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CONTENTS

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CORRIGENDA IN VOL. VI.

P. 197, line 10, *for* $+(1-s)\{\frac{1}{4}u+\frac{1}{2}r+\frac{1}{4}w\}$ *read* $+(1-s)\{\frac{1}{4}u+\frac{1}{2}c+\frac{1}{4}w\}^{n}$.

,, 12, *for* $F_r = s^r \left\{ \frac{2^{r+1}-1}{2^{r+2}} u + \frac{1}{2^{r+1}} c + \frac{2^{r+1}-1}{2^{r+2}} w \right\}$

read $F_r = s^r \left\{ \frac{2^{r+1}-1}{2^{r+2}} u + \frac{1}{2^{r+1}} c + \frac{2^{r+1}-1}{2^{r+2}} w \right\}^{n}$.

P. 200, line 2, *for* $\sqrt{\frac{3}{14}} \frac{1}{s} n \div \frac{n}{2(2-s)} = \sqrt{\frac{3(2-s)}{2(4-s)}}$

read $\sqrt{\frac{3}{1}} \frac{1}{1-s} n \div \frac{n}{2(2-s)} = \sqrt{\frac{3(2-s)^2}{n(4-s)}}$.

,, 5, *for* $\sqrt{\frac{3}{16}} n \div \frac{n}{4} \sqrt{\frac{3}{4}}$ *read* $\sqrt{\frac{3}{16}} n \div \frac{n}{4} = \sqrt{\frac{3}{n}}$.

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SCIENCE AND THE NATION

Essays by Cambridge Graduates

with an Introduction by the

Right Hon. Lord Moulton, K.C.B., F.R.S.

Edited by A. C. SEWARD, F.R.S., Master of Downing College, Cambridge.

CONTENTS

"All can see that after the world-war many industries will have to be rebuilt which rely wholly upon applied science; and there will be an enormous impetus given to the output of all sorts of commodities, the manufacture of which depends upon the use of high technical knowledge. Attempts to go forward on the commercial side without reference to the proper source of energy—namely, research—will be slow, ill-directed, and unsuccessful....We desire for this excellent little volume the widest possible circulation; it is a winning brief for those who have been advocating for years the endowment of pure research in this country. A start has been made, as far as medicine is concerned, with the Medical Research Bureau, but the satisfactory beginning must have far larger developments."—*Lancet*

STUDIES OF INHERITANCE AND EVOLUTION IN ORTHOPTERA. II[1].

By ROBERT K. NABOURS.

(With Plates I and II.)

Due to the efforts of many able and earnest workers the approximate end breeding results in numerous groups of plants and animals may now be predicted. If the ancestry of parents for one generation be known the characters and ratios of a resulting complex progeny may be approximately prognosticated. As well also may the characteristics of parents of unknown ancestry be analyzed by the appearance and ratios of their offspring. Although there is an approach to agreement in the matter of end results one finds wide diversity of judgment regarding the fundamental causes.

Most, if not all Mendelians consider the proof of the segregation of the germ plasm as an insulated substance in embryonic development adequate. It is considered a fundamental principle that the units contributed by two parents separate in the germ cells of the offspring without having had any influence on each other. The ideas of the definite location in the chromosomes of the factors giving rise to characters and explaining Mendelian phenomena by means of the manoeuvres of the chromosomes are thought to be satisfactorily supported by a large body of evidence. (Morgan and students.) On the other hand the idea of the insulation and continuity of the germ plasm as an entity independent of the rest of the organism is seriously questioned. There does not seem to be justification for the attempts to connect particular factors with particular chromosomes or parts of chromosomes, and the factorial hypothesis does not necessarily involve the assumption of factors as distinct entities in the germ. (Child.) These diametrically opposed ideas, each the consequence of extensive constructive experimentation and consideration, serve to indicate the difficulties involved in attempts to solve the problems of the mechanism of heredity, or the physiology of heredity, or both.

There is much confusion regarding the use of the terms dominant and recessive, the interpretation and application of ratios, and the definition, or determination, of characters. The terms dominant and recessive remain part of the nomenclature, as if they were realities, whereas they can have doubtful application only in crosses between characters allelomorphic to each other in which one character is more apparent (epistatic) and the other less apparent (hypostatic): or in case of characters which are allelomorphic only to their absences, a character being considered dominant and its absence recessive. Part of the confusion in this matter has undoubtedly resulted, as will be shown later, from the failure to recognize the distinction between the two classes of characters. The 9 : 3 : 3 : 1 and 3 : 1 ratios are used freely and with assurance, whereas there are in reality no such ratios. There appears to be a lack, in usage at least, of appreciation of the distinction between characters which are allelomorphic to each other, *never to an absence*, and those characters which are allelomorphic only to their absences, *never to each other or any other characters*, and which exist only in relation with, and in addition to, characters allelomorphic to each other. These matters are considered in the following paper which presents further records of end results and some applications of the breeding work with the Grouse locust, *Paratettix* Bol.

The colour patterns of the pronota and femora of the jumping legs are the characters considered. Observations have been continued on the characters of long and short wingedness, but nothing further has been ascertained than that these characters appear to be conditioned by the environment, a tentative conclusion supported by evidence presented in my former paper.

The suggestion that these forms be designated as species seems to have been premature and should be withdrawn: not that it is thought they may never be considered as such, but Orthopteran taxonomists are as yet uncertain regarding the taxonomic position these forms should occupy, and especially because this matter is not germane to the present study.

No names are assigned to the true breeding forms, or hybrids. They are designated by letters, the first eight being the same as before, with six additional ones, two of them, *LL* and *NN*, not being figured. (The *G*, *BG* and *CG* illustrated (*Journ. Gen.* Vol. III. Pl. VI), but not otherwise used, in the first instalment have subsequently been proven to have been *AA*, *AB* and *AC* carrying homozygous doses of Θ, respectively.) Each letter means that the pattern for which it stands is a unit which

cannot further be broken up, that *the pattern is allelomorphic to each of the others* (all of them having been tried with several, and some with all); in other words each letter represents one of a series of multiple allelomorphs, fourteen being used. The Greek letter Θ represents a melanic pattern which can exist either in the single or double dose only with, and in addition to, the true breeding patterns or their hybrids. *This pattern is allelomorphic only to its absence*, if indeed it may be considered allelomorphic at all. It shows well with any of the multiple allelomorphs, but perhaps best with *BB*, *BC* and *CC* where it is shown both in single and double doses (heterozygous and homozygous). At a given time soon after moulting, it can be determined whether most of the forms are heterozygous or homozygous for Θ, but after a few days those carrying only a single dose of Θ become melanic to the extent that they are not readily distinguishable from those carrying a double dose. The distinctions were not attempted except in a few instances, because it would have required practically constant watch to make the records at the proper time subsequent to moulting which occurs irregularly after the third or fourth instar. However, the groups were separated in matings (242), (244), (345), (246), (247), (254) and (255) (see table at end of summaries on p. 40), and this is being continued with extant cultures.

In most of the crossings between different pure types the resulting hybrid is readily discernible from either parent, usually intermediate, though in some cases the one pattern is more apparent than the other. In all crosses between any of the forms and *AA*, the hybrid superficially resembles *AA* less than the other parent form, and in some instances cannot be distinguished by casual examination; e.g., the crosses *AA × II*, *AA × PP*, and *AA × SS* produce progeny that can scarcely be discerned from *II*, *PP*, and *SS*, respectively. However, this is only an apparent dominance of *I*, *P*, and *S* and others over *A*; for when careful examinations are made it is found that the pigmental elements of each pattern are present in the hybrid in about equal proportions (5).

In most instances where *A* and single and double doses of Θ were involved I grouped together in the records the members of a progeny superficially similar in appearance. On this account some groupings were made that should give the apparent $9 : 3 : 3 : 1$ ratio (matings (175), (176), (177) (*ABΘ × ABΘ*), and (185) (*ACΘ × ACΘ*)). Also on this account there were from two to nine possibilities, including reciprocals, in the parents, and from one to four in the progenies (in matings (315), (446), (220), (221) and others), where the four kinds

($AB\Theta$, $A\Theta B\Theta$, $BB\Theta$, $B\Theta B\Theta$) so closely resemble each other that they were grouped together, and their progenies not bred out.

On Plate II it is attempted at this time to illustrate only twelve of the fourteen true forms (multiple allelomorphs) used in this paper and thirty-six of the hybrids, and those forms and hybrids carrying Θ. The distinctness of patterns is nowhere overdone and in some instances underdone. Some of the forms illustrated in my former paper appear again, a few of them, e.g., EE, II, and some of the hybrids, much better represented. The form QQ resembles CC greatly except for the red legs which are conspicuous, but it behaves as a true form. The form LL (not illustrated) has three light brown stripes running longitudinally along the pronotum, with the rest of the pattern somewhat mottled as in most of the others. The form NN (not illustrated) has a rufous brown, somewhat bronzed, pronotum as the striking feature of its pattern. Along with LL and NN, many hybrids, and forms and hybrids containing Θ, used in the matings are not illustrated.

The results are given in the form of tables. The arrangement is such that the ancestry of the individuals of any mating may be traced back, and the progeny traced forward, as far as there are any records. In the matings the gametic composition of the parents and the somatic composition of the offspring are given, and, unless marked (R), the male is on the left and the female on the right. The first line of figures (totals) gives the actual numbers and the second line the Mendelian expectation. The letters indicating the progeny are placed alphabetically, from left to right.

At this time the arrangements of the tables will suffice for the presentation of the data. Matings 1–159 show exclusively the behaviour of multiple allelomorphs, a continuation of the first instalment. Matings 160–468 exhibit the behaviour of the character Θ (or the factor for it). This part also indicates further the behaviour of the multiple allelomorphs; for there is no possibility of observing such a character, or factor, as Θ except along with characters like A, B, C, D, etc., and their hybrids, from which it is, by its nature, inseparable. (Two other characters apparently of the nature of Θ, one of them appearing as white specks on the femora and anterior pronotum and inconspicuous, the other a bright redness all over, head, body and legs, as well as pronotum, almost as conspicuous as Θ, have been discovered, but the forms bearing them are only now being bred.) The cultures of both groups have been carried on simultaneously, and, as the cross references indicate, individuals from one group were frequently used for matings in the others.

Table for Use in Making Pedigrees.

One or both of the parents of the numbers inside the parentheses came from the number outside. This table, with the source numbers in connection with the matings, enables one to trace the ancestry of any matings as far back, and the progeny as far forward, as there are any records.

1 (2, 314); 4 (5); 6 (7); 8 (9); 10 (15); 11 (1, 198); 13 (187); 14 (6, 12, 18, 45, 46, 47, 48, 53, 82, 131, 231); 15 (68); 17 (3); 18 (16, 54, 105, 338); 19 (112); 21 (115, 116, 117); 22 (25, 40, 189); 23 (69); 24 (52, 57, 58, 71, 292); 26 (74, 80, 106, 135); 27 (33, 53, 80, 145, 146, 147); 28 (71); 29 (64); 30 (4, 31, 211); 31 (152); 34 (106, 108, 109); 36 (115, 117); 37 (38, 197, 200, 201, 202, 203); 39 (11, 96); 40 (51); 43 (437); 44 (39, 40, 122, 186, 441, 444); 47 (37); 48 (41, 83, 144); 51 (81, 102, 123); 52 (77, 93, 334, 337, 372), 53 (103); 59 (92); 60 (67); 68 (136, 137); 69 (91, 119, 206); 70 (73, 90, 194); 71 (77); 72 (70, 76, 78); 73 (69, 84); 74 (75, 139, 142, 143); 78 (23); 85 (42, 43, 91, 287); 85 (38, 223, 224, 225, 349); 86 (76, 87, 348); 90 (283, 288, 289); 96 (42, 43, 95, 99, 155); 100 (107, 156, 279, 280, 408, 409, 412); 106 (93); 107 (109, 172, 407, 465); 108 (110); 114 (111); 115 (118); 116 (113, 114, 149, 428, 429); 119 (79); 120 (78, 141); 121 (267); 124 (434); 127 (67); 129 (138); 133 (128, 134); 135 (130); 137 (129); 140 (29, 92); 146 (144, 148, 464); 147 (463); 149 (150); 152 (109, 360, 415); 154 (110, 151); 156 (32); 157 (18, 131, 132, 133, 135); 158 (159); 165 (8); 166 (167); 169 (5, 161, 162, 163, 164, 168, 170, 177); 170 (172, 465); 173 (176, 178); 175 (1, 166, 173, 220); 176 (179, 181, 205); 178 (315); 179 (180, 192, 277, 405); 180 (160); 181 (195); 184 (192, 388); 186 (248, 249); 191 (15, 348, 434); 192 (163, 193); 194 (175); 196 (236); 198 (242, 243); 205 (156, 168, 183, 374); 206 (207, 215); 208 (89, 183, 195, 196, 209, 317); 211 (342, 264); 213 (427); 214 (363); 216 (217, 218, 219, 222, 224, 225, 226, 227, 228); 220 (221); 221a (239); 231 (464); 232 (210); 233 (268); 234 (132, 187, 231, 247, 359, 406); 235 (89, 270, 317); 236 (28, 234, 265, 425); 237 (257); 242 (199, 208, 211, 235, 258, 278); 243 (199); 244 (223); 245 (334); 249 (214, 250, 251, 358, 368); 256 (284); 258 (264, 279, 409, 412); 264 (32, 213, 236, 407, 415); 265 (85, 244, 245, 256, 286, 344, 357, 365); 266 (63, 222, 371); 268 (66, 320, 380); 275 (260, 261); 276 (280); 278 (374); 279 (408); 280 (360); 282 (25, 64, 188, 229, 233, 237, 283, 294, 295, 300, 305, 309, 354, 370, 375, 376, 377, 382, 389); 283 (49, 51, 268, 310, 316, 378, 431); 289 (299, 311, 381); 292 (88, 338, 369, 372, 463); 296 (291, 297, 313, 430, 431, 432); 300 (173); 303 (433); 305 (206, 221a, 316, 323, 324, 331, 453); 310 (66, 123, 238, 269, 321); 312 (62, 239, 240, 241, 304, 318, 325, 332, 385, 387, 391, 392, 393, 430, 452); 314 (235, 404); 315 (174, 196, 293, 322, 436, 438, 442, 443, 446); 316 (306, 319, 327, 328, 329, 330); 317 (213); 320 (315); 324 (212, 325); 325 (314, 333, 445, 455); 331 (240, 390, 392); 333 (298, 326); 335 (50, 52, 104, 232, 254, 255, 263, 271, 272, 273, 274, 275, 281, 285, 290, 396, 397, 398, 400, 401, 402, 403); 339 (193); 341 (37, 158, 216, 281, 290, 340, 343, 344, 345, 346, 357, 396, 467, 468); 348 (44, 282, 373); 351 (352); 360 (395, 413); 363 (252, 253, 258, 262, 270, 276, 277); 364 (198); 365 (200, 201, 202, 203, 210, 226, 227, 349, 366, 367, 371); 368 (363); 373 (94, 389); 380 (278); 382 (84, 221a, 364, 383, 384, 448); 383 (332, 385, 390); 384 (126, 391, 440); 386 (387, 393); 389 (457); 393 (184, 333, 445, 455); 395 (394, 428); 396 (197, 336, 337); 397 (350, 399); 407 (82, 265, 335, 341, 347, 355, 356, 411, 416, 417, 425, 426, 427); 408 (416); 411 (292); 413 (351, 353, 361, 362, 414, 423, 424, 429, 466); 416 (340, 410, 418, 419, 420, 421, 422); 417 (286); 425 (230, 246, 266, 343); 426 (263, 346, 397); 434 (439); 435 (312, 331, 379, 386); 436 (190); 439 (122, 125, 435, 441, 444, 447); 441 (296, 301, 302, 303, 307, 312); 444 (257); 445 (388); 447 (288, 289); 448 (287, 449); 449 (437, 450, 451); 453 (454); 457 (456, 458, 459, 460, 462); 465 (356); 468 (228).

Explanation of the Tables. Matings of the same kind are grouped. The ♂ is on the left and the ♀ on the right of the ×, except when (R), which indicates a reciprocal, is used. Beginning at the left, the (R), when used, equals a reciprocal; the number in heavy type (e.g. **3**) is that of the mating; the next number, or numbers, indicate the progeny; the last number, or numbers, in square type (e.g. 17) indicate the sources of the parents, the ♂ being on the left and the ♀ on the right when two numbers are given; (I in.) = from the cultures of the first instalment (*Journal of Genetics*, Vol. III. p. 141); (N) = from nature. The first line of totals gives the actual numbers and the second, in italics, the expectation.

AA × AA
|
AA

1	38	175 11	
2	5	1	
3	17	17	
4	7	N 30	
5	7	169 4	
6	22	14	
7	129	6	
8	74	165	
9	32	8	

Total   331

AA × FH

	AF	AH	
10	24	29	I in.
Expect.	*26·5*	*26·5*	

AB × AB

	AA	AB	BB	
11	1	1	39	
12	*5*	*29*	*14*	
Totals	6	30		
Expect.	*9*	*27*		

AB × AC

	AA	AB	AC	BC	
13	9	14	20	17	N
R **14**	30	32	23	15	N
Totals	39	46	43	32	
Expect.	*40*	*40*	*40*	*40*	

AB × AH

	AA	AB	AH	BH		
15	0	2	1	1	191 10	
Expect.	*1*	*1*	*1*	*1*		

AC × AC

	AA	AC	CC	
16	5	11		18
Expect.	*4*	*12*		

AC × AL

	AA	AC	AL	CL	
17	1	3	1	2	N
Expect.	*2·5*	*2·5*	*2·5*	*2·5*	

AQ × BC

	AB	AC	BQ	CQ		
18	12	10	23	14	157 14	
Expect.	*14·7*	*14·7*	*14·7*	*14·7*		

AD × AD

	AA	AD	DD	
19	12	55		N
Expect.	*16·7*	*50·2*		

AD × AJ

	AA	AD	AJ	DJ	
20	5	3	4	3	N
21	8	6	10	11	N
Totals	13	9	14	14	
Expect.	12·5	12·5	12·5	12·5	

AE × AP

	AA	AE	EP	AP	
22	2	3	3		N
Expect.	2	4	2		

AA × EI

	AE	AI	
23	4	1	N 78
Expect.	2·5	2·5	

(?) × AE

	AA	AB	AE	BE	AP	EP	
24	42	52	47	49	8	1	N

AE × BC

	AB	AC	BE	CE		
25	16	15	14	15	22	282
Expect.	15	15	15	15		

AI × AB

	AA	AB	AI	BI	
26	19	17	21	12	N
Expect.	17·2	17·2	17·2	17·2	

AI × AP

	AA	AI	AP	IP	
27	8	9	12	14	N
Expect.	10·7	10·7	10·7	10·7	

AI × BB

	AB	BI	
28	24	27	N 236
Expect.	24	24	

AI × CI

	AC	CI	AI	II	
29	8	7	10		N 140
Expect.	6·2	6·2	12·5		

AS × AJ

	AA	AJ	AS	JS	
30	4	4	4	0	N

AJ × SS

	AS	JS	
31	91	59	30 N
Expect.	75	75	

AN × BS

	AB	AS	BN	NS		
32	1	9	5	4	156	264
Expect.	5·5	5·5	5·5	5·5		

AP × AP

	AA	AP	PP	
33	18	51	27	
Expect.	17·2	51·7		

AS × AC

	JA	AC	AS	CS	
34	23	13	9	15	N
Expect.	15	15	15	15	

AS × AD

	JA	AD	AS	DS	
35	8	11	20	8	N
Expect.	11·7	11·7	11·7	11·7	

AS × DS

	AD	AS	SS	DS	
36	20	16		28	N
Expect.	23·5	47		23·5	

BB × BB
BB

37	31	341	47

BB × CC
BC

38	168	37	85

BC × AN

	AB	AC	BN	CN	
39	58	10	10	39	44 N
Expect.	14·2	14·2	14·2	14·2	

BC × AP

	AB	AC	BC	CP	
40	0	0	0	1	44 22

BC × BB

	BB	BC	
41	7	13	48
Expect.	10	10	

BC × BC

	BB	BC	CC	
42	1	11	7	96 84
43	14	27	9	84 96
44	14	26	13	348
45	8	7	6	14
46	15	21	14	14
47	1	0	0	14
48	24	57	32	14
49	13	29	13	283
50	11	27	11	335
Totals	101	208	105	
Expect.	103·5	207	103·5	

BC × CP

	BC	BP	CC	CP	
51	19	22	13	28	283 40
Expect.	20·5	20·5	20·5	20·5	

BC × EP

	BE	BP	CE	CP	
52	25	34	24	17	335 24
Expect.	25	25	25	25	

BC × IP

	BI	BP	CI	CP	
53	12	12	16	14	14 27
Expect.	13·5	13·5	13·5	13·5	

BQ × BQ

	BB	BQ	QQ	
54	11	20	17	18
Expect.	12·7	25·5	12·7	

BE × BC

	BB	BC	BE	CE	
55	7	7	6	9	1 in.
Expect.	7·2	7·2	7·2	7·2	

BE × BE

	BB	BE	EE	
56	8	19	6	1 in.
57	4	18	11	24
58	5	13	6	24
Totals	17	50	26	
Expect.	23·2	16·5	23·2	

BE × EE

	BE	EE	
59	16	7	1 in.
Expect.	11·5	11·5	

BF × BF

	BB	BF	FF	
60	0	1	0	1 in.
61	8	23	9	N
62	36	73	41	312
63	5	19	7	266
Totals	49	116	57	
Expect.	55·5	111	55·5	

BF × CI

	BC	BI	CF	FI	
64	13	12	8	6	282 29
Expect.	9·7	9·7	9·7	9·7	

BF × FF

	BF	FF	
65	6	5	1 in.
66	3	0	268 310
Totals	9	5	
Expect.	7	7	

BF × FH

	BF	BH	FF	FH	
67	6	6	2	8	60 127
Expect.	5·5	5·5	5·5	5·5	

BH × AS

	AB	AH	BS	HS	
68	1	5	2	3	15 N
Expect.	2·7	2·7	2·7	2·7	

BI × AE

	AB	AI	BE	EI	
69	8	8	7	10	73 23
Expect.	8·2	8·2	8·2	8·2	

BI × BB

	BB	BI	
70	5	7	72
Expect.	6	6	

BI × BE

	BB	BE	BI	EI	
71	12	15	10	13	28 24
Expect.	12·5	12·5	12·5	12·5	

BI × BI

	BB	BI	II	
72	3	13	5	1 in.
73	11	31	14	70
74	11	46	27	26
75	2	5	3	74
Totals	27	95	49	
Expect.	42·7	85·5	42·7	

BI × CE

	BC	BE	CI	EI	
R 76	10	12	4	12	86 72
77	2	0	3	1	71 52
Totals	12	12	7	13	
Expect.	11	11	11	11	

BI × EI

	BE	BI	EI	II	
78	0	1	1	0	72 120
79	1	4	3	1	119
Totals	1	5	4	1	
Expect.	2·7	2·7	2·7	2·7	

CE × CE

	CC	CE	EE	
86	8	6	3	I in.
87	4	1	2	86
88	12	17	14	292
Totals	24	24	19	
Expect.	16·7	33·5	16·7	

BI × IP

	BI	IP	IP	II	
80	4	5	8	5	26 27
Expect.	5·5	5·5	5·5	5·5	

CF × BB

	BC	BF	
89	17	29	235 208
Expect.	23	23	

BP × BP

	BB	BP	PP	
81	17	39	20	51
Expect.	19	38	19	

CH × BI

	BC	BH	CI	III	
90	11	12	7	6	N 70
Expect.	9	9	9	9	

CC × BC

	BC	CC	
82	25	30	407 14
83	33	28	48
Totals	58	58	
Expect.	58	58	

CI × BE

	BC	BI	CE	EI	
91	1	2	3	4	84 69
92	7	8	6	7	140 59
93	28	28	31	35	106 52
Totals	36	38	40	46	
Expect.	40	40	40	40	

CC × BI

	BC	CI	
84	4	4	382 73
Expect.	4	4	

CJ × CJ

	CC	CJ	JJ	
94	9	18	9	373
Expect.	9	18	9	

CC × CC

	CC	
85	59	265

CN × BN

	BC	BN	CN	NN	
95	23	23	25	16	96
R 96	13	9	6	11	39
Totals	36	32	31	27	
Expect.	31·5	31·5	31·5	31·5	

CN × CN

	CC	CN	NN	
97	4	9	3	N
98	6	12	5	N
Totals	10	21	8	
Expect.	9·7	19·5	9·7	

CN × NN

	CN	NN	
99	12	8	96
Expect.	10	10	

CN × SS

	CS	NS	
100	44	46	N
R 101	19	32	N
Totals	63	78	
Expect.	70·5	70·5	

CP × BP

	BC	BP	CP	PP	
102	6	11	8	11	51
103	5	7	5	8	53
Totals	11	18	13	19	
Expect.	15·2	15·2	15·2	15·2	

CP × CP

	CC	CP	PP	
104	19	19	16	335
Expect.	13·5	27	13·5	

CQ × CQ

	CC	CQ	QQ	
105	20	57	18	
Expect.	19·2	57·7		

CS × BI

	BC	BS	CI	IS		
106	5	8	4	3	34	26
Expect.	5	5	5	5		

CS × CS

	CC	CS	SS	
107	9	31	12	100
108	48	77	37	34
Totals	57	108	49	
Expect.	53·5	107	53·5	

CS × JJ

	CJ	JS		
109	7	7	107	152
R 110	3	10	154	108
Totals	10	17		
Expect.	13·5	13·5		

DD × DD
DD

111	32	114

DD × DD,
AD × DD or
DD × AD
DD or
AD and DD

112	10	19

DD × DJ

	DD	DJ	
R 113	2	0	116
114	31	36	116
Totals	33	36	
Expect.	34·5	34·5	

$DJ \times JS$

	AD	JJ	DS	JS		
115	42	32	43	39	21	36
Expect.	*39*	*39*	*39*	*39*		

$DJ \times DJ$

	DD	DJ	JJ	
116	49	66	22	21
Expect.	*34·2*	*68·5*	*34·2*	

$DJ \times DS$

	DD	DJ	DS	JS		
117	9	10	5	12	21	36
Expect.	*9*	*9*	*9*	*9*		

$DS \times JS$

	DJ	DS	JS	SS	
118	0	0	1	3	115
Expect.	*1*	*1*	*1*	*1*	

$EI \times BE$

	EE	BI	EE	EI	
119	7	9	11	10	69
Expect.	*9·2*	*9·2*	*9·2*	*9·2*	

$EI \times EI$

	EE	EI	II	
120	16	30	16	4 in.
Expect.	*15·5*	*31*	*15·5*	

$FF \times BC$

	BF	CF		
121	7	8	4 in.	
122	45	35	439	44
Totals	52	43		
Expect.	*47·5*	*47·5*		

$FF \times BP$

	BF	FP		
123	8	10	310	51
Expect.	*9*	*9*		

$FF \times FF$

	FF	
124	33	4 in.
125	20	439
126	3	384
Total	56	

$FF \times FH$

	FF	FH	
127	1	1	N
Expect.	*1*	*1*	

$HH \times HH$

	HH	
128	18	133

$HH \times SS$

	HS	
129	37	137

$HI \times HI$

	HH	HI	II	
130	3	2	2	135
Expect.	*1·7*	*3·5*	*1·7*	

$HQ \times BC$

	BH	BQ	CH	CQ		
131	4	11	7	2	157	14
R **132**	12	4	9	6	234	157
Totals	16	15	16	8		
Expect.	*13·7*	*13·7*	*13·7*	*13·7*		

HQ × HQ

	HH	HQ	QQ	
133	30	56	16	157
134	1	0	1	133
Totals	31	56	17	
Expect.	26	52	26	

HS × BI

	BH	BS	HI	IS	
135	21	14	30	9	157 26
Expect.	18·5	18·5	18·5	18·5	

HS × BS

	BH	BS	HS	SS	
136	86	80	72	67	68
Expect.	76·2	76·2	76·2	76·2	

HS × HS

	HH	HS	SS	
137	27	51	38	68
138	4	9	1	129
Totals	31	60	39	
Expect.	32·5	65	32·5	

II × BI

	BI	II	
139	29	12	74
Expect.	20·5	20·5	

II × CI

	CI	II	
140	10	12	1 in.
Expect.	11	11	

II × II

II

141	16	120
142	18	74
143	90	74
Total		124

IJ × BC

	BI	BJ	CI	CJ	
144	3	6	4	4	146 48
Expect.	4·2	4·2	4·2	4·2	

IP × AP

	AI	AP	PP	IP	
145	0	3	1		27
Expect.	1	2		1	

IP × JS

	IJ	IS	JP	PS	
146	3	9	7	9	27 N
R **147**	5	5	6	11	N 27
Totals	8	14	13	20	
Expect.	13·7	13·7	13·7	13·7	

IS × IS

	II	IS	SS	
148	1	8	5	146
Expect.	3·5	7	3·5	

JJ × DJ

	DJ	JJ	
149	3	4	116
Expect.	3·5	3·5	

JJ × JJ

JJ

150	12	149

JJ × JS

	JJ	*JS*	
151	23	20	154
Expect.	21·5	21·5	

JS × JS

	JJ	*JS*	*SS*	
152	3	11	6	31
153	6	10	5	N
154	14	40	25	N
Totals	23	61	36	
Expect.	30	60	30	

NN × NN

NN

155	23	96

NS × AB

	AN	*AS*	*BN*	*BS*		
156	5	4	4	4	100	205
Expect.	4·2	4·2	4·2	4·2		

QS × AH

	AQ	*AS*	*HS*	*QH*	
157	18	21	20	22	N
Expect.	20·2	20·2	20·2	20·2	

SS × SS

SS

158	127	341
159	95	158
Total	222	

AJ × AAO

	AJ	*AAO*	
160	9	13	180
161	30	26	169
162	11	20	169
Totals	50	59	
Expect.	51·5	51·5	

AAO × AAO

	AJ	*AAO*	*AOAO*		
163	13	54		169	192
164	2	4		169	
165	10	34		N	
Totals	25	89			
Expect.	28·5	85·5			

AAO × AB

	AA	*AB*	*AAO*	*ABO*		
166	0	1	2	1	175	
167	10	4	2	2	166	
168	1	4	2	1	169	205
169	10	12	17	9	N	
170	27	11	23	31	169	
171	13	15	21	16	N	
Totals	61	47	70	60		
Expect.	59·5	59·5	59·5	59·5		

AAO × SS

	AS	*ASO*		
172	6	5	170	107
Expect.	5·5	5·5		

AOAO × BF

	ABO	*AFO*		
173	11	7	175	300
Expect.	9	9		

$AB \times BFBOFO$

	AB	BB	AF	BF	ABO	BBO	AFO	BFO	
174	32		12	10	35		18	16	N 315
Expect.	30·7		15·3	15·3	30·7		15·3	15·3	

$ABAOBO \times ABAOBO$

	AA	AB	BB	AAO	AOAO	ABO	AOBO	BBO	BOBO	
175	1	26		25		49				194
176	0	6		4		19				173
177	1	11		14		48				169
Totals	2	43		43		116				
Expect.	12·7	38·2		38·2		114·6				

$ABAOBO \times AFAOFO$

	AA	AB	AF	BF	AAO	AOAO	ABO	AOBO	AFO	AOFO	BFO	BOFO	
178	0	4	0	3	2		3		3		3		173
Expect.	1·1	1·1	1·1	1·1	3·3		3·3		3·3		3·3		

$ABAOBO \times AS$

	AA	AB	AS	BS	AAO	ABO	ASO	BSO	
179	0	0	2	1	2	4	0	0	176 N
180	26	11	19	6	9	20	8	17	179 N
Totals	26	11	21	7	11	24	8	17	
Expect.	15·6	15·6	15·6	15·6	15·6	15·6	15·6	15·6	

$AOBO \times AAO$, or
$ABAOBO \times AOAO$

	AAO	AOAO	ABO	AOBO	
181	5		1		176
Expect.	3		3		

AOBΘ × AOFΘ,
AOBΘ × AFAOBΘ, or
ABAOBΘ × AOFΘ

	AOAO	*AAO*	*AOBΘ*	*ABΘ*	*AOFΘ*	*AFΘ*	*BΘFΘ*	*BFΘ*	
182	2		2		3		3		N
Expect.	2·5		2·5		2·5		2·5		

AOBΘ × BB, or
BOBΘ × BB

	BBΘ	*ABΘ*
183	19	205 208

AC × CΘFΘ

	ACΘ	*AFΘ*	*CCΘ*	*CFΘ*	
184	1	0	0	1	393
Expect.	0·5	0·5	0·5	0·5	

ACAOCO × ACAOCO

	AA	*AC*	*CC*	*AAO*	*AOAO*	*ACO*	*AOCO*	*CCO*	*COCO*	
185	0	3		9		14				N
Expect.	1·6	1·8		1·8		14·6				

ACAOCO BB

	AB	*BC*	*ABΘ*	*BCΘ*	
186	2	1	0	3	N 44
Expect.	1·5	1·5	1·5	1·5	

ACAOCO BC

	AB	*AC*	*CC*	*BC*	*ABΘ*	*ACO*	*CCO*	*BCΘ*	
187	17	29		10	9	24		21	234 13
Expect.	13·7	27·5		13·7	13·7	27·5		13·7	

ACAOCO BF

	AB	*AF*	*BC*	*CF*	*ABΘ*	*AFΘ*	*BCΘ*	*CFΘ*	
188	11	6	9	7	8	8	8	10	N 282
Expect.	8·3	8·3	8·3	8·3	8·3	8·3	8·5	8·3	

AE × CCΘ

	AC	CE	ACΘ	CEΘ		
189	6	8	9	7	22	N
Expect.	7·5	7·5	7·5	7·5		

AF × AFAΘFΘ

	AA	AF	FF	AAΘ	AFΘ	FFΘ	
190	0	8		2	6		436
Expect.	2	6		2	6		

AFAΘFΘ × BFBΘFΘ

	AB	AF	FF	BF	ABΘ AΘBΘ	AFΘ AΘFΘ FFΘ FΘFΘ	BFΘ BΘFΘ	
191	5	2	0	5	5	18	16	N
Expect.	2·8	5·7	2·8		8·6	17·2	8·6	

AS × ACAΘCΘ

	AA	AC	AS	CS	AAΘ	ACΘ	ASΘ	CSΘ	
192	9	10	12	7	6	5	9	1	179 184
Expect.	7·3	7·3	7·3	7·3	7·3	7·3	7·3	7·3	

ASAΘSΘ × ASAΘSΘ

	AA	AS SS	AAΘ AΘAΘ	ASΘ AΘSΘ SSΘ SΘSΘ	
193	3	0	0	3	192 339
Expect.	0·3	1·1	1·1	3·3	

BB × AAΘ

	AB	ABΘ		
194	19	16	70	N
195	8	10	208 181	
Totals	27	26		
Expect.	26·5	26·5		

BB × BFBΘFΘ

	BB	BF	BBΘ	BFΘ	
196	19	24	20	16	208 315
Expect.	19·7	19·7	19·7	19·7	

$BB \times BPBOPO$

	BB	BP	BBO	BPO		
197	12	11	17	9	37	396
Expect.	*12·2*	*12·2*	*12·2*	*12·2*		

$BOBO \times AS$

	ABO	BSO		
211	15	17	242	30
Expect.	*16*	*16*		

$BB \times COCO$

BCO

198	31	11	364
R **199**	19	242	243
200	310	37	365
201	131	37	365
R **202**	217	365	37
203	38	37	365

Total   749

$BOBO \times BOBO,$
$BBO \times BOBO,$ or
$BOBO \times BBO$

$BOBO$ BBO

212	89	324	
213	1	317	264
214	4	249	
215	40	206	

Total   131

$BBO \times ABAOBO$

	AB	BB	ABO	AOBO	BBO	BOBO		
205		17			44			176
Expect.		*15·2*			*45·7*			

$BOBO \times BOBO$

$BOBO$

216	171	341
217	106	216
218	172	216
219	150	216

Total   599

$BBO \times BBO$

	BB	BBO	BOBO
206	1	11	305
207	7	13	206
208	8	23	242
209	0	2	208
Totals	16	49	
Expect.	*16·2*	*·18·7*	

$ABAOBO \times BOBO,$
$BOBO \times ABAOBO,$
$BBO \times AOBO,$
$AOBO \times BBO,$
$AOBO \times BOBO,$
$BOBO \times AOBO,$
$BOBO \times BBO,$
$BBO \times BOBO,$ or
$BOBO \times BOBO$

	ABO	AOBO	BBO	BOBO
220		45	175	
221		30	220	

$BBO \times COCO$

BCO $BOCO$

210	42	32	232	365
Expect.	*37*	*37*		

Total   75

$B B \Theta \times C \Theta C \Theta$, or

$B \Theta B \Theta \times C C \Theta$

|
$B C \Theta$

221 a   1   305 382

$B \Theta B \Theta \times C C$

$B C \Theta$

223	104	244	85
224	91	216	85
R **225**	114	216	85
Total	309		

$B \Theta B \Theta \times B F B \Theta F \Theta$

$B B \Theta$	$B \Theta B \Theta$	$B F \Theta$	$B \Theta F \Theta$
222 7		7	216 266
Expect. 7		7	

$B \Theta B \Theta \times C \Theta C \Theta$

$B \Theta C \Theta$

226	52	216	365
R **227**	9	365	216
Total	61		

$B \Theta B \Theta \times S S$

$B S \Theta$

228   43   216 468

$B C B \Theta C \Theta \times B C$

	BB	BC	CC	$BB\Theta$	$BC\Theta$	$CC\Theta$	
229	15	13	5	3	21	17	282
230	27	46	12	10	30	15	425
231	2	10	10	8	15	1	234 14
R **232**	1	4	4	4	5	2	335
Totals	45	73	31	25	71	35	
Expect.	35	70	35	35	70	35	

$B C B \Theta C \Theta \times A C$

	AB	AC	CC	BC	$AB\Theta$	$AC\Theta$	$CC\Theta$	$BC\Theta$	
233	11	3		20	4	29		8	229 N
234	8	15		10	3	16		7	236 N
Totals	19	18		30	7	45		15	
Expect.	16·7	33·5		16·7	16·7	33·5		16·7	

$B C B \Theta C \Theta \times A F A \Theta F \Theta$

	AB	AC	BF	CF	$AB\Theta$	$A\Theta B\Theta$	$AC\Theta$	$A\Theta C\Theta$	$BF\Theta$	$B\Theta F\Theta$	$CF\Theta$	$C\Theta F\Theta$	
235	6	3	1	1	7		14		9		9		242 314
Expect.	3·1	3·1	3·1	3·1	9·3		9·3		9·3		9·3		

BCBOCO × BBO

	BB	BC	BBO	BOBO	BCO	BOCO		
236	7	3	7	5	9	7	264	196
237	1	0	7		6		282	N
Totals	8	3	19		22			
Expect.	6·5	6·5	19·5		19·5			

BCBOCO × BCBOCO

	BB	BC	CC	BOBO BBO	BOCO BCO	COCO CCO		
238	0	0	1	2	3	2	310	
239	1	0	0	1	3	1	312	221 a
240	9	7	3	9	15	5	312	331
241	2	5	2	17	27	10	312	
242	0	2	1	5	6	3	198	
243	1	6	1	4	10	3	198	
244	1	7	6	8	11	8	265	
245	1	5	3	8	20	5	265	
246	6	3	0	6	13	7	425	
247	2	5	1	3	11	6	234	
248	2	4	0	1	11	4	186	
249	9	18	5	20	65	30	186	
250	2	1	0	2	6	1	249	
251	1	0	1	1	5	3	249	
252	2	5	4	8	16	8	363	
253	1	0	0	2	3	2	363	
254	3	4	1	11	36	18	335	
255	13	13	7	27	49	20	335	
Totals	59	85	36	135	310	136		
Expect.	47·5	95	47·5	142·5	285	142·5		

BCBOCO × BF

	BB	BC	BF	CF	BBO	BCO	BFO	CFO		
256	3	3	2	3	5	0	4	1	265	N
Expect.	2·6	2·6	2·6	2·6	2·6	2·6	2·6	2·6		

BCBOCO × BFBOFO

	BB	BC	BF	CF	BFO BOBO	BCO BOCO	BFO BOFO	CFO COFO		
257	4	0	1	0	2	2	5	5	237	444
Expect.	1·1	1·1	1·1	1·1	3·5	3·5	3·5	3·5		

$BCBOCO \cdot BOCO$

	BBO	BOBO	BCO	BOCO	CCO	COCO		
258		4		10		5	363	242
Expect.		1·7		9·5		1·7		

$BCBOCO \times BP$

	BB	BC	BP	CP	BBO	BCO	BPO	CPO	
260	3	9	0	12	7	2	7	2	275
R **261**	3	5	1	4	3	3	2	3	275
Totals	6	14	1	16	10	5	9	5	
Expect.	8·2	8·2	8·2	8·2	8·2	8·2	8·2	8·2	

$BCBOCO \cdot BS$

	BB	BS	BC	CS	BBO	BCO	BSO	CSO		
262	5		3	3	6	1	3	2	363	N
263	8	9	2	3	3	8	5	7	335	426
Totals	22		5	6	9	9	8	9		
Expect.	17		8·5	8·5	8·5	8·5	8·5	8·5		

$BCBOCO \cdot BSBOSO$

	BB	BS	BC	CS	BBO	BOBO	BSO	BOSO	BCO	BOCO	CSO	COSO		
264	4	4	0		5		3		4		5		258	211
Expect.	3·1	1·5	1·5		4·6		1·6		1·6		1·6			

$BCBOCO \times CCO$

	BC	CC	BCO	BOCO	CCO	COCO		
265	2	4		15		15	236	407
Expect.	4·5	4·5		13·5		13·5		

BCBOCO × CF

	BC	BF	CC	CF	BCO	BFO	CCO	CFO	
266	22	9	0	10	13	2	25	13	425 N
267	0	1	2	1	3	2	1	0	N 121
Totals	22	10	2	11	16	4	26	13	
Expect.	13	13	13	13	13	13	13	13	

BCBOCO × CFCOFO

	BC	BF	CC	CF	BCO BOCO	BFO BOFO	CCO COCO	CFO COFO	
R **268**	14	4	6	8	9	19	15	30	283 233
269	2	0	1	2	0	3	2	2	310
R **270**	0	1	0	1	1	0	5	1	235 363
Totals	16	5	7	11	10	22	22	33	
Expect.	7·8	7·8	7·8	7·8	23·6	23·6	23·6	23·6	

BCBOCO × CP

	BC	BP	CC	CP	BCO	BPO	CCO	CFO	
271	18	8	5	1	6	5	7	12	335
272	10	3	1	4	3	1	3	9	335
273	25	22	4	1	5	2	20	19	335
R **274**	1	3	6	4	5	2	6	6	335
R **275**	11	8	6	2	6	8	2	10	335
Totals	68	44	22	12	25	18	38	56	
Expect.	35·3	35·3	35·3	35·3	35·3	35·3	35·3	35·3	

BOCO × BOCO, BCBOCO × BOCO, or BOCO × BCBOCO

	BOBO BBO	BOCO BCO	COCO CCO	
276	8	21	5	363
Expect.	8·5	17	8·5	

BOCO × BS

	BBO	BCO	BSO	CSO	
277	37	28	27	25	363 179
Expect.	29·2	29·2	29·2	29·2	

BOCO × COFO,
BCBOCO × COFO, or
BOCO × CFCOFO

	BCO	BOCO	BFO	BOFO	CCO	COCO	CFO	COFO		
278	3		2		1		3		242	380
Expect.	2·2		2·2		2·2		2·2			

BOCO × CS

	BCO	BSO	CCO	CSO		
R **279**	5	1	1	1	100	258
280	2	5	5	6	276	100
Totals	5	6	6	7		
Expect.	6	6	6	6		

BC × BSBOSO

	BB	BC	BS	CS	BBO	BCO	BSO	CSO		
281	3	1	5	2	5	2	5	1	335	341
Expect.	3·3	3·3	3·3	3·3	3·3	3·3	3·3	3·3		

BC × CFCOFO

	BC	BF	CC	CF	BCO	BFO	CCO	CFO		
282	11	3	5	6	2	4	3	6	348	
R **283**	3	0	0	1	0	2	0	2	282	90
284	2	13	5	1	4	4	5	3	256	
Totals	16	16	10	11	6	10	8	11		
Expect.	11	11	11	11	11	11	11	11		

BC × CPCOPO

	BC	BP	CC	CP	BCO	BPO	CCO	CPO	
285	23	27	21	30	30	24	28	20	335
Expect.	25·3	25·3	25·3	25·3	25·3	25·3	25·3	25·3	

BC × CSCOSO

	BC	BS	CC	CS	BCO	BSO	CCO	CSO		
286	7	4	3	4	2	4	2	1	265	417
Expect.	3·7	3·7	3·7	3·7	3·7	3·7	3·7	3·7		

BC × FFO

	BF	CF	BFO	CFO		
287	37	19	25	28	84	448
Expect.	*31·7*	*31·7*	*31·7*	*31·7*		

BC × FOFO

	BFO	CFO		
288	0	2	90	447
289	21	15	90	447
Totals	21	17		
Expect.	*19*	*19*		

BC × SSO

	BS	CS	BSO	CSO		
290	25	25	31	26	335	341
Expect.	*26·7*	*26·7*	*26·7*	*26·7*		

BE × BEFOEO

	BB	BE	BBO	BEO	EEO	EE	
291	1	12	6	9	17		296
Expect.	*6*	*12*	*6*	*12*	*12*		

BE × CCO

	BC	CE	BCO	CEO		
292	6	11	14	8	24	411
Expect.	*9·7*	*9·7*	*9·7*	*9·7*		

BFBOFO × AC

	AB	AF	BC	CF	ABO	AFO	BCO	CFO		
293	3	7	1	4	3	4	3	0	315	N
Expect.	*3·1*	*3·1*	*3·1*	*3·1*	*3·1*	*3·1*	*3·1*	*3·1*		

BFBOFO × BEO

	BB	BF	BEO	BOEO	BFO	BOFO		
294	7	2	16		10		282	N
Expect.	*1·3*	*1·3*	*13·1*		*13·1*			

BFBOFO × BC

	BB	BC	BF	CF	BBO	BFO	BCO	CFO	
295	7	9	2	4	5	3	4	6	282
Expect.	5	5	5	5	5	5	5	5	

BFBOFO × BE

	BB	BE	BF	EF	BBO	BEO	BFO	EFO		
296	11	8	1	0	2	1	4	8	441	69
297	6	6	2	0	2	0	5	7	296	
Totals	17	14	3	0	4	1	9	15		
Expect.	7·9	7·9	7·9	7·9	7·9	7·9	7·9	7·9		

BFBOFO × BS

	BB	BF	BS	FS	BBO	BFO	BSO	FSO	
298	2	0	1	1	0	1	1	2	333 N
Expect.	1	1	1	1	1	1	1	1	

BFBOFO × BFBOFO

	BB	BF	FF	BBO BOBO	BFO BOFO	FFO FOFO	
299	3	7	1	7	16	9	289
300	11	13	1	29	58	32	282
301	0	1	0	0	3	2	441
302	1	1	0	3	5	6	441
303	1	0	1	1	0	0	441
304	7	5	4	19	11	13	312
305	14	24	4	35	69	40	282
306	6	0	4	5	0	3	316
307	0	4	2	7	4	4	441
Totals	43	55	17	106	166	109	
Expect.	31	62	31	93	186	93	

BFBOFO × CC

	BC	CF	BCO	CFO	
309	31	7	3	19	282
Expect.	15	15	15	15	

BFBOFO × CFCOFO

	BC	BF	CF	FF	BCO BOCO	BFO BOFO	CFO COFO	FFO FOFO		
R 310	18	9	9	8	16	25	12	26	283	
R 311	3	0	0	0	4	1	2	4	289	
312	14	12	4	0	11	12	11	23	441	435
Totals	35	21	13	8	31	38	25	53		
Expect.	14	14	14	14	42	42	42	42		

BFBOFO × EFEOFO

	BE	BF	EF	FF	BEO BOEO	BFO BOFO	EFO EOFO FFO FOFO	
313	3	5	0	1	3	5	11	296
Expect.	1·7	1·7	1·7	1·7	5·2	5·2	10·5	

BOFO × AA

	ABO	AFO		
314	2	1	325	1
Expect.	1·5	1·5		

EOFO - BFBOFO, or
BFBOFO × BOFO

	BOBO BEO	BOFO BFO	FOFO FFO		
315	3	10	4	178	320
316	5	18	6	305	283
Totals	8	28	10		
Expect.	11·5	23	11·5		

BOFO BOBO,
BFBOFO × BOBO, or
BOFO - BFBOFO

	BEO BOBO	BFO BOFO		
317	1	0	235	208
Expect.	0·5	0·5		

BθFθ × BθCθ,
BFBθFθ × BθCθ, or
BθFθ × BCBθCθ

	BBθ	BθBθ	BCθ	BθCθ	BFθ	BθFθ	CFθ	CθFθ	
318	11		14		21		11		312
Expect.	14·2		14·2		14·2		14·2		

BFBθFθ · BθFθ

	BBθ	BθBθ	BFθ	BθFθ	FFθ	FθFθ	
319	1		2		1		316
Expect.	1		2		1		

BθFθ × BθFθ,
BFBθFθ × BθFθ, or
BθFθ × BFBθFθ

	BθBθ	BBθ	BθFθ	BFθ	FθFθ	FFθ	
320	0		2		1		268
321	1		1		1		310
322	18		35		12		315
323	3		4		1		305
324	2		4		1		305
325	31		46		33		324 312
326	3		4		1		333
327	26		88		31		316
328	5		21		2		316
329	10		19		8		316
330	6		13		6		316
Totals	105		237		97		
Expect.	109·7		219·5		109·7		

BθFθ × CFCθFθ

	ECθ	BθCθ	BFθ	BθFθ	CFθ	CθFθ	FFθ	FθFθ	
331	1		0		2		0		305 435
Expect.	0·7		0·7		0·7		0·7		

BOFO × COFO,
BFBOFO × COFO, or
BOFO × CFCOFO

	BOCO	BCO	BOFO	BFO	COFO	CFO	FOFO	FFO		
332	9		17		16		16		312	383
333	1		2		0		0		325	393
Totals	10		19		16		16			
Expect.	*15·2*		*15·2*		*15·2*		*15·2*			

BP × BOCO

	BBO	BCO	BPO	CPO		
334	11	13	9	6	52	245
Expect.	*10·5*	*10·5*	*10·5*	*10·5*		

BP × CCO

	BC	CP	BCO	CPO	
335	27	35	29	25	N 407
Expect.	*29*	*29*	*29*	*29*	

BPBOPO × BPBOPO

	BB	BP	PP	BBO BOBO	BPO BOPO	PPO POPO	
336	3	5	4	5	9	3	396
Expect.	*1·8*	*3·6*	*1·8*	*5·4*	*10·8*	*5·4*	

BPBOPO × CP

	BC	BP	CP	PP	BCO	BPO	CPO	PPO		
337	0	2	8	5	10	8	1	4	396	52
Expect.	*4·7*	*4·7*	*4·7*	*4·7*	*4·7*	*4·7*	*4·7*	*4·7*		

BQ × BC BOCO

	BB	BC	BQ	CQ	BBO	BCO	BQO	CQO		
338	21	22	12	11	15	17	16	22	18	292
Expect.	*17·3*	*17·3*	*17·3*	*17·3*	*17·3*	*17·3*	*17·3*	*17·3*		

BS × AAO

	AB	AS	ABO	ASO	
339	6	5	2	7	N
Expect.	*5*	*5*	*5*	*5*	

BS × COCO

	BCO	CSO		
340	18	16	341	416
Expect.	*17*	*17*		

BSBΘSΘ × BSBΘSΘ

	BB	BS	SS	BBΘ	BΘBΘ	BSΘ	BΘSΘ	SSΘ	SΘSΘ	
341	5	7	4	4	13	16	14	6	4	407
Expect.	4·5	9·1	1·5	9·1	1·5	18·2	9·1	9·1	4·5	

BSBΘSΘ × BSBΘSΘ

	BB	BS	SS	BBΘ	BΘBΘ	BSΘ	BΘSΘ	SSΘ	SΘSΘ	
342	1	0	3	1		3		1		211
343	3	4	0	4		10		7		425 341
Totals	4	4	3	5		13		8		
Expect.	2·3	4·6	2·3	6·9		13·8		6·9		

BSBΘSΘ × CC

	BC	CS	BCΘ	CSΘ	
344	1	6	11	1	341 265
Expect.	4·7	4·7	4·7	4·7	

CC × BFBΘFΘ

	BC	CF	BCΘ	CFΘ	
348	5	4	2	6	86 191
Expect.	4·2	4·2	4·2	4·2	

BΘSΘ × BB

	BBΘ	BSΘ	
345	32	21	341
Expect.	26·5	26·5	

CC × CΘCΘ
CCΘ

349	209	85 365

BΘSΘ × BS

	BBΘ	BSΘ	SSΘ	
346	22	30	13	341 426
Expect.	16·2	32·5	16·2	

CC × CPΘ

	CC	CP	CCΘ	CPΘ	
350	11	22	18	18	397
Expect.	18	18	18	18	

CC × BCBΘCΘ

	BC	CC	BCΘ	CCΘ	
347	31	36	34	29	407
Expect.	32·5	32·5	32·5	32·5	

CC × CSCΘSΘ

	CC	CS	CCΘ	CSΘ	
R **351**	43	5	12	34	413
352	9	12	14	5	351
Totals	52	17	26	39	
Expect.	33·5	33·5	33·5	33·5	

$CC \times SS\Theta$

	CS	$CS\Theta$	
353	9	5	413
Expect.	7	7	

$CC\Theta \times JS$

	CJ	CS	$CJ\Theta$	$CS\Theta$	
R **359**	30	30	28	27	N 234
360	0	3	6	3	280 152
Totals	30	33	34	30	
Expect.	31·7	31·7	31·7	31·7	

$CC\Theta \cdot BC$

	BC	CC	$BC\Theta$	$CC\Theta$	
354	20	20	16	19	N 282
355	5	10	10	12	407
Totals	25	30	26	31	
Expect.	28	28	28	28	

$CC\Theta \cdot SS$

	CS	$CS\Theta$	
R **361**	18	10	413
362	22	26	413
Totals	40	36	
Expect.	38	38	

$CC\Theta \cdot BS$

	BC	CS	$BC\Theta$	$CS\Theta$	
356	3	11	7	5	407 465
357	37	38	30	30	265 341
Totals	40	49	37	35	
Expect.	10·2	10·2	10·2	10·2	

$COC\Theta \cdot B\Theta B\Theta,$
$CC\Theta \cdot B\Theta B\Theta,$ or
$COC\Theta \cdot BB\Theta$

	$BC\Theta$	$B\Theta C\Theta$	
363		12	368 214

$CC\Theta \times CC\Theta$

	CC	$CC\Theta$	$COC\Theta$	
358	1	1		249
	0·5	1·5		

$COC\Theta \cdot COC\Theta,$
$CC\Theta \cdot C\Theta C\Theta,$ or
$COC\Theta \cdot CC\Theta$

	$CC\Theta$	$C\Theta C\Theta$	
364		1	382
365		89	265
366		135	365
367		114	365
368		26	249
Total		365	

$CE \times BCBOCO$

	BC	BE	CC	CE	$BC\Theta$	$BE\Theta$	$CC\Theta$	$CE\Theta$	
369	12	6	6	6	6	4	6	1	292
Expect.	6·2	6·2	6·2	6·2	6·2	6·2	6·2	6·2	

CFCӨFӨ × AC

	AC	CC	AF	CF	ACӨ	CCӨ	AFӨ	CFӨ	
370	45	1	4		17	23	14		282 N
Expect.	26	13	13		26	13	13		

CӨCӨ × BF

	BCӨ	CFӨ		
371	42	48	365	266
Expect.	45	45		

CECᴇӨEӨ × CE

	CC	CE	EE	CCӨ	CEӨ	EEӨ		
372	1	5	6	3	4	0	292	52
Expect.	2·3	4·7	2·3	2·3	4·7	2·3		

CFCӨFӨ × AJ

	AC	AF	CJ	FJ	ACӨ	AFӨ	CJӨ	FJӨ	
373	4	1	4	0	1	3	0	1	348 N
Expect.	1·7	1·7	1·7	1·7	1·7	1·7	1·7	1·7 .	

CFCӨFӨ × BB

	BC	BF	BCӨ	BFӨ		
374	5	5	5	3	278	205
Expect.	4·5	4·5	4·5	4·5		

CFCӨFӨ × CCӨ

	CC	CF	CCӨ	CӨCӨ	CFӨ	CӨFӨ	
375	15	4	22		22		282 N
Expect.	7·8	7·8	23·6		23·6		

CFCOFO × CF

	CC	CF	FF	CCO	CFO	FFO	
376	17	35	12	6	33	25	282
377	9	18	7	4	10	7	282
378	18	25	7	2	25	16	283
Totals	74	78	26	12	68	48	
Expect.	38·2	76·5	38·2	38·2	76·5	38·2	

CFCOFO × CFCOFO

	CC	CF	FF	CCO COCO	CFO COFO	FFO FOFO	
379	0	1	0	1	0	0	435
380	4	5	0	4	10	1	268
381	2	1	0	4	15	5	289
382	12	7	4	16	37	20	282
383	0	4	0	3	9	4	382
384	0	0	2	0	1	1	382
385	1	0	1	3	3	2	312 383
386	0	4	2	0	2	1	435
387	0	6	0	7	11	6	386 312
Totals	19	28	9	38	88	43	
Expect.	14	28·1	14	42·1	84·3	42·1	

CFCOFO × COFO

	CCO COCO	CFO COFO	FFO FOFO	
388	15	33	19	184 445
Expect.	16·7	33·5	16·7	

CFCOFO × FJFOJO

	CF	CJ	FF	FJ	CFO COFO	CJO COJO	FFO FOFO	FJO FOJO	
389	2	3	1	2	6	1	8	7	282 373
Expect.	1·8	1·8	1·8	1·8	5·6	5·6	5·6	5·6	

COFO × COFO,
CFCOFO × COFO, or
COFO × CFCOFO

	COCO CCO	COFO CFO	FOFO FFO	
390	7	7	10	383 331
391	3	4	1	312 384
392	15	40	15	331 312
393	12	36	18	312 386
Totals	37	87	44	
Expect.	42	84	42	

CJ × COCO

	CCO	CJO	
394	7	4	395
Expect.	5·5	5·5	

CJCOJO × CJCOJO

	CC	CJ	JJ	CCO COCO	CJO COJO	JJO JOJO	
395	3	15	13	31	79	19	360
Expect.	10·1	20·3	10·1	30·5	61·1	30·5	

CP × BBO

	BC	BP	BCO	BPO	
396	33	31	14	36	335 341
Expect.	36	36	36	36	

CP × CCO

	CC	CP	CCO	CPO	
397	16	13	14	13	335 426
Expect.	14	14	14	14	

CPCOPO × BCBOCO

	BC	BP	CC	CP	BCO BOCO	BPO BOPO	CCO COCO	CPO COPO	
398	1	2	0	1	3	3	2	6	335
Expect.	1·1	1·1	1·1	1·1	3·3	3·3	3·3	3·3	

CPCOPO × CPCOPO

	CC	CP	PP	CCO COCO	CPO COPO	PPO POPO	
399	1	1	1	0	2	0	397
400	0	4	5	10	10	5	335
401	0	3	0	2	2	1	335
402	0	10	6	23	34	11	335
403	0	2	2	7	15	8	335
Totals	1	20	14	42	63	25	
Expect.	10·3	20·6	10·3	30·9	61·8	30·9	

CS × ABAOBΘ

	AC	AS	BC	BS	ACΘ	ASΘ	BCΘ	BSΘ	
404	0	3	0	3	0	2	3	6	N 314
405	2	3	6	8	7	15	8	6	N 179
Totals	2	6	6	11	7	17	11	12	
Expect.	9	9	9	9	9	9	9	9	

CS × ACAΘCΘ

	AC	CC	AS	CS	ACΘ	CCΘ	ASΘ	CSΘ	
406	17		7	9	27		4	6	34 234
Expect.	17·5		8·7	8·7	17·5		8·7	8·7	

CS × BCBΘCΘ

	BC	BS	CC	CS	BCΘ	BSΘ	CCΘ	CSΘ	
407	1	2	3	2	2	2	6	3	107 264
Expect.	2·6	2·6	2·6	2·6	2·6	2·6	2·6	2·6	

CS × BSBΘSΘ

	BC	BS	CS	SS	BCΘ	BSΘ	CSΘ	SSΘ	
408	0	0	0	0	0	0	1	0	100 279

CS × CCΘ

	CC	CS	CCΘ	CSΘ	
409	5	4	4	3	100 258
410	6	5	13	11	N 416
411	21	28	26	25	407
Totals	32	37	43	39	
Expect.	37·7	37·7	37·7	37·7	

CS × CΘCΘ

	CCΘ	CSΘ	
412	5	5	100 258
Expect.	5	5	

CS × CSCΘSΘ

	CC	CS	SS	CCΘ	CSΘ	SSΘ	
413	20	30	19	16	30	15	360
R **414**	2	11	4	4	11	1	413
Totals	22	41	23	20	41	16	
Expect.	20·3	10·7	20·3	20·3	10·7	20·3	

CΘSΘ × JS

```
              CJΘ   CSΘ   JSΘ   SSΘ
     415      2     6     3     2    264 152
  Expect.    3·2   3·2   3·2   3·2
```

CSCΘSΘ × CCΘ

```
              CC    CS   CCΘ  CΘCΘ  CSΘ  CΘSΘ
     416      18    1        26         41    408 407
     417      1     3        17          8    407
  Totals      19    4        43         49
  Expect.    14·3  14·3      13·1       13·1
```

CΘSΘ × CΘSΘ,
CSCΘSΘ × CΘSΘ, or
CΘSΘ × CSCΘSΘ

```
           CCΘ  CΘCΘ  CSΘ  CΘSΘ  SSΘ  SΘSΘ
   418      11        38         14    416
   419      3         9           1    416
Totals      14        47         15
Expect.     19        38         19
```

CSCΘSΘ × CSCΘSΘ

```
           CC   CS   SS   CCΘ  CΘCΘ  CSΘ  CΘSΘ  SSΘ  SΘSΘ
  420      0    1    0        2          4          0    416
  421      2    1    1        5          4          0    416
  422      2    4    0        7         21          8    416
Totals     4    6    1        14        29          8
Expect.   3·8  7·7  3·8      11·6       23·2       11·6
```

CS × SSΘ

```
           CS   SS   CSΘ  SSΘ
  423      9    6    9    9    413
R 424      14   18   17   25   413
Totals     23   24   26   34
Expect.   26·7 26·7 26·7 26·7
```

CSCΘSΘ × BB

```
            BC   BS   BCΘ  BSΘ
  425       7    8    13   4    407 236
Expect.     8    8    8    8
```

3—2

CSCOSO × BCBOCO

	BC	BS	CC	CS	BCO	BOCO	BSO	BOSO	CCO	COCO	CSO	COSO	
426	0	4	1	0	4		3		6		2		407
Expect.	1·2	1·2	1·2	1·2	3·7		3·7		3·7		3·7		

CSCOSO × BOBO

	BCO	BOCO	BSO	BOSO		
427	2		4		407	213
Expect.	3		3		

DJ × CJCOJO

	CD	CJ	DJ	JJ	CDO	CJO	DJO	JJO		
428	0	2	0	1	2	0	3		116	395
Expect.	1	1	1	1	1	1	2		

DJ × CSCOSO

	CD	CJ	DS	JS	CDO	CJO	DSO	JSO		
429	7	6	4	7	8	11	11	6	116	413
Expect.	7·5	7·5	7·5	7·5	7·5	7·5	7·5	7·5	

EFEOFO × BC

	BE	BF	CF	CF	BFO	BFO	CEO	CFO		
430	1	1	2	1	0	5	0	4	296	312
431	2	0	1	2	0	4	0	2	296	283
Totals	3	1	3	3	0	9	0	6	
Expect.	3·4	3·4	3·4	3·4	3·4	3·4	3·4	3·4	

EFEOFO × EFEOFO

	EE	EF	FF	EEO	EOEO	EFO	EOFO	FFO	FOFO	
432	1	4	0	11		11		11		296
Expect.	2·5	5·1	2·5	7·6		15·3		7·6		

$FF \times BB\Theta$

BF $BF\Theta$

433   2   1   303

Expect.   1·5   1·5

$FF \times B\Theta F\Theta$

$BF\Theta$ $FF\Theta$

434   1   3   124 191

Expect.   2   2

$FF \times CC\Theta$

CF $CF\Theta$

435   56   47   439 N

Expect.   51·5   51·5

$FF\Theta \times AB A\Theta B\Theta$

AF BF $AF\Theta$ $A\Theta F\Theta$ $BF\Theta$ $B\Theta F\Theta$

436   6   4   20   22   315 N

Expect.   6·5   6·5   19·5   19·5

$FF\Theta \times BB$

BF $BF\Theta$

437   8   6   449 43

Expect.   7   7

$F\Theta F\Theta \times BB$

$BF\Theta$

441   80   439 44

$FF\Theta \times BS$

BF FS $BF\Theta$ $FS\Theta$

438   9   9   4   14   315 N

Expect.   9   9   9   9

$F\Theta F\Theta \times B\Theta B\Theta$,
$FF\Theta \times B\Theta B\Theta$, or
$F\Theta F\Theta \times BB\Theta$

$B\Theta F\Theta$ $BF\Theta$

442   14   315

R **443**   112   315

Total   126

$FF\Theta \times FF\Theta$

FF $FF\Theta$ $F\Theta F\Theta$

439   5   10   434

440   1   2   384

Totals   6   12

Expect.   4·5   13·5

$F\Theta F\Theta \times BC$

$BF\Theta$ $CF\Theta$

444   20   17   439 44

Expect.   18·5   18·5

FOFO   COFO,
FFO   COFO, or
FOFO   FFCOFO

|
COFO CFO FOFO FFO

445	1		0	325	393
Expect.	0·5		0·5		

FOFO   FOFO
FFO   FOFO
FOFO   FFO

|
FOFO   FFO

447	22	439	
448	16	382	
449	11	448	
450	15	449	
451	56	449	
452	13	312	
453	8	305	
454	50	453	
455	3	393	325

FOFO   BOFO,
FFO   BOFO, or
FOFO   FFBOFO

|
BOFO BFO FOFO FFO

446	22		21	315
Expect.	21·5		21·5	

Total   224

FJFOJO × FJFOJO

|
FF   FJ   JJ   FFO   FOFO   FJO   FOJO   JJO   JOJO

456	2	4	6	8		5		0	457
Expect.	1·5	3·1	1·5	1·6		9·3		1·6	

FJFOJO × FOJO, or
FOJO × FJFOJO

|
FOFO FFO FOJO FJO JOJO JJO

457	12		14		7	389
Expect.	8·2		16·5		8·2	

FOJO × FOJO
FJFOJO × FOJO
FOJO × FJFOJO

|
FOFO FFO FOJO FJO JOJO JJO

458	11		15		5	457
459	5		5		1	457
460	6		10		3	457
Totals	22		30		12	
Expect.	16		32		16	

HSHOSO   SS

HS   SS   HSO   SSO
461   2   4   5   4   N
Expect.   3·7   3·7   3·7   3·7

JOJO   JOJO
JJO   JOJO
JOJO   JJO

JOJO   JJO
462   40   457

JP   BCBOCO

BJ   BP   CJ   CP   BJO   BPO   CJO   CPO
463   42   48   29   27   28   28   25   27   147 292
Expect.   31·7 31·7 31·7 31·7 31·7   31·7   31·7   31·7

PS × BBO

BP   BS   BPO   BSO
464   7   9   5   6   146 231
Expect. 6·7   6·7   6·7   6·7

SS   CSCOSO

CS   SS   CSO   SSO
466   17   7   11   13   413
Expect. 12   12   12   12

SS   ABAOBO

AS   BS   ASO   BSO
465   3   1   1   1   107 170
Expect. 1·5   1·5   1·5   1·5

SS × SSO

SS   SSO
467   6   8   341
Expect.   7   7

SSO × SSO

SS   SOSO   SSO
468   25   78   341
Expect.   25·7   77·2

In a few matings separations of *BBO* from *BOBO*, *BCO* from *BOCO*, and *CCO* from *COCO* were made in the records. As has already been indicated, this is a very tedious and difficult undertaking, as the difference between an individual homozygous for O and one heterozygous for it is only slight at best. If the determinations are not made within a few days after moulting it is necessary to group them, as was done in most of the matings. Mating (341) (*BSO* × *BSO*) was separated with special care, the result being shown in the table. The following matings, grouped in the table, were thus separated, but the mortality

of the individuals mated from them was so great that the correctness of the separations was not adequately proven by further breeding.

					BΘ	BΘ			
	BB	CC	BC	BBΘ	BΘBΘ	CCΘ	CΘCΘ	BΘ	BΘCΘ
242	0	1	2	4	1	2	1	3	3
244	1	6	7	6	2	4	4	8	3
245	1	3	5	6	2	5	0	15	5
246	6	0	3	5	1	3	4	9	4
247	2	4	5	2	1	6	0	8	3
254	3	1	4	5	6	10	8	23	13
255	13	7	13	19	8	.11	9	34	15
Totals	26	19	39	47	21	41	26	100	46
Expect.	23	23	46	46	23	46	23	92	46

Note. The mortality on the whole due to fungus and other disease, lack of proper care, etc., was very great. However, recently, considerable improvement has been made. Of the 974 matings made in this experiment only 470 produced young that could be recorded. Of the 43,914 young transferred from the mating jars only 21,686 (those used in this paper) were recorded.

The nature of this material permits us to observe the difference in behaviour between the multiply allelomorphic characters, *allelomorphic to each other, never to absences*, and the character Θ, *allelomorphic only to its absence, never to anything*. Application of this conception may be made outside the *Paratettix* material: the case of inheritance of combs in fowls, for instance. Allowing P to represent the factor for pea, S the factor for single, each allelomorphic to the other, and Φ the factor, allelomorphic only to its absence, which, when present, modifies SS to make the two kinds of rose, and PP and PS to make the four kinds of walnut, we have the same situation that is produced by B, C, or any other two multiple allelomorphs and Θ in *Paratettix*. We then secure the same ratios, and exact parallelism in all respects. When Mr Bateson (2), p. 63, describes a cross, rose × single, with the resulting dominance of rose in F_1 and the usual 3 rose : 1 single in F_2, he really shows a cross of single homozygous for the modifying factor Φ and pure single ($SΦSΦ × SS$) which produces $SSΦ$. Then when these are inbred there results in F_2,

SS	SSΦ	SΦSΦ		SΦSΦ × SS	Parents
1	2	1		│	F_1
				SSΦ	
1	3			│	
				SSΦ × SSΦ	
				│	
				SS SSΦ SΦSΦ	F_2
				1 2 1	
				1 3	
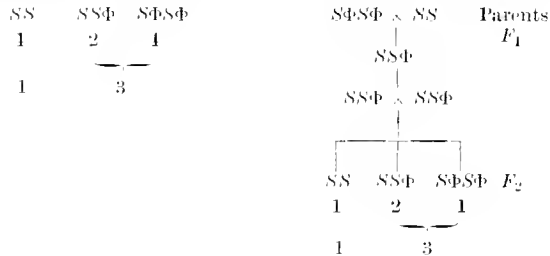
Rose × Pea: (2), pp. 63, 64. This cross was undoubtedly $PP \times S\Phi S\Phi$ which produced $PS\Phi$ (one of the four kinds of walnut) in F_1. These inbred would give F_2,

SS	PP	PS	SSΦ	SΦSΦ	PPΦ	PΦPΦ	PΦSΦ	PSΦ
1	1	2	2	1	2	1	2	4
Single	Pea		Rose		Walnut			
1	3		3		9			

This situation is exactly paralleled by matings (198), (242), and (243) in *Paratettix*:

Paratettix.

$$BB \cdot C\Theta C\Theta$$
$$\mid \quad (198)$$
$$BC\Theta$$

34

$$BC \ B\Theta C\Theta \times BCB\Theta C\Theta$$

	BB	BC	CC	BBΘ	BΘBΘ	BCΘ	BΘCΘ	CCΘ	CΘCΘ	
	0	2	1	5		6		3		242
	4	6	1	4		10		3		243
Totals	4	8	2	9		16		6		
	2·8	5·6	2·8	8·4		16·8		8·4		
		12	2	9			22			
		8·4	2·8	8·4			25·2			

Combs of Fowls.

$$PP \times S\Phi S\Phi$$
$$\mid$$
$$PS\Phi \quad F_1$$

$$PSP\Phi S\Phi \times PSP\Phi S\Phi$$

PP	PS	SS	PPΦ	PΦPΦ	PSΦ	PΦSΦ	SSΦ	SΦSΦ	
1	2	1	2	1	4	2	2	1	F_2
3		1	2		9		3		
Pea		Single			Walnut		Rose		

(See also matings at end of summaries, where those containing single and double doses of Θ were separated.)

The mating $RP \times S$, (2), p. 65, could not have been other than $PS\Phi \times SS$ which would produce

PS	SS	PSΦ and SSΦ
Pea	Single	Walnut Rose

Another case is that of comb behaviour in experiments 33, 40 and 41, (1), pp. 103, 106, 107. The ♀ in experiment 33 was well proven to have been homozygous for the modifying factor Φ which makes rose of single (experiments 30–33) and her composition therefore should read $S\Phi S\Phi$ and the ♂ was single (SS). A pedigree arrangement of these experiments would appear as follows:
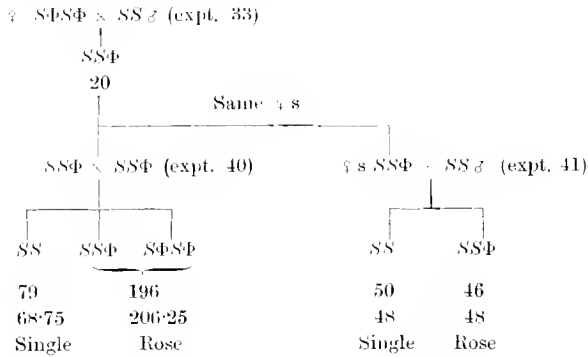
These experiments 33, 40, and 41 of Bateson and Saunders are exactly paralleled by matings (468) and (467) in *Paratettix*.

If P and S represent the factors for pea and single respectively and Φ the factor which modifies SS to make the two kinds of rose and PP and PS to make the four kinds of walnut, a revision of Bateson's 16-square diagram, (2), p. 75, to correspond with the one for *Paratettix* may be made:

	P	S	$P\Phi$	$S\Phi$
P	PP	PS	$PP\Phi$	$PS\Phi$
S	PS	SS	$PS\Phi$	$SS\Phi$
$P\Phi$	$PP\Phi$	$PS\Phi$	$P\Phi P\Phi$	$P\Phi S\Phi$
$S\Phi$	$PS\Phi$	$SS\Phi$	$P\Phi S\Phi$	$S\Phi S\Phi$

The essential difference between this conception and those prevailing in most of the literature and practically all text books on the subject is that two factors, P and S, which are paired, each with the other, and one factor, Φ, which is not paired, unless it be with its absence, are considered. Rose is a modified single and in no sense a character. Walnut is a modification by the factor Φ of pea and the combination of pea and single.

The same consideration may be given to the crossings of round yellow with wrinkled green peas. Having in mind the behaviour of Θ and any two multiple allelomorphs in *Paratettix*, it appears that Mendel's experiment, (2), pp. 333, 334, consisted of one pair of factors, round and wrinkled, each allelomorphic to the other, and a factor for yellow which is allelomorphic only to its absence as Θ in *Paratettix* and Φ in combs of fowls. Allowing R to represent the factor for round and W the factor for wrinkled, the two making an allelomorphic pair, and Δ the unpaired factor for yellow, we have a case of crossing $R\Delta R\Delta \times WW$, with the product in F_1, $RW\Delta$. These inbred produced in F_2, considering only those tested by Mendel,

RR	RW	WW	$RR\Delta$	$R\Delta R\Delta$	$RW\Delta$	$R\Delta W\Delta$	$WW\Delta$	$W\Delta W\Delta$
35	67	30	65	38	138	60	68	28
33	66	33	66	33	132	66	66	33

102	30	301	96
99	33	297	99
Round green	Wrinkled green	Round yellow	Wrinkled yellow

Green is common to the albumen of peas. It may be that peas are all homozygous for the factor, or factors, causing green, but the green does not pair, as an allelomorph, with yellow. It does not matter, in this consideration, whether the factor for yellow causes yellowness in addition to, and to the obscurity of, green, or whether it inhibits or destroys something to prevent the green from showing.

It may be remarked, in this connection, that if all fourteen *Paratettix* multiple allelomorphs, so far discovered, should be made homozygous for Θ, which could be easily accomplished, and all of them segregated, there would be no chance of securing pure multiple allelomorphs again from this group. As a matter of fact the forms with the double doses of Θ would themselves become multiple allelomorphs. This may be true now with respect to certain characters in *Paratettix*, e.g., the triangular black spots on each side of the mid-pronotum which are common to all forms. However, since all of them appear to have it

there is no possibility of proving the matter, unless a form without it, or only heterozygous for it, should be discovered.

