongruity in discussing any subject that has no obvious bearing on the greater problems of the hour. But I am convinced that we are following the right course in carrying on, with such help as remains available, the work of this Association, whose object is the advancement of Science, Literature and Art. In the short, swift cataracts of war, no less than in the gentler, steadier flow of peace, these matters of the mind have still their power.

In selecting a subject upon which to address you it has seemed to me best not to attempt to travel beyond the limits of that branch of Science with which my own studies have been chiefly concerned, and the science of Marine Biology is one which has special claims on a Devonshire Society. The work of Colonel Montagu at the beginning of the nineteenth century, which gave us the first descriptions of so many of our British marine animals, and by the acuteness and accuracy of its observations laid the foundation of future knowledge of their habits and life-histories, was practically all carried out in the Salcombe and Kingsbridge estuaries. Dr. Leach, the pioneer in the study of British Crustacea, was born at Hoe Gate House, within a few yards of Plymouth Hoe, and some of his collections still find a home in the museum of the Plymouth Athenæum. Philip Gosse studied the shore life of our Devonshire coast at Torquay and at Ilfracombe, and his book on those British Anemones, which he

E. J. ALLEN.

found in such profusion at both these spots, remains a classic. It was at Plymouth that Spence Bate first followed the remarkable transformations that occur in the development of the common crab of our shores, and it was here that he procured a large part of the material upon which was based the monograph on British Sessile-eyed Crustacea, which he wrote in collaboration with Westwood.

It was due to the wealth of marine life discovered by these and many other local naturalists, that when in 1884 an Association, chiefly under the influence of the biologists connected with the Universities of Oxford, Cambridge and London, was founded for the study of marine life and particularly for the study of marine fishes, the site of the first Laboratory was fixed at Plymouth. The researches which have been carried out at that Laboratory have fully confirmed the view that we possess off the Devon coast a fauna as extensive and as remarkable for the variety of its forms as is to be found anywhere in northern Europe.

The sea fisheries of Devonshire occupy also a unique position in the history of British Fisheries, for it was the trawl fishermen of Brixham who, gradually pressing eastwards, extended their industry to Dover, Ramsgate and Yarmouth, until finally at Grimsby and Hull they laid the foundations of that immense trade, which with the coming of the steam trawler has taken toll of the most distant waters, from Iceland and the White Sea in the north to the coast of Morocco in the south.

You will, I think, agree that it is fitting that I should here, in passing, pay a tribute to the sturdy character and indomitable courage of the men of our steam fishing fleets. The Brixham traditions have survived. Those of us who had known the men and had sailed with them in times of peace knew already something of their worth, but the cool daring and patient bravery of their work since the war began has surpassed all expectations. It is not too much to say that to them, as much as to any men, we owe the protection of our commerce from the ruthless warfare of mine and submarine.

It is now many years since the first attempts were made to apply scientific methods to the study of problems connected with sea-fisheries, and the subject has developed into what is almost a distinct department of marine biology. Were I to attempt to deal even with all the many branches of modern fishery research, it would be impossible within the limits of a single address to give more than a very superficial account of each of them. It will, I think, be more useful and offer a better prospect of securing your interest in the subject, if I confine myself to one limited question which has received in recent years a considerable amount of attention from fishery naturalists. The subject about which I propose to speak is that of the age of fishes and the rate at which they grow. It

THE AGE OF FISHES AND THE RATE AT WHICH THEY GROW. 401

requires no elaborate argument to prove that the study of this matter is of the first importance if we are to give a rational account of the possible productiveness of a fishery, of the rate at which the fishery can be replenished, and of the intensity of fishing which may be prosecuted without endangering its future prospects as a means of profit to the fishermen and a source of food supply for the people.

To begin at the beginning, I need hardly remind you of the now wellknown fact that the eggs of the majority of our marketable marine fishes are small, transparent, spherical bodies, which are buoyant and float freely in the sea. The fact that the eggs of a fish are of this character, which we describe as pelagic, was first discovered by G. O. Sars in Norway, in 1864, whose observations were made on the Cod. It was discovered independently in Cornwall in 1871, in the case of the Pilchard, by that enthusiastic fisherman-naturalist and acute observer, whose name will be well known to you, the late Matthias Dunn, of Mevagissey. The only important British sea-fish which is an exception to this rule of having pelagic eggs, apart from the skates and dogfishes, whose rate of growth I propose to leave out of consideration altogether, is the Herring, the spawn of which is deposited on the sea floor and attached to shells, stones and gravel.

The time occupied in the development of the eggs of different fishes, from the time they are spawned to the time of hatching, was shown by Dannevig (5) to be dependent upon the temperature of the water in which they float, the increase in the rate of development being in direct proportion to any increase of temperature.

The following table compiled by Dannevig shows the average number of days occupied in the development of the eggs of certain species of fish at different temperatures :—

Temperature in Centigrade	1°	$+3^{\circ}$	4°	5°	6°	8°	10°	12°	14°
Cod (Gadus morrhua)	42	23	$20\frac{1}{2}$	171	$15\frac{1}{2}$	$12\frac{3}{4}$	10^{1}_{2}	92	81
Whiting (Gadus merlangus)		11 2	<u>.</u>	$15\frac{1}{8}$	133	$10\frac{1}{4}$	8	$6\frac{1}{2}$	$5\frac{3}{4}$
Haddock (Gadus walefinus)	42	23	$20\frac{1}{2}$	172	151	13	10^{3}_{4}	$-9\frac{2}{3}$	83
Plaice (Pleuronectes platessa)				_	18]	141	12	101	
Flounder (<i>Pl. flesus</i>)	<u> 61</u>		-	$-\frac{1}{2}$	$6\frac{1}{2}$	51	$4\frac{1}{2}$	32	
Tin	ne of inc	ubatio	in da	us (24 h	ours).	1422		整构和	

These results have since been confirmed by Johansen and Krogh (16), working with more elaborate and accurate apparatus, and they have illustrated the relation between temperature and growth rate shown by Dannevig's figures by means of a graph,¹ in which the loci of the different

¹ The address was illustrated by lantern slides and the graph was shown. NEW SERIES, -VOL. XI. NO. 3. DECEMBER, 1917. $2 p^{1}$ observations for each kind of fish lie very nearly in a straight line, which means that the increase in rate of development, over the range of temperature examined, is directly proportional to the increase in temperature.

It follows, therefore, that the actual time, under natural conditions in the sea, which an egg takes to develop, from the time it is spawned until it is hatched, is by no means constant. There are, I believe, no actual observations on the point and direct evidence as to the time occupied would not be easy to get. If we suppose that temperature is the only factor that need be considered, it is possible to deduce from the data given by the laboratory experiments the time taken in particular instances. Thus, in the waters off Plymouth, Plaice spawn from December to March. Taking the temperature at 9° C., which is the mean for February, the coldest of the four months, the Plaice egg would, according to Dannevig's figures,¹ take thirteen days to hatch. In the southern part of the North Sea, on the other hand, which is a great spawning-ground for Plaice, the mean temperature for February is 7° C., at which temperature the eggs would take about sixteen days to hatch.

When they first emerge from the egg, the young fishes are small, transparent larvæ, whose form is very different from that of the adult fish, and the next points to consider are the time occupied by the period of transition from the larval to the adult form and the increase in size which accompanies this change of form.

In treating of this period of the life-history we will consider separately the ordinary round fishes such as Cod, Whiting, Mackerel and Herring, and flat-fishes like the Plaice, the Sole and the Turbot. In the case of the round fishes it is a little difficult to draw a sharp line of demarcation between the end of the larval and the commencement of the adult life, since both as regards structure of body and habits of life the one passes very gradually into the other.

