

GENETIC DATA ON *DROSOPHILA AFFINIS*, WITH  
A DISCUSSION OF THE RELATIONSHIPS  
IN THE SUBGENUS SOPHOPHORA

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INTRODUCTION

*DROSOPHILA affinis* Sturtevant is a member of the subgenus *Sophophora* (STURTEVANT 1939), closely related to *D. athabasca*, *azteca*, *algonquin*, *narragansett*, and *seminole* (STURTEVANT and DOBZHANSKY 1936b). Cytologically, all the members of this group (*seminole* has not been examined) are aberrant in the subgenus in that they have—in addition to a large V-shaped X chromosome and a small dot-like autosome—three two-armed autosomes (V-shaped or J-shaped—see figure 1). The short arm of one of the J's appears to be wholly heterochromatic, but there remain five autosomal euchromatic arms in addition to the dot—that is, including X and the dot, a total of eight. This was shown by MILLER 1939, for *algonquin*; for *azteca* and *athabasca* this conclusion rests on unpublished information communicated by PROF. T. DOBZHANSKY and MR. E. NOVITSKI. In most other members of the subgenus (*melanogaster*, *pseudoobscura*, *subobscura*, etc.), the total number of euchromatic arms is six. As indicated later in this paper, the European *obscura* probably agrees with the *affinis* group, *ananassae* has an extra X-arm, and in *willistoni*, *earlei*, and their relatives the dot has disappeared. The study of mutant genes in *affinis* was undertaken in order to throw some light on the relation between the distribution of genes in the *affinis* configuration and that in the other members of the subgenus.

MATERIAL

*D. affinis* occurs in the eastern United States, from central and southern Texas, to southeastern Kansas, the southern shores of the Great Lakes, Massachusetts, and the central portion of the Florida peninsula. Along its northern boundary *affinis* is gradually replaced by *athabasca* (subspecies *mahican*), along its western boundary (at least in Texas) by the ecologically similar *pseudoobscura*—these two species themselves showing a similar replacement along a zone from British Columbia to Colorado (STURTEVANT and DOBZHANSKY 1936b). *D. algonquin* is found along the whole western and northern replacement zone for *affinis*, being present, so far as known, only in areas where *affinis* occurs along with either *pseudoobscura* or *athabasca*. The *affinis-athabasca* replacement zone is also occupied by

*D. narragansett* (Woods Hole, Massachusetts; Darien, Connecticut; Ithaca, New York; Wooster, Ohio). *D. seminole* is known only from southern Alabama, deep within the range of *affinis*. It will not be surprising if the ranges of *D. azteca* and *affinis* are found to overlap on one side or the other of the Rio Grande. Thus this species is in contact, or nearly so, with all the other known members of its group, a relation scarcely possible for any of the others, since *seminole* at least seems very unlikely to occur with any of them.

Two subspecies of *D. affinis* have been recognized (STURTEVANT and DOBZHANSKY 1936b), the typical one being lighter in color and more southern in distribution than the subspecies *iroquois*. Study of a large series of living strains from many parts of the range shows that, in fact, southern strains average lighter in color than northern ones. However, both extremes of color may be found throughout the range, and there is no trace of cross-sterility or of any associated differences between the types. The few attempts that have been made to study the inheritance of the difference have not been encouraging. There is so great an age and environmental effect on the character as to make it very difficult to work with. For present purposes it has seemed simplest to ignore the subspecific distinction entirely.

The wild strains used in the present study have come from many regions, and many of them have been collected by friends. I am especially indebted to PROF. J. T. PATTERSON for material from Texas and Louisiana, to PROF. W. P. SPENCER for material from Kansas, Missouri, Tennessee, Ohio, and western New York, and to DR. D. F. POULSON for strains from Maryland and Connecticut. My own collections have been from Massachusetts and Alabama. The wild females have been brought in, and  $F_2$  generations reared from each one separately. In this way a number of mutant types have been isolated; others have appeared in old strains and in experiments concerning the linkage relations of previously found types.

There follows a catalogue of the mutant types studied, arranged by chromosomes, together with a discussion of the possible parallelism of each to types known in other species.