There are two classes of characters, the one such as A, B, C, D, etc., in *Paratettix*, pea and single in combs of fowls, and round and wrinkled in peas, and the other class such as Θ in *Paratettix*, Φ in combs of fowls and Δ in colour of the albumen in peas. In the first class two factors for any one suffice to make the whole character, and two for different ones produce a hybrid, intermediate in fact, though the one may be more apparent (epistatic) and the other less apparent (hypostatic). Two factors for either A, B, C, or either of the others in that series, suffice for a complete pattern; one factor for one and another factor for another make a hybrid. Two factors for pea make a complete pea comb; two factors for single produce a complete single comb; while one factor for pea and one factor for single produce the hybrid comb (with pea epistatic, though this hybrid is said to appear somewhat intermediate). Two factors for roundness produce the character of roundness, two factors for wrinkledness produce a wrinkled pea; one factor for wrinkledness and another for roundness produce an intermediate in fact (with the round epistatic, though this hybrid is said to be somewhat intermediate). In the other class (Θ, Φ and Δ) no one can exist except in connection with, and in addition to, characters of the first class. As already stated *these factors are allelomorphic to their absences, never to any other character.* For instance, in *Paratettix*, when BB contains a single dose of Θ (heterozygous for it), in the gametogenesis, every other gamete receives a dose of Θ, half the gametes formed carrying it and half without it. In neither case does the Θ factor affect the normal behaviour of the B gamete. The same conditions prevail for hybrids, such as BC; if Θ be present in the single dose, only every other gamete receives it, if Θ be present in double dose, no gamete is formed without it. In either case the gametogenesis in BC proceeds as though Θ were not present. (In the use of the word "dose" or "factor" there is no intention at this time of attempting to convey any conception of the condition or situation in the germ cells of the factor Θ.) It requires two gametes of any one multiple allelomorph to make a homozygote for that form, or a gamete of one and a gamete of another multiple allelomorph to make a hybrid or heterozygote. The situation is entirely different with regard to such characters as Θ, in *Paratettix*, Φ in combs of fowls and Δ in colour of peas; these are mere appurtenances of the gametes of the multiple allelomorphs.

This conception, if acceptable, has wide application. Besides applying

to colours of *Paratettix*, combs of fowls, and colours of the albumen of peas, it as readily applies to all the inheritance behaviour exhibiting the $1:3$ (actually $1:2:1$) ratios, and the $9:3:3:1$ (actually $1:1:1:1:2:2:2:2:4$) ratios described in the literature which I have had time so far to examine. I suggest also that those matings which result in the apparent $27:9:9:9:3:3:3:1$ ratios actually consist of one pair of allelomorphic characters, each allelomorphic to the other and two non-allelomorphic or unpaired characters, of the nature of Θ, each allelomorphic only to its absence, and neither one allelomorphic to the other, nor to any other, character.

One multiple allelomorphic factor of the nature of A, B, C, or others of this series, and two non-allelomorphic factors of the nature of Θ, or three factors of the nature of Θ and the factor, or factors, of the nature of A, B, C, etc., unnoticed, or ignored, though necessarily present, produce the $1:1:1:1:2:2:2:2:4$ ($9:3:3:1$) ratios. One multiple allelomorphic factor and three non-allelomorphic factors like Θ, or four factors of the nature of Θ and the factor, or factors, like A, B, C, D, etc., unnoticed or ignored, will give the $27:9:9:9:3:3:3:1$ ratios. In no instance can more than one multiple allelomorphic factor (A, B, C, D, etc.) be found in one gamete, or two in a zygote; but any number of factors like Θ can be accommodated in a gamete or zygote. The behaviour of these factors as illustrated in the tables lends emphasis to these distinctions which are of fundamental importance in studies of inheritance.

EXPLANATION OF PLATES.

PLATE I.

BFΘ and *BΘBΘ*, *BCΘ* and *BΘCΘ*, and *CCΘ* and *CΘCΘ* were photographed in pairs, respectively, on the same plates and were printed in pairs. All nine kinds are here easily distinguishable.

The series of phenomena is here represented as due to the combinations of one pair of allelomorphic characters, or factors, *B* and *C*, and a third character, or factor, Θ, which is not paired, or allelomorphic, except with its absence.

This conception is widely different from that which represents the phenomena as due to the combinations of two pairs of allelomorphic characters or factors. According to Mr Bateson (2), p. 65, *CΘCΘ*, or *BΘBΘ* might be considered one character of an allelomorphic pair.

PLATE II.

The top row (first twelve figures) represents the patterns which breed true and cannot be further analyzed. The form *AA* is most abundant in nature, most of the others being comparatively rare. Therefore it is common to find the other forms hybridized with *AA*, though they are sometimes found pure, or in combination with others than *AA*.

The eighteen figures (*BE*—*JS*) represent simple hybrids resulting from combinations of the pure forms.

The remaining fifteen figures (*BFΘ*—*CJΘ*) represent the pure forms and their hybrids carrying the melanic pattern Θ, heterozygously or homozygously, as indicated.

For an explanation of the three figures $\widehat{ISIS}$, $\widehat{BIS}$, and $\widehat{IIS}$ see third instalment, *Journal of Genetics*, Vol. VII. p. 47.

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Gametes

PLATE II

FF HH II JJ PP SS

BP BS CE CF CH CI

IS JP JS BFθ CFθ JJθ

CCθ CθCθ SSθ SθSθ CSθ CJθ
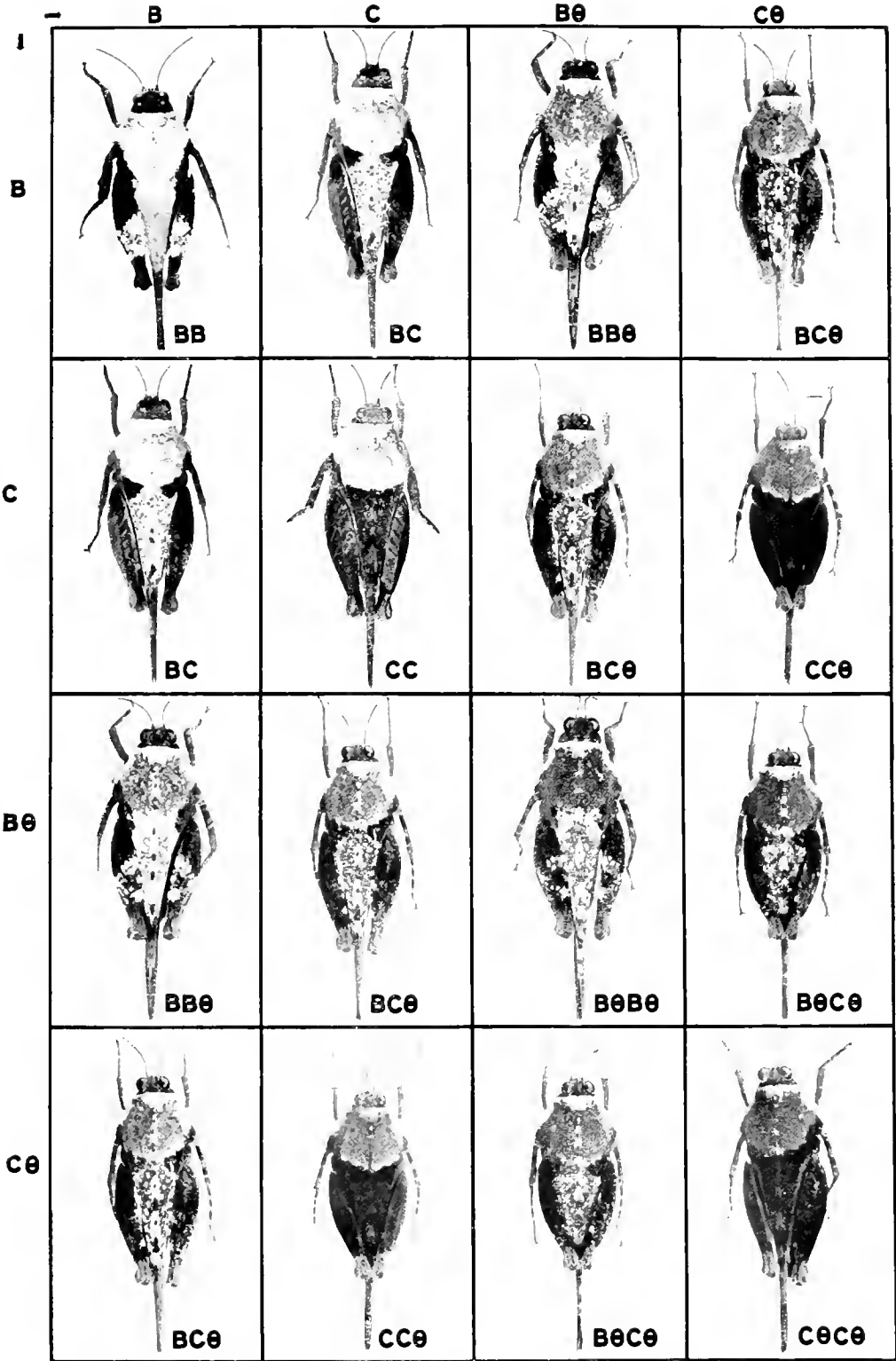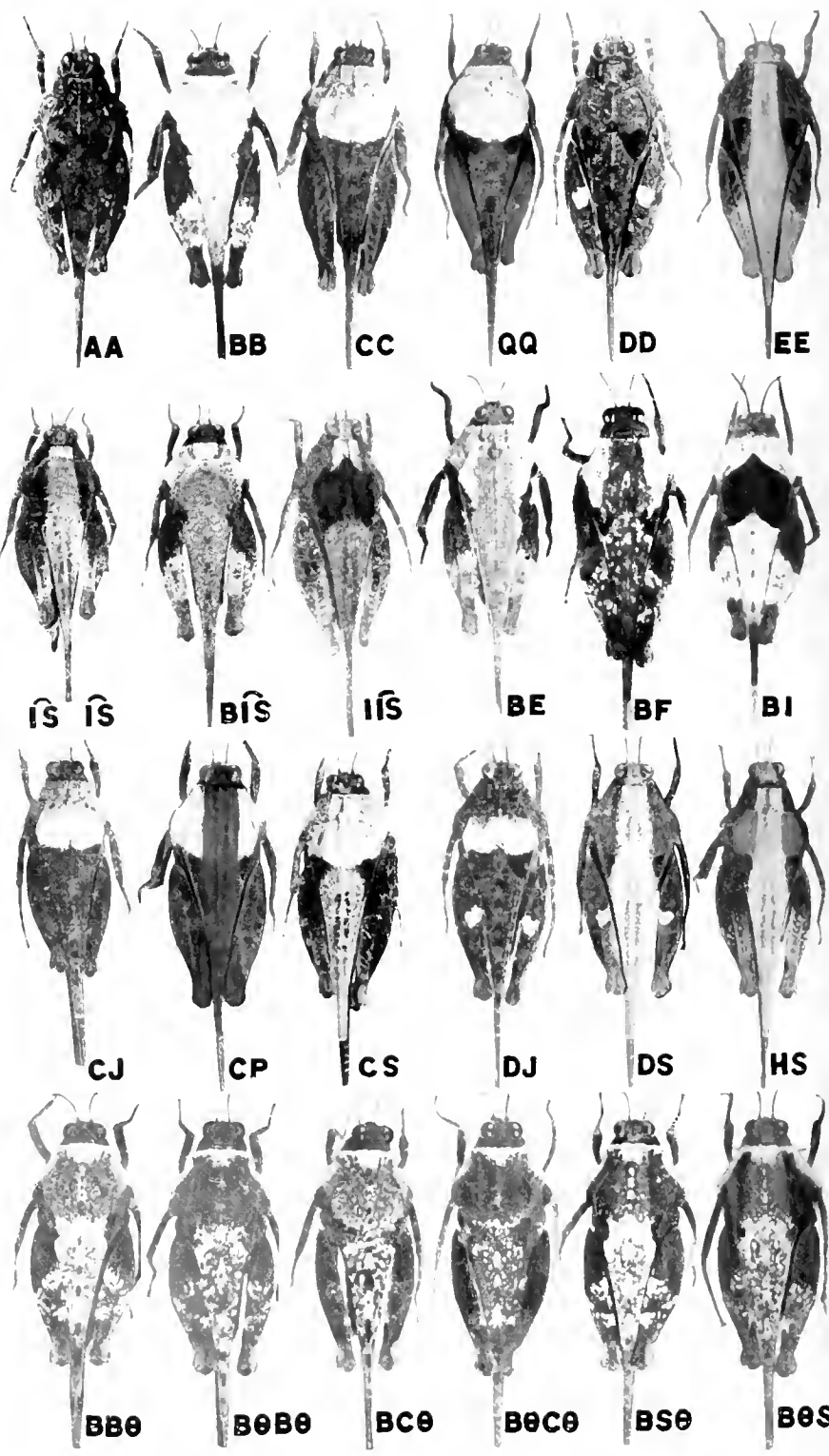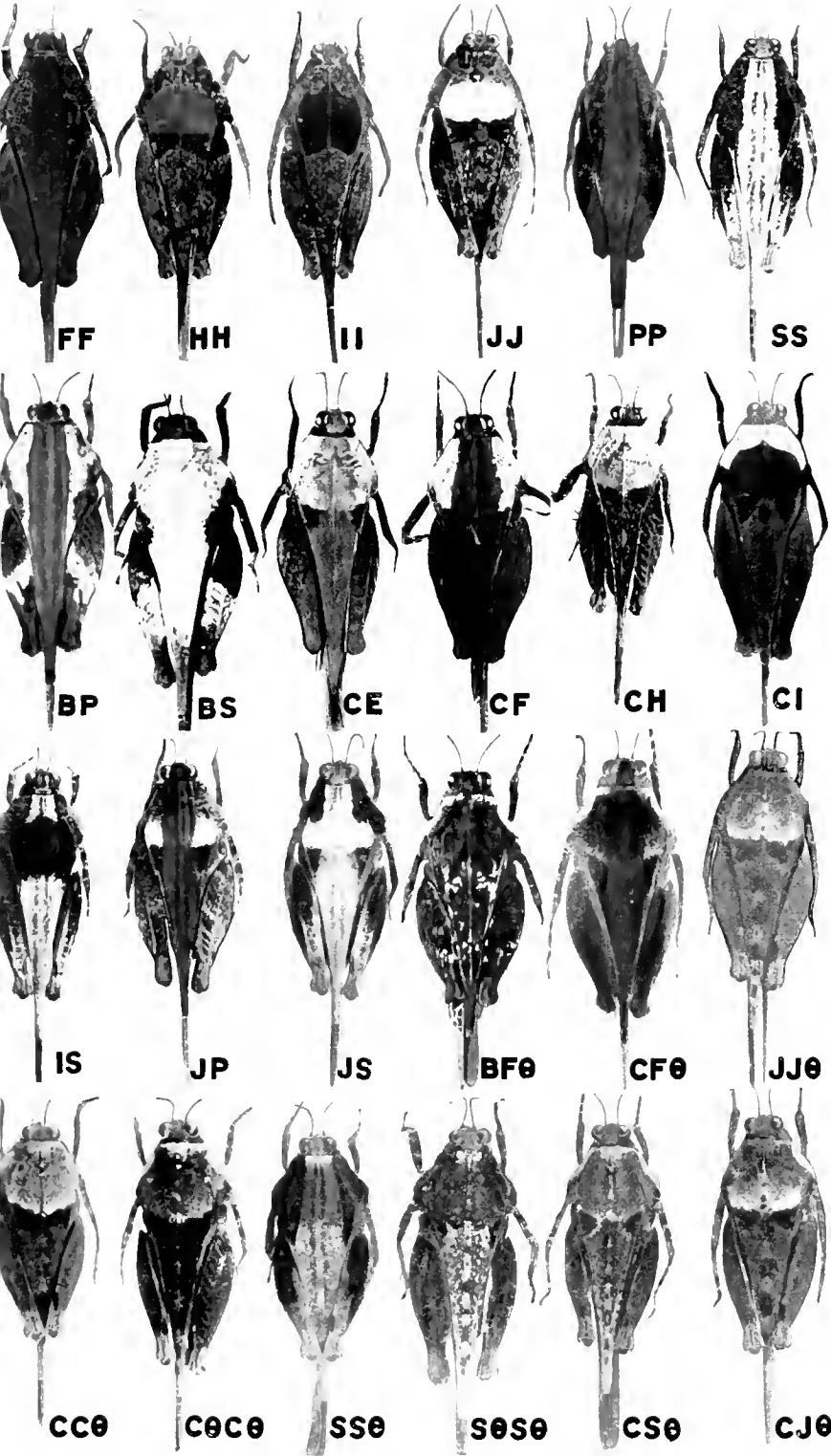
STUDIES OF INHERITANCE AND EVOLUTION IN ORTHOPTERA. III[1].

By ROBERT K. NABOURS.

In the first instalment of this study, *Journal of Genetics*, Vol. III. pp. 141—170, the crossing of the hybrid ♂ *CE* with a hybrid ♀ *BI*, Table III (*b*), was reported which produced the approximate normal expectation of *BC* 12, *BE* 11, *CI* 7, and *EI* 10, and an unexpected individual, a male, showing the combination of the three patterns *B*, *E*, and *I* (*BEI*). This aberrant individual was discovered at an early age and its pattern was clearly marked at all times, and especially well soon after moulting when patterns are always at their best. It became adult, but was lost before any matings were made. It was suggested in the report that perhaps the female had produced an abnormal gamete containing the factors for both *B* and *I*, and that this was fertilized by a normal gamete from the male containing the factor for *E*[2].

Explanations of the causes of this phenomenon have been proposed by Dexter ('14), and Bridges ('16), and comments have been made upon it by Castle ('14), and Morgan ('14).

No other such individual was observed in any of the *Paratettix* cultures until the summer of 1915, when a form combining the patterns of *B*, *S*, and a modified *I* appeared among the progeny of a mating (472) of *IS* × *BS*. This aberrant *BIS* individual, a male, was mated to three females, *BC* (mating 486), *BS* (mating 488), and *BB* (mating 482), respectively. Reference to the accompanying tables and to the tables in the second instalment will indicate the ancestry of the parents in this mating (472) and also show the breeding behaviour of the progeny and relatives. (See Plate II in second instalment.)

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[2] The other apparent exceptions referred to in the first instalment were those cases involving the factor O, which are considered in the second paper.

Table for Use in Making Pedigrees.

One or both of the parents of the numbers inside the parentheses came from the number outside. This table, with the source numbers in connection with the matings, enables one to trace the ancestry of any mating as far back, and the progeny as far forward, as there are any records.

470 (471, 472, 474); 472 (473, 479, 480, 482, 486, 488, 489); 473 (481, 490, 495, 496); 475 (476, 477, 478, 490, 504, 505, 506, 531, 532); 479 (491); 480 (481); 482 (483, 484, 485, 497, 498, 499, 502, 503, 528); 485 (487, 501, 512, 513, 536, 539); 486 (484, 509, 510, 515, 516, 517, 522); 488 (498); 489 (504, 505, 507, 508, 519); 491 (518); 492 (506, 508); 493 (519); 502 (518, 530); 503 (529, 531, 532, 533, 534, 538); 509 (525); 510 (487, 500, 514, 523, 524, 527, 529, 530, 535, 536, 540); 515 (500, 511, 520, 521, 523, 535); 522 (512, 513, 526, 537, 538, 540).

Explanation of the Tables. Matings of the same kind are grouped in summaries. The ♂ parent is on the left and the ♀ on the right of the ×, except when (R) is used, which indicates a reciprocal. Below the line, beginning at the left, (R) when used = reciprocal; the number in heavy type (e.g. **470**) is that of the mating; the next number, or numbers, indicate the progeny; the last number, or numbers, in square type (e.g. 26), indicate the sources of the parents, the ♂ being on the left and the ♀ on the right when two numbers are given. The numbers in the sources less than (470) refer to the tables of the second instalment. The first line of totals gives the actual numbers and the second the expectation.

TABLES.

CS × BI

	BC	BS	CI	IS		
470	10	9	3	9	407	26
Expect.	7·7	7·7	7·7	7·7		

CI × IS

	CI	CS	II	IS	
474	18	20	23	26	470
Expect.	21·7	21·7	21·7	21·7	

BC × CC

	BC	CC		
471	36	39	470	426
Expect.	37·5	37·5		

II × II

II

143	90	74	
475	19	143	
476	29	475	
477	69	475	
478	23	475	
Total	230		

IS × BS

	BI	BS	IS	SS	BIS	
472	9	8	7	10	1	470
473	18	12	19	17	0	472
Totals	27	20	26	27	1	
Expect.	25·2	25·2	25·2	25·2	0	

CE × BI

	BC	BE	CI	EI		
479	12	22	20	11	292	472
Expect.	16·2	16·2	16·2	16·2		

TABLES (continued).

IS × BI

	BI	BS	II	IS		
480	11	9	16	7	472	
481	24	10	12	10	480	473
Totals	35	19	28	17		
Expect.	24·7	24·7	24·7	24·7		

BIS × BB

	BB	BIS		
482	20	24	472	245
483	10	15	482	
484	10	9	486	482
485	22	31	482	
Totals	62	79		
Expect.	70·5	70·5		

BIS × BC

	BB	BC	BIS	CIS		
486	9	8	10	9	472	266
487	9	9	13	7	485	510
Totals	18	17	23	16		
Expect.	18·5	18·5	18·5	18·5		

BIS × BS

	BB	BIS	BS	ISS	
488	15	22	17	13	472
Expect.	16·7	16·7	16·7	16·7	

CE × IS

	CI	CS	EI	ES		
489	6	8	7	5	292	472
Expect.	6·5	6·5	6·5	6·5		

BS × II

	BI	IS		
490	30	31	473	475
Expect.	30·5	30·5		

CJ × CJ

	CC	CJ	JJ		
491	0	3	1	110	144
Expect.	1	2	1		

JS × DJ

	DJ	DS	JJ	JS		
492	1	3	3	0	151	149
Expect.	1·5	1·5	1·5	1·5		

BP × BP

	BB	BP	PP	
493	9	20	11	337
Expect.	10	20	10	

BC × CI

	BC	BI	CI	EI	
494	4	4	2	2	479
Expect.	3	3	3	3	

BΘBΘ × SS

	BSΘ		
495	91	218	473

TABLES (*continued*).

BS × BI

	BB	BI	BS	IS	
496	7	5	2	2	473
Expect.	4	4	4	1	

II × DS

	DI	IS		
506	13	15	475	492
Expect.	11	11		

II × BB
BI

497   72   143 482

CS × CI

	CC	CI	CS	IS	CIS	
507	14	9	15	14	1	489
Expect.	13·2	13·2	13·2	13·2	0	

BIS × BIS

	BB	BIS	ISIS		
498	5	3	2	482	488
499	3	4	2	482	
500	13	36	26	510	515
501	2	4	2	485	
Totals	23	47	32		
Expect.	25·5	51	25·5		

ES × DJ

	DE	DS	EJ	JS		
508	6	8	5	6	489	492
Expect.	6·2	6·2	6·2	6·2		

BIS × II

	BI	IIS		
502	21	14	482	143
503	16	17	482	143
Totals	37	31		
Expect.	34	34		

CIS × BIS

	BC	BIS	CIS	ISIS		
509	2	2	1	3	486	
510	8	15	10	9	486	
511	3	2	6	5	515	
512	18	11	15	16	522	485
513	10	10	10	8	522	485
R **514**	1	1	1	2	510	
Totals	42	41	43	43		
Expect.	42·2	42·2	42·2	42·2		

II × LS

	EI	IS		
504	19	16	475	489
Expect.	17·5	17·5		

EI × II

	EI	II		
505	2	4	489	475
Expect.	3	3		

CIS × BC

	BC	BIS	CC	CIS		
515	2	2	3	6	486	38
Expect.	3·2	3·2	3·2	3·2		

TABLES (continued).

$BC \times BFB\Theta F\Theta$

	BB	BC	BF	CF	BBΘ	BCΘ	BFΘ	CFΘ		
516	12	8	10	12	16	13	7	5	486	222
Expect.	10·3	10·3	10·3	10·3	10·3	10·3	10·3	10·3		

$BC \times B\Theta F\Theta$

	BBΘ	BCΘ	BFΘ	CFΘ		
517	9	8	11	8	486	222
Expect.	9	9	9	9		

$\widehat{ISIS} \times \widehat{ISIS}$

$\widehat{ISIS}$

524	33	510	
525	38	522	509
526	30	522	
527	31	510	
Total		132	

$\widehat{IIS} \times JJ$

	LJ	$\widehat{JIS}$		
518	2	4	502	491
Expect.	3	3		

$BB \times CEC\Theta E\Theta$

	BC	BE	BCΘ	BEΘ		
528	4	8	10	1	482	369
Expect.	5·7	5·7	5·7	5·7		

$CI \times BB$

	BC	BI		
519	8	9	489	493
Expect.	8·5	8·5		

$\widehat{IIS} \times BC$

	BI	$\widehat{BIS}$	CI	$\widehat{CIS}$		
529	31	30	22	24	503	510
R **530**	3	6	6	8	510	502
Totals	34	36	28	32		
Expect.	32·5	32·5	32·5	32·5		

$\widehat{CIS} \times \widehat{CIS}$

	CC	$\widehat{CIS}$	$\widehat{ISIS}$		
520	13	24	13	515	
521	25	51	17	515	
522	14	21	7	486	
523	10	27	12	510	515
Totals	62	123	49		
Expect.	58·5	117	58·5		

$\widehat{IIS} \times II$

	II	$\widehat{IIS}$		
531	4	7	503	475
Expect.	5·5	5·5		

TABLES (*continued*).

BI × II

	BI	II		
532	34	31	503	475
Expect.	32·5	32·5		

CC × CC
CC

537	26	522

IŜ × IŜ

	II	IIŜ	ISÎS	
533	4	5	4	503
534	1	1	1	503
Totals	5	6	5	
Expect.	1	8	1	

IIŜ × CÎS

	CI	CÎS	IIŜ	ISÎS		
538	31	35	28	26	503	522
Expect.	30	30	30	30		

ISÎS × BÎS

	BÎS	ISÎS		
535	32	32	510	515
536	33	21	510	485
Totals	65	53		
Expect.	59	59		

BB × BB
BB

539	88	485

BC × ISÎS

	BÎS	CÎS		
540	8	6	510	522
Expect.	7	7		

The *I* part of the pattern in this new combination is considerably modified. In the ÎS, BÎS or CÎS individuals the normal pigment of the dark mahogany spot which is most characteristic of *II*, and stands out sharply in the hybrids *BI, IS* and others, seems to be diffused or scattered over the area of the pronotum normally occupied by the spot, and in addition extends over all the posterior part of the pronotum. This scattering of the pigment, normally concentrated in the spot, gives the whole an appearance of being diluted, or diffused. The *SS* part of the pattern appears to be normal. The arrangement is indicated on Plate II.

The significant feature is the complete combination, or linkage, apparently permanent, of the factor for *S* and the factor for the modified *I* which is sufficiently demonstrated in the accompanying breeding tables. This combination, ÎS, becomes a new form, a new multiple allelomorph, pairing with, and allelomorphic to, any other multiple allelomorph with which it has been tried, including the forms (multiple

allelomorphs) *SS* and *II* from which it was itself derived. It also breeds true, matings (524), (525), (526), and (527).

Obviously it cannot be determined in this case, mating (472), whether the female gave an unusual gamete containing the factors for *B* and *S* and the male gave the gamete containing a factor for the modified *I*, or whether an abnormal gamete from the male carrying the factors for *S* and the modified *I* fertilized a normal gamete from the female carrying the factor for *B*. It is also not possible for me to suggest the means by which the combination, or linkage, was accomplished.

In mating (507), $CS \times CI$ (see table), another similar combination occurred, with *C* involved instead of *B* as in mating (472). Here an individual combining the *C*, *S*, and modified *I* patterns ($C\widehat{IS}$) appeared among the otherwise approximately normal expectation of *CC* 14, *CI* 9, *CS* 15, and *IS* 14. The *I* and *S* in this mating had come through one generation from the mating (472) which produced the original $B\widehat{IS}$ (see table). This $C\widehat{IS}$ was in all observable respects similar to the other $C\widehat{IS}$ individuals produced by descendants of the original $B\widehat{IS}$ aberrant form. It died before reaching adult stage. When this $C\widehat{IS}$ nymph, mating (507), was first observed, during its third instar, consideration was given to the possibility of its having been introduced into the breeding jar accidentally from some contemporaneous jar containing $C\widehat{IS}$, as matings (486), (510), and others. However, careful examination of the other breeding jars containing $C\widehat{IS}$ disclosed that none of these had arrived at the third instar stage, and, furthermore, this jar (507) had not been near enough these jars to make it likely that any accidental exchange might have been made. However, there remains the bare possibility of an accident in this case.

It appears that this strain of *I*, or *S*, or both, is subject to abnormal behaviour, and that the linkage, or modification, is permanent, thereby making a new and true breeding pattern. It may be that some of the numerous multiple allelomorphs in *Paratettix* have been developed in a similar way. The form *QQ* (see plate in second instalment) which so much resembles the form *CC*, may have secured the redness of its legs from some other form, just as the *SS*, in the experiment, mating (472), has become greatly modified through linkage with *I*. (In the new form, $\widehat{IS}$, the *S* pattern is more conspicuous than the *I* pattern.)

progress of the experiments and arrangement of the data. The expenses have been carried by the Adams fund and State fund of the Kansas Experiment Station, and I have had the most open-minded and complete encouragement from Director W. M. Jardine.

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STUDIES OF INHERITANCE AND EVOLUTION IN ORTHOPTERA. IV[1].

MULTIPLE ALLELOMORPHISM AND INHERITANCE OF COLOR PATTERNS IN TETTIGIDEA[2].

By ALBERT WILLIAM BELLAMY.

(With Plate III.)

INTRODUCTION.

ACCORDING to Bateson each character of an alternative pair is an allelomorphic one. He says ('09, p. 11) "The dissociation of characters from each other in the course of the formation of the germs, we speak of as *segregation*, and the characters which segregate from each other are described as *allelomorphic*, i.e. alternative to each other in the constitution of the gametes."

According to Morgan, allelomorphic characters are characters, the determiners for which have identical loci in homologous chromosomes. Shull ('15, p. 55) speaks of allelomorphism as "A relation between two characters such that the determiners of both do not enter the same gamete, but are separated into sister gametes." If instead of a single pair, a series of several characters exists, each of which behaves towards another as one of an alternative pair, it is said to constitute a system of multiple allelomorphs; the relation of the characters to one another being known as multiple allelomorphism.

Triple systems of allelomorphs have been described in rats, guinea-pigs, rabbits, Drosophila, beans, snapdragons, Lychnis, *et al.* Quadruple

systems are equally well known, having been studied in mice, guinea-pigs, Drosophila, and corn.   Nabours ('14) published an account of his work with *Paratettix* in which he described what has since been recognized (Dexter, '14) as a system of multiple allelomorphic characters,—the most extensive system yet reported.   Nabours showed the existence of eight colour patterns, each allelomorphic to any of the others.   Since that time, not only has the behaviour of the eight characters been fully confirmed, but the system has been extended to include in all, at least fourteen patterns and probably several more (Nabours, '17).

MATERIAL AND METHOD.

The material used in this study was collected near Houston, Texas, by Dr Robert K. Nabours and turned over to the writer in October, 1914. I am under deep obligation to him for aid by way of suggestion, encouragement, and criticism.

All the specimens used in the laboratory appear to conform most closely with Hancock's description of *Tettigidea parvipennis pennata* Morse.

Occurrence and distribution.   The *Tettigidea* are widely distributed, frequenting the damp surfaces of more or less deeply shaded areas, where mosses, lichens, algae, and decaying vegetation, upon which they feed, are to be found.

Life History.   That part of the life cycle from the egg to the adult may be completed in five or six weeks, although mating and deposition of eggs may not occur, at least in the laboratory, for several weeks after the last moult.   In one instance, e.g. series (9) of Table I, the first young of the parental generation hatched February 9, 1915.   Two females became adult March 9, one of which was mated on March 11, to her father, producing the second generation of young April 22, a little over eleven weeks from the hatching of the first generation to the hatching of the second.

Technique.   In the laboratory the grasshoppers are bred in cylindrical screen or glass jars set in pots of moist sandy loam, the surfaces of which are covered with a thin layer of peat.   The bottom of a small three-inch pot protrudes about one-half inch above the surface of the soil in the centre of each jar, affording a clean place upon which to

place the food. Some algae also grow upon it. The jars are of two sizes, the mating jars being $8'' \times 11''$ and the offspring jars $9' \times 15''$ (cf. Nabours, '14, pp. 143, 144, and Fig. 1).

The grasshoppers are fed on various filamentous algae which grow in abundance during the early spring, throughout the summer, and until late fall, in small streams, live-stock watering troughs, and similar places. In the winter, as well as in the summer, special troughs kept in the greenhouse supply a great deal of the food. If these food sources fail the supply is supplemented with algae and lichens that grow upon flower pots.

Characters under observation. The characters used in this study are the colour markings of the pronota and of the femora of the jumping legs. For present purposes, they may be considered as polyornate " forms " of the species *parvipennis*. For the sake of convenience in reference and recording, the different patterns are represented by capital letters. In instances where these letters are used apparently to indicate a single factor, or gene, it is to be understood that they indicate only the initiative reaction or impulse, or whatever it is, that ultimately results in the character as it appears in the adult animal. The different patterns may then be indicated as follows (see Plate III): $C =$ yellowish white striped pronotum. $D =$ white lined pronotum (*bilineata*), i.e. two whitish lines extend the full length of the lateral carinae. $E =$ slightly fulvo-aeneous plus blackish striped pronotum, i.e. the whole pronotum has an ill-defined blackish stripe on a pallid or slightly fulvo-aeneous background. $F =$ narrow banded femora ; this is subject to considerable variation, and in some individuals the pattern approaches a circle in outline, while in others it may appear as a white line. H (present only in connection with and in addition to some one or two of the other patterns) $=$ light brownish-red pronotum and femora of the jumping legs. $M =$ melanic, i.e. the whole animal is a dirty-brown to almost black individual.

Homozygous individuals, since they receive their determiners for the character in question from two parents, are indicated by doubling the letter representing that pattern and heterozygotes are indicated by a combination of the letters corresponding to the patterns represented in their constitution.

EXPERIMENTS.

Analysis of the original material. One male of the appearance of *DF* (see plate), one male of the appearance of *CF*, three females of the appearance of *MM*, and one female of the appearance of *EE*H, constituted the original material. They were mated as follows:

$$(3) \quad CF \times MM,$$
$$(5) \quad DF^1 \times MM,$$
$$(13) \quad DF^1 \times MM,$$
$$(9) \quad DF^1 \times EE\mathsf{H}.$$

These and the subsequent matings are shown in the table of matings which shows how all of the analyses were carried out.

It may be said that many of the matings were made, not so much in accordance with a previously arranged schedule, but because they represented the only available material. No doubt many of the analyses could have been carried out to better advantage, especially if one could have counted on having the right male and female adult at the *same time*, and if the contingency of the death of a valuable specimen did not have to be reckoned with.

Explanation of Table I. This table gives the entire pedigree. The matings are arranged in serial order reading in columns down the page and from left to right. The number in parentheses immediately above the horizontal line is the mating number; the number in parentheses above the mating is the mating from which the parents came. Take for example:

```
                     (9.3)
                  EF × EF
                     |        (9.16)
             ┌───────┴───────┐
            EE      EF       FF
             7      21        8
Expectation  9      18        9
```
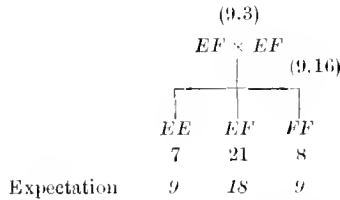
This is mating number (9.16), the parents coming from (9.3). The actual numbers are 7 : 21 : 8 and the expectations 9 : 18 : 9 respectively.

The original male *DF* was used in (5), (9), (9.1), and (13) and is indicated thus: **DF*.

---

[1] Same male.

TABLE I.

Nature
CF × MM
        (3)
```
   ┌──────┴──────┐
  CM          FM
  78          79
```
Expect.   78·5   78·5

(3)
CM × CM
        (3.4)
```
  ┌──────┬──────┐
 CC    CM    MM
```
       67   18
Expect.   63·75   21·25

(3)
FM × FM
        (3.5)
```
  ┌──────┬──────┐
 FF    FM    MM
```
       68   26
Expect.   70·5   23·5

(3)
CM × CM
        (3.6)
```
  ┌──────┬──────┐
 CC    CM    MM
```
       82   18
Expect.   75   25

(3)
FM × FM
        (3.7)
```
  ┌──────┬──────┐
 FF    FM    FM
```
       110   57
Expect.   125·25   41·75

(3.6)
CC × CC
        (3.8)
    CC
     9
Expect.   9

(3.8)
CC × CC
        (3.10)
    CC
    29
Expect.   29

(3.10)
CC × CC
        (3.11)
    CC
    10
Expect.   10

Nature
*DF × MM
        (5)
```
  ┌──────┴──────┐
 DM          FM
 39          50
```
Expect.   44·5   44·5

(5)
DM × DM
        (5.2)
```
  ┌──────┬──────┐
 DD    DM    MM
```
       63   27
Expect.   67·5   22·5

(5)
FM × DM
        (5.3)
```
  ┌─────┬─────┬─────┐
 DF   DM   FM   MM
  7    14   15   14
```
Expect.   12·5 12·5 12·5 12·5

(5)
FM × FM
        (5.5)
```
  ┌──────┬──────┐
 FF    FM    MM
```
       30   12
Expect.   31·5   10·5

TABLE I (*continued*).

(5.2)

$MM \times MM$

| (5.6)

MM

50

Expect.   50

(5.3)

$DF \times DF$

| (5.7)

	DD	DF	FF
	2	5	3
Expect.	2·5	5	2·5

Nature

$*DF \times EEH$

(9)

	DE	EF	DEH	EFH
	15	12	8	11
Expect.	11·5	11·5	11·5	11·5

---

(9)

$*DF \times DEH$

(9.1)

	DD	DE	DF	EF	DDH	DEH	DFH	EFH
	9	13	13	5	14	16	8	27
Expect.	13	13	13	13	13	13	13	13

---

(9)

$DEH \times DE$

(9.2)

	DD	DE	EE	DDH	DEH	EEH
	4	4	3	9	16	12
Expect.	6	12	6	6	12	6

---

(9)

$EF \times EF$

(9.3)

	EE	EF	FF
	35	81	12
Expect.	39·5	79	39·5

---

(9)

$EF \times DE$

(9.1)

	DF	DE	EE	EF
	38	71		25
Expect.	33·5	67		33·5

---

(9)

$EFH \times DE$

(9.5)

	DE	DF	EE	EF	EEH	DEH	DFH	EFH
	5	5	5	5	4	10	12	13
Expect.	7·3	7·3	7·3	7·3	7·3	7·3	7·3	7·3

TABLE I (*continued*).

(9.4)

DE × DE

(9.8)

DD	DE	EE
28	61	26

Expect. 28·7 57·5 28·7

(9.4)   (9.1)

DF · DD

(9.9)

DD	DF
8	13

Expect. 10·5 10·5

(9.4)

DF × DF

(9.11)

DD	DF	FF
25	39	14

Expect. 19·5 39 19·5

(9.4)   (9.3)

EE × FF

(9.12)

EF

4

Expect. 4

(9.3)   (9.1)

FF × DFH

(9.15)

DF	FF	DFH	FFH
18	17	19	11

Expect. 16·2 16·2 16·2 16·2

(9.3)

EF × EF

(9.16)

EE	EF	FF
7	21	8

Expect. 9 18 9

(9.3)

EE × EE

(9.17)

EE

2

Expect. 2

(9.5)

DFH × DFH

(9.18)

DD	DF	FF	DDH	DHDH	DFH	DHFH	FFH	FHFH
1	4	1	6		10		3	

Expect. 1·56 3·12 1·56 4·7 9·4 4·7

(9.4)

EE × EE

(9.21)

EE

5

Expect. 5

(9.4)

EF × EF

(9.22)

EE	EF	FF
9	43	15

Expect. 16·7 33·5 16·7

(9.3)   (9.5)

FF × EFH

(9.24)

EF	FF	EFH	FFH
9	8	3	10

Expect. 7·5 7·5 7·5 7·5

TABLE I (*continued*).

(9.5)
DEH × DEH
(9.25)

	DD	DE	EE	DDH	DHDH	DEH	DHEH	EEH	EHEH
	2	1	1	1		3		1	
Expect.	0·56	1	0·56	1·69		3·37		1·69	

(9.5) (9.1)
EEH × DDH
(9.26)

	DE	DEH	DHEH
	9	22	10
Expect.	10·25	20·5	10·25

(9.3) (9.1)
FF × EFH
(9.29)

	EF	FF	EFH	FFH
	10	16	24	20
Expect.	17·5	17·5	17·5	17·5

(9.3) (9.2)
FF × DEH
(9.27)

	DF	EF	DFH	EFH
	6	18	18	8
Expect.	12·5	12·5	12·5	12·5

(9.3) (9.8)
FF × DEH
(9.30)

	DF	EF	DFH	EFH
	9	16	33	6
Expect.	16	16	16	16

(9.5) (9.1)
FF × DD
(9.28)

	DE	DF
	6	5
Expect.	5·5	5·5

(9.11) (9.18)
DD × FFH
(9.31)

	DF	DFH
	0	2
Expect.	1	1

(9.8) (9.47)
DE × DEH
(9.37)

	DD	DE	EE	DDH	DEH	EEH
	3	8	4	2	12	5
Expect.	1·25	8·5	1·25	4·25	8·5	1·25

TABLE I (*continued*).

(9.6)   (9.17)
FFH × EE
                    (9.44)

EF   EFH
13   17
Expect.   15   15

(9.26)
DEH × DEH
                    (9.47)

DD   DE   EE   DDH   DHDH   DEH   DHEH   EEH   EHEH
1   5   4   3   4   4
Expect.   1·3   2·6   1·3   3·9   7·8   3·9

(9.18)   (9.29)
DFH × FF
                    (9.49)

DF   FF   DFH   FFH
7   4   3   7
Expect.   5·25   5·25   5·25   5·25

(9.11) (9.31)
DF × DFH
                    (9.51)

DD   DF   FF   DDH   DFH   FFH
0   3   1   1   1   2
Expect.   1   2   1   1   2   1

(9.26)   (9.24)
DEH × FFH
                    (9.52)

DF   EF   DFH   DHFH   EFH   EHFH
2   0   2   5
Expect.   1·1   1·1   3·3   3·3
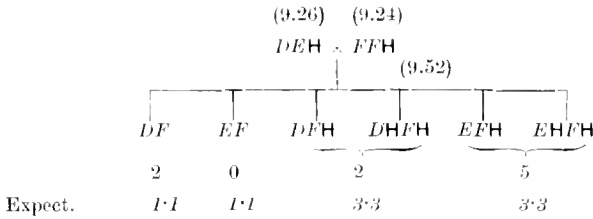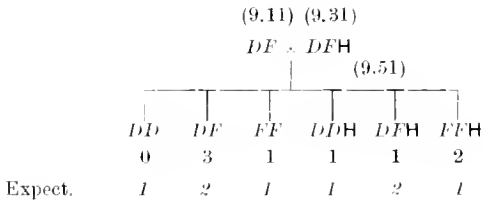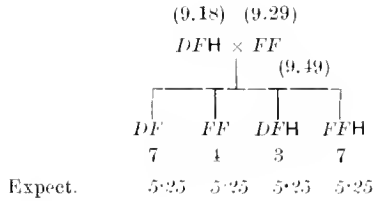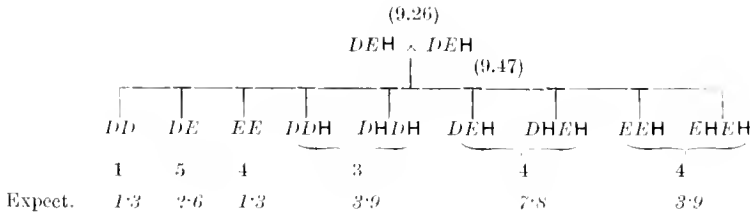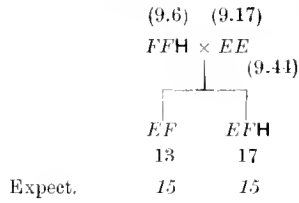
TABLE I (*continued*).

(9.6) (9.15)
EFH × FF
│ (9.53)

EF	FF	EFH	FFH
0	4	2	3
Expect.	1·75	1·75	1·75	1·75

Nature
+DF × MM
│ (13)

DM	FM
47	45
Expect.	46	46

(13)
DM × FM
│ (13.1)

DF	DM	FM	MM
9	8	10	15
Expect.	10·5	10·5	10·5	10·5

(13)
DF × DM
│ (13.2)

DD	DM	DF	FM
16	8	8	
Expect.	16	8	8	

(3)   (5)
FM   FM
│ (17)

FF	FM	MM
32		11
Expect.	32·25		10·75

(3)   (13)
CM × FM
│ (18)

CF	CM	FM	MM
11	17	13	8
Expect.	12·2	12·2	12·2	12·2

Nature
MMH × MMH
│ (19)

MM	MMH	MHMH
7	11	
Expect.	4·5	13·5	

(19)
MMH × MMH
│ (19.1)

MM	MMH	MHMH
2	7	
Expect.	2·25	6·75	

(3.6)   (5.2)
CM × DM
│ (22)

CD	CM	DM	MM
18	18	18	15
Expect.	17·2	17·2	17·2	17·2

(3.6)   (9.1)
CM × EFH
│ (24)

CE	CF	EM	FM	CEH	CFH	EMH	FMH
9	5	5	10	11	7	7	6
Expect.	7·5	7·5	7·5	7·5	7·5	7·5	7·5	7·5

TABLE I (*continued*).

(9.1)   (5.3)
DFH × DF
    (25)

	DD	DF	FF	DDH	DFH	FFH
	1	1	1	1	5	3
Expect.	1·5	3	1·5	1·5	3	1·5

(3.6)   (9)
CC × EFH
    (27)

	CE	CF	CEH	CFH
	7	9	0	10
Expect.	6·5	6·5	6·5	6·5

(17)   (9.1)
FF × DD
 | (28)
DF
52

Expect.	52

(3.6)   (9.2)
CC × EEH
    (29)

	CE	CEH
	23	26
Expect.	24·5	24·5

(29)
CEH × CEH
    (29.1)

	CC	CE	EE	CCH	CHCH	CEH	CHEH	EEH	EHEH
	5	6	3	3		11		4	
Expect.	2	4	2	6		12		6	

(3.8)   (9.26)
CC × DHEH
    (38)

	CDH	CEH
	23	20
Expect.	21·5	21·5

(9.18)   (29)
FFH × CEH
    (39)

	CF	EF	CFH	CHFH	EFH	EHFH
	0	1	3		3	
Expect.	0·87	0·87	2·6		2·6	

TABLE I (*continued*).

(19)   (9.17)

MMH × *EE*
| (40)

EM   *EMH*
1   5

Expect.   3   3

(22)   (28)

CD × *DF*
| (44)

CD   *CF*   *DD*   *DF*
5   5   4   5

Expect.   1·75   1·75   1·75   1·75

(3.8)   (5.6)

CC × *MM*
| (11)
CM
29

Expect.   29

(44)

CD × *CD*
| (44.3)

CC   *CD*   *DD*
8   16   9

Expect.   8·25   16·5   8·25

(3.8)   (38)

CC × *CDH*
| (42)

CC   *CD*   *CCH*   *CDH*
4   2   4   4

Expect.   3·5   3·5   3·5   3·5

(3.8)   (9.47)

CC × *EHEH*
| (43)
CEH
90

Expect.   90

(9.49)   (29.1)

DFH × *CC*
| (56)

CD   *CF*   *CDH*   *CFH*
5   5   3   5

Expect.   1·5   1·5   1·5   1·5

Table II.   Combination of matings (3.5), (3.7), (17), and (5.5).

FM × *FM*
|

FF   *FM*   *MM*

240   106

Expect.   259·5   86·5

Table III.   Combination of matings (3.6) and (3.4).

CM × *CM*
|

CC   *CM*   *MM*

149   36

Expect.   138·75   46·25

A combination of the results given in Tables II and III gives for the first two classes 389 and for the third class, composed entirely of MM, 142 : the expectations being 398·25 and 132·75 respectively.

Table IV. Combination of the results of the matings giving a "3 : 1" ratio, viz. (3.4), (3.5), (3.6), (3.7), (5.2), (5.5), and (17). The apparent dominance and recessiveness of certain of these patterns will be mentioned in another connection.

I	II	III
	552	169
Expect.	540·75	180·25

Table V. Combination of matings giving a "1 : 2 : 1" ratio directly.

DD	DF	FF	
2	5	3	(5.7)
25	39	14	(9.11)
DD	DE	DF	
28	61	26	(9.8)
EE	EF	FF	
35	81	42	(9.3)
7	21	8	(9.16)
9	43	15	(9.22)
CC	CD	DD	
8	16	9	(44.3)

Totals	114	266	117
Expect.	124·25	248·5	124·25

In Tables I, II, III, and IV, the results have been tabulated as though C, D, and F were each "dominant" or epistatic, and M "recessive" or hypostatic. This was due, in part, to the fact that when these records were made the writer lacked experience and familiarity with the material, which, because of the great similarity in the case of CC and CM, of the homozygous and heterozygous forms, made it seem desirable to record the two classes together; and in part due to the fact that CC and CM are not readily distinguishable until about a week after the last moult, and even then there are a few individuals which cannot readily be distinguished. In the case of FF and FM, the pattern FF is so small that it would be difficult to distinguish between FF and FM, even though the hybrids were exactly intermediate between them. The case is rare, if it ever occurs, where some detectable difference does not occur between a homozygous form and the hybrid.

The behaviour of H. An examination of Table I shows that the female EEH in (9) gave two sorts of gametes, viz. E and EH: that the female DEH in (9.1) gave four sorts of gametes, D, E, DH, EH, and that all the

possible combinations with the two gametes of the male give eight classes of young. However, (9.2), DEH × DE, produced six classes of young, which meets the expectation, because when all the possible combinations have been made the classes DE and DEH will each have occurred twice. Homozygotes, or heterozygotes containing H, are better analyzed by mating with homozygous individuals as has been done in (9.15) and (9.27), FF × DFH, and a number of others.

The mating (9.18), DFH × DFH, is of interest because among the nine possible combinations of gametes we should obtain three combinations in which H occurs twice, viz. DHDH, DHFH, and FHFH ; i.e. these individuals should have a double dose of H. In the sense that when inbred, all of the gametes will receive the factor (or factors) for H, they will be homozygous for it. It is interesting to note in this connection that a number of individuals appear in such matings as this which have the reddish pigmentation in an appreciably more intense condition than other individuals containing H in the same culture or other cultures. That such individuals may have a double dose of H is shown by matings (38), CC × DHEH, and (43), CC × EHEH ; (38) producing CDH 23 and CEH 20 ; and (43) producing CEH 90.

Homozygotic individuals with a single dose of H, as regards the characters in question, always give two sorts of gametes, while heterozygotic individuals with a single dose of H always give four sorts of gametes. Homozygotic individuals with a double dose of H always give one sort of gametes, while heterozygotic individuals with a double dose of H always give two sorts of gametes.

It is seen that while the zygotic constitution of, e.g., DFH is either D : FH or F : DH, its gametic formula is always D : F : DH : FH.

All the possible combinations of such a mating as has just been described may be obtained in the usual manner from the " 16-square " as for an organism differing in two "independent" characters, or they may be derived in the following manner and the ratios be made somewhat more apparent:

$$D : F : DH : FH \times D : F : DH : FH$$

DD	DF	FF	DDH	DHDH	DFH	DHFH	FFH	FHFH
	DF		DDH		DFH	DHFH	FFH	
					DFH			
					DFH			

1	2	1	2	1	4	2	2	1
1	3		3		6		3	
1	3		3		9		

PLATE III

CM

CF

CE

MM

FF

EE

DD

CC

EF*H*

EE*H*

DF*H*

DE*H*

DD*H*

CF*H*

EF

DF

DE
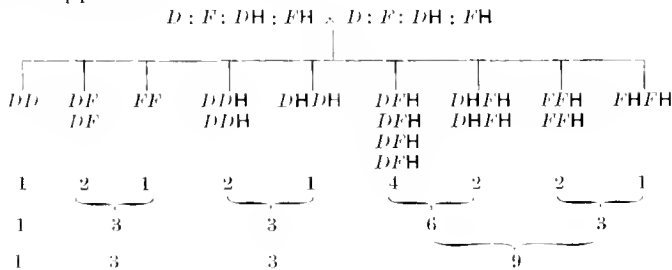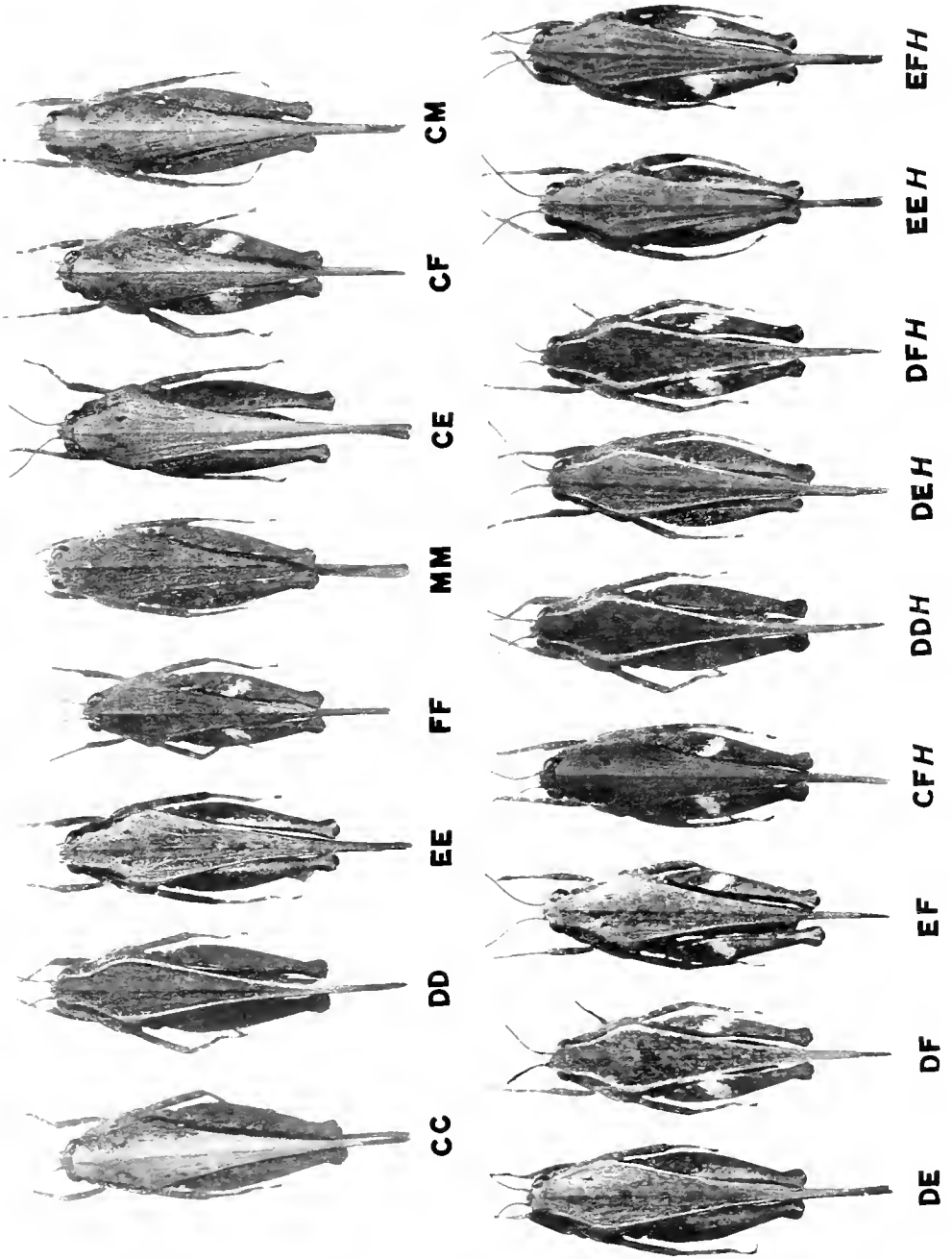
This ratio of $4:2:2:2:2:1:1:1:1$, or, when the single and double doses of **H** are counted in the same class as was done for (9.18) and others, of $6:3:3:2:1:1$, is actually a $9:3:3:1$ ratio; or better, as has been emphasized by Nabours ('17), the $9:3:3:1$ ratio is actually a $4:2:2:2:2:1:1:1:1$ ratio.

DISCUSSION.

The chief purpose of this paper has been to record the inheritance behaviour of several colour patterns in *Tettigidea* which constitute a system of " multiple allelomorphs "; and of another pigmental characteristic (**H**) "*which exists in connection with and in addition to the other patterns.*"

The theory of multiple allelomorphism as set forth by the Morgan school, postulates that the determiners for all the characters of a given system of multiple allelomorphs shall have identical loci in a pair of homologous chromosomes. There may be as many sets or groups of characters as there are chromosomes in the matured gametes. It is stated that the same results may be explained equally well by assuming that there is complete linkage, i.e. that the determiners lie so close together in the chromosomes that crossing over never takes place, and that the end results would be the same in either case.

If one wishes to interpret these results in the light of this hypothesis, it may be assumed that the " determiners " for the characters C, D, E, F, and M have identical loci in a single pair of homologous chromosomes. In the case of **H** it need only be assumed that its determiner is borne by some other chromosome. **H** is not sex linked and is apparently, as stated by Nabours for his $\ominus$ in *Paratettix*, allelomorphic only to its absence.

This report is based upon 3,219 recorded individuals.

EXPLANATION OF PLATE III.

Five " forms " of *Tettigidea parvipennis* are represented in the first five figures on the Plate, viz. CC, DD, EE, FF, and MM. The six figures, CE, CF, CM, DE, DF, EF, represent hybrids between certain of the preceding forms. The remaining six figures show the result of the addition of the factor **H**. For fuller explanation see text, p. 57.

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CONTENTS

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FERTILITY IN *CICHORIUM INTYBUS*: SELF-COMPATIBILITY AND SELF-INCOMPATIBILITY AMONG THE OFFSPRING OF SELF-FERTILE LINES OF DESCENT.

By A. B. STOUT.

(With Plates IV—VI.)

CONTENTS.

INTRODUCTION.

THE results presented in this paper pertain to the variation, the heredity and the results of selection in respect to seed production in progenies of self-fertile plants of chicory, such self-fertile plants having first appeared sporadically among the descendants of self-sterile parents.

It has already been noted (Stout, 1916, 1917) that the type of sterility involved in my studies with chicory can best be ascribed to a *physiological incompatibility* operating between sex organs that are

fully formed, anatomically perfect, potentially functional, and of simultaneous development. It is quite evident that the incompatibilities are not due to *anatomical incompatibility* (structural differences such as hercogamy) or to impotence (degeneration of sex organs or sex cells). *Embryo abortion* which results from a real gametic incompatibility that develops after fertilization may also be concerned in the decreased seed production and in the poor germinations observed. Such a type of abortion is to be considered as quite distinct from that which more purely involves nutrition.

As I have already shown (Stout, 1916, 1917) this sort of sexual incompatibility is very general in chicory. It is in evidence in the many instances of cross-sterility and in a very pronounced self-sterility both in wild and in cultivated varieties.

Self-fertile plants arise, however, among the progeny of self-sterile parents, and in some of my cultures of the variety "Red-leaved Treviso," such self-fertile plants first appeared after three generations of self-sterile parentage. Thus far, in my cultures, the self-fertile plants arising spontaneously have been relatively few in number, and they have exhibited various grades of self-compatibility as judged by seed production. In the lines of descent grown as offspring of the self-fertile plants, as already reported, the inheritance of self-compatibility was very irregular; self-incompatibility appeared in all progenies, even when these were offspring of two generations of highly self-fertile plants. I have now to report the results of another generation obtained in 1916.

As is pointed out in my previous papers, the behaviour of known progenies with reference to the development of compatibilities and incompatibilities is of special interest in its bearing on fundamental problems of sexuality and fertilization, especially as they are seen in the bisexual higher plants.

MATERIAL, METHODS, AND TERMINOLOGY.

All of the plants for which data are here presented descended from three self-sterile parents. Two of these parents were of the common unimproved cultivated chicory (Barbe de Capucin) designated in the records as *E3* and *E22*; these were crossed with a wild white-flowered plant designated as *A*. There are, therefore, two main families which may be referred to according to parentage as the *A × E3* family and the *A × E22* family (including reciprocals).

The group of sister plants grown from the same plant or from the same cross in any one season is called a *series*, and in these reports such a group bears the number of the plant that was the immediate parent, together with the numbers in serial order designating the previous parentage. Thus, for example, series $(A \times E22)$ is a generation of plants derived by using pollen of plant $E22$ on pistils of plant A; series $(A \times E22)-4-$ is a group of sister plants grown from self-fertilized seed of the F_1 plant $(A \times E22)$ no. 4. Thus the series $(A \times E22)-4-3-11-$, for which data are given in Table II, has had three generations of self-fertile ancestry, of the different series and numbers as designated, which indicate the line of descent from the original cross between A and $E22$. Although somewhat cumbersome, this treatment presents a complete record of pedigree, from which the performance of individuals, of lines of descent as a whole, and of families may be ascertained. All the plants of a sub-family will be given the designation of the common ancestor, thus all the descendants of plant $(A \times E22)$ no. 4 may be considered as family $(A \times E22)-4-$, and all the descendants of plant $(A \times E22)$ no. 10 will be designated as family $(A \times E22)-10-$, both, however, being sub-families in the main family $(A \times E22)$ but descending from two different sister plants.

The data in detail for any parents, or for any series referred to, but which were grown previously to 1916, are given in a report already published (Stout, 1916).

RESULTS OF THE EXPERIMENTAL STUDIES.

1. *Performance of a family of Barbe de Capucin × wild white-flowered: the family $(E3 \times A)-4-$.*

In 1916 two series from two generations of self-fertile ancestry were grown in the family $(E3 \times A)-4-$. The results obtained from the self-pollinations of these 49 plants are compiled in Table 1. Of the 23 plants of the series first presented in this table, all but five were self-fertile with percentages of fertility ranging from 4 to 48, and with an average fertility for the self-fertile plants of 20 °/₀. The percentage of fertility, frequently referred to in this paper, is determined on the basis of the proportion of seeds produced by the flowers involved in the controlled pollinations. Of the other series, 16 plants were self-fertile, and 10 were self-sterile; the fertilities of the self-fertile plants ranged from 2 to 60 °/₀ with an average of 15 °/₀.

TABLE I.

Self-compatibility and incompatibility in two series of a family of Barbe de Capucin (E3) × wild white-flowered (A); from two generations of self-fertile ancestry.

Plant with pedigree	Flower colour	Total heads	With no seed	With seed	Seed per head	Fertility per cent.
					Record for heads pollinated	
(E3 × A)–4–4–	B	—	—	— —	—	0·43
No.　4	W	8	5	5	3, 5, 5	0·09
,,　8	B	10	10	0	—	—
,,　12	B	11	5	6	4, 4, 5, 5, 7, 11	0·18
,,　14	W	11	4	7	4, 4, 4, 11, 12, 14, 18	0·23
,,　16	B	9	9	0	—	—
,,　17	B	10	2	9	1, 3+B, 4, 7, 7, 7, 12, 15	0·30
,,　18	W	10	1	9	1, 2, 2, 5, 6, 7, 8, 9, 13	0·29
,,　19	W	6	0	6	2, 2, 5, 5, 5, 6	0·22
,,　20	B	11	11	0	— —	—
,,　21	B	11	3	8	4, 4, 5, 5, 8, 8, 9, 12	0·27
,,　22	W	7	2	5	3, 5, 6, 10, 11	0·28
,,　23	W	13	8	5	1, 1, 8, 9, 12	0·31
,,　26	B	11	11	0	—	—
,,　27	W	7	4	3	1, 2, 4	0·04
,,　28	B	10	10	0	—	—
,,　29	W	9	0	9	1, 2, 5, 5, 9, 12, 12, 12, 16	0·48
,,　30	B	10	0	10	2, 3, 3, 4, 5, 6, 6, 7, 13, 15	0·32
,,　31	B	12	10	2	3, 4	0·03
,,　32	B	9	4	5	2, 3, 4, 5, 5	0·12
,,　34	W	10	8	2	2, 5	0·07
,,　35	B	10	4	6	1, 1, 2, 3, 4, 7	0·10
,,　37	W	10	2	8	2, 2, 2, 4, 5, 5, 6, 9	0·19
,,　38	W	8	5	3	1, 3, 8	0·09
(E3 × A)–4– Ser. II. 20	B	—	—	—	—	0·50
No.　1	B	9	9	0	—	—
,,　2	B	12	12	0	—	—
,,　5	B	7	3	4	3, 3, 5, 5	0·12
,,　6	B	10	2	8	1, 1, 2, 3, 3, 3, 3, 5	0·12
,,　7	B	10	10	0	-	—
,,　8	B	10	5	5	1, 2, 4, 7, 17	0·17
,,　10	B	12	4	8	3, 3, 3, 3, 4, 5, 6, 7	0·15
,,　11	B	6	0	6	5, 11, 11, 12, 15, 15	0·60
,,　14	B	9	9	0	....	—
,,　16	B	10	5	5	1, 3, 5, 6, 6	0·21
,,　17	B	12	10	2	2, 3	0·02
,,　18	B	9	5	4	1, 1, 3, 4	0·05
,,　19	B	7	3	4	2, 2, 5, 6	0·11
,,　21	B	9	6	3	1, 1, 2	0·03
,,　22	B	11	11	0	—	—
,,　23	B	9	0	9	4, 4, 5, 5, 7, 8, 10, 10, 14	0·42
,,　24	B	9	3	6	2, 2, 3, 3, 5, 17	0·19
,,　25	B	8	8	0	-	—
,,　26	B	10	7	3	1, 2, 4	0·03
,,　27	B	11	10	1	12	0·06
,,　29	B	10	10	0	·	—
,,　32	B	10	10	0	—	—
,,　33	B	11	9	2	1, 7	0·04
,,　34	B	15	15	0	—	—
,,　35	B	9	9	0	—	—
,,　36	B	9	4	5	1, 1, 2, 2, 10	0·10

A glance over this table shows that a rather large proportion of plants are self-fertile. Especially is this true of series $(E3 \times A)$-4-4-, which in this respect is perhaps the most highly self-fertile of the various series thus far grown.

The more complete summary of the record for the family $(E3 \times A)$ is presented in Table VII. As there indicated, the family is not a large one. From the cross between the two self-sterile plants $E3$ and A, 21 plants were grown in the F_1, of which four were self-fertile with fertilities of 2, 4, 13, and 48. Progeny were grown only from one plant having the highest fertility. Of the 18 grown, 10 were self-fertile, and the fertilities determined for 9 of these ranged from 3 to 50 %, with an average at 26. Selection for parents for the next generation was confined to the two plants most highly self-fertile. Thus the immediate parents of the two series were 43 and 50 % self-fertile respectively, and the common P_1 parent was 48 % self-fertile. The selection has here been continually of plants with highest fertility. The regression to a condition of complete self-sterility and to feeble self-sterility is most noticeable. The number of plants is perhaps not sufficient to determine the mathematical expression for such regression with accuracy, but the records indicate an irregular and incomplete inheritance of self-compatibility.

However, the proportion of self-fertile plants is higher in the series grown from self-fertile parents than that of the self-fertile plants appearing sporadically among the progeny of the original self-sterile parents. The average fertility for each of the two series from two generations of self-fertile ancestry is lower than that of the preceding generation $(E3 \times A)$-4-. (A series was grown in each of two different years from seed of the plant $(E3 \times A)$ no. 4; data for both are here compiled as for a single series.) The range of self-fertility has, however, been extended in the case of one plant to 60 %. This plant, however, is of the series which, as a whole, is of lowest average fertility. The summary for the progeny of the plant $(E3 \times A)$-4-, as a whole, shows that 65 % of all the plants were self-fertile in some degree, with a distribution on the basis of self-fertility that is decidedly irregular and skew, and with an average fertility of 0·197. It has already been suggested by the writer that there is evidence that complete self-sterility may involve different intensities of incompatibilities. If there were some means of determining comparative values for these, the distribution for a family and for the different series might be found to be more in agreement with a normally fluctuating variability. As

it is, the comparison may be based on the proportion of self-fertile plants and their fertilities, as has been done above.

2.   *Performance of families descended from crosses between the wild white-flowered plant A and plant E22 of Barbe de Capucin.*

By far the greater number of plants of the cultures were derived from crosses between the two plants *A* and *E22*.   Among the 75 F_1 progeny of the reciprocal crosses between these two self-sterile plants, there were 8 plants self-fertile to some degree.   Progenies of three of these plants constituting three families, $(A \times E22)-4-$, $(A \times E22)-9-$, and $(E22 \times A)-10-$, have now been grown for three further generations.   With the one exception of series $(E22 \times A)-10-$ *Ser. II. 10-* all the different series of these families grown in 1916 had three generations of self-fertile parentage.   The data for these various series will now be presented together with a discussion of the results obtained for these (sub) families.

(*a*)   *The family* $(A \times E22)-4-$.

Data for the three series of this family grown in 1916 are presented in Table II, and a summary of all the series of the family is given in Table VII.

Of the series $(A \times E22)-4-3-6-$ only two plants were grown.   These were both self-sterile.   The fertilities of the parental line of descent were respectively 4, **13**, and 5.

The series $(A \times E22)-4-3-11-$ comprised 29 plants, of which 20 were self-sterile and 9 self-fertile.   Not only was the proportion of self-fertile plants low, but the fertilities of such plants were low, ranging from 1 to 26 $°/_o$ with the average at 8 $°/_o$.   For this series the immediate parent was of rather high fertility (32 $°/_o$), but the ancestry previous to this was of 4 and 13 $°/_o$.   The feeble self-fertility of the series as a whole and of the various individuals comprising it is most noticeable, especially in comparison with the behaviour of such a series as $(E3 \times A)-4-4-$ reported in Table I.

Of the 16 plants of series $(A \times E22)-4-6-3-$, eight were self-fertile with range from 2 to 62 $°/_o$, and with an average of 25 $°/_o$.   The relative number of self-fertile plants, the range of fertilities, and the average fertility are all higher for this series than for $(A \times E22)-4-3-11-$.

A consideration of the family history shows that there has been no parent in this family with a fertility higher than 32 $/_o$.   The fertility

TABLE II.

Record for three series descended from plant (A × E3), No. 4. All have three generations of self-fertile parentage.

Plant with pedigree	Flower colour	Record for heads pollinated				Fertility per cent
		Total heads	With no seed	With seed	Seed per head	
(A × E22)–4–3–6–	W	—	—	—	—	0·05
No. 1	W	4	4	0	—	—
,, 2	W	11	11	0	—	—
(A × E22)–4–3–11–	W		—	—	—	0·37
No. 1	W	2	2	1	6	0·16
,, 3	W	14	12	2	2, 3	0·02
,, 5	W	7	7	0	—	—
,, 6	W	6	6	0	—	—
,, 7	W	10	7	3	1, 3, 4	0·04
,, 8	W	8	8	0	—	—
,, 9	W	5	1	4	3, 5, 8, 10	0·26
,, 10	W	7	2	5	1, 1, 3, 3, 10	0·14
,, 13	W	6	6	0	—	—
,, 14	W	6	6	0	—	—
,, 15	W	8	8	0	—	—
,, 16	W	6	6	0	—	—
,, 17	W	8	8	0	—	—
,, 18	W	12	10	2	1, 1	0·01
,, 19	W	3	3	0	—	—
,, 20	W	10	10	0	—	—
,, 21	W	5	3	2	4, 6	0·10
,, 22	W	4	4	0	—	—
,, 24	W	6	6	0	—	—
,, 25	W	10	9	1	2	0·01
,, 27	W	8	8	0	—	—
,, 28	W	6	6	0	—	—
,, 29	W	8	8	0	—	—
,, 31	W	7	7	0	—	—
,, 33	W	12	12	0	—	—
,, 34	W	7	7	0	—	—
,, 37	W	3	3	0	—	—
,, 38	W	6	6	0	—	—
,, 41	W	9	8	1	1	0·01
(A × E22)–4–6–3–	W	—	—	—	—	0·31
No. 1	W	3	0	3	5, 6, 12	0·41
,, 2	W	10	10	0	—	—
,, 3	W	4	4	0	—	—
,, 9	W	2	2	0	—	—
,, 11	W	8	5	3	1, 1, 1	0·02
,, 12	W	3	0	3	3, 8, 9	0·41
,, 13	W	5	3	2	5, 8	0·16
,, 14	W	2	2	0	—	—
,, 15	W	7	7	0	—	—
,, 16	W	6	0	6	1, 1, 2, 5, 8. 8	0·21
,, 17	W	9	6	3	2, 4, 5	0·07
,, 18	W	2	0	2	8, 14	0·62
,, 20	W	2	2	0	—	—
,, 21	W	6	4	2	2, 11	0·11
,, 22	W	3	3	0	—	—
,, 23	W	10	10	0	—	—

of the first self-fertile parent ($A \times E22$) *no. 4* was very low, being only 4°/₀. Although 7 of the 10 plants grown from its seed were self-fertile, the highest individual fertility was 23°/₀, and the average was 14°/₀. The four plants selected from this series as parents had fertilities of 12, 13, 16, and 22. The numbers of plants grown from these were too small for an adequate judgment of the various series, but from the two most highly self-fertile plants were derived the series ($A \times E22$)–4–3–11– and ($A \times E22$)–4–6–3– reported above. The first self-fertile parent was very feebly self-fertile, but with one exception parents for subsequent series were selected for highest individual fertility.

The behaviour of the various series indicates an irregular inheritance of the characteristics of self-compatibility and the frequent and decided regression to self-sterility. The range of the degree of self-fertility was rather decidedly extended in the series ($A \times E22$)–4–6–3–, and the average fertility was also high. This series was decidedly more fertile in every comparison than the series ($A \times E22$)–4–3–11–: the ancestral fertilities were only slightly higher, being 4, 22, and 31 as compared with 4, 13, and 32.

Considered as a whole, the family ($A \times E22$)–4– had 40°/₀ of the total plants self-fertile. The distribution on the basis of fertilities of the self-fertile plants is irregular and skew, the percentage of self-fertility observed in an individual is extended to 62, and the average percentage for all self-fertile plants is 16·5.

(b) The family ($A \times E22$)–9–.

As indicated in Table VII, the third filial generation in this family consisted of six series, which were derived from as many different plants of the second generation which had in turn descended from two plants of the first generation. Thus the series are of the two main sub-families ($A \times E22$)–9–4– and ($A \times E22$)–9–5–.

The data for the series which descended from plant ($A \times E22$)–9– *no. 4* are given in Table III. Of the 10 plants in series ($A \times E22$)–9–4–4–, four were self-fertile; of 13 in series ($A \times E22$)–9–4–10–, seven were self-fertile; and of the 4 plants in series ($A \times E22$)–9–4–11–, two were self-fertile. The fertilities of the immediate parentage were quite alike, the complete record of ancestry being 23, 43, and 20 for the first mentioned, 23, 43, and 17 for the second, and 23, 43 and 20 for the last named. As shown in the tables, the proportional number of self-fertile plants varies, as do the individual fertilities. The number of plants is perhaps insufficient for adequate comparisons of differences. It is to be

noted, however, that self-sterile plants appear in large proportions, and that there are various degrees of self-fertility in each series.

TABLE III.

Record for three series descended from plant (A × E22)–9–, No. 4. All from three generations of self-fertile parentage.

Plant with pedigree		Flower colour	Record for heads pollinated				Fertility per cent.
			Total heads	With no seed	With seed	Seed per head	
(A · E22)–9–4–4–		B	—	—	—	—	0·20
No.	1	B	11	5	6	1, 2, 3, 4, 5, 7	0·12
,,	2	W	11	11	0	—	—
,,	3	W	10	10	0	—	—
,,	6	W	10	10	0	—	—
,,	7	W	5	0	5	1, 2, 3, 7, 8	0·28
,,	8	B	7	0	7	1, 1, 2, 4, 4, 5, 5	0·18
,,	11	W	10	10	0	—	—
,,	12	B	7	6	1	6	0·06
,,	13	B	12	12	0	—	—
,,	15	B	12	12	0	—	—
(A · E22)–9–4–10–		B *	—	—	—	—	0·17
No.	1	B	10	10	0	—	—
,,	2	B	2	0	2	1, 5	0·20
,,	3	B	11	11	0	—	— —
,,	4	B	14	14	0	—	— —
,,	5	B	12	11	1	3	0·02
,,	6	B	9	5	4	1, 2, 4, 4	0·08
,,	8	B	10	9	1	2	0·01
,,	10	B	8	0	8	2, 4, 6, 6, 9, 10, 12, 12	0·51
,,	12	B	3	3	0	—	—
,,	13	B	10	10	0	—	—
,,	14	B	10	6	4	1, 3, 4, 8	0·10
,,	15	B	10	3	7	1, 3, 4, 4, 5, 6, 14	0·25
,,	19	B	11	11	0	—	—
(A · E22)–9–4–11–		B	—	—	—	—	0·20
No.	1	B	9	7	2	1, 1	0·01
,,	2	W	8	6	2	1, 3	0·03
,,	3	W	10	10	0	—	—
,,	4	W	11	11	0	—	—

Considering the three series together, 13 plants were self-fertile, and 14 were self-sterile. In only one plant was the fertility higher than 28 °/₀, and in this case the percentage was 51. The average for

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* In a former publication (Stout, 1916, Table 5) this plant was by error reported as white-flowered.