The time occupied by the larval period may be illustrated by one or two examples. The principal spawning time of the *Cod* in the North Sea begins in January and is at its height in February and March. The larvæ when first hatched have a length of about 4 mm., the length after absorption of the yolk being 4.5 mm. At a length of 25 mm, the adult form has practically been reached. Little cod of this size begin to appear, often hiding under the bell of a jelly-fish, from the middle of May onwards, that is to say about four months after the beginning of the spawning in January. We may say therefore with some confidence that these small cod of 25 mm. or 1 inch in length are from three to four months old.

Some observations on larval mackerel taken off Plymouth in the summer of 1914 will illustrate the method, a somewhat laborious one, it ¹ Ct: Apstein (1, p. 366). According to Apstein's figures the time would be nearer fourteen days at 9° C. and seventeen days at 7° C.

THE AGE OF FISHES AND THE RATE AT WHICH THEY GROW. 403

is true, by means of which the rate of growth of these young stages may be investigated. During May, June and July a large net of fine mesh the Petersen young-fish trawl—was used at frequent intervals, chiefly between Whitsand Bay and the Eddystone, for the purpose of collecting young stages of fish. Young Mackerel first appeared on the 25th of May and they continued to be caught fairly regularly until the end of June, whilst in July only three specimens of these early stages were found during the whole month. All the specimens captured were preserved and subsequently measured. The numbers taken at any one time were small, thirty-two being the largest number in a single haul of the net, but if we combine the figures obtained from the different hauls into two groups, certain interesting features appear. The following diagram represents the figures in a graphic form, the measurements being in millimetres¹ and each fish being represented by a dot :—

	Size in mm.
	5 3° (18010
	3 in systeme the training what the
1914.	6
May 25th	
to June 3rd.	7
6 HAULS.	86
Anonaga Sino	
7:15 mm	9 3 so and shill satisfy an another shall be governmented
/ 15 mm.	. 1 and H had) a share safar barran share share
Mode 6.5 mm.	10 2
	11
	.1
	12
	in the second proceeds and again the second
	52
	62
	7
1 10/1 00/1	75
June 10th-29th.	2
16 HAULS.	8 3
Average Size	97
5 5 mm.	9
Modes 6 5 and	105
9-5 mm.	
	11 3
	12 2
	2
	13

FIG. 1.-LARVAL MACKEREL.

¹ A table showing the relation between British and Metric measures will be found on p. 424.

In the first group of hauls, which we may call the end of May group, the size of greatest frequency is 6.5 mm. and the numbers form a fairly regular curve about this mode, the average size of all the measurements being 7.15 mm. In the second group of hauls, the middle of June group, the numbers range themselves round two centres of frequency or modes, one at 6.5 mm, the other at 9.5 mm. Although the numbers are not perhaps sufficiently large to be conclusive, they at least suggest that these 9.5 mm. fish belong to the same batch of larvæ as the 6.5 mm, fish of the end of May group, whilst the smaller fish represent a new batch of young, derived presumably from another shoal of spawning Mackerel. If this be so, we should, I think, be not far wrong in concluding that a growth of 3 mm. took place in the three weeks' interval from the middle of the period May 25th to June 3rd and the middle of the period June 10th to June 29th.

I give this actual instance from our own observations merely as an illustration of the way in which the problem of the rate of growth of larvæ in the sea under natural conditions may be attacked. To arrive at perfectly certain and definite results a much larger number of specimens would be necessary, and confirmation in different years would be required.

The Cod and the Mackerel, whose larval growth we have just been considering, are typical instances of ordinary round fishes. We will now look for a moment at the flat-fishes in which a distinct and rapid change both in structure and habit of life takes place at the end of the larval period. The young fish abandons its pelagic existence, during which it swam freely through the mass of the water snapping here and there at the small floating creatures upon which it feeds, and takes to lying on its side on the sand at the bottom, feeding on small worms, shellfish and crustaceans which the sand contains. This change of habit is accompanied by a twisting of the whole structure of the skull, in such a way that both eyes come to lie near together on one side of the fish, on the coloured side which is uppermost as the fish rests upon the sand. [A series of slides showing the metamorphosis of a flat-fish was shown.]

This change in structure and habit gives us a fixed point in the lifehistory of the fish, and for the purpose in hand we require to know for what length of time the free-swimming larval stage is continued, from the time that the larva leaves the egg until it settles down as a little flatfish adapted to life on the sand. Unfortunately the evidence available is not sufficiently detailed to enable us to fix this time with the degree of accuracy which we should desire, though an approximate estimate of its duration can be made for certain species. For instance, the Plaice in the southern part of the North Sea commences to spawn in January;

THE AGE OF FISHES AND THE RATE AT WHICH THEY GROW. 405

spawning is at its height in February and continues into March. The youngest bottom stages of the Plaice, immediately after the transformation, are found in quite shallow water along the margins of sandy bays and are often taken by shrimpers, working with push nets on the shore. According to the researches of Dutch naturalists (Redeke, **20**, p. 40) these small Plaice appear at the beginning of April on the Dutch coast and they become numerous in May. If, therefore, we allow two to three weeks for the eggs to hatch, we are left with about ten weeks for the larval stages. It must be admitted that this is a very indefinite statement, but it is, I think, as near as we can get on the evidence at present available. The times will doubtless vary considerably in different localities and also in different years, owing to differences of temperature and of the food-supply available.

In the case of the Sole, which was reared by Fabre-Domergue and Biétrix (6) in the laboratory at Concarneau, the pelagic larval stage lasted about seven weeks, but this of course does not give us a reliable figure for the time taken under natural conditions in the sea.

The length at which the transformation is complete and the bottom life commences is in the case of the Plaice from 14-15 mm., for the Sole it is 10-11 mm. The sizes at the time of hatching are 6-7.5 mm. for Plaice, 3.2 mm. for the Sole.

We may say in general, then, that the adult characters in most fishes are established at the end of about three months from the time of spawning, and when the length is from a quarter to half an inch.

In order to determine the rate of growth subsequent to this period various methods have been employed and for some years past considerable attention has been given to the subject. It is possible, of course, to study the matter directly by keeping fishes in confinement and measuring them from time to time. But we can get little really valuable information in that way, as it is soon seen that the rate of growth depends very largely on the conditions in which the fish are placed, on the volume of fresh seawater supplied to the tanks, on the temperature of the water, and on the amount and nature of the food which is supplied. This is an interesting study in itself, and from some points of view may prove to be of practical importance, but it really tells us little or nothing as to the rate at which the fishes grow under natural conditions in the sea, which is the point of main importance.

Dr. Petersen of Copenhagen was the first naturalist to place the study of the subject on a sound scientific basis (Petersen, **19**) and the method he employed is still perhaps the most useful for dealing with the first one or two years of a fish's life. It consists simply in making a large and representative collection of the fish to be studied, from a particular locality and as nearly as possible at the same time, measuring the length of each individual fish and then plotting the measurements in the form of a graph or curve.

The following curve [cf. Hjort and Petersen (11), Plate IV] in which 8046 Cod,¹ caught off the East Coast of Iceland in July, 1904, are graphically represented (Fig. 2), illustrates the method. Each fish was measured and the numbers found at each centimetre are plotted. It will be seen at once that the fish group themselves around certain definite lengths. The smallest sized fish in the collection was 3 cm. long, and of this size there were 6 fish. At 4 cm. there were 65, and at 5 cm. 189. The numbers then begin to fall, there being only 43 at 6 cm., 8 at 7 cm., and but one fish at 8 cm. Then they rise again until another maximum occurs at 12 cm., with 139 fish. At 17 cm. the number has fallen to 12, after which another rise occurs until at 22 cm. we have 107. In this way the fish fall naturally into the six groups O-V. This division into size groups is due to the fact that the spawning season of the Cod in each year is a limited one, extending over only two or three months at the beginning of the year-January, February and perhaps March. By July the fish born at that time will have reached about 5 cm. in length. The next maximum at 12 cm. represents the fishes born the year previously, and the difference between 12 cm. and 5 cm., i.e. 7 cm., expresses the growth in length during the year. Then at 22 cm. we have the fish which have completed two full years, these fish in July when the samples were taken being two and a half years old.

