Genetic analysis of modifier variability in Drosophila subobscura

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Summary. The previously detected modifier variability acting on the expression of the Bare (Ba) locus in Drosophila subobscura is demonstrated to be due to polygenes situated along the chromosome O. From crosses between isogenic lines of high and low modifier effect we ascertained the presence of approximately 5 modifier loci.

Modifier variability is one type of genetic variability frequently used to explain many evolutionary changes which cannot be understood by considering only structural loci. In spite of the great modifier variability acting on the expression of structural genes that has been found, little research has been devoted to the quantification of this type of variability in natural populations. With this in mind, we have studied the modifier variability in one of the chromosomes of Drosophila subobscura (the so-called O chromosome) in a natural population, inasmuch as it affects the expression of the dominant morphological mutant Bare (Ba). This mutant is precisely located on chromosome O of this species, and its phenotypic effect is to reduce variably the number of bristles.

The problem that arises is to define whether the variability we have studied is mainly due to the structural locus (isoallelic variability in wild O chromosomes) or to typical modifiers, namely allelic substitutions in loci on the chromosome O other than the Ba locus (polygenic loci). Although, in general, quantitative genetic variation is described in terms of typical polygenes, the possibility is not excluded that isoallelic variation constitutes an important component of this variation. Thus, Green has found several wild-type isoalleles acting on the eye color of Drosophila melanogaster, and Milkman and Scharloo have detected some isoalleles involved in several selection experiments. On the other hand, Thompson found that ci* (cubitus interruptus) isoalleles did not contribute to quantitative variability of veinlet expression.

The genetic basis for the variability we are studying could be established by considering that the effects of recombination on isoalleles at the Ba locus and on polygenic loci distributed along the chromosome O must be very different. If modifier variability of the wild O chromosomes is mainly due to polygenic loci, crossing over between chromosomes of high and low modifier effect will produce several recombinant chromosomes which will present intermediate modifier effects. On the contrary, if isoalleles at the Ba locus are principally responsible for the variability, crossing over between the 2 chromosomes will not be able to produce chromosomes of intermediate modifier effect and a bimodal distribution corresponding to the 2 parental chromosomes will arise.

To test these arguments, we performed an experiment with isogenic lines for the chromosome O of high and low modifier effect (lines 220 and 57, respectively). First of all, we obtained +220/+57 heterozygotes, which were mated with individuals of the balanced lethal Va/Ba strain (Va = Varicose, a dominant wing venation mutant) in 2 different ways, separately: via male and via female crosses (fig.1). In both via male and via female crosses, a single Va/+ male of the offspring was mated to Va/Ba females, and the bristles of 40 Ba/+ and 40 Va/Ba progeny individuals were counted (fig.1). 12 bristles per individual
(4 dorso-centrals, 4 scutellars, 2 supra-alars and 2 post-alar) were considered in our experiment. The difference (D) in mean number of bristles between Bα+/ + and Vα/Bα (control) individuals was used as a measure of the modifier effect of the chromosome O. A total of 83 Vα+/ + males were studied: 40 from via male and 43 from via female crosses. The results obtained (fig 2) show a clear bimodal distribution of D-values with only 2 classes in the via male crosses (absence of crossing over in the male), while several intermediate classes corresponding to the recombinant chromosomes appear in the via female crosses. These results clearly demonstrate that the modifier variability acting on the Bα locus is mainly polygenic, i.e., due to several loci situated on the chromosome O. However, this conclusion does not fully exclude the possibility that isoalleles at the Bα gene can effectuate a slight contribution to the modifier variability of the natural population studied.

Another interesting question is to define the number of polygenes or effective factors determining the modifier variability we are considering. Recently, a controversy on the number of polygenic loci involved in quantitative genetic traits has arisen and the problem remains an open question today. Thus, while Thoday and Thompson 16, and Thompson 17–18 have argued that many continuous distributions could be explained by segregation at a few loci, Vetta 19 has defended the common hypothesis that quantitative variation is produced by segregation in a large number of loci. The distribution of our D-values of chromosomes from via female crosses can be interpreted in terms of 6 discrete classes, as can easily be observed in figure 2. This is confirmed by y2 tests of heterogeneity 14, which were performed by using the variance of D-values from via male crosses as an estimate of the parametric variance. With a minimum of 6 classes these tests do not detect statistical significance inside each class. On this basis, a model of 5 polygenic loci could explain the distribution we observe. This assumption is consistent with an experiment on the location of modifiers that we have performed by using Thoday’s method 19 (unpublished results), which detects 5 effective factors distributed along the chromosome O. If these conclusions become definitive, we could explain the modifier variability of wild O chromosomes affecting the expression of the Bα gene in terms of a relatively small number of modifier loci.

Finally, we would like to point out that modifier variability and the main locus on which this variability is acting, could be considered as a particular case of a multilocus system. In the last years, multilocus systems have attracted the attention of many workers 20–23 as an alternative to the single gene as the unit of selection. Unfortunately, it is not easy to find other alternative units on which evolutionary forces could be operating. However, modifier systems could probably constitute evolutionary units themselves, and they could be analyzed with relatively little effort. The results reported in this article constitute an attempt to characterize such a system in preparation for further studies. On this basis, we are presently investigating the question of where selective forces are operating within a modifier system, in the hope of finding out whether selection is principally acting on modifiers of major genes, or whether selective changes are occurring primarily on the major genes themselves.

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4 J. N. Thompson, Genetics 52, 521 (1954).