TABLE IV.

Record for three series descended from plant (A × E22)–9––, No. 5.
All from three generations of self-fertile parentage.

Plant with pedigree		Flower colour	Total heads	With no seed	With seed	seed per head	Fertility per cent
(A × E22)–9–5–1–		W	—	—	—	—	0·07
No.	1	W	12	10	2	1, 2	0·02
,,	2	W	12	12	0	—	—
,,	3	W	10	10	0	—	—
,,	4	W	12	12	0	—	—
(A × E22)–9–5–6–		W	—	—	—	—	0·46
No.	2	W	12	12	0	—	—
,,	3	W	7	7	0	—	—
,,	4	W	11	11	0	—	—
,,	5	W	10	10	0	—	—
,,	6	W	11	10	1	2	0·01
,,	7	W	8	3	5	2, 4, 7, 11, 14	0·29
,,	8	W	9	9	0	—	—
,,	9	W	10	10	0	—	—
,,	10	W	12	12	0	—	—
,,	11	W	11	11	0	—	—
,,	12	W	11	9	2	3, 5	0·05
,,	13	W	11	4	7	1, 2, 3, 4, 7, 10, 10	0·21
,,	14	W	6	6	0	—	—
,,	15	W	11	11	0	—	—
,,	16	W	10	10	0	—	—
,,	17	W	11	5	6	2+B, 3, 6, 8, 8, 11	0·23
,,	19	W	9	6	3	1, 6, 11	0·15
,,	20	W	10	8	2	3, 7	0·06
,,	21	W	9	0	9	B, B, 1, 3, 4, 5, 9, 12, 13	0·42
,,	22	W	15	9	6	1, 2, I, 4, 4, 7	0·09
,,	23	W	10	7	3	2, 10, 18	0·20
,,	24	W	11	11	0	—	—
,,	25	W	11	11	0	—	—
,,	26	W	11	11	0	—	—
,,	27	W	10	10	0	—	—
,,	28	W	13	13	0	—	—
,,	29	W	11	9	2	3, 5	0·05
,,	30	W	13	13	0	—	—
,,	31	W	6	0	6	4, 10, 13, 14, 14, 15	0·77

TABLE IV—(continued).

Plant with pedigree		Flower colour	Total heads	With no seed	With seed	Record for heads pollinated Seed per head	Fertility per cent.
$(A \times E22)-9-5-12-$		W	—	—	—	—	0·70
No.	1	W	6	0	6	$5 + B$, 5, 7, 12, 13, 18	0·65
,,	2	W	11	7	4	1, 5, 5, 6	0·09
,,	3	W	12	0	12	7, 9, 9, 10, 10, 10, 11, 12, 13, 13, 14, 15	0·66
,,	4	W	13	11	2	1, 5	0·03
,,	5	W	13	13	0	—	—
,,	6	W	12	12	0	—	—
,,	7	W	10	10	0	—	—
,,	8	W	10	10	0	—	—
,,	9	W	11	5	6	5, 8, 10, 12, 14, 15	0·36
..	10	W	9	7	2	2, 4	0·04
,,	11	W	13	1	12	1, 4, 5, 5, 6, 6, 7, 8, 8, 9, 11, 12	0·38
,,	12	W	12	6	6	1, 1, 1, 2, 2, 3	0·10
,,	13	W	9	4	5	2, 2, 4, 5, 8	0·13
,,	14	W	10	0	10	2, 5, 7, 10, 10, 11, 11, 11, 14, 15	0·56
,,	15	W	10	0	10	2, 2, 2, 7, 8, 9, 10, 12, 13, 14	0·50
,,	16	W	11	11	0	—	—
,,	17	W	9	3	6	6, 6, 6, 8, 10, 15	0·34
,,	18	W	10	10	0	—	—
,,	19	W	14	0	14	1, 2, 2, 2, 3, 3, 3, 4, 5, 5, 6, 6, 6, 7	0·25
,,	20	W	9	8	1	2	0·01
,,	21	W	10	10	0	—	—
,,	22	W	13	8	5	1, 1, 2, 3, 5	0·06
,,	23	W	10	10	0	—	—
,,	24	W	10	10	0	—	—
,,	26	W	10	4	6	2, 2, 2, 3, 5, 6	0·12
,,	27	W	12	12	0	—	—
,,	29	W	13	13	0	—	—
,,	31	W	14	14	0	—	—
,,	32	W	12	12	0	—	—
,,	33	W	11	0	11	2, 3, 8, 9, 10, 10, 10, 12, 12, 13, 15	0·54
,,	34	W	12	12	0	—	—
,,	35	W	15	15	0	—	—
,,	37	W	11	11	0	—	—
,,	38	W	12	12	0	—	—

all self-fertile plants was 14 %. This sub-family therefore is one of rather low self-fertility. The parents have all been somewhat above the average of self-fertility, and that of the second ancestral generation was much higher than the average.

Data for the three series of the third filial generation derived from the plant $(A \times E22)$–9– *no.* 5 are given in Table IV. The immediate parent of one series was selected for low self-fertility; the parents of the other two were selected for high self-fertility, one in fact having the highest percentage of any plant thus far utilized in the cultures as a seed parent.

Of series $(A \times E22)$–9–5–1–, only four plants were grown, of which one was very feebly self-fertile.

Twenty-nine plants were grown and tested in series $(A \times E22)$–9–5–6–. Seventeen were self-sterile; twelve were self-fertile. As further shown in Table IV, the individual fertilities were below 30 %, except for two plants. One of these was 42 % self-fertile, and the other gave the percentage of 77, which is the highest thus far realized in any of the cultures. The line of parentage has been one of rather high fertility, being 23, 33, and 46, and the series to which the parents belonged have given high values for average fertility (38 and 29). Except for the one highly self-fertile plant regression has been very decided in this series.

The series $(A \times E22)$–9–5–12– is of special interest, for the immediate parent was one of 70 % self-fertility, the ancestral record being 23, 33, and 70. The series is also the largest of any thus far grown in these families. Of the 34 plants, exactly half were self-fertile. The fertilities range to 66 %, and are somewhat more evenly distributed than is usual. The average of the self-fertilities is 28 %. A comparison of the data for all the various series (Table VII) shows that, on the whole, this series is one of high fertility. However, half of the plants were self-sterile, a large number of the self-fertile plants were feebly self-fertile, none of the self-fertile plants were more self-fertile than the immediate parent, and the average is below that for any one of the line of self-fertile parentage. Still the fertilities of the two series as a whole are decidedly greater than that of the three series (Tables III and VII) derived from $(A \times E22)$–9– *no.* 4.

Considered as a whole, this family has been grown from parents selected for high self-fertility. With the exception of one series of four plants, no series had any parent of less than 17 % self-fertility. The value for the first parent in line of descent was 23; the values of the two parents of the next generation were 43 and 33; and the values for the

parents of the next generation ranged from 7 to 70. Self-sterile plants appeared in every series, and after three generations of ancestry of highest self-fertilities the proportional number of such plants was high. Of the total of 125 plants, 61 were self-fertile. The distribution of individual self-fertilities is decidedly skew. The average fertilities of self-fertile plants is 0·223.

(c) *The family ($E22 \times A$)–10–.*

In 1916, seven series were grown in this family. One of these was of the second generation in descent. This series consisted of 15 plants, all but one of which were self-sterile. The fertility of the one self-fertile plant was one of feeble self-fertility. Self-sterility was almost complete, although the plants had two generations of self-fertile parents with fertilities of 51 and 13.

TABLE V.

Record of a series having two generations of self-fertile ancestry.

Plant with pedigree	Flower colour	Record for heads pollinated				
		Total heads	With no seed	With seed	Seed per head	Fertility per cent.
($E22 \times A$)–10– Ser. 11. 10–	W	—	—	—	—	0·13
No. 1	W	11	11	0	—	—
,, 3	W	14	14	0	—	—
,, 4	W	10	10	0	—	—
,, 5	W	7	0	7	1, 1, 3, 3, 3, 8, 8	0·26
,, 6	W	10	10	0	—	—
,, 7	W	11	11	0	—	—
,, 8	W	10	10	0	—	—
,, 9	W	11	11	0	—	—
,, 10	W	12	12	0	—	—
,, 11	W	10	10	0	—	—
,, 12	W	12	12	0	—	—
,, 13	W	7	7	0	—	—
,, 14	W	12	12	0	—	—
,, 16	W	10	10	0	—	—
,, 17	W	9	9	0	—	—

The data for the six series of this family, having three generations of self-fertile ancestry, are given in Table VI. As shown in the pedigrees, the first two series given have the same parentage for the first two generations. The immediate parents of these series were therefore two sister plants, which, it may be noted, were very nearly identical in all vegetative characters, but differed considerably in the degree of self-fertility. From the parent of 51 fertility, 16 plants were grown and tested for self-fertility. All but two were self-sterile, and those were

TABLE VI.

Self-compatibility and self-incompatibility in six series descended from plant (E22 × A), No. 10. All series from three generations of self-fertile parentage.

Plant with pedigree	Flower colour	Total heads	With no seed	With seed	Seed per head	Fertility per cent
(E22 × A)-10-8-14-	W	—	—	—	.	0·15
No. 1	W	9	9	0	—	
,, 2	W	11	11	0	-	..
,, 3	W	9	9	0	—	..
,, 4	W	10	10	0	—	.
,, 5	W	11	11	0	—	...
,, 6	W	11	11	0	--	
,, 7	W	12	12	0	—	
,, 8	W	10	10	0	—	.
,, 9	W	9	9	0	—	..
,, 10	W	12	12	0	—	
,, 11	W	11	11	0	--	
,, 12	W	10	10	0	---	
,, 13	W	11	11	0	—	—
,, 15	W	9	2	7	1, 1, 1, 1, 2, 3, 7	0·10
,, 16	W	8	4	4	1, 3, 3, 6	0·10
,, 18	W	12	12	0	—	—
(E22 × A)-10-8-15-	W	—	—	—	—	0·40
No. 1	W	14	14	0	—	—
,, 2	W	10	2	8	3, 6, 7, 8, 10, 12, 15, 17	0·13
,, 3	W	10	5	5	1, 2, 2, 2, 7	0·08
,, 4	W	10	0	10	1, 2, 3, 4, 5, 7, 7, 13, 15	0·36
,, 5	W	9	3	6	2, 2, 3, 3, 4, 5	0·12
,, 6	W	13	10	3	1, 3, 9	0·06
,, 7	W	12	12	0	-	—
,, 8	W	8	1	7	1 + B, 3, 3, 3, 4, 7, 9	0·21
,, 9	W	10	9		12	0·07
,, 10	W	11	11	0	- -	--
,, 11	W	3	1	2	6, 5	0·23
,, 12	W	7	1	6	1, 2, 3, 4, 5, 12	0·23
,, 13	W	5	1	4	3, 5, 9, 12	0·31
,, 14	W	11	8	3	5, 7, 9	0·11
,, 15	W	6	0	6	1, 3, 3, 4, 4, 7	0·22
,, 16	W	6	3	3	2, 2, 11	0·13
,, 17	W	9	1	8	1, 2, 2, 2, 2, 2, 3, 9	0·15
(E22 × A)-10-13-5-	B	.				0·29
No. 1	B	7	4	3	4, 5, 8	0·14
,, 3	B	5	5	0		—
,, 4	B	10	10	0	-	—

Record for heads pollinated

TABLE VI—*(continued)*.

Plant with pedigree		Flower colour	Total heads	With no seed	With seed	Record for heads pollinated	Fertility per cent.
						Seed per head	
No.	5	*W*	10	10	0	—	—
,,	6	*B*	10	7	3	4, 5, 6	0·09
,,	8	*W*	7	2	5	1, 7, 8, 8, 9	0·28
,,	11	*B*	8	8	0	—	—
,,	12	*W*	6	6	0	—	—
,,	13	*B*	10	10	0	—	—
,,	15	*W*	9	9	0	—	—
,,	16	*W*	10	10	0	—	—
,,	17	*B*	8	5	3	2, 5, 9	0·12
,,	19	*B*	8	8	0	—	—
,,	20	*B*	8	8	0	—	—
,,	21	*B*	6	6	0	—	—
,,	22	*W*	10	10	0	—	—
,,	23	*B*	10	10	0	—	—
,,	24	*B*	5	5	0	—	—
,,	25	*W*	7	5	2	1, 1	0·02
,,	26	*B*	10	10	0	—	—
,,	27	*B*	11	11	0	—	—
,,	30	*W*	9	8	2	1, 2	0·02
,,	31	*B*	8	3	5	1, 2, 2, 3, 4	0·09
,,	33	*B*	11	11	0	—	—
,,	35	*B*	5	5	0	—	—
,,	37	*B*	10	10	0	—	—
,,	38	*B*	10	10	0	—	—
,,	39	*W*	11	4	7	1, 2, 3, 3, 4, 5, 6	0·13
,,	40	*B*	9	9	0	—	—
,,	41	*B*	9	7	2	1, 5	0·04
,,	44	*B*	5	3	2	2, 2	0·05
(E22 × A)–10–13–12–		*W*	—	—	—	—	0·25
No.	1	*W*	10	10	0	—	—
,,	2	*W*	14	14	0	—	—
,,	3	*W*	12	12	0	—	—
,,	4	*W*	8	8	0	—	—
,,	5	*W*	10	10	0	—	—
,,	6	*W*	10	10	0	—	—
,,	7	*W*	10	8	2	1, 5	0·04
,,	8	*W*	4	2	2	4, 5	0·13
,,	10	*W*	11	11	0	—	—
,,	11	*W*	9	4	5	1, 2, 2, 3, 4	0·08
,,	12	*W*	10	10	0	—	—
,,	13	*W*	12	12	0	—	—
,,	14	*W*	11	6	5	2, 2, 5, 7, 8	0·13
,,	15	*W*	10	0	10	1, 1, 2, 3, 3, 6, 7, 9, 9, 13	0·33
,,	16	*W*	11	5	6	3, 3, 5, 5, 6, 7	0·15
,,	17	*W*	11	11	0	—	—

TABLE VI—(*continued*).

Plant with pedigree	Flower colour	Total heads	With no seed	With seed	Seed per head	Fertility per cent.
					Record for heads pollinated	
No. 18	W	11	0	11	3, 4, 5, 5, 5, 6, 6, 8, 9, 12, 13	0·42
,, 19	W	10	10	0	—	—
,, 20	W	12	12	0	—	—
,, 21	W	10	8	2	1, 5	0·03
,, 22	W	10	10	0	—	—
,, 23	W	12	12	0	—	—
,, 25	W	10	10	0	—	—
(E22 × A)–10–13–13–	B	—	—	—	—	0·56
No. 1	B	10	10	0	·	—
,, 2	B	7	3	4	5, 7, 9, 15	0·33
,, 4	B	9	5	4	7, 9, 10, 14	0·28
,, 5	W	10	10	0	—	—
,, 6	B	10	9	1	5	0·03
,, 7	B	7	0	7	3, 5, 8, 10, 12, 13, 14	0·58
,, 8	B	11	8	3	6, 7, 9	0·13
,, 9	W	10	10	0	—	—
,, 12	B	9	9	0	—	—
,, 15	W	12	12	0	—	—
,, 16	W	11	11	0	—	—
,, 17	B	11	11	0	—	—
,, 18	W	11	11	0	·	—
,, ·19	B	12	12	0	—	—
,, 20	B	13	13	0	—	—
,, 21	W	10	6	4	7, 8, 10, 12	0·25
,, 22	B	15	3	12	1, 1, 2, 2, 2, 3, 4, 5, 6, 7, 8, 11	0·22
,, 24	· B	7	3	4	1, 2, 3, 5	0·10
,, 26	B	9	4	5	4, 6, 7, 7, 9	0·24
,, 27	W	9	6	3	2, 2, 11	0·12
,, 28	W	11	11	0		—
,, 30	W	9	2	7	2, 2, 2, 4, 8, 9, 13	0·30
,, 31	B	11	3	8	1, 2, 2, 3, 5, 5, 11, 13	0·25
,, 32	B	9	4	5	1, 2, 7, 7, 9	0·18
,, 33	W	8	8	0		—
,, 34	B	9	9	0		·
,, 35	W	12	12	0		·
,, 36	B	10	9	1	2	0·01
(E22 × A)–10–14 6–	W	—			·	0·13
No. 1	W	12	12	0	—	—
,, 2	W	13	13	0	·	—
,, 4	W	15	15	0		—
,, 5	W	12	12	0	·	—
,, 6	W	10	10	0		—
,, 7	W	12	12	0	·	—
,, 8	W	6	2	4	1, 1, 3, 5	0·10

rather feebly self-fertile. Of the 17 plants derived from $(E22 \times A)$–10–8– *no. 15*, all but 3 were self-fertile. The difference in self-fertility seen in these series is most marked, especially in respect to the number of plants self-fertile. Results in such individual cases as these seem to indicate that selection may be effective in increasing or decreasing the development of self-compatibilities.

The next three series recorded in Table VI were all descended from the plant $(E22 \times A)$–10– *no. 13*, which had a fertility of $38\,^{\circ}/_{\circ}$. The immediate parents of the three series had fertilities of 29, 25, and 56. Of series $(E22 \times A)$–10–13–5–, in a total of 31 plants, 21 were self-sterile. The fertilities of the 10 self-fertile plants were low, giving an average of $10\,^{\circ}/_{\circ}$ and a range extending only to $28\,^{\circ}/_{\circ}$. Considering the record of the line of parentage, with percents of 51, 38, and 29, and the series in the line of descent, the fertility of this series is decidedly low.

The ancestral record for series $(E22 \times A)$–10–13–12– is quite identical to that for the series just noted. Of the 23 plants in the series, 15 were self-sterile. The fertilities of the self-fertile plants ranged to $42\,^{\circ}/_{\circ}$, but the average was $16\,^{\circ}/_{\circ}$. This is also a low performance considering the parentage.

Of the 28 plants of series $(E22 \times A)$–10–13–13–, exactly half were self-fertile with percentages that extended to 58 and an average of 19. There has been, perhaps, no series grown with a more highly self-fertile ancestry. Here the selections have been from parents with percentages of 51, 38, and 56. Yet half of the series was self-sterile, and only one plant exhibited a percentage of self-fertility higher than 33.

The 7 plants of series $(E22 \times A)$–10–14–6– were derived from an ancestry with fertilities of 51, 14, and 13. Only one plant was self-fertile with a percentage of 10.

A summary of the ancestral records of the various lines of descent shows that although the various parents exhibited a considerable range in fertilities, the larger series and the greater number of plants in the family have an ancestry of rather high fertilities. The results in summary emphasize the irregular heredity and the continual sporadic or ever-sporting nature of self-fertility and self-sterility in chicory. Of the 196 plants descended from the highly self-fertile plant $(E22 \times A)$ *no. 10*, a total of 118 were self-sterile. The percentage of plants self-fertile is therefore 40. The distribution of the self-fertile plants on the basis of percentages is decidedly skew. Much the greater number of plants are feebly self-fertile, and the average fertility of all plants self-fertile is 0·185.

3.   *Fertilities in various Vegetative Types or Races.*

The continued growth of line progenies by self-fertilization of parents, as practised in my chicory cultures, has led to the isolation or segregation of various vegetative types or races that are very distinct, not only from each other but from the general character of the original parents crossed, or even from the first self-fertile parents of the F_1.

Marked uniformity among the sister plants of a single series first appeared in the F_3 generation, which was the second generation after self-fertile plants appeared. For example, the plants of series $(A \times E22)$–*10–13–* were very uniform in habit of growth, as is very well shown in Plate IV. (The field number of this series was 41.) The plants were abundantly branched, making rather bushy compact individuals constituting a semi-dwarf bushy race. In respect to flower colour, this series was variable. In the foreground of Plate IV, immediately in front of field label 41, is a typical plant of series $(E22 \times A)$–*10–8–*. The habit of growth here shown is very different from that of the semi-dwarf bush race. It is characterized by a tall well developed main stem with large conspicuous leaves. The branching is somewhat sparse and is erect; at the time the photograph was taken the branching of the plant in question had not developed. More mature plants of this type are shown in Plate V (see field label no. 49).

As has been noted above, and as shown in Table VII, two plants of $(E22 \times A)$–*10–8–* and three plants of $(E22 \times A)$–*10–13–* were selected as parents for a further generation. A part of each series of the latter is shown in Plate V. To the right of field label 49 is a row of $(E22 \times A)$–*10–13–5–* which, it may be said, had not fully developed when the photograph was taken; in front of this label are plants of $(E22 \times A)$–*10–13–13–*, and to the left are shown plants of $(E22 \times A)$–*10–13–12–*. All the plants of these three series were quite alike in having a general habit of growth that was quite identical to that of the parents.

The very different vegetative habit of the series $(E22 \times A)$–*10–8–* and of the next generation, series $(E22 \times A)$–*10–8–14–* and *–15–*, is shown in Plate V in the plants of field number 49.

Other equally well marked vegetative types appeared in the F_3, and bred as true in the F_4. Series $(A \times E22)$–*9–5–6–* is one of rather medium but scraggly growth, and with brittle branches and stems. (See Plate V, field number 53.)

Other races are shown in Plate VI. In the right foreground, extending to field label 63, are plants of $(A \times E22)$–4–6–3–, which were of a very decided dwarf habit with few brittle branches, and a very marked susceptibility to a stem-rot due to fungous or bacterial infection in the tips of the branches. The field no. 63 designates the 15 plants of $(E22 \times A)$–10 Ser. II. 10–, all but one of which were self-sterile; these, it will be noted, are of a rather tall and much-branched habit. Field no. 57 is for series $(A \times E22)$–9–4–10–, which exhibited the rather incongruous combination of large vigorous erect rosette leaves with a weakly developed and sparsely branched main stem. To the left of field no. 57 is a row of series $(A \times E22)$–4–3–11–. This series was somewhat like the dwarf series already noted, but was of more vigorous growth. The branches were brittle and very susceptible to the same disease. The dying tips of the branches are quite well shown in the reproduction of plants in the foreground.

The above rather brief description will give some idea of the various vegetative forms that have appeared in the various lines of descent. It is to be noted that the plants of each series of this F_4 generation and of most of the series of the F_3 are very uniform among themselves in general vigour and habit of growth, but that various vegetative types are very different from each other. The general data for flower colour are given in the various tables, which show that for some of the series the flower colour was quite uniform, while for others white-flowered and blue-flowered plants were both in evidence.

The data in detail given in Tables I—VI, and the summary of Table VII, show that self-incompatibility develops in these various races in quite the same degree. The most dwarf and the most robust races or lines are quite alike in performance. Plants that are widely dissimilar may be self-fertile or self-sterile. Also the performance within the various series indicates that plants that are quite identical in all vegetative characters may be either self-fertile or self-sterile.

4. General Summary of Results.

In Table VII, the results obtained in 1916 are compiled together with those obtained in previous years, thus presenting a summary for the various series and generations of each family. Here the summary for the F_1 generation derived by crossing the self-sterile plants A and $E3$ or A and $E22$ is presented in italics for comparison, but is not included in the summaries of families of self-fertile lines of descent, for

TABLE VII. Record for the various series summarised according to families and lines of descent.

Record of Ancestry Parentage	F₁	F₂	F₃	No. plants totals	self sterile	self fertile	Percentage self fertile	1-5	-10	-15	20	-25	30	-35	40	-45	-50	-55	-60	-65	70	75	-80	Average fertility of self-fertile plants
1-3 .A (with reciprocal)																								
(E33. A) 1	45			21	19	2		2		1								1						0·17
.. -4-4-		43		18	8	10*	55	1		1		3	2	2			1							0·26
.. -4- ...			50	23	5	18	78	2	4	1	2	2	1	2			1							0·20
.. -4- Ser. 11, 20				26	10	16	61	5	2	4	2	1			1		1		1					0·15
.. Summary				67	23	44*	65	8	6	6	4	6	6	2	2	2	2	1	1					0·197 0·133
A. E22 (with reciprocal)				25	65	8	11	4	2	3	1	1												0·111
(A. E22)-4-	64	16		10	3	7	70	1		3	1	2												0·14
.. -4-1-		15		10	10	0	00																	0·00
.. -4-3		22		8	2	6		1		1		2	1											0·21
.. -4-6		12		5	3	4		1	2	1			1											0·13
.. -4-10		13	65	3	3	0																		0·00
.. -4-3-6-			32	2	2	0																		0·00
.. -4-3-11		22	31	29	29	0			2	1														0·08
.. -4-6-3				16	8	8	50	5	1	1	1	1		1	2		1			1				0·25
.. Summary				85	51	34	40	8	4	7	3	4	3	2	2		2	1		1				0·165 0·136
(A. E22)-9-	23			6	4	2		2		1			1	1	1									0·38
.. -9-4-		43		12	6	6	50	2	1	1	3		1				1							0·12
.. -9-5-		33		13	3	10	77	2	2		1					2	1			1		1		0·29
.. -9-4-1		43	20	10	6	4	40	1	1	1	1													0·16
.. -9-4-10-			17	13	6	7	54	2	1		1	1	1		1									0·17
.. -9-4-11-			20	4	2	2		2	1															0·02
.. -9-5-1		33	07	4	3	1		1	1															0·02
.. -9-5-6-			46	29	17	12	41	3	2	1	1	2	1	1		1	1							0·21
.. -9-5-12-			70	34	17	17	50	3	3	2	2	1		1	1	1	1	3			1		1	0·28
.. Summary				125	64	61	49	15	9	5	6	5	3	3	2	2	2	3		1	2		1	0·223 ± 0·197
(E22. A)-10-	51			25	12	11	49	2		5	2	1	3			1								0·20
.. -10-6		23		2	0	2				2														0·07
.. -10-2-		62		3	2	1		1					1	1										0·04
.. -10-8-		16		10	4	6*	60	1	1	1	1	1				1			1					5·22
.. -10-13-		38		16	10	6*	34	1	1	2	1	1												0·29
.. -10-14-		11		5	3	2		1	1															0·12
.. -10 Ser. 11, 10-		13	33	15	14	1	66	1	2	2			1											0·26
.. -10-8-14		16	15	16	14	2	12	2		1														0·10
.. -10-8-15		40		17	3	14	83	4	2	5	1	1	2	1										0·20
.. -10-13-5		36	29	31	21	10	32	3	1	3	1	1	1	1	1									0·10
.. -10-13-12			25	33	15	8	35	2	1	3	1		2	1		1								0·16
.. -10-13-13			56	28	14	14	50	2	1	2	1					1			1					0·19
.. -10-14-6		11	13	7	6	1			1															0·10
.. Summary				196	118	78*	40	14	10	19	3	12	6	3	5	3				2			2	0·185 ± 0·118

the self-fertile plants in the F_1 series appeared sporadically. In the columns giving fertility of ancestry, the individual percentages are given for the parents in line of descent and the performance of the series to which these belonged is, of course, to be found from the pedigree. A general summary is given in bold face type for each family as a whole.

It is a most noticeable fact that at least some self-sterile plants appeared in every series but one, and this was a small series of only two plants. The proportion of self-fertile plants varies considerably. Considering the families as a whole, it is highest in the family $(E3 \times A)$–4–. In the three sub-families of A and $E22$ parentage, the percentages of the proportions are quite the same (40, 49, and 40). The distribution of the self-fertilities is quite similar in all families with the larger number of plants of low fertility. The range extends into somewhat higher values in the family $(A \times E22)$–9–. On the basis of the average fertility of the self-fertile plants, there is a range from 0·165 to 0·223.

Considering all these data, there appear to be no very decided family differences in regard to the heredity and variability of self-compatibilities and incompatibilities.

It is to be recognized that the data are not sufficient to give an adequate judgment of the performance of a family or a line of descent constituting a considerable progeny and having an ancestral record of feeble fertility. As I have conducted the experiments, to select continually for very feeble fertility is to greatly limit the number of the progeny. When the pollinations are made, there is no way of knowing with any certainty what the degree of fertility is. When this becomes known, it is usually too late to make in that year the large number of pollinations necessary for the production of considerable seed by feebly self-fertile plants. It would be quite possible, however, to keep feebly fertile plants, and by making large numbers of pollinations in succeeding years to obtain considerable seed.

Of the families grown thus far $(A \times E22)$–4– has an ancestry of the lowest fertility. The data for the first self-fertile ancestor (Stout, 1916, Table III) are quite adequate to establish its low fertility. Of 26 different heads pollinated on eight different days, 20 set no seed; in the six heads the number of seed were 1, 3, 3, 4, 4, 4, giving a percentage of 4. Of the ten plants grown to maturity from such seed, 7 were self-fertile, but the highest individual fertility was 23. In the next generation from four parents, 28 plants were grown. Ten plants of one series were all self-sterile, and in another series of 8 plants, 6 were self-fertile,

the widely different results in this case being obtained from almost identical ancestral records. After three generations of self-fertile parents with a record of 4, 13, and 32, one rather large series of 29 plants gave 31 °/₀ of plants self-fertile, but with ranges only to 26 °/₀, and the very low average of 8 °/₀. A sister series with ancestral record of 4, 22, and 31 °/₀ gave 50 °/₀ of plants self-fertile, of a range extending to 62°/₀ and an average of 25 °/₀. Such irregular and sporadic results seem characteristic so far as my data go.

However, on the whole, this family was one of relatively low ancestral fertility. Only three of the members have shown a fertility above 26 °/₀, and the average of 0·165 is for all offspring lower than that of any other family.

The record of ancestry for the family (*E22 × A*)-*10*- is one of high fertility. The fertility of the first self-fertile parent was 51 °/₀. The 23 plants of the first generation, 16 of the second, and 82 of the third all had self-fertile parents with no fertility lower than 25 °/₀, yet of these the percentage of self-fertile plants was 41, which was almost identical with the record for the whole family. The most highly self-fertile series yet obtained in regard to the percentage of self-fertile plants was in this family (see (*E22 × A*)-*10*–*8*–*15*–), but there were also two series that were almost completely self-sterile.

In the family (*A × E22*)-*9*-, the plants selected for parents have been, as a rule, of medium fertility, although, of course, these have been above the average. The range of fertility is considerably higher in the family, and the average fertility of self-fertile plants is also higher than in any other family.

Certain aspects of the results are perhaps clear. In every family, as a rule, the total fertility (proportion of plants self-fertile, range of fertilities, average percentage of fertility) is increased over that which evidently occurs in the progeny of self-sterile parents: at least the proportion of self-fertile plants is much greater. This increase is, as a rule, marked in the first generation of offspring grown from self-fertile parentage. Continued selection for parentage high in individual self-fertility does not steadily and continuously increase the fertilities of the progeny either as to individual or to average fertility. The marked tendency to the development of self-incompatibility has not been eliminated.

An inspection of the data presented will show that in several series the numbers of plants that are self-fertile are relatively high. For example, in series having 83, 78, and 77 °/₀ of the plants self-fertile it

might seem that the fertilities have been very much increased and that further selection might yield a race all of which would be self-fertile, at least to some degree. In every case, however, a large number of the offspring grown from highly self-fertile plants selected from such series have been self-sterile, and on the whole the record for such progeny has not been above that of the preceding generation.

In certain cases also, high records of fertility seem to be correlated with an ancestral record that is high. While the results in this respect are not uniformly in agreement, a number of the most highly fertile series do have an immediate parent of high self-fertility. Some evidence on this point may be gained by grouping the results according to the fertilities of the immediate parentage and without regard to the family or generation. This has been done in the following table.

TABLE VIII.

Summary according to degree of self-fertility of immediate parentage.

Record for progeny

Fertility of parent	Total no. plants	Number self-sterile	Number self-fertile	Percentage self-fertile	Frequency distribution, Percentage fertility																Average fertility of self-fertile
					1—5	—10	—15	—20	—25	—30	—35	—40	—45	—50	—55	—60	—65	—70	—75	—80	
—0·10	19	10	9	0·49	3	—	3	1	2	—	—	—	—	—	—	—	—	—	—	—	0·12
—0·20	101	70	31	0·31	6	6	5	2	3	5	1	1	—	—	1	—	—	—	—	—	0·17
—0·30	97	55	42	0·43	12	10	8	3	—	1	4	1	2	1	—	—	—	—	—	—	0·14
—0·10	91	44	47	0·52	9	5	7	2	8	3	2	4	3	1	—	1	1	1	—	—	0·21
—0·50	108	46	62	0·57	13	8	8	8	7	8	2	—	3	2	—	1	—	—	—	1	0·19
—0·56	51	26	25	0·49	4	2	4	3	5	2	1	2	1	—	—	1	—	—	—	—	0·22
	34	17	17	0·50	3	3	2	—	1	—	1	2	—	1	2	2	—	—	—	—	0·22

The results show that in respect to the proportion of self-fertile plants there were only slight differences in the progeny of parents of high or of low fertility: the lowest percentage (31) was obtained in the progeny of parents whose self-fertility ranged from ·11–·20. In regard to the range of the self-fertilities, the offspring of parents of the lowest fertilities (·01–·10) extended only to 23 %. The highest range is seen in offspring of the class 0·43–0·50. The number of offspring, especially of the lowest class of parentage, is not as large as one would wish. The evidence is quite conclusive, however, that there is strong regression, especially in the offspring of plants of high fertility, and that the various progenies do not differ in the degree that is decidedly correlated with the performance of the respective parents. Still the data are suggestive that the higher ranges and averages are to be

obtained in the offspring of parents whose self-fertility is higher than 30°/₀.

Discussion.

Physiological sexual compatibility in chicory is decidedly sporadic in its heredity. That its expression in the individuals of self-fertilized lines of descent is continually fluctuating is clearly in evidence from the behaviour of the various self-fertilized lines of descent reported above. The number of generations and the number of plants in the main sub-families have been, it would seem, sufficiently large to establish these points.

Starting with self-compatible plants that arose sporadically among the F_1 progeny of self-sterile parents, lines of descent have now been grown through three further generations (F_2, F_3, and F_4) and in every generation, and in every series (excepting a single one of only two plants) of each family, self-sterile plants have appeared, and usually these have been in considerable numbers. A general summary of the different generations and families shows that about half of the plants have been self-sterile: that is, there has been considerable regression in each generation, in each family, and in each series to the condition of self-incompatibility which appeared to be the rule in the original stocks from which these plants descended. Furthermore, the average performance has been quite the same for the successive generations.

The first self-fertile parents of these families and lines of descent were offspring of parents whose self-sterility had been thoroughly tested and found to be complete. As individuals they appeared to be completely self-sterile; the races or strains to which they belonged, however, are not to be considered as absolutely self-sterile. The self-fertile plants used as the first parents for the cultures here reported had thus one generation of parentage known to be self-sterile, but I have elsewhere shown (1917) that self-fertile plants may arise after three generations of ancestry self-sterile on both male and female sides. In the development of self-compatibility, these plants then differed sharply from their immediate parents, and from the greater number of their sister plants. The extremes, self-fertility and self-sterility, it would seem, are two quite decidedly contrasted characters. In the apparent suddenness of the occurrence of self-fertile plants among the offspring of self-sterile parents there is much that is suggestive of what is quite generally called mutation.

When the first self-fertile plants appeared in my cultures, I was of the opinion that the characteristic of self-fertility would be decidedly discontinuous, and that it would be transmitted as a fixed quality. In other words, it was thought that the occurrence of such self-fertile plants could be interpreted as "mutation," or possibly as a recombination of fixed heredity units which had been separated as a result of previous crossing. However, the various self-fertile plants which first appeared exhibited various grades of compatibility which are suggestive rather that compatibility is a highly variable quality. Furthermore, the self-fertilities of the offspring of self-fertile plants in all lines of descent are also of various grades. There is obviously a series of quantitative variations in the behaviour of the plants as wholes that grade from complete self-incompatibility to a very decided self-compatibility. Such a variability of expression of fertilities and such incomplete transmission of the characteristic of self-fertility, as is revealed in all my self-fertilized lines of descent, indicate that occurrence of self-fertility is not due to mutations which are at once fixed, or to recombinations of hereditary units. At least, such recombinations are decidedly not stable.

Darwin (1868, 1877) held that all the facts regarding the occurrence of self-incompatibility then known in such plants as *Eschscholtzia californica* and *Reseda odorata* show that the phenomenon is widely distributed and is of decidedly sporadic occurrence. In his opinion, self-sterility is due to "some change in the condition of life acting on the plants themselves or on their parents." The causes were held to be environmental, and the self-incompatibility was assumed to rest in too great a uniformity or similarity of the two kinds of sexual organs produced by a plant. The characteristic of functional fertility, according to Darwin, exhibits fluctuations and chance variation as do other characters.

Jost's (1907) theory of individual stuffs assumes that the causes of self-sterility (physiological incompatibility) are individual, internal, and epigenetic in that the sex organs fail to function because they are produced on the same plant: the sex organs have the same chemical individual stuff, and thereby lack the differentiation assumed to be necessary for successful fertilization. The causes were fluctuating, but were held to be solely internal.

Morgan's (1904, 1910) studies of self-incompatibility in the animal *Ciona intestinalis*, led to much the same conclusion as was reached by Jost. The failures to function are assumed to be due to too great similarity that involves cytoplasmic relations established in the

individual. The similarity is thus considered as independent of the degrees of dissimilarity in the germ plasm brought about by the crossing necessary to give fertility.

Beginning about 1910, the attention of various investigators was especially directed to a study of the breeding performance of plants with respect to self-sterility in the attempts to determine its heredity and obtain clues as to the nature of the processes involved.

In 1911, Baur claimed that the self-sterility of *Antirrhinum molle* was recessive to self-fertility in *A. majus*, giving complete self-fertility in all plants of the F_1. The F_2, it was reported, was composed of a large proportion of self-fertile plants. Compton (1912, 1913) likewise supports the view that self-fertility is a simple dominant over self-sterility, and further interprets breeding results in *Reseda* on the basis of a simple presence and absence hypothesis, the absence of some substance, either nutritive or stimulating to the growth of pollen-tubes giving self-sterility, while the presence of such a substance gives self-fertility. Neither Baur nor Compton presents adequate data for his conclusions, and evidently both assumed a Mendelian behaviour of self-sterility and self-fertility on *a priori* grounds. In regard to the later generations of these *Antirrhinum* hybrids, Lotsy (1913) reports that the F_2 generations are composed of self-fertile and self-sterile plants, and that there are various degrees of self-fertility in evidence. The statement is made by both Baur and Lotsy, however, that all plants of the species *A. molle* are self-sterile.

Such interpretations have an advantage of appearing definite, simple, and conclusive. However, the performance in chicory of pedigreed cultures of offspring of self-sterile plants does not show any such simple and regular behaviour. Similar methods of study may reveal quite identical conditions and results in the above named species.

Correns, in 1912, announced the very important discovery of physiological cross-incompatibility among sister plants grown in the F_1 seed progeny of a cross between two self-sterile plants of *Cardamine pratensis*, a species which had previously been known as self-sterile. Correns thus proved, for the first time, that cross-sterility may exist within a variety among plants of seed origin which exhibit no dimorphism or trimorphism. By a grouping of the results, Correns arrived at a Mendelian analysis of the hereditary performance. Line stuffs were assumed to be represented and transmitted in the germ cells by anlagen, and it was assumed that there could be no fertilization between gametes carrying the same line stuff. An examination of Correns' actual results

(Stout, 1916) shows that the inter-fertilities and sterilities do not fall into four nearly equal classes such as Correns has grouped them. Compton (1913) has also pointed out that if Correns' assumption holds, one-fourth of the F_1 generation which he studied should have been self-fertile. On this particular point Correns' data are incomplete: he seems to consider all plants self-sterile, but his report includes data for self-pollinations of only 13 out of 60 of the F_1 generation. Of these, however, three were partly self-fertile. The interpretation that self-sterility and cross-sterility are due to a few line stuffs that are transmitted as single hereditary units is obviously inadequate. The conclusion, however, has been given considerable credence, especially in Mendelian circles.

East (1915a and b) very soon pointed out the inadequacy of Correns' interpretation, and formulated a "near Mendelian" interpretation for the almost complete self-sterility and the almost complete cross-fertility which he observed in hybrids between two species of *Nicotiana*. While discarding the conception of factors directly concerned with fertility and sterility as such, East considers that these conditions arise as indirect properties of Mendelian units; plants are self-sterile because the male gametophyte produced by a plant can possess no hereditary unit not possessed by the somatic cells of the pistil. He assumes that this degree or element of similarity between pollen-tube and pistil in self-pollination prohibits the formation of secretions in the pistil which are necessary for the nourishment and growth of the pollen-tubes.

As to the facts of breeding performance, we may note that neither East nor Correns gives adequate data as to the fluctuations in the degree of fertility, or in the behaviour of pedigreed lines of descent from self-sterile parents of a variety or a species, and there have been no data published regarding the behaviour of pedigreed lines of descent from self-fertile individuals which originated sporadically from self-sterile parentage. A few such plants were in evidence in the F_1 crop studied by Correns quite as I found them in chicory.

It is especially to be noted that there are no published data regarding the performance with reference to sterility and fertility of cultures of the so-called self-sterile species *Antirrhinum molle* and *Nicotiana Forgetiana*. Detailed studies of the performance of these, as well as of other species reported self-sterile, are greatly to be desired.

Moore (1917) recently reports that: "The species of *Tradescantia*, alsike clover, alfalfa, and Shirley poppy showed different degrees of self-sterility. *Tradescantia* was completely self-sterile; in alsike clover about

2 $\mathrm{^0/_0}$ of the flowers set seed when self-pollinated; in alfalfa 27 $\mathrm{^0/_0}$ of the flowers were fertilized with self-pollen, and when Shirley poppies were self-pollinated 39 $\mathrm{^0/_0}$ of the flowers set seed." The performance of individual plants is not indicated in these results, so it is impossible to judge of the variability in fertility that occurs in the various individuals involved. Evidently some individuals are self-sterile (except in *Tradescantia ?*) and some are self-fertile.

At this point one may venture to recognize that most of our misunderstanding (and assumed understanding as well) of the transmission of characters and of the nature of variation of all sorts is, no doubt, due to attempts to analyze all sorts of characters in terms of hereditary units. There has been a tendency to ascribe all sorts of characters, superficial, fundamental, all sorts of pattern effects in pigment distribution, minutely qualitative or quantitative differences of highly specialized organs, and general qualities of an organism as a whole to factors which, it would seem, are mostly thought of as corpuscular units serially arranged in the germ plasm. The inadequacies of the attempts to analyze self-sterility on this basis are quite apparent both as to methods and results.

To speak of the occasional appearance of self-compatible individuals in an ordinarily self-sterile race as sporadic, and to refer the processes determining the possibility of fertilization to variable interactions between tissues and cells as such, may to many seem less definite than an interpretation on the basis of assumed hereditary units. But the irregular behaviour of compatibility and incompatibility both in ontogeny and heredity in chicory is clear. Neither compatibility nor incompatibility are fixed and unchanging characters in transmission and in expression, and are not to be considered as directly represented in the germ plasm by hereditary elements.

In general it has been held that functional sex-vigor is congenital, and that fertility in the sense of ability to produce large numbers of offspring is hereditary. In many hermaphrodite plants, perhaps the majority, self-fertility appears complete; within many species cross-compatibility is perhaps complete; the functional compatibility between the sexes is so general in the plant and animal kingdoms that it has been held to be congenital.

The presence of sexual incompatibility, therefore, between individuals of a single race or variety, or even single line of descent, as it is found in chicory, strikes one at first as a decided anomaly, and it seems still more an anomaly that the sex organs produced on the same plant, and

even in the same flower, may be as incompatible in function as though they were produced by plants of unrelated genera.

There has been much speculation as to the nature and operation of the physiological processes operating in such incompatibilities as are seen in physiological self- and cross-sterility. In many cases of self-incompatibility it has been reported that there is a limited or restricted growth of pollen-tubes. These facts have led to views that the determining factors in compatibility and incompatibility are limited to the relations between pollen-tubes and pistils alone. Jost (1907) considers that the poor growth of pollen-tubes in such cases is due to the action of individual stuff which inhibits growth of pollen-tubes having the same stuff. Compton (1912, 1913) believes that self-sterility is due to the absence of a stimulating stuff, the presence of which gives fertility. East (1915 a) attributes self-sterility to absence of food stuffs which are not secreted because the pollen-tubes involved do not possess any hereditary element not possessed by the diploid cells of the pistil. Moore (1917) considers that the limited growth in length of pollen-tubes observed in self-sterility in *Tradescantia* is really due to the presence of too much food.

Some of these views appear to regard the determining factors as conditions of the pistil alone; others consider that the conditions arise through a reciprocal reaction between tubes and pistil. All of them fail to recognize that a critical period in the growth of the pollen-tube may result from secretions of the egg, and that the different qualities of the pistil may be due to the diffusion of hormones from the gameto-phytes. As I have earlier pointed out, there is some evidence that some cases of embryo abortion may be due to incompatibility, expressing itself after fertilization and during the development of the embryo. This may be true in some cases in chicory. Further studies are in progress on this point.

Cross-sterility (within a species) without self-sterility might be explained as are isoprecipitation phenomena on the basis of an intra-specific specificity of individuals, or groups of individuals, as such. Self-compatibility, however, shows that an equally-marked differential specificity may develop in sex organs and gametes produced by a single individual: such specificity is not characteristic of the sporophytic individual as a whole, but of the pollen-tubes, pistils, embryo sacs and eggs as such.

Conclusions.

1. *Self- and cross-incompatibilities in chicory develop independently* of either (*a*) *anatomical incompatibility* with its marked structural differences and adaptations for cross-pollination; or (*b*) *embryo abortion*, at least of the sort that is due to the malnutrition of embryos by the parent plant, and which in many fruit-bearing plants involves various conditions of seed and flesh formation.

2. There is some evidence that both impotence and embryo abortion are also present in some degree in chicory.

3. The experiments with chicory already reported (1916, 1917) indicate (*a*) that self- and cross-incompatibilities are strongly in evidence; (*b*) that a few self-compatible plants may arise sporadically from parents that are self-sterile, even after three generations of self-sterile parentage; (*c*) that the progeny of such self-fertile plants do not breed true as to this character; (*d*) that the degree of self-compatibility varies; (*e*) and that selection for increased self-fertility after two generations was not effective in isolating a completely self-fertile strain.

4. The new data reported in this paper are fully in accord with the results obtained in previous years. A new generation, the third having self-fertile ancestry, exhibited quite the same irregular heredity and sporadic development of self-sterility (or regression to the condition of self-sterility) as was seen in the former generation. In this respect every family, every line, and every series were in close agreement.

5. *Self-compatibility is entirely independent of differences in vegetative rigor.* The various series of the crops grown in 1915 and 1916 showed widely different types in respect to vegetative vigor. Self-sterility appeared in all these races with practically equal frequency. Sister plants of the least vigorous dwarf race or sister plants of the most vigorous vegetative race were either self-fertile or self-sterile indiscriminately.

6. *Self-compatibility and self-incompatibility operate independently of potential sex-rigor.* The total production of flowers varied greatly among the various series. Plants with large numbers of sex organs were either self-sterile or self-fertile, as were plants with the fewest number.

7. *Self-compatibility and self-incompatibility operate independently of the purely nutritive relations of the embryos to their parent plants.*

Ten flower heads self-pollinated on a completely self-sterile plant will set no seed, while ten heads on the same plant pollinated on the same day with pollen from a highly cross-compatible plant will set abundant seed. The fruits are rather small achenes having no endosperm, and are practically composed only of the embryo: provided the pollination is compatible, they develop equally well throughout the season (Data, see 1916, Tables XV and XVI).

8. *Self-compatibility and self-incompatibility appear independently of any combination of germ plasm elements* in so far as these can be judged by the expression of characters. Each operates alike between gametes that are similar or those that are dissimilar in respect to hereditary units of genetic analysis. Plants widely different in such qualities as colour of flowers, type of branching, shape of leaves, etc. are either self-fertile or self-sterile, and plants of a sister series quite similar in all respects are either self-fertile or self-sterile. When an F_1 plant of hybrid origin is self-fertile in any degree the evidence indicates that any of the sex cells may function in any recombination; on the other hand in self-sterile sister plants whose sex cells must, it would seem, be of much the same diversity none are compatible. Also all the sex cells of an F_4 plant which must have much the same germ-plasm constitution may fail to function together, while those of a sister plant may be highly functional. Two self-sterile plants, sisters of an F_1 cross or sisters of any generation, may be cross-fertile or cross-sterile quite indiscriminately.

9. *The development of either self-compatibility or self-incompatibility occurs in both cross-bred and inbred races, the latter often being highly constant races for vegetative characters.* Both self-fertile and self-sterile plants occurred among sister plants that were F_1 hybrids of rather wide crosses (Stout, 1916, 1917); they also appeared among inbred strains derived by crossing self-sterile parents for as many as three generations (1917), and they occurred, as here reported, among the progeny of self-fertile plants, even after three generations of self-fertile parentage. The positive evidence at hand, however, makes it clear that self-compatibilities do not decrease in self-fertilized lines of descent which are so uniform that they constitute decidedly pure races.

10. *The results obtained in the cultures of chicory make it clear that self-incompatibility and self-compatibility are here not to be described as dominant and recessive characters,* or paired allelomorphs, and that there is no simple Mendelian formula that fits the results. The evidence

at hand for the behaviour of similar phenomena in other species is also quite in agreement with this conclusion.

11. *The conditions controlling sex-fusions,* judged by the behaviour of compatibilities and incompatibilities in such species as *Cichorium Intybus, arise in connection with the development of the sex organs and sex cells as such.* In this sense the controlling factors are of epigenetic and individual development.

12. *The factors which determine or prohibit successful fertilization in chicory, whatever their essential nature may be, are highly variable as to degree, specificity, and transmission in heredity.*

New York Botanical Garden,
May 10, 1917.

EXPLANATION OF PLATES.

PLATE IV.

View of series $(A \times E22)$-10-13- of the semi-dwarf bushy race showing very decided uniformity in general vegetative habit. Ten of this series were self-sterile and six were self-fertile. In the foreground is a plant of series $(A \times E22)$-10-8- showing a tall sparsely branched habit of growth. These plants are from two generations of self-fertile ancestry.

PLATE V.

View of chicory in experimental plot. Crop of 1916. Several races are shown.

PLATE VI.

Another view in experimental plot. Crop of 1916. Dwarf and semi-dwarf races are especially prominent. Plants shown in Plates V and VI are from three generations of self-fertile ancestry. Plants here shown were self-compatible or self-incompatible quite indiscriminately.

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PLATE IV

PLATE VI

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RACIAL STUDIES IN FISHES.

I. STATISTICAL INVESTIGATIONS WITH *ZOARCES VIVIPARUS* L.

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(With Plate VII and seven text-figures.)

DURING the past few decades, variation-statistical investigations have been carried out on a large scale with several species of the food fishes having their habitat in our northern seas; a classical example is the great work by Heincke on the Races of the Herring (*Clupea harengus*). This appeared in 1898, and was of great importance, both in methodical respects and also by reason of the results arrived at.

Heincke's work, with that of several others dealing with the same question[1], showed that the herrings of North and West Europe do not make up a single coherent and homogeneous shoal. They are on the contrary divided up into numerous more or less highly localised "communities" or "populations," each leading an isolated existence, and each to be characterised as distinct from other populations by average structural conditions, spawning time, etc.

Similar, more or less marked differences have been found among practically all the species of fish which have been sufficiently investigated in detail. A characteristic exception from this rule, however, is the common freshwater eel (*Anguilla vulgaris*) which will be referred to later on.

[1] Readers wishing for further information on the subject of Herring investigations may refer to the recent paper by H. Chas. Williamson: "A short résumé of the researches into the European Races of Herrings and the method of investigation" (*Fishery Board for Scotland, Scientific Investigations*, 1914, No. I. Edinburgh, 1914).

In trying to characterise these populations, various quantitative features are employed, both such as are determinable by counting (e.g. the number of vertebrae or of fin rays), and such as involve measurement (as for instance the size and shape of the head). We have thus in the former case to deal with integrated, in the latter with graduated variates.

Where two populations have been found, by statistical examination of a great number of specimens, to differ in the mean of one or more characters, it is customary, in fishery biology, to say that each belongs to its own *race* of the species in question. The word "race" is, however, not employed by all writers; some prefer the term "local forms" or "families," while others again use all three indiscriminately.

This uncertainty in the terminology itself serves to indicate the incompleteness of our knowledge as to the true nature of races in fishes. We do not even know whether they are genotypically determined or merely phenotypical phenomena. And a genetic analysis is still wanting in this sphere. The reason for this lack of knowledge must be sought, partly in the great experimental difficulties attending investigation of our marine food fishes, partly also in the fact that fishery biologists most frequently regard their problems as solved when once they have shown that two or more populations actually are distinct and biologically independent.

The question then is still before us: What is the cause of the racial differences found? Why, for instance, should the race of herrings living on the east coast of Scotland have a higher average number of vertebrae than that—or those—of the Baltic, and why have the Baltic herrings again a higher figure for this character than the herrings of the White Sea? Or how is it that the plaice (*Pleuronectes platessa*) in the North Sea manage to develop a greater number of rays in the anal fin than the plaice of the Baltic waters?

The generally accepted view among fishery biologists is that racial differences arise from the influence of differing external conditions under which the races in question live, such as for instance salinity of the water, its temperature, etc. It is thought that the average values for the differing qualities, i.e. the racial characters, are actually dependent upon this or that temperature, salinity, or the like, which happens to be peculiar to the water in question. Certain writers, such as Heincke, imagine these external conditions as exerting a directly determinative effect; others are more inclined to regard them as acting indirectly, through a process of selection. In this latter case, the variates not

suited to the surroundings would be rejected, whereby the average values for the different characters would of course be indirectly altered.

The object which I had set before me was to elucidate as far as possible, by means of suitable material, some of the conditions responsible for the racial differences found among our marine fish species in nature. From the outset, I had a clear appreciation of two points: first, that the investigation would have to be of an even more detailed character than any of those previously carried out (though these might seem detailed enough, for instance, in the case of the herring and plaice investigations!). And secondly, that experimental aids would be necessary, as without such, it would hardly be possible to arrive at any decisive result.

The necessity of experimental investigations again forced me to abandon the two species in which the question of race has been best investigated (statistically), viz. the herring and the plaice, since experiments with these seemed out of the question at present, at any rate with the means at my disposal. In addition, I wished to have a species even more " variable " and more local than the herring or the plaice. Both of these are, as we know, pelagic for a more or less considerable part of their life, and consequently subject to important passive or active dislocations which may lead to an intermingling of the individuals from different populations.

A species which appears to fulfil the required conditions is the common *Viviparous Blenny* (*Zoarces viviparus*, L.) with which I have now been working since the autumn of 1914. I have made both statistical and experimental investigations with this species; only the former, however, have up to the present been brought to a conclusion, and only these are therefore so far advanced as to be suitable for publication.

In course of time, a great number of specimens, over 25,000, have been examined, with regard to several characters. A detailed account, with the figures pertaining thereto, appears in Vol. XIII of the *Comptes rendus des travaux du Laboratoire de Carlsbery*, Copenhagen, and I must here restrict myself to mentioning some of the principal results.

Zoarces viviparus is an extremely common fish in our Danish waters, where it plays a far greater part than in the British. It lives as a rule in quite shallow water, inside the 10 metre curve. Its distribution in Europe has a marked *north-easterly* character. It is found from the

White Sea in the north to the English Channel in the south, is common on the east coasts of Scotland and England but rare on the west, and is not known with certainty from Ireland. Eastward, however, it penetrates into the innermost waters of the Baltic, to the base of the Gulf of Bothnia and Gulf of Finland. A striking feature is the fact that it is not found at the Faroes or Iceland.

One of the most prominent points in the natural history of *Zoarces* is that it is viviparous. Pairing takes place late in the summer, and by the close of the winter a considerable number of young, up to 400, are brought into the world. These are at birth 4—5 cm. long, exactly resembling their parents in all main features, and, like these, keeping to the bottom from the very first. The quality of being viviparous is almost unique among our northern teleosteans, and this is also one of the essential reasons for my taking *Zoarces* for the purposes of investigation, as we have here the great advantage of being able to examine the progeny of a single female and compare the qualities with those of the mother. For the young have, before they are born, all the qualities with which we are here concerned fully developed in numerical respects.

Besides a great number of characters which have not been investigated throughout in all samples, we have devoted particular attention to the following four: (1) number of vertebrae ("vert"), (2) of rays in the right pectoral fin (" Pd "), (3) of hard rays in the dorsal fin (" D_2 "), and (4) of pigment spots on the dorsal fin (" Pigm. D_1 "). All these qualities are determined by counting, so that we have only to deal with integrated variates. This is an advantage, as the qualities in question are not altered from long before the birth of the individual until its death.

The characters investigated are of essential physiognomical importance, the number of pectoral rays, however, to a lesser degree than the others. This will be seen from the three sketches (Pl. VII, figs. 1—3). The specimen shown in Fig. 1 has a large number of vertebrae, viz. 121, and thus appears much more slender than those in Figs. 2 and 3, with 105 and 109 vertebrae respectively.

Highly characteristic of *Zoarces* is the fact that the dorsal fin has an incurvation extending for a more or less considerable length down its posterior part. This portion of the fin contains only hard rays, the number of which will thus determine the length of the incurvation. In the specimen Fig. 1, where there are no less than 12 hard rays, the incurvate part is long; in the specimen Fig. 2, where the number is only 5, it is much shorter. Finally, the dorsal fin in the specimen

Fig. 3, where hard rays are altogether lacking, exhibits no incurvation at all.

The number of pigment spots is also, as will be seen from the figures, of physiognomical importance.

The number of vertebrae has been found to vary from 101 to 126 inclusive, a range of variation which is very considerable, and greater than in any other species of fish hitherto investigated. The other characters also have a wide range of variation. Thus we find, for the hard rays 0—17, for the pigment spots 7—21, and for the pectoral rays 16—22. For the sake of brevity I will here restrict myself mainly to the mention of a single character, viz. the number of vertebrae.

Preliminary investigations soon showed that there was no difference between the sexes in respect of the characters here in question. It was further found, on repeated analyses of the same population, that most of the characters exhibited a high degree of *constancy from year to year*, as far as the scope of the investigations extends up to now. An instance of such constancy is shown in the graphs of Fig. 4, representing the number of vertebrae in the years 1914, 1915 and 1916 for the same population (St. 31, Ise Fjord, Sealand, Denmark). The number of vertebrae is noted in figures along the vertical lines, each dot denoting a single specimen of *Zoarces*. It will be seen that the three graphs agree excellently well together, and therewith also the average values for the three years, viz. *113.42* ($\pm$ 0.49), *113.23* ($\pm$ 0.43) and *113.40* ($\pm$ 0.44).

Altogether about 80 population analyses were made, embracing material from the greater part of the area of distribution of *Zoarces*. The separate population samples consisted as a rule of about 200 specimens, which permit of a very good degree of accuracy in the determinations. For vertebrae, the highest mean found was 119.44, and the lowest 107.98; similar results were arrived at in the case of the other characters, least in the case of the pectoral rays, where there are also, it must be noted, very rarely more than four variates.

The mean values for the various characters may appear in highly differing combinations in the different populations. Disregarding the pectoral rays, where the range of variation is but slight, and using A, B and C to denote a high value, a, b and c a low mean value for number of vertebrae, hard rays and pigment spots respectively, we find, out of the eight possible combinations, six were realised in our 80 population analyses: ABC, ABc, AbC, Abc, abC and abc. Up to the present, however, we have encountered no instance of aBc and aBC,

and of the six combinations noted above as found, not all were of the same frequency.

An attempt has been made to characterise the various larger regions of sea within the *Zoarces* area by means of the average qualities of the
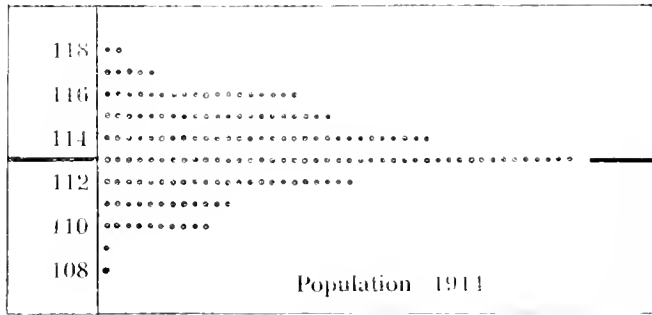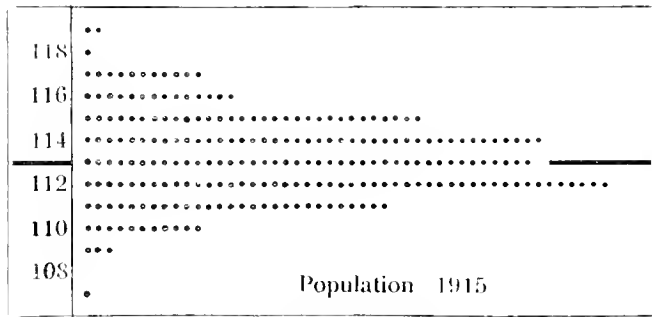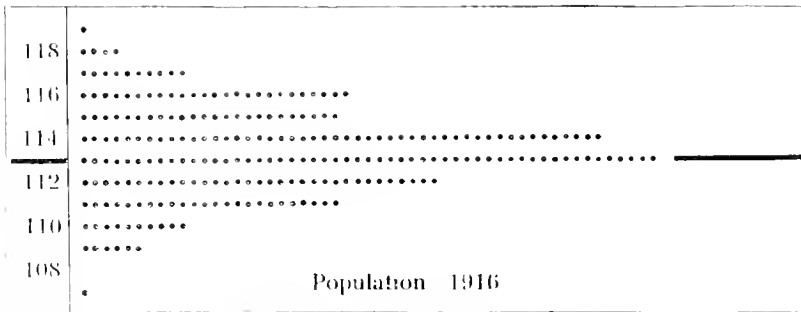
Fig. 4. *Zoarces viviparus*, L. Number of vertebrae. Population analyses for three successive years from Station 31, Ise Fjord, Sealand, Denmark.

Outside Fjord

Mouth of Fjord
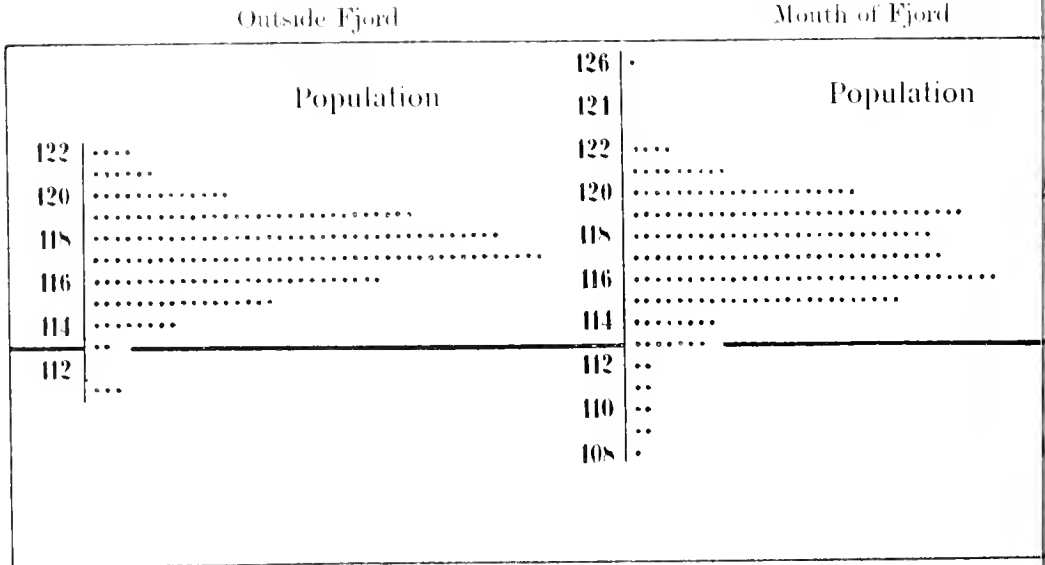
a = 117·37 (±0·48).

a = 117·10 (±0·62).

Fig. 5. *Zoarces viviparus*, L. Number of vertebrae. Four population analyses from the e
from the mouth

Mouth of Fjord
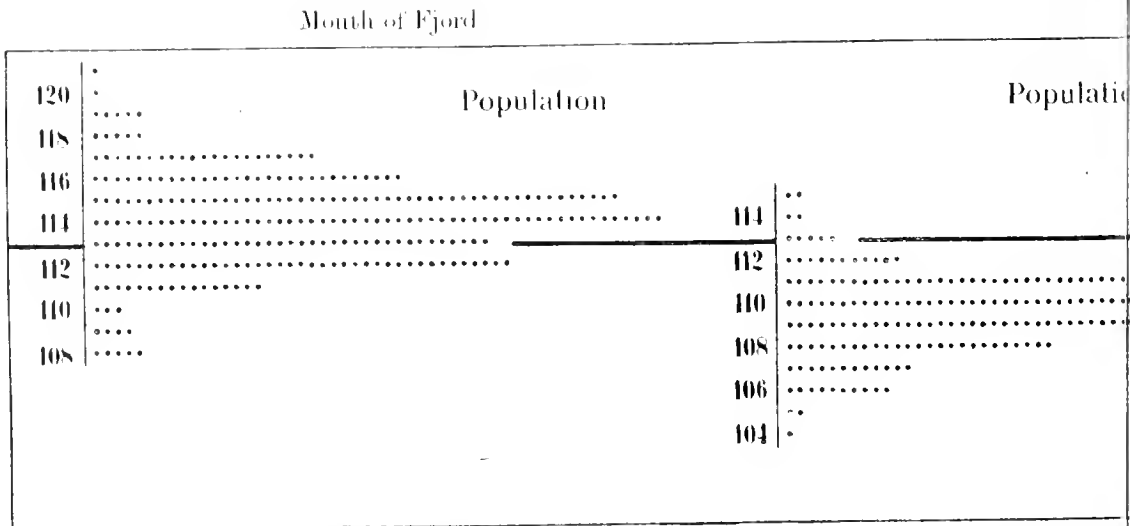
a = 111·01 (±0·16).

a = 109·46 (±0·49)

Fig. 6. *Zoarces viviparus*, L. Number of vertebrae. Three population analyses from Ise Fjord, Roskilde

Inner part of Fjord

Population   Population
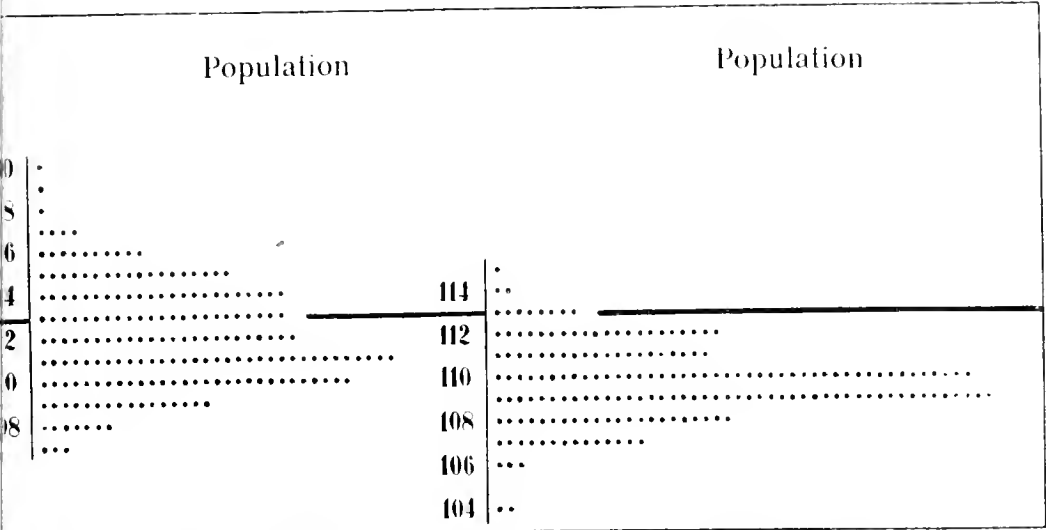
$a = 112 \cdot 11 \, (\_ 0 \cdot 59).$ $a = 109 \cdot 69 \, (\pm 0 \cdot 45).$

ern part of Liim Fjord, Jutland, Denmark. Showing how the number of vertebrae decreases the fjord inwards.

Inner part of Fjord

Population

$a = 107 \cdot 95 \, (\pm 0 \cdot 36).$

ord, Sealand, Denmark. Showing how the number of vertebrae decreases from the mouth of the fjord inwards.

populations there found. Dividing up the area into four parts, and utilising the same symbols as above, we obtain the following : (1) western North Sea, **Abc**: (2) eastern North Sea, **abc**; (3) west Baltic region, **ABC**; (4) east Baltic region, **ABc**. On taking together three populations, typical as far as possible, from each of the four regions, we obtain the following mean values :

TABLE I.

			Average value for	Vert.	Pd	D_2	Pigm. D_1
I.	North Sea	1.	Western part	116·2	18 71	7·2	12·7
	,,	2.	Eastern part	111·2	18·48	6·0	12·3
II.	Baltic	3.	Western part	117·7	19·35	8·0	14·3
	,,	4.	Eastern part	117·2	18·66	11·1	12·3

On going into details, we find many discrepancies and irregularities in the geographical distribution of the mean values. A certain regularity, on the other hand, and also highly peculiar conditions are noted in the shallow Danish and other *fjords* of the western Baltic. The rule here is that the average number of vertebrae, hard rays and pigment spots will be essentially *lower* up in the fjords than outside, and this applies even where the distance between the two populations only amounts to some few miles. The graphs in Figs. 5, 6 show some instances of this as regards the number of vertebrae. Table II, giving the values for Mariager Fjord, east coast of Jutland, Denmark, shows the same also for the other characters.

TABLE II.

Mariager Fjord, Denmark.

Average value for	Vert.	D_2	Pigm. D_1
Stat. 14	117·37	9·21	13·30
,, 15	115·43	8·74	13·06
,, 16	110·99	7·21	12·32
,, 17	110·18	6·87	11·80
,, 19	109·30	6·40	11·83

St. 14 lies outside the fjord; the remaining stations up in the fjord; St. 19 at its base.

The lower number of vertebrae in the *Zources* of the fjords gives them a physiognomy differing greatly from that of their relatives on the coasts, the former being of short and stumpy build, the latter slender and elongated in shape.

Our population analyses have thus shown that *Zoarces* is split up into numerous "races," often highly localised, and differing widely one from another. In this respect, however, there is no difference of principle between *Zoarces* and the other well investigated fish species such as herring and plaice. The difference is only one of degree, depending upon the fact that *Zoarces* is an even more "variable" and even less migratory species than either of the other two.

One species of fish, however, to which I have also devoted particular attention, viz. the common freshwater eel (*Anguilla vulgaris*), does differ in principle, and a comparison with this species, which has about the same number of vertebrae, etc. as *Zoarces*, is therefore highly instructive.

On going through a large amount of material, it was found that in contrast to *Zoarces*, which, as we have seen, is split up into numerous local races, all the eel populations of Europe are identical (see graphs, Fig. 7). The explanation of this most remarkable fact must be sought in the great biological difference between the two species; *Zoarces* spends the whole of its life in the same very restricted area, whereas all the freshwater eels of Europe undertake migrations of thousands of miles out into the Atlantic to spawn, the young thereafter journeying the same way back. Long before the young, or rather larvae (*Leptocephalus brevirostris*), reach the coasts of Europe, they have developed their full complement of vertebrae, etc., and we have here a natural explanation of the fact that all the eel populations of Europe are identical, or belong to one and the same "race."

As mentioned above, *Zoarces* gives birth to a great number of young, which have already, long before they are born, developed their full number of vertebrae, fin rays, pigment spots, etc. This renders it possible for us to carry out *individual offspring analyses* with this species, the offspring of each gravid female being separately investigated.

Examples of such individual offspring analyses will be found in the graphs (Fig. 8). The material is from the same population (St. 31) as the three population analyses for 1914, 1915 and 1916 in Fig. 4. On comparing Fig. 4 with Fig. 8 we find that the average number of vertebrae in various offspring samples can exhibit considerable variation among themselves, and differ greatly from the average for the population. Thus in the case of the three offspring samples in Fig. 8; the mean values for number of vertebrae were about 117·83, 112·36 and 109·48 respectively, whereas the number for the population was in all the three years 1914–16 between about 113·2 and 113·4.

Iceland
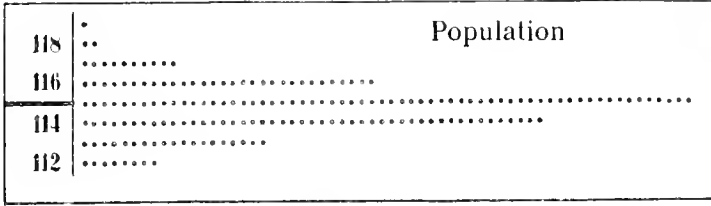
$a = 114.73 \, (\pm 0.32).$

Copenhagen
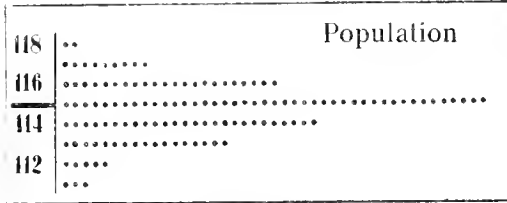
$a = 114.68 \, (\pm 0.30).$

Bayonne
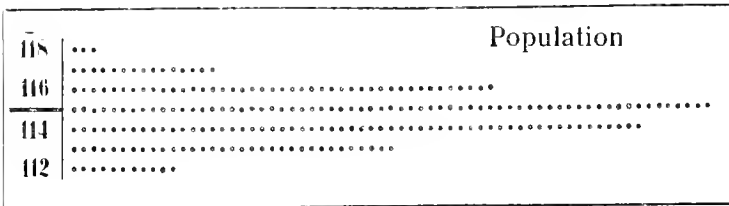
$a = 114.67 \, (\pm 0.21).$

Azores
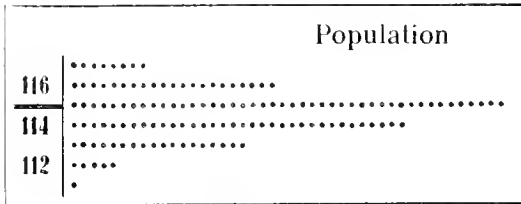
$a = 114.60 \, (\pm 0.38).$

Comacchio (Adriatic).
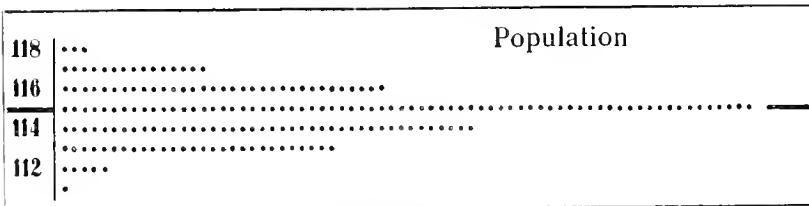
$a = 114.77 \, (\pm 0.31).$

Fig. 7. Common freshwater eel (*Anguilla vulgaris*). Number of vertebrae. Five population analyses of material from Iceland, Copenhagen, Bayonne (France), Azores, Comacchio (Adriatic). Showing that the eel populations of Europe are identical.
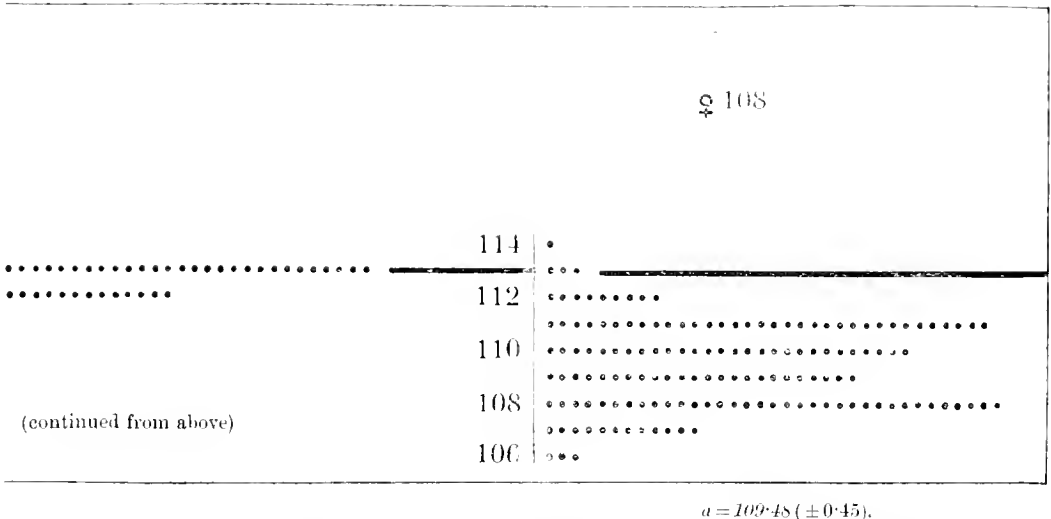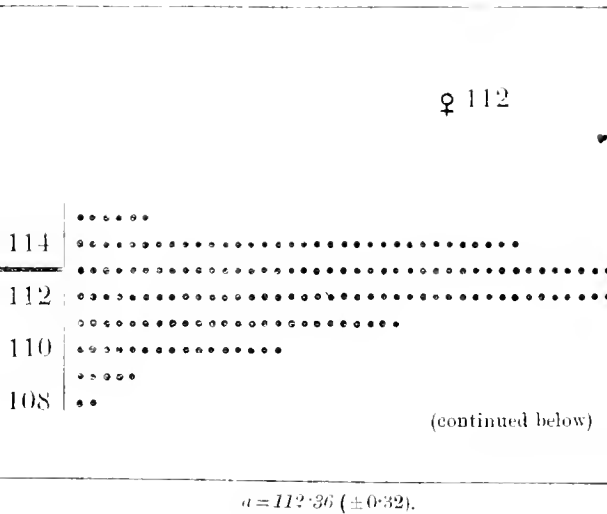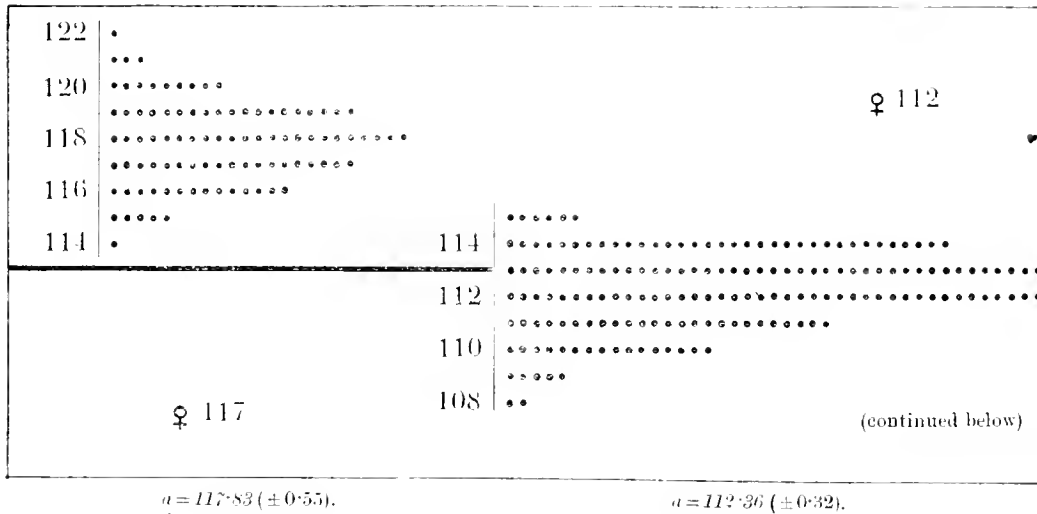
Fig. 8. *Zoarces viviparus*, L. Number of vertebrae. Three individual offspring analyses of gravid females from the 1914 population at St. 31, Ise Fjord, Sealand, Denmark ; the same population as shown in Fig. 4. On comparing with Fig. 4 it will be seen that the number of vertebrae in individual offspring samples may differ greatly from that of the population. For each of the graphs of offspring samples, the number of vertebrae in the mother is noted.