Since all the fish were caught in 1904 we are able to say in what year each group was born, the V group, with a maximum frequency at 88 cm., being Cod born in 1899.

Now, although this method is satisfactory for the early years, the distinction between the groups becomes much less marked as the fish grow older, until finally the different year-groups run into one another and become indistinguishable. Fortunately, however, other methods have been discovered which enable us to attack the problem of age and rate of growth with even greater precision.

In the year 1898 Hoffbauer (13) published a paper in which he showed that the age of a fresh-water carp could be determined by an examination of the markings on the scale. In 1902 Stuart Thompson (22) published an account of some work carried out at the Plymouth Marine Laboratory in which he showed, for the first time, that a similar method was applicable to sea-fisheries, his researches having been made upon fishes of the Cod family—the Gadidæ—especially on Whiting and Pollock.

¹ The number of fish at 45 cm. has been taken at forty-seven instead of ninety-seven given by Hjort, which appears to be a misprint. Forty-seven agrees with what is shown in the graph and is in accordance with expectation.



THE AGE OF FISHES AND THE RATE AT WHICH THEY GROW.
E. J. ALLEN.

Fig. 3 is from a drawing of the scale of a coal-fish (*Gadus virens*). The surface of the scale appears covered with a series of concentric rings or ridges. When growth is proceeding rapidly there is a considerable space between succeeding ridges, when growth becomes slow the ridges crowd



FIG. 3.—Scale of Coal-fish (Gadus virens). (After Damas.)

closely together. But the fish grows most rapidly during the summer months, when the water is warm and food is plentiful, whereas during the winter growth becomes slower and slower, and even ceases altogether. It is during this winter period of very slow growth that the concentric ridges on the scale become crowded together and give the appearance of a darker ring on the surface of the scale. On the scale figured there are two such winter rings and the growth of the third summer is well advanced.

That this explanation of the appearance presented by the scale is the correct one has been proved by the examination of scales taken from fish caught at different times of the year. A fish captured in summer, such as the one illustrated, has the ridges far apart at the margin of the scale, whilst in fishes captured as the season advances towards winter the ridges round the margin become crowded together.

In the case of the Cod family these markings on the scale are especially distinct and the examination of a few scales is generally sufficient to fix the age (Winge, 25). The number of winter rings formed by the crowding together of the ridges tell us at once the number of years of life which the fish has completed. It must be remarked, however, that the appearance of these winter rings is not in the case of each individual fish as clear and definite as that shown by the scale illustrated, and in a large batch of fish a certain number will be doubtful and the exact age a little uncertain.

By examining large samples these exceptional instances cease to have any importance, as they are not sufficiently numerous to alter the average values obtained.

The Salmon is one of the fish the age of which is often well shown on the scale, and a good deal of work has been done upon it (Masterman, 18). The Herring is another case which I shall consider in more detail presently.

In certain other fishes, as for example the Plaice, the scales, although they show indications of similar winter rings, are not marked sufficiently clearly to make them easily available for age determination. Fortunately, however, other structures of the fish have been found which show in a very definite way alternating rings expressing different rates of growth, which enable us to estimate age with great accuracy. These structures are (1) the otoliths or ear-stones, and (2) certain of the bones of the fish-In the Plaice, the fish to which this method has been chiefly applied, the age of the younger fishes up to about six or seven years old is best seen on the otolith, that of older ones on the bones.

The otoliths or ear-stones (Fig. 4) are small, oval, calcareous bodies which lie in the cavity of the inner ear. They can be removed easily for



FIG. 4.—Otoliths of mature male Plaice. Upper row—Otoliths of Plaice from the West Bay (English Channel). Lower row—Otoliths of Plaice taken in the southern deep water of the North Sea, near the Gabbard Light Vessel. (After Wallace.)

examination from the dead fish by making a single incision in the head in an appropriate direction, and an inspection with a simple lens generally suffices to make an age determination (cf. Reibisch, **21**).

As will be seen from the figure, alternate white and dark rings are seen, when the otolith is examined by reflected light. The white rings are formed in spring and early summer, the dark rings in late summer and autumn. During the winter practically no growth of the otolith takes place. The first white ring is formed in the spring following the year of birth, that is when the fish is just one year old, and the total number of white rings will therefore give us the number of years of life which the fish has completed.

As the Plaice gets older, however, the rings at the edges of the otoliths are so crowded together that it becomes impossible to count them. For these older fishes Heincke (9) has shown that an examination of the bones, after special treatment, gives the information required.

It is clear that if we can determine the age of individual fishes, and if we do this on sufficiently large samples, we at once obtain some information as to their rate of growth, for if, say, the average size of the two-yearold Plaice in a particular locality is 20 cm. and the average size of the three-year-olds is 25 cm. we shall not be far wrong in concluding that a Plaice of 20 cm. will grow about 5 cm. during the next year of its life. This conclusion, however, assumes that the conditions of growth are the same each year, and from information now available we know that this is not always true, but that some years are more favourable for growth than others. Growth in different localities, also, even though they may not be very distant from each other, may differ greatly. What we can obtain by the use of the methods already described, if the observations are repeated for a number of years, is the *average* rate of growth for each year of age.

There are, however, other methods by means of which we can get an idea of the actual rate of growth in a particular area at a particular time. The one which has been most used and has yielded the most reliable results is the method of marking experiments. In these experiments a healthy fish is measured soon after being caught and a small metal label is attached to it, generally at the base of the dorsal fin. The label is numbered and the fish is returned to the sea. When it is subsequently caught again by the fishermen it can be identified by its number and measured a second time. The actual amount of growth will then be known. A great many experiments of this kind have been made on both Plaice and Cod, and large numbers of the fish have been caught and returned by the fishermen to the various laboratories. Even these experiments, however, which were carried out primarily to give information as to the migrations of the fish, are subject to at least one possibility of error, owing to the fact that the future growth of a fish may be considerably retarded by any slight injury it may have sustained when it was first caught. This source of error has to some extent been overcome by keeping the fish in tanks of running sea-water for some time before

they are measured and marked, and only using such fish as appear to be quite uninjured and full of vigour.

We must now pass on to consider some of the conclusions which have resulted from the use of these methods of investigating age and growth rate. In the case of the Plaice, the researches of Dr. Wallace, which were carried out at the Lowestoft Laboratory of the Marine Biological Association, are amongst the most important. The method he employed was the study of the otoliths, his results being based on a total of 20,000 fish, each of which was measured and its age determined. In addition to this Wallace makes use of the records of the otoliths of another 20,000 measured Plaice collected by the Board of Agriculture and Fisheries (24). These numbers will give some idea of the extent of the investigations which have been made.

The following table embodies the result of the analysis as regards age of two series of samples of Plaice trawled by Wallace along a line nearly at right angles to the Dutch coast, from Texel to the Leman Banks, commencing about three miles from the shore and running out some eighty or ninety miles into the North Sea. The samples were taken in May and September, 1905. (Wallace, **23**, Rep. II, Pt. I, p. 26.)

