

orbit, temporal and nasal regions, and the visceral arch derivatives are considered separately. The author publishes, for the first time, two new views of the skull of a twenty-millimeter embryo which combine numerous interesting relations. It is a pity that the details of these figures are not better shown in the half-tones. Anatomical illustrations are being steadily improved, and this is shown in many figures in this edition; but far more care is yet required in both the printing and selection of suitable paper, before the standard of German editions can be approached. The chapter closes with an extended account of the ossification of the individual bones of the skull.

The development of the muscular system is described by W. H. Lewis in about seventy pages. We find this an excellent account, well planned and comprehensive, while at the same time concise and logical. The influence of a participation on the part of the writer in embryological studies of an experimental nature is quite evident and gives a modern point of view.

The chapter is well illustrated, many of the figures being original, and some published here first. It is possible to obtain from them and the text a good idea of the origin and development of the various muscle groups. The author's contributions to the development of the muscles of trunk and limbs, and more recently of the head, tongue and larynx, are outlined here with figures from his new models. Futamura's striking series of pictures representing the stages of spreading of the facial musculature forms an interesting feature.

Only twenty-four pages are allotted to the last section, including the septum transversum diaphragm, and the coelom, but the subject is brought up to-date by Mall with the aid of new investigations in addition to his previous extensive studies and the conditions found in a number of recently described young human ova. Broman's work is also incorporated to advantage.

One praiseworthy feature is the extensive bibliography at the end of each chapter.

Though the printing of the illustrations and the general make-up of the German edition is decidedly superior to the English, the American publishers have, on the whole, succeeded in making the volume a creditable one. The second volume, now in press, will be anticipated with much interest.

H. MCE. KNOWER

CINCINNATI, OHIO,
February 18, 1911

SPECIAL ARTICLES

THE ORIGIN OF NINE WING MUTATIONS IN *DROSOPHILA*¹

IN the following preliminary report I wish to put on record some of the principal wing mutations that have appeared in cultures of the fruit fly, *Drosophila ampelophila*. In another communication I shall describe five mutations in eye color that have been found in the same cultures, and their modes of inheritance. The theoretical questions involved must be deferred until the complete data can be published. These mutations have appeared in such rapid succession that my time has been almost entirely consumed in producing pure strains of the new forms, which can be utilized later for a thorough study of the inheritance of the new types. I wish here merely to call attention to the fact that while most of the new types breed true from the start, others do not; and also to the fact that while certain of the mutations are sex-limited other mutations involving the same organs do not show this form of inheritance. It may appear that we have here an opportunity to learn something further of these different modes of inheritance appearing in the same animal. One fact especially will impress itself on any one who follows the history of these new types, viz., the "segregation" of the characters, and in most cases the absence of intergrades.

Beaded Wings.—In May, 1910, a number of flies, pupæ, larvæ and eggs of *Drosophila* were subjected to radium rays. One fly was pro-

¹ The main facts in this paper were given before the American Society of Zoologists, December 29, 1910.

duced, the marginal vein of whose wings was beaded. Bred to his sisters, the beaded condition appeared in one fly in sixty of the next generation. The beaded flies were inbred and produced in the third generation, one beaded winged fly to thirty-five normal. The beaded flies produced in the next generation one beaded to twelve normal wings. The same process continued through many generations has finally produced stock that gives in certain cultures nearly 100 per cent. beaded wings.

Not only has selection slowly increased the percentage of abnormal wings, but much more extreme forms of the same variation have appeared, and an attempt is now being made to fix some of these extreme variations.

When a beaded male of the stock in its present condition was bred back to the wild females the beaded condition appeared in one fly in twelve of the first generation. In the second generation from non-beaded flies the proportion was one to twenty.

In the further course of the experiment eight other modifications have appeared that are undoubtedly mutations; one confined largely to females, some of the others showing strictly alternate inheritance, combined with "sex-limited transmission." These modifications may be described under the following headings.