My own interpretation of the offspring analyses, which is supported
by the results arrived at in 1903 by W. Johannsen in his studies on bean
communities, is roughly as follows.   It was found possible by population
analyses to subdivide *Zoarces viviparus* into numerous local "races."
The individual offspring analyses showed that the smallest unit hitherto
considered, the "race," may be resolved into still smaller elements, ex-
pressed by the means of the offspring samples.   These smaller elements
may differ widely one from another, and likewise from the average of
the population ("race"), but when added together they reproduce the
picture of the race itself as the latter is expressed in the results of the
population analyses.

As already mentioned above, it is a generally accepted view among
fishery biologists that racial differences are due to the differing external
conditions under which the various races live.   The salinity of the water
is here as a rule considered of great importance, and as this factor is also
the best elucidated up to date, I have endeavoured to ascertain how far
any agreement could be found to exist between the salinity and the
average values characterising the races of *Zoarces*.   A few examples
may be quoted.   Of the populations we have analysed, that of St. 57
in the North Sea (Anstruther, Scotland) is the one living in saltest
water, St. 52 in the Gulf of Bothnia in the Baltic (Hudiksvall, Sweden)
that with lowest salinity.   The difference between these two places is
very great, the salinity at the Scottish station being about $34 \,^{\circ}/_{\circ\circ}$, and
in the Gulf of Bothnia about $5 \,^{\circ}/_{\circ\circ}$ only.   The population at St. 57 thus
lives in a salt solution more than six times the strength of the water at
St. 52.   The graphs in Fig. 9 show the values for number of vertebrae
in these two populations.   It will be noticed that there is no difference
to speak of between the two graphs, either as regards course or average
values, the latter being about 116·0 and about 116·4 respectively.   This
example thus seems to suggest that the salinity is not of any real im-
portance.

Another example is illustrated in Fig. 10.   The two populations
here shown are from Roskilde Fjord, Sealand, Denmark, and Kjelds
Nor, Langeland, Denmark.   At these two places the salinity is very
nearly the same and rather low, viz. about $12 \,^{\circ}/_{\circ\circ}$.   But it is at once
noticeable that the values for number of vertebrae exhibit an enormous
difference as between the two populations, amounting to no less than
about 11·5 mean.   So great is the dissimilarity indeed that the two
populations have not a single common variate.   The picture presented

is such that the uninitiated might well take it as representing two distinct species, and yet as a matter of fact we have here only to deal with two populations living within the same area of sea, and, as far as we are aware, under uniform external conditions.

St. 52.　Gulf of Bothnia (Sweden).

120 ∘•
⠀⠀•••••
118 •••••••••••••
⠀⠀•••••••••••••••••••••
116 ••••••••••••••••••••••••••••••••
⠀⠀••••••••••••••••
114 ••••
⠀⠀•••
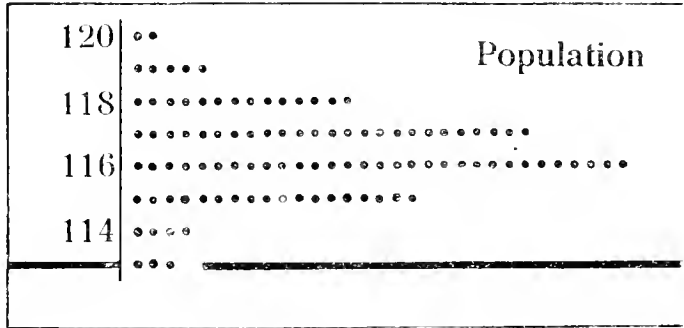
Population

$a = 116 \cdot 10 \; (\pm 0 \cdot 47)$.

St. 57.　Scotland (Anstruther).

120 ••
⠀⠀•••
118 ••••••••••••••••
⠀⠀•••••••••••••••••••••••••••
116 •••••••••••••••••••••••••
⠀⠀•••••••••••••••••••••••••
114 •••••••••••••••
⠀⠀•••
112 ••
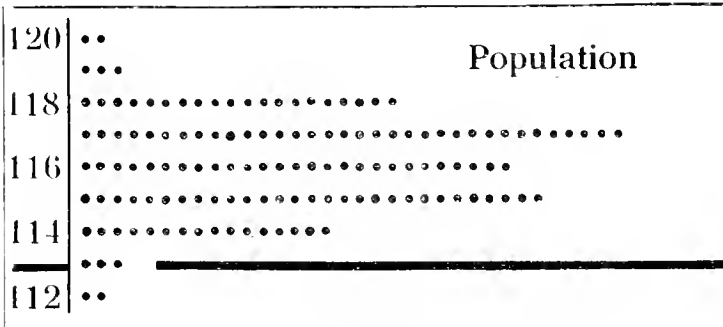
Population

$a = 116 \cdot 10 \; (\pm 0 \cdot 45)$.

Fig. 9.　*Zoarces viviparus*, L.　Number of vertebrae.　Two population analyses from St. 57 (Anstruther, Scotland) and St. 52 (Hudiksvall, Gulf of Bothnia).　At St. 57 the salinity of the water is about 34 ‰; at St. 52 only about 5 ‰.

Our investigations thus by no means support the hypothesis that the racial characters are determined exclusively by environment.　On the contrary, they seem rather to indicate that differences of environment are not sufficient to explain the structural differences between the races, and that the importance of the salinity especially has doubtless been greatly over-estimated.

On the other hand, the very distinct gradation of average qualities found in the fjord populations seems to suggest that the surroundings may be of importance, either directly or indirectly, but what factors here come into play we cannot as yet determine.

My view then, with regard to the nature of "races" in fishes, as characterised by our population analyses, is briefly this: A fish "race"
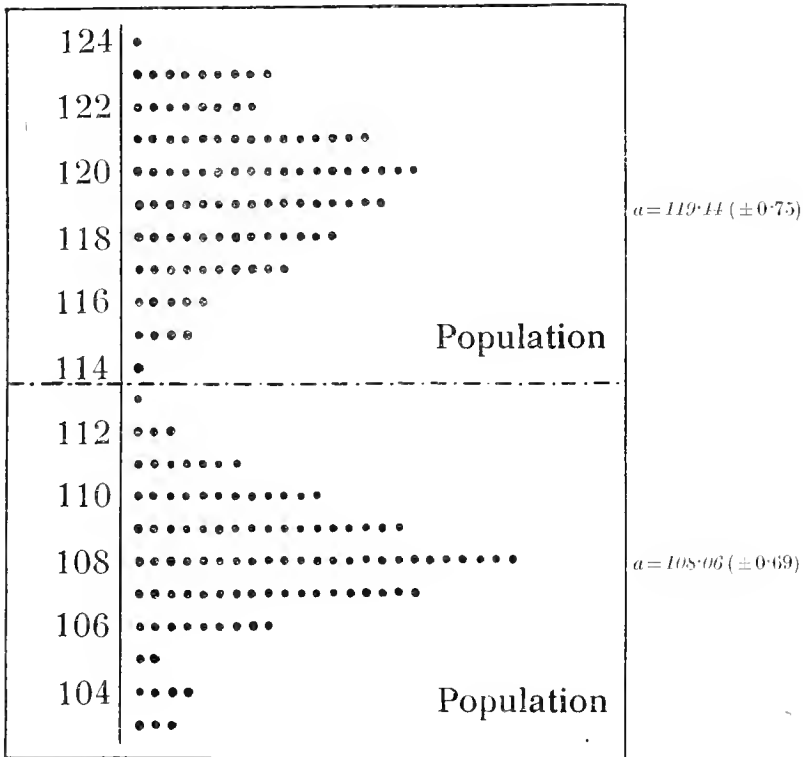
Fig. 10. *Zoarces viviparus*, L. Number of vertebrae. Two population analyses from Kjelds Nor, Langeland, Denmark (above), and Roskilde Fjord, Sealand, Denmark (below). At both places the salinity is about 12 ‰. The boundary between the populations indicated by a dotted line.

is largely a statistical conception. It implies a mixing of different genotypes, and the average values characterising the "race" are primarily dependent upon the quantitative proportion between these; only secondarily on the environment.

It should nevertheless be pointed out that we cannot expect to arrive at any final decision before the results of the experimental

analysis are available. I hope therefore to revert to the question on a subsequent occasion, after conclusion of the experiments, of which the individual offspring analyses briefly referred to above form a part.

DESCRIPTION OF PLATE VII.

Fig. 1.   *Zoarces viviparus*, L.   Sketch of a specimen about 26 cm. in length from the Sound.   Number of vertebrae 121, of hard rays 12, and of pigment spots on dorsal 16.

Fig. 2.   *Zoarces viviparus*, L.   Sketch of a specimen about 25 cm. in length from Roskilde Fjord, Sealand, Denmark.   Number of vertebrae 105, of hard rays 5, and of pigment spots on dorsal 11.

Fig. 3.   *Zoarces viviparus*, L.   Sketch of a specimen about 33 cm. in length, from Gullmar Fjord, Sweden.   Hard rays lacking.   Number of vertebrae 109.

In all three figures the foremost pigment spot is situated on the front margin of the dorsal fin.

Note.   In calculating the probable fluctuation of the average number of vertebrae etc. the following formula was employed, viz. $\pm \frac{\sigma}{\sqrt{n}} \cdot 0.67449 \cdot 5$ This value is always given in brackets after each average value of the character in question.

Fig. 1.

Fig. 2.

Fig. 3.

PLATE VII
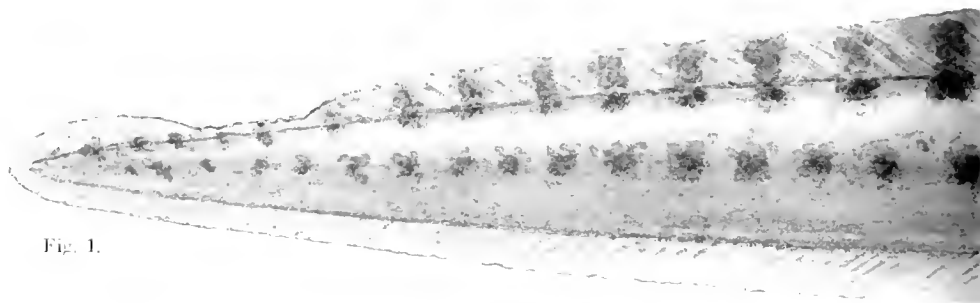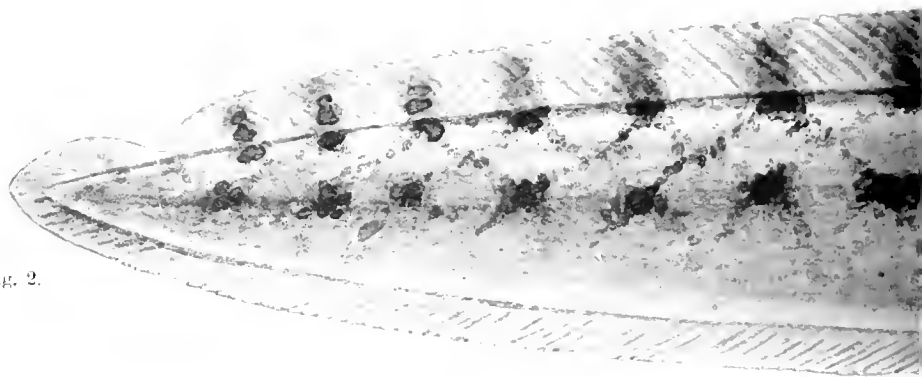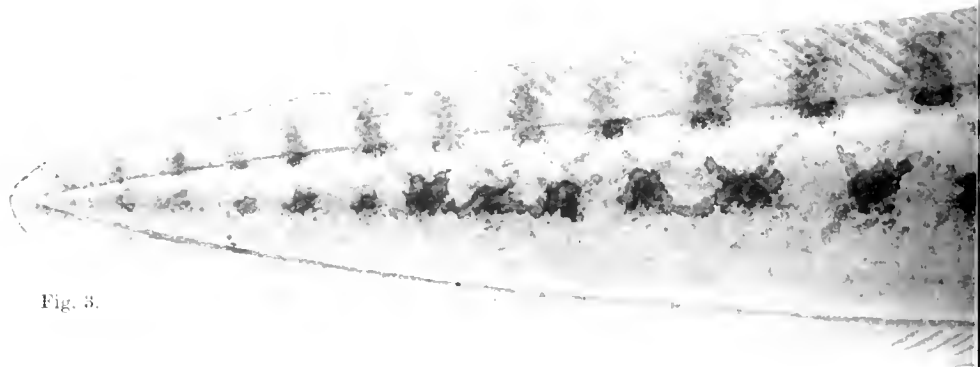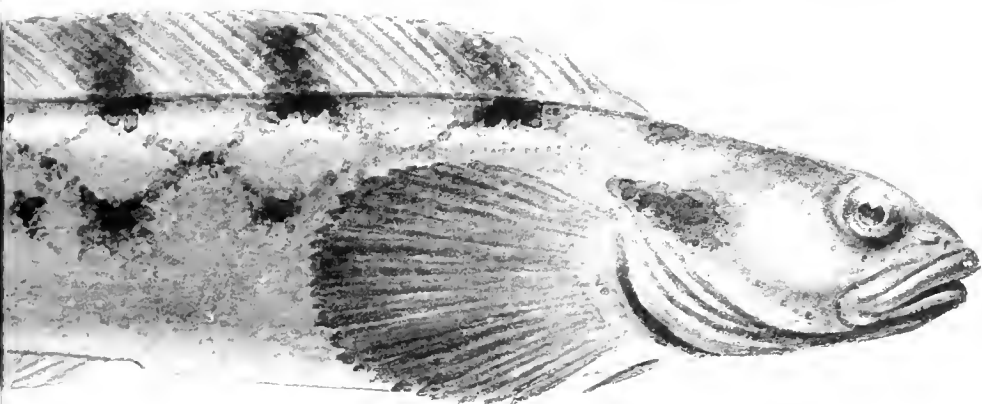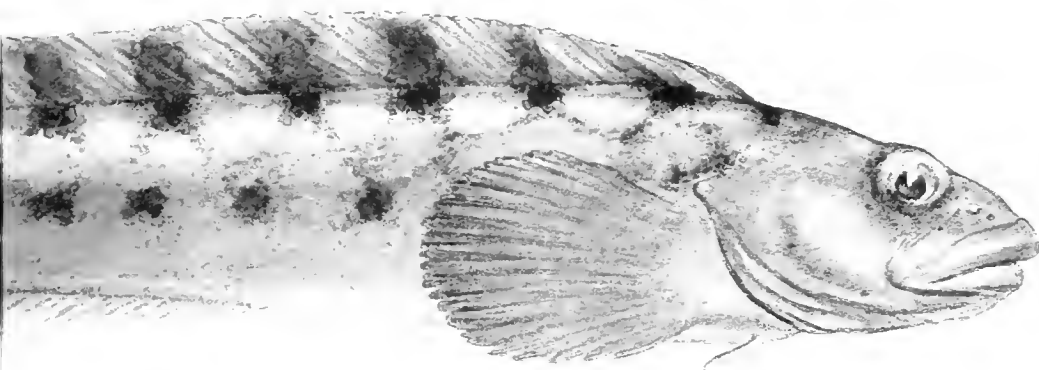
A NOTE ON THE INHERITANCE OF COLOUR IN ONE BREED OF PIGEONS—AN ATTEMPT TO DEMONSTRATE A MENDELIAN TYPE OF TRANSMISSION.

By J. S. W. NUTTALL, M.B.

THE inheritance of feather colour in domestic pigeons having proved so difficult to fit into any scheme, I determined, in 1914, to investigate the matter afresh, confining my energies to one breed and to a small series of colours. I am strongly of opinion that when distinct types or breeds are crossed, the results are complicated by the occurrence of reversion. The matter is obviously complex; a simple beginning was indicated. The work done completes the preliminary stage only; the onset of war, of necessity, seriously interrupted further experiments. The results are given in bare outline, but it was thought advisable to publish some details of what has been done.

The breed of pigeons used is known to fanciers as the "Racing Pigeon," a variety which is being used in the present war in the Overseas Pigeon Service, and is doing useful work. This breed has been firmly established in this country, and more firmly in Belgium, for many years. Various colours are to be found, but the vast majority of the hundreds of thousands bred yearly are of the following colours— blue, blue chequered, red chequered and mealy. A short description of these colours is necessary.

The blue birds are similar in colouring to the *Columba livia*, except that the ground colour is, as a rule, brighter or "cleaner" in appearance, though distinctly slaty-blue. They present, in common with *Columba livia*, the typical wing-bars, the white (albescent) or blue croup and the tail-bar. The ground colour of the primary and secondary wing-quills, and the tail-quills, is dark blue. The blue chequered birds are similar to the blues with the addition of chequering. The wing-bars of the blue are mainly due to spots on the outer sides of the secondary wing feathers; the chequering arises from an extension of these spots to the

smaller wing coverts and other feathers. The wing-bars and the tail-bar are present as in the blue.

The colour of the so-called mealy birds is difficult to describe. The ground colour is somewhat like that of fine oat-meal; the wing-bars are reddish—approaching the colour of damp sand. The mealy birds differ in two salient points from the blues—the wing- and tail-quills are, as a rule, pale in colour, and the tail-bar is absent.

The red chequered birds stand in the same relation to the mealies as the blue chequers do to the blues, i.e., they are mealies with the addition of chequering. The wing-quills and tail-quills are generally pale in colour; there is no tail-bar.

The colour of the birds used being of unknown composition, the results have been based on group, rather than individual, matings. The calculated results have been arrived at by considering all the types of gametic combinations theoretically possible, and by assuming that each pair of birds produces 16 offspring.

The experiments have led to the following conclusions:

1. Red (of red chequer or mealy) is dominant to blue.

2. Presence of chequering is dominant to absence of chequering.

3. Red chequers may be homozygous or heterozygous for colour or chequering.

4. Mealies may be homozygous or heterozygous for colour.

5. Blue chequers may be heterozygous or homozygous for chequering, but are homozygous for colour.

6. Blues are homozygous.

Two pairs of allelomorphic factors may therefore be considered:

R (domt.), presence of red. r (rec.) absence of red.

C (domt.), presence of chequering. c (rec.) absence of chequering.

Red chequer may then be represented by RC, blue chequer by rC, mealy by Rc, and blue by rc.

Group 1. Red Chequer × Red Chequer.

Composition of parents, $RCRC$, $RCRc$, $RCrC$, $RCrc$, $RcrC$.
Types of mating possible, 15.
Number of offspring (16 from each mating), 240.
Calculated appearance:

(240)   196 Red cheq. : 20 Blue cheq. : 20 Mealy : 4 Blue.

(70·8)   57·9   :   5·9   :   5·9   :   1·4.

Observed appearance of 71 birds produced in this group:

    (71)   50 Red cheq. : 11 Blue cheq. : 8 Mealy : 2 Blue.

Group 2.   Red Chequer × Blue Chequer.

Composition of parents—five red chequers as in group 1, two blue chequers *rCrC* and *rCrc*.

Types of mating possible, 10.

Number of offspring, 160.

Calculated appearance:

    (160)   100 Red cheq. : 44 Blue cheq. : 8 Mealy : 8 Blue.

    (94·8)   59·3   :   26·1   :   4·7 : 4·7.

Observed appearance of 95 birds produced in this group:

    (95)   41 Red cheq. : 50 Blue cheq. : 2 Mealy : 2 Blue.

Group 3.   Red Chequer × Mealy.

Composition of parents, red chequers as in group 1, mealies *RcRc* and *Rcrc*.

Types of mating possible, 10.

Number of offspring, 160.

Calculated appearance:

    (160)   104 Red cheq. : 46 Mealy : 8 Blue cheq. : 2 Blue.

    (44·9)   29·2   : 12·9   :   2·2   : 0·6.

Observed appearance of 45 birds produced in this group:

    (45)   28 Red cheq. : 11 Mealy : 4 Blue cheq. : 2 Blue.

Group 4.   Red Chequer × Blue.

Composition of parents, five types of red chequers as in group 1, a single type of blue, *rcrc*.

Types of mating possible, 5.

Number of offspring, 80.

Calculated appearance:

    (80)   40 Red cheq. : 16 Mealy : 16 Blue cheq. : 8 Blue.

    (40)   20   :   8 :   8   : 4.

Observed appearance of 40 birds produced in this group:

    (40)   17 Red cheq. : 7 Mealy : 11 Blue cheq. : 5 Blue.

Group 5.   Mealy × Mealy.

Composition of parents, *RcRc* and *Rcrc*.

Types of mating possible, 3.

Number of offspring, 48.

Calculated appearance :

(48)   44 Mealy : 4 Blue.

(33)   30·2   :   2·8.

Observed appearance of 33 birds produced in this group :

(33)   28 Mealy : 5 Blue.

Group 6.   Blue Chequer × Blue Chequer.

Composition of parents, *rCrC* and *rcrC*.

Types of mating possible, 3.

Number of offspring, 48.

Calculated appearance :

(48)   44 Blue cheq. : 4 Blue.

(72)   66   :   6

Observed appearance of 72 birds produced in this group :

(72)   67 Blue cheq. : 5 Blue.

Group 7.   Blue Chequer × Blue.

Composition of parents, *rCrC, rcrC, rcrc.*

Types of mating possible, 2.

Number of offspring, 32.

Calculated appearance :

(32)   24 Blue cheq. : 8 Blue.

Observed appearance of 32 birds produced in this group :

(32)   20 Blue cheq. : 10 Blue : 1 Red cheq. : 1 Mealy.

Group 8.   Blue × Blue.

Composition of parents, *rcrc.*

Types of mating possible, 1.

Number of offspring, 16.

Calculated appearance :

(16)   16 Blue.

Observed appearance of 32 birds produced in this group :

(32)   32 Blue.

Group 1.   In this group the observed red chequer and mealy figures are lower, the blue chequer and blue higher, than the estimated figures. To my mind there is a simple explanation of this.   Fanciers generally object to this type of mating, preferring to " mix the colours"; it thus naturally follows that the majority of red chequers are heterozygous for colour, and when mated red to red, they will produce less than the

expected number of red chequers and more than the expected number of blue chequers. The experiments having been for the present almost suspended, the testing of the extracted colours is incomplete. As far as this has been carried out, the anticipated results have been obtained.

The blue chequers have proved to be homozygous for colour, some being heterozygous for chequering; the mealies homozygous for absence of chequering, some giving rise to blues; the blues have proved to be homozygous for colour and absence of chequering. (See comments on group 6 for occurrence of white in these extracted colours.)

Group 2. The heterozygous composition of red chequers may be expected to have a greater effect in this type of mating than in group 1 type. The blue chequers being homozygous, and probably the majority of the red chequers heterozygous for colour, it follows that the observed red chequer figure will be low and that for blue chequer high. It is worthy of mention that the colour of red chequers bred from dissimilarly coloured parents (red chequer and blue chequer, or red chequer and blue) is, as a rule, richer than that of birds bred from two reds. This probably accounts for the popular aversion to red chequer and red chequer mating. Red chequer cock birds from red chequer × blue chequer almost invariably possess black ticks. I have not found an example of these black ticks in hen birds; brown ticks may however sometimes be met with.

All the red chequered cocks which have come under my notice, having one parent blue or blue chequered, present some degree of ticking. A proportion of those from two red chequers and of those from red chequer × mealy, are free from ticks and do not appear to develop any with age. On this may rest the possibility of separating the homozygous and heterozygous red chequers of the male sex.

Group 3. As, in this group, red may come from either parent, the effect of the heterozygous composition of red chequer is modified and the observed approaches closely to the estimated result. The extracted blue chequers and blues have so far proved to be pure for colour.

Group 4. The results obtained in this group and in group 3, suggest that chequering depends on a single factor, and that it may produce its full effect even when contributed by one parent. The eleven blue chequers in this group were typical of the chequered type.

Group 5. A correlation was observed between paleness of plumage (ground colour especially) and light coloured beaks and claws in some of the mealies in this group. Of the blues, however, two in particular were exceptionally sound in colour with dark beaks and claws. Blues

from this group have been tested at greater length than most of the extracted colours and have been found to be pure.

Group 6. The results from this group do not support the generally accepted view of fanciers that almost any colour may arise from blue chequer × blue chequer. I have examined the results of many breeders, and where cross-mating can be definitely excluded, the results agree with my own. The majority of the birds used in this group had at least one red parent. This fact is strong evidence of their recessive and homozygous nature.

Some blue chequers from two reds have a reddish brown tinge in some of the wing-quills especially. I expected to obtain reds from these, but so far have failed. This type of blue chequer appears to give an increased proportion of reds when mated to reds.

Pied types. The behaviour of white is difficult to follow. Two main types are met with, the "gay" pied and the type with a few white feathers. The majority of gay pied birds follow a fairly uniform pattern in the distribution of white. This "pattern" type is probably dominant to self colour. On the other hand the type with a few white feathers is recessive. In testing the extracted colours several examples of this recessive type arose. No pied birds were used in any of the experiments.

Group 7. The red chequer and mealy in this group arose from the same pair and in the same nest. Their occurrence is disconcerting as the likelihood of cross-mating was no greater in their particular case than in any other. However, that cross-mating is the explanation, I feel assured of by the subsequent offspring of the parents of these two exceptions. Thus far 14 birds have been produced from this one pair in complete isolation. The seventh pair of young now (Mar. 15th, 1917) three weeks old provides no single atypically coloured specimen.

The appearance of this single family is :

(14)   8 Blue cheq. : 6 Blue.

It may be allowed that the composition of the blue parent is *rcrc* and that of the blue chequer *rCrc*.

Group 8. In this group one of the birds had two white primary wing-quills. Of the remaining 31 birds, 30 were typical blues, one had grizzle primaries and a general colouring approaching more closely to grizzle than blue. Grizzle being a macroscopic admixture of blue and white, all the birds in this group have been considered to be substantially blue.

THE INHERITANCE OF GLUME LENGTH IN *TRITICUM POLONICUM.*

A CASE OF ZYGOTIC INHIBITION.

By W. O. BACKHOUSE,
Economic Botanist to the Argentine Government.

(With Chart.)

THE sub-species of *Triticum* known as *T. polonicum* is characterised by long glumes which, in extreme cases, can attain a length of 40 mm. whereas that of an ordinary wheat is in the neighbourhood of 10 mm. only. There is a large number of varieties of *T. polonicum* known, varying considerably in minor characters such as colour of leaf, colour and shape of grain, degree of felting, etc., also in glume length itself, some having an average length of about 19 mm., others as high as 28 mm. The sub-species *T. polonicum* hybridises easily with both *T. durum* and *turgidum* and shows[1], by the total lack of sterile individuals in F_2 when crossed with varieties of the former, that it might be considered, genetically speaking, merely an aberrant form of the sub-species *T. durum.* The result of hybridising the long and the short glume lengths is a first generation intermediate in this respect, splitting in the second into long, intermediate and short in the ordinary 1 : 2 : 1 ratio, but not in a manner possible to classify by eye and necessitating the plotting of a curve to show the segregation.

When at Verrières, in 1911, through the kindness of M. Ph. de Vilmorin, the writer was able to examine a collection of varieties of *T. polonicum* grown there and was struck by the fact that there were none with perfectly smooth glumes and, furthermore, that the shorter the glume of the variety, the more felted did it seem to be. The longest glumed varieties, being only faintly pubescent, would roughly speaking

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[1] R. H. Biffen, *Journal of Genetics*, Vol. v. p. 225.

be classed as smooth. With the object of investigating this, in 1912 a cross was made between a variety of *T. polonicum*, with an average glume length of 29 mm. and very faintly pubescent, and a variety of *T. durum*, which will be referred to in this paper as *Kubanka*. This last is a smooth and otherwise typical example of *T. durum*, with an average glume length of 12 mm. The first generation was a hybrid of intermediate length—actually of an average of 18 or 19 mm. It was, however, remarkable in that it was distinctly pubescent—very much more so than the *polonicum* parent. The second generation was surprising, for it was soon observed that there was a proportion of plants bearing fully pubescent ears—pubescence, be it remembered, is a dominant character—yet the variety of Polish wheat used as a parent would have been classed as smooth in comparison with such a wheat as Rivet or Essex Rough Chaff.

At harvest time, a middle glume in the ear of each plant was measured and a curve plotted of the number of plants of each glume length in millimetres (Chart[1], Fig. 1 a). The plants were also classified into pubescent, intermediate and smooth, by means of a hand lens. The *polonicum* parent would have fallen among the intermediates in this classification, while the smooths were, as far as could be seen, perfectly glabrous. The numbers observed, considering glume length alone, were as follows:

	Long and Intermediate	Short
	172	55
Expectation ...	170·25	56·75

A glance at the curve of this family will show that there is no dividing line between the longs and the intermediates but, actually, the shorts can be distinguished by eye—that is to say, an extra short glumed heterozygote. A starved plant, for example, which might fall in the 14 or 15 mm. lengths class, has an indefinable something about it which points to its really belonging to the heterozygote class.

The carrying of large numbers of plants into the F_3 generation showed that, while only two mistakes were made at the short end of the curves, it had been impossible to pick out any but the extreme longs with the certainty that they would be pure to their particular length. Considering those with a glume length varying between 10 and 14 mm. as being pure short segregates and those between 15 and 31 mm. as including both the longs and the heterozygotes, a count of the proportion of pubescent individuals shows that in the short glumed

[1] See pp. 130, 131 and explanation on p. 133.

class, the roughs predominate in the ordinary 3 : 1 proportion (Chart, Fig. 1 b).

	Felted Glume	Smooth
	40	15
Expectation ...	*41·25*	*13·75*

Examining 56 individuals, the theoretical expectation of homozygous longs, and beginning at the extreme long end of the curve, it was found that there were, among them, no individuals which could be called felted, though with a lens a short velvety pubescence was seen on most. Among the individuals with glume length between 15 mm. and 22 mm., which may roughly be said to comprise the heterozygotes, the proportion was 85 felted to 31 smooth; but here there were only 15 individuals which could confidently be called felted—in the majority of cases the closest scrutiny was needed to determine to which category they belonged.

Finally the long class were examined critically—with the help of a lens and the individuals selected which appeared to be absolutely smooth —as smooth as the original short glumed *Kubanka*. These plants were grown the succeeding year and found to be all pure longs except two, and, what is more important, a careful inspection with a lens showed them to be also breeding true to this smoothness: a smoothness which, however, turned out to be only apparent in some cases.

Test crosses were made between these smooth lines and the original *Kubanka*, also other *durums*, to see whether the presence of the pubescence in any way affected the segregation of glume length. The second generations from these test crosses were surprising for, while some were all smooth, others behaved in the same way as the original cross (giving a 3 to 1 proportion of roughs and smooths among the short glumed class), differing only in that the pubescence was of a minor degree, as exemplified in the Canadian variety *Prelude*. From this it will be seen that the long glume was able to inhibit the expression of a dominant character and, furthermore, that there was a direct relation between the length of the glume and the degree of felting—the greater the glume length, the less being the pubescence, even among the variable heterozygotes. This will be better illustrated in the following case.

The same variety of *T. polonicum* used in the first experiment was crossed with a felted, black glumed variety of *T. turgidum*, not unlike Rivet wheat of which it is, in fact, a descendant. The average glume length of the *turgidum* is 11 mm. and of the *polonicum* 28 or 29 mm. The first generation was intermediate in glume length—varying between 14 mm. and 17 mm. It was fairly felted and in colour white or faintly

tinged. In this experiment the *polonicum* will be considered smooth, as indeed it is in comparison with the other; the classification was done by eye, unaided by a lens. The second generation was plotted as a curve (Chart, Figs. 2, 3, 4 and 5) in the same way as the Kubanka Polish cross. Here again it was impossible to separate the pure longs from the heterozygotes and statistically there is no sharp dividing line between the shorts and the heterozygotes (Chart, Fig. 5). However it is fairly safe to say that the pure shorts are comprised among those with a glume length between 9 and 13 mm.—though undoubtedly several of 13 mm. are poorly grown heterozygotes.

The ratio of short glume to long is:

	Long and Intermediate	Short
	514	178
Expectation ...	*519*	*173*

There were 692 plants in this family, besides 39 which were not noted, being too green at the time of harvesting to determine the colour.

The second curve (Chart, Fig. 4) shows the total analysed into those individuals which were felted like the short glumed parent and those (shown by the dotted line) which were practically smooth, like the Polish parent. Here again, it will be seen, the length of the glume has acted as an inhibitor of pubescence. A study of the colour shows this inhibiting nature even more clearly (Chart, Figs. 2 and 3). With the single exception of one plant of 16 mm. glume length, *all* the fully coloured individuals are between 8 and 13 mm.—among the shorts, in fact. The proportion is:

	Tinged and White	Coloured
	129	49
Expectation ...	*133·5*	*44·5*

It was impossible to draw a really satisfactory distinction between the heterozygous tinged or faintly coloured, and the colourless, as the faintly tinged individuals were easily confused with stained whites, but the pure blacks were easily classified. Nevertheless Chart, Fig. 3, shows a curve of those individuals which were considered to be tinged.

The point of interest which attaches to this curve is the distribution of the tinged individuals; it will be seen (Fig. 3) that they are not quite evenly distributed among those with glume length varying between 13 and 20 mm., but that they occur with greater frequency at the short end of the heterozygote curve. The colour seemed to be quite independent of the pubescence. To ascertain whether, among the

longs, there existed some which, though they could not show it, were, in fact, homozygous for colour, five long glumed individuals were crossed with the short glumed *Kubanka* and the first generation plants grown this year (1916). There is no need to wait for the second generation for the results. Two individuals gave all tinged, one gave all white, and two gave a mixture of tinged and whites. There can be no doubt, therefore, that when the second generation is grown and true shorts appear, there will also appear fully coloured individuals.

Only two families of long × short have been described but they are typical of no less than seven second generations grown, all of which show that the long glume in wheat behaves as an inhibitor which, in extreme cases, is as complete as though it were a case of genetic repulsion. There remains only one thing more to note—that from such long and short glumed crosses it is possible to isolate a number of pure lines, each with a different average length and breeding perfectly true to its particular length.

It is possible that the greater variation in length of glume among the *polonicums* is merely due to the effect of magnified small differences, these escaping observation in the ordinary short glumed wheats. If a curve be plotted of the variation in short glumed wheats, this is always steep and acute ; long glumed varieties, on the other hand, however often reduced to single plant cultures and so purified, always give a long low curve. The heterozygote curve is more or less intermediate in shape between the two parents[1].

Should it be the case that the apparent greater variation in glume length is only due to a magnifying effect of the extra long glume, then it seems possible to regard *T. polonicum*, which has always been considered a good sub-species in wheat, as merely a number of variations of *T. durum*, differing from the short glumed type in one single unit character which makes the long glume. Thus, had the existence of black and fully pubescent *polonicums* been possible, a separate sub-species would possibly never have been created.

Further experiments with *T. polonicum* throw some light on the strange behaviour of Polish Rivet crosses[2].

I have been able to examine some of Professor R. H. Biffen's material and am familiar with the behaviour of this cross in England. When leaving for this country, I took with me, in the form of grain, hybrids

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[1] R. H. Biffen, *Journal of Agricultural Science*, Vol. i. Part 1.

[2] "Suppression of Characters on Crossing," R. H. Biffen, *Journal of Genetics*, Vol. v. Part 4.

Fig.1a

Fig.1b

Fig.2

Fig.3
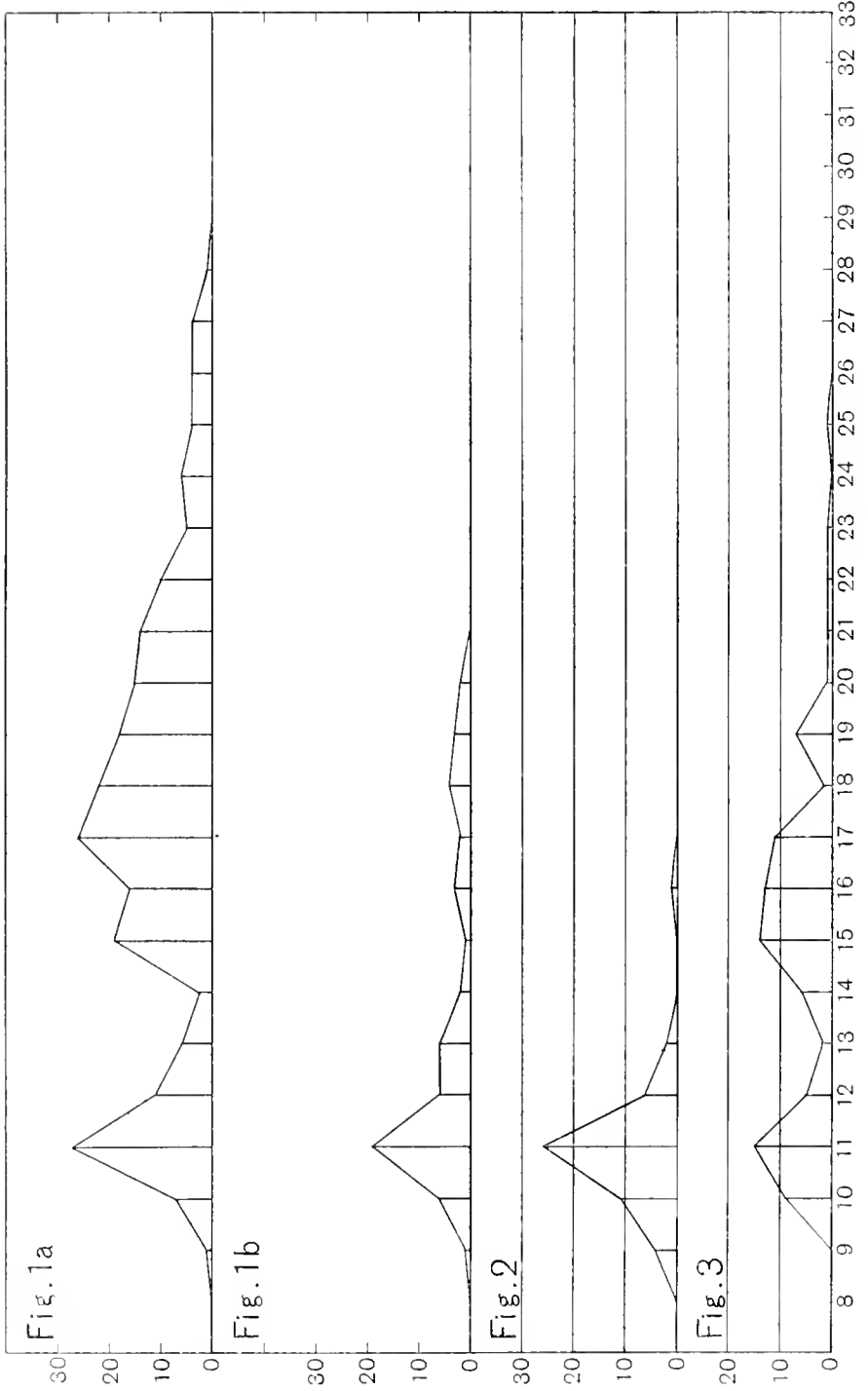
Fig. 4
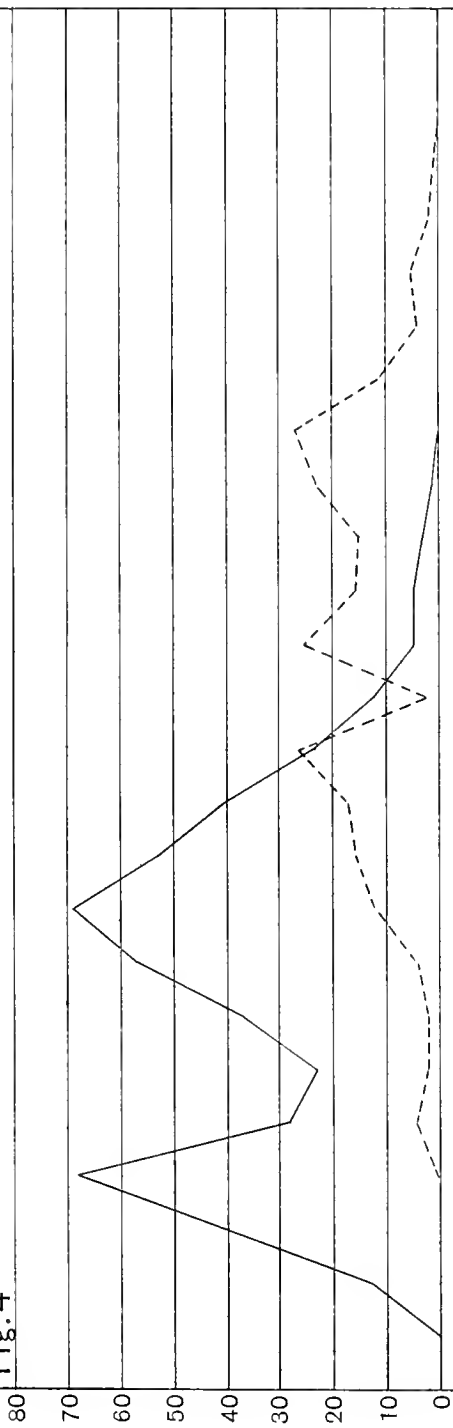
Fig. 5
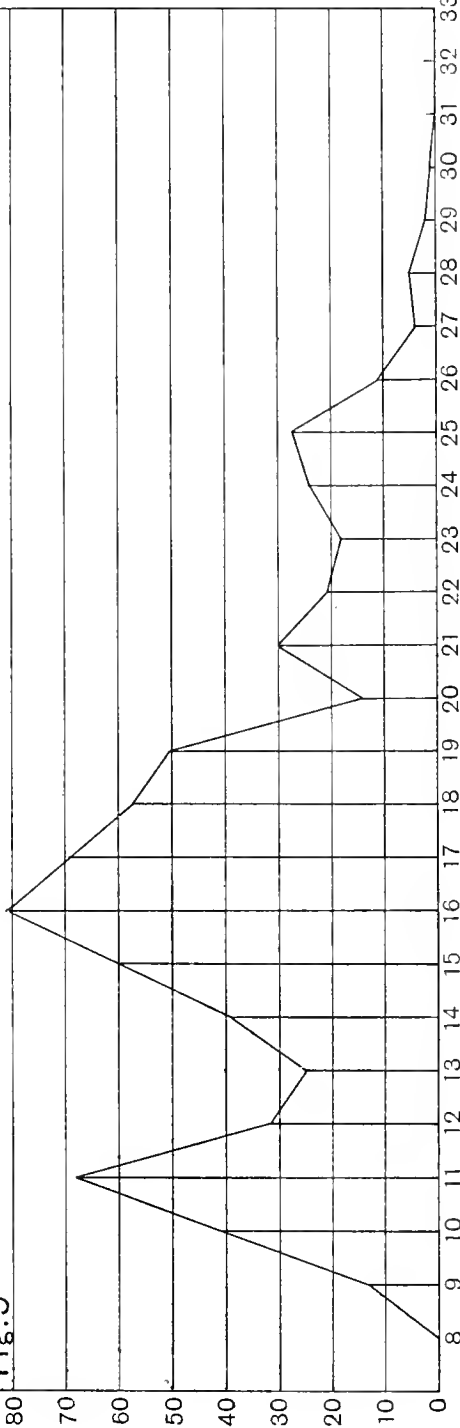
For explanation see p. 133.

already made with the same strains of Rivet and of Polish wheats as used by Biffen. The first generation was grown at Pergamino, in 1913, and was notable from the start as being decidedly tinged. The second generation was divided and grown, in 1914, in three different places, viz. in the north, centre and south of the wheat producing area of the Argentine Republic. In the north, all the individuals were colourless, as in England. In the centre, at the latitude of Buenos Aires, some of the short glumed individuals were tinged. In the south, in the Pampa, the coloured ones were fairly clearly defined and could be classified, giving the following proportions:

Rivet × Polish F_2. *Guatraché, Pampa.*

Long and Intermediate glume length		Short glume length	
72		30	
Coloured	White	Coloured	White
0	72	7	23

Three doubtful shorts grown in 1915, to test, bred true to short glume, but not to colour, and gave a total of 7 white to 13 coloured. The proportion is peculiar but it is always difficult to distinguish the homozygous coloured individuals from the heterozygous tinged ones.

Polish × Rivet F_2. (*Reciprocal of the other cross.*)

Long and Intermediate glume length		Short glume length	
25		9	
Coloured	White	Coloured	White
0	25	4	5

It will be observed that here again the coloured individuals are only found among the short glumed category. The coloured segregates of these crosses are never quite so deeply coloured as Pedigree Rivet wheat itself and grade almost imperceptibly from coloured to tinged and tinged to colourless.

The interest of the experiment, however, lies in the fact that, whereas in England the colour disappears and does not return in any subsequent generation, the result of growing F_2s, obtained in identically the same way, in the Argentine, is to prove that at any rate the colour is there and, given suitable climatic conditions, will show itself. Rivet wheat, grown for comparison, had the same peculiar mouse-grey colour as in England and was no darker in this climate.

The cause of the suppression of colour in this particular cross must be sought for in the shape of an inhibitor, brought in, either by Polish wheat and meeting something in Rivet to release it, as it were, or *vice versa*; for this particular strain of *polonicum* crossed with coloured varieties other than Rivet gives coloured descendants, in climatic conditions under which, crossed with Rivet, they are colourless.

EXPLANATION OF CHART (on pp. 130, 131).

Fig. 1a.   Family 74/14.   *Kubanka × Polonicum.*

Curve of glume length plotted for 227 individuals, showing that, whereas the short glumed individuals, namely those whose glume length varies between 9 and 14 mm., are easily distinguished from the rest, there is no discontinuity in the curve between the heterozygotes (of, say 15 mm. to 22 mm.) and the bulk of the homozygous longs.

Fig. 1b.   Curve of those individuals which were completely felted. It will be seen that there are few of heterozygote glume length and no longs.

Fig. 2.   Family 104/16.   *Polonicum × Turgidum* 179.

The fully coloured individuals. These, with one single exception, are among the short glumed plants.

Fig. 3.   Those individuals which were not fully coloured and classed as tinged. Owing to gradation in colour from plainly tinged to faintly tinged or stained white, this curve is only of relative value, but serves to show that among the real longs there were only three or four with a trace of colour.

Fig. 4.   The same curve as in Fig. 5, resolved into felted individuals—shown by the whole line—and those classified, without the aid of a hand lens, as smooth—shown by the dotted line.

Fig. 5.   Curve of the whole family of 692 plants, plotted for glume length alone.

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

By Mrs ONERA A. MERRITT HAWKES, M.Sc., B.Sc.

Number I.   ON LARVAL CHARACTERS.

(With Plate VIII and two text-figures.)

Section I.   On the Inheritance of Spots in the Larva.

THE larvae of *P. ricini* and *P. cynthia* are alike in general body colour but differ from one another as regards the number of black spots present in the last instar.

When an adult larva, *P. cynthia* has seven longitudinal series of black spots, consisting, in all segments except the anal and cephalic, of two mid-dorsal, two upper lateral, two or three spiracular and one or two lower lateral spots.   The upper lateral, spiracular and lower lateral are arranged bisymmetrically.   The spots of the lower lateral series occur above the thoracic legs, on the abdominal legs and at a low level on the legless segments.   In the thoracic segments there is an extra spot on each side at the base of the thoracic legs (Fig. 1).   I have not been able to breed *P. cynthia* (Drury) from Ning-po, so give this description from the verbal statement of Mr J. W. Watson.   Packard(9) gives a description and figure of *P. cynthia advena* (Walkeri), the nearly related American species, but does not mention the moth from Ning-po.   Packard's description of *P. cynthia advena* would do perfectly for the Ning-po variety, not only as regards spots but also in other details, but as I have found the scales of the Ning-po *cynthia* considerably different from those of *advena*, and as they may differ considerably in genetic constitution, it is possible that further observation may show an increasing number of distinguishing points between the two.

P. ricini differs from *P. cynthia* in the absence of the mid-dorsal, upper lateral and spiracular series of spots. I bred a number of the wild *P. ricini* and found that the lower lateral spots varied considerably— there was every condition between two spots in each segment and none. (Text-figure 1.) I did not inbreed the *ricini*, hence do not know whether,
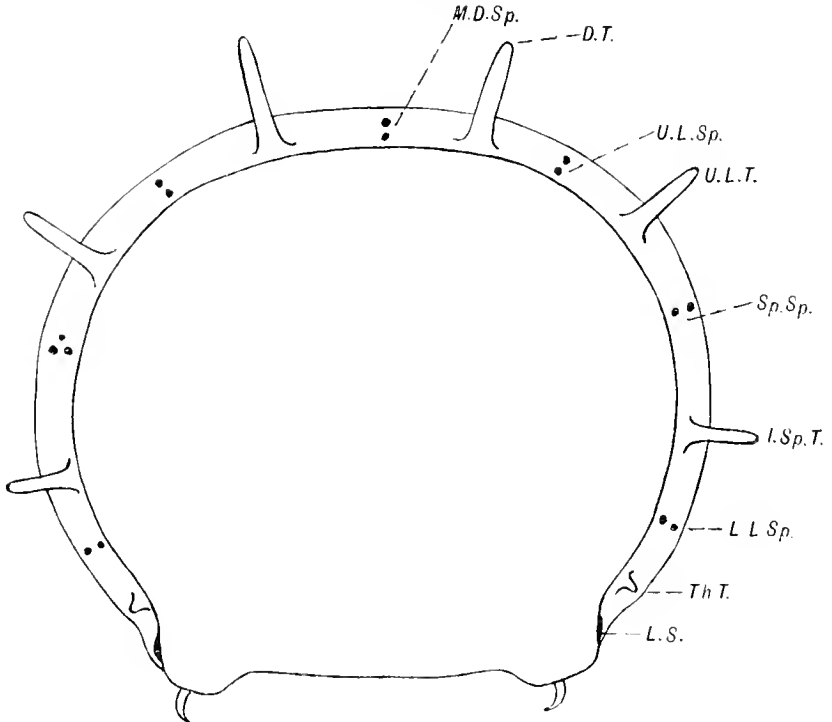
Fig. 1. Diagrammatic drawing of the second and third thoracic segments in *P. cynthia.*

D.T. = Dorsal tubercle.	*Sp.Sp.* = Spiracular spots.
I.Sp.T. = Infra-spiracular tubercle.	*Th.T.* = Thoracic tubercle.
L.L.Sp. = Lower lateral spots.	*U.L.Sp.* = Upper lateral spots.
L.S. = Leg spots.	*U.L.T.* = Upper lateral tubercle.
M.D.Sp. = Mid-dorsal spots.	

as regards this variation, there is or is not segregation within the species. Lefroy(8) when describing *P. ricini* (Eri worm) gives two types of adult larvae, spotted and plain. Mr Watson however believes this is an impure race due to a former mixture with *P. canningi* (Hutton). The description of the spotless larva suggests that it has no spots in any position, but the statement made in reference to this point is not

definite. The drawing on Plate V (8), which is not sufficiently clear to be authoritative, shows no spots.

The difference between the two species therefore is, that whilst *cynthia* has seven complete series of black spots, five of these are entirely lacking in *ricini* and the remaining two are generally partially present but are variable. The condition in *cynthia* is therefore called spotted and denoted by *S*, whereas that in *ricini*, which superficially looks plain, in spite of the lower lateral series, is called plain and is represented by *P*. (Plate VIII, figures B 2, C 3, C 4.)

Method of Rearing.

The larvae were reared at first in glass-lidded boxes, and later in zinc cages covered with black net. The room used for breeding purposes was heated by steam pipes and kept damp by water boxes on the pipes and damp cloths over the open cages. The minimum of handling was resorted to—I soon dropped the usual method of moving the young larvae by means of a camel's hair brush, as it seemed unsuitable to a larva so well provided with setae, preferring the more tedious method of waiting until the larvae had crawled on to a leaf or stem which could be moved by forceps. The greatest care was taken to keep the boxes clean; when changed they were sterilised with boiling water and in the later stages, when disease appeared, by boiling water plus carbolic. Periodically the larvae were all turned out of the room and the room was sterilised with a formalin apparatus, but as the experiment and the War progressed coincidentally, it became impossible to obtain the formalin and finally, after nearly two years, there was much disease. The larvae were doubtless very susceptible to disease as, owing to inadequate warmth, they were eating little and growing slowly.

Cynthia and *ricini* were crossed by Mr J. W. Watson at Manchester. He divided the eggs between a number of entomologists, giving me 180 eggs from which 149 adult larvae were reared. Unfortunately, the other breeders reared only a very small proportion of their larvae and kept no record of the characteristics.

The F_1 generation.

All the 149 larvae of this generation had spots on the upper part of the body; most had the full complement of spots characteristic of *cynthia* and were therefore spotted (*S*), but some had only a portion of

these spots and were called "reduced spots" (*RS*). The two types were distributed among the 110 imagines as follows :

	S		RS	
	♂	♀	♂	♀
	38	28	8	36
Totals	66		44	

This table shows a preponderance of males among the spotted forms, but further investigation showed that the character was not sex-limited.

TABLE 1.

Table to show results of various matings in the F_1 *generation.*

	♂ ♀	♂ ♀	♂ ♀	♂ ♀
Types of matings ...	$S \Longleftrightarrow S$	$S \diagdown RS$	$S \cdot RS$	$RS \Longleftrightarrow RS$
Types of larvae ...	P S RS	P S RS	P S RS	P S RS
M 5. 6. 7. 12 ...	76. 194. 56	—	—	—
	58. 125. 29	—	—	—
M 2. 11	—	40. 138. 36	—	—
	—	*19. 63. 18*	—	—
M 4	—	—	18. 44. 23	—
	—	—	*14. 25. 13*	—
M 3. 9. 10	—	—	—	54. 123. 49
	—	—	—	*29. 51. 36*
Ratio of *P* to *S* · *RS*	1 : 3·28	1 : 4·35	1 : 3·72	1 : 3·48
Ditto	*1 : 2·65*	*1 : 4·26*	*1 : 2·71*	*1 : 3·0*

The first column contains the numbers given to the matings and used throughout the records; thus *M* 5 means mating five.

The ordinary numerals refer to the larvae and the italics to the imagines.

The F_2 *generation.*

Twelve matings produced twelve F_2 families, which consisted of *S*, *RS* and *P* types of larvae in the proportions 3 (*S* × *RS*) to 1 *P*. Every variety of mating (see Table I) was made to test whether *S* and *RS* had different hereditary values, but these few matings gave no indication of any difference. It is equally clear that no mating took place between homozygous forms of either *S* or *RS*. This generation only showed that some type of spotted form was dominant. The *particular S* and *RS* parents used in these particular matings appear to have the same inheritance value, as judged by their offspring.

It was observed that there appeared a regularity in the disappearance of the spots, for example, when only one spot was lacking, it was

usually from the mid-dorsal region of the second abdominal segment. The mid-dorsal spots had usually entirely disappeared before the upper lateral series were affected, although there might be a simultaneous diminution in the size of the spots all over the body. This suggested that one was not dealing with spottedness (S) as a simple character but as a compound of a large number of characters, each of which was related primarily to a definite segment and subsequently to a segment as a part of a longitudinal series.

The above statement, "every variety of mating," must be qualified— the RS condition represents the loss of anything between 1 and 140 (approx.) spots. On account of the small space and limited amount of food at my disposal, I have had to experiment as if the S condition acted as a heritable unit; ideally, the matings should have been made between each different type of reduction. But as the S and P types occur naturally, the method of experiment used may be considered as a useful and justifiable introduction to further detailed and more analytical experiments. Also, as the lower lateral row of spots occurs in *ricini* and the upper rows are absent, may it not be that there is a connecting link between the gens for the upper rows of spots, which has, somewhere in the past, made them act as a unit, in appearance or disappearance, independent of the lowest rows of spots?

Table I shows that the proportions among the larvae and imagines are approximately the same, in spite of the numbers, which appear so small when compared with those of the Japanese workers. This means that, under domesticated conditions, there is no selective death rate as regards spotted and plain larvae in the pupae: this in an important point in deducing results from an animal which appears in three stages in its life history and where, in artificial conditions, the death rate is so great. It should not be forgotten however that, even in its native haunts, the death rate must be very high. Thus Crampton(2) states in reference to *Philosamia cynthia* (*adrena*)—"the perfect imagines constituted only $16 \cdot 6 \, ^{\circ}/_{\circ}$ of the whole number of individuals which entered the cocoons, from which we may gain an idea of the severity of the conditions under which the quiescent pupa exists."

In the early stages the majority of deaths are due to the strain at ecdysis, but in the later stages, deaths are mostly due to disease. An attempt was made to find if there was a differential death rate for the S, RS and P types during the first instars, but it was unsuccessful. The larvae are all spotted when they emerge and become RS and P at later ecdyses; but whereas these changes take place at regular and

known stages in the pure-bred larva, in the hybrid the reductions took place at various stages in the same and in different families. Although Table I shows that there is no differential death rate in the pupal stage, one cannot make any deduction from it as regards the larval death rate.

The plain (*P*) larvae usually appeared in the third and fourth instars, but in one family the change took place in the second instar. Lefroy(8), p. 21, writes: "From the second stage onwards, the black spots are retained by some larvae, while in others they entirely disappear in the second stage: in a few, a few black spots may be present faintly till the third stage and then disappear." This irregularity supports Mr Watson's contention that the commercial Eri worm is a hybrid and hence makes it imperative that scientific work should be done only with the wild *ricini*, collected from the forests.

The *RS* condition is particularly difficult, as close observation showed that during the last stage itself spots may disappear. Entomologists usually consider that any larval change in colour and marking only takes place at an ecdysis, but that is certainly not the case in this hybrid. It is this which has made the work of separating the *S* from the *RS* very difficult and has allowed possibilities of error to creep in. Thus a larva labelled *S* may, between examination and spinning-up, have lost some spots and should therefore be called *RS*, or again, a larva labelled *RS* may, during the same period, have lost all its few spots and hence be a *P*. The latter occurrence is much rarer than the former. The daily examination took place in the morning, on account of the light, and the spinning usually began in the late afternoon or evening; as the changes noted took place between the daily examinations, they may have taken place without my cognisance before spinning up.

Healthy larvae are covered with a white powder which does not hide the black spots; nevertheless, in all intermediate (*RS*) conditions the powder was brushed off before the final decision was made.

The F₃ generation.

Nineteen matings were made to produce this generation, seven were between plain parents and the others were as follows:

> *S* × *S*—*S* matings (*M* 27, 15, 17, 42, 47, 41, 25, 30).
> *S* × *S*—2 matings (*M* 24, 22).
> *RS* × *RS*—2 matings (*M* 49, 52).

No matings produced only full spotted (S) larvae, but three matings (30, 47, 17) produced S and RS larvae but no plain ones—the results of these matings are as follows :

Types of larvae			P	S	RS
Mating 30	...	...	0	34	14
,, 47	...	...	0	19	4
,, 17	...	...	0	6	6
Totals		...	—	59	24

The history of mating 30 is interesting, for it had a series of descendants, all of which were S and RS, none being P, until in F_6 there appeared a family consisting entirely of S larvae (see Table II).   Evi-

TABLE II.

Table to show the Inheritance of a Pure S Family.

P (ricini) × S (cynthia)

F_1 S 1 (67) × S 1 (68) and RS larvae

F_2 S 6 (22) × S 6 (19) and RS and P larvae

F_3 RS 30 (15) and S and RS but no P larvae × S 42 (7) and RS and P larvae

F_4 S 75 (12) × S 75 (11) and RS but no P larvae

F_5 S 93 (1) × S 93 (2) and RS but no P larvae

F_6 The offspring of mating 107 which consisted entirely of S larvae
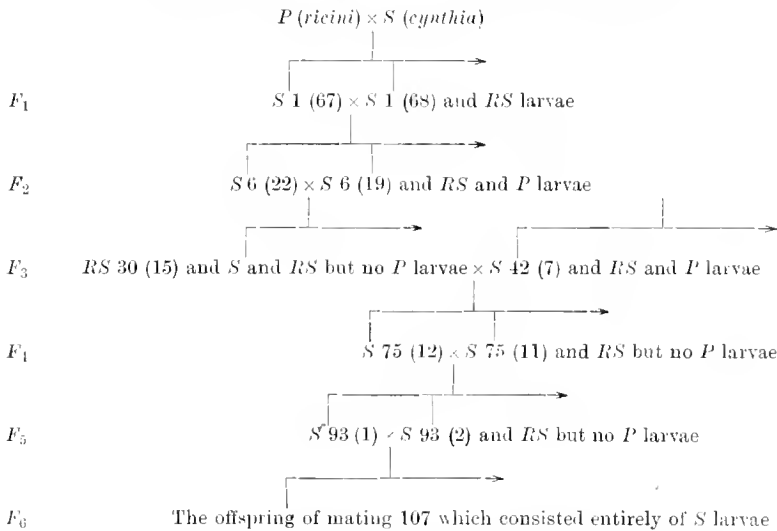
The formulae used are to be interpreted thus : for example, RS 30 (15) and S and RS but no P larvae means, the individual was a larva with reduced (RS) spots, the offspring of mating 30, of which it was the fifteenth member, and in its fraternity were produced S and RS, but no P larvae.

dently the parents of this mating (30) had all the reproductive cells supplied with some factors or gens for spots, but it was only in the F_5 generation that two parents were chosen, which had *all the gens* which are necessary for a complete (S) or *cynthia* type of larva.   It may be that the results would have been reached more quickly if there had been

more brother and sister matings, but these were not always possible, as in each family the males tended to emerge some days before the females and as the time during which the males will mate is only a few days even when retarded by dark and cold, no matings could be effected; secondly, I did not wish at first to go contrary to the advice of experienced entomological breeders who were sure that inbreeding was disastrous for moths.

The F_4 generation.

Ten families were reared but only three produced only S and RS larvae, the results being as follows:

Types of larvae		P	S	RS
Mating 60	$RS \times RS$ ...	0	8	5
,, 64	$S \times RS$ ...	0	12	3
,, 75	$RS \times S$ ...	0	15	4
Totals	...	0	35	12

The proportion of S to RS is very different in this generation from that in F_3, but the numbers here are excessively small and the constitution is doubtless different.

Mating 64 had no fertile descendants and so the family came to an end. Mating 75 is the descendant of mating 30 mentioned above. Mating 60 is interesting as a demonstration that the RS form may be either homo- or heterozygous as regards the character of full spots.

The probability is that full spots are due to a series of unit characters, which are linked to one another rather more closely than they are to other characters. To demonstrate this would have required much more space than was at my disposal.

Mating 60 was produced by mating ♂ 25 (3) RS with ♀ 22 (7) RS; a large number of eggs were laid, but there was great mortality at the first three ecdyses. No P larvae were produced. Only 13 larvae spun up, eight S and five RS, and of these few only ten moths emerged, viz. 7 S, 3 RS. If RS is a constantly heterozygous form, some P larvae would be expected in the family. But as there was such a large mortality all the P larvae might have died, especially if there was an extra large death rate for the P type. Two members of this family, 60 (5) and 60 (6), mated (mating 88, F_5 generation), and produced all types of offspring, viz. S, RS and P, hence one of the grandparents was a heterozygote. But, when another member of the family, 60 (10), mated with the heterozygote 79 (23) S, in mating 90, only S and RS larvae were produced. This suggests that the other RS grandparent was a homozygous

form for full spots, otherwise P larvae would have been found since 79(23) is a heterozygous form although an S larva, being produced by the union of an RS and a P parent. The heterozygous nature of this RS parent is shown by the number of the offspring—40 P to 44 $S + RS$, approximately equal numbers of the recessive and the other types. The heterozygous nature of these S types was proved by the P, S and RS larvae which appeared in the subsequent generation (matings 92, 91, 84).

One of the disadvantages in breeding animals with a short life is that they are dead long before one knows their genetic content, as judged by their progeny—on the other hand the families should be large and hence certain judgments can be made as a result of a study of the fraternity.

The F_5 generation.

In this generation, for the first time, I did a large amount of fraternal inbreeding, but the results, as far as the numbers were concerned, were very poor, thirteen matings producing only 171 imagines. A much smaller number of eggs were laid—in one case as few as 25—but this may have been due to the fact that I was also doing selective breeding for a smaller type of moth. There was also a much reduced percentage in the number of eggs hatched, which was as low as 25% and never higher than 45%. In this generation only one mating (90) was not fraternal, but that also was non-productive; only 45 eggs were laid of which 40 hatched, but in the end only one imago resulted.

The fraternal matings (90, 93) produced only S and RS offspring. Three matings between brother and sister, both S (84, 85, 91), produced all types of larvae.

The F_6 generation.

This generation has been a failure for several reasons; mice ate more than two-thirds of the F_5 cocoons, the moths that did emerge could not be kept, on account of war conditions, at an adequate temperature, very few eggs were laid, and finally the larvae grew so slowly in the cool breeding room that many succumbed to disease. This generation produced one family (107), whose adult larvae all had the full complement of spots. The larvae, numbering 23, were about to cocoon when they died of cold. As the number of larvae which hatched was only 50, the 23 which reached maturity were probably a good average lot, so that one is justified in supposing that at last two parents with all the

gens for full spots were isolated and mated. It is clear that forms which are homo- and heterozygous for the full number of spots may appear either as S or as RS larvae. It is possible that $P.$ *cynthia* may have two forms, one with the full range of spots and another or others in which certain spots are missing; no picture or description indicates that this is the case, but as entomologists seek "type" such variations may well pass unnoticed.

No families have been bred which produced only RS forms. Eleven matings have been made between RS parents in F_2, F_3, F_4, and F_5 generations, nine of which produced all types of larvae, the proportion being as follows: S 162 : RS 87 : P 90, or $S \times RS : P = 249 : 90$, approximately the same proportions as were found in the F_1 generation.

Review of literature.

Lefroy at Pusa(8) evidently made experiments to segregate spotted and unspotted larvae, for he writes, p. 22 : "The offspring of either has been seen to be spotted and unspotted mixed. If only unspotted ones are bred, the majority tend to be unspotted. On the other hand, if spotted ones are bred, the majority tend to be spotted...it is possible to eliminate either spotted or unspotted worms wholly...of worms from the eggs of these moths (spotted), more than 50 (but not all) were black spotted." These observations were made from mass matings, not from individual matings as in this present work, hence the somewhat confused statements. It would be surprising to find that Lefroy was right in his statement that spotted larvae appear in the progeny of unspotted forms. He makes no distinction between completely and partly spotted larvae.

Kellogg(7) crossed white (plain larvae) and moricand types of silkworm, and as a result of his work he says, p. 16 : "White is regularly recessive to all the other larval colour pattern types. And white larvae mated with white never produce any but white larvae." He does not distinguish between a homo- and a heterozygous type and indeed, considering the nature of the markings, it does not seem possible to do so, except by breeding and judgment from the offspring. Whilst Kellogg found that white cocoon colour might be dominant or recessive, according to race, the white colour of the larva was always recessive. But Tanaka(11) states, p. 24, "the quail factor is partially dominant and partially recessive to the plain. These facts show that the relation of dominance and recessiveness is more complex than is generally supposed." The Japanese workers have made the following general state-

ment(12), p. 148 : " In the first generation of the crossing between white and common marking worms, all the worms were of the common marking and in the second generation two kinds appeared : of the common marking 77°/₂ and of the white 23°/₂. In the fourth generation the worms produced by the mating of the white worms were all white." This looks like a case of simple dominance, but later work of Tanaka(11), p. 211, states : "There is great variation of pigment intensity in the normal... type. In this we find almost every gradation from the lightest to the darkest, apparently presenting a continuous variation....Provisionally I have divided the normal, according to the heritable characteristics into four sub-types : namely normal 1, 2, 3, 4." At the bottom of the series is a form ' hardly distinguishable from the pure plain " and he further adds in a footnote, p. 211, " I assume the existence of different genes respectively for the different sub-types of marking and colour." Now this is what I also am inclined to do as regards the series of spots, although it is stated already that there have not been enough experiments done to prove the point, but it is strongly suggested by the fact that the spots disappear in an orderly and continuous manner. The experiments in Japan by Tanaka, Toyama, etc. and those above recorded all confirm the statement of Kellogg, p. 68 : " In larval colour-pattern characters, the inheritance behaviour is rigorously alternative and Mendelian, dominance always being consistent in relation to a given colour pattern as related to another."

Experiments have been made in crossing certain allied Saturnians : thus Joutel(6) and Pollard crossed *Philosamia cynthia* (*adrena*) and *Callosamia promethia*, but as this cross was made for the sake of the imago rather than the larva, the results with regard to the latter are not stated in detail, but it seems clear that there is a sex-linked inheritance as the reciprocal crosses gave different results. Soule(10) also crossed these species, but her findings are different from those of Joutel. Her results are shown in Plate LXXI of Packard(9), which shows plain larvae as a result of the cross between a plain (*P*) and a spotted (*S*) parent. This indicates that although *P. cynthia adrena* and its Chinese relative *P. cynthia* (Ning-po) appear so alike, genetically they are very different—if these results are confirmed it will be an interesting point in insect heredity.

Section II. The Inheritance of the Plain Larvae.

The plain larvae, as stated in Section I, appeared in the F_2 generation in the proportion of a simple Mendelian recessive, viz. one of the recessive to three of the other types.

The matings of plain to plain produced only plain larvae; of such matings, there were six in the F_3 generation, one in the F_4, seven in the F_5, and six in the F_6 generation.

These results agree with those of Kellogg and the Japanese workers (see p. 144).

Mr J. W. Watson crossed *P. ricini* ♂ (plain larva) with *P pryeri* ♀ (spotted larva) and produced a hybrid which he called *Rothschildi* (13). These F_1 larvae were all spotted, there being both *S* and *RS* forms. He inbred the F_1 generation and gave me some of the eggs. These eggs produced an F_2 generation which consisted of *P*, *S* and *RS* larvae in the proportion of 1 *P* to 3 *S* × *RS*. Only one mating was made between *P* parents, but that produced only *P* larvae. In this mating with *pryeri*, *ricini* behaved genetically exactly as in the mating with *cynthia*.

Section III. On Larvae with reduced Tubercles (Scoli).

P. cynthia and *P. ricini* have throughout their larval life six complete longitudinal series of tubercles, three on each side, the upper rows being the best developed; the lowest row is shorter than the others. In the three thoracic segments there is also present a fourth bi-lateral series of tubercles, situated at the base of the thoracic legs; these are very short, especially the first pair, which may be reduced to mere knobs. The setae borne by the tubercles vary in proportionate length in the various stages, being fewest and shortest in the last. (Text-fig. L)

The tubercles of the two species are alike in all anatomical features, but differ in colour, those of *cynthia* (Ning-po) having a slightly pink tip.

The tubercles in F_1 were normal in appearance, but among the twelve families of F_2 five matings produced a few larvae with abnormal tubercles. These larvae were very variable, the tubercles being entirely absent, very short or varying in length on the various segments of the body. (Plate VIII.)

Before proceeding to a statement of the breeding experiments, it will be as well to define the term tubercle, which is often used very vaguely, and hence denotes a variety of larval appendages. Fracker(3), p. 44, states that the term " tubercle has been used to mean any cuticular

projection of the body wall, from a minute papilla to a conspicuous prominence," but he considers that the word tubercle should be used, p. 16, "as a general term to indicate the location of a seta or a group of setae or a process of the body wall bearing such a group." Fracker has given the name scoli to the particular tubercles which occur in Saturnian and Nymphalidian larvae, scoli being defined as thorny processes bearing spine-like setae.

The three upper rows of scoli of both *cynthia* and *ricini* are, to use Fracker's words, " well developed, conspicuous, cylindrical. higher than wide," but the infra-spiracular series are short and the thoracic are dumpy.

The larvae with reduced tubercles appeared after the last ecdysis and seemed, within their individual lives, to reverse the process by means of which the typical Saturnian scolus has been developed within the species. Fracker(3), p. 44, states that the scolus has been evolved from papillae, i.e. "setae surrounded at the base by a small chitinized ring." The larvae which had the most perfectly reduced tubercles showed in some segments, on careful examination, traces of the chitinized ring, but the setae had disappeared, just as they have disappeared on the short infra-spiracular papillae of the normal larvae.

The number of abnormal larvae in F_2 was small, only 47 occurring out of a total number of approximately 900 adult larvae. Only the adult larvae can be counted as this condition appeared in the last instar. These 47 larvae were S, RS, and P forms, of both sexes and gave rise to both dark and light moths; this particular phenomenon was therefore not correlated with any of the other characters studied in this series of papers.

In order to know the anatomical value of the scoli, Dr A. D. Imms, of Manchester University, very kindly cut sections for me, as I did not have the adequate apparatus at my disposal. The scoli (Fig. 2) consist of two parts, a basal portion with a greatly thickened cuticle, presumably for support, and a distal portion over which the cuticle is thinner and quite smooth. This cuticle is evidently different from that on the basal portion and the general body surface, as it stains much less deeply. The hypodermis consists of columnar cells, among which are the large trichogenous cells with their large flattened nuclei—this layer is at places invaginated to form what are apparently glands, although they are not connected with any opening in the cuticle.

The general body cavity extends into the distal portion of the tubercles, through a somewhat narrow passage, which perhaps acts as a
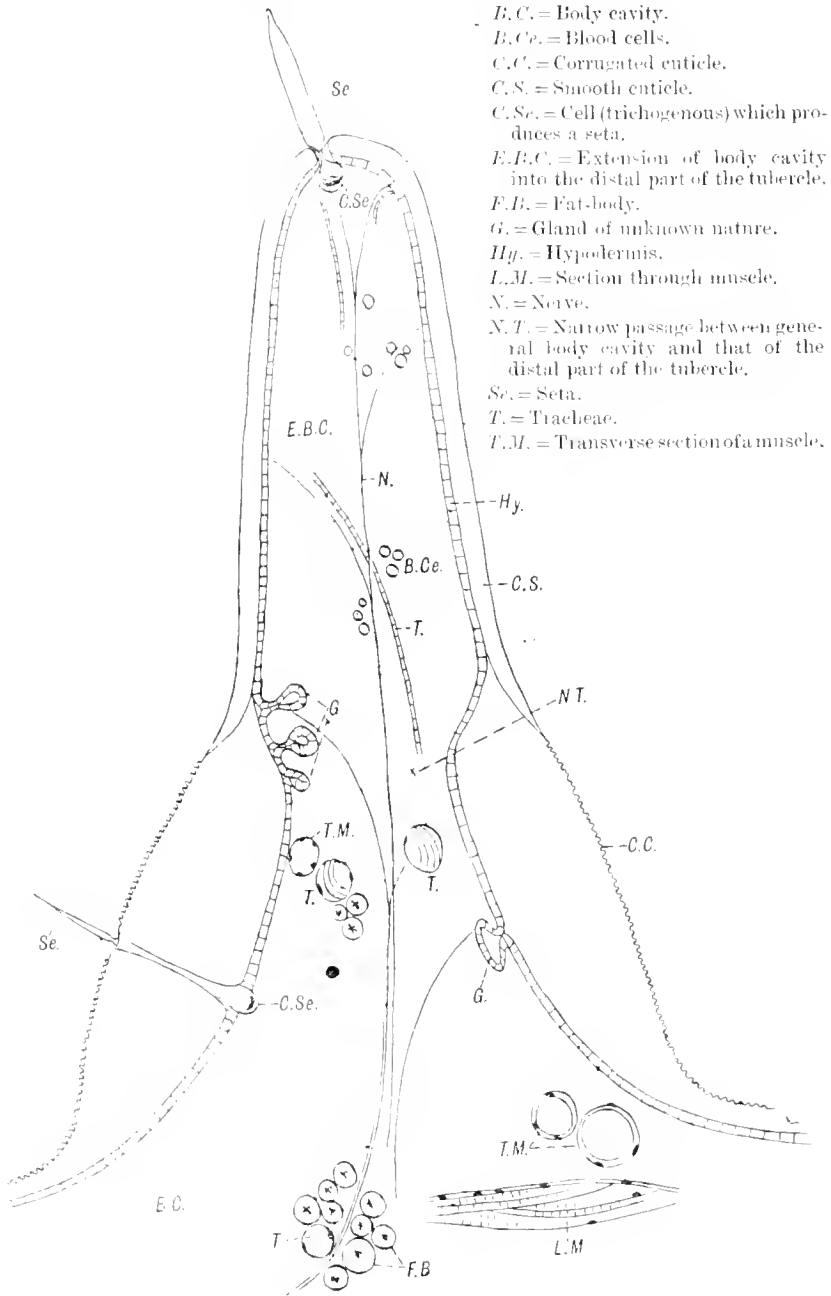
B.C. = Body cavity.
B.Ce. = Blood cells.
C.C. = Corrugated cuticle.
C.S. = Smooth cuticle.
C.Se. = Cell (trichogenous) which pro-
    duces a seta.
E.B.C. = Extension of body cavity
    into the distal part of the tubercle.
F.B. = Fat-body.
G. = Gland of unknown nature.
Hy. = Hypodermis.
L.M. = Section through muscle.
N. = Nerve.
N.T. = Narrow passage between gene-
    ral body cavity and that of the
    distal part of the tubercle.
Se. = Seta.
T. = Tracheae.
T.M. = Transverse section of a muscle.