1. Males.

The	I group	averaged	9.4 cm. in	May and	14.9 cm. i	n Sept.
,,	II	,,	16·2 cm.	····· ,,	19·9 cm.	,,
,,	III	,,	22·2 cm.	,,	25·4 cm.	,,
,,	IV	,,	27·2 cm.	,,	29·3 cm.	,,
,,	V	,,	31.6 cm.	,,	33·7 cm.	,,
,,	VI	,,	34·8 cm.	haz "	34.5 cm.	,,
2. F	emales.					
The	I group	averaged	10.3 cm.	in May and	d 15.2 cm.	in Sept.
,,	II	,,	16·8 cm.	al al ,,	20.9 cm.	.,
·,·	III	"	23.6 cm.	at 18 .,	25.8 cm.	., ···
,,	IV	,,	28.3 cm.	,, iii	30.9 cm.	,,
,,	V	,,	34·3 cm.	"	37.7 cm.	,,
,,	VI	,,	38.5 cm.	,,	41.3 cm.	·

[A number of diagrams were also shown illustrating Wallace's results.]

The samples of fish from which these figures were derived were taken, as already stated, upon a line extending from the Dutch coast seawards to a distance of eighty or ninety miles. Wallace was the first to point out that if we are to obtain really accurate values for the average size of the Plaice belonging to any particular age-group in a given locality, we can only do so by collecting samples uniformly in this way at different distances from the shore. In order to make it clear why this is so, it will be necessary to give a short account of the distribution of the Plaice according to size, and for this purpose we will consider its distribution in the North Sea.

When we were dealing with the larval stages of the Plaice, you will recollect that we left the earliest bottom stages inhabiting the margins of the sandy shores in quite shallow water. During the first year of their life the young Plaice remain close to the shore in depths under ten fathoms. As they grow larger they move further and further seawards



FIG. 5.—Plaice. Catch per hour of the III Group. (After Wallace.) O = May, 1906 (Covered Beam Trawl). D = September, 1905 (Otter Trawl).

away from these nursery grounds, and in the North Sea it may be taken as a general rule that the average size of the Plaice becomes larger the further out into the open sea we get.

This is well illustrated by the charts published by Garstang (8) showing the distribution of Plaice in the North Sea according to average size.

This seaward movement, it is important to note, depends upon the size of the fish rather than upon their age, so that the larger individuals of any year class are found further out to sea than the smaller ones. If we now look at the next Chart by Wallace (Fig. 5), which illustrates the catch per hour of Plaice of the III Group, that is fish between three and four years old, on the line running out from the Dutch coast—from Texel to the Leman Bank—we shall see that this group is taken along the whole line. It is most abundant near the coast, where the average size of the fish is small, and the numbers captured gradually diminish as we move seawards, the size of the fish at the same time becoming larger. The chart also shows that between May (represented by the circles) and

412

September (the squares) there has been a distinct shifting of the group of fish seawards as they have grown larger.

It will be clear, therefore, that if the fish are distributed in this way according to size, we must take uniform samples all along the line in order to obtain the true average of those belonging to any age-group. If, for instance, in the case of this III Group we took samples only near the coast we should miss all the larger fish belonging to the group, whereas if we took samples only at the seaward end of the line we should miss all the small ones. In the latter case our average would be far too high, in the former case it would be far too low. Wallace therefore is quite justified in maintaining that samples of Plaice for age determination must be taken upon such radial lines, if accurate average sizes for the different years of age are to be obtained.

One of the points which has come out most clearly in the course of these studies is the great differences in rate of growth which are found, firstly at different seasons of the year, secondly in different years, and thirdly in different localities.

As regards seasonal differences we may say that in the North Sea the year's growth begins in the spring, about the month of April; it goes on vigorously during the summer until September, slows down in October, and from that time until the following April there is practically no growth at all, at any rate in the shallow water near the coasts. In the central portions of the North Sea, for example on the Dogger Bank, a certain amount of growth does seem to take place in the winter.

The evidence for differences in the rate of growth of Plaice in different years is chiefly based on the work of the Danish naturalist Johansen (14), who has studied the question by means of marking experiments carried out off the North Sea coast of Denmark. Thus the average annual growth for specimens of 20 to 29 cm. liberated in the Horn Reef area in 1903 was only about 4 cm., whilst in 1904, 1905, 1906 and 1907 it was from 6 to 7.5 cm. In this connection Johansen notes the interesting fact that in 1903, when the growth was abnormally low, there was an unusually rich stock of under-sized fish on the Horn Reef grounds, which suggests that the rate of growth may depend, amongst other things, upon the density of the Plaice population (Johansen, 14, III, p. 37).

It is possible, therefore, that a certain amount of fishing on grounds overcrowded with young fish may tend to increase the rate of growth of the fish that remain.

That the rate of growth of Plaice differs widely in different localities may be inferred from the fact that the average length of the different age-groups is different in different areas, provided always that the samples on which the figures are based are adequately distributed or at least properly comparable. Thus Wallace's samples show that Plaice of the II Group in August, that is fish two and a half years old, average 6 cm. longer in Tor Bay on the South Devon Coast than those in deeper water on the Leman Banks in the North Sea, and 11 cm. longer than those from the shallow water off the coast of Lincolnshire, the Devon fish being thus from one to two full years ahead of those from the North Sea.

This rapid growth of the Devon fish is clearly reflected in the structure of the otolith, as will be seen from Fig. 4. The broad white rings are in marked contrast to the narrow rings of the North Sea fish (Wallace, 23, Rep. III, p. 142A, Figs. 6 and 7).

The following table (p. 415) summarizes Wallace's results as to the average size of Plaice of the different age-groups in different localities.

From this table it is possible also to compare the difference in rate of growth of males and females. It will be seen that on the whole females grow more rapidly than males, and that this difference tends to increase as the fish grow older.

The great differences which may occur in the rate of growth of Plaice on different grounds are strikingly shown by the results of the transplantation experiments carried out by Garstang and Borley in the North Sea [Garstang (7), Borley (2), Lee and Atkinson (17)]. Small Plaice





caught on the shallow young-fish nurseries off the Danish and Dutch coasts were carried in sea-water tanks to the Dogger Bank, which lies in the middle of the North Sea. They were then measured, marked with

AVERAGE SIZES OF THE PRINCIPAL AGE GROUPS OF PLAICE FROM DIFFERENT FISHING GROUNDS.

From Wallace [23], Report III, Tables 11 to 16, pp. 136-141. Length in centimetres.

AGE GROUPS			MA	LES.					I	EMALE	s.							
AGE GROOPS.		II	III	IV	V	VI	Ι	II	III	IV	V	VI	VII					
Texel to Leman Banks. Sep- tember, 1905. 7–17 fms.	14.9	20.0	25.4	29.3	_	_	15.1	20.9	25.8	30.9	Clease Elan	repay -	led k					
Texel to Leman Banks. May, 1906. 13–17 fms		14.6	21.3	27.3	30.9	nda Uk vel	tad:	od [14·9	22.5	28.8	32·9							
Scheveningen and Southern Deep Water. May, 1906. 12–23 fms.		16.5	21.9	27.7	31.1		_	17.7	22.7	29.1	32.4		_					
South Dogger and Flamboro' Off. Winter (OctMarch)			29.1	34.1	37.0	38.1		_	* 30·4	36.6	41.0	44.1	47.5					
Great West Bay (English Channel). Winter (NovFeb.). 3–7 fms., 17–30 fms.	20.3	27.1	31.0	32.9		a banna Baang	20.4	28.3	31.8	35.5	that cost is the second	1912 1912 1912						
Tor Bay and Start Bay. August, 1909. 3–8 fms.	18.3	27.9	31.3	_			18.4	27.7	33.5	37.4	41.3							

numbered labels and liberated. The transplantation was carried out in May, and during the following year large numbers of the marked fishes were returned by the fishermen. The amount of growth shown by the following autumn and winter was very remarkable. Small, under-sized fish of little or no market value had become fine Plaice, of good size and in excellent condition. The preceding diagram (Fig. 6) shows the growth of these transplanted fish, compared with the growth of fish of the same size which had remained on the inshore grounds. Taking the figures for, say, the following January, whereas the average length of the transplanted fish was 11 cm. the size of those left on the Horn Reef ground was about 5.5 cm.

