

THE INTERSEXUAL MALES OF THE BEADED MINUTE
COMBINATION IN *DROSOPHILA MELANOGASTER*

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Dr. A. H. Sturtevant kindly sent me a copy of the manuscript of his paper on the Beaded Minute males of *Drosophila melanogaster*. He holds that these males described by me as intersexual males are not real intersexes, but products of rudimentation of the genital and anal discs. There is no doubt that many individuals might be described this way if they stood alone. But this is also true for many triploid intersexes of Dobzhansky's classes I-III (Dobzhansky, 1930). Actually, these types are only one in a series of morphological changes which indicate clearly that we are dealing with male intersexes. It seems that, by chance, Sturtevant met only with the one type which usually, though not always, is the most frequent one. Detailed statistics on the frequency and genetics of the different types will be published in time together with the necessary illustrations of all the types, grades and transitions.

It should be stated first that the lower grade Bd-M intersexes are different from the triploid intersexes (Dobzhansky's classes I, II). Both the anal plates and the type of reduction of the armature are very different. Sturtevant is much impressed by this fact. But it should be pointed out that, thus far, the only male intersexes available for comparison are the triploid ones. For female intersexes a number of different strains are known, all of which have their specific features, which show that the details of intersexual transformation vary with the different genetic backgrounds. Thus, I cannot regard the triploid intersexes as an absolute standard of intersexual structure. But it is a fact that the internal structure of the Bd-M intersexes is exactly the same as that described by Dobzhansky for the triploids of his classes I-III. Unfortunately, the higher classes of intersexuality are rather rare in the Bd-M case.

As Sturtevant mentions only the one type of intersexuality which I call the "reduction type" it should be proved first that this type is also actually an expression of intersexuality in which the reduction and final disappearance of the male genital armature is more prominent than the secondary appearance of female characters. This type is a combination of two phenomena, namely, the reduction and disappearance of the anal plates and that of the genital armature proper. It is the conspicuous reduction of the anal plates found in this type only, but absent in the other types, which led Sturtevant astray. I think that his statements and interpretations are correct as far as the anal plates are concerned. In a rather good correlation with the intensity of the Bd-M effect upon the males, the anal plates and even the

abdominal tip are reduced in a part of the females, and some not Beaded-Minutes may show this also. But it will be shown below that the involution of the anal plates is independent of the reduction of the genital armature. In the reduction type, now under discussion, the genital armature is retracted and found (if not completely lost) below the surface, in conditions which indicate that it had developed to a certain degree—all degrees from completeness to total absence—and then stopped growing. (This includes also stoppage at different times of the well-known 360° rotation in the pupa.) These conditions parallel closely those described by Dobzhansky for the triploid intersexes, although not in every detail. The highest grade of this reduction type is characterized by a rather large abdomen without any genital structure at the tip. As obviously the entire disc region degenerated early, no further female differentiation is possible. But in less extreme grades (called in my work class III) the disc is still present below the integument, and in this stage I twice found (in not too many dissections of this specific type, as yet) individuals with rudimentary testes, without any male ducts, but with a complete vagina with its characteristic histological differentiation, and with a ventral receptacle complete in one, not perfect in the other case. In the higher grades of this type, hairs are found rather frequently on the 7th sternite. This is a female character. Examination of innumerable normal brothers of the same genetic constitution never showed this phenomenon.

A second type of intersex appears rather irregularly in the F_1 and F_2 broods. In our earlier work it was just as frequent as the reduction type in certain Bd-M combinations. Recently it was found rather rarely, indicating that specific modifiers may control these types. (All types may appear in the same brood. Statistics will be published in time.) In this second type there is no degeneration of the anal plates. Instead, they even hypertrophy. They grow out beyond the tip of the abdomen into two large plates which frequently unite dorsally (a female trait). The dorsal part of the genital arch to which the plates are attached is also pushed out as a socket, which, if sufficiently large, develops hairs of the type of the female 8th tergite, which it clearly represents. The genital armature proper undergoes the same stages of reduction as described for the first type until the ventral side of the abdomen below the large beak-like protruding anal plates is free of differentiations. In still higher grades this ventral surface becomes depressed and forms a deep cup. In more extreme individuals, the anterior lip of the cup-like depression grows backward until only a curved slit remains. In the only three dissections of this type made thus far the bottom of the covered cup was found to have the histological structure of the vagina (uterus) and is therefore considered as the secondary invagination of a vagina. (I agree with those authors who think the vaginal disc is not identical with the male disc.)

A third type, which we call the direct type is rather frequent in its lower grades, but thus far rather rare in the higher grades. It represents a simple and direct transformation of the male abdominal tip into an almost female one. There are, of course, also transitions and combinations between the three main types, e.g., degeneration of the anal plates with progressive differentiation of the female segment. The only male parts to become rudimentary in this type are the claspers and the penis, which assume very characteristic shapes during this process. The first step is the fusion of the two ventral tips of the genital arch with their characteristic tufts of hair into a single median one, which protrudes as a knob. The genital arch then broadens and becomes oriented as an 8th segment. The possibility that a 9th segment is involved will be discussed another time. The knob becomes larger and is transformed into a protruding structure—still with the tufts of hair—resembling the female abdominal tip and assumes the spatial relation to the anal plates typical of the female. Finally the genital arch forms a typical female eighth (or 8th and 9th?) segment with its normal pigmentation and arrangement of hairs. Also, the tuft of hairs on the "knob" scatters over the sternite. In one such extreme type the anterior surface of the knob carried a disc which might have been a vaginal disc or the anlage of the vaginal plates. Only rarely are the anal plates arranged in a dorsal and ventral position, as in females.

An accurate record of these facts requires many illustrations which will be published when all dissections are completed. It should be added that in these experiments thousands of brothers of the intersexes of other genetic constitutions, i.e., Bd or M or neither, were constantly watched as controls without a single case of intersexuality or reduction of the genital armature occurring. There is no doubt in my mind that the types described are male intersexes, which leaves the theoretical considerations which I made in my earlier paper (Goldschmidt, 1948) and in another one now in press (Goldschmidt, 1949) as they were originally formulated.

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