Fig. 2.

Semi-diagrammatic drawing of a well developed tubercle (Scolus).

valve in the erection of the tubercles. The tubercles are well supplied by tracheae and nerves. The fat-body and muscles extend into the basal, but not into the distal portion of the tubercles. The tubercles are similar to those of the Tortoise-shell butterfly (*Vanessa urticae*), described by Berlese(1). This being their anatomy the tubercles are not a simple character like colour, etc., but they have a certain anatomical importance, and must be represented in the chromosome by a large number of correlated factors.

An attempt was made to mate these abnormal forms, but two were never fit for mating at the same time and it was not until the following generation (F_3) that resort was finally made to a mating between a normal and an abnormal larva. The abnormal form used in the successful mating (m. 79) was not one with perfectly reduced tubercles, but had them represented only by stumps (papillae) except in the infra-spiracular row, where the position of each tubercle was indicated by a chitinous ring. In this family 86 adult larvae were reared (see Table III). These larvae all had normal tubercles, the abnormal form had disappeared. These were then inbred, ten families being reared, and amongst them, larvae occurred with long, with short, and with no tubercles—an obvious Mendelian segregation. The individuals with some or all tubercles absent were separated from those that had tubercles, but the long and short tubercled forms were not separated from one another—partly because of lack of space and partly because I had no satisfactory standard of size by which to effect a satisfactory separation. The tubercles vary in distention and also in individuals. Unfortunately the completely non-tubercled forms failed to mate with one another. A large number of the long and short tubercled forms were eaten by mice, and those that appeared as imagines did not mate well and laid very few eggs. These results, as stated in the earlier section, may have been due to inbreeding for five generations, or simply to the unsatisfactory heat of the breeding room. As a result of breeding in F_2 four small families were reared (98, 96, 100, 103). In two of the families, 100 and 103, the larvae all had short tubercles, but no tubercles were absent. In another family (96) most of the larvae were normal, but a few had short tubercles. In mating 98 one of the parents (83·7) was from the cage which contained a mixture of larvae with both long and short tubercles, and the other was from a larva (81·21) with reduced tubercles; this larva was as follows: the two rows of dorsal tubercles were very short, those on the seventh and eleventh segments being represented only by minute protrusions, the other rows of tubercles were not quite as short

as those just described, but on the left side of the seventh segment there was no infra-spiracular tubercle. The offspring from this mating had all the tubercles present, but the upper lateral and the infra-spiracular were only stumps. Again there is an indication of Mendelian segregation, but of course further breeding is necessary. The weather conditions were so severe early in 1917, that privet, the food on which the larvae lived, could not be obtained and the families died out.

TABLE III.

Normal larva × Abnormal larva

F_1 86 Normal larvae F_4

F_2 10 families which had normal tubercles, short tubercles and no tubercles F_5

F_3 m. 96 (nearly all normal) ; m. 100 and m. 103 (short tubercles); m. 98 F_6
         (reduced tubercles)

There is no recorded direct ancestor of the normal or abnormal parents used in this particular mating which had reduced tubercles in the three proceeding generations reared. But they both had ancestors in the five original families which produced the tubercled forms.

The generations on the left side refer to the breeding for the absence of tubercles, whilst those on the right side are the total generations bred.

Not only from the general heredity view-point but also in relation to the question of the origin of certain unusual forms in the Saturnidae, these experiments are interesting.

Most of the Saturnidae have larvae with tubercles, but a few, *Callosamia angulifera, Brahmaea japonica, Rhodia fugax*, etc., have no tubercles in the last instar. Apparently the smooth form has arisen as a mutation from the tubercled forms within the group. What is the relation of the abnormal forms with reduced tubercles which occurred in the F_2 generation to the smooth forms in the group of Saturniids? Did they arise because there was in the parent *cynthia* or in the parent *ricini* a dormant gen for smoothness which appeared when inbreeding took place in F_2 or was the original *cynthia* or *ricini* from a larva which had mutated and then passed on the character? Presumably the gen was not present on both sides or some non-tubercled forms would have appeared in the F_1 generation. As soon as material can be obtained the cross will be repeated, when it will be known if one is dealing with a mutation or not. Among the silkworms, normally with caudal horns, with which Kellogg experimented, were found a number without a horn ; these he mated, but he states(7), p. 58, "that the character is not

heritable; it does not behave Mendelianly and cannot be fixed." Packard(9), p. 152, writes: "The single median tubercle on the eighth abdominal segment of the specialised Saturnian larvae represents the 'caudal horn' of *Bombyx mori* and is evidently the fusion before the end of embryonic life of what was originally two separate tubercles." The tubercles of this *cynthia* × *ricini* cross and the caudal horn being thus equivalent structures, it will be interesting to compare their inheritance behaviour when it is fully worked out, although the indication so far is that the smooth form in this hybrid does behave as a Mendelian recessive. I do not know if the structures are anatomically the same, but even if they were it would not necessarily follow that they would behave in the same way in a crossing. Thus one may instance the variability of the dominance or recessiveness of white cocoon colour, and again, whilst I find that the black spots of the *cynthia* larva are dominant over the plain condition of the *ricini* larva, Soule(10) found the black spots of the nearly related *P. cynthia advena* were recessive when crossed with the plain *Callosamia promethea*.

Tanaka(11), p. 197, mentions a knobbed race of *Bombyx mori*. The knobs, he writes, "are large paired evaginations of the skin formed in the sub-dorsal line."..."No permanent peculiarity is seen in the larvae until they have passed through the third moult, when the knobs come forth for the first time, and their full development is attained only in the last stage of larval life." He found segregation of knobbed and smooth from the hybrid, but does not say whether the extracted dominants and recessives remain pure.

This character appears to be very different from the tubercles of *Philosamia* or the caudal horns of *Bombyx mori*, as it is an addition which originates late in larval life, and Tanaka continues, p. 197, "the remnants of certain knobs are still visible in the pupal and imaginal stages." The tubercle belongs to an early stage of Saturnian evolution, but this knob is a mutation added so late that it is even ceasing to be a purely larval structure and is carried over into the imago. There may also be a fundamental difference between the two, for whilst Tanaka writes of the knob as an "evagination of the skin," the tubercle is an evagination of the body wall related to a definite group of setae.

Packard(9), p. 151, writes: "The larval characters of this group tend to show that the family has originated from a spiny group and most probably, when we take into account the transformations of *Aglia tau*, from the Ceratocampidae....In the European Saturni...we have the perhaps most generalised and primitive members of the group."..."It is

not unreasonable to suppose that all the more specialised genera must have been derived from a Saturnia-like ancestral form, i.e. a larva in which all the tubercles, whether the thoracic or the abdominal, were of the same shape, size and colour on all the segments; those on the eighth abdominal segment being of the same number (6) as on the segments in front "; p. 19, "The larva of *Aglia* after its last moult becomes like a Saturnian, possibly of the type of *Telea* and especially like a smooth form of the larva of *Attacus betis* (Walker) (also called *Rothschildia*). It is clear that the Saturnian larva, although well tubercled in the earlier stages, has, as a whole, a less complicated tubercle in the last stage than the Ceratocampidae and that it is only in the Saturniidae that a number of forms occur which have much reduced tubercles in the last stage."

The complete reduction of tubercles (except on one segment) has reached its limit in two forms, one belonging to the Ceratocampidae, viz. *Cercophana frauenfeldii* (*venusta* variety) and one of the Saturniidae, viz. *Rhodia fugax*. In appearance these two are remarkably alike and so abnormal in appearance that they must be regarded as highly specialised forms which have approached one another perhaps because of a similar environment. These forms being so highly specialised it is necessary to seek the relation of the present non-tubercled hybrid, if any relation exists, among the more ordinary forms which occur in the Saturniae in which the tubercles are much reduced rather than entirely absent, such as *Telea polyphemea*, *Callosamia promethea*, *Tropea luna*, *Aglia tau*, etc.

Apparently a form with simplified tubercles, similar to *Aglia*, arose as a mutation within the Ceratocampidae, and from this form some of the Saturniidae were certainly descended—it is difficult when a study is made of the larvae, to suppose that all the Saturnians are derived from the same ancestor since they are divided into two natural groups by the condition of the tubercles on the eighth abdominal segment.

Has there been a repetition *de novo* in this hybrid of the same phenomenon which produced *Aglia tau*, or through the ages since the latter originated, have the gens for a reduced tubercular condition in the last instar, been waiting in *ricini* or in *cynthia*?

Fig. A 1.
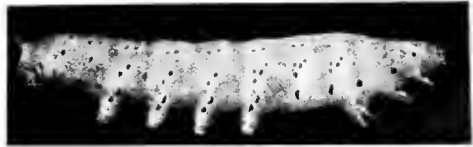
Fig. C 1.
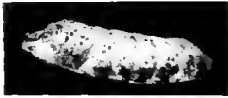
Fig. A 2.
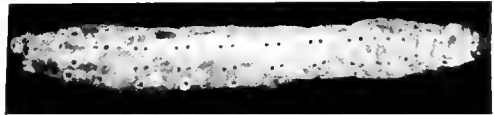
Fig. C 2.

Fig. A 3.

Fig. C 3.
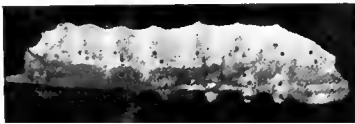
Fig. A 4.

Fig. C 4.

Fig. B 1.

Fig. B 2.

SUMMARY.

1. The plain or non-spotted condition of the larva of *P. ricini* is recessive to the spotted condition of the larva of *P. cynthia* (Ning-po variety).

2. The dominance in the F_1 generation is incomplete; all the larvae are spotted but not all have the full complement of spots.

3. The spots are probably represented, not by one, but by a group of related gens in the chromosome.

4. The dominant homozygous and the heterozygous forms can be distinguished only by breeding, as both may be either full- or partly-spotted.

5. A number of abnormal larvae with reduced tubercles occurred in the F_2 generation; when mated with normal larvae, this character behaved as a recessive; whether it was a mutation which occurred *de novo* as a result of this particular cross or whether it is a result always to be expected from this hybrid, has not yet been determined. This non-tubercled mutation (?) is interesting in relation to the few non-tubercled species among the Saturniids.

EXPLANATION OF PLATE VIII.

Figures A 1, A 2, A 3, A 4 are larvae of F_2.

    A 1—½ natural size. Normal tubercles. Full spots (*S*).

    A 2—¾ natural size. No trace of tubercles. Full spots (*S*).

    A 3—¾ natural size. Irregular tubercles. Full spots (*S*).

    A 4—½ natural size. Slight vestiges of tubercles. Reduced spots (*RS*).

Figures B 1, B 2 are larvae of F_1 and F_2 of the cross between a normal and an abnormal larva. (See Table III.)

    B 1.—Natural size. Normal tubercles. Full spots (*S*).

    B 2.—Upper larva—½ natural size. Traces of tubercles as chitinous rings. No spots (*P*). Lower larva—½ natural size. Normal tubercles. No spots (*P*).

Figures C 1, C 2, C 3, C 4 are larvae of F_2. They were blown by Mr J. W. Watson. ¾ natural size.

    C 1, C 2 are lateral and dorsal views of a non-tubercled, full-spotted larva (*S*).

    C 3, C 4 are lateral and dorsal views of a tubercled, plain (*P*) larva. This specimen shows some spots of the lower lateral series on the abdominal legs. The large spots at the side are the spiracles.

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CONTENTS

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with an Introduction by the
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ON THE STERILITY OF HYBRIDS BETWEEN THE PHEASANT AND THE GOLD CAMPINE FOWL.

By D. W. CUTLER, M.A. (Cantab.),

Assistant Lecturer in Zoology, Manchester University.

(With Plate IX.)

OUR knowledge of the changes that occur in the constituents of the nucleus during the maturation of the reproductive cells of animals and plants, renders the cytological study of the gonads of hybrids of great interest and importance.   However, it is only within comparatively recent times that such investigations have been undertaken.   Guyer's work on the gonads of hybrid pigeons was one of the first made, and this has been followed by the publication of the results of research on other hybrid material.

In 1915 Dr Doncaster and I published the result of investigation of the testes of a sterile tortoiseshell cat.   The condition of the organ was so interesting in comparison with that found in other cases of sterility, that I very gladly undertook to study the gonads of some hybrid birds kindly given to me by Dr Doncaster.   The progress of the research has been slow owing to the pressure of other work and some of the problems connected with it still remain unsolved.   I have, however, been able to discover the cause of sterility, which seems to justify the publication of this paper.

MATERIAL.

The hybrids were bred by the Rev. Lewis Jones, who crossed pheasant males with hens of the Gold Campine breed.   About a dozen chicks were obtained, which were of two kinds :

(*a*)   dark variety,   (*b*)   light variety.

All the chicks, however, were males. There is a possibility that the absence of females was accidental and that the males are more viable than the females, which died in the shell: indeed in support of this Mr Lewis Jones says that he thinks he was able to identify one of the offspring, which died soon after hatching, as a female.

The well-marked colour varieties present a very complicated, but interesting problem. There are two breeds of Campine fowl, silver and gold, which differ from one another in the fact that the silver race possesses a dominant sex limited (sex linked) character that is absent in the gold race. The silver female transmits therefore this dominant factor for silver only to her sons, while the gold female transmits a recessive gold factor to the offspring of both sexes. Since the female parent of the hybrid chicks was a Gold Campine, the existence of the two distinct colour varieties cannot be explained by assuming the presence of the silver factor in some, but not in others of the offspring. If, however, the fact that all the hybrids reared were males is not due to the mortality of the female embryos, but is caused by the development into males of eggs which, if normally fertilised by sperms of their own species would have been females; then it is possible that the two colour classes of hybrids may be due to the presence of some other sex limited factor derived from the Gold Campine female parent. Such a factor would normally be transmitted to the male offspring only and not to the female; but if the potentially female eggs are transformed into males by the pheasant spermatozoa, then in this way two colour classes might arise among the hybrids.

METHODS.

The tissues were fixed in Bouin's formal-picro-acetic mixture and in corrosive sublimate. Both these fixatives gave very satisfactory results, but the former seemed to be a little the better of the two. A large variety of stains were employed, but Heidenhain's Iron Haematoxylin was much superior to them all.

At an early stage in the work it became obvious that it would be necessary to study the spermatogenesis of the parents used in the cross. This I was able to do owing to the kindness of Mrs Haig Thomas and Mr Lewis Jones, who supplied me with pheasant and campine material.

Spermatogenesis of the Pheasant.

The spermatogenesis of the pheasant is exceedingly difficult to eluci-
date, owing to the tendency of the chromosomes to stick together, thus
making it very hard to separate one from another, also the linin of the
nucleus takes up the stain, though not to the same extent as the
chromosomes, making clear figures very difficult to find.

I have examined many sections of the testes, but in no case has it
been possible to determine the exact number of chromosomes in the
spermatogonial cells. It has frequently happened that the chromosomes
were all separated one from another, with the exception of one or two,
which were so closely associated that it was impossible to decide the
exact number representing the complex. However, from the examination
of many spermatogonial division figures I conclude that the chromosome
number is from twenty to twenty-two. Fig. 1 shows very well the
appearance which most of the spermatogonial cells have when seen in
polar view. When viewed from the side they appear quite typical in
character.

Primary Spermatocytes. The growth of the spermatogonia into
primary spermatocytes is initiated by the nucleus increasing a little in
size ; the chromatin is scattered through it in the form of small granules
lying on a fine network (Fig. 2). The next stage is the formation of a
thin spireme, which gradually contracts to form the synizesis stage in
which the threads pass into a tangled condition. It is very characteristic
of this stage to find the chromatin threads aggregated together at one
side of the nucleus (Fig. 3). I have not been able to follow the details
of this process or to determine in what manner the bivalent chromosomes
arise. The next stage, which immediately follows synizesis, is shown in
Fig. 4 where the threads fill the whole of the nucleus and are thickened.
The question of the number of double chromosomes that arise from these
threads is again exceedingly difficult to decide. In most cases the
number appears to be either 10 or 11, but even in the best of the figures
one cannot be absolutely certain. The arrangement of the chromosomes
is, however, characteristic. In polar view there is seen a ring of chromo-
somes with one or two lying in the centre (Figs. 5, and 6). Also it is
common to find one of the chromosomes protruded far outside the others,
making it a very conspicuous element. Fig. 6 exhibits this well and
corresponds very closely with some of the figures published by Guyer in
his recent paper on the chromosomes of the fowl.

11—2

The division stages of the primary spermatocytes, when seen from the side, do not present any features of interest, except that one of the chromosomes is often sharply differentiated from the rest (Fig. 8) I have not been able to find any trace of a lagging element, though many division stages have been carefully examined.

Secondary Spermatocytes. These cells are usually a little smaller than are those of the primary spermatocytes. There is, however, at this stage, a great tendency for the chromosomes to undergo secondary fusion, which is in many cases in pairs. As a result of this, in the majority of cells, five or six clumps of chromatin are seen (Fig. 9). This fusion in pairs, however, is by no means a regular occurrence as the number of chromatin masses in the secondary spermatocytes varies from 1 to 7 or 8 (Fig. 10). I have not observed a secondary spermatocyte with more than eight chromatin elements so that it appears as though a certain amount of pairing always takes place.

This phenomenon is not of rare occurrence and has been recorded in the spermatogenesis of insects and mammals. The spermatids and spermatozoa are of the normal type and do not require any special description.

Spermatogenesis of Gold Campine Cock.

The phases in the development of the spermatozoa are very like those described for the male pheasant. Guyer has recently published the results of research on the spermatogenesis of the fowl and arrives at the following conclusions :

1. The somatic chromosome number is 18 of which two are sex chromosomes.

2. During synapsis pairing of the chromosomes takes place so that nine bivalent chromosomes appear in the primary spermatocytes. The two sex chromosomes pair together, but during the division of the cell they behave as a single bivalent, so that two kinds of spermatocytes are formed, one with $8 + 2X$ chromosomes, the other with 8 chromosomes.

3. Secondary fusion occurs in the secondary spermatocytes so that the majority of the cells contain four or five clumps of chromatin.

4. Spermatocytes with four chromatin masses frequently show abnormal characters, which leads to the conclusion that only one class of spermatid, that with the X chromosomes, develops into functional spermatozoa.

I am at present unable either to confirm or dispute these results as I have not obtained figures which are sufficiently clear to make an accurate count of the chromosomes possible. Spermatogonial mitoses in which an accurate count can be made are exceedingly rare, but from the few figures I have observed I should conclude that the number is from 18 to 20.

In the primary spermatocytes the chromosomes are arranged in a ring with one element projecting beyond the others, as described by Guyer, and the number is from 8 to 10.

The aggregation of the chromosomes into clumps during the growth of the secondary spermatocytes is very obvious in the sections, but I have not been able to find any trace of degenerating spermatids, though I have made a special search for them.

Spermatogenesis of Hybrids.

A careful examination of the testes of the two colour classes of hybrid birds failed to show any differences whatsoever between them: the two types will therefore be treated under the same heading. The testicular tubules do not differ from those of the parent species, nor is there any increase in the amount of interstitial tissue as was found in the sterile tortoiseshell tom cat investigated by Doncaster and myself.

The spermatogonial cells are arranged round the margin of the tubules and many are found in the dividing condition, which is in sharp contrast with that of the parent species where dividing spermatogonia are rare. The divisions are normal, the chromosomes arrange themselves in a regular way on the spindle and pass to each pole without any trace of lagging (Figs. 11, 12, 13). When seen in side view the impression is given that good countable figures would be obtained from a face view; this, however, is not the case for the chromosomes stick together, as in the parent birds, rendering it impossible to make an accurate estimation of the number. It is probable, however, that it is from 18 to 20 (Figs. 14, 15). It is not possible to distinguish between the maternal and paternal chromosomes.

The early development of the primary spermatocytes is normal; a granular spireme is formed (Fig. 16) which retracts to one side of the nucleus (Fig. 18), producing a closely packed mass of threads (Figs. 17, 19). The next stage is the one of interest in connection with the problem of sterility for it is now that spermatogenesis becomes abnormal. The synaptic threads, instead of breaking into bivalent chromosomes,

form a varying number of irregularly shaped clumps of chromatin. There is no uniformity as regards the number produced and a series can easily be formed in which the number varies from two to three large masses (Fig. 20), up to the condition where the chromosomes are almost all bivalent, or where many have separated as univalents (Fig. 21). This failure of the synaptic threads to form bivalent chromosomes is evidently the cause of the sterility in the hybrids. The conditions are seen in Figs. 20 to 27.

This is the final stage in spermatogenesis, for divisions of the primary spermatocytes do not occur, nor is there any trace of abnormal mitoses. The formation of giant spermatids recorded for hybrid pigeons by Geoffrey Smith does not take place, nor is there any evidence of the production of multiple spindles, as found by Guyer in hybrid pigeons and by Wodsedalek in the testes of the mule.

DISCUSSION.

As was pointed out at the beginning of the paper, our knowledge of the cytology of the gonads of hybrids is still small; the results, however, of investigations which have been made, are extremely interesting as regards the behaviour of the chromosomes during the maturation of the germ cells. In both animals and plants the offspring of a cross may be completely sterile, partially so, or entirely fertile, and the evidence which we have points to the conclusion that one or the other of the results is largely dependent upon whether the paternal and maternal germ plasms are able to co-operate one with another during maturation.

Guyer concluded, from investigations on hybrid pigeons, that there was something repellent in the two germ plasms, which had contributed to the cross, so that the chromosomes were unable to pair, causing an irregularity in synapsis.

Geoffrey Smith obtained three sterile male birds from the cross domestic dove female with Magpie pigeon male. Synapsis was disturbed, but not to the same extent as with Guyer's birds, for abnormal spermatozoa were produced. The reductive divisions, however, were abnormal for no bivalent chromosomes were produced. The second division was entirely suppressed and the spermatocytes proceeded without further development to form giant spermatids from which spermatozoa of abnormal size developed.

In a further paper two years later this observer and Mrs Haig Thomas published the results of experiments on the hybridisation of pheasants.

From the cross *P. reevesii* ♀ with *P. formosanus* ♂ a sterile male was produced, and a second one from the cross *P. reevesii* ♀ with *P. versicolor* ♂.

On examination of the testes of these hybrids it was found that the spermatogonial cells were normal, but all subsequent stages were abnormal, owing to the failure of the two sets of chromosomes to pair during synapsis.

On another occasion from the same crosses three sterile females were obtained. The ovaries of two of these were investigated, but there was no trace of sexual cells, the whole organ being composed of interstitial cells mixed with stroma and fibrous tissue.

The sterility of the male hybrids is therefore due, as in other cases enumerated above, to the inability of the chromosomes derived from the two parents to co-operate during maturation.

Although in the female hybrids degeneration of the ovaries occurred before maturation, it is probable that here also sterility is assignable to the same cause as in the males: for as G. Smith points out, in his paper on pigeon hybrids, there is evidence that a precocious temporary synapsis takes place in the female germ cells. Probably it was at this period that the chromosomes failed to pair, thus leading to degeneration of the gonads.

A paper by Wodsedalek dealing with the sterility of the mule has appeared recently. He finds that the maturation divisions are further suppressed than in the above cases, for there is no trace of normal synapsis, and the spireme condition which usually follows it is entirely lacking. The conflict between the paternal and maternal chromosomes begins in the primary spermatocytes leading to the production of abnormal cells. The spermatogonial chromosomes are 51 in number, but in the spermatocytes the number varies from 34—49. Thus it appears that there is some attempt on the part of a few chromosomes to pair. Wodsedalek found, however, that the most pronounced signs of decay were to be seen in the cells where pairing had been greatest.

Finally there is the case of sterile moths, hybrids of the genus Bistoninae, which has been investigated by Harrison and Doncaster. The parents of the hybrids were *Biston hirtaria* and *Nyssia zonaria*. Reciprocal crosses were made but the resulting offspring were all sterile. An interesting change in the sex ratio was produced according as to the manner in which the cross was made; this will be dealt with later in the paper. In both spermatocytes and oocytes the first stages in synapsis are normal, but there is no production of a thick coiled spireme. Complete pairing of the chromosomes does not occur and only a few are able to find mates. It was estimated that in the cross *zonaria* female with *hirtaria*

male about 10 chromosomes paired, but in the converse cross the number was greater.

The reduced number in *zonaria* is 56, while that of *hirtaria* is 14. It will be noticed that the number in the latter species is four times that of the former, and Doncaster suggests that in *hirtaria* the chromosomes are compound and the *zonaria* units are here united together, but in a different order. If this is so the further suggestion is made that sterility is due to the chromosomes not being able to pair normally because of the different grouping of the units.

In connection with the foregoing, the results of Federley's work are of interest. *Pygaera curtula* male and *Pygaera anachoreta* female were mated and the offspring, which were fertile, showed certain characters of one species dominant and other characters intermediate. On crossing the hybrids back to one of the parent species segregation of a few characters occurred.

Cytological investigation showed that during maturation of the original hybrids there was practically no pairing of the chromosomes; one or two did mate, but at division they segregated, while the remainder divided equationally, giving rise to apparently normal spermatocytes.

In the gonads of a hybrid formed by mating a male of the original hybrids back to a pure *anachoreta* female, there was a triple set of chromosomes composed of a double set of *anachoreta* and a single set of *curtula*. Pairing of the *anachoreta* chromosomes occurred at maturation, while the *curtula* ones divided equationally. The gametes produced, therefore, had a haploid set of *anachoreta* and *curtula* chromosomes.

The fertility of these hybrids may then be due to the almost entire lack of pairing of the chromosomes in the first hybrids produced.

Reviewing the cases enumerated above it is apparent that sterility is primarily due to the incompatibility of the maternal and paternal germ plasms; this is sometimes manifested by the inability of the chromosomes to pair and separate in a normal way during synapsis, while in other cases the repellent nature of the germ plasms seems to be so great that pairing occurs only to a slight degree. In other hybrids, however, synapsis takes place, but bivalent chromosomes are not formed, the chromatin threads breaking into irregular masses.

It is evident, however, that whatever may be the cause of the incompatibility of the chromosomes, it is not sufficient to prevent the functioning of the rest of the cells of the body, which appear to perform their several duties in a normal manner. Further we saw that in the *Pygaera* hybrids, which were quite fertile, there was little or no pairing

of the chromosomes. Thus it seems that although the failure of the chromosomes to pair and separate is not the direct cause of sterility, yet it is often the manifestation of the antagonistic nature of the constituents of the germ plasm.

Up to this I have dealt entirely with sterility of hybrids: there is, however, a second type where sterility is found in a pure species of animal. Two such examples were investigated by Doncaster and myself. The first was that of a sterile tortoiseshell tom cat. These animals are exceedingly rare and, when produced, are usually sterile, or fertile to only a slight degree. The colour is normally found only in the female and can be produced by mating a yellow male with a black female. The male offspring are then black. The yellow colour is sex-limited in inheritance and goes only with female producing gametes. On occasion, however, this yellow factor goes with male producing gametes and tortoiseshell toms result. Such a cat we had in our possession and though repeatedly mated no offspring were developed. Investigation of the testes demonstrated that the sterility was caused by the complete failure of the spermatogonia to form. Sterility produced in this way was also found in a hen-feathered cock, extracted from the cross Sebright hen with Hamburgh cock. Hen-feathering is undoubtedly an inherited character, so that these two cases suggest that, when a factor normally confined to the female, is received by the male animal, there is a tendency for sterility to result. Though there appears at present to be no connection between these cases and those of sterile hybrids it is possible that there is a common basis to both. That many of the factors which behave in a Mendelian way are chemical ones seems to be extremely probable. If then a factor common to the constitution of the female is on rare occasions transmitted to the male, the general metabolism of the sex cells may be so upset that they are unable to perform their usual functions. In the same way in hybrids the composition of the germ cells of the parents may be so divergent, that when the two sets of chromosomes are brought together in the nuclei of the gonads, they are unable to co-operate during the complicated phases of maturation but are still quite capable of performing the activities characteristic of the nuclei of the various somatic cells, and also of some germ cells so long as they are not brought into intimate contact with one another.

It is by no means uncommon to find that the sex ratio of hybrids is unequal, as was discovered by Guyer and Geoffrey Smith in hybrid pigeons, by Mrs Haig Thomas in pheasant hybrids, and by Mr Lewis Jones in the hybrids which I have been able to investigate.

In the *Biston* hybrids Harrison and Doncaster found that reciprocal crosses gave very different results: thus from *hirtaria* female and *zonaria* male both sexes were formed, but from the converse cross only males developed. An explanation of this was offered which assumed that in the *zonaria* egg a certain amount of male-determining substance must be present if fertilisation was to produce a male. The *hirtaria* sperm, however, is supposed to possess a much greater amount of this substance than does the *zonaria* sperm, and thus from any *zonaria* egg which is fertilised by a *hirtaria* sperm, male offspring will develop. This assumption is supported by the fact that the *hirtaria* chromosomes are four times as large as the *zonaria* ones, and if the male-determining substance is carried by a sex chromosome it will contain four times as much as does any single *zonaria* sex chromosome.

It is possible that the high male production in the hybrids I have investigated is due to a similar cause, and that the pheasant sperm is preponderately male producing when it fertilises the egg of the fowl. No definite evidence of this has as yet been obtained, but I hope to conduct research on these lines in the future.

I wish to express my thanks to Mrs Haig Thomas and Mr Lewis Jones for supplying me with material, and especially am I grateful to Dr Doncaster, who has read over this manuscript and offered me many valuable suggestions.

EXPLANATION OF PLATE IX.

All the figures were drawn to the same scale. The outlines were drawn by means of a Zeiss-Greil drawing apparatus, and the details filled in free hand.

Figures 1—10. Spermatogenesis of male pheasant.

Fig. 1. Equatorial plates of three spermatogonial cells.

Fig. 2. Young primary spermatocyte.

Fig. 3. Early synapsis stage: fine threads are withdrawn to one side of the nucleus.

Fig. 4. Later synapsis stage with thick coiled threads.

Fig. 5. Primary spermatocyte, equatorial plate probably with 10 chromosomes.

Fig. 6. Primary spermatocyte, equatorial plate probably with 11 chromosomes, one projecting beyond the others.

Figs. 7, 8. Division of primary spermatocytes: in Fig. 8 one of the chromosomes is differentiated from the others.

Figs. 9, 10. Secondary spermatocytes, equatorial plates.

5 μ   10 μ
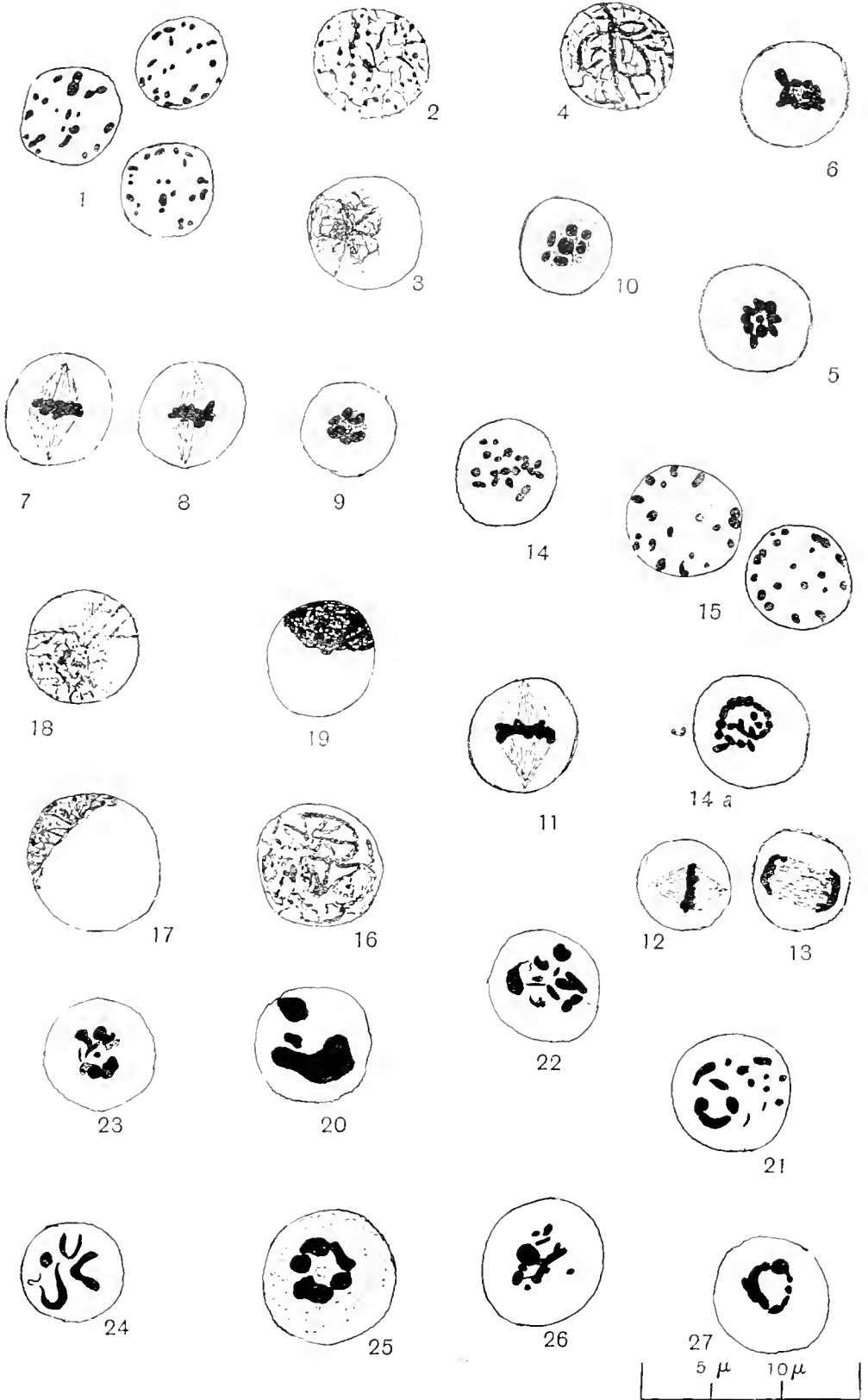
Figures 11—27. Spermatogenesis of hybrids.

Fig. 11. Spermatogonial division of dark coloured hybrids.

Figs. 12, 13. Spermatogonial divisions of light coloured hybrids.

Figs. 14, 14 a. Spermatogonial equatorial plates of dark coloured hybrids showing in Fig. 14 probably 20 chromosomes, and in Fig. 14a 19 or 20.

Fig. 15. Spermatogonial equatorial plates of light coloured hybrids, showing probably 19 chromosomes on the left, and 20 on the right hand figure.

Fig. 16. Spireme stage of dark coloured hybrids.

Figs. 17, 18, 19. Stages in synapsis of dark coloured hybrids, showing the concentration of the threads to one side of the nucleus.

Fig. 20. Three large chromatin masses in the primary spermatocytes of light coloured hybrids.

Figs. 21, 22, 23. Irregular number of chromatin masses in the primary spermatocytes of light coloured hybrids.

Figs. 24—27. Irregular number of chromatin masses in the primary spermatocytes of dark coloured hybrids.

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A FURTHER NOTE ON THE GENETICS
OF *FRAGARIA*.

By C. W. RICHARDSON.

My work on *Fragaria* has been somewhat intermittent in character for the last three years owing to other calls on my time, accordingly many experiments I hoped to continue, when I wrote my first "note" to this *Journal* (Vol. III. No. 3, Feb. 1914), I have been obliged to leave on one side for a future date; also a considerable amount of seed gathered from plants in 1914 has either failed to germinate or germinated badly. But there is an ever growing bundle of facts which time might tend to render stale or to submerge under fresh detail, and it is this accumulation I would add to the record.

Once again I express my gratitude to the John Innes Horticultural Institution for the facilities they have afforded me in carrying on my work, at a time when labour is very short and there are few to answer the numerous calls of a garden "in being."

Flower Colour. It is difficult to distinguish between very light pinks and pure whites, so much so that I have found it impossible to draw a clear line between them after 5 P.M. in June, when, as a rule, in England the light tends to become red.

As stated, in my previous paper, the cross pink flowering *vesca* × white flowering *vesca* produced pink flowering F_1's. These selfed produced 20 Pink, 57 Pale pink, 10 White or very nearly white (of the latter at least 3 were absolutely white).

Expectation 1 to 15—81·57 Pink to 5·43 White.

Double flowering. My original double *vesca* parents were hardly so consistent in their double quality as one might desire, but they were quite as double as any I have seen elsewhere or obtained in my F_2 generations, the leading flowers in a truss are generally the most double and are frequently perfect.

The cross double-flowering *vesca* × single produced in the F_1 generation single flowers with occasional extra petals. The F_1's selfed produced

60 Single	24 Double
37 Single	13 Double
Total 97 Single	37 Double.

Expectation (3 to 1)   100·5 Single   33·5 Double.

The cross Single × Double produced F_1's single.

The F_1 generation selfed produced

58 Single   25 Double.

Expectation (3 to 1)   62·25 Single   20·75 Double.

It is worth noting that some dark pink doubles were very beautiful flowers: my experiment was not on a large enough scale to make certain of my figures but they pointed to a 1 to 15 ratio, the white double being the 1.

Hairy leaf stems and front of leaf. In reality all stems are to some extent hairy, but some appear to be " hairy " because the hairs stand out from the stems and are more numerous. On the other hand, the front of the leaf may be quite glabrous.

In a cross *Virginiana* × *Chiloensis* the F_1's had " hairy " stems and the front of the leaves was hairy. The F_1's selfed produced

32 " Hairy " stems   10 not " hairy "

29 + 3 (marked ? " consider hairy ") Hairy front of leaf   10 Glabrous.

Clearly a 3 to 1 in each case.

An F_2 generation, from a selfed F_1 of a cross *Chiloensis* × *Virginiana*, have yielded plants showing marked segregation of numerous characters —too numerous for me to go into carefully in the short time at my disposal.

Leaving these simple matters I pass to the much more difficult problem—Sex.

Chinensis ♀ × *Chiloensis* ♂ gave

26 ♀   21 ♂ or ♀.

Chinensis ♀ × *Virginiana* ♂ gave

18 ♀   14 ♂ or ♀.

Virginiana ♀ × *Mexicana* ♂ gave

                    20 ♀   15 ♂ or ☿ .

Virginiana ♀ × *Virginiana* ♂ gave

                    17 ♀   16 ♂ or ☿ .

The total of my recorded figures now stands

                    183 ♀   155 ♂ or ☿ .

The noteworthy fact is the persistent dominance of the females which seems to fit a 9 to 7 ratio. The chief difficulty in this line of work is classification—and I fear to a large extent this must remain a matter of individual preference. At present I find it *simpler* to group all sterile flowers with the sex to which they appear to belong, and to consider males and hermaphrodites as one sex, rather than two, as it is almost impossible to say that a given apparently male plant (e.g. a *Virginiana*) will not set an occasional well-developed fruit or an occasional seed.

Up to the present I have no recorded case of a female flowering plant becoming male or hermaphrodite—once a female always a female.

I have failed to produce by crossing species any fruit markedly larger than either of its original parents, but I have not received the results of Hautbois crosses.

James Barnet in a description of the plants in the Society's garden (*Tr. Hort. Soc.* VI.) makes special mention of " Hudson Bay " and other Canadian plants as giving large fruit—it is possible the key may lie in these fruits slowly developed in the long light of the far North summer: when opportunity for continuous work comes once more I hope to make use of some Canadian species.

From a cross *Virginiana* × *vesca* I have now 5 F_2 plants from selfed F_1 hermaphrodite plants, they are still too young to draw conclusions from except that they have the leaf-colour of *Virginiana* and only one has normal leaves, the remainder having five or six malformed. It is not surprising that this cross has been generally considered sterile. Out of some 200 plants flowering freely in the open I found 4 females which set one or two seeds on each plant and 3 hermaphrodites which behaved in the same manner. Last year from 4 large free flowering runners, obtained from the most fertile of these 3 hermaphrodites, I obtained 13 seeds five of which were fertile. I counted 260 flowers on one of these plants! No flower set more than two seeds, and any one might have set from 80—150.

From 12 chance seeds gathered from F_1's in the open, with garden varieties in rows next to them, I obtained four plants, which produced

malformed hermaphrodite or male flowers of no set shape and up to the present sterile.

From crosses made with *Vesca* × *Daltoniana*, garden varieties and *Chiloensis*, I have never obtained free fruiting plants, and am now very strongly inclined to believe that *Vesca* has nothing to do with the present garden varieties.

From my own experience in crossing *Fragaria*, I may perhaps be allowed to add the following note which may be useful to others engaged on similar work.

In gathering strawberries for seed it is essential to gather them when the seed is quite ripe. I find the best plan is—gather dry, i.e. not wet, ripe fruit without handling it—place in a strong paper seed packet—gum up—and keep in a fairly dry room. The fruit becomes nearly desiccated, most of the liquid passing into the air and some into the paper. There may be some mildew produced, but it does not matter. Seeds when wanted can be rubbed from the dried fruit. I have found most seed fertile after three years, but, when the fruit has been very small, and the seed, through lack of pulp, become very dry, the fertility is largely lost.

There is nothing to be gained by sowing in July-October, but some gain *is* made by sowing during November in a hot-house. When seed is valuable or hard to obtain it is an excellent plan to place it between two thin folds of wet cotton wool and keep in a warm house (about 70° F.).

On the least sign of germination the seeds should be placed in pans in a cool house, where they can remain till planted out or potted up: the first seeds generally germinate within 12 days, the last may take months. Wood lice take kindly to very young strawberry seedlings, so it is wise to place pans or boxes on glass jars until plants develop two leaves.

Vesca or *vesca*-like plants or crosses should be renewed by runners or subdivision, as they *wear out* after two years. On the whole the only real disadvantage the strawberry presents as a subject for study is that it requires a considerable amount of space all the year round, and it is extremely doubtful policy to grow catch crops between the rows of plants.

GYNANDRY IN ARACHNIDA.

By the Rev. J. E. HULL.

(With one Text-figure.)

i. I WRITE under the general heading of Arachnida though actual cases of gynandry are known in one order only—Araneae. In the concluding section of this paper, however, I shall have something to say concerning the other orders: meanwhile I proceed to discuss the spiders.

It may be well in the first place to review the general sexual characters, beginning with the external structures of the genitalia. These lie on the median line of the epigaster—the anterior segment of the venter—flanked on either hand by the anterior spiracles. In the female this sexual area is a more or less specialised epigynium, sometimes simple, sometimes elaborately sculptured (affording excellent specific characters), in or under which the vulvar apertures are situated. In the male there is no special epiandrium: the paired apertures open on the epigastral margin, and are practically invisible under ordinary powers of magnification. There is no penis; the copulatory apparatus is a special modification of the terminal article of the palp.

The outstanding secondary sexual characters are the following:

1. **Size.** The female is almost invariably larger than the male, sometimes considerably larger: but none of the known instances of gynandry have occurred where the difference in size is unusually great; all the records are of species in which the total length of the female does not exceed that of the male by more than 15 per cent. of the latter. The difference is always sufficient to cause asymmetry of the body in the gynandromorph, though in some cases it is not very conspicuous.

2. **Palpi.** As the tarsus in the male is expanded and hollowed out beneath to accommodate the highly specialised copulatory apparatus, it becomes an organ of the greatest importance, affording, like the epigyne of the female, excellent specific characters. The 'genital bulb,' as it is

generally called, may briefly be described as a more or less elaborated syringe, capable of sucking up the seminal fluid[1] and expelling it again gradually in the act of coition. The corresponding article of the female is a plain cylindrical joint more or less acuminate at the apex.

3. **Other characters.** So far as the species enumerated below are concerned these are all associated with the cephalic region, including the pair of prae-oral appendages (falces or mandibles). Up to the time of the penultimate moult these differences do not show (nor any other, as a matter of fact); but as the final moult approaches, the tarsus of the male palp enlarges rapidly, and in the case of the Linyphiidae (to which family belong nearly all species now to be dealt with) there is often a special development of the male caput, and of the form and armature of the falces.

ii. Gynandromorphs of three species have been figured and described:

Oedothorax fuscus Bl. (sub *Erigone fusca*). Kulczyński, *Potworek Obojnakowy Pajaka*, Cracow, 1885.

Maso sundevallii Westr. Falconer, *Naturalist*, 1910, p. 229.

Lophomma herbigradum Bl. Hull, *Trans. Nat. Hist. Society of Northumberland*, etc., Vol. IV. (New Series), p. 48.

No two of these agree, as it happens, in the distribution of sexuality, and they may be regarded therefore as types of three different classes. I take them in order, as above.

1. *One side male, the other female—sexual structures perfect except for the distortion resulting from the union of dissimilar halves on the median line.*

Of this Kulczyński's *Oedothorax fuscus* is an excellent example. I translate his description, and add some of his figures.

The right half of the cephalothorax is longer and wider than the left (width: 380μ, left 350μ; length from fore middle eyes to the hind margin: right 970μ, left 910μ), the difference mainly accounted for by the asymmetry of the hind margin, of which the shape is shown in Fig. 1.

The eye area is slightly asymmetrical, the right eyes being a little in advance of the left: what difference there is in the size of the corresponding eyes is hardly per-

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[1] The peculiar interest of this operation will excuse a note. I have twice witnessed the exclusion of the seminal fluid. In each instance it was deposited on a leaf—the living leaf of a tree in the case of *Linyphia montana*, a dead leaf on the ground in the case of *Lycosa amentata*; in both cases it was immediately taken up into the bulb. Coition was effected a few minutes afterwards in the former case; in the latter I could only watch about half-an-hour, and courtship was still proceeding when I left.
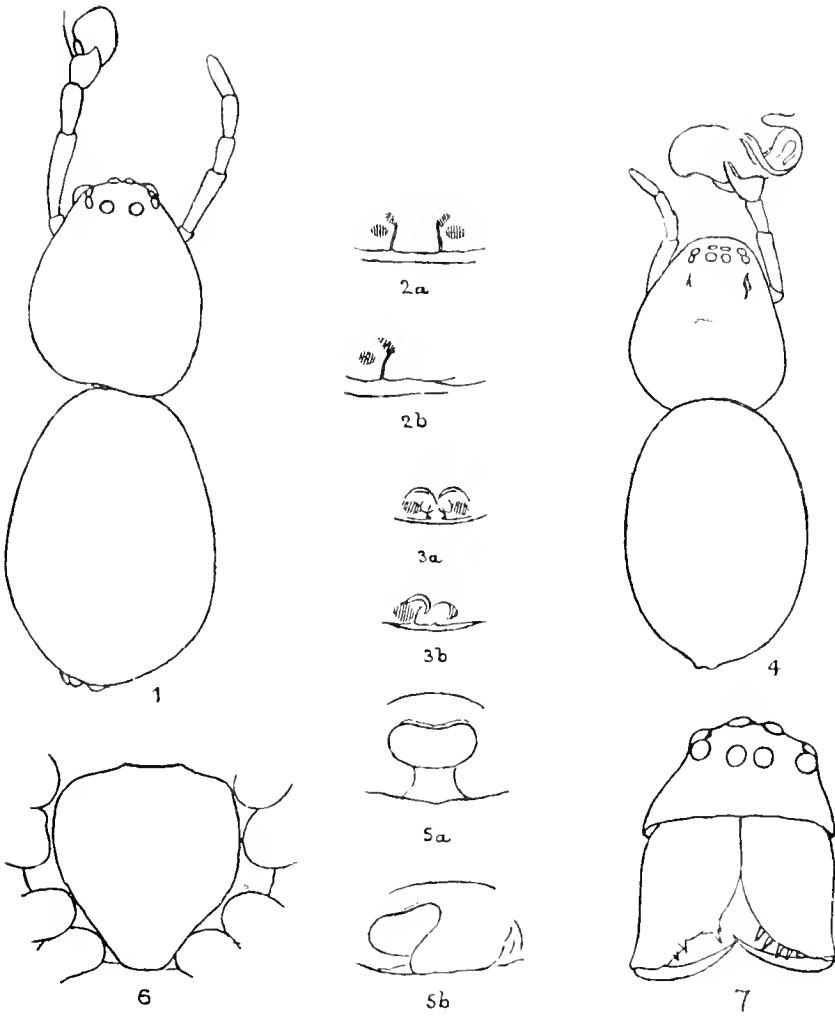
Fig. 1.

1. *Oedothorax fuscus* Bl. ♂. After Kulczyński.
2.   ,,   ,,   ,,   *a*—epigyne of normal ♀; *b*—genital area (after Kulczyński).
3. *Maso sundevallii* Westr. *a*—♀ epigyne; *b*—♂ genital area (after Falconer).
4. *Lophomma herbigradum* Bl. ♂.
5.   ,,   ,,   ,,   *a*—♀ epigyne; *b*—♂ genital area.
6.   ,,   ,,   ,,   ♂ sternum.
7.   ,,   ,,   ,,   ♂ frons and falces.

ceptible. Looked at from the front the cephalothorax seems a little distorted, because the front row of eyes is more strongly curved on the left than on the right, and the lateral slope of the caput is steeper.

The mandibles are about equal in length (330μ), but the right is rather broader (190μ) than the left (170μ), an d the setae are somewhat differently distributed. The fore margin of the fang-groove bears on the right mandible 4, and on the left 5 teeth: the former are slightly larger and unequally spaced ; the latter are equidistant, the first and last being obviously smaller than the three between them. The sternum is asymmetrical ; the left maxilla, seen from below, appears shorter than the right. The left palp is a completely normal and fully developed male palp ; the right is female without trace of abnormality.

It is remarkable that in spite of the marked inequality of the two body-halves the corresponding legs have joint for joint exactly the same length : but there is an obvious difference between the metatarsi, and more particularly between the tarsi of the first pair. The latter differ both in shape and pubescence : the left is slightly clavate, at the base 55μ, near the apex 70μ wide ; while the right is of uniform thickness (55μ) except for the very apex ; the pubescence of the male (left) tarsus is much denser and finer than that of the female right....

The asymmetry of the abdomen (1270μ long, 880μ broad) is pretty obvious, the right half being broader and more strongly curved than the left : a line from the pedicle bisecting the fore part of the abdomen leaves all the spinners on its left side. The right inferior spinner is 138μ long, the left 130μ, the former 95μ, the latter 80μ wide at the base.

Very striking is the asymmetry of the genital area. The right half is more strongly chitinized, the hind margin from the middle to the right dark, to the left light ; the fissure on the left in which lies the entrance to the spermatheca, is abnormally bent inwards, whereas in the normal female it runs straight forward : on the outer side of this fissure are two conspicuous spots— that in front oblong blackish, reaching the fissure ; that behind it round reddish and at some distance from the fissure. The latter spot is caused by the underlying spermatheca, the former by the duct leading from it to the external aperture. Of all this the left half of the genital area shews no trace.

This careful description simply means that (externally)[1] the spider was wholly and completely male on the left side and female on the right, the structures being strictly normal except for junctional distortion. It is interesting to note that the careful examination of this spider revealed the sexual differences in tarsus I which had previously escaped notice.

2.   As 1, *but one side imperfectly developed before, the other behind.*

This is exemplified (according to my own reading of it!) by Falconer's *Maso sundevallii,*—a British example captured by Dr A. Randell Jackson, time and place unknown. But I have not seen the actual specimen, and Falconer's opinion is different. I quote his brief description :

[1] This qualification is to be understood throughout this paper. No dissections have been made of any of the gynandromorphs here enumerated.

The left palpus is of the male form, the palpal organs being well developed; the right palpus is somewhat tumid with the appearance of being loosely covered at the apex, and is thus not quite of the normal female shape. The epigyne is very imperfect, the parts on the left side being obsolete, and those on the right being very much distorted....The specimen is thus male on the left side, but not quite female on the right.

It should be remarked that asymmetry of the body is not to be expected in this species as the two sexes are of approximately the same size: indeed sexual dimorphism is very feeble.

Not having seen the specimen, I can only judge the description of the genital area—loosely called the 'epigyne'—by the figure given. To me this figure (in the explanation of the plate—*Naturalist*, 1910, p. 229—described by error as 'epigyne of female') presents much the appearance one would expect from an amalgamation of the right half (perfectly developed) of an epigynium with the left half (probably imperfect) of an epiandrium. The spermatheca on the right seems quite normal—in fact nothing abnormal save the inevitable disturbance of the median septum. If there be defect it seems to me to be on the left, which in a normal epiandrium is wholly covered by the dark pubescent cuticle of the epigaster, but here unmistakably exhibits vestiges of a female element of about the same strength as the male element in the right palp. If I interpret it rightly this particular gynandromorph presents a reciprocal combination—a left side perfectly male in front, imperfectly male behind; and a right side imperfectly female in front and perfectly female behind.

I am the more confirmed in this opinion because it seems to agree with a *Hilaira excisa* Cb. taken by me near Haltwhistle, Northumberland, in August 1898. The specimen was accidentally destroyed and never recorded. It was certainly male on the right as regards palp and carapace, the tarsus of the left palp being crassate and the occipital tuber (characteristic of the male) nearly bilaterally perfect; so that the left anterior region was, at most, predominantly female. I unfortunately cannot speak with certainty of the genital area. There was asymmetry both of cephalothorax and abdomen, but I have no accurate note of it.

3. *One side perfectly female before and male behind, the other perfectly male in front and female behind.*

This is the condition of things in my *Lophomma herbigradum.* I reproduce my original note.

A fine gynandrous example of this common species was taken at Ninebanks in the spring of 1910. For the most part this specimen exhibits the usual phenomena

of bisexuality; that is, one side is male and the other female, with no atrophy or distortion of parts except where mutual accommodation is necessary on the median line. Naturally this disturbance of structure shows itself chiefly in the sexual region of the epigaster. In the present instance the female side of the external genitalia suffers less modification than the male side. In one particular, however, this individual differs from all other bisexual spiders I have ever seen or heard of; for while the right side of the cephalothorax is male and the left female, in the case of the abdomen the sexes are reversed—the right side being female and the left male.

In view of the unusual character of this specimen I now supply further details.

The first two pairs of appendages of the cephalothorax, being unconnected, retain their sexual characters undisturbed. Thus the right falx (or mandible) is typically male—attenuate and divergent distally, with four teeth on the forward border of the fang-groove, a proximal pair of which the first is smallest of all and the second largest, and a distal pair of intermediate size, the larger (the third) being slightly out of the line of the rest on the side farthest from the fang-groove. The left falx is typically female, equal in breadth to the right at the base, but wider at the apex (i.e. not attenuate or divergent), with five fang-teeth, all in the same line and equal, except the last, which is smaller than the rest.

Similarly the right palp is typically male. In this particular specimen the copulatory organs were nearly fully exserted at the time of capture and are so shown in the figure. They are fully developed in every detail without the slightest variation from the normal. The same may be said of the left palp which is completely and perfectly female.

As the cephalothorax differs in form and dimensions in the two sexes, there is inevitably asymmetry of the carapace. In the first place the clypeus of the male is rather higher than that of the female: consequently there is in our gynandromorph a certain distortion of the 'face.' The front row of eyes is straight but tilted upwards on the right (male) side, on which side also the eyes are slightly nearer together and more prominent. Another effect of the distortion is that the larger part of the eye area falls to the left of the median line; but it must be remembered that part of this excess is normal, the eye area of a female being slightly wider than that of a male.

In the group of genera to which the present species belongs it is usual for the occipital area (including the two posterior middle eyes or not) of the male to be raised into a tuber varying in form according to the species, limited on either side by a furrow or indentation or pit. In several species this occipital tuber is so slightly developed as to be scarcely perceptible, though the lateral grooves (called the post-ocular

furrows) are generally well marked. This is the case in *Lophomma herbigradum*; and accordingly in our gynandromorph the right post-ocular furrow is present, quite normal in form and dimensions. But on the left side there is a corresponding longitudinal impression, very slight but still obvious, which of course does not exist in a normal female. This I take to be a merely mechanical effect, and not due to a subordinate male element on the left side.

The normal female exceeds the male more in breadth of cephalothorax and abdomen than in length, so that there is less displacement of the axis of the body than in Kulczyński's *Oedothorax* (where the difference of the sexes in length is considerable); but the difference in breadth makes itself visible in carapace, sternum, and abdomen. In the last, the sexes being reversed, the lateral gibbosity is of course on the right side. It will suffice to give illustrative dimensions of the sternum. The greatest width of the left half is 263μ, of the right 236μ.

The legs present no special feature, but I append measurements of the five distal articles—tarsus, metatarsus, tibia, patella, femur—in the order named. As it is the *proportions* that matter, I take no definite unit of measurement but use the length of metatarsus I ($= 100$) as a standard of reference:

First pair of legs ..	Right :	95	100	133	50	153
	Left :	90	106	132	49	158
Second pair of legs ..	Right :	85	95	112	49	135
	Left :	85	95	110	48	140
Third pair of legs ...	Right :	75	80	92	45	120
	Left :	73	80	85	44	115
Fourth pair of legs ..	Right .	87	105	140	45	155
	Left :	85	105	135	45	150

To these three I must add a fourth of more dubious nature—an example of *Oedothorax retusus* Westr. taken by Mr W. Falconer on the sandhills near Southport in May 1904, and included by him in the paper on *Abnormality in Spiders* already quoted above (see *Naturalist*, 1910, p. 199). He describes it thus:

The cephalothorax is raised behind the eyes as in a normal male, but the elevation is much less lofty, not so massive and totally devoid of the lateral impressions which are [not][1] so conspicuous in the latter, while the descent to the ocular area is also less abrupt. Both palpi are of the male form, but some of their parts, including the palpal organs, are abnormal in shape, size, and structure. In a normal example the tibial joint is shorter than the patella, and provided at the extremity with an

[1] The brackets are mine. The 'not' is obviously a printer's error.

angular prominence directed outwards, and ending in a small pointed apophysis, a little distance from which is a small, black, sharp-pointed, slightly curved spine, directed downwards. In the abnormal specimen both palpi are without the angular prominence, possessing only the curved spine ; the right [tibia][1] is equal in length to the patella ; the left [tibia][1] is in normal proportion, but towards the extremity has an irregular false articulation....The epigyne is imperfectly formed but all the details may be distinctly traced.

It will be observed that the sexual development is everywhere imperfect, and that the two halves are sexually dissimilar. Both palps superficially resemble a normal male palp, but neither is fully developed. The right palp, for instance, is farther from the normal than the left, as is indicated by the form of the tibial joint, which makes an approach to the dimensions of the normal female palpal tibia. If the explanation of the arrest of male development be the presence of a female element, it is stronger on the right than on the left.

Similarly the genital area has a general resemblance to that of the normal female (so much so that Falconer as above quoted calls it an epigyne), slightly imperfect on the right and still less perfect on the left. If a male element is the disturbing cause, it is stronger on the left than on the right.

This state of things may be represented diagrammatically thus:

<div align="center">

Anterior

M_3F_1	M_2F_2

Left   Right

F_2M_2	F_3M_1

Posterior

</div>
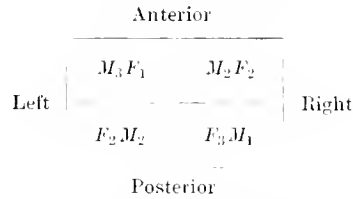
Here M and F represent the male and female element respectively, the subscript figures varying degrees of influence, of which the figures may or may not be a measure.

iii. The following British records stand in the names of the Rev. O. Pickard Cambridge and Dr A. Randell Jackson.

Hilaira excisa Cb. Cambridge : *Proc. Dorset.* etc., *Field Club,* 1902, p. 21.

Adults of both sexes found near Glamorgan[2] and sent to me by Dr A. R. Jackson in 1901. Among them was a remarkable bisexual form. One of the palpi was that of the male spider, the other that of the female ; the form of the caput was that of

[1] 'Palpus' in the original ; obviously a slip of the pen.

[2] I quote *verbatim.* The specimen was actually taken on Maendy Hill, near Ystrad in the Rhondda valley.

the male, and the abdomen was of the male form. I have seen a somewhat similar form in an exotic spider, but never before among the many thousands of British spiders I have had occasion to examine.

In all probability this specimen will still be preserved in the Cambridge collection, now (or presently to be) in the Hope Museum at Oxford.

Dr Jackson mentions this spider in a list of the spiders of Glamorgan (*Cardiff Nat. Soc. Trans.*, Vol. XXXIX. 1907). Like Cambridge he says the caput is the caput of a male, but he does not mention the abdomen.

Porrhomma pallidum Jacks. Jackson: *Trans. Nat. Hist. Soc. Northd.* etc., Vol. I. (new series), part iii, p. 384 (*sub P. oblongum* Bl.).

A gynandrous specimen taken at Hexham. It has one male palpus, one female palpus, and a distorted epigyne.

Probably this specimen is still in existence, but Dr Jackson is on active service and his collection for the time being inaccessible : so it is impossible to say whether this gynandromorph falls into Class 1 or 3.

Leptyphantes pallidus Cb. Jackson: *Trans. Nat. Hist. Soc. Northd.* etc., vol. III (new series), part ii, p. 435.

A fine gynandrous form occurred at Cudham at the end of May (1908). In this specimen the right palpus was of the male form with well-developed palpal organs. The left palpus was of the female type. The epigyne was large but asymmetrical. The central portion was of the normal female type, and so was the left part of the scapus. The right portion of the scapus was quite short. Thus the specimen was male on the right side and female on the left.

Agroeca proxima Cb. Cambridge : *Proc. Dorset*, etc., *Field Club*, 1913, p. 112.

No figure or description is given—merely the record of the capture (in Dorset) of a 'hermaphrodite' of this species. It is, however, important as being the only definite record of a gynandrous spider which does not belong to the family of the Linyphiidae.

iv. I believe Dr Thorell somewhere casually records the occurrence of a 'hermaphrodite' of the family Lycosidae (*Lycosa* sp.), but I cannot trace the reference. The authentic cases here included may be classified thus :

  LINYPHIIDAE :

    § **Linyphiina**—2 species.
      Leptyphantes pallidus Cb.
      Porrhomma pallidum Jacks.

    § **Hilairina**—1 species (twice).
      Hilaira excisa Cb.

§ **Coryphaeina**—2 species.

> *Oedothorax fuscus* Bl.
> *Oedothorax retusus* Westr.

§ **Nerienina**—2 species.

> *Maso sundevallii* Westr.
> *Lophomma herbigradum* Bl.

DRASSIDAE :

§ **Clubionina**—1 species.

> *Agroeca proxima* Cb.

Kulczyński's *Oedothorax* was taken in Galicia in 1880: the rest are British (England, 7 : Wales, 1); and of these eight species seven belong to one family, Linyphiidae.

It is perhaps important to have a just conception of some reasons why the Linyphiidae should take so large a place in this list. The family is only one of seventeen represented in Britain; but it is by far the largest. I have just completed a revision of the British list of spiders, and make the total of British species 539. Of these the Linyphiidae claim no less than 232: *proxime accessit*, the Drassid family, 58—exactly one-fourth of the Linyphiid total. Thus, of every 5 British species, 2 are Linyphiids. In the north of England, which supplies 5 of our 8 gynandromorphs, the proportion of Linyphiids is still higher; in Northumberland quite a half. Moreover, the family includes nearly all the very small and critical species, which the collector finds it necessary to take for closer examination. I shall not be over the mark if I say that in an ordinary way 80 per cent. of my own captures (in Northumberland) are Linyphiidae.

Still the difference in size of the sexes is so general that the consequent asymmetry of the body, together with the conspicuous difference of the palps (to say nothing of every collector's keen interest in practically *every* adult male!) would make it difficult for a gynandromorph to be overlooked whatever family it belonged to.

On the whole therefore we may conclude that the preponderance of Linyphiidae in the records of gynandry fairly represents the actual state of things. And, briefly, the British figures stand thus—in 232 species of the Linyphiidae we have 7 cases of gynandry : in 377 species of other families 1 only. Taking the figures as they stand, they indicate that cases of gynandry are a little more than nine times as frequent among the Linyphiidae than in all the rest taken together.

Whatever the reason may be, it is obviously indisputable, after making every allowance for the imperfection of the numerical test, that the liability to gynandry (in Britain) is strikingly greater in the Linyphiid family than in any other. But I do not think that the tendency can be ascribed to any particular alliance within that family, for the two great branches into which it is divided—the Linyphiine and the Erigonine—are about equally represented among the known gynandromorphs.

v. Examples of gynandry in other orders of the Arachnida are yet to seek. In recent years I have had through my hands many thousands of specimens, chiefly Acari (particularly Gamasidae, Thrombidiidae, Oribatidae, and Tyroglyphidae) and have never seen a true gynandromorph; nor do I know of any record of one. I may, however, here refer to an observation of Canestrini (*Prospetto dell' Acarofauna Italiana*, III, p. 364) on a Tyroglyphid—*Rhizoglyphus echinopus* F. and R.—which has some bearing on the subject. In maintaining that *Hypopus dujardinii* of Claparède and *Rhizoglyphus robinii* of Michael are dimorphic males of the same species, he says: " My conviction is strengthened still more by the discovery of a male in which one leg of the third pair is incrassate as in *Rhizoglyphus robinii*, while the other is of ordinary dimensions " (which is the case with both in the female and in the other form of male, i.e. *Hypopus dujardinii* Clap.). It would be interesting to know something of the genitalia of this abnormal individual : for the normal third leg might be either male or female.

But the total lack of records of gynandry in orders other than Araneae is by no means surprising, for (the Gamasidae and a few other Acari excepted) sexual dimorphism is so slight that the sexes cannot be separated without very close examination. Indeed, in the case of the Oribatidae, it is impossible to distinguish male from female by an external examination, however close.

NOTES ON THE GENETICS OF *TEUCRIUM SCORODONIA CRISPUM* (STANSFIELD).

By M. C. RAYNER, D.Sc.

(With Plate X.)

AN interesting variety of the common "Wood-sage" came into my possession some years ago and has since been crossbred with typical plants of the species in order to investigate the genetic behaviour of the varietal leaf characters.

The results of these experiments are recorded in the present note which is preliminary to a more detailed account of the structural peculiarities and behaviour of the plant.

The type species, *Teucrium Scorodonia* L., the "Wood-sage" or "Germander," is a common plant, especially of dry open woods, commons and heaths, locally abundant but often absent from certain areas. The leaves are variable as to size, details of shape and incision; two characteristic examples are figured in Plate X, fig. 1. A variety, *Teucrium Scorodonia dentatum* Bab., with deeply cut leaves, is recorded but does not appear to be common.

The variety under discussion, recorded as *Teucrium Scorodonia crispum* (Stansfield) is of rather more compact habit than the species, the leaves are broader and blunter and the leaf margins are characteristically "crisped" or "crested" as shown in the photograph (Plate X, fig. 2).

The inflorescences, flowers and fruits resemble those of *T. Scorodonia*.

The variety is very distinct and is of some interest for taxonomic reasons, inasmuch as there appears to be no previous record of such a form of *Teucrium* in this country, nor have I noticed any tendency towards leaf variations of this kind in wild plants in localities where the plant is abundant. The deviation from type is quite clean and well-marked in the variety and I have not been able to find a reference to a

"crested" variety of *Teucrium Scorodonia* as a local form, or to the species as one in which the abnormality of leaf-structure known as "cresting" has been observed.

For the original material, I am indebted to Dr F. Stansfield, in whose garden the plant has been cultivated for many years.

Dr Stansfield's plants are vegetative descendants of a wild plant found in Devonshire at least 50 years ago,—exact date and locality unknown. The plants are readily increased by division and by cuttings and have remained true to type during this long period of vegetative propagation.

There is no tendency for the leaves to revert to the type normal for the species, such as is exhibited, for instance, in similar crested leaf-varieties of *Anemone japonica* and of *Viola* sp., in both of which corresponding forms with crisped leaves are known but are not permanent under cultivation. The flowers of these crested *Teucrium* plants are normal, viable seed is formed and the plant sows itself freely under cultivation.

Dr Stansfield has observed many generations of such self-sown seedlings in his garden, and they are invariably of the normal type, showing no trace of the "crested" character.

The possibility of accidental crossing appeared to be excluded, since the nearest wild plants of *T. Scorodonia* are at least two miles distant. The correctness of this view is confirmed by the results of the experiments recorded below.

In 1913 flowers of a "crested" plant were pollinated from wild plants of *T. Scorodonia* and also from plants growing in the Cambridge Botanic Gardens.

These crosses gave about 20 seeds, the majority of which germinated, yielding an F_1 generation with normal leaves (Pl. X, fig. 3).

These F_1 plants have been under cultivation since that time and have never given the slightest indication of their hybrid origin.

The cross has not been made in the reverse direction.

In 1915 several of the F_1 plants were selfed and were also crossed with the "crested" grandparent, using the latter as pollen parent.

These crosses yielded an F_2 generation of approximately 200 seeds in the first case and of 12 seeds in the second case. From the 200 seeds 89 seedlings were raised, all of which grew to maturity and have continued to grow without showing any trace of the "crested" habit (Pl. X, fig. 4).

None of the seeds obtained from the other cross germinated.

The experimental results may be tabulated briefly as follows:

Crested Type
|
F_1, 20 seeds, of which the majority germinated giving
plants exactly like the pollen parent.

F_1 selfed. F_1 crested.
| |
F_2, 200 seeds, of which 89 reached   12 seeds, none of which germinated.
    maturity giving plants exactly
    like parents: no trace of 'crest-
    ing.'

The experiments are obviously incomplete and must be repeated and extended before exact hypothesis can be founded upon them.

The mortality among the F_2 generation seedlings may be significant or may be accidental: it requires investigation and analysis and there is at present no evidence as to its cause.

It is conceivable, for instance, that the seeds carrying the " crested " character are not viable or die off soon after germination. This would account for the non-appearance of " crested " plants under experimental conditions and also for their absence in a wild state.

Such a hypothesis, however, offers no explanation of the apparent non-inheritance of the " crested " character when the variety is selfed.

If, on the other hand, the mortality was due to accidental causes and the " crested " character is never inherited by seedlings, the possibility that the original plant was of the nature of a periclinal chimaera suggests itself as an explanation.

Microscopic examination of the epidermal tissues of the two parents has not yielded any evidence in support of this view, nor is it easy to imagine how a plant of this constitution could have arisen in the first instance. The possibility is being experimentally tested.

The case seems to be worth recording at this stage if for no other reason than to put on record the appearance of a well-marked and apparently isolated case of leaf-variation in a wild plant.

A tendency to excessive marginal growth of the leaves resulting in the " crested " or " crisped " habit is common among ferns and not uncommon among Angiosperms and in the former it is often inherited by the sporelings.

There is no record, as far as I have been able to ascertain, of such a general tendency showing itself in *Teucrium Scorodonia*, in which plant it seems to have manifested itself as a sudden and rare variation.

UNIVERSITY COLLEGE,
    READING,
        November 1917.

DESCRIPTION OF PLATE X.

Fig. 1.   Leaves from a wild plant of *Teucrium Scorodonia* L.

Fig. 2.   Leaves from a plant of the "crisped" variety of *T. Scorodonia* L. recorded as *T. Scorodonia crispum* (Stansfield).

Fig. 3.   Leaves from plants of the F_1 generation of the cross *T. Scorodonia crispum* × *T. Scorodonia.*

Fig. 4.   Representative leaves from plants of the F_2 generation resulting from the selfing of plants of Fig. 3.

Fig 1

Fig 2

Fig 3

F1

Fig 4

F2
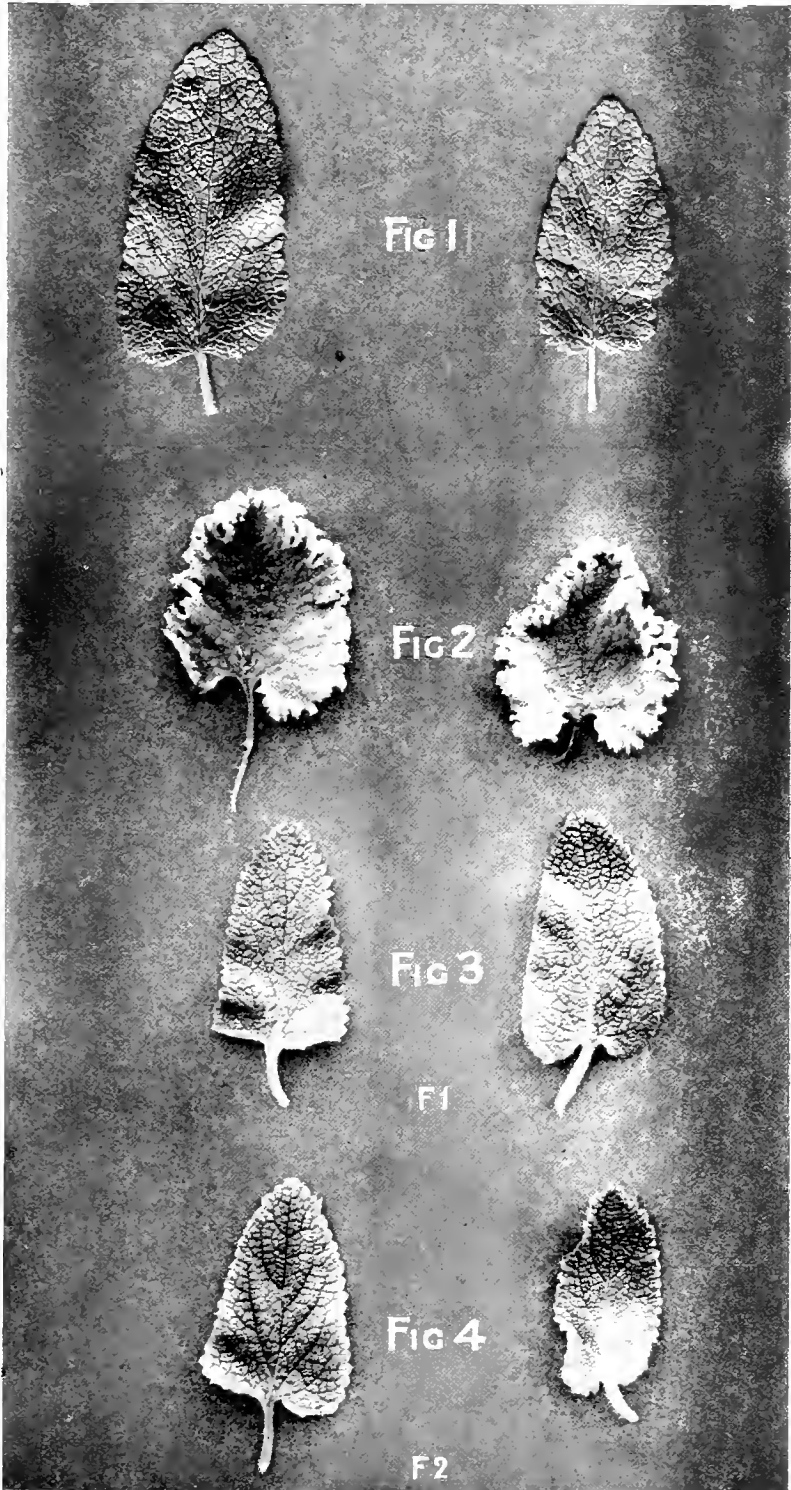
SOME EXPERIMENTS ON THE ROTIFER HYDATINA.

By EDITH E. HODGKINSON.

Six years ago I began some tests and experiments on the rotifer *Hydatina* which were brought to a close in the summer of 1913. The principal object was to test for strains producing no arrhenotokous females. Many tests were made but arrhenotokous females occurred in all the families tested; no pure thelytokous strain was found. The Rotifers were isolated in watch glasses during the tests and the food used was a horse manure solution prepared in the same way as that used by Whitney[1] for his experiments on *Hydatina*. The results of the testing of one family are given in the table below (p. 188). The rotifer laid 42 eggs six of which hatched into arrhenotokous females. The descendants of the thelytokous females from these eggs were tested through a varying number of generations. The generations were rarely completed. The table shows the number of generations tested from each female and the number of thelytokons and arrhenotokous females in these generations.