If instead of considering the length of the fish we take the percentage increase of weight the result is even more striking. Whereas by the following spring the fish that remained on the Danish Horn Reef ground had increased in weight by 100 per cent., that is to say, had doubled their weight, those put out on the Dogger had increased their weight by 400 per cent., that is to say, they were five times as heavy as they were originally.

Since well-grown Plaice command a much higher price per lb. than small ones this increase of weight means that the value has increased to perhaps seven times the original value.

These results of investigations on the age of Plaice and their rate of growth have several important practical aspects, apart from the suggestion of a direct improvement of the fishery by the transplantation of young fish from crowded nursery grounds to rich feeding grounds such as the Dogger Bank, where the rate of growth is much more rapid. It would seem that the most profitable fishery would result from concentrating the fishing as much as possible on Plaice of the Age Groups IV, V and VI. that is to say, on fish in the fifth, sixth and seventh years of their life. Before this they are small, but capable of rapid growth and rapid increase in value. After the seventh year the growth gets slower, and as long as a sufficient supply of mature fish is allowed to remain to ensure an adequate amount of spawn for the perpetuation of the race, it would appear that from a commercial point of view it is of greater advantage to put the seven year olds on the market rather than to allow them to remain in the sea. They would increase in value very little compared with the amount of nourishment they would consume, whilst when they are removed the food they would have eaten becomes available for the younger fishes, which grow in size and value at a much more rapid rate.

In this connection the *age* at which the majority of Plaice mature for the first time is important. According to Wallace (24, p. 40) for female Plaice this "age of first maturity" in the Southern North Sea is five

416

years, in the middle North Sea six years, and further north seven years. In the English Channel, on the other hand, the bulk of the females reach maturity at *four* years of age. The average age for the males may be a year earlier than for the females.

We have now perhaps devoted sufficient attention to the Plaice, and will pass on to consider certain investigations into the age of the Herring, which bring out very clearly another application of a knowledge of the age of fishes, which may have an important practical bearing. These investigations we owe especially to the energy and enterprise of Norwegian naturalists under the leadership of Dr. Johan Hjort.



(After Hjort.)

As with most marine fishes, the growth of the Herring comes practically to a standstill during the winter. This winter rest is clearly indicated by a ring-like mark on the surface of the scale, these rings being often very definite and precise.

That each ring really does represent the cessation of growth during the winter has been proved by Lea, by examining samples of Herrings month by month during the year (12), in the same way as was done by Wallace with the otoliths of the Plaice. It was possible to follow the band of summer growth becoming wider and wider, until as winter came on it ceased, and the darker ring was found at the margin of the scales. This being so it is obvious that an examination of the scale can tell us a good deal more about a fish's history than merely its age. We can indeed infer the length of the fish at the end of any particular year of its life, for it has been possible to show that the length of the fish is always proportional to the length of a particular scale. If, therefore, we magnify the scale until its total length from the median transverse line to the edge is equal to the length of the fish, the distance from this line to each of the winter

2 E

NEW SERIES.-VOL. XI. NO. 3. DECEMBER, 1917.

rings will be the length which the fish had at the time the ring was formed. This will be clear from the diagram Fig. 7.

Fig. 8 illustrates the composition of three samples of Norwegian Spring Herring taken in March, 1907, and analysed by Dahl (3), by an examination of the scales, into age groups. It will be seen that the majority of



FIG. 8.—Analysis of three samples of Norwegian Spring Herring taken in March, 1907, into age groups. (After Dahl.)

the fish belong to the IV, V, VI, VII and VIII year-classes, the bestrepresented class being IV. The position of the apex of each curve gives us the size of fish most frequently found in each age group.

Samples of Norwegian Spring Herring have been examined in this way every year since 1907 and the results obtained are given in the following table (p. 419), the number of fish belonging to each year-class being expressed as a percentage of the whole sample (Hjort, **12**, p. 219, Table I).

An examination of the figures in this table reveals a very remarkable fact. If we commence with the year 1908, we see that 34.8 per cent. of the fish belong to the year-class IV, that is to say, they are fish which were born in the year 1904. We see further that no other year-class is nearly as well represented, the next in order being the IX year-class, of which the sample contains 14.4 per cent. Now look at the percentages for the year 1909; the best represented class is the V year-class, with 43.7 per cent. But in 1909 the V year-class is composed of fish born in

418

AGE OF NORWEGIAN SPRING HERRING IN THE YEARS 1907-1914.

THE REPRESENTATION OF EACH YEAR-CLASS IS GIVEN IN PERCENTAGES.

12	Ye.	AR-CL	ASSES	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1907				1.6	22.2	18.5	14.8	12.6	19.4	3.4	$2 \cdot 3$	1.7	$2 \cdot 2$	0.9	0.5	_		_	_
1908			• .	_	34.8	12.2	11.6	11.1	8.5	14.4	1.9	1.1	1.5	1.5	0.6	0.3	0.1	0.1	_
1909				-	0.4	43.7	11.9	$4 \cdot 1$	4.8	6.7	17.6	3.3	2.6	1.6	$2 \cdot 3$	0.4	0.2	0.4	0
1910					1.2	9.9	77.3	6.7	1.0	0.4	$1 \cdot 1$	2.0	_	_	_	-			-
1911	•	•		-	0.6	4.1	17.3	70.0	5.5	1.5	0.6	0.5	0.1	-	-	-	-		-
1912				-	1.6	$3 \cdot 1$	3.9	14.5	64·3	6.4	1.6	1.2	1.2	1.5	0.6	0.1	-	0.1	-
1913				0.1	0.7	$2 \cdot 2$	3.4	4.8	13.3	64·7	$5 \cdot 1$	1.2	1.2	0.5	0.2	0.2			T
1914	•	•		-	0.6	3.3	6.9	$5 \cdot 2$	$7 \cdot 2$	13.9	54·3	5.0	1.5	1.2	0.4	0.5	_	-	-

1904. In 1910 the VI year-class, with 77.3 per cent., completely dominates the others; still the fish born in 1904. In 1911 the VII year-class, in 1912 the VIII year-class, and in 1913 the IX year-class still form from 64 to 70 per cent. of the whole population, the fish in each case being those born in 1904. In 1914 these fish still form 54.3 per cent. of the whole. Thus it will be seen that for six or seven years this one year-class of 1904 dominates the fishery. If we look at the figures still more closely we shall see further evidence that a particular year-class may be of special importance over a series of years. In 1910 the fish of year-class V formed 9.9 per cent. of the sample, being the second largest of the year-classes present. These fish were born in 1905. In 1911 these 1905



FIG. 9.—Yield of the Norwegian spring herring fisheries for the years 1896-1913. 15=1.500,000 hectolitres. 1 hectolitre=22 gallons. (After Hjort.)

born fish belong to the VI class, and again they are second in importance with 17.3 per cent. The class occupies the same position in 1912 and in 1913, when the fish are seven and eight years old respectively. Similarly the fish born in 1899 form the VIII group in 1907, the IX group in 1908, and the X group in 1909, the group in each case being present in considerably greater numbers than fish of the adjacent groups.

The herring fishery is one which is subject to very great fluctuations from year to year, and to those who have watched the fishery for many years it is a well-recognized fact that bad and good years often run in

series. After a number of poor or average years the fishing begins to improve and remains successful for three or four years in succession. In the case of the Norwegian Spring Herring fishery the years from 1909 to 1913, when the fish of the 1904 class predominated, were exceptionally good years, with a very high yield, the year 1913 especially being the best fishery during the whole period from 1896 to 1913 (Fig. 9).

