

## STUDIES OF INHERITANCE AND EVOLUTION IN ORTHOPTERA. III<sup>1</sup>.

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*<sup>2</sup>.

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.)

<sup>1</sup> Contribution from the Zoological Laboratory of the Kansas State Agricultural College and Experiment Station, No. 11.

The first instalment appeared in the *Journal of Genetics*, Vol. III., and the second in *Ibid.* Vol. VII. pp. 1—46.

<sup>2</sup> The other apparent exceptions referred to in the first instalment were those cases involving the factor  $\Theta$ , which are considered in the second paper.

48 *Inheritance and Evolution in Orthoptera III*

*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 (494); 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.

<i>CS × BI</i>					
	BC	BS	CI	IS	
<b>470</b>	10	9	3	9	407 26
Expect.	7·7	7·7	7·7	7·7	

<i>CI × IS</i>					
	CI	CS	II	IS	
<b>474</b>	18	20	23	26	470
Expect.	21·7	21·7	21·7	21·7	

<i>BC × CC</i>				
	BC	CC		
<b>471</b>	36	39	470	426
Expect.	37·5	37·5		

<i>II × II</i>		
	II	
* <b>143</b>	90	74
<b>475</b>	19	143
<b>476</b>	29	475
<b>477</b>	69	475
<b>478</b>	23	475
Total	230	

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

<i>CE × BI</i>					
	BC	BE	CI	EI	
<b>479</b>	12	22	20	11	292 472
Expect.	16·2	16·2	16·2	16·2	

TABLES (continued).

$IS \times BI$

	$BI$	$BS$	$II$	$IS$	
<b>480</b>	11	9	16	7	472
<b>481</b>	24	10	12	10	480 473
Totals	35	19	28	17	
Expect.	24.7	24.7	24.7	24.7	

$BS \times II$

	$BI$	$IS$	
<b>490</b>	30	31	473 475
Expect.	30.5	30.5	

$BIS \times BB$

	$BB$	$BIS$	
<b>482</b>	20	24	472 245
<b>483</b>	10	15	482
<b>484</b>	10	9	486 482
<b>485</b>	22	31	482
Totals	62	79	
Expect.	70.5	70.5	

$CJ \times CJ$

	$CC$	$CJ$	$JJ$	
<b>491</b>	0	3	1	110 144
Expect.	1	2	1	

$JS \times DJ$

	$DJ$	$DS$	$JJ$	$JS$	
<b>492</b>	1	3	3	0	151 149
Expect.	1.5	1.5	1.5	1.5	

$BIS \times BC$

	$BB$	$BC$	$BIS$	$CIS$	
<b>486</b>	9	8	10	9	472 266
<b>487</b>	9	9	13	7	485 510
Totals	18	17	23	16	
Expect.	18.5	18.5	18.5	18.5	

$BP \times BP$

	$BB$	$BP$	$PP$	
<b>493</b>	9	20	11	337
Expect.	10	20	10	

$BIS \times BS$

	$BB$	$BIS$	$BS$	$ISS$	
<b>488</b>	15	22	17	13	472
Expect.	16.7	16.7	16.7	16.7	

$BC \times CI$

	$BC$	$BI$	$CI$	$EI$	
<b>494</b>	4	4	2	2	479
Expect.	3	3	3	3	

$CE \times IS$

	$CI$	$CS$	$EI$	$ES$	
<b>489</b>	6	8	7	5	292 472
Expect.	6.5	6.5	6.5	6.5	

$BEB\theta \times SS$

	$BSE\theta$	
<b>495</b>	91	218 473

50 *Inheritance and Evolution in Orthoptera III*

TABLES (continued).

$BS \times BI$					
	BB	BI	BS	IS	
<b>496</b>	7	5	2	2	473
Expect.	4	4	4	4	

$II \times DS$			
	DI	IS	
<b>506</b>	13	15	475 492
Expect.	14	14	

$II \times BB$				
	$BI$			
<b>497</b>	72	143	482	

$CS \times CI$					
	CC	CI	CS	IS	$\widehat{CIS}$
<b>507</b>	14	9	15	14	1 489
Expect.	13.2	13.2	13.2	13.2	0

$\widehat{BIS} \times \widehat{BIS}$					
	$\widehat{BB}$	$\widehat{BIS}$	$\widehat{ISIS}$		
<b>498</b>	5	3	2	482	488
<b>499</b>	3	4	2	482	
<b>500</b>	13	36	26	510	515
<b>501</b>	2	4	2	485	
Totals	23	47	32		
Expect.	25.5	51	25.5		

$ES \times DJ$				
	DE	DS	EJ	JS
<b>508</b>	6	8	5	6 489 492
Expect.	6.2	6.2	6.2	6.2

$\widehat{BIS} \times II$				
	$\widehat{BI}$	$\widehat{IIS}$		
<b>502</b>	21	14	482	143
<b>503</b>	16	17	482	143
Totals	37	31		
Expect.	34	34		

$\widehat{CIS} \times \widehat{BIS}$				
	$\widehat{BC}$	$\widehat{BIS}$	$\widehat{CIS}$	$\widehat{ISIS}$
<b>509</b>	2	2	1	3 486
<b>510</b>	8	15	10	9 486
<b>511</b>	3	2	6	5 515
<b>512</b>	18	11	15	16 522 485
<b>513</b>	10	10	10	8 522 485
R <b>514</b>	1	1	1	2 510
Totals	42	41	43	43
Expect.	42.2	42.2	42.2	42.2