Out of the thelytokous females tested all gave arrhenotokous females in the first generation except 1, XXXIV and XXXIX and these gave them subsequently.

Attempts were made to alter the relative proportion of arrhenotokous and thelytokous females by using solutions of horse manure of different ages and concentrations, but the results were not definite. Other methods were tried to produce an increase in the number of arrhenotokous females but also with no definite results. Protozoa bred in horse manure solution were removed from the solution and put in spring water and these served as the liquid and food for the rotifers. The protozoa were removed from the horse manure solution by centrifuging some of the solution in a tube. The protozoa sank to the

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[1] *Science*, xxxii, No. 819, 1910.

bottom of the tube and as much liquid as possible was drawn off with a pipette, then spring water was added. The process was repeated several times until it could be assumed little or no horse manure solution remained. Judging from Shull's[1] results, it was thought this method would give a very definite increase in arrhenotokous females, as the horse manure liquid was practically removed; but very few were hatched. The rotifers were kept well supplied with fresh protozoa during this experiment. Again, the temperature was varied, the horse manure solution was oxygenated, but no definite change in the proportion of the sexes could be produced.

		No. of generations tested	T females	A females			No. of generations tested	T females	A females
I	T	5	39	16	XXII	T	2	33	11
II	T	4	60	9	XXIII	T	4	29	8
III	T	5	70	13	XXIV	T	3	20	5
IV	T	4	45	8	XXV	A	—	—	—
V	T	5	48	11	XXVI	T	2	16	9
VI	T	5	42	9	XXVII	T	3	7	5
VII	A	—	—	—	XXVIII	T	3	20	8
VIII	A	—	—	—	XXIX	T	2	27	7
IX	T	3	16	13	XXX	T	15	134	9
X	T	5	56	7	XXXI	T	2	19	5
XI	T	4	32	11	XXXII	T	1	20	3
XII	A	—	—	—	XXXIII	T	4	21	3
XIII	T	5	50	16	XXXIV	T	17	115	5
XIV	T	2	24	7	XXXV	T	14	104	17
XV	T	5	51	9	XXXVI	T	4	18	12
XVI	T	5	34	11	XXXVII	T	4	23	7
XVII	T	5	26	16	XXXVIII	T	2	8	2
XVIII	A	—	—	—	XXXIX	T	12	93	11
XIX	T	5	28	14	XL	T	2	19	5
XX	T	4	31	11	XLI	T	3	23	7
XXI	A	—	—	—	XLII	T	2	11	6

During one period of the testing of the family given in detail above no arrhenotokous females were produced. A *very* concentrated solution of horse manure was used but it was not an old solution. This was suspected of producing the results and on the completion of the test rotifers were bred in a highly concentrated solution of horse manure which was swarming with protozoa. The solution was more concentrated and the protozoa more numerous than in any test previously made. No arrhenotokous females were produced by these rotifers.

I then decided to try the effect of a culture of green protozoa used as food instead of the colourless protozoa in the horse manure solution

[1] *Journ. Exp. Zool.* 1911.

and subsequently learned that in his paper of 1910 Whitney stated that an apparently thelytokous strain could be made to produce arrhenotokous ♀ ♀ when fed upon the green flagellate, *Chlamydomonas*. I found that rich cultures of green protozoa could be made by the following method. Bones and meat are covered with water and allowed to stand for a few days. A little of the solution is put in a glass jar, filled up with spring water and infected with green protozoa—*Euglena*, etc. This is placed in sunlight and in 3 to 5 days a rich culture is formed and is ready for use. By this means cultures of different ages and in different conditions can be used, if required.

Experiment I. A thelytokous female, a descendant of XXX in the test given above, was selected, as few arrhenotokous females had occurred in this line, and put in the green protozoa culture. The details of the descendants of XXX when in the horse manure solution are given

Generation	T female	A female
1	8	1
2	3	0
*3	1	0
4	3	0
5	6	0
6	12	0
7	6	0
*8	15	0
9	5	0
10	10	0
11	17	2
12	10	4
13	26	2
14	8	0
15	5	0
Totals ...	135	9

* A break occurred here in the continuity of the generations as generations 3 to 7 were bred away from the laboratory.

These are the details of the descendants of the thelytokous female in the green protozoa culture.

	T		T	A
A A A A A A A A A A T T T A A A A T T A A T T T T A T A A A A T T A A A A A			12	27
A T T T A T A T T T A A A A A A T A A T A T A			10	14
A A ↓ A A A ↓ A A A A (parent died)			0	9
A A A A A ↓ A A A T A A A A A A A A			1	16
A T T T T A			4	2

13—2

These are the details of a similar experiment. A thelytokous female was taken from XXXIV shown in the detailed test, which was producing few arrhenotokous females. The results in the horse manure solution were 115 thelytokous females and 5 arrhenotokous females. The table shows the results of a thelytokous female in the green protozoa culture.

	T	*A*
A A A A T T T T T A A A A A A A A A A A A	5	16
A A T T T T A T T A A	6	5

These experiments indicate that the increase in the number of arrhenotokous females is due to the change from the horse manure solution to the green protozoa culture and this is proved by subsequent experiments. It is to be noted that an increase takes place in the first generation.

Experiment II. A thelytokous female not taken from a tested family was put in the green protozoa culture. A thelytokous female of the second generation was transferred to the horse manure solution which was very concentrated and the protozoa of which were very numerous. The family was continued in this solution

T in green protozoa food	*T*	*A*
** *T T A A T T A T A T A T T A A A A*	8	9
** *A A A A A *T T A A A A T A T*	4	10

T in horse manure solution	*T*	*A*
A A A T T T	3	3
T T T A T T T T T T T A T T T T T	15	2
T T T A T A T T T A T T A A A T A T A T T A A A A A T T T T T T T T T A	22	14
T T T T T T T T A T T T T T T T T T T A T T T T T T T T T T T T T T T	34	2
T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T	40	0
T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T	37	0
T T	2	0
T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T	39	0
T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T	33	0

** The parents and many eggs in these two generations were killed through being exposed to the sun's rays on a hot day.

It is to be noted that the arrhenotokous females persisted through 4 generations when the rotifers were transferred to the horse manure solution, after which none were produced.

Experiment III. A thelytokous female was put in green protozoa culture; after laying a certain number of eggs it was transferred to concentrated horse manure solution in which the remainder of the eggs of that generation were laid. This was repeated through two more generations, the parent in each case being a rotifer that had hatched out in the green protozoa culture. The table gives the results

Green protozoa culture	T	Horse manure solution
T A A A A A T T T		T T T T T T T T T T T T T T T T T T T T T T T T
A A A A A A T T		T T T T T T T T T T T T T T
T T T A A T T T A T A T T		T T T T T T T T T T T T T T T

A definite change occurred in the same generation: whilst the parent was in the green protozoa culture numerous eggs were laid which hatched out into arrhenotokous females, but after transfer to the horse manure solution no arrhenotokous females were produced. This change occurred in each generation.

Experiment IV. A rotifer and its descendants were put in a culture of green protozoa kept diluted with spring water so that it was comparatively poor in protozoa. The results were

Generation	T	A
1	17	11
2	17	9
3	25	19
4	6	10

Further experiments are needed here to show if a decrease in the food supply and in the assimilation of the green protozoa affects the output of males.

Experiment V. Four rotifers were isolated and put in green protozoa culture. They were kept in sunlight during the day and in electric light during the night so that assimilation by the green protozoa was continuous. The results were

	T	A
I	16	13
II	24	5
III	12	26
IV	7	19

The results are too scanty to prove that increased assimilation by the green protozoa causes a rise in the proportion of arrhenotokous females. This is however not unlikely in view of the fact that Shull and Ladoff[1] have found that increased oxygenation leads to the output of a higher proportion of arrhenotokous ♀♀.

The results recorded in this paper serve to confirm the conclusions of other observers as to the alteration in the proportion of arrheno-tokous females brought about by a change of diet from protozoa without chlorophyll to protozoa which contain this substance. Both Whitney and Shull have attempted to push the analysis further and to bring about the alteration in the relative proportions of the two kinds of females by means of substances of more simple constitution chemically. Their attempts have shewn that a wide field of inquiry is still open here, and I do not feel that at present I can add anything to the full and suggestive discussions which are to be found in their papers.

[1] *Journ. Exp. Zool.* 1916.

THE HISTORY OF *PRIMULA MALACOIDES*, FRANCHET, UNDER CULTIVATION.

By ARTHUR W. HILL.

(With Plates XI and XII and one Text-figure.)

THE history of *Primula malacoides* under cultivation is of some interest, as though of only recent introduction it has been very extensively grown in this country and has already displayed a considerable range of variation.

The species was discovered by Père Delavay in March, 1884, in cultivated fields at Tali, Yunnan, a locality to which it appears to be restricted, and a description of the plant was drawn up by Franchet in 1886[1]. The introduction of the plant to cultivation is due to Mr G. Forrest, who collected specimens in the Tali valley in 1905 and 1906. From the seed sent home to Mr Bully of Ness (of the firm of Messrs Bees, Ltd, of Liverpool, for whom Mr Forrest was collecting) plants were raised which flowered in 1908[2]. Mr Forrest records that it is abundant in the Tali valley near the city at elevations of from 5000 to 7000 feet, and that it was thriving in rather moist sunny situations. The illustration of a plant raised by Messrs Bees in 1908 is given in *Notes of the Royal Botanic Garden Edinburgh*, Vol. IV. Pl. XXVII B, and shews the slender, graceful inflorescences of the original plants[3]. A figure of a more robust specimen is given in the *Gardener's Magazine* for Dec. 5, 1908. The plant figured was shown by Messrs Bees, Ltd, and given an award of merit at the meeting of the Royal Horticultural Society's meeting of Nov. 24.

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[1] Franchet, in *Bull. Soc. Bot. Fr.* Vol. XXXIII. 1886, p. 64.

[2] Messrs Vilmorin had received seeds in 1895 but they failed to germinate.

[3] The same figure is reproduced in the *Gardeners' Chronicle* of Dec. 5, 1908, p. 397, in connection with a short note on the plant by Prof. Bayley Balfour.

According to Franchet's original description the colour of the wild flowers is rose and the limb of the corolla is said to be 10—12 mm. in diameter.

Prof. Balfour in his note in 1908 says: "To some its tint of pink or lavender-pink, in contrast with the grey mealy surface of the flower stems, will be hardly pronounced enough for effect, but time and cultivation will alter that, and it may be predicted that this Primula is likely to become a general favourite...." This prophecy was quickly fulfilled. It may be remembered that in the case of *Primula obconica*[1] no striking variations occurred until the plant had been in cultivation for some fifteen years, and double flowers were only developed in the twenty-first year of its cultivated existence. With *P. malacoides* however the whole range of variations was initiated in about four years from the date of its introduction to this country. A figure in *The Garden*[2] for 1912 shows the more robust character of the plant as compared with those first cultivated in this country.

The only coloured illustration of *P. malacoides* of which we are aware is that published in the *Revue Horticole* for 1912, p. 156, which depicts a plant very like the type as originally introduced. The plant does not appear to have been cultivated in France until 1911 when it was exhibited by Messrs Vilmorin at a meeting of the French Horticultural Society in the spring of that year[3]. M. Mottet, the author of the article, gives a short historical account of the plant and, what is of considerable value, has drawn up a detailed description from living specimens cultivated in Paris in 1911.

According to this description the corolla measured 15—20 mm. across, the segments were deeply notched and the colour was a soft rose-lilac with a greenish-white centre. The leaves were 6—8 cm. long, oval rounded at the apex and cordiform at the base.

The leaves on our collected specimens are up to 9 cm. long.

From this account it appears that the effect of cultivation has been to increase the size of the flowers from the maximum of 12 mm. in diameter given by Franchet to 25 mm., which is the dimension of the largest flower yet noticed.

In England about this time apparently the plant varied in several directions. Messrs Sutton and Sons sent to Kew on April 6, 1912, a

[1] A. W. Hill, "The history of *Primula obconica*, Hance, under cultivation, &c." in *Journ. Genetics*, Vol. II. 1912, p. 1, with plates.
[2] *The Garden*, March 30, 1912, pp. 157, 158, with fig.
[3] *Rev. Hort.* 1911, p. 218; *Journ. Soc. Nat. Hort. Fr.* 1911, p. 181.

white sport of *P. malacoides* (Pl. XI, Fig. 3) and informed us that they had also a "deep mauve quite distinct from the type."

The flowers of the white sport measured only 1 cm. across, the corolla segments were narrow, only 4 mm. broad at the apex and almost oblong with a shallow notch. The eye was deep yellow. The calyces were very mealy and the inflorescences much more slender than in the type.

Messrs Bees, Ltd, who also had the white sport, remarked that the habit of the plant is very distinct from that of the rose-coloured form, the inflorescences being much more erect and the distances between the whorls of flowers much shorter. The flowers of the white form sent by them to Kew measured 2 cm. across, whilst the largest lilac flowers measured 2·5 cm. The more robust character attained by the plant in its fifth year of cultivation is well shewn in the figure in *The Garden* for March 30, 1912, p. 157.

In this same year *P. malacoides* also produced double flowers for the first time, and this sport occurred among a large batch of plants grown by Mr L. R. Russell at his Cedar Nursery, Ham, Surrey (Pl. XI, Figs. 5—12; Pl. XII, Figs. 2 and 3). All stages in the doubling of the flowers were noticed, and on the same inflorescence in some plants every gradation from single to fully double flowers could be found. The doubling is like that of the old double white *P. sinensis* and of *P. obconica*, being due to out-growths from the apex of the connective of the anther resulting in a "hose-in-hose" type of flower. In the best cases one or more whorls of extra segments have been developed, each segment having the characteristic apical notch.

A good figure of the double form was given in *The Garden* of Dec. 13, 1913, p. 624, from a plant grown by Messrs Bees, Ltd, and the sport appears to have originated in Cheshire independently of its appearance at Messrs Russell's nursery[1].

The double white variety was produced at Kew as a result of crossing the double lilac with the single white form and flowered in 1915. This spring (1917) Messrs W. and J. Brown of Stamford, showed double white[2], double lilac and double mauve forms at a meeting of the Royal Horticultural Society.

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[1] Although the double form of *P. malacoides* originated first with Messrs Russell in 1912 it was Messrs Bees' plant shown at the meeting of the R. H. S. on December 2, 1913, which received an Award of Merit, see *G. C.* March 14, 1914, p. 180.

[2] A figure of the double white form is given in *Gardeners' Chronicle*, March 2, 1918, p. 91, and the foliage of the plant is distinctly "fern-like."

The seed of these three doubles was obtained from a private grower and sown in the autumn of 1916.

Another break which occurred in 1912 also at Messrs Russell's nursery consisted in the fimbriation of the corolla segments, a variation which has commonly developed in primulas under cultivation (Pl. XI, Fig. 13; Pl. XII, Fig. 4). In the examples seen in 1912 the apical notch still existed, but the lobes of the segment were more or less deeply cut or laciniated and there was also a tendency to the formation of tooth-like projections in the sinuses between the segments.

This latter tendency is especially noticeable in the forms with narrow segments and wide sinuses (Pl. XI, Fig. 15; Pl. XII, Fig. 5).

In some cases only a single segment or one side of a segment of a flower may show fimbriation.

With fimbriation of the corolla is associated also a fimbriation of the calyx. Normally the calyx bears five simple acute teeth, but where the corolla segments are laciniate the calyx teeth tend to be conspicuously and sharply toothed (Pl. XI, Figs. 13 and 14). With the double flowers the calyx is like that of the type.

Fimbriation and doubling then appear to be two quite independent variations and fundamentally different, though the inception of both is undoubtedly due to cultivation.

Yet another variation was noticed this same year with regard to the scent of the plants, the foliage of some being almost scentless, while in other cases it was distinctly scented, the odour being like that of pine apples. Attention has also been called to this fact by Dr MacWatt, who states that the pine-apple scented form is more robust and sets seed freely, while the scentless form has smaller flowers and does not set seed according to his experience[1].

Variation in the direction of greater intensity of flower colour has also been marked in *P. malacoides*; though the range of variation is not yet so wide as in *P. obconica*, both lilac and deep mauve forms are common, and a deep pink shade was exhibited by Mr James Box in 1914[2]. This particular form was further distinguished by its vigorous growth. The plant having "stouter stems, a more robust habit, and flowers twice the size of those of the type." The flowers measured 2·5 cm. in diameter. This giant form appears to be the result of beneficial cultivation rather than of any hybridisation, the suggestion that *Primula Forbesii* may have been accidentally crossed with *P.*

[1] *The Garden*, January 6, 1912, p. 2.
[2] *Gardener's Chronicle*, March 14, 1914, p. 180, fig. 82.

malacoides seems no more tenable than that the deep rose colour of some forms recently exhibited is due to the influence of the pollen of *P. rosea*. According to the editorial note in the *Gardeners' Chronicle* numerous experiments have been made to cross *P. malacoides* and *P. Forbesii*, but no fertile seed has resulted.

The most distinct colour form of *P. malacoides* is that known as " Rose Queen," the flowers of which are of rich rosy colour. A figure of this is given in *The Garden* of Feb. 27, 1915, p. 104. The variety, was raised by Mrs Denison of Little Gaddesden, Berkhamsted, and is very vigorous in habit with fine trusses of flowers. It differs from other forms chiefly in the breadth of the perianth segments which have become so much broadened that they touch one another and the flower has a rounded outline more like that of a polyanthus.
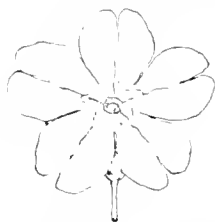
As in the case of *P. obconica*, the hybridisation of *P. malacoides* with other species of *Primula* has been attempted by many gardeners, but there is no evidence that success has attended any of the experiments. The species in a remarkably short space of time has responded to cultural conditions and has sported in the directions of doubling, fimbriation of the corolla segments, albinism, and various colour changes as well as in the direction of increased vegetative vigour. All these changes however must be attributed to the skill of the gardener rather than to the efforts of the hybridiser.

P. malacoides has varied under the influence of cultivation in precisely the same manner as have *P. sinensis* and *P. obconica*[1], but the time interval required for the disturbance of its equilibrium has been very short.

[1] It is of interest that *P. denticulata* which in 1912 was being grown in large quantities by Messrs Russell at Cedar Nursery, Ham, showed a great range of colour forms, through every shade of lilac, pale purple and violet to a distinct bluish shade and also white. The shape and form of the flowers was also very varied from small with narrow sharply pointed segments to very large flowers with rounded segments very far removed from the type. Fimbriated flowers were also noticed but no doubling. The leaves were also very diverse in form in some cases being quite coarse. In this species there is no question of any hybridisation having been attempted.

EXPLANATION OF PLATES.

PLATE XI.

Figs. 1 and 2.   *Primula malacoides* grown at Kew in 1912, very similar to the plant as originally introduced.

Fig. 3.   White variety which appeared at Messrs Sutton and Sons in 1912.

Fig. 4.   A deep coloured form flowered at Kew in 1914.

Figs. 5, 6, 7.   Stages in doubling Fig. 7 being a complete double, see Fig. 11, from Messrs Russell in 1912.

Fig. 8.   An enlarged drawing of the flower seen in Fig. 6, cut open to show the extra segments developed from the connective of the anther.

Figs. 9 and 10.   Details of the development of the perianth-segments from the connective.

Fig. 11.   An enlarged drawing of Fig. 8, the perianth cut open showing a complete inner perianth and further developments commencing from the anthers.

Fig. 12.   An extra segment and anther from the flower represented in Fig. 11.

Fig. 13.   A large fimbriated flower grown at Kew in 1914 the flower measured 2·35 cm. in diameter.

Fig. 14.   The calyx of the above magnified showing the toothed margins of the segments.

Fig. 15.   A flower showing incipient lobes in the sinuses.

The drawings are by Miss M. Smith.

PLATE XII.

Flowers from a group of seedling plants of *P. malacoides* exhibited by Messrs R. L. Russell, Nurserymen, Richmond, at the Royal Horticultural Society's show, April 9th, 1912.   The plants were raised at Cedar Nursery, Ham, and selected from a batch of 15,000 plants.

All the flowers are natural size.

Fig. 1.   Flowers showing early stages in fimbriation.

Figs. 2 and 3.   Early stages of doubling with two more or less completely double flowers.

Fig. 4.   A flower with the segments conspicuously fimbriated.

Fig. 5.   Three flowers showing an attempt to produce outgrowths from the sinuses.

Fig. 6.   Three large single flowers measuring 2·2—2·35 cm. in diameter.

Photographed by C. P. Raffill.

1

2

5   6   7

8

9   10

13

14

12

15   11
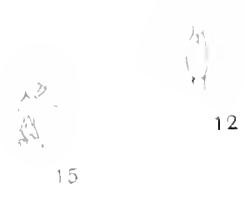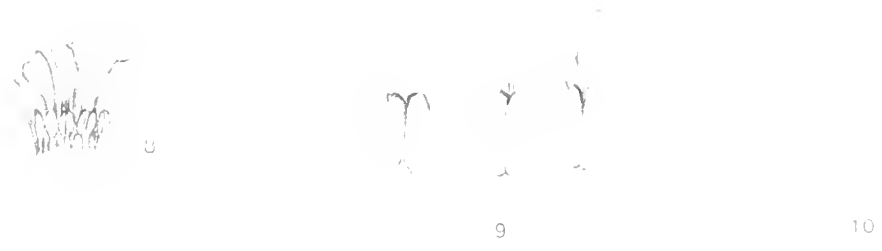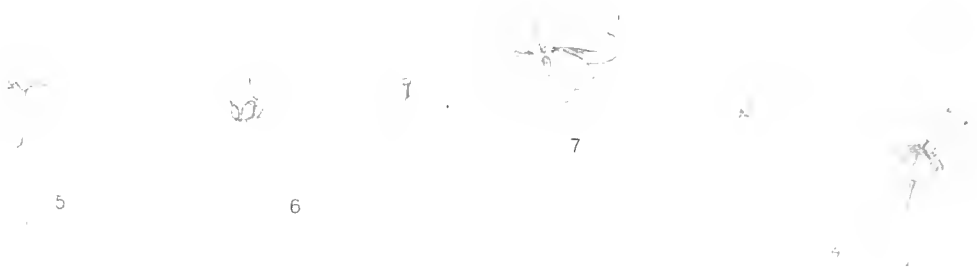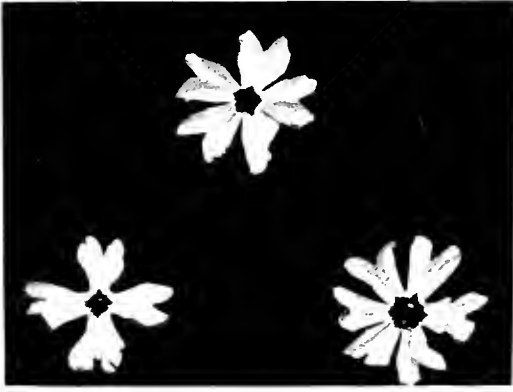
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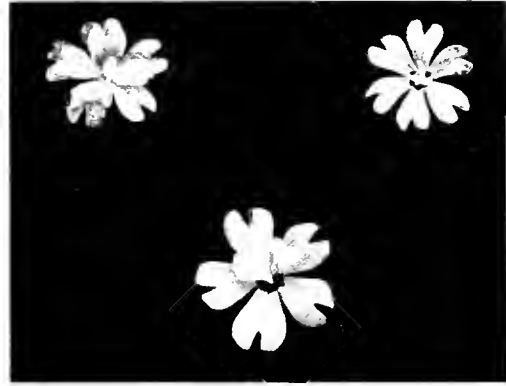
Fig. 2.

Fig. 3
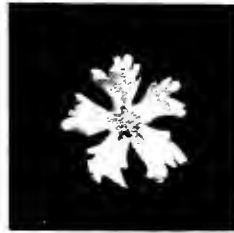
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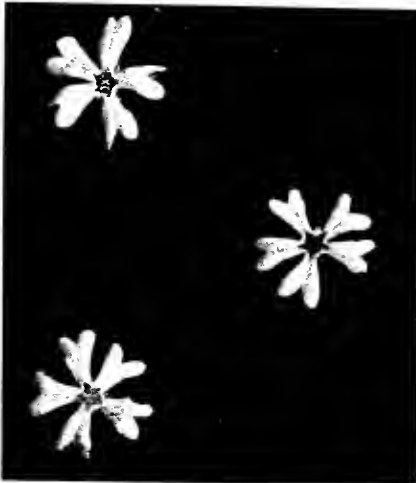
Fig. 5.
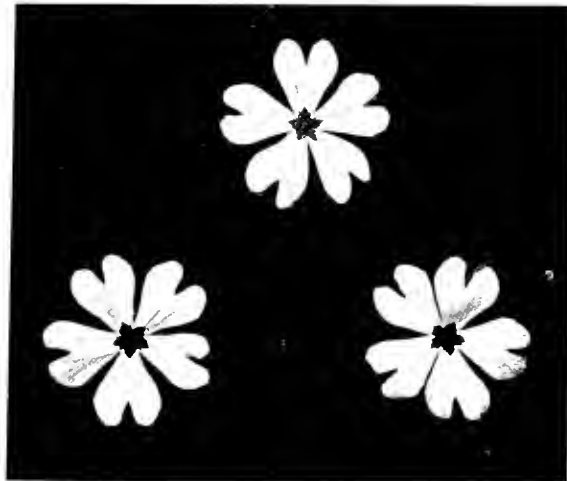
Fig. 6

PARTIAL SELF-FERTILIZATION CONTRASTED WITH BROTHER AND SISTER MATING.

By RAINARD B. ROBBINS,

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In a recent issue of this *Journal*, A. B. Bruce(1) has published an article entitled "Inbreeding," the purpose of which was "to express the genetic consequences if, in each generation, selfing and mating at random take place in the fixed ratio $s : (1 - s)$." Bruce gives as one of the reasons for the importance of such a problem, that the results of brother and sister mating may be assumed to be given by a proper choice of s. The excuse for such an assumption is suggestive parallelism in particular cases. The fact is that the assumption is erroneous, as the results of this paper will show.

The theory will now be developed for combined selfing and random mating. The results for the general case of brother and sister mating have already appeared(2). It is by comparing these results that our conclusions are drawn. Only one pair of simple Mendelian factors will be considered.

Suppose we start with a population which can be represented by

$$r_0 AA + s_0 Aa + t_0 aa.$$

This means that the pure dominants, the heterozygotes and the recessives occur in numbers proportional to r_0, s_0, t_0. For convenience we choose r_0, s_0, t_0 such that

$$r_0 + s_0 + t_0 = 1.$$

Suppose that self-fertilization occurs in a part of each generation indicated by the proper fraction σ and that mating is at random in the remainder of each generation. Of course we assume that the individuals which are self-fertilized are chosen at random in each generation.

Let r_n, s_n, t_n represent the proportions of the three types of zygotes in the nth generation, and let

$$r_n + s_n + t_n = 1.$$

The analysis of the formation of the zygotes of the nth generation gives the following recurrence relations:

$$r_n = \sigma\,(r_{n-1} + s_{n-1}/4) + (1 - \sigma)\,(2r_{n-1} + s_{n-1})^2/4, \quad \ldots\ldots\ldots(1)$$

$$s_n = \sigma\,s_{n-1}/2 + (1 - \sigma)\,(2r_{n-1} + s_{n-1})(2t_{n-1} + s_{n-1})/2, \quad \ldots\ldots(2)$$

$$t_n = \sigma\,(t_{n-1} + s_{n-1}/4) + (1 - \sigma)\,(2t_{n-1} + s_{n-1})^2/4. \quad \ldots\ldots\ldots\ldots(3)$$

On the right hand side of each of these equations, the first term is the contribution of self-fertilization, and the second term is the contribution of random mating. To solve these equations we notice that

$$2r_n + s_n = 2r_{n-1} + s_{n-1} = \ldots\ldots = 2r_0 + s_0.$$

Thus we have that $2r_n + s_n$ is constant. Let

$$\rho = 2r_0 + s_0.$$

Then equations (1), (2), (3) simplify giving,

$$r_n = \sigma\,r_{n-1}/2 + [\sigma\rho + (1 - \sigma)\,\rho^2]/4, \quad \ldots\ldots\ldots\ldots\ldots\ldots(4)$$

$$s_n = \sigma\,s_{n-1}/2 + \rho\,(1 - \sigma)(2 - \rho)/2. \quad \ldots\ldots\ldots\ldots\ldots\ldots(5)$$

$$t_n = \sigma\,t_{n-1}/2 + [\sigma\,(2 - \rho) + (1 - \sigma)(2 - \rho)^2]/4. \quad \ldots\ldots\ldots(6)$$

The solutions of these equations are,

$$r_n = \left(\frac{\sigma}{2}\right)^n c_0 + \frac{\rho\sigma\,(1 - \rho) + \rho^2}{2\,(2 - \sigma)}, \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots(7)$$

$$s_n = \left(\frac{\sigma}{2}\right)^n d_0 + \frac{\rho\,(1 - \sigma)(2 - \rho)}{2 - \sigma}, \quad \ldots\ldots\ldots\ldots\ldots\ldots(8)$$

$$t_n = \left(\frac{\sigma}{2}\right)^n e_0 + \frac{(2 - \rho)(2 - \sigma - \rho + \rho\sigma)}{2\,(2 - \sigma)}. \quad \ldots\ldots\ldots\ldots(9)$$

The constants c_0, d_0, e_0 are determined by the initial conditions and are

$$c_0 = r_0 + \rho\,(\rho\sigma - \rho - \sigma)/2\,(2 - \sigma), \quad \ldots\ldots\ldots\ldots\ldots(10)$$

$$d_0 = s_0 + \rho\,(2 - \rho)(\sigma - 1)/(2 - \sigma), \quad \ldots\ldots\ldots\ldots\ldots(11)$$

$$e_0 = t_0 + (2 - \rho)(\rho + \sigma - \rho\sigma - 2)/2\,(2 - \sigma). \quad \ldots\ldots\ldots(12)$$

Equations (7), (8), (9) give the results for our problem of combined selfing and random mating. Incidentally we may specialize these

equations so as to get the results for random mating and for self-fertilization.   If we set $\sigma = 0$, we have, for random mating,

$$r_n = (2r_0 + s_0)^2/4; \quad s_n = (2r_0 + s_0)(2t_0 + s_0)/2; \quad t_n = (2t_0 + s_0)^2/4.$$

Setting $\sigma = 1$ gives for self-fertilization

$$r_n = r_0 + s_0(1 - 1/2^n)/2; \quad s_n = s_0/2^n; \quad t_n = t_0 + s_0(1 - 1/2^n)/2$$

The results for brother and sister mating, starting with a family $r_0 AA + s_0 Aa + t_0 aa$, have been published by the present author (2). They are

$$r_n = \rho/2 - L_n/4^{n+1}, \quad \dots\dots\dots\dots\dots\dots\dots(13)$$

$$s_n = 2L_n/4^{n+1}, \quad \dots\dots\dots\dots\dots\dots\dots\dots(14)$$

$$t_n = (2 - \rho)/2 - L_n/4^{n+1}, \quad \dots\dots\dots\dots\dots(15)$$

in which $\qquad L_n = \dfrac{\sqrt{5}}{2}[K_3(1 + \sqrt{5})^{n+1} - K_4(1 - \sqrt{5})^{n+1}],$

and $\qquad K_3 = \dfrac{(1 + \sqrt{5})}{5} s_0 + \dfrac{(1 - \sqrt{5})}{5}(s_0 - 4r_0 t_0),$

$$K_4 = \dfrac{1 - \sqrt{5}}{5} s_0 + \dfrac{(1 + \sqrt{5})}{5}(s_0^2 - 4r_0 t_0).$$

From these results we readily calculate that as n increases indefinitely, r_n, s_n, t_n approach respectively the values $2r_0 + s_0$, 0, $2t_0 + s_0$. In words, *the heterozygous type tends to disappear in brother and sister mating and the homozygous types approach a proportion equal to that of their respective gametes in the original population.*

But equation (8) *shows that in our combination of self-fertilization and random mating, the heterozygous type can never disappear, if σ is different from unity.*   In fact equation (8) shows that

$$\lim_{n=\infty} s_n = \rho(1 - \sigma)(2 - \rho)/(2 - \sigma).$$

Thus it is clear that no such combination of random mating and self-fertilization can represent brother and sister mating.   In every case of inbreeding which the present writer has examined, the proportion of heterozygotes approaches zero as the number of generations increases. Equation (8) shows that so long as $\sigma \neq 1$, i.e. so long as we have a fixed proportion of each generation mating at random while the others are self-fertilized, the proportion of homozygotes cannot vanish.   It would

therefore seem unwise to assume without pretty good evidence that any form of inbreeding is equivalent to such a problem.

However, as Bruce points out, the combined problem of random mating and self-fertilization is directly important, since it is just the sort of mating which occurs in certain problems.

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November 23, 1917.

GENETIC STUDIES IN POULTRY.

I. INHERITANCE OF LEG-FEATHERING.

By R. C. PUNNETT, F.R.S., and the late
Major P. G. BAILEY, R.F.A.

[THE results recorded in this paper are the outcome of some experiments started in 1910 and designed to throw light upon the inheritance of certain features in poultry, more particularly of weight, broodiness, and egg-colour. The data presented here are but a by-product of these other investigations, but in view of the economic importance of the species to which they relate I have thought it worth while to place them on record. From 1911 until the outbreak of war the work was carried on jointly by Mr Bailey and myself. Thenceforward he was unable to take any active part in it though his interest never flagged until his death in action last year. Nevertheless, deep as is my regret that it must be so, responsibility for the views expressed in this paper rests with me alone. R. C. P.]

The data recorded below were derived from two distinct crosses. In each case the Langshan was the parent with feathered leg, the clean-legged parent being in one case the Brown Leghorn and in the other the Gold-pencilled Hamburgh.

Some of the later experiments involved a mating between a bird derived from the Langshan-Hamburgh crosses and an F_2 hen ex Langshan × Leghorn.

The relation between the various birds used in the whole series of experiments is set out in the pedigree on p. 204; the actual data are given in the tables on pp. 206–207.

The type of Langshan used was what is known as the Croad Langshan. In our experience the leg-feathering is not very heavy but extends fairly uniformly down the leg. It was found in all the birds

PEDIGREE CHART.

Langshan ♀ ——— Leghorn ♂ × Langshan ♀ ——— Langshan ♂ × Leghorn ♀

♀ 216/11
♀ 240/11
243 11
344/11

♂ 123/11

♀♀ 465/10
468/10
469/10
470/10
471/10

♂ 467/10

♀ 124/11

♀ 129/11

Langshan ♀

♀♀ 459/10
463/10
464/10

♂ 461/10

♀ 55/11

♂ 133/11

♀ 43/11

♂ 219/11

——— Hamburgh ♂ ×

♀ 452/13

♀ 454/13

♀ 453/13

♀ 263/12
♀ 220/12

♀ 262/12

♀ 487/13

♂ 64/12 × ♂ 90^s/12

♀ 250/13 × Hamburgh ♂

♂ 271/16 × ♀ 210/16

♂ 55/15

♂ 388/16 × ♂ 44/16

This chart gives the record numbers of the birds actually bred from. The composition of the families in which they appeared, as well as of the families which they produced, is given in Tables I and II.

which we bred, 38 in number (cf. Table, Pen 6, 1911, and Pen 3, 1912), and did not shew much variation.

44 F_1 birds were bred from the mating Langshan ♀ × Brown Leghorn ♂ and its reciprocal. All of them exhibited some degree of leg-feathering though in all cases it was less than that of the pure Langshan. The extent of the feathering varied but no attempt was made to grade the birds into different classes. Of the F_1 birds 4 ♂♂ and 14 ♀♀ were used to produce an F_2 generation, viz. Pen 10 and Pen 11 in 1911, Pen 13 in 1912, Pen 4 and Pen 11 in 1913. The number of F_2 birds from these pens was 429. Of these 323 shewed feathering on the leg while 106 had clean legs—a very close approach to a 3 : 1 ratio. The extent of the leg-feathering varied considerably though here again no grading was attempted. But our records make it clear that in some cases the feathering was rather heavier than in the average Langshan, while in others it was quite slight. In three cases F_2 birds from this cross were bred together. Pen 16, 1912, consisted of two such birds, both with feathered leg. The distribution of feathered and clean-legged birds, 34 to 15, suggest that both parents were here heterozygous. In Pen 11, 1912, an F_2 ♂ with feathered leg was mated with an F_2 ♀ which had clean legs. Of the 23 chickens hatched 11 had feathered and 12 had clean legs, a near approach to the expected equality on the assumption that the cock used was heterozygous. In the third pen, Pen 13, 1912, two feathered-legged birds bred together gave 7 chickens all with feathered legs. The numbers are too small to draw any definite conclusion, but it is not unlikely that at any rate one of the parents here was homozygous for the character. One other F_2 bird, ♀ 487 ex Pen 11, 1913, was subsequently tested in Pen 5, 1916, by mating her with ♂ 35 which, from his breeding, must be supposed to have been heterozygous. As all the 22 children produced had feathered legs ♀ 487 must be regarded as in all probability a homozygous F_2 bird. All the data from the Langshan-Leghorn cross are evidently consistent with the view that leg-feathering behaves as a simple dominant to clean leg. On this view we must suppose that the variation in the extent of the feathering, though partly dependent upon whether the bird is homozygous or heterozygous for the feathered-leg factor, must be dependent also upon some other factor or factors not yet analysed.

The Langshan-Hamburgh results, with one exception, are not dissimilar. 12 F_1 birds were raised in Pen 9, 1912, and Pen 15, 1913 Of these 11 had feathered legs, while one, which will be referred to

14—2

TABLE 1.

Langshan-Leghorn cross.

Year	Pen	Male	Origin	Female	Origin	Type of Mating	Offspring f.l	Offspring n.f.l
1910	Pen 6	Langshan	—	Leghorn	—	f.l. × n.f.l.	14	—
1911	Pen 6	Langshan	—	Langshan	—	f.l. × f.l.	18	—
		"	—	Leghorn	—	f.l. × n.f.l.	18	—
	Pen 10	461/10	F_1 ex Pen 6, 1910	459/10, 463/10, 464/10	F_1 ex Pen 6, 1910	f.l. × f.l.	66	23
	Pen 11	467 10	F_1 ex Pen 6, 1910	165/10, 468/10, 469/10, 470/10, 471/10	F_1 ex Pen 6, 1910	f.l. f.l.	79	30
	Pen 10 or Pen 11	—	—	—	—	f.l. × f.l.	23	10
1912	Pen 3	Langshan	ex Pen 6, 1911	Langshan	ex Pen 6, 1911	f.l. × f.l.	20	—
	Pen 10	123/11	ex Pen 6, 1911	216/11, 240/11, 243/11, 344/11	ex Pen 6, 1911	f.l. × f.l.	108	28
	Pen 11	133/11	F_2 ex Pen 10, 1911	55/11	F_2 ex Pen 10, 1911	f.l. × n.t.l.	11	12
	Pen 13	219/11	F_2 ex Pen 10, 1911	43/11	F_2 ex Pen 10, 1911	f.l. × f.l.	7	—
	Pen 16	129/11	F_2 ex Pen 10, 1911	124/11	F_2 ex Pen 10, 1911	f.l. × f.l.	34	15
	Pen 28	Leghorn	—	Langshan	—	n.f.l. × f.l.	12	—
1913	Pen 4	Same birds as in Pen 10, 1912			—	f.l. × f.l.	9	2
	Pen 11	202/12	F_1 ex Pen 28, 1912	203/12, 220/12	F_1 ex Pen 28, 1912	f.l. × f.l	40	13

TABLE II.

Langshan-Hamburgh cross.

Year	Pen	Male	Origin	Female	Origin	Type of Mating	Offspring f.l.	Offspring n.f.l.
1912	Pen 9	Hamburgh	—	Langshan	—	n.f.l. × f.l.	6	1
1913	Pen 15	Hamburgh	—	Langshan	—	n.f.l. × f.l.	5	—
1914	Pen 18	908/12	F_1 ex Pen 9, 1912	64/12	ex Pen 3, 1912	f.l. × n.f.l.	41	14
	Pen 5	Hamburgh	—	64/12	F_1 ex Pen 9, 1912	n.f.l. × n.f.l.	13	12
	Pen 7	908/12	F_1 ex Pen 9, 1912	453/13	F_1 ex Pen 15, 1913	f.l. × f.l.	36	8
1915	Pen 7	Same birds as in Pen 7, 1914		—	—	f.l. × f.l.	15	6
	Pen 13	908/12	—	2 Hamburgh ♀♀	—	f.l. × n.f.l.	7	16
	Pen 11 {	Hamburgh	—	250/13	F_2 ex Pen 18, 1913	n.f.l. × f.l.	7	—
	Pen 11 {	452/13	F_1 ex Pen 15, 1913	454/13	F_1 ex Pen 15, 1913	f.l. × f.l.	13	5
1916	Pen 5	35/15	ex Pen 13, 1915	2 Hamburgh ♀♀	—	f.l. × n.f.l.	22	28
	Pen 6 {	452/13	F_1 ex Pen 15, 1913	187/13	F_2 ex Pen 11, 1913	f.l. × f.l.	22	—
	Pen 6 {	452/13	F_1 ex Pen 15, 1913	451/13	F_1 ex Pen 15, 1913	f.l. × f.l.	41	8
1917	Pen 7	908/12	F_1 ex Pen 9, 1912	2 Hamburgh ♀♀	—	f.l. × n.f.l.	8	12
	Pen 10 {	271/15	ex Pen 5, 1916	453/13	F_1 ex Pen 15, 1913	f.l. × f.l.	12	4
	Pen 10 {	271/15	ex Pen 5, 1916	451/13	F_1 ex Pen 15, 1913	f.l. × f.l.	18	8
	Pen 20 {	44/16	ex Pen 5, 1916	210/16	ex Pen 24, 1916	f.l. × n.f.l.	12	9
	Pen 20 {	44/16	ex Pen 5, 1916	250/13	F_2 ex Pen 18, 1913	f.l. × f.l.	5	—
	Pen 20 {	44/16	ex Pen 5, 1916	388/16	ex Pen 24, 1916	f.l. × n.f.l.	16	20

below, was recorded as clean-legged. F_1 birds with feathered legs were mated together in Pen 7, 1914 and 1915, Pen 14, 1915, Pen 6 and Pen 7, 1915. Of the 148 birds produced 117 had feathered and 31 had clean legs—expectation being 111 and 37. F_1 birds were also mated with pure Hamburghs in Pen 7, 1915, Pen 14, 1915, and Pen 6, 1916. They gave 93 offspring of which 37 were feathered and 56 were clean in the leg, the latter class being more numerous than was expected.

One F_2 bird, ♀ 250/13, was mated with a Hamburgh cock and gave 7 chickens, all with feathered legs. Probably she was homozygous for the character[1]. Of her sons, one, ♂ 35/15, was mated with ♀ 487/13, an F_2 bird from the Langshan-Leghorn cross (cf. p. 204). Two birds from this mating were tested in Pens 10 and 20, 1917. Both proved to be heterozygous. ♂ 271/16 was mated with ♀ 454/13, an F_1 Langshan-Hamburgh hen. The result, 18 feathered and 8 clean-legged chicks, is close to the expected 3 : 1 ratio on the assumption that he was heterozygous. Further, with ♀ 210/16, a hen of mixed Hamburgh-Sebright-Leghorn origin, he gave 12 chicks with feathered and 9 with clean legs—a proportion near the expected equality of the two classes— ♂ 44/16, a brother of ♂ 271/16, was mated with a sister of ♀ 210/16. The 36 chickens produced are nearly equally distributed between the two expected classes.

So far the results of the Langshan-Hamburgh crosses may be said to have borne out those derived from the cross between the Langshan and the Leghorn. There is however the aberrant case above referred to where a clean-legged bird, ♀ 64/12, came from the Langshan-Hamburgh cross. This bird behaved as though she had feathered legs : with her brother she gave (in Pen 18, 1913) 55 chickens of which those with and those without feathered legs were almost exactly in the proportion 3 : 1. In the following year she was mated with a pure Hamburgh (Pen 5, 1914). Of the 25 chickens produced 13 had feathered and 12 had clean legs. One of her daughters, ♀ 250/13, has already been referred to as being in all probability homozygous for the feathered leg.

Occasionally therefore a heterozygous bird may fail to put up any leg-feathering. Sometimes the leg-feathering may be reduced to one or two small feathers at the base of the outermost toe. In two cases chicks on hatching were recorded as clean-legged though subsequent

[1] She was also mated with ♂ 44 in Pen 20, 1917, a bird known to be heterozygous. Here again, though only five chickens were hatched, all had feathered legs.

examination, when they were nearly full grown, revealed the presence of one or two very small feathers in this position. Instances of this extreme reduction of the feathering are comparatively rare. In the great majority of cases there is no difficulty in appreciating the presence of the feathering either at hatching or at any later stage in the bird's life. But apparently in a few cases the feathers fail to break through in early life, and occasionally, as in ♀ 64/12, they never break through at all.

In 1917 a few observations were made on the extent of the feathering in Pens 10 and 20. Both cocks were birds with legs slightly feathered though not of the very reduced type. Each was mated with a hen of mixed Hamburgh-Sebright-Leghorn origin. Presumably these hens were pure for the clean-leg character for during the past eight years many hundreds have been bred from birds involving these three breeds without the appearance of a single case of feathered leg.

There are two points of interest in connection with the feathered-leg birds from these two pens. In the first place the offspring may shew a grade of leg-feathering much heavier than that of the male parent. In Table III these chickens[1] have been graded roughly into three classes: (a) strong, in which the feathering is not dissimilar to that of the pure Langshan, (b) moderate and (c) slight, including birds with feathering similar to or less in extent than that of the male parents.

TABLE III.

Father	Mother	Male offspring			Female offspring		
		Strong	Moderate	Slight	Strong	Moderate	Slight
♂ 44	♀ 388	2	1	1	—	—	4
♂ 271	♀ 210	1	1	3	—	1	3
♂ 271	♀ 454	6	—	—	2	3	2
	Totals ...	9	2	4	2	4	9

In 6 cases out of 17 from ♀♀ 388 and 210 the leg-feathering was markedly heavier than in the father, suggesting that the clean-legged bird may carry some modifier affecting the extent to which the feathering developes. ♂ 271 was also mated with ♀ 454, an F_1 bird with feathering well marked though not as heavy as in the Pure Langshan. Here again some of the offspring were more strongly feathered than either of the parents.

[1] The numbers are rather less than those given in Table II. Some of the chickens died without their sex being determined.

The second point of interest appears in all three of the matings. There is a marked tendency throughout for the ♂♂ to be more heavily feathered than the ♀♀. More than half the ♂♂ are found in the highest of the three grades, while the majority of the ♀♀ occur in the lowest one. In his experiments on leg-feathering ("booting") Davenport ('09) grades his results but he does not appear to have noticed any connection between the degree of leg-feathering and sex. Since the sex of the offspring is not recorded in his tables it is not possible to test this point by his data. It is however one that may well be borne in mind by any future investigator of this character.

Several observers have published data on the inheritance of feathered leg in poultry. Of these the results recorded by Davenport are the most extensive and at the same time the most instructive. Many of his crosses, especially those in which birds of the F_2 and later generations were used (cf. Table 38, pp. 52, 53) are too involved for analysis, but for the Cochin and Dark Brahma crosses (Table 34, pp. 48, 49) the data are more favourable, and consideration of them has led me to the conclusion that a simpler interpretation can be found for them than that which Davenport has suggested. If we suppose that in these feathered-legged races two factors A and B may be present, either of which determines leg-feathering, the different proportions of clean-legged birds in the various F_2 matings recorded by Davenport may very well occur. In demonstration of this I have constructed Table IV on p. 211 from the data given on pp. 48 and 49 of Davenport's paper. The assumption is made that the original parents on the feathered-leg side all transmitted the factor A to the F_1 offspring subsequently tested. In many instances they also transmitted factor B while in others this factor was not passed on. It is assumed that the clean-legged breeds used, whether white Leghorn or Minorca, lacked both of these two factors. The restatement of Davenport's results set out on p. 211 clearly supports the view I have just advocated as to the factors which give rise to the feathered leg. The actual numbers are in fair accordance with expectation throughout and in many cases the two sets of figures are practically identical. It is probable therefore that in Cochins and Brahmas two factors are concerned in leg feathering, and not one only as in Langshans. This tallies with the grade of leg-feathering found in the two former breeds, in which the feathers are more numerous and more highly developed than in the last named.

Cochins were also used by Hurst who found that the F_1 birds pro-

TABLE IV.

Pen	Nature of cross			Ref. nos. of F_1 Mothers	Ref nos. of F_1 Father	Suggested constitutions of F_1 Parents	F_2 offspring		Expectation	
							f.l.	n.f.l.	f.l.	n.f.l.
650	Black Cochin × Wh. Leghorn			170, 263, 278, 364	265	$AaBb × Aabb$	133	11	126	18
,,	,,	×	,,	361	265	$Aabb × Aabb$	26	9	26	9
654	Wh. Leghorn × Buff Cochin			602, 828, 640, 696, 767, 697	704	$Aabb × Aabb$	72	25	73	24
608	Wh. Leghorn × Dk. Brahma			384, 248	409	$AaBb × Aabb$	78	7	75	10
,,	,,	×	,,	249, 395, 385	409	$Aabb × Aabb$	107	37	108	36
659	,,	×	,,	762, 503, 382, 250, 737, 387	375	$AaBb × Aabb$	146	16	142	20
655	,,	×	,,	720, 724, 728, 730, 732, 734, 761, 800, 721	666	$AaBb × AaBb$	53	1	51	3
,,	,,	×	,,	724, 734, 800, 720, 728, 761, 732, 730, 721	254	$AaBb × Aabb$	96	14	96	14
632	Minorca × Dk. Brahma			742, 690, 631, 618, 700, 703, 743, 599	637	$AaBb × Aabb$	221	17	208	30
,,	,,	×	,,	524, 576, 638	637	$Aabb × Aabb$	57	17	56	18

duced from crosses with clean-shanked breeds such as the White Leghorn and Hamburgh all shewed leg-feathering, though in less degree than the Cochin parent. At the time of Hurst's experiments the idea of multiple factors had not yet been put forward. It was not at that time fully realised how important it was to keep entirely separate the record of each bird used as a parent. Many similarly bred hens were run with a given cock on the assumption that they were of like constitution though, as we know to-day, this was not necessarily the case.

Nevertheless Hurst's results can to some extent be reconciled with those of Davenport. In Exp. 6 (p. 135) a number of F_1 birds were raised from (a) 2 Hamburgh ♀ ♀ × Buff Cochin ♂ and (b) from Buff Cochin ♀ × Hamburgh ♂. The 107 birds reared all had feathered legs, though the feathering was distinctly less than that of the Cochin. In Exp. 8 (p. 138), 12 of these F_1 ♀ ♀ were mated with an F_1 ♂, and gave 115 chicks with feathered and 4 with clean legs.

Assuming that all of these birds were **AaBb** in constitution expectation would be 111·5 f.l. : 7·5 n.f.l. Twelve F_1 ♀ ♀ (presumably different ones from the above since the experiment was also made in 1903) were

run with a Hamburgh ♂ to give 35 f.l. and 21 n.f.l. chicks, expectation being 42 : 14. The number of clean-shanked chicks is rather higher than expectation, but we do not know for certain that all of the hens were in constitution **AaBb**. If one or two were **Aabb** the excess in the n.f.l. class would be easily accounted for.

Lastly a Hamburgh-Cochin from Exp. 6 was mated with 12 Leghorn-Houdan ♀ ♀ (Exp. 13, p. 141). Here again expectation is f.l. and n.f.l. in the ratio 3 : 1. The actual numbers were 195 f.l. and 112 n.f.l. The considerable excess of n.f.l. birds suggests some complication. Possibly some of the potentially f.l. birds do not shew the feathering as in ♀ 64 (cf. p. 209 above). There is also the possibility that some of the Leghorn-Houdan hens may have carried a factor inhibiting the development of the leg feathers. This possibility is indicated by some experiments of Bonhote. From the Silky as the feathered and the Yokohama as the clean-legged parent he obtained $2F_1$ birds of which both had clean legs. Bred together this pair gave 24 chicks of which 8 were f.l. and 16 were n.f.l. If the Silky carried a factor **A** for feathered leg and the Yokohama an inhibitor factor I, the constitution of the F_1 birds might be regarded as **Aali**. Such birds in F_2 should give f.l. and n.f.l. in the ratio 3 : 13. The figures obtained by Bonhote, viz. 16 n.f.l. and 8 f.l. are not hopelessly out of accord with those expected, viz. 19·5 n.f.l. : 4·5 f.l., when the smallness of the numbers is taken into account.

In the only other experiments of this nature with which I am acquainted, those of Cunningham dealing with a Jungle fowl—Silky cross, the birds reared were too few to give a result of much value. The F_1 birds had feathered legs, while of 10 F_2 birds 9 were f.l. and 1 was n.f.l.

In so far as our present knowledge of the heredity of leg-feathering goes we may say that in certain crosses it may behave as a simple dominant, though dominance is always incomplete. In breeds with more heavily feathered legs there are grounds for supposing that two factors for leg-feathering may be present. Further, it is possible that some strains of clean-legged birds may carry an inhibitor for the feathered-leg character. The extent of the feathering shews considerable variation even in birds similarly constituted in respect of the factor or factors for feathered leg. Rarely a potentially leg-feathered bird may fail to shew even traces of the feathering. Probably clean-legged birds will be found in some cases to carry factors, hitherto not identified, which affect the extent to which the feathering is developed. In support of this is the fact that a clean-legged bird, mated with a bird

in which the leg-feathering is slight, may give offspring in which the legs are strongly feathered (cf. p. 209).

The experiments of which an account is given above form part of a series of investigations on heredity in poultry for which the means have been provided out of the Fund controlled by the Development Commission.

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ON THE OCCURRENCE, BEHAVIOUR AND ORIGIN OF A SMOOTH-STEMMED FORM OF THE COMMON FOXGLOVE (*DIGITALIS PURPUREA*).

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In the course of an earlier investigation on the inheritance of the peculiar modification of the flower known as heptandry, which is occasionally met with in *Digitalis purpurea*, it was incidentally noted that some individuals exhibited a distinct variation from the recognised type as regards surface character[1]. The typical plant is generally described as having all the aerial green parts covered with hairs, those on the stem and petioles being so abundant as to give these structures a downy, grey appearance. In the particular individuals in question, on the other hand, the vegetative region of the stem was conspicuously green, smooth and shining, and the leaves were distinctly less hairy on the upper surface and deeper green in colour, so that the eye was at once attracted to these plants. The data obtained in regard to this partially glabrous condition pointed to its relation to the completely hairy state being that of dominant to recessive, but the records were neither large enough nor derived from a sufficient number of generations to furnish conclusive evidence on this point, nor did they serve to show whether or not this character is constant and breeds true. In order to obtain decisive proof as to the behaviour of this form the experiments were continued through several further generations. In passing it is worth mention that a further object of the investigation was to ascertain whether the two distinct abnormalities, peloria and heptandry, exhibited any phenomenon of the nature of linkage, or whether each recessive character was inherited without relation to the other. The later work showed that these two modifications are, in fact, inherited quite independently and that in

[1] *The New Phytologist*, Vol. x. 1911, p. 60.

peloria, as in heptandry, the degree in which the abnormality is mani-
fested, as indicated by the size of the peloric "flower" has some relation
to the order of the axis, whether main or lateral, on which it is borne,
as is the case with numerous other abnormalities which exhibit grada-
tions. A further remarkable peculiarity observed in all the members
(40) of one heptandrous non-peloric family was the thickening of the
margins of the sepals, on which were borne bodies having the appearance
of rudimentary ovules. Unfortunately no offspring were raised from
these particular plants, and as the character never reappeared in any
later crop there is nothing to add to the bare record.

A serious difficulty all through the work was the almost unavoidable
contamination of the whole available ground with a large quantity of
self-sown seed. In spite of the precautions taken to meet this contin-
gency the appearance of an occasional plant here and there gave ground
for suspicion that it was a "stray" and sufficed to render the evidence not
wholly beyond question. Eventually, however, by breeding exclusively
from white-flowered peloric, heptandrous (i.e. triple recessive)[1] parents
whereby the detection of "strays" red-flowered or normal was at least
ensured, unimpeachable records were obtained. These results have now
fully established the fact that the smooth-stemmed condition in *Digitalis
purpurea* is a well-defined character[2] and that pure-bred individuals
exhibiting this character but otherwise identical with the completely
hairy plant, breed strictly true. We have in fact in the partially glabrous
D. purpurea a form as definite as the partially glabrous (half-hoary)
Matthiola incana which I have described elsewhere[3], to which indeed it
appears to be somewhat analogous. For the half-hoary Stock similarly
has a glabrous stem though the type plant is tomentose throughout.

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[1] The recessive nature of peloria was established by Keeble, Pellew and Jones (see
The New Phytologist, Vol. IX. 1910). In my earlier paper (*loc. cit.*) I showed that
heptandry is similarly recessive to the normal, and the same result has been obtained by
Tine Tammes and Shull (see Shull, *Zeitschr. f. induk. Abstammungs- u. Vererbungslehre*,
Bd. VI. 1912). The white-flowered plants employed were of the pure white form with
greenish spots which behaves as a recessive to the coloured type.

[2] Although I have consistently referred for convenience only to the *stem* character, it will
be understood that this feature is always associated with the smoother leaf surface though
the difference in the leaves is less striking to the eye. And here I may add that the extent of
the stem which is smooth is not a definite proportion of the total length but is determined by
the amount of vegetative growth which takes place before the reproductive stage approaches.
A practical outcome resulting from this variability is that in many herbarium specimens
barely sufficient of the stem is preserved to permit of its character being certainly determined.

[3] See Reports of the Evolution Committee to the Royal Society, Rep. 1, 1902, p. 33.
For a fuller account later see *J. of Genetics*, Vol. V. No. 3, 1916, p. 145.

The leaves which succeed the cotyledons are also glabrous except for one or two minute marginal hairs near the apex. But as the plant develops the successive leaves attain a greater degree of hoariness until the lower surface becomes covered nearly if not quite as densely as in the fully hoary type plant, though on the upper surface the covering of hairs remains throughout appreciably thinner. As we ascend from the vegetative region of the stem to the bractless racemes hairs usually gradually extend down on to the axis from the pedicels which become distinctly hoary on their abaxial surface. In the smooth-stemmed Foxglove, as stated above, the stem is glabrous, deep green and of a polished appearance from the radical rosette upwards. The leaves, though hairy on both surfaces, are distinctly less so on the upper surface than in the hairy form, and are deeper green in colour. The midrib on the under side of the last-formed leaves of the rosette appears as a smooth green demarcation line halving the greyer lamina and petiole, whereas, in the hairy form, the grey surface appears unbroken. This feature serves as a useful means of identification in young plants which have not yet developed the flowering axis. Proceeding up the stem we find that an overflow as it were of the hairs from the leaf may extend down from the point of insertion as a hairy streak or band. As we approach the flower spike these decurrent bands from the uppermost leaves and bracts coalesce more or less completely so that the axis becomes as completely downy as in the hairy form. Thus in both Stock and Foxglove we have the same feature, a transition from the glabrous condition characteristic of the vegetative region to a more hairy condition in the inflorescence, the change being much more marked however in the Foxglove.

As appeared probable from the results obtained incidentally in the course of the earlier experiments on heptandry the smooth-stemmed form in *D. purpurea* is found to behave as a simple dominant. The statistical evidence proving this to be the case is given in the accompanying tables where it will be seen

(1) that both forms, when pure, breed true ;

(2) that the F_1 generation from a mating between the two is all smooth-stemmed ;

(3) that F_1 plants yield the simple ratio of 3 smooth to 1 hairy when self-fertilised, and 1 smooth to 1 hairy when crossed back with the hairy form.

These results are in marked contrast to the complex relations which are found to hold in the Stock, a full account of which it is hoped to

complete shortly. For the moment the general statement that the half-hoary condition in the Stock is dependent upon several factors, and that it behaves as a recessive to the fully hoary type will suffice to show that the underlying factorial relationships are here quite different notwithstanding the apparent similarity of the two cases.

That the smooth-stemmed plant represents a distinct form of *purpurea* sharply separated from the accepted type and not a *fluctuating* condition of the species does not appear, so far as I can discover, to have been recognised by systematists. I have searched in vain in both British

TABLE I.

Results obtained when the two forms of Digitalis purpurea *were self- or inter-bred.*

Reference to these two forms by name being more convenient than by a lengthy description I have designated the hairy-stemmed form *pubescens*, the smooth-stemmed *nudicaulis*.

Experiment 1 shewing that *pubescens* (recessive) breeds true.				Experiment 2 shewing that pure bred *nudicaulis* (dominant) breeds true.			
		Offspring				Offspring	
Parentage	No of family	*pubescens*	*nudicaulis*	Parentage	No of family	*pubescens*	*nudicaulis*
pubescens - self	1	208	None	*nudicaulis* - self	1	None	303
or fertilised	2	115	,,	or fertilised	2	,,	263
inter se	3	77	,,	*inter se*	3	,,	162
	4	75	,,		4	,,	49
	5	55	,,				
	6	47	,,		Total		777
	7	46	,,				
	8	37	,,				
	9	32	,,				
	10	30	,,				
	11	28	,,				
	12	26	,,				
	13	12	,,				
	14	87	,,				
	15	47	,,				
	16	43	,,				
	17	41	,,				
	18	39	,,				
	19	29	,,				
	20	21	,,				
	21	21	,,				
	22	19	,,				
	23	19	,,				
	24	12	,,				
Total		1166	None				

TABLE II.

Results obtained when crossbreds were self-fertilised or bred back with the hairy-stemmed form.

Experiment 3* shewing that *nudicaulis* erossbreds × self or fertilised *inter se* yield both forms in the simple Mendelian ratio of 3 *nudicaulis* : 1 *pubescens*.

| Parentage | No. of family | Offspring | |
		pubescens	nudicaulis
nudicaulis cross-	1	15	55
breds × self or	2	16	37
fertilised *inter se*	3	24	65
	4	36	104
	5	8	42
	6	28	75
	7	21	69
	8	36	94
	9	28	78
	10	47	128
	11	27	73
	12	10	64
	13	24	53
	14	50	191
	15	18	75
	16	10	25
	17	14	42
	18	1	7
	19	28	108
	20	1	6
	21	15	57
	22	6	22
	23	6	23
	24	5	13
	25	53	130
Totals ...		527	1636
Expectation		*541*	*1622*

Experiment 4* shewing that *nudicaulis* crossbreds when crossed back with *pubescens*, in accordance with expectation yield the two forms in the ratio of 1 *nudicaulis* : 1 *pubescens*.

| Parentage | No. of family | Offspring | |
		pubescens	nudicaulis
nudicaulis cross-	1	388	394
breds × *pubescens*	2	377	343
	3	205	228
	4	15	18
	5	74	62
	6	83	88
	7	116	146
	8	145	173
	9	40	38
	10	145	158
	11	177	156
	12	140	144
	13	55	57
	14	70	48
	15	41	33
	16	68	87
	17	31	31
	18	74	60
	19	144	141
	20	103	116
	21	11	12
	22	13	9
Totals ...		2515	2542
Expectation		*2528·5*	*2528·5*

* Reciprocal crosses were made in each case.

and Continental Floras and in numerous works devoted to detailed descriptions of British Wild Flowers and Garden Plants for any hint as to the definite nature of the variation above mentioned. In descriptions containing direct reference to this character of the stem as apart from the plant as a whole, and such are the exception rather than the rule, it is usually stated simply to be tomentose or pubescent, or at most with the amplification "especially above," but without in such case precise

reference to any sharp contrast presented by the lower region. This is the more surprising as the two forms very frequently occur together in copses, woods and hedgebanks through the length and breadth of England. I had hoped to be able to give a more or less full list of the areas in this country where the smooth-stemmed form occurs mixed with the hairy, and where it appears not to accompany it, but I have been obliged to postpone further investigation in this direction owing to the difficulties which have arisen in consequence of the war. That it is widely distributed as a wild or naturalised plant there is no doubt. I have myself observed it as far north and south as Northumberland and the New Forest; in the Midlands; and as far east and west as Kent and Surrey and Somersetshire and Carnarvonshire. Also wherever I have chanced to examine plants in gardens I have invariably found both forms growing mixed together. In herbarium material, whether British or Continental, I find *purpurea* represented *by either form indifferently and without distinction.* In the Cambridge collections, for example, specimens from Surrey, Gloucestershire, Wales and Scotland, and from the Black Forest and the Vosges appear to be smooth[1], while other specimens from Scotland and Germany, from Gibraltar and Castile, Portugal, France and the English counties Shropshire, Sussex and Worcestershire (Malvern Hills)[2] are hairy. Again in the Kew collections, out of some score of specimens examined, about two-thirds were found to be *nudicaulis* and one-third only of the recognised type. There appear, however, to be localities in England, and no doubt abroad, where *pubescens* occurs alone—*nudicaulis* alone I have never met[3]. For the following information on this point I am indebted to the kindness of friends who were good enough to make observations in response to my enquiries. Dr J. C. Willis tells me that of some hundreds of plants examined on Worcestershire and Herefordshire Beacons (Malvern Hills) he and his daughter noticed only *pubescens*. Statements to the same effect were sent to me by Dr O. Withers in regard to the neighbourhood of Sidmouth and to his own garden there where plants had appeared spontaneously from self-sown "wild" seed; by

[1] Although in some of these specimens only the upper part of the stem is preserved, I have no doubt as to the identification being correct in these cases.

[2] On the Lickey Hills on the other hand I found both forms.

[3] In the only two districts where I attempted an actual count over a small area—a copse at Holmwood (Surrey) and a cleared piece of land near Stocksfield (Northumberland)—I found in the former case a slight, and in the latter a considerable predominance of the smooth form. Information kindly sent to me by a friend in regard to a wood in Somersetshire on the other hand was to the effect that *pubescens* was much more abundant than *nudicaulis*.

Dr D. H. Scott regarding a wood near Oakley (Hampshire), although both forms were to be found in his garden about a mile away, here however commercial seed had been introduced[1]; by other correspondents in regard to the plants which occur abundantly on shingle in the neighbourhood of Dungeness and in woods and coppices around Peasmarsh (Sussex).

These facts naturally give rise to the question as to when and where the smooth-stemmed form first appeared. Did it arise spontaneously as a wild plant or did it originate in cultivation and then become generally distributed as a "garden escape." Or is the premise here involved not really established and should we more properly enquire whether indeed *pubescens*, as seems to be always assumed, or *nudicaulis* represents the original type ? Whichever be the view adopted there remains to be considered the further question whether the one form arose from the other by direct mutation, or as the result of hybridisation either with a hairy species on the second supposition, or with a glabrous or partially glabrous one on the first. If a direct mutation has taken place, then, according to the accepted view we should have the case of a dominant mutant arising from a recessive type. As a comparable case in another member of the Scrophulareaceae we may cite *Linaria alpina* where the self-coloured form *concolor*, though dominant, is regarded as a variety, the recessive form with the orange patch on the lower lip as the type[2]. Here as in *Digitalis* the two forms are distinguished by a solitary characteristic, in every other respect they are identical. Such instances of mutation—if mutation it be, and in *Linaria* there seems no ground for regarding it otherwise—from a recessive to a dominant form, when only one factor appears to be involved, are exceptional, and it is obvious that on the "presence and absence" theory of factors they present a certain difficulty. But the alternative hypothesis which supposes that the smooth-stemmed Foxglove or the self-coloured *Linaria* is derived from a cross with another species is also not free from difficulty. On this supposition we should look in these forms for larger or smaller differences from the parent type in a considerable number of characters such as are enumerated by Neilson Jones[3] as characterising his artificially raised (and hence authentic)

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[1] I am indebted to Dr Scott for the further information that this was essentially an oak and hazel wood, and that the soil was "clay with flints" resting upon chalk. So far however the results of investigation do not seem to indicate that the appearance of *nudicaulis* is conditioned by the character of the soil.

[2] See *The New Phytologist*, Vol. xi. 1912, p. 167

[3] "Species Hybrids of Digitalis," *J. of Genetics*, Vol. ii. No. 2, 1912.

purpurea-grandiflora (= -*ambigua* Murr.) hybrids which were found to differ to a greater or less extent from the parent species in every particular: by Henslow[1] in his detailed comparison of a spontaneously occurring garden hybrid with its supposed parents *purpurea* and *lutea*: and again in the still earlier account by Roth[2] of the wild form *media* presumed to be a hybrid between *ambigua* Murr. and *lutea*. In the case of *Digitalis* certainly we should look too for some trace of that sterility which is so marked a feature of indubitable species hybrids in this genus[3]. But we do not find either the one or the other. For except as regards surface character the two forms *nudicaulis* and *pubescens* are precisely similar, and both set seed abundantly. Moreover it is to be noted that such spontaneously occurring forms as are judged to be of hybrid origin exist for the most part in small numbers, only a single plant perhaps being found wild or in a garden from time to time[4], whereas, as stated above, *purpurea nudicaulis* is not only of very general occurrence, but where it occurs it is abundant. Furthermore, reference to other species of *Digitalis* makes it evident that the *nature* of the differentiating character in the present case cannot be taken as in itself necessarily

[1] *Trans. Camb. Phil. Soc.*, Vol. IV. Part 2, 1831, p. 257.

[2] *Cat. Bot.* II. 1800.

[3] Among many references to this fact since the early work of Koelreuter and Gärtner may be mentioned Focke's account of the following hybrids—*purpurea-lutea*, *ambigua-purpurea*, *ambigua-obscura*, *ambigua-lutea*, *ambigua-lanata*, *ambigua-laevigata*, *laevigata-lanata* (*Die Pflanzen-Mischlinge*, 1881). In each case greater or less difficulty was experienced in obtaining the hybrid artificially, and the hybrids themselves proved in most cases to be completely sterile. Of these various forms *purpurea-lutea* has been recorded from time to time by various observers in the wild state. It was noticed by A. Saint-Hilaire and de Salvert growing mixed with *purpurea* and *lutea* in a valley in the Auvergne district in 1808, and for several consecutive years the capsules were examined for seed, but each season they were found to be shrivelled and to contain only aborted ovules (" Observations sur la Stérilité des Hybrides," *Mém Soc. d'hist. nat. Paris*, I. 1825, p. 373). It is stated by Wilson who raised a number of hybrids between these two species that the stamens were often wanting, and that when present the pollen was found to be bad and he obtained no seed (see *Report of the third International Conference on Genetics*, Roy. Hort. Soc., 1906).

[4] Among such cases may be instanced the single plant identified as *D. purpurascens* Roth. found by Le Jolis growing in the environs of Cherbourg amid plants of *D. purpurea* (*Ann. Sci. Nat.*, 3rd Sér. T. VII. 1847, p. 220): the single specimen of *D. longiflora* noticed by Lejeune near Verviers and regarded by him as answering closely to Koelreuter's *hybrida* (*Revue de la Flore des Environs de Spa*, 1824, p. 126): the single *purpurea-lutea* hybrid described by Henslow which appeared in his garden among plants of the two parent species (*loc. cit*): and other similar records to be found scattered through the literature of the subject which emphasise the rarity of occurrence of these natural hybrids, their variability of form, and the fact that when they arise they are often little durable (see Lamarck and De Candolle, *Flore Française*, Vol. VI. 1815, p. 412, and Vaucher, *Histoire Physiologique des Plantes d'Europe*, T. III. 1841, p. 520).

pointing to a hybrid origin. For we find within the genus, besides the group of types closely allied to *purpurea* and like *pubescens* having the stem pubescent or tomentose throughout, as e.g. *Thapsi* L., *tomentosa* Link and Hoffmgg., *Mariana* Boiss., *nevadensis* Kze. and *dubia* Rodr.[1], and those on the other hand which like *laevigata* W. and K., *laciniata* Lindl., *obscura* L. and *ferruginea* L. are smooth-stemmed throughout, a considerable number of forms which exhibit *as a recognised normal feature* a similar transition from a glabrous condition in the vegetative to a hairy condition in the flowering region of the stem. Well-marked examples of this class are *D. lanata* Ehrh., a Hungarian species, and the Portuguese form *D. miniana* discovered by Sampaio and described by him in 1905, in both of which the transition in surface character is definitely recognised as a diagnostic character. Among cases less pronounced or possibly only less clearly recognised we may probably include *ambigua* Murr., *sibirica* Lindl., *leucophaea* Sibth., *parviflora* Jacq.[2] and perhaps *orientalis* Lam. and *lutea* L.[3]; also *purpurascens* Roth. considered by some as a hybrid form and *fuscencens* W. and K., the last-mentioned a rare Hungarian plant

[1] All these types appear to be closely related to *purpurea*. Beautiful illustrations of *tomentosa* and *Thapsi* are given in *Flore Portugaise* by Link and Hoffmansegg, where *tomentosa* and *purpurea* are compared in detail. According to Brotero (*Phytographie*, T. II. 1827, tab. 149, p. 159) *tomentosa* is not to be regarded as distinct from *purpurea* but merely as a southern race of that species to which it is linked by intermediate forms. *Thapsi* is described by Lindley (*loc. cit.*) as also very similar to *purpurea*, and by Koelreuter (*Acta Acad. Petropol.*, 1777) is regarded in the same light as *tomentosa*. G. W. F. Meyer takes the same view (*Chloris Hanoverana*, 1836, p. 323). *Mariana* is another form, according to Boissier (*Voy. Bot.* T. II) closely akin to *purpurea*, while *dubia* is considered by Rodriguez (*Plantas vasculares de Menorca*, 1874) to be intermediate between *Thapsi* and *minor*, the flowers of the latter species being described by Linnaeus as again very similar to those of *purpurea*.

[2] From systematic descriptions of these species where little importance attaches to the nature of the stem surface as a diagnostic character it is less easy to gather the precise degree of difference between the upper and lower region. Though no specific statement may be met with in the text reference to the illustration, where such is given, will sometimes clearly show that the plant exhibited this transition character, as is seen, for example, in the case of *D. ochroleuca* described and figured by Jacquin in *Fl. Aust.* I. p. 36, pl. 58, 1773.

[3] Though *lutea* is generally spoken of as glabrous Lindley describes the stem as very glabrous *or pubescent*, and Henslow also draws attention to the possibility that absence of hairs in this species is not a fixed character. Specimens from near Siena in the Bunbury Collection (Cambridge) show numerous hairs on the margins and on the veins of the under surface of the leaves, and on bracts and sepals, but the stem appears to be hairless. Whether the appearance of hairs on the stem in this case is a fluctuating character and varies with conditions or whether there are two distinct and constant forms I have not sufficient data to determine. It is possible that the same question may arise in regard to *orientalis* and perhaps also with *laevigata* as well.

universally regarded as a hybrid, but whether on other grounds than its intermediate character does not appear. It has not yet apparently been artificially bred since statements as to its parentage commonly indicate uncertainty as to whether it should be regarded as derived from a cross between *ambigua* and *lanata* or *ambigua* and *laevigata*.

D. lanata was originally described by Ehrhart[1] as having the stem glabrous, the raceme woolly. The figure and description of this plant in Curtis's *Botanical Magazine*[2] emphasises the same character, the stem being described as "smooth at the lower part, woolly above." So also does the account given by Waldstein and Kitaibel[3] of the plant referred by them to this species. They describe the stem as naked but woolly with white hairs among the flowers, this feature being also clearly seen in the coloured plate which shows the stem destitute of hairs and purplish-red in the lower portion, becoming green and covered with hairs in the region of the inflorescence. Similarly Sampaio's description of *D. miniana* as quoted by Coutinho states that the stem is everywhere glabrous except the axis of the inflorescence which is more or less tomentose[4]. Comparison of the descriptions by numerous writers of the other forms enumerated above and examination of herbarium material indicate that this same feature is characteristic of all of them in varying degree. Now to several of these types, if not to all, systematists are agreed in according specific rank, hence in the particular case of *purpurea* the stem character cannot be held to afford ground for regarding *nudicaulis* as a crossbred. But there is yet another alternative supposition which is not excluded and which appears to me worthy of consideration. May it not be that *nudicaulis* is a precursor rather than a derivative of *pubescens*? As between such forms our conception of which is type and which variety, in the absence of any historical record is largely determined by our knowledge of the relative numerical abundance of the two forms and possibly may not invariably reflect the true genealogical order. A mutation in this reverse direction, i.e. from *nudicaulis* to *pubescens* would on the "presence and absence" view be simply the usual case of variation by the loss or dropping out of a factor. Once in existence the new recessive (on this supposition *pubescens*), in any area to which it chanced to spread unaccompanied by *nudicaulis*, might well continue to

[1] *Beiträge* vii. p. 152.

[2] Vol. xxix. Pl. 1159.

[3] *Descript. et Icon. Plant. rar. Hungariae*, i. p. 76, pl. 74.

[4] I have been unable to see or obtain Sampaio's original paper in *A Revista, Porto*, iii. 1905, but his account is quoted by Coutinho in the *Bol. Soc. Broter.*, xxxii. p. 199. See also Coutinho, *A Flora de Portugal*, 1913, p. 561.

remain pure for a considerable period, and be taken in such areas to represent the type form of the species. It is possible that the Malvern Hills afford a case in point, for according to Anne Pratt the Foxglove suddenly appeared in abundance on one of these hills after, for some reason, the soil had been turned up[1]. The same argument may be advanced in the analogous case of *Linaria alpina* mentioned above, where indeed a hybrid origin seems even more improbable.