We are furnished, therefore, with what appears to be a distinct step in advance in our attempts to find a rational explanation of the fluctuations in the fisheries. A season occurs in which the conditions are exceptionally favourable for the production of young fish, either owing to an exceptional supply of nourishment upon which the larvæ and fry can feed, or to the absence of enemies, or to some other cause which at present has not been traced. As these fish grow up they year by year come to form a more important factor in the yield of the fishery and the abundance of fish caught increases. In the case we have considered the Herrings born in 1904 dominated and rendered fruitful the fishing of the six years from 1909 to 1914. How much longer their influence will be felt remains to be seen.

What appears to be an exactly parallel case occurred in the North Sea Haddock fishery, and curiously enough it was again fish of the year 1904 that were exceptionally abundant. The young fish of 1904 began to show in the catches in 1905, and in 1906 they were present in extraordinary numbers (Helland-Hansen, **10**, p. 33). Although the case has not been worked out in the same detail as for the Herring, the statistics show an exceptional quantity of medium-sized Haddock in 1907, and of large Haddock from 1907 to 1910. This is just what we should expect from the gradual growth of the fish born in 1904, which were so exceptionally abundant in 1906.

For the Plaice also it has been shown that the abundance of the young brood on the nursery grounds varies greatly from year to year (Johansen, **14**, Pts. III and VI), and there is little doubt that the same sequence of events occurs in the case of this fish, though it has not up to the present been followed in detail.

These investigations, then, seem to give us one of the keys necessary for a proper understanding of much in relation to the fluctuations of the fisheries which was previously difficult to understand. Moreover, they offer a prospect of enabling us to predict the probable course of the fishery some years ahead, for when the exceptional abundance of the young fish of any year has been discovered, we shall be able to say, from a knowledge of the growth-rate of the fish, in how many years these fish will reach marketable size and if all goes well with them give rise to an abundant fishery. Information of this kind, intelligently applied, ought to be of some use to the practical fisherman. To those whose duty it is to study the fisheries from the point of view of legislative or administrative control, it is of course of the very greatest importance.

As was explained at the beginning of this address, I have attempted to lay before you some account of one single branch of fishery research, and as I have proceeded you will no doubt have felt that a subject which at first sight seemed fairly straightforward and simple developed quite unexpected complexity, and yielded in the end quite unexpected results. This is indeed only the common experience of those who break new ground or explore new territories in any branch of knowledge whatever, but in the case of marine research the difficulties are perhaps exceptionally great and the calls on the patience and perseverance of the investigator are almost unlimited. But those who have been most intimately associated with this research and have followed it in greatest detail are the most convinced of its promise of fruitful result. We must look to the growing intelligence of the larger public, grown wiser, may we hope, in the stern school of war, for that appreciation which will enable it to be continued with the means and resources which its difficulties demand.

LIST OF LITERATURE.

- APSTEIN. Die Bestimmung des Alters pelagisch lebender Fischeier. Mitt. Deutsch. Seefisch. Ver. XXV. 1909, p. 364.
- BORLEY, J. O. Report on the Experimental Transplantation of Plaice to the Dogger Bank. Mar. Biol. Assocn. Internat. Invest. Report. IV. [Cd. 6125.] 1912.
- DAHL, K. The Scales of the Herring as a means of determining Age, Growth and Migration. Rep. Norw. Fish. and Marine Invest. Vol. II. No. 6. 1907.
- DAMAS, D. Contribution à la Biologie des Gadides. Conseil Internat. pour l'Explor. de la Mer. Rapp. et Proc. Verb. X. 1909.
- DANNEVIG, H. The Influence of Temperature on the Development of the Eggs of Fishes. 13th Ann. Rep. Fish. Board Scotland. Pt. III, p. 147. 1895.
- FABRE-DOMERGUE ET BIÉTRIX. Développement de la Sole. Paris. 1905.
- GARSTANG, W. Experiments in the Transplantation of small Plaice to the Dogger Bank. Mar. Biol. Assocn. Internat. Invest. Report. I. [Cd. 2670.] 1905.

- 8. GARSTANG, W. The Distribution of the Plaice in the North Sea, Skagerak and Kattegat, according to Size, Age and Frequency. Cons. Internat. p. l'Explor. de la Mer. Rapp. et Proc. Verb. XI. 1909.
- HEINCKE, FR. Bericht über die Untersuchungen der Biologischen Anstalt auf Helgoland zur Naturgeschichte der Nutzfische. Beteil. Deutschl. Internat. Meeresforsch. IV-V. 1908.
- HELLAND-HANSEN, B. Statistical Research into the Biology of the Haddock and Cod in the North Sea. Conseil Internat. pour l'Explor. de la Mer. Rapp. et Proc. Verb. X. 1909.
- HJORT, J., and PETERSEN, C. G. J. Short Review of the results of the International Fisheries Investigations. *Conseil Internat. pour l'Exploration de la Mer. Rapp. et Proc. Verb.* III. Appendix G. 1905.
- HJORT, J. Fluctuations in the Great Fisheries of Northern Europe viewed in the light of Biological Research. Cons. Internat. pour *l'Explor. de la Mer. Rapp. et Proc. Verb.* Vol. XX. 1914. (Contains on pp. 10–13 a list of the principal memoirs on the Age of the Herring.)
- HOFFBAUER, C. Die Altersbestimmung des Karpfens an seiner Schuppe. Allgemeine Fisch. Zeit. 1898. No. 19.
- JOHANSEN, A. C. Contributions to the Biology of the Plaice. Medd. Komm. Havunters. Fisk. Pt. I in Bd. I, No. 2, 1905; Pt. II in Bd. II, No. 5, 1907; Pt. III in Bd. III, No. 4, 1908; Pt. IV in Bd. III, No. 5, 1908; Pt. V in Bd. IV, No. 1, 1912; Pt. VI, Bd. IV, No. 4, 1913; Pt. VII, Bd. IV, No. 9, 1915.
- 16. JOHANSEN and KROGH. The Influence of Temperature and certain other Factors upon the Rate of Development of the Eggs of Fishes. Cons. Internat. p. l'Expl. de la Mer. Publ. de Circons. No. 68. 1914.
- LEE, R. M., and ATKINSON, G. T. Report on Plaice Transplantation Experiments to various Fishing Grounds in the North Sea. *Mar. Biol. Assocn. Internat. Invest. Report.* IV. [Cd. 6125.] 1912.
- MASTERMAN, A. T. Report on Investigations upon the Salmon with special reference to Age-determination by Study of Scales. Bd. of Agric. and Fisheries. Fishery Investigations. Ser. I. Vol. I. 1913.
- PETERSEN, C. G. J. On the Biology of our Flatfishes. Report Danish Biol. Sta. IV. 1893 [1894].

E. J. ALLEN.

- REDEKE, H. C. Bericht über die hollandische Schollenfischerei und über die Naturgeschichte der Scholle in der südlichen Nordsee. Verhand. Rijks. Instit. v. onderzoek der Zee. II, 5. 1909.
- REIBISCH, J. Eizahl bei *Pl. platessa* und die Altersbestimmung dieser Form aus den Otolithen. *Wissensch. Meeresunters*. N.F. Bd. IV. Kiel. 1899.
- THOMPSON, STUART. The Periodic Growth of Scales in Gadidæ as an index of Age. Journ. Mar. Biol. Assoc. VI, 1902, and VII, 1904.
- WALLACE, W. Mar. Biol. Assoc. International Investigations. Report I (1902–03) [Publ. 1905];
 Report II (1904–05) Pt. I [Publ. 1907];
 Report II (1904–05) Pt. II [Publ. 1909];
 Report III (1906–08) [Publ. 1911].
- WALLACE, W. Report on the Age, Growth and Sexual Maturity of the Plaice in certain parts of the North Sea. Bd. of Agric. and Fisheries. Fishery Investigations. Ser. II. Vol. II. No. 2, 1915.
- WINGE, O. On the Value of the Rings in the Scales of the Cod as a means of Age Determination. Illustrated by Marking Experiments. *Medd. Komm. Havunders. Fisk.* IV. No. 8, 1915.