#### MUTANT TYPES

##### *Left limb of the X chromosome*

bobbed. Found in a wild strain originally from Chautauqua, New York. Bristles small, abdominal tergites with rather few bristles and with etched margins. Resembles the bobbed of *melanogaster*, *simulans*, *pseudoobscura*, etc. (see LÜERS 1937). So far as tested, the Y chromosome is without effect on the bobbed character, there being no noticeable sexual dimorphism for it. Y chromosomes from Massachusetts, New York, Tennessee, and Kansas have been studied. Bobbed females have been sterile so far as tested.

cut. Found in a wild strain originally from Woods Hole, Massachusetts. Wings with nicks in margin; often extreme, sometimes overlapping wild type, especially in females. Often the humeri are more separate from the mesonotum than usual, suggesting epaulets. Except in this last respect the character is much like the beaded of *pseudoobscura*, and also resembles cut of *melanogaster*.

pebbled. Found in experiments with a cut vermilion chromosome. Wing surface coarsely granular. Often of low viability and fertility, but is easily kept in one homozygous strain that apparently happens to have modifiers favorable for it.

scute-1. Arose in linkage experiments. Resembles the scutes of *melanogaster*, scutellar of *pseudoobscura*, etc. Both scutellar bristles are usually absent, and the anterior and middle orbitals are often absent. In some cultures a dorsocentral is also missing. The character is variable, and sometimes overlaps wild type, especially in females.

scute-2. Arose in experiments involving scute-1, and was at first confused with it. Resembles scute-1, but is less viable and fertile, and less frequently affects the dorsocentral bristles.

stubby. Found in linkage experiments. Bristles slightly shortened and curved. Perhaps a slight allele of either forked or singed (*melanogaster*, *simulans*, *pseudoobscura*, and other species).

vermilion. Arose in the cut stock. Quite similar to the vermilion of *melanogaster* and other species. MR. C. W. CLANCY tested it for me by the feeding technique of BEADLE and LAW (1938), and reports that it lacks the  $v^+$  substance that is present in wild-type *affinis* (vermilion brown *melanogaster* larvae were used as test material). There can therefore be no doubt of the identity of the locus.

white-1. Arose in the same culture as scute-1, but in the other X of the mother of that culture. Eyes completely white, as in the well-known types of *melanogaster* and other species.

white-2. Arose in a scute-1 scarlet chromosome. Completely white eyes, allelic to white-1.

#### *Right limb of the X chromosome*

ascute. Two males were found in a linkage experiment. Resembles ascute and grooveless of *melanogaster* or of *pseudoobscura*.

hairy. Found in a strain from Gatlinburg, Tennessee. There are a few hairs on the dorsal surface of the scutellum. The character is variable; often only one hair is visible, and sometimes the specimens look wild type. In many crosses some of the heterozygous females have one or two of these hairs present. The resemblance to hairy of *melanogaster* would be of doubtful significance were it not in agreement with the other parallels in this arm.

hairy-2. Found in linkage experiments with cut and scarlet. It is indistinguishable from hairy-1, and allelic to it.

scarlet. Arose in a cut vermilion stock, where its presence was only detected as a result of apparent inconsistencies in linkage experiments, since vermilion, scarlet, and vermilion scarlet are indistinguishable in eye color. The resemblance to scarlet of *melanogaster* or *pseudoobscura* is clear.

sex-ratio. Found frequently in wild strains from various localities (Woods Hole, Massachusetts; Coffeyville, Kansas; Gatlinburg, Tennessee—see STURTEVANT and DOBZHANSKY 1936a). This gene is not easy to study in *affinis*, since its expression is variable; males carrying it often give essentially normal sex-ratios, yet descendants carrying the same X may give large families with few or no sons. For this reason statistics concerning the frequency of the gene in wild populations are of little value. Sex-ratio has been found associated with only one of the two sequences referred to below (the inverted one); it remains uncertain whether it is always present in chromosomes having that sequence.

tilt. Found in the original white-1 chromosome. The wings are often curved upwards slightly at their tips, but a more useful index is the presence of extra veins between the second and third longitudinal veins at about the level of the anterior crossvein, the two longitudinals often being fused here into a knot. The character is variable, frequently overlapping wild type, especially in females. Resembles tilt of *melanogaster*.

veinlet. Found in early experiments with white-1, of the same series of cultures as that in which tilt was found. The third, fourth, and fifth longitudinal veins are often incomplete at their distal ends. Overlaps wild type. Resembles short of *pseudoobscura*, or veinlet of *melanogaster*, though it is less extreme than the latter.

