

NOTE ON A CASE OF LINKAGE IN *PARATETTIX*.

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NABOURS (1) has shown that the various colour patterns in the grouse-locust, *Paratettix texanus*, are due to a series of Mendelian factors *A, B, C, D, E, F, H, I, J, L, N, P, Q*, and *S*, which are multiple allelomorphs or else very intensely repelled (this repulsion has been changed to coupling for one pair only), and a factor Θ allelomorphic to its absence only. Nabours regarded this factor as being inherited quite independently of the others. A close examination of his data shows however that in spermatogenesis Θ and any of the other factors exhibit linkage with a cross-over value of about 24% or nearly that of the 1:3:3:1 system, whilst in oögenesis they exhibit a small linkage, the cross-over value being about 46%.

The notation used below is that of Nabours, except that the absence of Θ is represented in the usual manner by θ , and a zygote known to have been formed from gametes carrying $A\Theta$ and $B\theta$ is represented by $A\Theta.B\theta$, and so on. In all matings the composition of the father is shown on the left. In Table I are shown the results of Nabours' matings in which the male was doubly heterozygous, and his composition can be determined from that of his parents. Those matings where such a male was mated to a female carrying the same factors are excluded, as we have here no means of determining how much of the observed linkage was due to each parent. Column 1 gives the composition of the parents, Column 2 the number in Nabours' catalogue, Column 3 the total number of young produced, and Column 4 the number of these which were due to "crossing-over" or rearrangement of the factors during spermatogenesis.

For example in Mating 180 the male was of composition $A\theta.B\Theta$, since his parents were $AB\Theta\theta$ and $A\theta.S\theta$. When mated to the female $A\theta.S\theta$ he begot:

	45	$A\theta . A\theta$	and	$A\theta . S\theta$,
	17	$B\theta . A\theta$	„	$B\theta . S\theta$,
	17	$A\Theta . A\theta$	„	$A\Theta . S\theta$,
and	37	$B\Theta . A\theta$	„	$B\Theta . S\theta$.

Hence out of 116 spermatozoa he must have produced :

$$45 A\theta, \quad 17 B\theta, \quad 17 A\ominus, \quad 37 B\ominus,$$

or 34 cross-overs out of 116. When the mother was also heterozygous for \ominus certain classes of zygotes could not be distinguished, and hence only those classes are considered which enable us to measure the linkage directly. Thus in mating 178 all the $A\theta B\theta$ and $B\theta F\theta$ zygotes were formed from non-cross-over spermatozoa, whilst $A\theta A\theta$ or $A\theta F\theta$ would have been due to crossing-over.

TABLE I.

Male doubly heterozygous.

Mating	Number	Totals	Cross-overs
$A\theta . B\theta \times A\theta . F\theta$	178	7	0
$A\theta . B\theta \times A\theta . S\theta$	180	116	34
$A\theta . C\theta \times B\theta . C\theta$	187	57	19
$B\theta . C\theta \times B\theta . C\theta$	231	21	3
$B\theta . C\theta \times B\theta . P\theta$	260	42	7
$B\theta . C\theta \times B\theta . B\theta$	237	1	0
$B\theta . C\theta \times B\theta . C\theta$	229, 230	104	30
$B\theta . C\theta \times B\theta . S\theta$	263	45	13
$B\theta . C\theta \times C\theta . F\theta$	266	94	25
$B\theta . C\theta \times C\theta . P\theta$	271, 272, 273	194	38
$B\theta . F\theta \times B\theta . B\theta$	294	9	2
$B\theta . F\theta \times B\theta . C\theta$	295	40	15
$B\theta . F\theta \times B\theta . E\theta$	296, 297	63	8
$B\theta . F\theta \times C\theta . C\theta$	309	60	10
$B\theta . F\theta \times C\theta . F\theta$	312	30	4
$B\theta . F\theta \times E\theta . F\theta$	313	9	1
$B\theta . P\theta \times C\theta . P\theta$	337	38	7
$C\theta . E\theta \times C\theta . E\theta$	372	10	1
$C\theta . F\theta \times A\theta . C\theta$	370	104	22
$C\theta . F\theta \times A\theta . J\theta$	373	14	2
$C\theta . F\theta \times B\theta . C\theta$	268	32	12
$C\theta . F\theta \times B\theta . C\theta$	283	8	1
$C\theta . F\theta \times B\theta . F\theta$	310, 311	47	17
$C\theta . F\theta \times C\theta . C\theta$	375	19	4
$C\theta . F\theta \times C\theta . F\theta$	376, 377, 378	160	38
$C\theta . F\theta \times F\theta . J\theta$	389	8	3
$C\theta . P\theta \times B\theta . C\theta$	398	4	1
$C\theta . S\theta \times B\theta . B\theta$	425	32	11
$C\theta . S\theta \times B\theta . C\theta$	426	5	1
$C\theta . S\theta \times C\theta . C\theta$	417	4	1
$C\theta . S\theta \times C\theta . C\theta$	416	19	1
$E\theta . F\theta \times B\theta . C\theta$	430, 431	25	4
Totals	...	1421	335

