

Some Remarks on Symbols, Multiple Allelomorphism, Crossing Over and Linkage Groups in The Silkworm

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SOME REMARKS ON SYMBOLS, MULTIPLE ALLE- LOMORPHISM, CROSSING OVER AND LINKAGE GROUPS IN THE SILKWORM¹

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I. REVISION OF SYMBOLS FOR TWO LARVAL MARKINGS

According to the nomenclature of genes in *Drosophila*, a recessive mutation is to be represented by a small letter or letters significant to the mutated character, and its normal allelomorph by the corresponding capital letter with or without the suffix of the small letters. Since 1917 I have followed this method of nomenclature, though a different scheme was used in my earlier works. For instance, the plain marking was represented by P, to which q was added whenever necessary to distinguish the plain from normal. Thus it is actually not P or p that distinguishes the plain from the other markings. This is at least confusing if not absurd especially when there are many recessive genes affecting the same organ as already pointed out by MORGAN (1913). It seems, therefore, desirable to revise the symbols for recessive larval markings, i. e. plain and quail. To make clear the history of changes, the symbols are listed below:

| Papers | Normal | Plain | Quail | Pale quail |
|------------------------------|---------|----------|---------------|----------------|
| TANAKA 1913a, b. 1914. 1915. | N | n | — | — |
| TANAKA 1916. | PQ | Pq | pQ | pq |
| New symbols | PQ | p | q | pq |
| Consequently, | | | | |
| | Striped | Moricaud | Striped quail | Moricaud quail |
| TANAKA 1916. | SPQ | MPQ | SpQ | MpQ |
| New symbols | S | M | Sq | Mq |

Bombyx mori has been domesticated for thousands of years, and no one can tell exactly the origin of our silkworms, though the wild mulberry silkworm is generally presumed to be their ancestral form. The wild mulberry silkworm is sometimes called *Theophila mandarina*, and sometimes *Bombyx mandarina*, but *Bombyx mori* var. *mandarina* seems to me better fitting as its scientific name. Besides the unsettled systematic position, the genetic characters of the wild silkworm are not yet fully worked out. It seems, therefore, more convenient, in *Bombyx*, to take the more common type as the standard, and the less common form as the mutant as BRIDGES and MORGAN propose (1923) for the cases where the wild type is unknown or not certainly known. Some important standard characters are compared to those of *mandarina*.

| | Standard form of <i>B. mori</i> | <i>Mandarina</i> form |
|---------------------------------|---------------------------------|-----------------------|
| Larval marking | Normal | Moricaud |
| Blood color | Colorless | Light yellowish |
| Cocoon color | White | Light green |
| Voltinism | Univoltine | Polyvoltine |
| Number of molts before spinning | Four | Four |
| Skin | Opaque | Opaque |

Determination of the standard form may sometimes be arbitrary, because we can not say which larval marking, "normal" or "plain," for example, is really more common in the world. It is, however, true that we can pick the more common type as the standard without difficulty in majority of cases.

II. MULTIPLE ALLELOMORPHISM

Special relations between four larval markings, striped, moricaud, normal and plain described in my previous papers (1913b, 1914) were pointed out by STURTEVANT (1915) as they form a series of multiple allelomorphs. Though I adopted the explanation by complete coupling and repulsion in my paper of 1916 as I did in the preceding work, I have later accepted the idea of multiple allelomorphism for this case. The students of *Drosophila* make use of exponents to denote multiple allelomorphs, as w^e , e^s etc. for example. But I am, for the time being, content with the use of the simpler expressions, S (striped) and M (moricaud) instead of symbols p^s and p^m .

III. CROSSING OVER VALUE

It may be somewhat useful that the phenotypic ratios published in my previous paper (1916) to be expressed in terms of the crossing over

value. As there is no crossing over in the female sex in *Bombyx*, the cross over value in diheterozygous males may be calculated from F_2 results by the following formula, in which k , l , m and n represent the numbers of individuals belonging to AB, Ab, aB and ab F_2 phenotypes.

$$\text{Cross-over value} = 1 \div \left\{ \frac{k+n}{2(l+m)} + 0.5 \right\} \times 100$$

This formula is available for F_2 ratios in "coupling" only, while in case of "repulsion" the F_2 ratio is uniformly 2 : 1 : 1 whatever the linkage value may be (TANAKA 1916), which makes calculation of cross-over per cents impossible. The crossing over per cents are to be obtained only through back-crossing, when two dominants are introduced from different parents.

a) Striped-yellow linkage.

| | SY | Sy | sY | sy | Totals | c.o. % |
|--------------------------|-------|------|------|------|--------|--------|
| "Coupling" { Back cross | 4421 | 1631 | 1735 | 4418 | 12205 | 27.58 |
| { F_2 | 10958 | 1075 | 1101 | 3017 | 16151 | 26.95 |
| "Repulsion" (back cross) | 112 | 338 | 372 | 119 | 941 | 24.55 |
| Weighted mean of c.o. | | | | | | 27.22 |

b) Moricaud-yellow linkage.