### *Second chromosome*

abnormal. Found in a strain from Baltimore, Maryland. Abdominal bands irregular, tergites often failing to meet in the mid-dorsal line. Overlaps wild type.

arc. Found in a wild stock from Woods Hole, Massachusetts. Wings rather short, bowed as in the arc of *melanogaster*, but with no approximation of the crossveins. Overlaps wild type.

bithorax. Found in linkage experiments with chromosome 5. The balancers are wing-like. Overlaps wild type. Resembles some of the alleles of bithorax in *melanogaster* or *pseudoobscura*.

claret. Present in a wild strain from Baton Rouge, Louisiana. Resembles pinkish and pink-like of *affinis*, pink and claret (as well as other eye colors) of *melanogaster*, *simulans*, or *pseudoobscura*.

crossveinless. Found in the stock of pinkish, of pure Woods Hole ancestry. Posterior crossvein broken or absent. Overlaps wild type frequently. Resembles crossveinless-d of *melanogaster*; not like crossveinless of *melanogaster* (X) or of *pseudoobscura* (2).

crumpled-1. Found in  $F_2$  from a wild female from Litchfield, Connecticut. Wings abnormal, distal part often folded back under proximal part; branches of arista bent anteriorly near their bases, so that distal parts are parallel to main axis; bristles blunt, somewhat shortened; fertility greatly reduced. Resembles crumpled of *melanogaster* or *pseudoobscura*.

crumpled-2. Found in linkage experiments. Phenotypically not distinguishable from crumpled-1; allelism and linkage not tested.

Delta. Found as two individuals in a linkage experiment. Dominant. Veins thickened, especially at junctions, acrostichal hairs numerous and in irregular rows, eyes somewhat roughened, tarsi short and thick. Lethal in homozygous condition. Resembles Delta of *melanogaster* or *simulans* and Smoky of *pseudoobscura*.

knot. Found in a strain from Woods Hole. Slight thickening of junctions of veins. Overlaps wild type. Not easily classified.

pinkish. Found in  $F_2$  from a wild female from Woods Hole, Massachusetts. Pink eye color, resembling pink, claret, ruby, garnet, etc. of *melanogaster*, or pink, claret, magenta and ruby, of *pseudoobscura*.

pauciseta. In a wild stock from Gatlinburg, Tennessee. Many of the bristles and hairs are reduced in size or absent, in an irregular pattern. Often so nearly wild type as to be difficult to classify. Resembles pauciseta of *pseudoobscura*, and may also be compared to recessive hairless of *simulans*.

rugose. Found in  $F_2$  from a wild female from Lake of the Ozarks, Missouri. Eyes distinctly rough, of normal size and convexity.

short-wing. In the wild stock from Woods Hole, Massachusetts that contained knot. The two genes were originally associated in the same chromosome. Wings short, blunt, of uneven texture. Variable, and sometimes overlaps wild type.

short-1. Found in linkage experiments. Character similar to veinlet, but somewhat more extreme and less often overlapping wild type.

short-2. Found in  $F_2$  from a wild female from Gatlinburg, Tennessee. Not different phenotypically from short-1, to which it is allelic.

short-tarsi. Found in  $F_2$  from a wild female from Mendham, New Jersey. Legs, especially tarsi, short. Often a strong constriction in the tarsi, leaving the terminal segments attached to the rest of the legs by a thread-like connection. Arista often with a thickened axis.

tiny-bristle. Found in a stock from Wooster, Ohio. Bristles fine, not shortened. No marked effect on development rate.

*Third chromosome*

cinnabar. Present in a wild strain from Austin, Texas. Bright eye color, not separable from vermilion or scarlet. Feeding experiments made for me by MR. D. D. MILLER show that it has  $v^+$  but not  $cn^+$  substances, that is, that it corresponds to cinnabar of *melanogaster* and orange of *pseudoobscura*.

narrow. Found in linkage experiments. Wings narrow, cross veins approximated; legs rather short; head and mesonotum rather short and broad, sometimes slightly concave in mid-dorsal line. Resembles lanceolate of *melanogaster*, or narrow of *pseudoobscura*.

pink-like. Found in  $F_2$  from a wild female from Woods Hole, Massachusetts. Like pinkish, but slightly more extreme. This, like pinkish, gives, when combined with vermilion, a clear yellow eye-color.

roughish. Found in a strain from Coffeyville, Kansas. Eyes rough, often somewhat wrinkled; various head and thoracic bristles may be absent; variable, sometimes quite extreme but may overlap wild type.

straw. Found in linkage experiments. Yellowish body-color, quite similar to the straw of *melanogaster* or of *simulans*.