Out of 1421 spermatozoa produced by the doubly heterozygous males 335, or 23.6%, were due to crossing-over. The cross-over value appears to vary slightly with the pair of "multiple allelomorphs" concerned, but the only variation which is probably significant is as follows. Where one of the factors concerned is A , i.e. in matings 178, 180, and 187, the cross-overs number 53 out of 180, giving a cross-over value of $29.4 \pm 2.3\%$.

whilst for the other factors together the cross-over value is $22.7 \pm 8\%$. The probable errors given are those due to random sampling only. The divergence may probably be explained on the following hypothesis, which is substantially that of Dexter (2). The factors *B*, *C*, *D*, etc. are incompletely dominant over their absence, which is represented by *A*, and are not allelomorphic to one another, but very strongly repelled. This is undoubtedly true of *B* and *I*, since they may become coupled. We may then more accurately represent the zygote $A\Theta . B\theta$ as $bc\Theta . Bc\theta$ $B\Theta . C\theta$ as $Bc\Theta . bC\theta$, and so on. Now it has been shown by Sturtevant (3) and Muller (4) that in *Drosophila melanogaster* certain factors, when present in the heterozygous condition, cause great increases in linkage, while Gowen (5) has shown that numerous factors cause small increases. If then the factors *B*, *C*, *D*, etc. have this effect in a slight degree, we should expect the linkage to be greater where the zygote is triply

TABLE II.

Female doubly heterozygous.

Mating	Number	Totals	Cross-overs
<i>SO . Sθ × Aθ . Bθ</i>	465	6	4
<i>Cθ . Sθ × Aθ . Bθ</i>	401, 405	72	41
<i>Aθ . Sθ × Aθ . Cθ</i>	192	59	32
<i>Cθ . Sθ × Aθ . Cθ</i>	406	26	13
<i>Aθ . Bθ × Aθ . Fθ</i>	178	7	4
<i>BC . θθ × Aθ . Fθ</i>	235	11	2
<i>Bθ . Pθ × Bθ . Cθ</i>	261	24	10
<i>Cθ . Cθ × Bθ . Cθ</i>	347	130	60
<i>Cθ . Fθ × Bθ . Cθ</i>	268	32	18
<i>Cθ . Sθ × Bθ . Cθ</i>	426	5	4
<i>Bθ . Cθ × Bθ . Cθ</i>	232	11	8
<i>Bθ . Qθ × Bθ . Cθ</i>	338	139	67
<i>Cθ . Fθ × Bθ . Cθ</i>	369	50	22
<i>Cθ . Pθ × Bθ . Cθ</i>	398	4	1
<i>Cθ . Pθ × Bθ . Cθ</i>	274, 275	89	39
<i>Jθ . Pθ × Bθ . Cθ</i>	463	254	112
<i>Bθ . Eθ × Bθ . Eθ</i>	291	10	4
<i>BC . θθ × Bθ . Fθ</i>	257	5	1
<i>Cθ . Fθ × Bθ . Fθ</i>	310, 311	47	17
<i>Bθ . Bθ × Bθ . Pθ</i>	197	49	21
<i>BC . θθ × Bθ . Sθ</i>	264	4	4
<i>Cθ . Sθ × Bθ . Sθ</i>	408	1	1
<i>Bθ . Bθ × Cθ . Eθ</i>	528	23	5
<i>Bθ . Cθ × Cθ . Fθ</i>	284	40	14
<i>Bθ . Fθ × Cθ . Fθ</i>	312	30	18
<i>Bθ . Cθ × Cθ . Fθ</i>	282	40	14
<i>Bθ . Cθ × Cθ . Pθ</i>	235	203	88
<i>Cθ . Cθ × Cθ . Pθ</i>	350	72	32
<i>Cθ . Sθ × Cθ . Sθ</i>	413	70	35
<i>Cθ . Cθ × Cθ . Sθ</i>	352	40	26
<i>Bθ . Fθ × Eθ . Fθ</i>	313	9	6
<i>Cθ . Fθ × Fθ . Jθ</i>	389	8	3
Totals		1570	726