| | MY | My | mY | my | Totals | c.o. % |
|--------------------------|-------|------|------|------|--------|--------|
| "Coupling" { Back cross | 3053 | 1030 | 1057 | 3129 | 8269 | 25.24 |
| { F_2 | 10512 | 873 | 858 | 2949 | 15192 | 22.78 |
| "Repulsion" (back cross) | 86 | 453 | 483 | 104 | 1126 | 24.02 |
| Weighted mean of c.o. | | | | | | 23.66 |

c) Plain-yellow linkage.

| | PY | Py | pY | py | Totals | c.o. % |
|--------------------------|------|-----|-----|-----|--------|--------|
| "Coupling" { Back cross | 719 | 207 | 186 | 614 | 1726 | 22.77 |
| { F_2 | 3361 | 376 | 294 | 910 | 4941 | 27.12 |
| "Repulsion" (back cross) | 280 | 827 | 756 | 222 | 2085 | 24.08 |
| Weighted mean of c.o. | | | | | | 25.54 |

As the genes S, M and p are multiple allelomorphs, they ought to be all the same in cross over percentage, but there is actually remarkable deviation from expectation. This is, however, not astonishing when we take into consideration the fact that very different numbers were obtained from back-crossing and F_2 results even between the same genes. For instance, crossing over value calculated from back-crossing in p-Y linkage is 22.77, while that derived from F_2 figures is 27.12, showing a difference of 4.35%. KOGURE (1926) studied, in my laboratory, on the crossing over variation between S and Y, and discovered the existence of a

dominant modifier which partly suppresses crossing over between them and reduces it as low as 12%. He finds also that the crossing over percentage is influenced by the room temperature where the heterozygotes were reared: the average crossing over value of his "high crossing over" strain was 21.48 in about 30° C, while it was 25.86% in about 19°C, and some intermediate figures were obtained in intermediate thermometric degrees. The weighted mean of cross-over per cents between Y and the locus of p, S,M is 25.6 in my experiments.

IV. LINKAGE GROUPS AND CHROMOSOME MAPS

Four linkage groups have hitherto been described in the silkworm. They are as follow:

| Linkage groups or chromosomes | Genes contained | Authors |
|-------------------------------|-----------------|----------------------------------|
| I (Sex-chromosome) | os | TANAKA (1921), NISHIKAWA (1922) |
| | e | TANAKA (1924) |
| | od ² | TANAKA (1926) |
| II | S,M,p,Y | TANAKA (1913b, 1914, 1915, 1916) |
| III | Z,I | OGURA (1922) |
| IV | sk,L | TANAKA and MATSUNO (1927) |

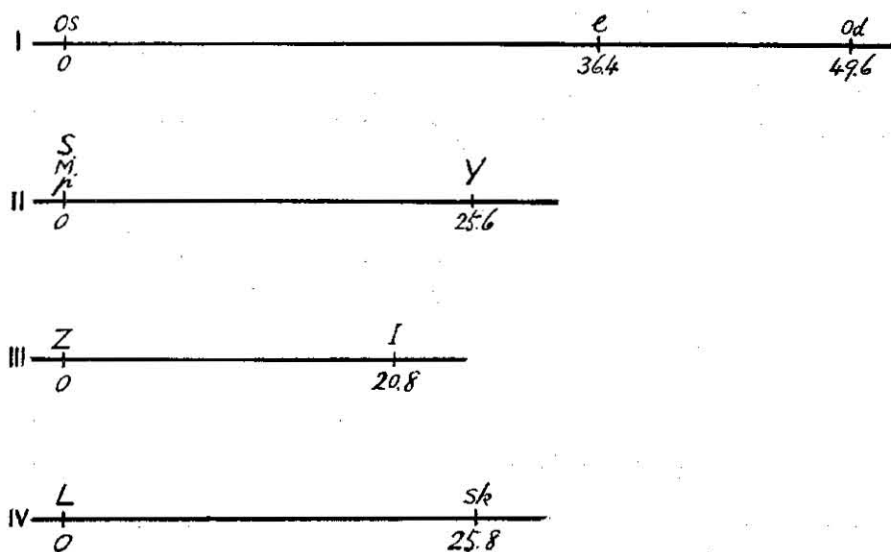


Fig. 1.

Chromosome maps I to IV in the silkworm.

² The description in English will soon appear.

A few more possible cases of linkage are known to me at present, but they have not been fully worked out.

The chromosome maps of the silkworm are drawn on basis of published data, taking the cross-over per cents as units as such.

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