*Fourth chromosome*

antennipedia. Found in  $F_2$  from a wild female from Litchfield, Connecticut. The antennae are more or less leg-like, varying from normal antennae up to an extreme in which a practically complete leg (femur, tibia, basal tarsal segments), bearing a rudimentary arista at its tip, is attached to the rudimentary base of the third antennal segment. The type differs radically from the aristapedia of *melanogaster* or *simulans*, where the normal antenna becomes more or less leg-like—the second antennal segment becoming femur-like, the third tibia-like, and the arista quite tarsus-like. In antennipedia all the normal antennal parts persist, including an arista (which may be short, thick, or rudimentary, but is inserted at the normal position), while the apex of the third segment has some portions of a leg attached to it. Another property of antennipedia is that, in the males, sex-combs are often present on the tarsi of the second and third pairs of legs (more often the second) as well as the first where they normally occur. This applies more particularly to the longer sex-comb of the basal tarsal segment; the single tooth of the comb on the second segment is sometimes present on the second leg, but has not been seen on the third.

jaunty-1. Found in  $F_2$  from a wild female from Gatlinburg, Tennessee. Resembles jaunty of *melanogaster* or of *pseudoobscura*, curled of *melanogaster*, upturned of *pseudoobscura*, etc.

jaunty-2. Found in  $F_2$  from a wild female from Mendham, New Jersey. Like jaunty-1 and allelic to it.

jaunty-3. Found in F<sub>2</sub> from a wild female from Baton Rouge, Louisiana. Like jaunty-1 and allelic to it.

TABLE I  
Corresponding mutant types.

<i>affinis</i>	<i>pseudoobscura</i>	<i>melanogaster</i>
XL	XL	X
bobbed	bobbed	bobbed
cut	beaded	cut
miniature	miniature	miniature
scute	scutellar	scute
vermilion	vermilion	vermilion
white	white	white
yellow	yellow	yellow
XR	XR	3L
ascute	ascute	ascute
hairy	—	hairy
scarlet	scarlet	scarlet
sex-ratio	sex-ratio	—
tilt	tilt	tilt
veinlet	short	veinlet
2	2	3R
bithorax	bithorax	bithorax
claret	pink, claret	pink, claret
crossveinless	—	crossveinless-d
crumpled	crumpled	crumpled
Delta	Smoky	Delta
pinkish	pink, claret	pink, claret
pauciseta	pauciseta	(Hairless ?)
3	3	2R
cinnabar	orange	cinnabar
narrow	narrow	lanceolate
straw	—	straw
4	4	2L
jaunty	jaunty	jaunty
net	tangled	net
truncate	—	dummy
5	5	4
abdomen rotatum	—	abdomen rotatum
reduced	—	(shaven ?)

net. Present (heterozygous) in a wild male from Ithaca, New York. Extra wing-veins, especially between the distal ends of the second and third veins, and around the posterior crossvein. Resembles net of *melanogaster*, or plexus and tangled of *pseudoobscura*.

truncate. Found in linkage experiments. Wings short, often with the characteristic "truncate" shape, that is, strongly indented at the posterior distal corner, but with intact margin. Overlaps wild type. Resembles some of the dumpy alleles of *melanogaster*

#### *Fifth chromosome*

abdomen rotatum. Found in linkage experiments. The abdomen is twisted about its longitudinal axis in a counterclockwise spiral. Both sexes are sterile. Resembles the abdomen rotatum of *melanogaster*.

Fused. Arose in a cross between a strain from Woodstock, Maryland, and one that carried several mutant genes. Dominant, lethal when homozygous. Third and fourth veins strongly convergent at their distal ends; ocelli and ocellar bristles usually absent. Resembles the fused of *melanogaster*, except that that type is recessive and has a peculiar type of lethal action (LYNCH 1919) that is not evident in *affinis*.

reduced. Found in a strain from Woodstock, Maryland. Posterior scutellar bristles (occasionally also the anterior ones, rarely a few other thoracic bristles) very short, thick, and blunt. Suggests the shaven of *melanogaster*, though not a convincing parallel.