heterozygous, as in $Bc\Theta . bC\theta$ (or $B\Theta . C\theta$) than where it is only doubly heterozygous, as in $bc\Theta . Bc\theta$ (or $A\Theta . B\theta$).

In Table II the offspring of doubly and triply heterozygous females is tabulated. Here there were 726 cross-overs out of 1570, giving a cross-over value of 46.2%. Where A was one of the factors concerned, or on the above hypothesis the females were only doubly heterozygous, there were 96 cross-overs out of 181, giving a cross-over value of $53.0 \pm 2.5\%$ (the true value is presumably under 50%). When A was not concerned, or the females were triply heterozygous, there were 630 cross-overs out of 1389, giving a cross-over value of $45.4 \pm 0.9\%$. Hence in the female also linkage appears to be stronger in triple than in double heterozygotes.

These results are confirmed by an examination of the families where both parents were of the same doubly (or triply) heterozygous composition. For example the matings 175, 176, and 177 (all $A\Theta . B\theta \times A\Theta . B\theta$) gave :

116 $BB\Theta$ and $BA\Theta$, 43 $AA\Theta$, 43 $BB\theta\theta$ and $BA\theta\theta$, 2 $AA\theta\theta$,

a typical F_2 repulsion series.

The type of linkage found is similar to though far less intense than that found by Nabours (6) in *Apotettix*, where cross-over values up to 12% were found in the female and much smaller values in the male. It is thus intermediate between the type found in *Drosophila* and *Bombyx*, where no crossing-over occurs in the digametic sex, and the type found in plants and mammals where the linkage is approximately equal in the two sexes.

Since according to Robertson (7) and Harman (8) the haploid number of chromosomes in *Paratettix* is 6 or 7, it is somewhat surprising that the loci of all the 15 factors so far discovered should be in one chromosome, which must be the case on Morgan's theory of linkage. Even if only I , S , and Θ were in different loci, the odds against finding three loci running in the same chromosome would be of the order of 48 to 1, though somewhat lessened by the unequal sizes of the chromosomes. This difficulty would be diminished if we assumed that the individual chromosomes were very rigid, but that moderate linkage occurred between chromosomes formed from adjacent parts of the spireme. This latter possibility is suggested by certain cytological observations.

The above deductions were only rendered possible by the unusual fullness of Nabours' published records, which enable the complete pedigree of any individual to be traced with the greatest ease.

SUMMARY.

Linkage between two Mendelian colour factors occurs in *Paratettix texanus*, the cross-over value being about 24% in the male, 46% in the female. This linkage is probably more intense in triply than in doubly heterozygous animals.

REFERENCES.

1. NABOURS, R. K. "Studies of Inheritance and Evolution in Orthoptera," I, II, III. *Journal of Genetics*, Vol. III. p. 141, Vol. VII. p. 1.
2. DEXTER, J. S. "Nabours' breeding experiments with grasshoppers." *American Naturalist*, Vol. XLVIII. p. 317.
3. STURTEVANT, A. H. "Genetic factors affecting the strength of linkage in *Drosophila*." *Proc. Am. Nat. Ac. Sci.* Vol. III. p. 555.
4. MULLER, H. J. "The Mechanism of Crossing-over." *American Naturalist*, Vol. L. p. 193.
5. GOWEN, J. W. "A Biometrical Study of crossing-over." *Genetics*, Vol. IV. p. 205.
6. NABOURS, R. K. "Parthenogenesis and crossing-over in the Grouse locust *Apotettix*." *American Naturalist*, Vol. LIII. p. 131.
7. ROBERTSON, W. R. B. "Chromosome Studies," I. *Journal of Morphology*, Vol. XXVII. No. 2.
8. HARMAN, M. T. "Spermatogenesis in *Paratettix*." *Biological Bulletin*, Vol. XXIX. No. 4.