$II \times ES$			
	EI	IS	
<b>504</b>	19	16	475 489
Expect.	17.5	17.5	

$EI \times II$			
	EI	II	
<b>505</b>	2	4	489 475
Expect.	3	3	

$\widehat{CIS} \times \widehat{BC}$				
	$\widehat{BC}$	$\widehat{BIS}$	$\widehat{CC}$	$\widehat{CIS}$
<b>515</b>	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	BB $\theta$	BC $\theta$	BF $\theta$	CF $\theta$		
<b>516</b>	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		

$BC \times B\theta F\theta$

	BB $\theta$	BC $\theta$	BF $\theta$	CF $\theta$		
<b>517</b>	9	8	11	8	486	222
Expect.	9	9	9	9		

$\widehat{I}S\widehat{I}S \times \widehat{I}S\widehat{I}S$

	$\widehat{I}S\widehat{I}S$		
<b>524</b>	33	510	
<b>525</b>	38	522	509
<b>526</b>	30	522	
<b>527</b>	31	510	
Total	132		

$\widehat{I}S \times JJ$

	IJ	JIS		
<b>518</b>	2	4	502	491
Expect.	3	3		

$BB \times CEC\theta E\theta$

	BC	BE	BC $\theta$	BE $\theta$		
<b>528</b>	4	8	10	1	482	369
Expect.	5.7	5.7	5.7	5.7		

$CI \times BB$

	BC	BI		
<b>519</b>	8	9	489	493
Expect.	8.5	8.5		

$\widehat{I}S \times BC$

	BI	BIS	CI	CIS		
<b>529</b>	31	30	22	24	503	510
<b>R 530</b>	3	6	6	8	510	502
Totals	34	36	28	32		
Expect.	32.5	32.5	32.5	32.5		

$C\widehat{I}S \times C\widehat{I}S$

	CC	CIS	ISIS		
<b>520</b>	13	24	13	515	
<b>521</b>	25	51	17	515	
<b>522</b>	14	21	7	486	
<b>523</b>	10	27	12	510	515
Totals	62	123	49		
Expect.	58.5	117	58.5		

$\widehat{I}S \times II$

	II	IIS		
<b>531</b>	4	7	503	475
Expect.	5.5	5.5		

TABLES (continued).

	$BI \times II$			
	┌───┐			
	│			
	└───┘	└───┘		
	$BI$	$II$		
<b>532</b>	34	31	503	475
Expect.	32.5	32.5		

	$CC \times CC$	
	┌───┐	
	│	
	└───┘	
	$CC$	
<b>537</b>	26	522

	$\widehat{IIS} \times \widehat{IIS}$			
	┌───┐			
	│			
	└───┘			
	$II$	$\widehat{IIS}$	$\widehat{ISIS}$	
<b>533</b>	4	5	4	503
<b>534</b>	1	1	1	503
Totals	5	6	5	
Expect.	4	8	4	

	$\widehat{IIS} \times \widehat{CIS}$			
	┌───┐			
	│			
	└───┘			
	$CI$	$\widehat{CIS}$	$\widehat{IIS}$	$\widehat{ISIS}$
<b>538</b>	31	35	28	26
Expect.	30	30	30	30
	503			

	$BB \times BB$	
	┌───┐	
	│	
	└───┘	
	$BB$	
<b>539</b>	88	485

	$\widehat{ISIS} \times \widehat{BIS}$			
	┌───┐			
	│			
	└───┘			
	$\widehat{BIS}$	$\widehat{ISIS}$		
<b>535</b>	32	32	510	515
<b>536</b>	33	21	510	485
Totals	65	53		
Expect.	59	59		

	$BC \times \widehat{ISIS}$		
	┌───┐		
	│		
	└───┘		
	$\widehat{BIS}$	$\widehat{CIS}$	
<b>540</b>	8	6	510
Expect.	7	7	522

The *I* part of the pattern in this new combination is considerably modified. In the  $\widehat{IS}$ ,  $\widehat{BIS}$  or  $\widehat{CIS}$  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,  $\widehat{IS}$ , becomes a new form, a new multiple allelomorph, pairing with, and allelomorphous 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* × *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 (*CIS*) 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 *BIS* (see table). This *CIS* was in all observable respects similar to the other *CIS* individuals produced by descendants of the original *BIS* aberrant form. It died before reaching adult stage. When this *CIS* 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 *CIS*, as matings (486), (510), and others. However, careful examination of the other breeding jars containing *CIS* 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, *IS*, the *S* pattern is more conspicuous than the *I* pattern.)

I am under obligation to Mr A. W. Bellamy (1916—Fellow in Zoology in the University of Chicago) for valuable help during the

54 *Inheritance and Evolution in Orthoptera III*

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.

LITERATURE CITED.

- BRIDGES, C. B. 1916. "Non-disjunction as a proof of the Chromosome Theory of Heredity." *Genetics*, Vol. I. pp. 1—52; 107—163.
- CASTLE, W. E. 1914. "Nabours' Grasshoppers, Multiple Allelomorphism, Linkage, and Misleading Terminologies in Genetics." *Amer. Nat.* Vol. XLVIII. pp. 383, 384; 503, 504.
- DEXTER, JOHN S. 1914. "Nabours' Breeding Experiments with Grasshoppers." *Amer. Nat.* Vol. XLVIII. pp. 317—320.
- MORGAN, T. H. 1914. "The Theoretical Distinction between Multiple Allelomorphs and Close Linkage." *Amer. Nat.* Vol. XLVIII. pp. 502, 503.
- NABOURS, R. K. 1914. "Studies of Inheritance and Evolution in Orthoptera. I." *Journal of Genetics*, Vol. III. pp. 141—170.
- 1917. "Studies of Inheritance and Evolution in Orthoptera. II." *Journal of Genetics*, Vol. VII. pp. 1—46.