How far a fuller knowledge of the geographical distribution of the two *D. purpurea* forms will serve to throw light on their genealogical relation remains to be seen. The home of the genus appears to be in Central and Southern Europe, numerous species occurring in Germany, France, Spain, Italy, Austria; it is also represented by several forms in Russia, Belgium, and Portugal, *purpurea* itself being found in all these countries, as well as in England, Denmark, Norway and Sweden where it is the only recorded species. I have already drawn attention to the wide distribution over Great Britain of *purpurea nudicaulis* in company with *purpurea pubescens*. The further fact that herbarium material examined at Kew was found to include specimens of *nudicaulis* as well as *pubescens* both from Norway and Sweden, taken together with the descriptions of the species in Neuman's *Swedish Flora* (stem cylindrical, hairy *above*) and in Blytt's *Norwegian Flora* ([plant] covered with short downy hairs *especially above*) renders it highly probable that *nudicaulis* will very generally be found with *pubescens* in these countries, as in England. If this should prove to be the case it strengthens still further the argument against hybridisation as an explanation of the appearance of *nudicaulis*. It may be urged no doubt that the absence of all mention of glabrousness as a feature of the stem in the early descriptions of *D. purpurea*, such as those of the older herbalists, renders the view here suggested improbable. But seeing that neither in modern works do we find any clear reference to the existence of two forms despite the abundance and wide distribution of *nudicaulis* this objection may be put aside. A similar omission is very general in the case of *Linaria alpina*; many botanical works dealing with the flora of regions where *both* forms are to be found make no mention of the *concolor* form. And here perhaps the matter must rest until further evidence throwing light on the question is available.

[1] *The Flowering Plants and Ferns of Great Britain*, Vol. IV.

Summary of Conclusions.

1.   *Digitalis purpurea* occurs under two distinct forms, the one commonly accepted as the type with the stem grey and densely pubescent throughout, and the leaves very hairy, here designated *pubescens*; the other, not apparently hitherto distinguished, with the stem green, polished and smooth from the base to the flowering region where it becomes pubescent, and leaves less hairy, designated *nudicaulis*.

2.   The two forms are similar in every respect except as regards surface character.

3.   No difference in fertility was observed between the two forms which set seed abundantly.

4.   The distinguishing feature of *purpurea nudicaulis* is a character common to several other species within the genus.

5.   Both forms, when of pure parentage, breed true.

6.   *Nudicaulis* behaves as a Mendelian dominant when crossed . with *pubescens* and the crossbreds yield the monohybrid ratio 3 *nudicaulis* : 1 *pubescens* when self-fertilised and 1 *nudicaulis* : 1 *pubescens* when crossed back with the recessive *pubescens*.

7.   The facts stated under 2, 3, 4, 5 and 6 do not support the idea that *nudicaulis* is of hybrid origin.

8.   The alternative hypothesis of the origin of the one from the other by direct mutation raises the question as to which represents the original type, unless we postulate parallel development from a common ancestor.

9.   In the absence of conclusive historical or geographical evidence to the contrary, and in view of the fact that there is a certain difficulty in supposing the origin of a dominant mutant form a recessive type, the view that *nudicaulis* may be the earlier form and *pubescens* the derivative seems at least worthy of consideration.

10.   The same argument may be advanced in the case of *Linaria alpina* where also, according to the accepted view, we have in the recessive spotted form the type and in the dominant *concolor* form the variety.

And further in regard to certain abnormal features :—

11. That the two modifications of the corolla, peloria and heptandry, both recessive to the normal, are inherited quite independently.

12. That as a rare occurrence the margins of the sepals may be thickened and bear structures having the appearance of rudimentary ovules.

The expenses incurred in the course of this investigation have been defrayed in part by grants from the Royal Society and from the British Association for the Advancement of Science.

After the foregoing account had been written I received from Professor Coutinho, to whom I here wish to tender my most cordial thanks, in response to my enquiry, a specimen of *D. miniana* obtained from the same region as Sampaio's original plant (Duriminia, Serro de Castro, Laboreiro, near Alcebaça, about lat. 42° N.), and also further interesting information regarding the occurrence of this form. Professor Coutinho writes that *D. miniana* is a rare plant, occurring within a very restricted area *mixed with* purpurea; that it was found again last year by one of his assistants in the original locality, the specimen sent being one of those obtained on this occasion. The appearance of the specimen, taken together with Sampaio's account, and the further details supplied by Professor Coutinho, make clear the close affinity of this form with *purpurea*. In fact whether it is really distinct from that species seems to me open to question seeing that the smooth stem emphasised as the distinctive character of *miniana* is a constant character of *purpurea nudicaulis*. The dimensions given for the stem (2 cm. in diameter at the base, 17 dcm. in height), the deeper colour, smaller size (10—18 mm. long) and narrower form of the corolla which is only slightly ventricose may possibly be fluctuating characters, and in that case may be discovered associated with the *pubescens* habit, although having hitherto escaped detection. The description of the leaves of *miniana* would be quite applicable to a plant of *purpurea*. Although the length of the pedicels in *purpurea* is generally not more than equal to that of the bracts whereas in this particular specimen of *miniana* they far exceed the bract-length, this appears to be a decidedly variable character since in his description of *miniana* Sampaio states the precise contrary, and in *purpurea* I have occasionally found a pedicel exceed the bract by perhaps 2 mm. or more. Beyond the corolla characters therefore there seems to be no very sharp distinction between *purpurea nudicaulis* and *miniana*, and it remains to be seen whether the latter

form will remain constant under different conditions, a point which I hope now to be able to test on the material received from Professor Coutinho.   Hybridisation as an explanation seems improbable since *D. Amandiana* Samp., the only other native form with a glabrous habit, is not mentioned by Sampaio as an inhabitant of this region but as occurring in arid and stony places along a certain part of the course of the Douro, and the Tua and elsewhere.

CONTENTS

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THE INHERITANCE OF TIGHT AND LOOSE
PALEAE IN AVENA NUDA CROSSES[1].

By A. St CLAIR CAPORN.

(With six text-figures.)

EXPERIMENTS were conducted with three varieties of ordinary oats with tight paleae, viz. :—

> Thousand Dollar.
> Ligowo.
> Nubischer Schwarzer (Nubian Black).

As the F_2 generation of the cross with Nubischer Schwarzer has not yet been harvested, being part of this year's crop, it may be necessary to issue the results obtained from it in a supplementary account, though reference to its earlier stages will be made in this paper.

A short description of each of the parents will indicate the nature of the characters involved.

Thousand Dollar.

This is a typical tight grained oat of the spreading, or open, panicle kind. The grains are of good size, fairly long, and firmly ensheathed in the paleae. They do not, except when it is exceptionally prolonged and violent, become naked on threshing. The inner paleae are thin but stiff, the outer thick and curled round the edges of the inner. So well developed is the intervascular sclerotic tissue that the fine longitudinal ribs of the outer paleae appear only as faint markings, the whole surface, save at the extreme tip, being perfectly smooth.

The spikelets are usually two-grained, though a panicle will often contain a few which are 3-grained. Very rarely a plant will be found which has two or three 4-grained spikelets. In this case the uppermost grain is generally very small and all the peduncles are short and

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[1] The work herein described was taken up at the F_2 stage. The data concerning the parents and the F_1 generation, however, were rather vague and scanty, and had to be reinvestigated by me concurrently with the analysis of the F_3 crop.

straight. It is important to note this condensation of the occasional large spikelet in the tight oat as compared with the extreme laxity of the Avena nuda type.

Ligowo.

In all its essentials this variety resembles Thousand Dollar. It also has white, tight, awned outer paleae and spreading panicles. The grain, however, is somewhat plumper and there seems a greater tendency towards 3-grained spikelets, though no 4-grained have been noticed, possibly because no large field crop has been available for inspection as in the case of Thousand Dollar.
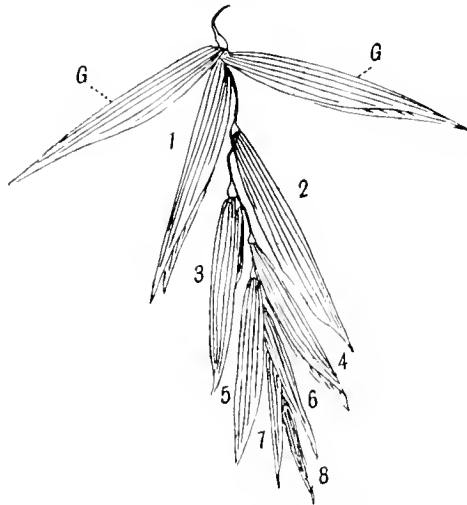
Fig. 1.   Characteristic spikelet from a " pure loose "
containing 8 flowers.

Nubischer Schwarzer

is a shorter strawed oat than the two just described. It also differs in being a black tartarian. Save for the size and shape of the grain all other points are similar.

Avena nuda.

Two distinct features characterise the spreading panicles of this species :—

(*a*)   The long, dangling spikelets in which there may be as many as nine flowers (cf. Fig. 1), and

(*b*)   The readiness with which the grain drops out from between the paleae when mature.

The parental stock used showed impurity if the "nuda" type be taken as one in which the paleae are *all* absolutely membranous, that is to say, with no trace whatever of intervascular sclerosis. For some plants had at least one obviously tight grain, often more, the proportion of tights even rising to 40 % in extreme cases, while others would have a grain or two with paleae moderately stiffened in a broadened midrib region.

One important character, however, is common to all these forms: *they never throw offspring with* ALL *the grains tight.* In this respect, therefore, even if not in others also possibly concerned in the *partial* tightening of the paleae, they may be regarded as constituting a pure line.

In colour the parent plants were mixed greys and whites. Greys are very easily overlooked in *Avena nuda* because colour is developed only on the small inner paleae.

THE F_1 GENERATION.

Spikelets.

The panicles of the F_1 plants contained a varying proportion of many-flowered spikelets of the " nuda " type. In the basal regions the two-flowered spikelet predominated.

Paleae.

Every conceivable gradation from the "pure tight" of the tight grained parents to the wholly membranous palea occurred.

On rubbing out, it was noticed that sometimes there was an excess of tight grains, and sometimes not. Six separate panicles, which all threw the same range and similar proportions of F_2 types, and must therefore have been F_1 heterozygotes of the same factorial composition, were constituted as follows

TABLE I.

Avena nuda ♀ × *Thousand Dollar* ♂.

Panicle 1.	Excess of loose grains.		Tights about $\frac{1}{4}$ of total			
,, 2.	,,	,,	,,	,,	$\frac{1}{3}$	,,
,, 3.	,,	tight	,,	,,	$\frac{1}{2}$	,,

Ligowo ♀ × *Avena nuda* ♂.

Panicle 4.	Excess of tight grains.		Tights about $\frac{3}{5}$ of total			
., 5.	,,	,,	,,	,,	$\frac{1}{2}$	,,
,, 6.	,,	loose	,,	,,	$\frac{1}{5}$	,,

It was at first thought that the reason for this fluctuation might lie in the fact that single panicles were examined instead of whole plants; but

a more detailed analysis of the entire plants in this generation of the Nubischer cross proved that, although there are cases in which the exact nature can only be ascertained when the basal tillers are also taken into consideration, the main panicle is generally indicative of the whole plant. The necessity for inspecting the other panicles arises chiefly when the excess of either tight or loose grains is very great. In such cases all, or most, of the paleae of the preponderating type may be concentrated into the largest panicle, and the opposite extremes have to be searched for on the subsidiary panicles.

In the detailed analysis just referred to the panicles on each F_1 plant were taken separately, in the manner shown in Table II, and the paleae borne on the different branches classified node by node, commencing at the base. A " pure tight" palea has no paperiness, a "pure loose" is entirely membranous, while an "intermediate" is a very variable mixture of these two extremes (cf. Fig. 2).
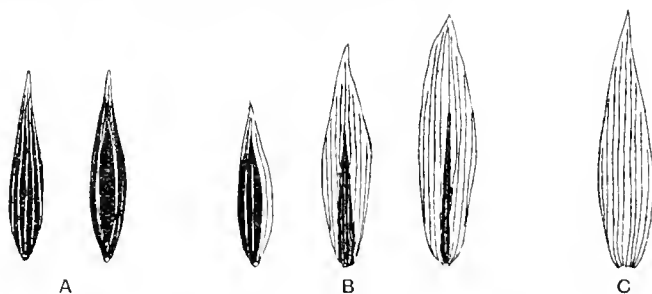
Fig. 2. Types of paleae found on F_1 plants. **A** = pure tight; a grain is shown in both dorsal and ventral view, the latter showing the margins of the outer pale clasping the inner one.   **B** = intermediate forms. **C** = a pure loose palea. The sclerotised parts are represented black.

The percentage of "pure tights," it will be observed, ranges from 20·4 % to 68·7 %; that of the "pure looses" from 7·8 % to 46·8 %. The rise of the one appears to be correlated by the fall of the other, not only when different plants are compared, but also in different zones in the same plant. In plant *A*, for example, the first nodes of the four panicles bear 77 pure tight and 7 pure loose paleae out of a total of 115, *i.e.* the relative proportions are as 67 % : 6·1 %.

In the case of the second nodes they are as 45·8 % : 20·8 %.
For the third nodes they are as   ...   26·8 % : 39 %.
For the fourth they are as   ...   ...   5 % : 45 %.
And for the last they are as   ...   ...   7·4 % : 44·4 %.

TABLE II.

Nubischer Schwarzer × Avena nuda.

Analysis of paleae on 5 F_1 plants.

[P.t. = pure tight.   P.l. = pure loose.   Int. = ± membranous.]

Distribution of paleae at

Plant	Panicle	1st node			2nd node			3rd node			4th node			5th node			Percentage	
		P.t.	Int.	P.l.	P.t.	Int.	P.l.	P.t.	Int.	P.l.	P.t.	Int.	P.l.	P.t.	Int.	P.l.	P.t.	P.l.
A	1	27	8	2	22	15	15	2	4	5	0	1	3	0	0	0		
	2	16	18	4	9	10	9	0	3	7	0	2	5	0	2	4		
	3	23	5	1	15	3	0	5	3	2	1	3	1	1	5	7		
	4	11	0	0	9	12	1	4	4	2	0	4	0	1	6	1		
	Totals	77	31	7	55	40	25	11	14	16	1	10	9	2	13	12	45·2 %	21·4 %
B	1	4	17	12	5	9	20	2	5	7	0	5	8	0	3	8		
	2	27	4	2	13	11	0	5	10	11	1	1	12	2	7	19		
	3	4	7	6	5	17	10	5	10	11	5	5	6	0	5	18		
	4	4	2	1	0	8	10	1	3	7	0	2	8	0	2	14		
	Totals	39	30	21	23	45	40	13	28	36	6	13	34	2	17	59	20·4 %	46·8 %
C	1	7	10	7	2	13	12	1	8	10	0	5	7	0	1	10		
	2	26	9	4	13	9	7	7	8	5	0	6	7	0	2	4		
	3	11	14	9	7	15	6	3	8	5	0	3	2	0	3	5		
	4	6	3	0	10	6	2	9	4	1	5	3	0	2	3	7		
	5	10	6	2	3	8	5	10	1	5	2	3	6	0	4	6		
	6	13	2	2	5	12	10	1	5	3	6	5	15	0	0	8		
	7	7	2	0	11	11	5	8	4	4	3	3	8	3	2	7		
	8	24	1	0	11	7	2	8	6	3	4	1	2	4	1	2		
	Totals	104	47	24	62	81	49	47	41	36	20	29	47	9	16	49	36·4 %	30·9 %
D	1	30	0	0	18	0	0	5	2	2	1	1	0	1	1	0		
	2	10	8	2	12	12	2	3	4	3	0	2	6	0	2	6		
	3	12	0	0	6	0	0	10	1	1	1	1	2	0	2	4		
	Totals	52	8	2	36	12	2	18	7	6	2	4	8	1	5	10	63 %	16·2 %
E	1	11	8	0	16	5	0	10	3	0	2	0	0	2	2	2		
	2	3	0	0	4	1	0	4	1	0	1	1	0	0	2	0		
	3	19	1	5	5	1	1	1	1	0	1	1	1	tip broken off				
	Totals	33	9	5	25	7	1	15	5	0	4	2	1	2	4	2	68·7 %	7·8 %
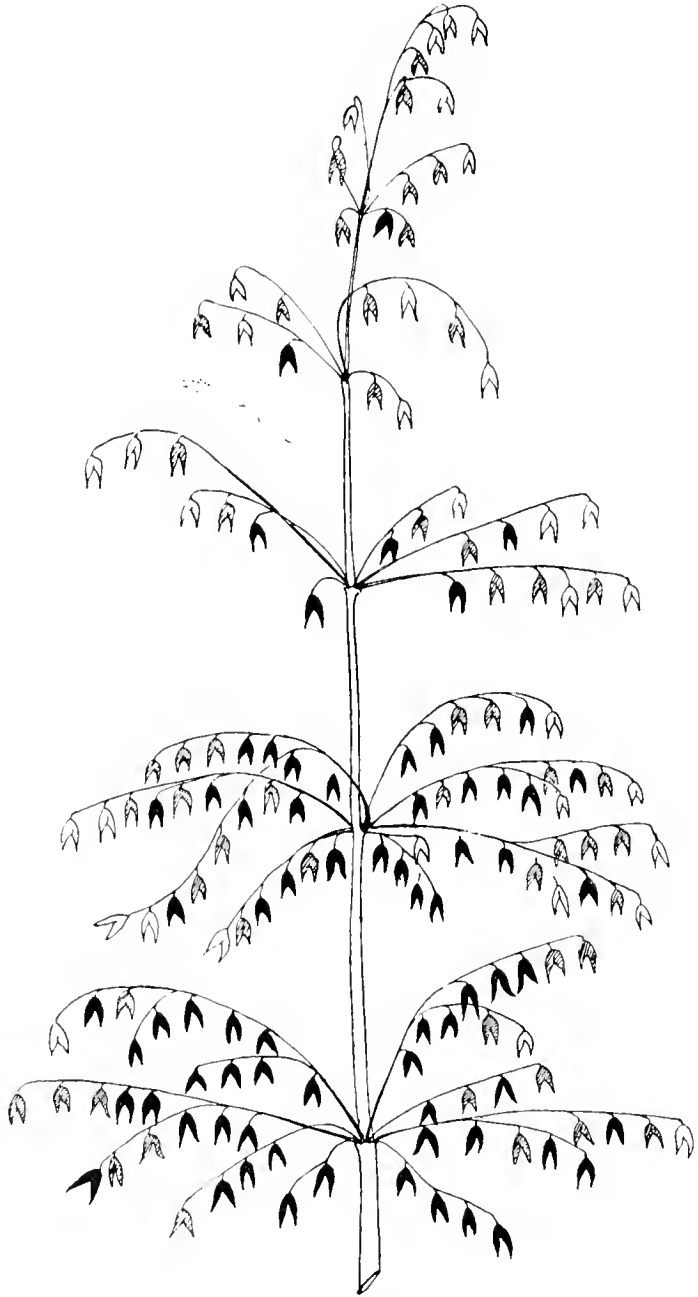
Fig. 3.   Diagrammatic representation of an F_1 plant as a single panicle.   For
purposes of the diagram the different types of paleae are indicated each in
a separate spikelet, though naturally all three kinds frequently reenr in the
same spikelet.

⋀ = Pure tight type of paleae.

⋀ = Intermediate type of paleae.

⋀ = Pure loose type of paleae.

This gradual diminution in the number of tight paleae, and increase in the number of loose, towards the tip is a tendency noticeable in every heterozygous panicle.

Colour.

Owing to the impure condition of the Nuda parent as regards colour, the plants raised from the crosses with the white husked varieties, Thousand Dollar and Ligowo, were a mixture of greys and whites. The presence of greys, however, demonstrated the dominance of the grey colour whenever the cross grey × white actually occurred.

In the case of Nubischer Schwarzer × Avena nuda the F_1 colour was a bright brown sometimes overlaid with a faint greyish flush. Here the variability of the F_1 may also be due to the fact—established in another experiment—that the black parent is really made up of at least three different kinds of blacks, represented zygotically by the formulae

$$BB \cdot B'B' \cdot GG$$
$$BB \cdot B'B' \cdot gg$$
$$BB \cdot b'b' \cdot gg$$

where B and B' are factors for blackness, and G for grey colour.

The F_2 and F_3 Generations.

Paleae.

No meticulous examination of the pales in the F_2 generation was made. The mixture of types looked so bewildering that there seemed no alternative but to rub out the panicles and note the actual proportion of tight and loose grains. This was done.

TABLE III.

1	Thousand Dollar ♂ × Avena nuda ♀	213 panicles gave 64 with all grains tight				
2	Avena nuda ♂ × Ligowo ♀	172	,,	,,	49	,, ,,
3	Reciprocal Cross	133	,,	,,	31	,, ,,
	Grand Total ...	518	,,	,,	144	,, ,,

Here appeared to be some evidence of a 3 : 1 segregation, though the approximation is rough, expectation on the ratio mentioned being 129·5 instead of 144. When, however, it is remembered that only single panicles were examined, that these were occasionally damaged at the tips, or had lost a few spikelets elsewhere, and that although, as was subsequently proved in the case of pure tight-grained forms, at any rate, the single panicle is indicative of the whole plant about

85 times in every 100, the possibility of the number 144 being an abnormally augmented figure is not difficult to conceive.

The likelihood of a heterozygous panicle being taken to indicate a homozygous plant is well illustrated in Table II, plant D, panicle 1. If such a panicle were only slightly damaged, the chances are all in favour of the two loose grains with membranous paleae being the first to break off, while it is also possible that the four paleae classified as "intermediate" might be such near approaches to the pure tight form as to be separable from the grains only by extra hard rubbing.

A random selection of 26 taken out of the 144 apparently "pure tights" yielded an F_3 generation fairly representative of the whole group. The plants of 22 rows were uniformly tight grained on every panicle. The remaining 4 rows showed distinct splitting. Twenty-two out of twenty-six is equivalent to 122 "pure tight" out of 144 tentatively considered pure. This is a much better agreement with the 129·5 expected on a 1 to 3 basis, the corrected result for the F_2 generation reading :—

			Pure loose and heterozygotes	Pure tight
Observed	...	...	396	122
Expected	..	...	388·5	129·5

More substantial evidence of this agreement will now be offered in connection with the detailed classification of other F_3 results.

A large number of sowings was made from F_2 heads having a mixed character. Double rows were planted, so that the tight grains in each sowing might be placed in one section, and the loose in the other. This was done in case the nature of the husk should in any way be related to the zygotic constitution of the embryo, and hence have some bearing on the segregation, though it was hardly expected that maternal characters would so affect it. As a matter of fact they did not. The double rows, however, if for no other purpose, were very useful in that they enabled one to obtain a few more F_3 plants.

In order to determine just which among these F_3 rows were showing splitting after the manner of offspring of F_1 plants, and could therefore be regarded as an exact repetition[1] of an F_2 generation derived from actual F_1 individuals, the seed from half a dozen F_1 panicles which had been saved over was sown at the same time. These F_1 panicles had shown on rubbing out a proportion of "pure tight" grains varying from one-fifth to three-fifths of the total. Allowing for a reasonable

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[1] In regard to the throwing of one-quarter pure tights, that is to say.

amount of variation in the relative numbers of the different constituents, the six F_2 rows were essentially alike. All included "pure tights," tight-containing types similar to the F_1 parents, and one or more of the forms such as have been described as occurring in the original samples of Avena nuda.

It was found that practically all[1] the plants of mixed type picked out of the F_2 generation gave rise to F_3 rows of the kind just described, no matter what the relative proportions of tight and loose grains. Some even among the panicles sown as "pure tight" and "pure loose" behaved in the same way, these, as has been explained before, being obviously either damaged panicles or cases in which the preponderance of one type of grain was so great as to render classification uncertain unless the whole plant were examined. The number of these imagined "pure" types which split in this way was small, and it has already been shown (p. 236) that in the case of the pure tights, in which the observed figures were too high, the excess over expectation was due simply to these mistakenly placed heterozygotes.

According to the nature of the paleae the progeny thrown by each of the similarly segregating F_3 rows were placed in the following groups.

I. *Pure tights.*—All the grains on the plant enclosed in tough, wholly sclerotised paleae (cf. the respective tight parents).

II. *Tight-containers*[2].—One or more "pure tight" paleae, the rest varied.

III. *Hardbacks.*—No "pure tight" pales. Pales partly membranous, partly hardened, the hard portion varying from a slightly thickened midrib to the stiffening of nearly the whole palea.

IV. *Penulti-looses.*—As in III, but the hardening is never found above the lowest palea in any of the spikelets. These verge very closely on the

V. *Pure looses.*—All paleae absolutely membranous.

119 sowings gave rows containing 2445 plants and exhibiting the splitting just described. The following table shows the distribution of the various forms.

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[1] Exceptions are the "tight-containers" dealt with subsequently. See Table IV et seq.

[2] To avoid possible misapprehension it may be stated that this term is devoid of any implication as regards the genetic properties of the plants to which it applies. Most "tight-containers" throw "pure tight" plants among their offspring, but there are some which do not throw any (cf. p. 239).

TABLE IV.

		Total F_3 plants	Pure tights	Tight-containers	Hard-backs	Penulti-looses	Pure looses
1	Thousand Dollar ♂ × Avena nuda ♀	1133	283	610	161	61	18
2	Avena nuda ♂ × Ligowo ♀	657	163	341	113	24	16
3	Ligowo ♂ × Avena nuda ♀	655	164	359	95	25	12
	Grand Total ...	2445	610	1310	369	110	46
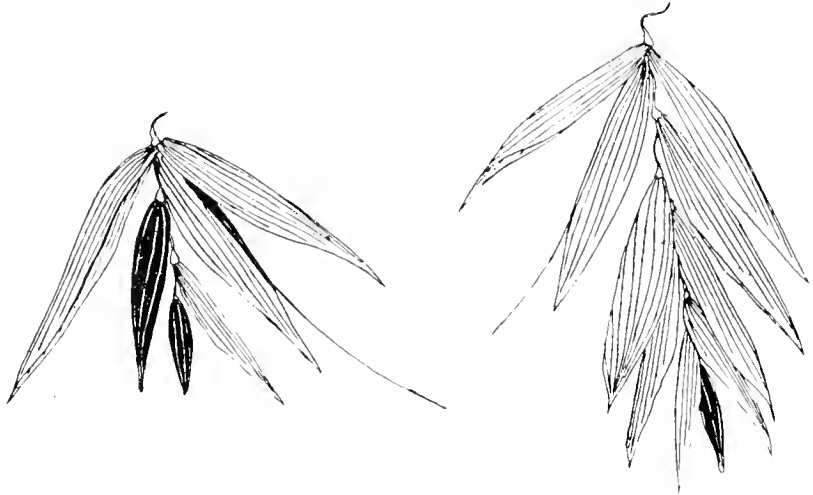
Fig. 4. Two characteristic spikelets from "tight-containers." Sclerotised parts represented black.

Fig. 5. Characteristic spikelet from a "hardback." Sclerotised parts represented black.

Fig. 6. Characteristic spikelet from a "penulti-loose." Sclerotised parts represented black.

The first thing to notice is that the pure tights make up almost exactly one-quarter of the total. The agreement with expectation is remarkably good.

The tight-containers call for closer study, as their group is really a mixture of two. These groups can only be defined and separated by further breeding. For whereas the one type always throws pure tights, the other, which is outwardly indistinguishable from it, never does so. In some cases as many as 35—65 plants and more have been raised from tight-containers of this second kind without any pure tights appearing among them. It was also found that out of a fair random sample of 118 tight-containers 7 behaved in this way. 7 out of 118 is equal to 78 out of 1310; so that the results in Table IV may now be summarised as follows:

$$610 \text{ Pure tights} : 1232 \text{ Tight-containers} : \begin{cases} 78 \text{ Tight-containers } not \\ \qquad \text{throwing pure tights.} \\ 369 \text{ Hardbacks.} \\ 110 \text{ Penulti-looses.} \\ \underline{46} \text{ Pure looses.} \\ 603 \end{cases}$$

with the middle group labelled "throwing pure tights".

This definitely establishes the 1 : 2 : 1 ratio, or, in other words, the determination of *complete* tightness by a single independent factor.

But what is it that causes the heterogeneity of the last term in the ratio, the 603 plants which, while so obviously of different sorts, have the one common property of being unable to give rise to pure tights? The 46 pure looses compose roughly one-sixteenth of the group. Added to the penulti-looses they form one-quarter. These proportions are significant: plainly other factors must be coming into play.

At the present stage of the investigation, mainly through an insufficiency of available experimental evidence, it is not possible to give the exact number and mechanism of these factors (whether they are complementary or cumulative, or even inhibitory, for example), but it seems tolerably certain they are there, and that only through them can the very variable constitution of the F_1 individuals (see Table II) be accounted for.

Let us suppose, in order to illustrate this view, that there are 3 factors:

X = a factor capable of rendering *all* the paleae on the plant pure tight.

Y = a factor capable of rendering some of the paleae on the plant pure tight.

Z = a factor capable of rendering some of the paleae on the plant more or less sclerotised but never wholly tight.

It follows that all pure tight forms must be homozygous for X, no matter whether they contain Y or Z, separately or together, or not. Similarly all plants which never throw pure tights, *i.e.* all "nuda" forms, must be recessive for X. They, too, may or may not contain X and Y. Now let any two individuals of these two classes be crossed. It is evident that quite a number of F_1 combinations may result:

$$\left.\begin{array}{l} XYZ \cdot xYZ \\ Xyz \cdot xyz \\ XYz \cdot xyz \\ XYZ \cdot xyz \end{array}\right\} \text{ are a few.}$$

One feature will alone be constant: the heterozygosity of X. All, therefore, will throw one-quarter pure tights in the F_2 generation. This is consonant with our proven results. Now if in the F_1 combination the presence of one dose of X determine that, say, $x°/_0$ of the paleae shall be pure tight, then it is not unnatural to infer that the remainder will be variably tightened and hardbacked according as Y and Z are present both homozygously, both heterozygously, one homozygously and one heterozygously, and so on, or both absent.

It should be added that the functions assigned to the factors Y and Z are, of course, merely hypothetical. Just as possibly either or both may have some negative, inhibiting action, thus lowering the basic $x°/_0$ of pure tight grains in the F_1 plant (cf. Plant B in Table II), while quite possibly they may govern the number of grains per spikelet and thus have an indirect influence on the hardening of the paleae. For it has been noted that progressive tightening of the paleae always reduces the number of flowers in a spikelet, until, in the pure tight forms, the repulsion between the many-flowered habit and tightness of paleae is complete.

Some further light is cast on the complex nature of the various "nuda" types in Table V; but admittedly it is only a glimmer. A few interesting points, however, stand out. The results of two seasons' plantings are contained in the table, as, owing to the tediousness of the classification, with its careful scrutiny of every palea, only a limited number could be undertaken at one time. In 1916 the parents were simply single panicles rubbed out and called "various nuda forms";

TABLE V.

| | | Progeny | | | | |
Group	Parental Number	Tight-containers	Hard-backs	Penulti-looses	Pure looses	Nature of Parent
A	5/8	2	6	11	1	—
	5/25	7	13	1	1	Tight-container
	9/3	2	17	1	1	—
	5.4/3	4	1	5	2	—
	5.4/7	4	5	2	2	—
	5.4/17	5	5	2	1	Tight-container
	5/32/1	12	12	7	6	Hardback
	9/5/2	1	27	11	7	Hardback
	9/5/3	11	35	28	15	Hardback
	9/5/4	39	23	17	5	Tight-container
	Totals	87	144	85	41	
B	5.4/1	12	6	—	1	—
	9/3/2	61	6	—	5	Tight-container
	Totals	73	12	—	6	
C	5/1	6	8	2	—	—
	5/2	6	9	1	—	—
	5/3	3	16	6	—	—
	9/5	6	12	2	—	—
	9/7	6	9	6	—	—
	9/5/1	6	21	2	—	Penulti-loose
	9/5/5	22	32	8	—	Tight-container
	Totals	55	107	27	—	
D	5/4	16	6	—	—	—
	5/23	32	3	—	—	Tight-container
	5/26	42	4	—	—	Tight-container
	9/4	7	9	—	—	—
	9/10	3	12	—	—	—
	9/43	14	4	—	—	Tight-container
	5.4/19	16	1	—	—	Tight-container
	9/3/1	33	28	—	—	Tight-container
	9/4/1	54	6	—	—	Tight-container
	9/4/2	34	5	—	—	Tight-container
	Totals	251	78	—	—	
E	5/5	—	8	10	11	—
	5/6	—	9	5	24	—
	9/6	—	3	1	8	—
	5.4/2	—	5	11	7	—
	5.4/8	—	4	3	6	—
	Totals	—	29	30	59	—
F	5/8/1	—	—	9	30	Pure loose

but in 1917, when whole plants were used, the exact type was always noted. Hence the indication in the table of only some of the parents.

Groupings have been made; but they are not meant to show the identity of the members in more than one broad, fundamental character. Thus in group *A*, where some parents were tight-containers and others hardbacks, the different progenies have one common feature in that they cover the whole range of the four "nuda" forms. The total for the group is 87 tight-containers, 144 hardbacks, 85 penulti-looses, and 41 pure looses. The fact that the tight-containers make up almost exactly one-quarter (expectation is 89) is of interest. On the other hand it must be recognised that there is some lack of uniformity in this first section of the table. This is even more marked in the next section, in which two families each lacking penulti-looses have been placed. It is very possible that No. 5*A*/1 may really belong to group *A*, and that No. 9/3/2, with its huge preponderance of tight-containers, should go to group *D*, especially as the five pure looses were in this case wretchedly small plants all under two feet high, and with only a few spikelets each on most.

In the following set of seven, however, a moderate degree of uniformity exists, though the two known parents were of distinctly unlike kinds. Here pure looses are not found, but on a rough approximation the tight-containers again form a quarter of the total (expectation 47).

The plants in Group *D* threw neither penulti-looses nor pure looses. The proportion of hardbacks in the individual families fluctuated considerably; yet it is noteworthy that all the classified parents were of the same sort. It was also remarked that among the offspring tight-containers the tendency to produce a large relative number of pure tight grains was much greater than in any other group. Numerous plants had from 35—45 % of pure tight grains. Taken as a whole the group exhibits a 3 : 1 ratio.

Tight-containers were entirely absent from the last two parts of the table. In *E* the hardbacks form a very uniform quarter of the progeny, while in *F*, which has even less variety, the same is true of the penulti-looses. Group *E* consists of 1916 sowings only and unfortunately nothing definite can be said about the parents.

Five distinct breeding systems, therefore, have been recognised among the "nuda" types:

Group *A*. Forms throwing tight-containers, hardbacks, penultilooses, and pure looses.

Group *C*. Forms throwing tight-containers, hardbacks, and penulti-looses.

Group *D*. Forms throwing tight-containers and hardbacks.

Group *E*. Forms throwing hardbacks, penulti-looses, and pure looses.

Group *F*. Forms throwing penulti-looses and pure looses.

Very likely more exist. A pure line of pure looses could probably be isolated from No. 5/8/1, and Nos. 5/23 and 5A/19 of group *D* may conceivably serve as a basis for obtaining tight-containers which breed pure. Very likely, too, the lack of uniformity in the large groups may signify a mixture of different lesser groups. But so far as the experiment has at present been carried, and with a limited amount of data available, nothing beyond this one important empirical result has come into prominence; namely, that irrespective of the actual proportions of the offspring-constituents in individual members, certain groups broadly similar in the nature of their progeny can be established.

Spikelets.

One of the main objects for which the crosses were made was to ascertain whether it would be possible to transfer the many-flowered habit of the Avena nuda spikelet to the tight-grained forms. A type with a combination of these two characters would plainly be of pre-eminent agricultural value; for not only would it yield a very heavy crop, but the grain would also not be liable to shake out. Occasionally seedsmen have put on the market new varieties which have been extracted from Avena nuda crosses, and for which it has been claimed that the slightly higher yield they gave was due to this combination; but the observations set forth in this paper, dealing with some thousands of plants of all sorts, do not support these contentions. Far from doing so: they tend rather to foster the idea that the presence of these two features fully developed in one and the same plant is physiologically impossible.

The many-flowered spikelet appears to be a function of the membranous palea. In "nuda" forms the spikelet with 6—10 flowers is found right through the panicle. As soon as tight grains occur in it, however, as in the F_1 generation, the multiflority is partly suppressed, the reduction always taking place in those spikelets bearing the tight grains. When one comes to the pure tight type extracted from the F_2 generation, the maximum number of grains per spikelet ever found is four, and that very uncommonly. Only a few of the spikelets on the

whole plant are 4-grained, and when bred on for another year the character often fails to appear in any of the offspring.

Now none of the varieties sold ever go beyond four grains to the spikelet; they are never 4-grained throughout; and they do not remain constant throwers of 4-grained forms. Moreover, it has been noted at the beginning of this paper that four grains may occur sporadically in varieties normally with two. (Specimen XI.) It can hardly be held, therefore, that extracted pure tights with some 4-grained spikelets really show a transfer of the high "nuda" number. It is more likely that they are just exhibiting the effect of superabundant nutrition.

These facts incline one to conclude that when membranous paleae are replaced by thick, stiff husks, the extra growth which would have produced the additional grains is used up instead in the process of strengthening the paleae.

Colour.

In this investigation the inheritance of colour has been followed merely for the subsidiary purpose of discovering whether there might be any connection between it and the different degrees of sclerosis of the paleae. The figures from the crosses involving the white tight-grained parents seemed in some respects to point to a preferential linkage between white colour and tight husk; but the results lacked consistency, and adverse conditions so weathered the crop in 1916 that the correct classification of light greys was rendered extremely difficult. The F_2 generation (raised this season) of the cross Nubian Black × Avena nuda, moreover, did not show any signs of the supposed coupling being perfectly normal. In Table VI are 1225 plants raised from 60 coloured F_2 plants showing splitting. The second cross suffered the least from weathering and mice.

TABLE VI.

	Total F_2 plants		Pure tights		Tight-containers		Hard-backs		Penulti-looses		Pure looses	
	G	W	G	W	G	W	G	W	G	W	G	W
Thousand Dollar ♂ × Avena nuda ♀	439	170	93	48	253	92	58	18	27	9	8	3
Avena nuda ♂ × Ligowo ♀	259	87	55	22	145	45	44	17	10	1	5	2
Ligowo ♂ × Avena nuda ♀	182	88	43	26	107	47	21	15	7		4	—
Grand Total	880	345	191	96	505	184	123	50	44	10	17	5
Expected	919	306	$229\frac{1}{2}$	$76\frac{1}{2}$								

The whole group showed a rough approximation to a ratio of 3 grey : 1 white, but among the pure tights the ratio was practically 2 : 1. If, however, it were a case of partial coupling of tight paleae with whiteness, a much greater bias in favour of greys than actually exists should occur at the opposite end of the scale.

Nothing similar was found among the pure tights in the Nubian Black crosses carried on to the F_2 generation this year. Segregations in four families are shown in Table VII. All these are quite normal

TABLE VII.

Nubischer schwarzer × A. nuda.

Pure tights only from F_2 generations.

	F_2 Colours			Parent Gametes	
F_1 plant	Black-brown	Grey	White	Nubian	Nuda
A	34	13[1]	—	Bb′G × bb′G	
B	40	2[2]	1	BB′G × bb′g[3]	
C	87	7[1]	—	BB′G × bbG	
D	13	1[1]	—	BB′G × bbG	

[1] All dark.
[2] One dark, one very light.
[3] Or BB′g × bb′G.

segregations. The first conforms to the ratio 3 : 1, the second 60 : 3 : 1, and the last two 15 : 1, the parent gametes producing the F_1 plants being as shown, where B and B′ are factors for black, and G for grey colour. This cumulative black in the Nubian parent will be discussed in another paper. The point to note here is that the colour inheritance is on ordinary lines and that no linkage of a particular colour with tight paleae is manifested. The apparent indications, inconsistent and irregular, of coupling seen in parts of Table VI must therefore be ascribed to the weathering, damage by mice, and consequent experimental error. For even on the whole count the error is large.

SUMMARY.

1. In "pure tight" varieties complete sclerosis of *all* the outer paleae is found. The spikelets are from 2 to 4-flowered.

2. In Avena nuda all, or most, of the paleae are membranous : a few tight grains may occur up to a proportion of over 40 °/₀ ; but "pure tight" forms are never thrown. 6 to 10-flowered spikelets are found.

3. The F_1 plants have grains enclosed in pure tight, pure loose, and several intermediate kinds of paleae. The range of variation is very great.

4. The method of segregation in the F_2 generation shows that the inheritance of what may be called the "pure tight" character depends on a single factor. At first sight the number of F_1 types appearing in this generation seems to exceed expectation. This is because they include tight-containing "nuda" forms which can be separated out only by further breeding. Such forms never throw pure tights.

5. Much diversity exists in the quarter of the F_2 generation incapable of yielding any pure tights. These "nuda" forms appear to result from secondary factors; for, according to their type and the manner of their breeding, empirical groupings can be made among them. They require more extensive study.

6. In extracted pure tights the number of grains per spikelet never exceeds four, no cross-over of the large "nuda" number taking place.

7. There is no repulsion between grey or brown colour and pure tight paleae.

AN ACCOUNT OF AN EXPERIMENT TO DETERMINE THE HEREDITY OF EARLY AND LATE RIPENING IN AN OAT CROSS.

By A. St CLAIR CAPORN.

(With one text-figure.)

SYSTEMATIC experiments on the maturation of cereal crops have not commended themselves to Mendelian workers, partly because the matter involved the study of characters obviously influenced to a certain extent by climatic and edaphic conditions, and partly because the amount of labour necessary seemed hardly commensurate with the results apparently to be expected. Observations therefore have been of a rough and ready kind, generally incidental notes made during the course of experiments with some other principal object in view. It was known, for instance, that when a spring wheat like *T. polonicum* was crossed with a winter Rivett, the F_1 generation was more or less an intermediate in regard to time of ripening. It was also known that in the F_2 generation a very extensive scatter took place, though the bulk of the crop tended to be earlier than the late parent. But there was always uncertainty as to precisely how much stress to lay on the fact that one parent was a winter wheat and the other a spring, and it was largely on this account that no fixed standard of ripeness was determined on, and complete statistical analyses made. While the results of the investigation described in this paper cannot be said to be other than puzzling and empirical, they can at any rate claim to present in tabular form the exact maturation values of a whole F_2 generation as established by the F_3 progeny.

The two parents chosen were Mesdag and Hopetown. Their ripening times in 1913 were

Mesdag. July 26th.

Hopetown. August 13th.

These dates, while giving the time when the whole mass of each variety was mature, take no account of the extremes of the ripening periods. It will be seen, however, that there is a reasonably large gap between them, and it may be stated here as well that all the individuals of a sowing of the early parent are always completely ripe some time before the first Hopetown panicles can be harvested. There is no overlapping whatever.

Fig. 1.   For explanation see p. 249.

In some respects Mesdag has distinct affinities with the wild oat, *A. fatua*, which may possibly figure in the pedigree. The panicles are extremely long and with a great drooping spread. They are borne on a tall weak straw, as in the wild oat, but the considerably larger and heavier grain makes it appear even weaker. The lower grain in each spikelet is strongly awned and of a dark brown colour which resembles that of the wild oat in that it masks a grey factor. By way of contrast, however, hairiness is absent and the grain is of exceptionally fine size and plumpness.

Hopetown grains are a good deal smaller and narrower. They have white husks and stiff, twisted awns. The straw is of medium length.

The two parents present a marked difference in habit in their earlier stages. In Fig. 1 the taller plant on the left is Mesdag, that on the right Hopetown.

Both are of the same age and were grown in adjacent rows. The Mesdag plant is just about to send up the floriferous shoots, here limited to one main head. The late ripening Hopetown, on the other hand, tillers profusely; so that at the time when the Mesdag panicles are completely out of their sheaths, its own more numerous panicles have yet to burst through.

The F_1 and F_2 Generations.

Little information as to the rate of ripening in these two generations was available[1]. As far as can be gathered, the F_1 plants, which were strongly awned, with brown grains somewhat lighter in shade than those of Mesdag, and also with more compact panicles, were ripe before the late parent, yet not quite so soon as the early parent.

The F_2 generation was harvested when the majority of the plants were fully mature; that is to say, when a certain proportion must have been over ripe. Even then, however, there was a number of very green plants to be seen. A sample of 24 plants contained 4 without any yellowness at all in the glumes. This sample probably gave a rough idea of the general composition of the whole F_2; but the possibility of picking out entirely green panicles from an assortment made up of so many different stages in ripeness not occurring until most of the crop had been rubbed out for the next sowings, no real confirmation of this assumption can be brought forward. Nevertheless it will be worth noting here that the F_3 rows derived from the 4 green panicles all tended to ripen late. (Table I, Nos. 103—106 inclusive.)

The F_3 Generation.

A far more detailed study of the F_3 generation was made. 106 F_2 heads were rubbed out and planted, all on the same day. A row of each of the parents was also sown in proximity to the rest of the crop.

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[1] The experiment, which came into my hands after the F_2 crop had been harvested, was unfortunately the victim of several interruptions, and suffered accordingly from want of attention. All that could be done was simply to grow on the first two generations without making any careful observations. Needless to say, the lack of a concise conception of the F_1 ripening period is keenly felt in any attempt to explain later results.

TABLE I.

F₃ Rows, Numbers

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Aug. 10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	—	2	—	—	—
14	—	—	1	—	—	—	3	—	1	1	—	3	—	—	1	1	2	—	2	3	—	2	—
15	—	1	—	—	1	—	2	—	—	—	1	—	—	—	—	1	1	—	2	1	—	1	1
16	—	—	—	—	—	1	1	1	—	—	—	1	—	1	1	—	2	—	2	3	1	2	—
17	—	1	1	—	—	—	4	—	—	1	2	1	—	1	—	4	1	1	1	—	3	3	—
18	—	2	2	4	2	1	1	—	—	3	—	3	1	1	2[*]	1	2	1	1	2	3	—	—
19	—	—	1	1	—	—	1	1	—	1	1	—	—	—	—	1	2	2	—	2	—	—	—
20	—	1	—	—	1	1	1	—	—	1	2	2	—	—	1	1	1	3	2	1	1	—	1
21	1	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22	2	1	—	—	—	1	1	—	—	1	1	1	—	—	1	—	—	2	—	1	—	—	—
23	1	—	—	1	—	2	—	1	—	—	1	1	—	—	—	—	1	1	—	—	2	1	—
24	—	3	—	1	—	1	—	—	1	—	1	1	1	1	2	—	2	1	—	2	—	1	—
25	1	1	1	—	—	—	—	1	—	—	1	—	—	—	—	1	—	2	—	—	—	2	1
26	1	—	—	2	1	—	—	1	1	—	2	2	2	—	1	2	1	—	1	—	3	—	—
27	2	1	—	—	2	—	—	—	2	2	—	—	—	1	3	—	—	2	2	1	1	2	1
28	—	1	1	1	1	2	2	1	1	—	1	—	—	—	1	—	—	—	—	—	1	1	5
29	—	—	—	2	—	—	—	—	—	—	—	—	1	—	1	—	—	2	—	—	—	—	3
30	2	—	—	3	1	2	2	—	—	—	1	—	—	—	1	—	—	2	—	—	—	—	—
31	1	—	1	1	2	—	—	2	1	—	—	—	—	—	4	—	—	—	—	2	—	—	—
Sept. 1	—	—	—	4	—	—	1	—	1	—	2	2	—	1	2	2	—	—	—	—	—	—	—
2	—	2	—	—	1	—	—	5	1	—	1	2	1	—	—	1	—	2	—	—	—	—	1
3	1	—	3	1	—	1	—	—	3	2	—	2	4	3	—	2	—	—	—	—	—	—	—
4	1	—	—	—	1	1	—	3	4	4	—	—	—	—	3	—	—	—	—	—	—	—	—
5	2	—	2	1	—	1	2	—	1	—	—	—	2	—	—	—	—	—	1	1[†]	1	1	1
6	2	1	1	—	—	—	—	3	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—
7	—	—	1	1	3	—	2	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—
8	2	—	—	—	—	—	—	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	1
9	—	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10	—	—	1	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
14	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Later	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* One taken a little prematurely.

† Stem nearly severed before ripe. Date therefore unreliable.

TABLE I (*continued*).

F₃ Rows, Numbers

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Aug. 10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	1	—	—	—	—	—	—	—	—	1	1	—	—	—	1	1	1	—	—	2	2
13	1	—	—	1	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	—	—	1	1
14	1	—	1	—	1	—	1	2	—	1	—	—	—	—	2	—	—	—	4	1	2	—	3
15	—	1	—	—	—	—	1	2	—	3	—	—	—	—	—	1	—	—	1	—	1	2	—
16	—	1	1	1	1	—	—	—	1	1	—	—	1	1	1	—	1	2	—	—	1	—	—
17	2	1	3	—	2	2	2	1	1	1	1	1	1	1	1	1	—	1	—	—	1	1	—
18	3	—	2	1	2	1	—	2	1	—	—	—	1	1	—	—	—	—	—	1	—	1	—
19	1	2	—	—	2	—	1	3	—	—	1	—	1	4	1	—	1	1	3	1	1	—	2
20	1	—	—	—	2	—	2	—	2	1	1	2	1	1	1	1	3	—	2	1	—	—	1
21	1	2	1	3	—	—	1	1	—	—	—	—	2	—	1	—	—	—	—	2	—	2	—
22	—	—	1	1	2	—	1	2	—	—	1	2	—	2	1	1	1	1	—	1	—	3	—
23	1	—	1	1	—	1	—	—	—	1	—	—	—	—	1	—	1	—	2	1	—	—	—
24	—	—	2	1	1	2	1	2	2	—	1	3	—	3	—	—	2	1	1	1	1	1	1
25	—	2	1	2	1	—	—	—	1	—	4	—	1	—	2	1	1	—	1	2	1	1	2
26	1	—	—	—	1	2	—	—	3	—	—	2	—	3	2	1	—	4	3	1	2	1	1
27	—	2	—	—	—	—	—	1	1	1	2	1	1	1	—	2	—	1	—	1	3	—	3
28	2	3	—	—	1	—	3	1	2	4	2	1	1	1	1	1	2	1	1	—	—	—	1
29	—	—	—	1	1	1	2	—	—	1	1	1	1	—	—	1	—	—	1	1	—	—	—
30	—	1	2	—	—	1	—	1	—	1	2	1	1	—	—	1	1	—	—	1	—	1	—
31	—	—	—	—	—	—	2	1	—	—	2	—	1	1	—	1	—	—	—	—	—	1	—
Sept. 1	—	—	3	—	1	3	—	2	—	—	—	2	1	—	—	1	1	—	—	—	1	—	—
2	—	—	—	1	—	—	—	1	1	—	1	2	2	2	—	2	1	—	—	—	1	—	—
3	—	2	—	—	—	—	1	—	1	—	—	—	1	—	—	—	—	3	—	1	—	—	1
4	—	1	—	—	—	2	—	—	—	—	—	—	—	—	—	1	—	—	—	2	—	1	1
5	—	—	—	2	—	—	—	1	1	—	—	1	1	—	1	1	—	1	—	1	—	—	—
6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
7	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Later	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE I (continued).

F_3 Rows, Numbers

	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
Aug. 10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	—	—	—	1	—	1	—	—	—	—	—	1	—	1	—	—	1	—	—	—	—
13	1	2	—	1	1	1	—	2	—	—	—	—	—	2	1	—	—	1	—	—	1	—	1
14	—	—	—	1	—	4	—	—	2	—	—	—	1	1	—	—	—	2	—	—	1	—	—
15	—	1	—	—	1	4	1	—	—	—	1	—	—	2	—	2	1	—	—	1	—	—	1
16	—	1	—	3	2	3	1	—	3	2	2	1	2	2	2	1	—	—	1	3	—	1	1
17	1	1	1	1	2	—	1	1	1	—	2	1	2	—	—	2	—	2	1	1	—	2	—
18	1	2	—	—	2	1	2	1	1	4	1	—	—	1	—	3	—	1	1	—	—	—	—
19	3	—	1	—	—	3	1	—	1	1	1	—	1	1	4	1	4	1	—	—	1	1	—
20	1	2	3	—	—	—	—	3	1	—	—	1	—	1	2	—	—	1	—	2	—	—	—
21	—	1	—	—	—	—	2	—	—	1	—	1	1	1	1	2	—	—	—	1	2	—	2
22	—	1	—	—	—	—	1	1	—	2	3	—	2	—	—	2	3	—	2	2	1	—	—
23	2	1	—	1	1	—	—	2	—	—	2	—	—	2	—	—	—	1	3	1	—	1	—
24	—	—	2	—	1	—	—	1	—	—	1	—	—	3	1	—	1	3	1	—	1	—	—
25	1	1	1	1	1	1	1	1	1	—	—	2	2	—	—	—	—	3	1	1	1	1	1
26	1	2	—	1	6	—	2	—	—	1	—	—	—	—	4	2	—	1	—	—	1	1	—
27	1	—	1	1	—	—	4	3	2	—	1	—	4	—	—	—	1	3	—	—	2	1	—
28	1	—	—	—	—	—	—	—	1	—	1	1	1	1	—	—	1	—	—	2	3	1	—
29	—	—	2	—	—	—	1	—	1	—	—	—	—	—	1	—	—	—	—	1	—	—	—
30	—	—	1	—	—	—	—	—	1	1	—	—	—	1*	—	—	2	—	—	—	2	—	—
31	1	—	1	—	1	—	—	1	—	3	—	2	—	2	1	—	1	—	2	—	—	1	3
Sept. 1	1	—	3	—	—	1	—	—	—	1	—	2	—	1	—	—	1	—	—	2	—	1	1
2	—	3	1	—	—	—	—	—	—	—	—	1	—	—	1	—	1	1	1	2	—	—	—
3	—	—	1	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—
4	—	1	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	2	1	—	3	—	3
5	1	—	—	—	—	—	—	—	—	—	2	—	—	—	1	—	3	2	—	—	1	—	—
6	—	—	2	—	—	1	—	1	1	—	1	1†	1	—	—	1	—	1	—	—	2	1	—
7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
8	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	1
9	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—
10	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
13	1‡	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Later	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* Probably earlier.

† Sheath not fully split open. Therefore possibly earlier.

‡ The first panicle aborted.

TABLE I (continued).

F_3 Rows, Numbers

	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
Aug. 10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	—
13	1	—	—	1	—	—	—	—	—	—	—	3	—	1	—	—	—	—	—	1	—	—	—
14	1	—	2	—	4	—	—	—	1	1	—	2	—	1	—	—	—	—	2	2	—	—	—
15	—	—	1	—	—	—	—	—	3	1	—	—	1	1	—	1	—	—	—	—	1	—	—
16	1	—	—	1	1	1	1	—	—	1	1	2	2	1	—	—	—	1	1	—	—	1	—
17	—	2	1	1	—	—	1	—	—	1	2	3	1	2	—	—	1	—	—	1	—	—	—
18	1	1	—	—	—	—	—	—	1	1	2	—	1	1	—	2	—	—	1	1	1	2	1
19	—	1	1	1	—	—	—	—	—	1	—	—	—	1	—	—	—	3	—	1	3	—	—
20	1	—	2	—	—	1	—	—	—	1	2	2	1	—	—	2	—	1	2	—	—	—	—
21	—	1	1	—	—	—	—	—	—	—	—	3	2	—	1	—	—	—	—	—	—	2	—
22	—	1	2	—	1	1	—	2	1	1	1	—	1	—	2	—	1	—	—	—	1	2	—
23	—	1	—	—	1	—	—	1	—	—	1	—	—	1	1	1	3	3	1	—	—	1	—
24	—	—	1	1	—	—	1	—	—	—	—	—	—	2	1	1	—	—	—	—	1	1	—
25	4	—	1	—	—	—	—	1	2	2	2	—	—	—	—	2	—	—	—	—	2	—	—
26	—	1	1	—	—	1	2	—	2	—	2	—	1	3	—	—	—	1	—	—	—	—	—
27	1	2	1	—	—	1	—	1	1	—	1	—	2	1	4	1	4	4	1	3	1	1
28	—	3	1	—	1	—	—	2	2	—	—	1	—	—	—	—	1	—	2	1	1	1	—
29	—	—	1	3	1	2	—	—	—	—	—	—	1	1	—	—	—	1	—	—	—	—	4
30	—	—	—	2	—	—	—	2	—	—	2	—	—	—	—	—	—	1	—	—	—	—	—
31	—	1	—	3	—	1	1	3	—	—	—	2	2	—	3	1*	1	2	—	—	1	1	4
Sept. 1	—	—	1	2	2	1	3	1	—	1	—	1	—	—	4	—	2	—	—	—	1	—	—
2	4	3	1	1	—	1	—	3	—	1	—	—	1	—	2	—	1	1	—	—	1	—	—
3	—	1	—	1	3	—	—	—	—	—	—	—	—	3	1	—	1	1	—	—	—	—	—
4	—	1	3	1	—	—	1	—	1	—	—	—	1	1	1	—	—	—	2	—	1	—	—
5	—	—	—	—	—	1	—	3	—	1	1	—	1	—	—	—	—	1	—	2	—	1	—
6	—	—	—	—	1	—	1	—	—	1	2	—	—	—	—	—	—	—	—	1	—	—	—
7	1	—	—	1	—	2	—	1	1	—	1	—	1	—	2	—	—	—	—	—	2	—	—
8	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—
9	—	—	—	2	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—
11	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
12	1	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	1	—	—
13	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
14	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
17	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Later	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* 1st panicle damaged. Therefore probably earlier.

TABLE I (*continued*).

| | | | | | | F_3 Rows, Numbers | | | | | | | | | | Parents | |
	93	94	95	96	97	98	99	100	101	102	103	104	105	106	Mesdag	Hopetown
Aug. 10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
12	—	—	—	—	2	—	—	—	—	—	—	—	—	—	1	—
13	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	—
14	—	1	—	1	1	—	1	—	—	—	—	—	—	—	3	—
15	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—
16	—	—	1	—	—	—	—	1	—	—	1	—	—	—	—	—
17	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—
18	—	2	2	—	2	—	—	1	—	—	—	—	—	—	1	—
19	—	—	1	3	1	—	—	—	1	—	1	—	1	—	—	—
20	—	2	2	—	—	1	1	—	—	1	—	1	—	—	—	—
21	—	1	—	—	—	—	1	—	—	1	—	1	1	—	—	—
22	—	—	—	—	—	—	1	—	—	2	—	—	—	2	—	—
23	1	1	3	—	—	2	—	—	—	—	1	1	—	1	2	—
24	—	—	1	—	—	—	—	2	1	—	—	1	—	—	1	—
25	—	1	—	1	2	—	1	1	—	2	—	1	—	—	—	—
26	—	—	—	1	1	—	3	1	—	2	—	—	3	2	—	—
27	2	—	—	—	2	—	—	1	3	—	—	—	—	1	—	—
28	—	—	2	—	—	3	2	—	1	—	—	—	—	—	—	—
29	—	—	1	—	—	—	1	—	1	2	—	2	1	—	—	—
30	1	—	—	1	—	2	—	1	—	—	1	—	—	—	—	—
31	—	—	—	1	—	1	—	2	—	4	3	—	—	1	—	—
Sept. 1	—	2	—	—	—	—	—	—	—	2	—	—	—	—	—	—
2	—	—	—	1	—	—	—	—	1	—	—	—	2	—	—	—
3	1	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—
4	1	—	1	—	—	—	1	2	—	—	—	—	—	1	—	1
5	2	—	—	1	—	1	—	—	—	—	—	—	—	3	—	—
6	—	—	2	2	—	1	2	2	1	1	1	—	2	—	—	2
7	—	—	—	1	—	—	—	1	—	1*	1	—	2	—	—	—
8	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	1
9	—	—	1	—	—	1	—	—	2	—	—	—	1	—	—	—
10	1	—	1	—	—	—	—	—	—	—	1	—	—	—	—	1
11	2	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—
12	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
14	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
19	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Later	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	2
															Parents	

* 1st panicle damaged.   Therefore probably earlier

Between the plots 1 ft. 3 in. paths were left to facilitate examination of the growing rows from both ends. The same object was also attained by shortening the rows a trifle, so as to make them contain 24 grains instead of the usual 28.

A panicle was held to be fully mature when the last trace of greenness had vanished from the tips of the paleae. Finding the ripe heads by this method is not so laborious as might at first be imagined. For the colour of the glumes is more or less an indication of the ripeness of the grains they enclose. To pick out the ripe ones, therefore, it is only necessary to peep in between the glumes at the base of the yellowest panicles. This system of gauging ripeness was preferred to any based on the times at which the panicles emerged from their sheaths, because the rate of ripening of any two panicles leafing at the same time appears to vary a good deal.

At every daily inspection the heads cut out were given separate labels bearing the number of the row and the date. After the whole crop had been thus gradually harvested, the ripening period for each row was obtained and recorded. The results are collected together in Table I.

The Mesdag row started ripening on Aug. 10th. It had finished on Aug. 24th. Over 70 $\%$ of the plants came to maturity within the first five days. Ten days elapsed before the first panicle in the Hopetown row could be cut. Here again the period was 15 days, but the sequence of the ripenings was much more regular. (See end of Table.)

On examining the table it will be noticed that *no* row is as late as the late parent, and none capable even of reasonable approximation to it. Nor is there any exactly as early as Mesdag, although two, Nos. 17 and 97, extend only two and three days respectively beyond the Mesdag period. If, however, as is likely, a certain amount of latitude must be given, then these two rows are to be reckoned equivalent to parental Mesdag in earliness. Two out of 106 may possibly indicate a 1 : 63 ratio.

Another survey of the table reveals the fact that there are 24 rows whose ripening period, starting early, extends over the gap between the parental times and finishes on the first day of the Hopetown harvest (Sept. 4th). The reverse condition, in which ripening starts immediately after the last Mesdag, is not found at all. The number 24, however, is possibly significant; for it offers a very close agreement with 26·5, which is the expectation on a 1 : 3 basis.

The general conclusion arrived at as the result of this experiment therefore is that there is ground for supposing that early and late ripening are mendelian characters, but that they are dependent on more than one factor, possibly three. F_2 plants homozygous for one of these, it would seem, are definitely early in the sense that their F_3 rows all reach complete ripeness before any individuals of the late parent are mature; yet, in all except 2 cases out of 24, they cannot be called *exactly* as early as Mesdag. Apparently it required homozygosis in all three factors to produce these two perfectly early rows. The diversity of the remaining 22 early ripeners, where in some cases (*e.g.* Nos. 20, 52) the accumulation of the ripening occurs during the first part, in others (*e.g.* Nos. 28, 44, 54, 61, 72) in the middle, in others again (*e.g.* Nos. 29, 49, 71) at the end of the period from Aug 10th to Sept. 4th, certainly supports the inference that although one factor is here constant and homozygous, thus imparting a common measure of earliness, the other two, in various heterozygous and homozygous combinations, are responsible for the different incidences of the greatest intensity of this earliness.

There can be little doubt, too, that the extent of the tillering has much to do with the rate of ripening. The tillering power of late forms is always good; that of early, very poor. Owing to the concentration of growth among early plants into one or two panicles only, these are generally bigger and bear better grain than those of late plants; but this advantage does not compensate for the diminished yield due to the small number of heads. There is thus an inevitable sacrifice of crop when it is attempted to render a late kind early. The only hope, apparently, lies in increasing the output, per individual panicle, of an *already early variety*. This can best be done by extracting it again from a fair-sized F_2 generation of a cross with a type which, quite apart from any ability to tiller profusely, has above all *larger panicles* and *larger grain* of better quality.

SUMMARY.

1.   Earliness and lateness are not instantaneous, sharply defined characters: they are spread over a period.

2.   The ripening times of the parents used did not overlap.

3.   Poor tillering power was characteristic of the early parent.

4. F_1 plants more or less intermediate.

5. The F_2 crop was harvested all at once. Hence no definite data were available. Evidence of early, late, and many intermediate forms, however, was visible.

6. Systematic, gradual harvesting of the F_3 generation was undertaken, together with parent rows grown under exactly the same conditions, to determine the constitution of the individual F_2 plants.

7. Analysis of results. Earliness is possibly a function of 3 factors. A type which is *comparatively* early, in that its F_3 period never extends into the period of the late parent, is segregated on a 1 : 3 basis.

8. Suggestions are made with regard to the improvement of early varieties.

Since completing this paper the writer has been referred to the work of Hoshino (1915) on peas and rice. In the case of the latter this investigator made observations on the "shooting times" in a cross between an early and a late variety. By "shooting time" is meant the time at which the first spikelet of the inflorescence emerges above the ligule of the sheathing leaf Apparently in rice this is also an exact measure of the relative maturing time of the grain later on. Hoshino's F_3 results were remarkably similar to those given in this paper for a different cereal examined on a different system. Two only out of forty-six randomly taken F_3 rows were as early as the early parent, while twenty-one stretched across the "gap-period," but not into that of the late parent. As only ten plants per row were raised, the number twenty-one is probably too high, and would, had there been more plants, have been nearer 11—12, which is the expectation on the 1 : 3 ratio. Although he overlooks this important fact, however, Hoshino nevertheless strongly favours the multiple-factor hypothesis as an explanation, deducing from the very small number of pure earlies like the original early parent that there are three factors.

The value of this present paper, therefore, does not lie in the originality of its inferences, but rather in that similar conclusions to those of the Japanese worker have been reached perfectly independently by different methods, and also in a cereal.

LITERATURE.

Hoshino. 1915. *Imperial University, Sopporo, Japan.* Vol. vi. November.

ON A CASE OF PERMANENT VARIATION IN THE GLUME LENGTHS OF EXTRACTED PARENTAL TYPES AND THE INHERITANCE OF PURPLE COLOUR IN THE CROSS *TRITICUM POLONICUM* × *T. ELOBONI*.

By A. St CLAIR CAPORN.

(With Plates XIII and XIV, three charts, and one text-figure.)

THE work set forth in this paper was initiated by Professor Biffen, who made the cross in 1913 and carried it on to the F_2 generation. Thereafter, from the analysis of the F_2 figures, the experiment has been in the hands of the writer. Rust, together with weakness of straw, was often responsible for considerable damage, lowering and shrivelling the grain output per plant, and thus increasing the difficulty of discovering faint colour traces usually borne on only a few of the riper grains.

THE POLONICUM PARENT.

Triticum polonicum is a tallish wheat about 4—$4\frac{1}{2}$ feet high. The tillering is poor, most of the plants having only two stems which differ from ordinary straws in being solid. The species is moderately susceptible to rust.

The ear is very long, lax, and bearded. Owing to their great length the outer glumes are a characteristic feature. Practically smooth, flat, and deeply keeled, they spread out stiffly at flowering time, giving to the ear the appearance of having been rubbed from the tip downwards. (Plate XIII, figs. 1 and 2.)

Average glume length (82 ears) = *29·23* mms.

The frequency distribution is shown in Chart I.

For purposes of measurement the glume of the fourth grain-containing spikelet from the base of the ear was always used.   Empty

CHART I.

Glume Lengths in mms.
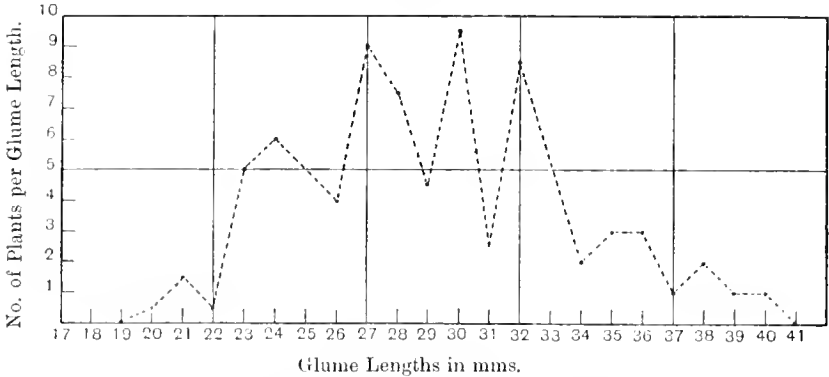
basal spikelets were never counted.   As the number of measurements available in this experiment was not over large, and the separate plotting of the lengths involving fractions of the unit would have jolted the curve considerably, it was decided to record them as nearest whole numbers.   The method of dealing with these non-integral numbers is shown in Table I which contains the data for Chart I.

TABLE I.

Glume Lengths in Millimetres

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Whole Numbers	0	1	0	4	4	2	1	6	5	3	7	0	7	4	1	2	2	0	2	1	1
$\frac{1}{2}$ below	0	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{2}$	$1\frac{1}{2}$	$1\frac{1}{2}$	$1\frac{1}{2}$	$1\frac{1}{2}$	1	$\frac{1}{2}$	2	$\frac{1}{2}$	1	0	1	0	1	0	0	0
$\frac{1}{2}$ above	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{2}$	$1\frac{1}{2}$	$1\frac{1}{2}$	$1\frac{1}{2}$	$1\frac{1}{2}$	1	$\frac{1}{2}$	2	$\frac{1}{2}$	1	0	1	0	1	0	0	0	0
Totals for each length	$\frac{1}{2}$	$1\frac{1}{2}$	$\frac{1}{2}$	5	6	5	4	9	$7\frac{1}{2}$	$4\frac{1}{2}$	$9\frac{1}{2}$	$2\frac{1}{2}$	$8\frac{1}{2}$	5	2	3	3	1	2	1	1

The only fraction considered was the half unit, or ·5 mm.   An example taken from it will explain how the table has been compiled. In addition to the six ears with a glume length of 27 mms. and the five of 28 mms. there were three of 27·5 mms.   Of these three, half (*i.e.* $1\frac{1}{2}$ ears) go to the whole number which 27·5 mms. is immediately below (*i.e.* to the 28 mm. length), and half to that which it is ·5 mm. above (*i.e.* to the 27 mm. length).   This method of tabulation has been employed in every case where a series of glume measurements has been taken.

As is to be generally expected when the glumes are so elongated, the grain is also longer than that of ordinary wheat. It is hard and pointed, has a very deep furrow, a whitish colour, and a translucent appearance.

Plate XIV, fig. 4 (*a, a'*), shows typical Polonicum glumes—maximum and minimum.

The Eloboni Parent.

The parent stock was raised from a sample of grain brought from Abyssinia; but, owing to the ravages of rust, to which this variety is extremely susceptible, the strain was unfortunately lost in the second and third years of the experiment.

Here again the tillering is poor and the plants small. The ears are of small size, narrow, fairly lax, and bearded. (Plate XIII, fig. 3.) In contrast to *T. polonicum* the chaff is very short, the glume lengths ranging from 8 mms. to 13 mms. A series of 51 short-glumed Elobonis in the F_3 generation had an average length of 10·58 mms.; but, as will be shown later, there is reason to believe that the extracted parental types have a markedly different average from the original, for which the figure, in all probability, would be fully 1 mm. lower. No extensive measurements of the glumes of the Eloboni parent, however, were made, and as the stock had entirely died out when the experiment was handed over to me, the conjectured average glume length is based mainly on an analogy with the behaviour of the "pure long" glume.

The grain is short, stumpy, hard. It has a tendency to shrink and become slightly wrinkled.

It is in the purple colour, however, that the chief feature of this wheat is to be found. Unlike maize, where the aleurone layer contains it, the pigment is located in the pericarp and therefore belongs to the same generation as the plant which bears the grain. When the grain has been well soaked in water, the pericarp of the caryopsis may readily be peeled off. It consists of

The Epicarp. A tissue of narrow cells elongated in the direction of the long axis of the fruit and with pitted lateral walls. At the apex of the grain it bears a few hairs.

The Hypoderm and Mesocarp. Similar to the epicarp but with fewer pits and firmly united to it.

The first careful peeling generally removes these three as one skin.

The Girdle Cells. Very regular, delicate cells with pitted lateral walls and long axes at right angles to those of the components of the first skin.

The Tube Cells, or *Endocarp.* Scattered vermiform cells, often coalescing, running lengthwise in the grain. They resemble later tubes and the longer the grain the more conspicuous they are. They are always best developed at the embryo end and on the side remote from the groove. To them often adhere

The Spermoderm and the *Perisperm,* two delicate cell laminae which are not strictly pericarp, but the outermost layers of the seed.

The second skin.

The purple colour is found in the sap of the girdle cells, staining all or part of it according to the distribution and intensity. The position of this pigmentiferous layer is shown in Plate XIV, figs. 9 and 10, the first of which shows it in a transverse section of the grain, and the other in a superficial view of the girdle cells, more particularly where they are not covered over by the fragment of epicarp. After immersion in dilute sulphuric acid (1 in 20) for a short time, the grain turns a deep crimson. This reaction, in conjunction with microscopical examination, has proved very useful in the detection of faint purple tinges in grains which showed a slight streak to which the overlying portions of the pericarp gave a doubtful, brownish appearance. For whereas the acid produces a distinctive coloration, water causes the anthocyanin first to fade and then to become dull green,—a colour which is much commoner than crimson, far less vivid, and by no means distinctive.

In both figures the acid reaction colour is illustrated.

THE F_1 GENERATION.

A type of F_1 ear is shown on Plate XIV, fig. 5. All the ears approximate to this type, of which the glumes are intermediate in shape and size between those of the parents, though the fluctuations range from glumes slightly longer than those of Eloboni to others a little shorter than the minimum Polonicum glume. Plate XIV, fig. 6, illustrates these two types (*c* and *a*) as well as the more general average (*b*). The grain is also of intermediate dimensions, as will be seen from Plate XIV, fig. 7, in which it is placed between the parent grains for comparison.

The F_1 grains were all purple.

The F_2 and F_3 Generations.

Glumes.

183 F_2 plants were examined. As is usual in *T. polonicum* crosses, it was found that, while certain ears were clearly long- or short-glumed, there was a very large proportion which verged on these extremes, as well as those which were obviously intermediates. The glume lengths were therefore measured and plotted in the form of a curve (Table II and Chart II).

The curve (dotted), it will be seen, falls into three periods, indicating that segregation, although indistinct, has nevertheless taken place. Professor Biffen[1] has already explained the real significance of such a curve in other crosses of this kind. It results from the overlapping of three separate curves representing the lengths of homozygous short, homozygous long, and heterozygous short-long glumes. Where the curves overlap there is a piling up effect equal to the sum of the values of the constituent curves at these points. Thus:—
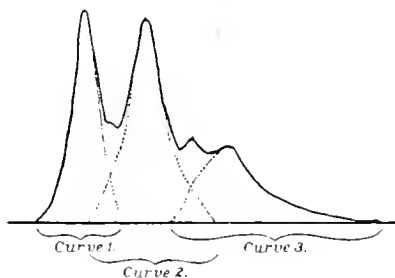

The triple nature of this type of compound curve is more plainly recognisable when a greater number of glume lengths is available for measurement. The dot-and-dash curve on Chart II represents the glume lengths of 151 F_3 individuals derived from 10 heterozygous F_2 ears, and when added to the first curve, produces the large continuous-line curve in which the three periods are far more distinct. It must be admitted that the third region is far from smooth. This is due to its diffuse character. By adopting the smoothing line (*sm*), however, one can indicate the real position. The point P marks the summit of the overlapping curves—always very pronounced where a high curve overlies a very low one.

[1] Biffen, R. H., *Journ. Agr. Sc.*, 1905,

TABLE II.

Glume Lengths in Millimetres

	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Whole Numbers	0	2	1	15	3	4	6	5	11	13	9	7	5	7	6	2	2	1	0	2	0	0	0	0	0
½ below	0	½	0	3	6	4	2½	2	3	4	3	3	2½	½	1½	1½	½	1	½	0	1	½	1	0	0
½ above	½	0	3	6	4	2½	2	3	4	3	3	2½	½	1½	1½	½	1	½	0	1	½	1	0	0	½
Totals for each length	½	2½	4	22	13	10½	10½	10	18	20	15	12½	8	9	9	4	3½	2½	½	3	1½	1½	1	0	½

CHART II.

No. of Plants per Glume Length.

Glume Lengths in mms.

The 183 F_2 ears, each representing a separate plant, were all rubbed out and planted; but although all had been measured for the purpose of compiling Table II, they were not specifically identified in the sowings. They yielded 170 F_3 rows with a sufficient number of plants per row to permit of accurate classification. The segregation—an undoubted $1 : 2 : 1$ ratio—is shown in Table II A.

TABLE II A.

|	Number of F_3 Rows	
Character of F_2 Segregation	Observed	Expected
Short only	41	42·5
Short, medium, and long ...	87	85
Long only	42	42·5

A series of sowings in which the glumes of the parents had been carefully measured proved that the maximum for pure shorts was 12·5 mms. and the minimum for pure longs 18 mms., while the upper and lower extremes of heterozygosity were 20·5 and 12 mms. respectively. The extracted pure long types, it was frequently noticed, seemed to be somewhat more compact than *T. polonicum*, and a more careful study of them was therefore made. The glumes of the progeny of certain pure longs of known size were measured and compared with those of an equal number of Polonicum plants grown in the same season and under identical conditions. 82 plants of each kind were examined. The influence of the parental glume length on the progeny in the case of these pure long forms was nil; for a plant with a 19 mm. value gave a row of offspring with the same average length as did one of 27·5 mms.

In Chart III the taller curve has been plotted from the extracted pure longs (Table III), while the dotted curve represents the frequency distribution of an equal number of Polonicum ears. The average length of the former was 24·15 mms.; that of the latter 29·23 mms. The difference is very considerable. Furthermore, there is a tendency towards greater uniformity among the extracted longs (cf. the large proportion of glumes 24 and 25 mms. long). In all probability the extracted pure shorts exhibit much the same sort of alteration in average value of the glume length when compared with the Eloboni parent, with the difference that instead of being lowered, the average length is increased. For although no proper comparison could be made, owing to the destruction of the Eloboni stock, nevertheless, as far as could be judged by instinctive eye tests, most of the extracted Elobonis appeared to be appreciably longer in the glume.