For further references to the literature of the subject see :

DAHL, K. The Assessment of Age and Growth in Fish. Internat. Rev. Hydrobiol. and Hydrogr. II, 1909, p. 758.

BRITISH AND METRIC MEASURES.

To convert millimetres to inches multiply by .039. ,, ,, centimetres ,, ,, ,, .39.

The following equivalents will be useful in reading this paper :---

 $1 \text{ mm.} = \frac{1}{25} \text{ inch.}$ $3 \quad ,, \quad = \frac{1}{10} \quad ,,$ $6 \quad ,, \quad = \frac{1}{4} \quad ,,$ $13 \quad ,, \quad = \frac{1}{2} \quad ,,$

1	cm.	$= \frac{2}{5}$ inch.	$25\cdot4$ cm.	= 10 inches.
2.5	,,	= 1 ,,	30.5 ,,	= 12 ,,
5	,,	= 2 inches.	35.6 ,,	= 14 ,,
10	,,	= 4 ,,	40.6 ,,	= 16 ,,
$15 \cdot 2$,,	= 6 ,,	50.8 ,,	= 20 ,,
20.3	,,	= 8 ,,	100 ,,	= 39 ,,

424

Marine Biological Association of the United Kingdom.

Report of the Council, 1916.

The Council and Officers.

Four ordinary meetings of the Council have been held during the year, at which the average attendance was nine. A Committee of the Council visited and inspected the Plymouth Laboratory during the Easter Vacation.

The Council has to record with regret the death of Sir Richard Martin, Bart., who for a number of years was a Governor, representing the Worshipful Company of Fishmongers.

The meetings of the Council have been held in the Rooms of the Royal Society, and the thanks of the Association are due to the Society for its hospitality.

The Plymouth Laboratory.

It has been found necessary to replace the gas engine used for circulating the sea-water through the tanks of the Aquarium and of the upstairs Laboratory. The old engine had worked continuously, for practically twenty-four hours a day, for fifteen years, so that good service had been rendered. A new engine was obtained from Messrs. Crossley Bros., fitted with the latest improvements. The other machinery has been maintained in working order, and the buildings are in a satisfactory state of repair, though expenditure under these heads has been kept as low as possible on account of the war.

The Boats.

The steamer *Oithona* is still laid up at Hooe Lake and it is not_{ν} proposed to put her in commission at present. The eighteen-foot sailing-boat has been used for such collecting work as has been

possible in the immediate neighbourhood of Plymouth Sound. As in former years many specimens have been obtained from the local fishermen.

The Staff.

The salaried staff has consisted of the Director (Dr. E. J. Allen, F.R.S.), Mr. D. J. Matthews, Miss M. V. Lebour, and Mrs. Matthews.

The Council is glad to be able to report that Mr. R. S. Clark, who left the Laboratory in 1914 as biologist to Sir Ernest Shackleton's Antarctic Expedition, has returned safely and in good health to this country, after forming one of the party who remained on Elephant Island.

Dr. Allen was appointed President of the Devonshire Association for the Advancement of Science, Literature and Art for the meeting held in Plymouth in July, 1916, and delivered an address on the age of fishes and the rate at which they grow.

Occupation of Tables.

The following Naturalists have occupied tables at the Plymouth Laboratory during the year :—

Miss CRUMP, London (Oscarella).
W. DE MORGAN, Plymouth (Protozoa).
H. S. HOLDEN, M.SC., Nottingham (Marine Algæ).
Mrs. E. W. SEXTON, Plymouth (Gammarus).
Dr. C. SHEARER, F.R.S., Cambridge (Dinophilus).

The usual Easter Vacation Course in Marine Biology for University students was not held this year.

General Work at the Plymouth Laboratory.

In the number of the Journal issued during the year Miss M. V. Lebour has published a description, with detailed illustrations, of the different stages in the life history of the Copepod, *Calanus finmarchicus*. The material upon which this description is based was obtained by Mr. L. R. Crawshay, who reared the animals from the egg, under experimental conditions in the Laboratory.

In the same number of the Journal Dr. Orton gave an account of the researches which had been carried out in the Laboratory on races of herrings, and Mr. D. J. Matthews reported on the amount of Phosphoric Acid found in sea-water off Plymouth Sound. Two further

REPORT OF THE COUNCIL.

papers by Miss Lebour dealt with the life history of the sea-spider *Anaphia petiolata*, the larvæ of which are carried about by medusæ, and also recorded the fact that medusæ act as hosts for larval Trematodes, the adult form of the worm found in the jelly-fish being known to occur in the mackerel.

A paper by Mrs. Sexton and Miss Wing gave an account of a lengthy series of experiments on the inheritance of eye-colour in the Amphipod *Gammarus chevreuxi*, which was found to be in accordance with Mendel's law.

During the year the Director has completed a report upon the postlarval stages of fishes collected off Plymouth in 1914. A number of interesting stages not previously known have been found.

The experiments on the growth of the scales of fishes kept in the Laboratory tanks under different conditions, especially as regards temperature, were continued until the autumn of 1916. The material is being examined and reported upon by Mr. D. W. Cutler.

Mrs. Matthews' experiments on the rate of growth of fishes kept in the Laboratory and fed with food of different kinds have been continued and extended, and a considerable number of data have been brought together, which will, it is hoped, yield results of importance.

Mr. Matthews, working half-time, has completed his determinations of Phosphoric Acid in the sea off Plymouth. The results extend over a period of sixteen months, showing a large seasonal variation, and will be published in the next number of the Journal. He has also continued his experiments on the methods of determining nitrates in sea-water. The other half of his time has been given to investigations into cerebro-spinal meningitis for the Medical Research Committee, the chemical work being carried out in the Laboratory of the Association.

Miss M. V. Lebour has carried out for a complete year the periodical examination of the micro-plankton found at the mouth of Plymouth Sound. The material has been obtained by centrifuging samples of sea-water taken at different depths, and the results have been worked out quantitatively. At the same time samples of plankton taken with ordinary silk tow-nets have been examined. Miss Lebour's work has added greatly to our knowledge of the smallest plankton organisms and many new records have been obtained, especially amongst the Peridinidæ. A full account of this work has been prepared for publication in the Journal.

REPORT OF THE COUNCIL.

Miss Lebour has since commenced to study the actual food found in larval and post-larval fishes, which feed upon plankton organisms. This is largely a new field of investigation, which is already giving promise of results of considerable interest.

Mr. W. De Morgan has been again engaged in studying the marine protozoa, and Mrs. E. W. Sexton has extended and developed the studies on the Mendelian inheritance of eye-colour in *Gammarus* referred to above.

Published Memoirs.

The following papers, either wholly or in part the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association :—

DUNCAN, F. MARTIN. Studies in Marine Biology. Journ. Roy. Mier. Soc., 1916, pp. 257-261.

KRAMP, P. L. Spontaneous Fission in Hydroids. Vidensk. Meddel. fra Danske naturh. Foren., Bd. 67, 1915, pp. 211-219.

MATTHEWS, A. The Development of Alcyonium digitatum, with some notes on the Early Colony Formation. Quart. Jour. Micr. Sci., vol. 62, 1916, pp. 43-94.

The Library.

The thanks of the Association are due to numerous Government Departments, Universities and other institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library. The list is similar to that published in the Reports of Council of former years. A number of authors have been good enough to send reprints of their papers for the Library, and to these also thanks are due.

Donations and Receipts.