Truncated Wings.—The normal wings of *Drosophila* are longer than the abdomen, extending for about one third their length beyond the end of the body. The wings have a rather pointed end. In the seventh generation of the beaded wing stock a fly appeared with the end of the wings cut off nearly squarely, and indented at the end or somewhat scalloped. Bred to sister flies there were produced in the next generation twenty-one flies with truncated wings to 230 with normal wings. In the next generation some of these truncated winged flies produced nearly 50 per cent. of flies with truncated wings. It has proved difficult to pass beyond this point, although certain of the later cultures have produced over 90 per cent. of truncated winged flies. This high average has not, however, been maintained in the next generation. There are

indications, nevertheless, that the inheritance may be raised even to this high standard. Two main points of interest have appeared in the breeding of this modification. First, the condition is confined almost exclusively to the female line. A comparison of many cultures shows that the offspring of truncated parents consist of almost equal numbers of males and females with normal wings, while the truncated winged forms are, as stated, confined almost exclusively to the females. The deficiency of males in the entire culture is due, therefore, to the absence of males with truncated wings. Yet such males appear in small numbers, and especially in cultures in which truncated males are the fathers of the next generation.

Secondly, by selecting the shortest-winged individuals in each generation the wings have been reduced in some cases until they are not longer than the abdomen, and in a few cases they were even much shorter than the abdomen, and are not superficially different in this respect from the type to be next described, although in their inheritance they follow an entirely different procedure. The character can not be said to be sex-limited to the female in the conventional sense. When a female with truncated wings was bred to a normal wild male all of the offspring in the first generation had long wings. These inbred produced in the second generation 1,826 normal flies to 36 truncated individuals, males and females. When a truncated male was bred to a normal wild female all the flies in the first generation were normal, and in the second generation, when these were inbred, there were produced 1,408 normals to 14 truncated males and females. These facts indicate that this condition is not connected with sex-limited inheritance, although other wing modifications, as will be shown, are intimately connected with sex transmission. It should be added that normal winged flies of this modified stock throw a high, though variable, percentage of flies with truncated wings.

Rudimentary Wings.—In the second generation of the beaded winged flies a male ap-

peared with wings shorter than the abdomen. The square, short wings were broad and often blistered; in individuals obtained later their ends were crenated at times as though incompletely unfolded, but at other times the ends were quite even. This fly, bred to his sisters, reproduced the same condition in a few of his male offspring, and in closely related stock a few males of this kind appeared in successive generations. By repeated intercrossing a large number of these males have been produced and some females. It is important to note that although I have paired numbers of these males and females together I have obtained offspring in only a very few cases and these were all normal flies. Inbred these normal flies have produced 964 normal males and females; 6 short winged males and 2 females. Whether the original short winged females were virgins may appear doubtful from these facts. On the other hand the males and females with rudimentary wings are fertile, both with wild flies and with the mutations to be next described. The frequent failure to obtain fertile eggs from pairs of flies with rudimentary wings may seem therefore to indicate that this combination is generally sterile, but whether because the eggs are not fertilized or being fertilized do not develop is uncertain. This point is being further investigated. The extraordinary deficiency of individuals of this class in the second filial generation (see below), may be due to the same causes that account for the deficiency when inbred. Similar deficiencies, though not so extreme (see the second generation of white-red eyed and black-yellow crosses), run through nearly all of the results with my new races.

If a male with rudimentary wings is bred to normal females of *the original stock* all of the offspring have long wings. These inbred produce variable percentages of long and rudimentary wings. A partial census of the results gave 5,850 normal wings to 83 males with rudimentary wings. No intermediate types appeared. Later several males with rudimentary wings were bred to a new *wild stock*. The offspring had long wings. These flies inbred produced in the next generation

8,459 normals, males and females, and only 32 males with rudimentary wings. The experiments show that the condition of rudimentary wings is sex-limited. By suitable combinations this sex-limited character has been combined with another sex-limited character, viz., white eyes. The theoretical questions involved in such a combination have been discussed elsewhere.²

Miniature Wings.—In the seventh generation of the beaded wing stock a fly appeared with wings like the normal in form, but extending no further than the end of the abdomen. Flies with wings of this kind are much more viable than those with rudimentary wings. Pure cultures of thousands of individuals are now on hand. The character also shows itself to be sex-limited. Many combinations between these flies and those with other modifications have been made. Only a few of these can be now mentioned. Miniature wings have been combined with the white eyes, also a sex-limited character.