TABLE III.

Glume Lengths in Millimetres

	18	19	20	21	22	23	24	25	26	27	28	29	30
Whole Numbers	1	1	5	7	4	1	8	12	3	3	5	0	2
$\frac{1}{2}$ below	0	$\frac{1}{2}$	$\frac{1}{2}$	0	$2\frac{1}{2}$	$\frac{1}{2}$	2	$2\frac{1}{2}$	2	2	$1\frac{1}{2}$	0	1
$\frac{1}{2}$ above	$\frac{1}{2}$	$\frac{1}{2}$	0	$2\frac{1}{2}$	$\frac{1}{2}$	2	$2\frac{1}{2}$	2	2	$1\frac{1}{2}$	0	1	0
Totals for each length	$1\frac{1}{2}$	2	$5\frac{1}{2}$	$9\frac{1}{2}$	7	$3\frac{1}{2}$	$12\frac{1}{2}$	$16\frac{1}{2}$	7	$6\frac{1}{2}$	$6\frac{1}{2}$	1	3

CHART III.

Glume Length in mms.
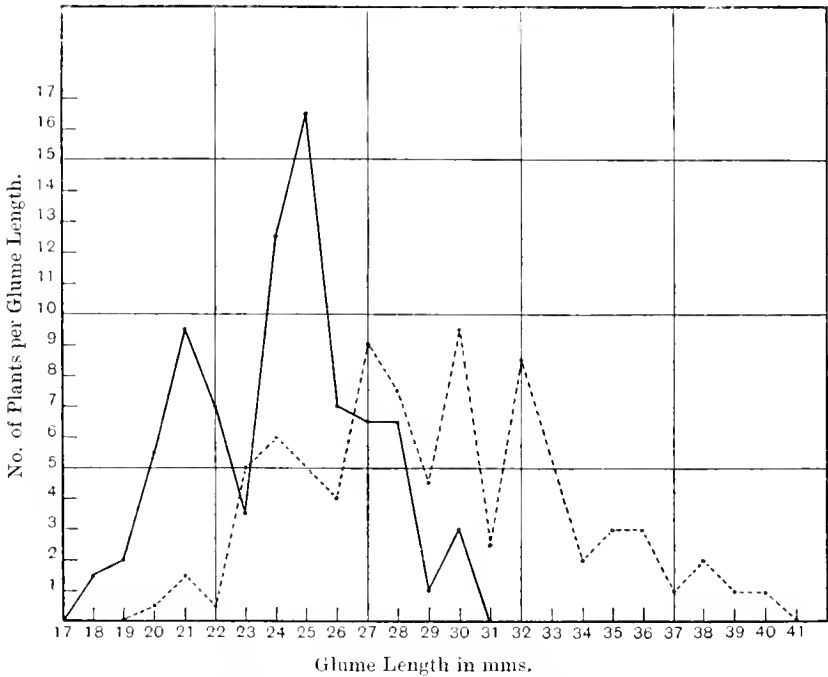
Average Length of Extracted Longs = 24·15 mms.
„   „   Parent   „   = 29·23 mms.

Briefly, the result of crossing a long-glumed wheat with a short-glumed is this :—

Along with the ordinary segregation there is established in the F_2 generation a kind of telescopic effect, whereby the means of the two homozygote curves are brought nearer to that of the heterozygotes than the means of the parents would actually be. This condensation persists right through into the F_3 generation in which, owing to the possibility of isolating the 'pure long' and 'pure short' curves, it can

be the more readily observed. There is thus every indication that this slight change in regard to the average glume length of extracted pure types as compared with the parents is a permanent one.

Grain Colour.

Before detailing the numerical results of this aspect of the experiment it will be convenient to describe here the different colour types found in the F_2 generation. Full coloured purples resembling the Eloboni parent, but of light and dark shades, were thrown. Besides these, however, a number of streaked individuals appeared. The colour of the streak is a dull brownish purple. The purple element is always intensified by treatment with dilute sulphuric acid, which turns it bright crimson. In Plate XIV, fig. 8, the various colour types are shown. Grain *a* is the ordinary Polish type, of a light yellow translucent appearance, but with no purple colour in the girdle cells, and hence, as far as this cross is concerned, classifiable as ' Non-coloured.' The grain *b* is a full purple, or ' Flushed ' form, while *c* and *d* illustrate the ' Streaked.' *b'*, *c'*, *d'* show the colour changes in acid. The streak shown in *d* is by no means the minutest recognisable, which may be so extremely faint, possibly because the place for the strongest streak on the plant may be on an unripe secondary tiller grain, as to be nearly invisible to the naked eye, even when treated with acid and examined in the brightest light. In such a case microscopic inspection reveals crimson stained nuclei in a small cluster of girdle cells, but very little pigmentation of the sap. (Plate XIV, fig. 10, *x*.) Care has to be taken, in circumstances like these, to ensure that the colour is really crimson in acid, not reddish or pinkish-brown ; for nuclei and their adjacent protoplasm often take on these tints in the grains of non-coloureds which have been much weathered or somewhat rusted. In Plate XIV, fig. 10, some of these potentially misleading colours have been introduced for the sake of comparison with the acid reaction of the real purple pigment.

A noticeable feature in ears containing full coloured purple grains is the way in which the same kind of flush stains the glumes. The glume purple is most intense just before the grain hardens. As complete maturity is slowly attained it fades away altogether. In pale or particoloured forms its presence is less vividly marked, a faint purplish margin to the glume being the sole indication.

Development of colour in the grain seems to be dependent to a variable extent on direct exposure to sunlight. This is especially the case in streaked forms where the width of the gape of the paleae,

occurring when the grain is at its plumpest, appears largely to determine the size and intensity of the streak. No doubt this also accounts for the fact that only some of the grains in the ears of a streaked plant actually bear the streak, as but few get exposed in this way, in the long-glumed plants particularly. That direct sunlight exposure does not alone determine colour production, however, is proved by the existence of the flushed forms, wherein the greatest colour area is developed in well covered up portions of the grain. The action of direct light may *start* in these grains the chemical change which renders the colour visible, but that it is essential for its continuance is a matter of doubt.

On the basis of the colour classification already indicated the F_2 generation consisted of

> 28 Flushed, 8 Streaked, 136 Non-coloured.

Or, eliminating all which gave less than F_3 plants next season,

> 27 Flushed, 8 Streaked, 123 Non-coloured.

The nature of these F_2 plants was determined firstly by examination of their grain in the ordinary way, and subsequently, after the more accurate acid test had been adopted, by re-examination of any seed left over from sowings for the F_3 rows, or, when none remained, by considering the F_3 segregations analogically.

Thus, in the case of the 8 streakeds, only one (which had a very strong streak) was detected on rubbing out by the rough, hurried, unaided eye test then used. Later, after the sowings for the F_3 generation had been made, the grain left over from three of these was tested in acid and streaks were discovered microscopically. Now as no grain remained over from the other four F_3 sowings, that the streak was present in their F_2 parents was deduced from the fact that the progeny showed exactly the same type of segregation as that of the undoubted streaked forms.

In the same way the 123 non-coloureds were definitely identified as such. After sowing, surplus seed was left over from 37 F_2 plants. It averaged about 8 grains per plant, and, coming from short-, intermediate- and long-glumed forms indiscriminately, constituted a good random sample. All these grains gave a negative colour reaction in sulphuric acid, and the analogous segregation in the F_3 rows of the remaining 86,—roughly eye-tested even though no grains were left over for subsequent microtesting,—settled the correct classification of the whole group.

It should be emphasized that whenever an insufficient number of plants for judging was present in an F_3 row of which the parental colour was doubtful, or roguing was suspected, these cases were not included in the count; so that the 27 flusheds, 8 streakeds, and 123 non-coloureds contain no individuals about which any uncertainty exists. Furthermore, although no particular note was made regarding the matter, very probably the grains from which these 180 or so F_2 plants were derived all came off a single F_1 plant. For, in spite of poor tillering power, plants of later generations with a fair amount of room, such as those at the end of rows, were observed with five or six well filled ears; whereas among the F_1 individuals the encouragement to tiller is considerably greater, since they are always purposely well spaced.

Apparently, then, one, and only one, heterozygous combination gave rise to the F_2 generation. This conclusion is supported by the simplicity of the ratio: it is too even to be a fortuitous mixture of different F_2 segregation systems. For 27 : 8 : 123 is, considering the not very large number of plants involved, a reasonably close approximation to 3 : 1 : 12, the actual expectation being 30 : 10 : 118.

In view of the full purple colour of the F_1 grains, the minor proportion of flushed forms in the F_2 generation is very striking. No less so is the behaviour of the 123 non-coloureds, of which

111 threw non-coloureds only, and

12   „   „   „   + streakeds.

[In the 12 non-coloureds absence of colour was apparently a dominant, as the streakeds made up the smaller part of the offspring.]

Now if the ratio 3 : 1 : 12 be expressed in the form 48 : 16 : 192, the third term can be conveniently split up on a 15 : 1 basis so that the whole may be restated thus,

$$48 : 16 : (180 + 12).$$

On applying this to the F_2 results the comparison with expectation reads as follows:

Observed.   27 flusheds : 8 streakeds : (111 + 12) non-coloureds.

Expected.   30   „   : 10   „   : (111 + 7)   „   „

While, therefore, the probability cannot be pressed to the verge of certainty, there is still ground for believing that the two kinds of non-coloureds in the F_2 generation were to each other as 15 to 1.

To speculate on the Mendelism of these figures at this stage were

eminently unsound. Additional data are needed. Further breeding on of all the colour-yielding forms in the cross furnishes us with them; but, as will be seen from Table IV, into which they have been gathered, although of precise and distinctive kinds, by their very multiplicity they tend rather to complicate than to clarify the problem.

For the sake of convenience letters have been used to denote the various glume and colour types in the table. Whenever the parental colour is enclosed in brackets, the identity of the F_3 segregation with others of definitely known parentage has been the means of its determination.

In the first part of Table IV are the flushed forms which bred true. They are followed by one which gave rise to 18 flusheds and 6 streakeds. The possibility that this may really belong to the next group, which possesses non-coloured elements besides and conforms to the ratio $12F : 3S : 1N$, is admitted; but other examples of the same sort of segregation (picked out of F_4 results and therefore not included here) show that in any case a type throwing $3F : 1S$ does exist. Some members of the $12 : 3 : 1$ section, perhaps, by reason of their incompleteness will call for a few words of explanation. No. 4 has 17 flusheds and 4 streakeds but no non-coloured. Although it is quite conceivable that it may belong to the $3F : 1S$ class, the low proportion of streakeds gives cause for hesitation in so placing it. Unfortunately only one of the 17 flusheds was carried on for another generation; but as it yielded 15 flusheds and 3 streakeds—again a low proportion of the latter— with one of the streakeds very faint indeed and very likely heterozygous, it was decided to retain No. 4 where originally placed. In No. 3 there were no streakeds. Out of four of the flusheds which were grown on for another year, however, one gave rise to 14 flusheds and 6 streakeds. The other three bred true. If it were a case of two cumulative factors making for the 'flush' character, and no 'streak' factor in the zygote at all, this type of segregation could not have been produced. A 15 flushed : 1 non-coloured ratio must therefore be rejected. Moreover, as the single non-coloured forms less than one quarter of the total, No. 3 goes to the $12F : 3S : 1N$ group instead of to the following set, wherein the non-coloureds are produced in considerably greater relative numbers and the streakeds constitute the smallest term in the ratio $27 : 9 : 28$. By analogy No. 7 does likewise.

Two more groups bred from flushed parents remain. In neither do any streakeds appear. The first has flusheds to non-coloureds in the ratio $3 : 1$, the second $9 : 7$.

TABLE IV.

[L = Long.   M = Intermediate.   St = Short.   F = Flush.   S = Streak.   N = Non-coloured.]

F_3 Nos.	Glume character	No. of F_3 plants in row	Colour Segregation F	S	N	Parental F_2 grain colour	Group Totals F	S	N	Ratio
13	St	8	8	—	—	F				
14	St	23	23	—	—	F	72	—	—	Pure F
20	M	21	21	—	—	F				
102	St	20	20	—	—	F				
8	St	24	18	6	—	F	18	6	—	3 : 1
2	L	16	12	2	2	F				
3	M	10	9	—	1	F				
4	M	21	17	4	—	F				
6	L	25	22	2	1	F				
7	L	13	12	—	1	F	119 (115·4)	22 (28·9)	13 (9·6)	12 : 3 : 1
9	M	21	15	3	3	F				
10	L	12	8	3	1	F				
12	St	15	8	4	3	F				
15	M	21	16	4	1	F				
17	St	25	9	6	10	F				
18	M	22	8	2	12	F	44 (40·9)	15 (13·6)	38 (42·4)	27 : 9 : 28
21	M	26	12	5	9	F				
106	M	24	15	2	7	F				
11	M	25	19	—	6	F				
16	M	26	20	—	6	F	70 (68·25)	—	21 (22·75)	3 : — : 1
19	M	18	14	—	4	F				
103	L	22	17	—	5	F				
1	L	20	11	—	9	F				
101	M	25	16	—	9	F	43 (45)	—	37 (35)	9 : — : 7
105	L	12	5	—	7	F				
j	M	23	11	—	12	F				
72	St	8	—	8	—	[S]				
86	M	6	—	6	—	[S]	—	63	—	Pure S
93	M	27	—	27	—	S				
100	M	22	—	22	—	S				
60	St	23	—	17	6	S^1				
129	M	21	—	15	6	S	—	71 (69)	21 (23)	— : 3 : 1
g	M	21	—	17	4	[S]				
h	M	27	—	22	5	[S]				
45	M	7	—	2	5	[N]				
49	St	22	—	6	16	[N]				
84	L	11	—	1	10	[N]	—	21 (21·75)	66 (65·25)	— : 1 : 3 and or 3 : 13
110	M	23	—	6	17	N				
112	St	24	—	6	18	[N]				
74	L	16	—	8	8	N				
85	M	25	—	8	17	N				
96	M	16	—	8	8	[N]				
109	M	25	—	11	14	N	—	58 (59·5)	78 (76·5)	— : 7 : 9
136	M	17	—	7	10	[N]				
145	M	18	—	8	10	[N]				
159	M	19	—	8	11	N				
104	M	4	2	—	2	F	—	—	—	—
35	?	1	1	—	—	?	—	—	—	—
a	St	5	2	—	3	F	—	—	—	—
160	M	8	2	—	6	N	—	—	—	—
146	M	23	1	5	17	N	—	—	—	—
34	M	5	1	—	4	?	—	—	—	—

[1] Very faint.

The 8 F_2 plants with streaked grains were divisible into two classes of 4 each :—

        (1)   Pure streakeds.

        (2)   Heterozygous streakeds.

The latter provided a mixed progeny exhibiting a 3 : 1 segregation.

The next two groups of F_3 generations, both derived from non-coloured parents, have already been mentioned. Their chief characteristic is the dominance, or pseudo-dominance, of absence of colour. The first is composed of one quarter streakeds; in the second the proportion is seven-sixteenths.

At the base of the table all the anomalous colour-throwing F_2 plants have been collected. That the cause of the anomaly is traceable in several would sufficiently justify their being cast out altogether, but in the interests of exactitude and to avoid criticism on the score of deliberate omission, they have all been inserted. No. 104 contains only 4 plants—too small a number for an accurate determination of the proper ratio. No. 35 has a similar fault. In addition the three or four parental grains were so badly shrivelled and rusted that the colour question had to be left unanswered. The mere germination of the one was in itself a surprise. In three out of the remaining four the facts all point to certain rogning. *T. polonicum* and its derivatives are clearly susceptible to more rogning than most wheats on account of the wide gaping apart of the flowering glumes when the anthers are dangling out. It is quite likely that sometimes cleistogamy has not been effected before this occurs, and that very occasionally a stigma receives foreign pollen. In certain cases this rogning and its origin are readily discoverable. For instance, a purple-grained F_3 ear with long glumes derived from a long-glumed F_2 ear gave an F_4 row containing 14 plants, all of which were long-glumed and bearded. The exception had slight scurs, intermediate glumes, and purple grain— obviously the result of one of the stigmas on the parent ear receiving pollen from a beardless, short chaffed non-purple belonging to another culture altogether. Something similar happened to No. *a* in which it would seem that a purple F_1 grain was contaminated with pollen from a beardless non-purple. For the F_2 ear was a beardless purple which threw an F_3 row containing 4 beardless plants, of which one was plainly of Squarehead origin. No. *a* may be a pure purple, and the unravelling of the F_3 figures would doubtless result in the settling of this point: but they are too few. More troublesome to explain is No. 160. Beardless in the F_2, thus indicating rogning of an F_1 grain, and of a very

dark, translucent colour, which, however, was not purple, it nevertheless gave rise to an F_3 in which two flushed purples appeared (both beardless). It is of course not at all unlikely that here the foreign pollen came from another kind of non-coloured altogether, namely, one possessing an inhibitory factor; but in a case like this, with only 8 F_3 plants to study and the roguing as far back as the F_1 generation, it is not safe to attempt deductions. In No. 146, on the other hand, the roguing took place later,—in a single F_2 grain to judge by the bearded nature of the F_2 ear and the F_3 of 22 bearded + 1 beardless flushed. Hence if the purple plant be not a stray from some other row, and the rogue pollen from a non-coloured form, the F_3 segregation may possibly be correct, though I doubt it.

Bearded like the parent the last F_3 row, No. 34, came from one of about half a dozen F_2 ears with such shrivelled, sprouted grains that it was not thought they would grow, and they were consequently planted speculatively with the colour undetermined. In any case, however, five plants are scarcely enough on which to decide the dominance or otherwise of purple in this particular row. But although extraneous pollination does not appear to have taken place, it is not unlikely that the purple individual came out of No. 35 which possessed but a single plant: mistakes are easily made in harvesting two adjacent rows such as these with extremely few and scattered plants in each.

To sum up this group of doubtfuls: of the six, Nos. 104, 35, a, and 160 can be totally rejected on account either of insufficient numbers or of hopeless roguing at an early stage, while only the remaining two, in which the degree of doubt is slightly less, though still very strong, may qualify for a few further words in the following discussion of the results.

At the outset let it be understood that no attempt is being made to formulate a theory to fit the facts. Tentative suggestions and interpretations may have to be adopted to explain *some* of them and also to aid in the readier appreciation of certain aspects of the problem; but for all that, the contradictory nature of the figures makes them so thoroughly baffling that at present it must be honestly confessed no scheme which will embrace them *as a whole* can be advanced.

In some general features the colour inheritance has points in common with that of aleurone colour in maize. East and Hayes[1], in dealing with a case involving purple, red, and non-coloured forms, write that "the only difficulty in alining the results obtained with the ordinary

[1] East and Hayes, 1911, p. 83.

behaviour of the known factors, is the fact that almost none of the F_3 generation show the same ratios as the F_2 generation." They then instance a ratio of 1843 purples : 188 reds : 545 non-purples obtained from F_1 seeds which is obviously 12 : 1 : 3. Nothing like it appeared in the following generation, but, while admitting later that the deficiency of reds is too great to justify this step fully, they seize upon the slender chance of their figures representing a ratio of 9 : 3 : 4 and thence unfold a carefully formulated theory with which most of the other results accord fairly well.

Now a 12 : 1 : 3 ratio appeared in the F_2 generation of this wheat cross, but the opportunity for harmonising it,—or, at any rate, attempting to do so,—with any even remotely similar F_3 segregation was absolutely lacking. For in all the subsequent 12 : 1 : 3 ratios the colours of the terms were transposed. In F_2, 12 : 1 : 3 represented non-coloureds, streakeds, and flusheds respectively; in F_3, flusheds, non-coloureds, and streakeds. The nearest approach to the F_2 ratio, if one ignore the far too high proportion of streakeds, was in the rogued row, No. 146; but because of the adulteration no confidence can be put in it. Furthermore the F_2 seeds which gave rise to the row differed from the F_1 grains in one vitally important point. They were *not* purple. In any case, however, even were as many as 4 factors involved in the production of colour, out of 256 plants 16 heterozygotes identical with the F_1 type would be expected,—in other words at least 9 out of 158.

It may be pretty definitely asserted, therefore, that as far as this particular purple × non-purple cross is concerned *no F_3 ratio arising from purple seeds like those in F_1 and resembling the ratio of the F_2 generation exists.*

If the full flushed purples yielding offspring free from streaked forms be lifted out of Table IV and separately studied, it will be noted how very much akin in their behaviour they are to certain of the dark maize purples investigated by East and Hayes. The production of flusheds to non-coloureds in the ratios 3 : 1 and 9 : 7 indicates F_2 mono- and di-hybrids which are functions of two complementary colour-making factors. When also these data are taken in with those of the remaining full coloured plants in the F_2 generation, 4 pure purples out of 27 give further support to this idea. Nevertheless, as East and Hayes point out in a very similar situation[1], as soon as these individual ratios are taken in conjunction with the main mass of data, it has to be recognised that " tri-hybrids and tetra-hybrids *are possible* which give such results."

[1] East and Hayes, p. 85.

This is particularly conceivable when some of the relations of the streaked forms are considered.

In maize certain 'splashed' purples are found; but "they are zygotic variations which are not inherited, for their progeny are exactly like the progeny of the dark purple seeds. Further, the patches are not in a regular pattern nor does the selection of seeds of this nature have the slightest tendency to fix the phenomenon as a separate character[1]." Evidently, then, in wheat the streaked plants, many of which are capable of being bred true, are of an entirely different kind.

But there is another colour type in maize with which the appearances of structural affinity are in some respects quite well developed, though only in some. This type is known as 'particoloured,' the colour being a very faint purple. If we imagine such diluted pigmentation localised in one or two areas, and may be occasionally a little intensified owing to this concentration, the 'streaked' form results. In view of certain similarities in the behaviour of their segregates which will now be described, the visible differences between particoloureds and streakeds are thus best likened to those between chemical allotropes.

East and Hayes describe the occurrence of particoloureds in two crosses[2]. In the second they are designated 'light purples,' not because they are unlike particoloureds in outward appearance, but presumably to emphasize an important difference in the gametic formulae.

Where two factors, P and a colour factor C, are concerned in the production of colour, it is held in the first cross the absence of C from the combinations ccPP and ccPp does not prevent the formation of a very small amount of colour. Hence the particoloureds. The ratio of 9 purple : 3 particoloured : 4 non-coloured in the F_2 generation lends support to the theory. Moreover, if allowance be made for the fact that "particoloureds especially when non-starchy are not always distinguishable from whites," the agreement is fairly good. It is better in F_3 if pure starchy groups be chosen. Again, ratios of 3 purple : 1 particoloured, 3 purple : 1 non-purple, and 3 particoloureds : 1 non-purple, as well as pure purples and particoloureds, occurred in the F_3 generation. All these facts uphold the theory. But there is clearly a weakness when it is stated[3] later that pure white races, apparently devoid of any inhibitor of colour, may also have the gametic formula cP. Moreover in yet another family, wherein it is alleged

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[1] East and Hayes, p. 68.
[2]   ,,   ,,   p. 67, Family (8 × 54) and p. 81, Family (60 × 54).
[3]   ,,   ,,   p. 102 (foot)—103.

particoloureds of exactly the same nature are thrown, the selfed whites gave one particoloured ear out of every four in the next generation[1]. Now this last is a feature which marked certain non-purples in the second cross. One is inclined to ask whether there is really any difference between the particoloureds of the two crosses. Surely in the circumstances the **cP** hypothesis cannot *alone* account for the particolouring in the first maize cross any more than, as will shortly be questioned, the action of an inhibitor can alone be responsible in the second.

Here, however, a useful interpolation may be made to note that nearly all the above segregations of the first cross, with the exception of the 9 : 3 : 4 ratio, are also to be found among the results set out in this paper. It is even possible that the ratio 9 flushed : 3 streaked : 4 non-coloured is present too; for if the two groups in Table IV throwing all three colour types be added together, then comparison with expectation is as follows:—

$$\text{Observed.} \quad 163F : 37S : 51N.$$

$$\text{Expected.} \quad 141F : 47S : 63N.$$

Bearing in mind the small number of plants, one can hardly say the discrepancy is very much worse than in East and Hayes'

Observed.   638 purple : 210 particoloured : 306 non-coloured.

Expected.   649   „   : 216   „   : 289   „   [2]

To return to the second maize cross. Here East and Hayes hold that the **cP** seeds are whites and that the particoloureds develop when the colour inhibitor **I** undoubtedly operating in this cross is present heterozygously along with **P** and **C**. The fact that in this case no particoloureds breed true favours the conception. But if this be so, why do quite as many of these light purples (particoloureds) yield ratios of 3 particoloured : 1 non-purple and 1 particoloured : 3 non-purple as give 1 : 1 (possibly 9 : 7 or 7 : 9)? [Note that the first of these is also thrown by streakeds in the wheat cross, but not the others, which come from non-coloureds.] Also, unless the non-purples lacked **P** and **C**, they must by the theory be homozygous for **I** and therefore incapable of throwing particoloureds. But this is not so. For in two cases the following proportions were found[3]:

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[1] East and Hayes, p. 78.

[2] East and Hayes, p. 72.   Table 21 A.   Starchy seeds only, *i.e.* the most favourable selection.

[3] East and Hayes, p. 100.   Table 25 E.

Non-coloureds throwing

80 particoloured : 294 non-coloured

80	,,	: 216	,,	
160	,,	: 510	,,	$= 1 : 3 \left(\begin{matrix}\text{and}\\\text{or}\end{matrix}\ 3 : 13\right).$

While another had

105 particoloured : 204 non-coloured,

which is probably equal to 7 : 9 as the classification would err on the side of the non-coloureds[1].

Again this is a point of similarity to the wheat: the non-coloureds shown in Table IV behaved in this manner.

In brief, then, the 'streaked' and 'non-coloured' aspect of the wheat cross in its relation to the same in the two maize families can be synopsised thus:—

Resemblances to 1st cross.   Streakeds (particoloureds) throwing

All particoloureds.

3 particoloureds : 1 non-coloured.

Resemblances to 2nd cross.   Streakeds (particoloureds) throwing

3 particoloureds : 1 non-coloured.

Non-coloureds throwing

1 particoloured : 3 non-coloureds $\left(\begin{matrix}\text{and}\\\text{or}\end{matrix}\ 3 : 13\right)$

$\frac{1}{2}$,, $+\frac{1}{2}$,,   (approx.).

The outstanding point is that in one and the same cross (wheat) the inheritance of streaking gives support to two separate, radically opposed theories on the transmission of particolouring (maize). The conclusion is either that one of these two schemes is incorrect and the other as yet imperfectly elaborated, or that both are incomplete ways of expressing what may be in reality two kinds of particolouring dependent on the same system. The evidence of this paper seems to support the latter idea. For as at present expressed by East and Hayes, although each does so *in part*, neither hypothesis by itself will fit the wheat cross *completely*. On the cP hypothesis the origin of streakeds from non-coloureds is left unexplained, while the full flushed purple of the F_1 grains and the failure of F_2 non-coloureds to throw flusheds are against the presence of the usual type of inhibitor. To the

[1] East and Hayes, p. 96.   Table 25 A.

writer it seems not at all impossible that streaking is dependent on an entirely different factor (or factors) from flushing, and that apparent reversal of dominance in the non-coloureds throwing streakeds may be due to an inhibitor affecting 'streak' alone.   For I cannot inhibit 'flush' as in maize, because, as has just been remarked, no non-coloured forms throw flusheds, nor do any streakeds[1].   But whether or not this same factor I affects flushing to any extent in an indirect manner is not clear.   It plainly has no visible action in the F_1 generation, where the purple flush is fully dominant; but the remarkable deficiency of full coloured forms in the F_2 generation is a puzzle to explain otherwise. That, and the lack of any F_3 segregation with the F_2 ratio, is the snag on which every theory so far launched seems fated to founder.

Stabilisation.

Several pure lines have been extracted during the experiment. Most are full coloured purples with long glumes.   That no pure long-glumed flusheds appeared in the F_2 generation is to be attributed to the very small number of pure flusheds produced rather than to any coupling of 'short glume' with 'flush.'   The glume distribution in the intermediate No. 20 disproved the latter suggestion and no difficulty was experienced in obtaining them in numerous F_4 cultures.   Outwardly similar, genetically they are very varied.   Three pure flushed lines which were bred from the $12F : 3S : 1N$ group, for instance, may or may not be alike.   They may give F_1 mono- or di-hybrids on crossing, they may mask a streak even as a black oat will contain, but not show, hypostatic grey, or they may be pure for the flushed character alone. The same remarks apply to the pure purples of the $27F : 9S : 28N$ section in Table IV, although no F_4 cultures of them were actually isolated in quantity.

No streaking occurred in the $3F : 1N$ and $9F : 7N$ groups, and, assuming that in both cases the colour is due to the interaction of the factors **C** and **P**, then the extracted pure purple races must all have the formula **CCPP**.

As for the various pure cultures obtained from No. 20, all that can be said of them is simply that they are pure flusheds, but whether alike or different and of exactly what nature can only be decided from their behaviour after being crossed with whites of known constitution.

Pure streakeds, both long- and short-glumed, have also been stabilised, and lastly non-coloured Elobonis.

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[1] An extremely doubtful exception which may or may not contain a stray, and of unknown parentage, is No. 34.   But see remarks on p. 273.

PLATE XIII

I.   II.   III.
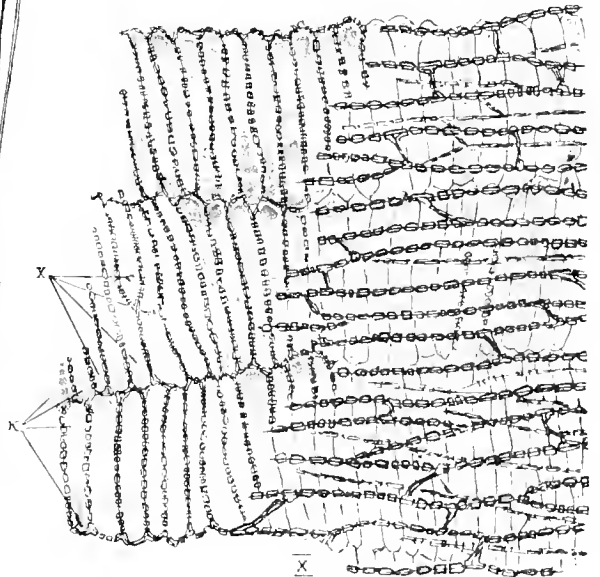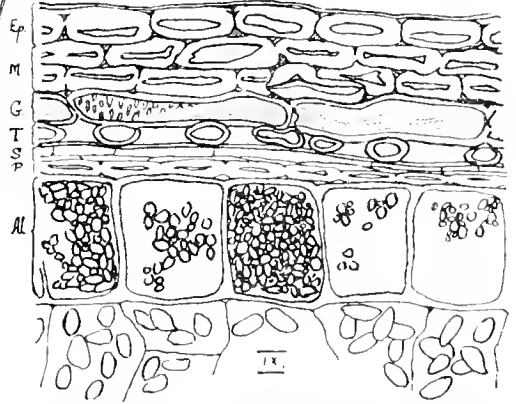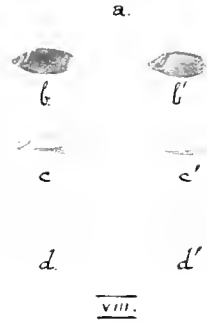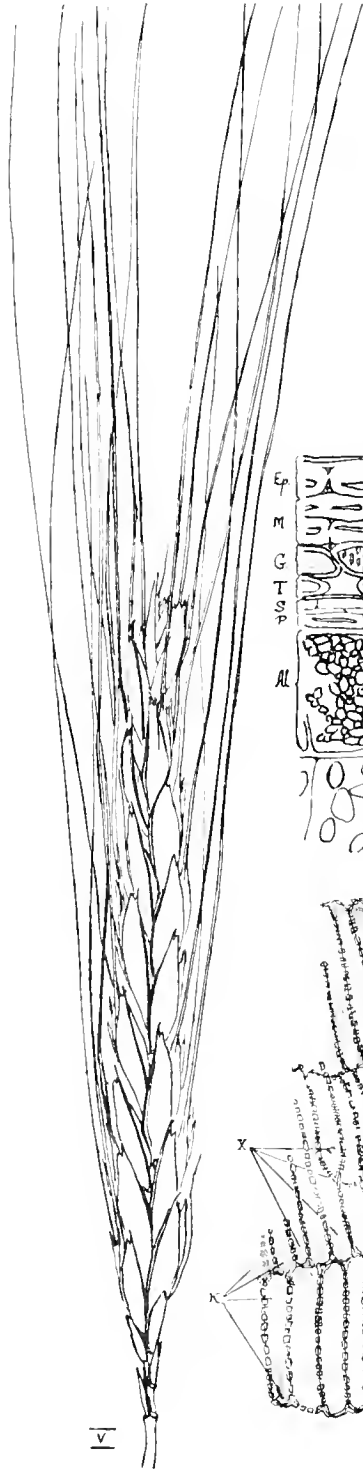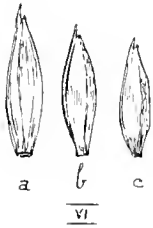
SUMMARY.

In the first part of the paper the parents are fully described; an accurate method of measuring and tabulating glume lengths explained; and it is shown how in the F_2 generation a marked change in the average glume length of homozygous 'longs' as compared with the average of the parent, *T. polonicum*, under equal conditions persists right through into the F_3 generation.

The second half is concerned with the purple pericarp colour,—the manner and extent of distribution in the tissues, its development and detection in minute quantities, and the inheritance. The latter is distinguished by one cardinal and unaccounted for anomaly: segregations analogous to the F_2 segregation have not been found in the F_3 generation. Streaking, a character which suddenly appeared in the F_2 generation, has resemblances to particolouring in maize. These are discussed.

Various cultures have been stabilised in respect of colour and glume length.

EXPLANATION OF PLATES.

PLATE XIII.

Fig. 1. Ear of *T. polonicum*. Spikelets in frontal view. Natural size.
Fig. 2. ,, ,, ,, lateral ,, ,,
Fig. 3. Ear of *T. eloboni*. ,, ,, ,, ,,

PLATE XIV.

Fig. 4. a, a'. Extreme forms of *T. polonicum* glumes $\begin{cases} a. & 32 \times 4\frac{1}{2} \text{ mms.} \\ a'. & 21 \times 4 \quad ,, \end{cases}$
       b. Typical *T. eloboni* glume. 10×4 mms.
Fig. 5. An F_1 ear. Spikelets in lateral view. Natural size.
Fig. 6. a. 'Long' type of intermediate glume. $17\frac{1}{2} \times 4\frac{3}{4}$ mms.
       b. 'Average' ,, ,, ,, $16 \times 4\frac{1}{2}$,,
       c. 'Short' ,, ,, ,, $14\frac{1}{2} \times 4$,,
Fig. 7. a. *T. polonicum* grain. $11\frac{1}{2} \times 3\frac{1}{2}$ mms.
       b. F_1 grain. 10×4 mms.
       c. *T. eloboni* grain. $9 \times 3\frac{1}{2}$ mms.
Fig. 8. Colour types.
       a. *T. polonicum* grain
       b. 'Flushed' grain
       c. 'Streaked' grain
       d. Faintly 'streaked' grain
       } Natural colours.
       b', c', d'. Acid colours.

Fig. 9.   Portion of transverse section of a purple grain showing pericarp and adjacent tissues.   × 190.

  Al = aleurone.   *Ep* = epicarp.   *G* = girdle cells.   *M* = mesoderm and hypoderm. *P* = perisperm.   *S* = spermoderm.   *T* = tube cells.

Fig. 10.   Superficial view of girdle cells in part overlaid by epicarp and mesocarp after removal of the underlying tissues.   × 190.

  K = False sap tints,—tannin yellow, dark reddish brown, and pink. *X* = Colour content of an extremely minute streak.

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REPORT ON TESTS OF SELF-STERILITY IN PLUMS, CHERRIES, AND APPLES AT THE JOHN INNES HORTICULTURAL INSTITUTION.

PREPARED BY IDA SUTTON,
Student in the Institution.

(With Plate XV.)

THE work to which this report relates was begun in 1911 by Mr W. O. Backhouse and Mr M. B. Crane. It has been continued in each succeeding year, and among others who took part in it must be mentioned Lt. Sherrard, Prof. Kusano, Prof. Chibber, and Miss Garlick. My responsibility in connexion with the observations began in 1915.

Preliminary reports on the earlier stages of the work were made by Backhouse (1, 2, 3). It is greatly to be regretted that this report had to be prepared without consultation with those who preceded me in the work, most of whom are absent on foreign service.

The objects were in part economic, for since the work of Waite and others it has been recognized that failure of fruit crops is not unfrequently due to self-sterility; and in addition it was expected that the work might elucidate the physiological nature of this phenomenon. At the present stage no comprehensive discussion of the genetic problems can be offered. In view of the recent experiments of others two main questions arise, (1) whether self-sterility is a simple Mendelian recessive character; (2) whether the older observers were right in considering that in such cases self-steriles are fertile with the pollen of *any* other variety, or whether there are not, rather, several classes of individuals, between which there is what East has called "Cross-incompatibility." As regards the first question there is nothing in our results which negatives the view that the property of self-sterility may be a recessive, but until a later generation can be tested, the only evidence bearing on this aspect of the matter is the fact that the results with plums and cherries are consistent with the supposition that the plants consist of two larger classes, self-fertiles and self-steriles, with a smaller number of plants of intermediate properties. These and presumably some of the self-fertiles may be supposed to be heterozygous. The self-sterile class forms a fairly homogeneous group, and the occasional indications

of partial self-fertility are probably attributable for the most part to errors. When, for instance, in the case of Coe's Golden Drop fertilized by Jefferson, the record shows a few fruits formed, out of a large number of flowers pollinated, the fact may mean that compatibility exists in a very slight degree, and if this could be confidently asserted, it would be tempting to suppose that the tree may be mosaic in that respect; but conceivably some error may have occurred. Between these interpretations we have at present no means of deciding, and the facts can only be given as they stand. The characters of the seedlings will in some cases hereafter provide a criterion.

As regards the question of cross-incompatibility the work was begun in the expectation that this was the only acceptable account of the facts. The older belief implied the paradox that there are as many categories as individuals; that, as a friend put it, "each lock would open with *every* key but its own." Nevertheless the results obtained have not favoured the theory of cross-incompatibility. Of clear incompatibles we have found four only, Coe's Golden Drop, Crimson Drop, Coe's Violet and Jefferson. But Crimson Drop and Coe's Violet are known to have arisen as bud-sports from Golden Drop[1] and it is not altogether impossible that Jefferson had a similar origin[2]. In apples no such case was seen. Cherries have not been so fully investigated and some records of failure with certain pollens may possibly be an indication of incompatibility, but pending repetition and confirmation their significance is doubtful. We are thus driven to suppose that at least in plums and apples the former belief is at least approximately true, improbable as this may appear.

The evidence from apples is not strictly applicable in this connexion, for as our records relate primarily to the formation of *fruits* the power of the pollen in producing seeds is very imperfectly recorded. In plums and cherries well-formed fruits with rarest exceptions contain developed seeds, but in apples seedless fruits are common, and indeed in Duchess of Oldenburg and Antonowka are almost the rule, nor does seedlessness necessarily involve any diminution in the size of the fruit (e.g.

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[1] As to the origin of Coe's Violet, see O. Thomas, *Rev. Hort.*, 1870, XLII. p. 515. Mention is also made of the independent occurrence of a sport, presumably identical, in *Trans. Hort. Soc.* Vol. VI. 1826, p. 393. Another violet sport was observed by Mr Vert of Ruabon (*in litt.*). For the origin of Crimson Drop see *R.H.S.J.* 1901, XXVI. p. ccxxvi.

[2] Hedrick, U. P., *Plums of New York*, 1911, p. 256, writes : "The parentage of the variety is unknown ; Floy thought it was a seedling of Washington ; Elliott suggested that it was 'from a seed of Coe's Golden Drop, which in growth and wood it closely resembles.'"

Antonowka) though in Lord Derby, for example, such diminution was observed.

In work of this kind where the measure of sterility or fertility must be the proportion of fruits actually set, it is obvious that many circumstances must inevitably blur the accuracy of the final result, for in almost all varieties only a proportion, generally small, of flowers can in any case succeed in forming fruits. The allowances to be made for these irregularities must depend largely on personal judgment, experience of each variety, and details which could only be recorded at great length. The classified lists appended are therefore given as representing approximate interpretations of the results recorded in the Tables.

The stage at which fertilisation fails probably differs in various forms. Mr Collins has made preliminary investigations on this subject. In Coe's Golden Drop, typically self-sterile, he finds that whether the flowers be selfed, crossed, or left unpollinated, the style is definitely cut off by an abscission-layer at its base on about the fifteenth day after the flower opens. The plant's own pollen germinates on the stigmatic surface and tubes penetrate the nutrient stylar tissue, a phenomenon seen by previous observers in other self-sterile plants.

At the beginning of the work the flowers were bagged on trees in the garden, but from 1912 all experiments were done on trees grown in pots in an orchard-house. This house is provided with mosquito-bars, and various other elaborate precautions were taken to ensure the exclusion of insects. It is believed that errors from that disturbance have been almost wholly avoided.

The numbers of flowers given are in general accurate, but some of these numbers were obtained by estimation based on the number of corymbs used. The word "em" means that the flowers were emasculated. In the absence of this expression, the anthers were not removed. All flowers were hand-pollinated. The number of flowers tested is given when a record was made. At first this was not always done.

The trees, with very few exceptions, were in the finest condition, being for the most part in exhibition state. The horticultural treatment was under the continual supervision of Mr Allard, the Superintendent, and great credit is due to him for the fine health in which the plants were kept, without which such observations would be altogether unreliable.

From the horticultural point of view the conclusions to be drawn from our experiments are (1) that many important commercial varieties set little or nothing unless cross-pollinated; (2) that for the pollination

of these self-sterile kinds pollinisers must be planted; (3) that provided that a variety produces plenty of pollen and flowers simultaneously with the variety which it is intended to pollinate, any variety, at least of plums and apples, will probably serve for this purpose, apart from the special case of the Coe varieties of plums and their presumable co-derivative, Jefferson.

The paper by Stout published in this volume gives (p. 102) references to the more important papers on the physiology of self-sterility. To these may be added the following, relating for the most part to horti-cultural observations made in this country.

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PLUMS.

Self-Sterile	*Partly Self-Fertile*	*Self-Fertile*
Coe's Golden Drop	Rivers' Early Prolific	Denniston Superb
Coe's Violet	Early Favourite	Early Transparent
Crimson Drop	Cox's Emperor	Reine Claude Violette
Jefferson	Early Orleans	Golden Transparent
Bryanston Gage	Farleigh Damson	Reine Claude Bavay
McLaughlin's Gage		Oullin's Golden Gage
Early Green Gage		Belle de Louvain
Old Green Gage		Monarch
Reine Claude d'Althan		Prince Engelbert
Pond's Seedling		Prune Géante
Wyedale		Gisborne
Frogmore Orleans		Victoria
Late Orleans		Czar
Prune d'Agen		Pershore
		Yellow Magnum Bonum
Primate (small numbers of		Early Mirabelle
Flowers selfed, but no		Myrobalan Red
other cross on tree)		Belgian Purple
Frogmore Damson		

CHERRIES.

Self-Sterile	*Partly Self-Fertile*	*Self-Fertile*
Amber Heart	May Duke	Flemish Red
Black Eagle	Archduke	Late Duke
Black Heart		Morello
Black Tartarian		
Bigarreau de Schreken		
,, Noir de Guben		
,, Napoleon		
,, Jaboulay		
,, Frogmore Early		
Early Rivers		
Elton		
Governor Wood		
Guigne d'Annonay		
Kentish Red		
Toussaint ?		
Waterloo		
White Heart		

APPLES.

Self-Sterile	*Partly Self-Fertile*	*Self-Fertile*
Beauty of Bath	Worcester Pearmain	Antonowka
Cox's Orange Pippin	Bramley's Seedling	Annie Elizabeth
Gascoyne's Scarlet	Lord Hindlip	Baldwin
Lane's Prince Albert	Lady Sudeley	Cellini Pippin
Norfolk Beauty	Old English Broadleaf	Coronation
Northern Greening	Doucin	Duchess of Oldenburg
	Improved Doucin	Golden Spire
Grimes's Golden ⎰Very small	*P. prunifolia*	King of the Pippins
Yellow Newtown ⎱number of	*P. baccata*	Lord Derby
flowers selfed	Golden Russet	Red Winter Reinette
		Ribston Pippin
		Stirling Castle
		Sturmer Pippin
		Washington
		French Paradise
		Crimson Bramley

PLUMS.

	Selfed		Crossed					
	Flowers	Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Coe's Golden Drop ...	Many	0	Reine Claude Violet	—	Many	—	—	—
	Many	0	Denniston Superb	—	Many	—	—	—
			Golden Transparent	314	79	—	—	—
			Bryanston Gage ...	207	30	—	—	—
			,, ,,	136	33	—	—	—
			,, ,,	—	Many	Reine Claude d'Althan...	—	Mod.
			McLaughlin's Gage	336	77	,, ,,	—	Many
			Reine Claude d'Althan	—	Many	Old Green Gage	—	Few
			Old Green Gage .	140	Many	...	—	—
			Early Green Gage	180	V. Many	...	—	—
			Oullin's Golden Gage	—	Many	—	—	—
			Monarch ...	—	Many	—	—	—
			Rivers' Early Prolific	—	Many	—	—	—
			Pond's Seedling ...	—	Many	—	—	—
			Wyedale ...	—	Many	Wyedale	—	V. Many
			Prune d'Agen	175	Mod.	—	—	—
			,, ,,	117	21	—	—	—
			Frogmore Orleans	117	28	Frogmore Orleans ...	118	62
			Late Orleans ...	206	42	Late Orleans ...	244	20
			Myrobalan Red ...	70	7	—	—	—
			Early Mirabelle ...	Many	Many	—	—	—
			Crimson Drop ...	166	0	Crimson Drop ...	87	0
			,, ,,	100—200	0	—	—	—
			Coe's Violet ...	100—200	0	Coe's Violet ...	88	0
			,,	Many	0	—	—	—
			Jefferson ...	507	4	Jefferson ...	Many	0
			,,	100—200	4	,,	200	0
			,,	Many	1	,,	240	0
			,,	150	0	,,	296	0
			Farleigh Damson	506	4	Farleigh Damson	167	V. Many
			Myrobalan Yellow ...	40	1 (seed bad)	—	—	—
			,, ,,	41	0	—	—	—
Coe's Violet ...	150	0	Bryanston Gage ...	60	44	—	—	—
	51	0	Reine Claude d'Althan ...	3	2	Reine Claude d'Althan...	—	Many
			Pond's Seedling ...	—	V. Many	—	—	—
			Orleans	78	Many	—	—	—

Seed parent	Pollen parent	Flowers	Fruit	Pollen parent	Flowers	Fruit
Coe's Violet	Rivers' Early Prolific	157	Many	—	—	—
	,, ,,	6	0	Jefferson	214	0
	Jefferson	—	0	,,	200	2
	,,	121	0	—	—	—
	,,	150	0	Coe's Golden Drop	100—200	0
	Coe's Golden Drop	—	—	,,	Many	0
	,,	—	0	Crimson Drop	88	0
	Crimson Drop	141	1*	—	—	—
Crimson Drop (294)	Wyedale	3	3	Jefferson	200	0
	Belle de Louvain	37	13	,,	238	0
	Jefferson	124	1 (seed bad)	,,	166	0
	Coe's Golden Drop	87	0	Coe's Golden Drop	100—200	0
	Coe's Violet	88	0	,,	—	0
		—	—	Coe's Violet	141	1*
Jefferson (114)	Early Transparent	—	V. Many	Reine Claude d'Althan	—	Many
	Reine Claude d'Althan	—	V. Many	,, ,,	—	Mod.
	Bryanston Gage	114	V. Many	Bryanston Gage	4	3
	Gisborne	105	39	Wyedale	—	V. Many
	Monarch	—	V. Many	Old Green Gage	75	1
	Rivers' Early Prolific	—	V. Many	,,	—	4
	Pond's Seedling	190	V. Many	—	—	—
	Prune Géante	234	52	Prune d'Agen	503	20
	Prune d'Agen	367	47	Cox's Emperor	129	41
	Frogmore Orleans	164	57	Farleigh Damson	108	V. Many
	Farleigh Damson	349	30	—	—	—
	,, ,,	70	6	—	—	—
	,, ,,	268	10	—	—	—
	Myrobalan Red	10	8	—	—	—
	,, ,,	97	1	Coe's Golden Drop	150	1
	Myrobalan Yellow	296	0	,,	507	0
	,, ,,	240	0	,,	100—200	4
	Coe's Golden Drop	200	0	,,	124	4
	,, ,,	238	0	Crimson Drop	124	1 (bad seed)
	Crimson Drop	200	0	Coe's Violet	121	0

* There are reasons for suspecting error in this case.

PLUMS	Selfed		Crossed					
	Flowers	Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Jefferson	—	—	Coe's Violet	214	0	Coe's Violet	150	0
			" "	200	2	" "	—	0
Bryanston Gage	465	0	Rivers' Early Prolific	369	59	Rivers' Early Prolific	—	150
	24	0	Old Green Gage	81	40	Old Green Gage	172	24
			—	—	—	—	—	1
			Jefferson	4	3	Jefferson	114	65
			Prune d'Agen	48	17	Prune d'Agen	675	23
			Farleigh Damson	48	2	Coe's Golden Drop	136	Many
			Myrobalan Red	50	10	" , "	207	33
			" Yellow	60	0	" , "	—	30
Denniston Superb	162	120	Burbank	Many : em	0	Coe's Violet	60	44
	Many	175				Early Green Gage	—	Many
	—	Many				Coe's Golden Drop	—	Many
Early Transparent	Many	110						
	126	80				Jefferson	—	Many
	Mod.	152						
	Many	Many						
Reine Claude Violette	Mod.	28	Rivers' Early Prolific	239	2	Coe's Golden Drop	—	Many
	Mod.	8						
	—	V. few						
	—	V. few						
	Many	Many						
Golden Transparent	Many	288				Coe's Golden Drop	314	79
	Mod.	Many				Primate	Many	30
	875	V. Many						
McLaughlin's Gage	291	1	Rivers' Early Prolific	14	2	Rivers' Early Prolific	55	2
	365	0	" , "	147	71	" , "	280	60
			Prune Géante	55	11	Coe's Golden Drop	336	77
			Old Green Gage	195	10	Old Green Gage	471	45
Early Green Gage	Many	0	Bryanston Gage	—	Many	Coe's Golden Drop	180	V. Many
	1162	0	Pond's Seedling	—	Many	Wyedale	—	V. Many
			Victoria	—	V. Many			
			Rivers' Early Prolific	—	Many			

Female variety			Pollen parent			Pollen parent		
Early Green Gage ...	—	—	Cox's Emperor	333	22	Early Green Gage	195	10
			Black Bullace	Few	7	Bryanston Gage	81	40
			Frogmore Damson	Mod.				
Old Green Gage ...	Many	2	Early Green Gago	471	45	Coe's Golden Drop	140	Many
	,,	0	Bryanston Gage	172	24	Farleigh Damson	225	Many
			,, Oullin's Golden Gage	—	1	Pond's Seedling	Few	2
			Jefferson	—	Few	,, ,,	41	30
			,,	75	4			
			Coe's Golden Drop	—	Few			
			Victoria	—	V. Many			
			Wyedale	—	Few			
			Pond's Seedling	—	V. Many			
			Prune Géante	66	5			
Reine Claude d'Althan	Many	0	Oullin's Golden Gage	—	Mod.	Jefferson	—	V. Many
	,,	1	Jefferson	—	Mod.			
	72	0	,,	—	Many			
	—	0	Coe's Violet	—	Many	Coe's Violet	3	2
			Coe's Golden Drop	—	Many	Coe's Golden Drop	—	V. Many
			,,	—	Mod.			
Reine Claude Bavay	26	6	Monarch	—	Mod.			
	Many	42	Rivers' Early Prolific	—	Mod.			
	Mod.	28	Burbank	Few	0			
	478 (Tree sickly)	Few	,,	Few	0			
Oullin's Golden Gage	—	46	McLaughlin's	280	60	Coe's Golden Drop	147	Many
	33	30	Early Favourite	55	2	Old Green Gage	14	Few
	Many	Mod.	Pond's Seedling	—	Few	Reine Claude d'Althan	—	Mod.
Rivers' Early Prolific	114	6	Belle de Louvain	410	Many	McLaughlin's	147	71
	Many	3	Bryanston Gage	—	32	,,		14
	114	0	Frogmore Orleans	491	150	Pond's Seedling	46	—
	681	0	Gisborne	346	2	Orleans	—	6
	Mod.	9			77	Bryanston Gage	369	59
	110	10				Reine Claude d'Althan...	—	Mod.
						,, ,, Violette	239	2

PLUMS.	Selfed Flowers	Selfed Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Rivers' Early Prolific	—	2	Prune Géante	270	23	Early Green Gage	—	Many
			Prune d'Agen	570	11	Jefferson	—	V. Many
			Farleigh Damson	262	9	Coe's Golden Drop	—	V. Many
			" "	324	0	Coe's Violet	157	Many
							6	0
						Wyedale	—	V. Many
						Cox's Emperor	125	41
						Prune d'Agen	827	47
						Farleigh Damson	200	V. Many
						Rivers' Early Prolific	—	Few
Early Favourite	—	Mod.	—	—	—	—	—	—
	—	Mod.	—	—	—	—	—	—
Cox's Emperor	159	6	Jefferson	129	44	Early Green Gage	333	22
	523	2	Early Rivers' Prolific	125	41	Late Orleans	251	22
	135	2	Gisborne	40	9	Frogmore Orleans	190	29
	—	—	Prune Géante	112	15		—	—
			Farleigh Damson	96	3		—	—
Belle de Louvain	355	21				Rivers' Early Prolific	410	32
	69	16				Crimson Drop	37	13
Pond's Seedling	Mod.	2	Old Green Gage	Few	2	Old Green Gage	—	V. Many
	—	0	" "	41	30	Early Green Gage	—	Many
	—	—	Rivers' Early Prolific	—	Many	Jefferson	—	V. Many
			P. cerasifera var. Pissardii	Few	0	Coe's Golden Drop	—	Many
						Coe's Violet	—	V. Many
						Rivers' Early Prolific	—	V. Many
						Wyedale	—	V. Many
Wyedale	Many	0	Early Green Gage	—	V. Many	Old Green Gage	—	Few
			Jefferson	—	V. Many	Primate	Few	5
			Coe's Golden Drop	—	V. Many	Coe's Golden Drop	—	V. Many
			Rivers' Early Prolific	—	V. Many	Rivers' Early Prolific	—	Mod.
			Pond's Seedling	—	V. Many	Pond's Seedling	—	Mod.
			P. cerasifera var. Pissardii	—	0			
Monarch	19	6 Tree sickly				Crimson Drop	3	3
	Many	Mod. but tree sickly				Coe's Golden Drop	—	Many
Prince Engelbert	Few	Few	Burbank	17	0	Jefferson	—	V. Many
	Few	V. Few				Reine Claude d'Althan	—	Mod.

Seed Parent			Pollen Parent			Pollen Parent		
Prince Engelbert	—	Many				Belgian Purple	—	2
Early Orleans	157	12	Coe's Golden Drop	418	62	Coe's Golden Drop	147	28
	846	0	Cox's Emperor	190	29	Rivers' Early Prolific	491	2
†Frogmore Orleans	1592	0	Late Orleans	415	0	Jefferson	367	57
	205	0	Coe's Golden Drop	244	20	Coe's Golden Drop	206	42
†Late Orleans	556	1	Cox's Emperor	251	22	Frogmore Orleans	415	0
	194	0				Coe's Golden Drop	175	21
Prune d'Agen	Many	0	Prune Géante	—	3	,, ,,	—	Mod.
	75	0	Rivers' Early Prolific	827	47	Rivers' Early Prolific	570	11
	—	—	Bryanston Gage	675	23	Bryanston Gage	48	17
			Jefferson	503	20	Jefferson	234	47
			Farleigh Damson	533	2	Farleigh Damson	269	V. Many
			P. cerasifera var. Pissardii	—	0	Prune d'Agen	—	3
Prune Géante	Few	14				Jefferson	190	52
	251	25				Old Green Gage	66	5
	254	Many				McLaughlin's Gage	55	11
						Cox's Emperor	112	15
						Early Rivers' Prolific	270	23
						Frogmore Damson	277	70
						Farleigh Damson	137	Many
Gisborne	524	198				Cox's Emperor	40	9
	647	Many				Early Rivers' Prolific	346	77
Belgian Purple	60	8	Early Orleans	2	2	Jefferson	105	39
	307	23						
Primate	36	0	Golden Transparent	Many	30			
			Wyedale	Few	5			
Victoria	—	V. Many				Early Green Gage	—	V. Many
	Mod.	V. Many				Old Green Gage	—	V. Many
Czar	Mod.	V. Many						
Pershore	Mod.	V. Many						
Yellow Magnum Bonum	Mod.	V. Many						
Myrobalan Red	Many	Many	P. cerasifera var. Pissardii	7 em	6	Coe's Golden Drop	70	7
	—	127	Myrobalan Yellow	— em	33	Jefferson	70	10
	41	38	,, ,,	— em	37	,, ,,	268	8
	35	5				Bryanston Gage	50	10

† Frogmore Orleans and Late Orleans are apparently identical.

PLUMS.

	Selfed		Crossed					
	Flowers	Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Farleigh Damson	82	3	Jefferson...	108	V. Many	Coe's Golden Drop	506	4
	75	0	Coe's Golden Drop	167	V. Many	Jefferson...	164	30
	*1530	Few	Old Green Gage	225	Many	Jefferson...	349	6
	80	0	Rivers' Early Prolific	200	V. Many	Rivers' Early Prolific	262	9
	—	1	Prune d'Agen	269	V. Many	" "	324	0
			Prune Géante	137	Many	Prune d'Agen	533	2
			Orleans	115	34	Bryanston Gage	48	2
						Cox's Emperor	96	3
						Frogmore Damson	238	22
Frogmore Damson	243	0	Farleigh Damson	238	22	Early Green Gage	—	Mod.
	—	—	Prune Géante	277	70			
Early Mirabelle	422	240		—	—	Coe's Golden Drop	—	Many

CHERRIES.

	Selfed		Crossed					
	Flowers	Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Archduke	Many	24	Big. de Schreken	Few	20		—	—
	794	17	Morello	136	2		—	—
			Governor Wood	266	9		—	—
			Royal Duke	Many	Few		—	—
Amber Heart	270	0	Big. Napoleon	Mod.	1	Elton	84	40
Black Eagle	320	0	Big. Napoleon	677	111	Big. de Schreken	117	42
			Waterloo	—	28	Waterloo	—	25
Black Heart	Many	1 (seed bad)	Morello	219	57	Early Rivers	173	5
			Royal Duke	582	26		—	—
			Big. de Schreken	151	0		—	—
			Big. Frogmore Early	222	0		—	—
Black Tartarian	Many	0	Early Rivers	Few	Some		—	—
			" "	283	0		—	—
			Guigne d'Annonay	Few	Few		—	—
Bigarreau de Schreken	140	0	Big. Noir de Guben	21	8	Archduke	20	V. Many
			Black Eagle	117	42	Big. Noir de Guben	330	24
						Big. Frogmore Early	63	0
						White Heart	50	14
						Black Heart	151	0
Bigarreau Noir de Guben	Many	0	Big. Frogmore Early	36	26	Big. de Schreken	21	8
			Big. de Schreken	330	24		—	—

* There are reasons for suspecting error in this case.

Seed parent			Pollen parent			Pollen parent		
Bigarreau Napoleon	—	0	Governor Wood	51	33	Archduke	—	1
						Amber Heart	677	111
						Morello	11 cm	3
						Morello	8 cm	4
Bigarreau Jaboulay	Many	0	Early Rivers	105	11	Elton	80	30
			Royal Duke	134	12	Early Rivers	230	9
			May Duke	202	3	Big. Nor de Guben	36	26
						Black Heart	222	0
Bigarreau Frogmore Early	—	1	Elton	53	15	Big. Frogmore Early	53	6
			Early Rivers	301	6	White Heart	205	72
			May Duke	55	21	Kentish Red	50	0
			" "	166	6			
			Flemish	129	22	Governor Wood	62	V. Many (all seed bad)
			Morello	80	3	Black Tartarian	Few	Some
			Late Duke	63	0	"	283	0
			Big. de Schr-ken	—	0	Big. Jaboulay	105	14
Early Rivers	20	0	Big. Frogmore Early	230	9	Big. Frogmore Early	—	15
	—	0	May Duke	170	16			
			Kentish Red	34	5 (2 are abnormal)			
			Black Heart	173	5 (? some fallen)			
Elton	Many	1 (seed bad)	Governor Wood	37	1	Big. Frogmore Early	—	—
	12	15	Morello	9	Many			
			Big. Frogmore Early	80	0			
			Late Duke	80	30			
			May Duke	150	4			
					10			
Flemish Red	84		Amber Heart	84	(Tree sickly) 40	Big. Frogmore Early	166	22
	267					Kentish Red	124	1
						Morello	56 cm	14
Governor Wood	267	0	Early Rivers	62	V. Many (all seed bad)	Early Rivers	37	1
						Archduke	266	9
						Big. Napoleon	51	33
						May Duke	393	7
						Morello	80 cm	15

There are reasons for suspecting error in this case.

		Selfed			Crossed		
CHERRIES.	Flowers	Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Governor Wood	Many	0	May Duke	20	11	Kentish Red ...	132	0
Guigne D'Annonay	—	—	Morello ...	105	36	Black Tartarain	Few	Few
Kentish Red	—	0	Flemish Red	124	1	—	—	—
	87	0	Late Duke	98	5	Early Rivers ...	34	5
			Morello	65 + ?	13	White Heart ...	—	22
			Governor Wood	132	0	—	—	—
Late Duke	1086	105	Early Rivers	50	0	May Duke ...	334	4
	—	Many				Kentish Red ...	98	5
	Many	Many				Elton ...	80	4
	—	Mod.				May Duke ...	246	6
						Big. Frogmore Early	80	0
May Duke	1115	8	Morello	271	6	Morello ...	16 cm	19
	1697	8	Kentish	334	4	Big. Jaboulay ...	202	3
	370	7	Governor Wood	393	7	Big. Frogmore Early	304	24
			Old Bigarreau	266	16	—	55	6
			Late Duke	246	6	Early Rivers ,,	170	16
			Also pollen from varieties	Many	7	Elton (tree sickly)	150	10
						Guigne d'Annonay	20	11
						White Heart ...	200	30
Morello	205	84	Big. Jaboulay	8 cm	4	Archduke ...	136	2
	—	Mod.	Governor Wood	80 cm	18	May Duke ...	271	6
	977	279	May Duke	46 cm	19	Black Heart ...	219	57
	406	390	Flemish Red	56 cm	14	Big. Frogmore Early	129	3
			Big. Napoleon	11 cm	3	Elton ...	9	Many
						,, ...	—	0
						Guigne d'Annonay	105	36
						Kentish Red ...	65 + ?	13
						Toussaint ...	Few	0
Toussaint	Few	0	à Brindelles	Few	set	—	—	—
			St Margaret Big.	—	set freely			
			Morello	Few	0			
Waterloo	414	0	Black Eagle	—	25	Black Eagle	—	28
White Heart	Many	0	Kentish Red	200	22	—	—	—
			May Duke	205	30	—	—	—
			Early Rivers	50	72	—	—	—
			Big. de Schreken		14	—	—	—

APPLES

Table 1 (first set of trials)

Variety			Pollinator		
Antonowka	1	1†	Gascoyne's Scarlet	6 em	Some
	209	17†	Worcester Pearmain	6 em	Some
	41	4†	Coronation	6 em	Some
			Cox's Orange Pippin	45 em	10
Annie Elizabeth		4†	,, ,,	212	9
	294	6+?	,, ,,	114 em	5+?
			Bramley Seedling	150 em	11
			Lane's Prince Albert	316	9
Beauty of Bath	Many	0	Cox's Orange Pippin	Many	13
	26	0	Annie Elizabeth	9	1
			Lady Sudeley	264	4
			P. baccata	259	10
Baldwin	Many	67	—		
	Many	49†	—		
Bramley's Seedling	187	5	Cox's Orange Pippin	—	7
	271	8	,, ,, ,,	170 cm	11
	17	12	,, ,, ,,	41 cm	3
	26	6	Annie Elizabeth	257 cm	20
		0	P. baccata	75 em	14
				129 cm	22
Cellini Pippin	160	10†	—		
		14†	—		
	113	11	—		
Coronation		15†	—		
Crimson Bramley	50	4	Worcester Pearmain	8 em	1
	64	3	Cox's Orange Pippin	99 em	8
		—	Antonowka	12	0*
Cox's Orange Pippin	180	0	Beauty of Bath	Many	9
	100	0	,, ,,	193	8+?
			Norfolk Beauty	114	7
			Lane's Prince Albert	—	6
			Worcester Pearmain		22
			Lord Derby	198	4
			Ribston Pippin		5
			Crimson Bramley	317	14

Table 2 (second set of trials)

Variety	Pollinator		
Antonowka	—		
Annie Elizabeth	Cox's Orange Pippin	12	0*
	Beauty of Bath	9	18
	Bramley Seedling	257 em	1
	—		20
Beauty of Bath	Cox's Orange Pippin	Many	8+?
	Lady Sudeley	288	9
	,, ,,	17	8
	P. baccata	11	0
	P. prunifolia	—	6
Baldwin	—		
Bramley's Seedling	Cox's Orange Pippin	Many	11+ fallen
	Annie Elizabeth	40	0
	,, ,,	150 em	11
	Golden Spire	—	3+
	Worcester Pearmain	56 em	0
	Lord Hindlip	—	6
	King of the Pippins	—	6
	Lane's Prince Albert	231	8
	P. baccata	55	2
	P. prunifolia	120 em	19
Cellini Pippin	P. prunifolia	12	6
Coronation	—		
Crimson Bramley	Antonowka	6 em	Some
	Cox's Orange Pippin	155	9
Cox's Orange Pippin	,, ,,	317	14
	,, ,,	130	16
	Antonowka	45	16
	Beauty of Bath	Many	13
	Norfolk Beauty	318	4
	Lane's Prince Albert	210	11+
	Worcester Pearmain	177	14
	Lord Derby	— em	4
	Ribston Pippin	189	3
	Crimson Bramley	99 cm	8
	Golden Spire		32

* Pollen old.

† Some of the apples had no seeds.

+? means some apples had fallen.

APPLES.

Variety	Selfed Flowers	Selfed Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Fruit
Cox's Orange Pippin	—	—	Crimson Bramley	130	16	Golden Spire	Few em	1+
			Coronation	155	9	King of the Pippins	—	2
			King of the Pippins	—	5	Lord Hindip	—	11
			Stunner Pippin	221	4	Newton Wonder	270 em	18
			"	—	1	Northern Greening	—	20
			Stirling Castle	450	7	Bramley's Seedling	—	7
			Bramley Seedling	Many	11+?	"	170 em	11
			"	40	0	"	41 em	3
			Wellington	54	9	Duchess Favourite	68	4
			Duchess Favourite	108	10	"	—	6-?
			Duchess of Oldenburg	—	20	Annie Elizabeth	212	9
			Annie Elizabeth	—	18	"	114 em	5+?
			Newton Wonder	153	1	Yellow Newtown	7	6
			"	—	3	Duchess of Oldenburg	60	10+?
				—		Sturmer Pippin	104 em	25
				—		Doncin	15 em	2
				—		Grime's Golden	5 em	0
				—		Stirling Castle	30 em	0
			Gascoyne's Scarlet	174	17	Gascoyne's Scarlet	77	10
			P. baccata	252	26	Golden Russet	180 em	23
				—		P. baccata	286 em	5
				—			9	1
Duchess of Oldenburg	Many	20+	Cox's Orange Pippin	69	10+?	Cox's Orange Pippin	—	20
			Golden Spire	24 em	9	Golden Spire	Few	1
			Lord Derby	—	14+?	Lord Derby	—	20
				—			—	3
Gascoyne's Scarlet	Many	0	Norfolk Beauty ...	160	10	Antonowka	— em	Some
	47	0	Cox's Orange Pippin	77	10	Cox's Orange Pippin	174	17
			Stirling Castle ...	102	1	Norfolk Beauty ...	3	0
			P. baccata ...	81	14			
Golden Spire	Many	7+	Cox's Orange Pippin	Many	32	Duchess of Oldenburg	24 em	9
	181	1	Duchess of Oldenburg ...	Few	1+?			
			Bramley's Seedling ...	—	3+?			
			Lord Derby ...	—	2+?			
			Lady Sudeley ...	70 em	2			

Selfed   Crossed

† Some of the apples had no seeds.   +? means some apples had fallen.

Variety			Pollinator			Pollinator		
Golden Spire	—	—	Lady Sudeley … …	129	2		—	—
			P. baccata .	46 em	1		—	—
			" … … :	314	5		—	—
Golden Russet	275	1	Cox's Orange Pippin	180 em	23	Cox's Orange Pippin	—	—
Grime's Golden	36	0	" … …	5	0		—	—
King of the Pippins	522	1+	Worcester Pearmain …	Few em	1		—	—
		10+	Cox's Orange Pippin .	Few em	2	Cox's Orange Pippin	—	—
			Bramley's Seedling …	Few em	0		—	7
Lane's Prince Albert	—	0	Cox's Orange Pippin …	210	11+	Cox's Orange Pippin	114	6
			Bramley's Seedling …	231	8	Annie Elizabeth	316	9
			P. baccata …	213	6			
Lady Sudeley	—	1+	Beauty of Bath …	288 em	8	Beauty of Bath	264	4
	44	0	P. baccata …	244 em	1	P. baccata	29	1
						P. prunifolia	6	4
						Northern Greening	70 em	V. Many
						Golden Spire …	129	2
								2+
Lord Hindlip	—	2+	Cox's Orange Pippin	11		"	—	—
			Duchess Favourite …	7		"	—	—
			Bramley's Seedling …	6				
			Northern Greening	9				
Lord Derby	40	4+	Cox's Orange Pippin …	— em	4	Cox's Orange Pippin .	—	4
			Stirling Castle …	— em	1	Stirling Castle …	30 em	1
						Golden Spire …	—	2+
			Duchess of Oldenburg	— em	3	Duchess of Oldenburg …	—	14
						Yellow Newtown .	—	5
Newton Wonder	Few+	Few+	Cox's Orange Pippin	270 em	20	Cox's Orange Pippin	153	1
		1			18			3
Norfolk Beauty	Few	0	Cox's Orange Pippin …	318	4	Gascoyne's Scarlet	160	10
			Gascoyne's Scarlet …	3	0	Cox's Orange Pippin …	193	7
						Lord Hindlip	—	9
Northern Greening	—	1	Cox's Orange Pippin …	—	20		—	—
			Lady Sudeley … …	—	V. Many		—	—
Red Winter Reinette	60	10					—	—
	166	7					—	—
Ribston Pippin	140	4	Cox's Orange Pippin …	189 em	3	Cox's Orange Pippin .	198	5
	196	4					—	—
Stirling Castle	—	18+	Lord Derby …	30 em	1	Cox's Orange Pippin …	450	7
		21+	Cox's Orange Pippin …	30 em	0	Lord Derby …	— em	1
	194	9				Gascoyne's Scarlet …	102	1
	303	24+					—	—

† Some of the apples had no seeds.   +? means some apples had fallen.

APPLES.

APPLES.	Selfed Flowers	Selfed Fruit	Ovules fertilized by	Flowers	Fruit	Pollen put on	Flowers	Frrnt
Stirling Castle	261	Mod. 304	—	—	—	—	—	—
Sturmer Pippin	Many 44	5+ 6	Cox's Orange Pippin	104 cm	25	Cox's Orange Pippin	221	4
						King of the Pippins		1
						Cox's Orange Pippin	54	9
Washington	152	12						—
		18						—
		6+						—
	249	17+						—
		12						—
		9						—
	206	9+						—
	84	0						—
	249	8						—
	247	17+						—
Worcester Pearmain	204	8+	Cox's Orange Pippin	177 cm	14	Cox's Orange Pippin	—	22 V. Many
	214	7	P. baccata	230 cm	6	Antonowka	6 cm	Some
		2	P. prunifolia	226 cm	5	Duchess Favourite		3 + ?
			Bramley's Seedling	56 cm	0	Crimson Bramley	8 cm	1
						King of the Pippins	— cm	1
Yellow Newtown	13	—	Lord Derby	—	5		—	—
			Cox's Orange Pippin	7	6			
			P. baccata	6 cm	1		—	—
P. baccata	315	0	Lady Sudeley	29	1	Lady Sudeley	244	4
	1231	3	Bramley's Seedling	55	2	Bramley's Seedling	75 cm	14
	20	1	Old English Broadleaf	120 cm	19		129 cm	22
			Cox's Orange Pippin	136 cm	10	Old English Broadleaf	122 cm	18
				286 cm	5	Cox's Orange Pippin	252	26
			Beauty of Bath	9	1			
				17	0	Beauty of Bath	259	10
						Gascoyne's Scarlet	81	14
						Golden Spire	46 cm	1
						Yellow Newtown	314	54
						Worcester Pearmain	6 cm	1
							230 cm	6

† Some of the apples had no seeds.

+ ? means some apples had fallen.

P. baccata		—		—			Lane's Prince Albert	213	6
P. prunifolia	41	1	Beauty of Bath	11	6	Worcester Pearmain	—	226 cm	5
			Bramley's Seedling	12	6		—		
			Lady Sudeley	6	4		—		
Old English Broadleaf	60	1	Doucin	60 em	18	Doucin	6 em	4
	50	5	French Paradise	175 cm	29	French Paradise	24 cm	10
			P. baccata	122 cm	18	P. baccata	136 em	10
Doucin	20	2	Old English Broadleaf	6 em	4	Old English Broadleaf	60 cm	18
	92	1	Improved Doucin	155 cm	9	Improved Doucin	71 cm	3
	93	5	Cox's Orange Pippin	15 em	2		—	
Improved Doucin	30	2	Doucin	74 em	3	Doucin	155 em	9
French Paradise	15	4†	Old English Broadleaf	24 cm	10	Old English Broadleaf	175 em	29

† Some of the apples had no seeds.

EXPLANATION OF FIGURES.

Fig. 1. Jefferson. Tree was covered with flowers ; different branches were crossed with pollen from Coe's Golden Drop, Coe's Violet, Crimson Drop, and Pond's Seedling. No fruits set by the pollen of Coe's Golden Drop, or Crimson Drop, only two fruits set by Coe's Violet, whereas a heavy crop set on the one branch pollinated with Pond's Seedling—see lowest branch on right-hand side of figure.

Fig. 2. Governor Wood. Tree in flower ; the flowers on one large branch (on left-hand side of figure) were crossed with pollen from Early Rivers : the rest of the flowers were self-pollinated.

Fig. 3. Governor Wood. The same tree as in Fig. 2. No self-pollinated flowers set fruit ; a good crop set by the pollen of Early Rivers. Note that this photograph was taken from the opposite side of the tree so that the crossed branch shows on the right-hand side of the figure.

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Fig. 1. Jefferson.

PLATE XV
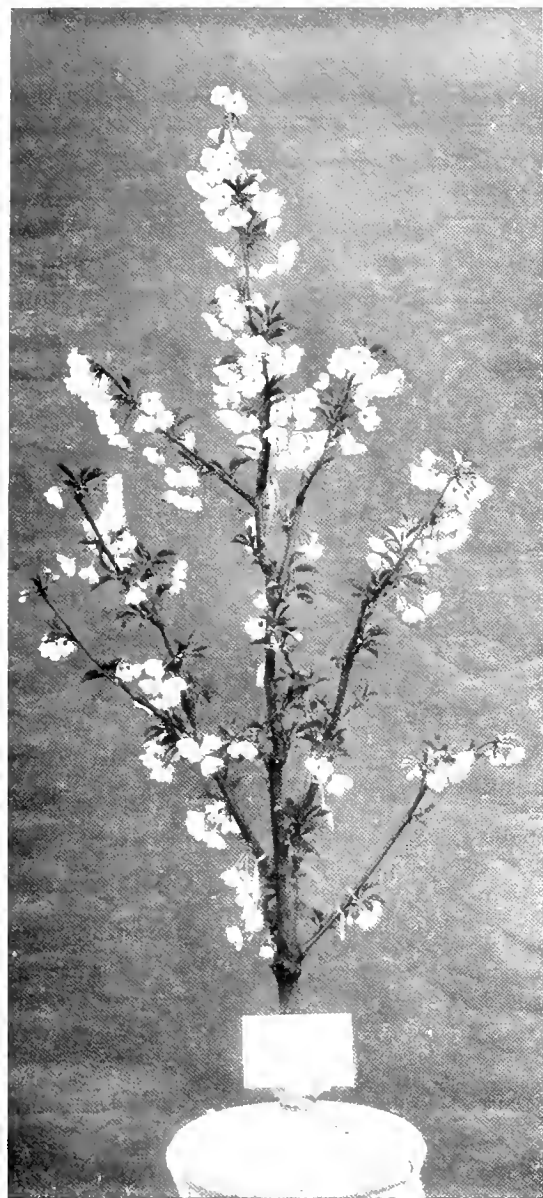
Fig. 2.   Cherry in Flower.

Fig. 3.   Cherry in Fruit.

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