The receipts for the year include a grant from H.M. Treasury of $\pounds 500$, being on account of the war one-half of the sum granted in recent years, a grant from the Board of Agriculture and Fisheries' Development Fund ($\pounds 400$), and one from the Fishmongers' Company ($\pounds 600$). In addition to these grants there have been received Annual Subscriptions ($\pounds 104$), Rent of Tables in the Laboratory, including $\pounds 25$ from the University of London and $\pounds 20$ from the Trustees of the Ray Lankester Fund ($\pounds 50$); Sale of Specimens ($\pounds 313$) and Admission to Tank Room ($\pounds 89$).

428

Vice-Presidents, Officers, and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1917-18:—

President.

Sir E. RAY LANKESTER, K.C.B., LL.D., F.R.S.

Vice-Presidents.

The Duke of BEDFORD, K.G. The Earl of DUCIE, F.R.S. The Earl of STRADBROKE, C.V.O., C.B. Lord MONTAGU OF BEAULIEU. Lord WALSINGHAM, F.R.S. The Right Hon. A. J. BALFOUR, M.P., F.R.S. The Right Hon. Austen Chamber-Lain, M.P.
W. Astor, Esq., M.P.
G. A. Boulenger, Esq., f.r.s.
A. R. Steel-Maitland, Esq., M.P.
Rev. Canon Norman, d.c.l., f.r.s.
Edwin Waterhouse, Esq.

Members of Council.

Prof. W. M. BAYLISS, F.R.S.
E. T. BROWNE, Esq.
L. W. BYRNE, Esq.
W. C. DE MORGAN, Esq.
Prof. H. J. FLEURE, D.Sc.
E. S. GOODRICH, Esq., D.Sc., F.R.S.
E. W. L. HOLT, Esq.
Prof. E. W. MACBRIDE, F.R.S.

H. G. MAURICE, Esq., C.B.
P. CHALMERS MITCHELL, Esq., D.Sc., F.R.S.
C. C. MORLEY, Esq.
F. A. POTTS, Esq.
C. TATE REGAN, Esq., F.R.S.
Prof. D'ARCY W. THOMPSON, C.B., F.R.S.

Chairman of Council. A. E. Shipley, Esq., D.Sc., F.R.S.

Hon. Treasurer.

GEORGE EVANS, Esq., 1 Wood Street, London, E.C. 2.

Hon. Secretary.

E. J. ALLEN, Esq., D.Sc., F.R.S., The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council :---

- G. P. BIDDER, Esq., Sc.D.
- Sir MATTHEW I. JOYCE (Prime Warden of the Fishmongers' Company).
- The Earl of PORTSMOUTH (Fishmongers' Company).
- The Hon. NATHANIEL CHARLES ROTHS-CHILD (Fishmongers' Company).
- T. T. GREG, Esq. (Fishmongers' Co.).

GEORGE EVANS, Esq. (Fishmongers' Company).

- Prof. G. C. BOURNE, D.Sc., F.R.S. (Oxford University).
- A. E. SHIPLEY, Esq., D.Sc., F.R.S. (Cambridge University).
- Prof. W. A. HERDMAN, D.Sc., F.R.S. (British Association).

THE MARINE BIOLOGICAL ASSOCIATION

Statement of Receipts and Payments for

	e		d	£		à
To Balance from Last Year :	æ	5.	и.	2	5.	a.
Cash at Bankers	852	0	2			
Cash in hand	17	12	10	869	13	0
,, Current Receipts :						
H.M. Treasury for the year ending 31st March, 1917	500	0	0			
The Worshipful Company of Fishmongers	600	0	0			
Annual Subscriptions Rent of Tables (including Ray Lankester's Trustees,	104	7	11			
£20; University of London, £25)	50	0	0			
Interest on Investments	12	18	8			
" Deposit	6	16	9	1,274	3	4
,, Extraordinary Receipts :						
Donation, G. H. Fox	0	10	6			
Board of Agriculture and Fisheries, Grant from Development Fund for year ending 31st March,						
1917	400	0	0			
Naval Bank—Dividend	3	19	7	404	10	1
,, Laboratory Boats and Sundry Receipts :-						
Sales of Apparatus	14	10	2			
,, ,, Specimens	313	9	6			
,, ,, Nets, Gear, etc	0	7	6			
Other Items	1	1	. 0	329	.8	2

Dr.

£2,877 14 7

The Association's Bankers hold on its behalf £410 14s. 8d. New Zealand 4% Stock, 1943-63.

OF THE UNITED KINGDOM.

the Year ending 31st December, 1916.

By	Salaries and Wages-	£	s.	đ.	£	8.	d.
e.	Director	200	0	0			
	Hydrographer	150	0	0			
	Senior Naturalist	51	3	0			
	Additional	191	15	6			
	Temporary	150	19	0			
	Assistant	190	15	0			
	(temporary)	12	10	0			
	Salaries and Wages	470	11	3	1.268	2	9
					-,		
,,	Travelling Expenses				17	15	9
	• • • • • • • • • • • • • • • • • • •						
,,	Library				47	19	6
	Journal	00	0	11			
,,	Less Sales.	18	15	7	71	5	4
		-10	10	-	11	0	1
,,	Buildings and Public Tank Room-						
	Gas, Water, and Coal	140	13	11			
	Stocking Tanks and Feeding	34	16	0			
	Maintenance and Renewals	97	18	7			
	Rent, Rates, Taxes, and Insurance	54	17	6			
		328	6	0			
	Less Admission to Tank Room	89	4	8	239	1	4
,,	Laboratory, Boats, and Sundry Expenses-						
	Glass, Apparatus, and Chemicals	81	6	11			
	Purchase of Specimens	27	2	1			
	Maintenance and Renewals of Boats, Nets, etc	95	4	1			
	Boat Hire and Collecting Expenses	4	5	0			
	Coal for Steamer	1	1	0			
	Stationery, Office Expenses, Carriage, Printing, etc.	85	14	2	294	13	3
	Balance						
"	Datatice ;—						
	Cash at Bankers	927	16	6			
	Cash in hand	11	0	2	938	16	8
					£2,877	14	7

Examined and found correct,

(Signed) N. E. WATERHOUSE. PORTSMOUTH. THOMAS T. GREG. C. TATE REGAN.

⁹ Frederick's Place, Old Jewry, London, E.C. 25th January, 1917.

OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

The late Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the late Duke of ARGYLL, the late Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr. CARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY, the late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the great st return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000. Since that time investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the seawater circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the hire and maintenance of fishing-boats, and the salary of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council, by an Honorary Secretary and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances. The reader is referred to page 4 of the Cover for information as to membership of the Association.

CONTENTS OF NEW SERIES, Vol. XI., No. 3.

PAGE

1.	THE LOSS OF THE EYE-PI STUDY. BY E. J. ALLE	GMENT I	E. W.	MMARI SEXTO	US CH. N. W	EVREUX Vith 7 P	I. A M lates	ENDEL	(AN	273
2.	HEREDITY IN PLANTS, A Diagrams in the Text	ANIMALS,	AND	Man.	Ву	E. J.	ALLEN.	With	11	354
3.	FOOD FROM THE SEA. B	Y E. J.	ALLEN							380
4.	THE AGE OF FISHES AND With 9 Text Figures	THE RAT	E AT V	vhich	THEY	GROW.	By E.	J. All	EN.	399
5.	REPORT OF THE COUNCIL,	1916 .								425
6.	BALANCE SHEET, 1916									430

NOTICE.

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this Journal excepting when those statements are contained in an official report of the Council.

TERMS OF MEMBERSHIP.

Annual Members		. per annun	1 1	s. 1	<i>a</i> .0
Life Members		Composition Fee	15	15	0
Founders			100	0	0
Governors			500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, &c.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Plymouth.