If a male with miniature wings is crossed with a wild female all of the offspring have long wings. These inbred have produced 409 flies with normal wings, males and females, and 178 *males* with miniature wings. No females with miniature wings appeared in the second generation. Miniature wings are, therefore, sex-limited in inheritance. The reciprocal cross, viz., females with miniature wings by wild males, gave in the first generation 50 females with normal wings and 51 males with miniature wings. Evidently the male-producing sperm of the wild fly does not carry the character essential for the formation of long wings. This same spermatozoon also lacks, as I have tried to show, one of the factors essential for the formation of red eyes, likewise a sex-limited character. The F_1 flies, inbred, produced 785 normal males and females (in approximately equal numbers) and 827 flies with miniature wings, of which 430 were females and 397 were males. This result gives the expectation for this combination.

² *Proc. Soc. Experimental Biology and Medicine*, Vol. 8, October, 1910, and *American Naturalist*, February, 1911.

It will be noted that the flies with miniature wings are even more numerous in this generation than the normal flies. Their chances for development are therefore at least equal.

Balloon Wings.—Occasionally flies have appeared, especially in the truncated winged stock, with each wing swollen up into a balloon or bladder filled with fluid. When these become dry the walls collapse and form flat plates that are carried at right angles to the body. Some of these flies have been isolated and have produced practically pure stock with the character present in all of the individuals, and this condition has been carried through two generations. The flies are exceedingly active and look like small X's running about in the bottles. They can not of course fly. They seem to be very sterile and produce only a few offspring, but nevertheless I have more than a thousand of these flies alive at present.

Albino Flies.—Several times flies have appeared that failed to develop black pigment in the body. The eyes were red, *i. e.*, unmodified by the lack of body pigment. One of the albinos had white eyes, it is true, but it arose in white-eyed stock, so that the colorless eye bore no relation to the absence of pigment in the body. The wings of these albinos were almost white with a faint brownish edge. The hairs of the body were brown instead of black. Although some of these flies lived for nearly a week they left no offspring. When the normal fly emerges it lacks pigment except in the eyes.

Melanistic Flies.—In some of the crosses between wild flies and those with miniature wings there have appeared in the second generation some flies, males and females, with black wings. The veins of the wings are broad and conspicuous. Pure stock of these flies was easily, and at once produced. The dark color is not confined to the wings, but the entire body is black. The type is clearly a melanistic variation of *Drosophila*. Crossed with wild stock the flies of the first generation are intermediate in color between the black and the normal type. The color does not seem to be sex-limited in relation to the normal, so far as the experiments have been carried.

Yellow Wings.—A male appeared in the black-winged stock with golden yellow wings. In fact, the entire fly is conspicuously yellow, and makes a striking contrast with his dark companions. He was bred to his black sisters, and gave only black flies in the first generation. These were inbred and have produced 233 black females, 127 black males and 76 golden-winged males. Evidently the color is sex-limited in relation to the melanic type from which it arose. The same, or a similar mutation, has appeared again in a stock not related to the first, except in so far as both came originally from flies with miniature wings. As yet only males have appeared. These have given in the first generation (when crossed to their normally colored sisters) normal flies.

Wingless Flies.—Occasionally flies appear without wings, but this character is not inherited, as a rule, and is due to some difficulty in unfolding the primordia of the wings. But in some of the stock of truncated wings I have obtained a considerable number of flies with tiny scales in place of wings. In one culture there appeared 11 flies with scales, instead of wings, amongst 125 winged flies. Although this stock is very sterile it seems not improbable that, in time, a wingless fly can be produced.

T. H. MORGAN

COLUMBIA UNIVERSITY

THE NATIONAL CONFERENCE COMMITTEE
ON STANDARDS OF COLLEGES AND
SECONDARY SCHOOLS

THE fifth annual meeting of the National Conference Committee on Standards of Colleges and Secondary Schools was held at the rooms of the Carnegie Foundation for the Advancement of Teaching, 576 Fifth Avenue, New York, N. Y., on Saturday, January 28, 1911.

All the organizations which send delegates to the conferences of this committee were represented, those in attendance being as follows:

President George E. MacLean, The State University of Iowa, representing the National Association of State Universities.

Headmaster Wilson Farrand, Newark Academy, representing the College Entrance Examination Board.