#### CHROMOSOME MAPS

##### *The X chromosome*

Two different sequences occur in each arm, the "standard" sequence of XL being regularly associated with the standard of XR, and the inverted sequences being likewise associated. Both sequences have been found in strains from Woods Hole, Tennessee, Missouri, Kansas, and Texas. The association between the two limbs remains unexplained, but can probably be interpreted when salivary gland preparations are studied.

Scute-1, white-2, and hairy-1 arose in the inverted sequence; scute-2, white-1 and hairy-2 in the standard. Ascute, tilt, and scarlet all arose in standard, but were later transferred to the inverted sequence by crossing over. These six genes are therefore known in both sequences; the others only in one or in the other. Maps are shown for each sequence.

The maps are unsatisfactory, since many of the mutant types are unsuited to exact linkage studies. Pebbled, bobbed, scute-2, and ascute all have markedly low viability; cut, both scutes, both hairys, tilt, and veinlet, all overlap wild-type; and white, vermilion, and scarlet interfere with each other's classification.

In females heterozygous for the two sequences there is very little crossing over, not over one percent for the whole known region. Most or all of that which occurs is in the region to the right of hairy. Patroclinous sons have been found rarely from such females, but it is not certain that they



were XO in constitution, so no definite conclusions can be drawn from them.

Perhaps the most unusual relation shown here is that yellow and scute are not close to each other as in most species, but are separated by cut, vermilion, and pebbled.

TABLE 2

*Linkage maps of X, second and fourth chromosomes of D. affinis.*

STANDARD SEQUENCE	INVERTED SEQUENCE
stubby..... 0	miniature..... 0
white..... 2	scute..... 6
yellow..... 12	white..... 12
cut..... 17	hairy..... 28
vermilion..... 22	veinlet..... 40±
pebbled..... 24	tilt..... 40±
scute..... 27	ascute..... 60
bobbed..... 40±	scarlet..... 90
hairy..... 40±	
veinlet..... 50±	
tilt..... 50±	
ascute..... 60	
scarlet..... 99	

## SECOND CHROMOSOME

pauciseta..... 0
short-wing..... 1±
rugose..... 25
pinkish..... 33
crumpled..... 45
short..... 67±
Delta..... 68
crossveinless..... 68±
bithorax..... Between 66 and 70
abnormal..... 73±
tiny-bristle..... 98
short-tarsi..... 98±

## FOURTH CHROMOSOME

net..... 0
antennipedia..... 31
jaunty..... 67

(Loci marked "±" are uncertain as to order, as well as to numerical value.)

## MAPS OF AUTOSOMES

The second chromosome map shown is more satisfactory than that of the X, since there are more useful characters here. No variations in linkage have been found, indicating that the sequence shown is the usual one throughout the range of the species.

The possible combinations of the three third chromosome characters pink-like, narrow, and roughish have all been studied rather extensively, but no double recessive has yet been obtained. Either all three loci are close

together, or the chromosomes concerned have different sequences. The other mutant genes in this chromosome have not yet been adequately tested.

The fourth chromosome map, like that for the second, shows values that have been obtained repeatedly from crosses to a wide variety of strains. It must represent the sequence usual throughout the range of the species. Preliminary studies show that truncate is approximately 34 units from net; it has not yet been placed with respect to the other two loci shown on the map.

The fifth chromosome has been little studied. Reduced is not favorable for study, since it overlaps wild type frequently, and the complete sterility of abdomen-rotatum makes it also unfavorable. The few tests carried out have not yielded any crossovers between either of these and Fused.

#### PARALLELISM WITH MUTANT TYPES OF OTHER SPECIES

Comparison of the mutant types here described with those known in *melanogaster* or in *pseudoobscura* (see DONALD 1936, STURTEVANT and TAN 1937) leaves little doubt as to the homologies, which are evidently as follows:

<i>affinis</i>	XL	XR	2	3	4	5
<i>pseudoobscura</i>	XL	XR	2	3	4	5
<i>melanogaster</i>	X	3L	3R	2R	2L	4

In the case of the X this relation was to have been expected, since the X of *melanogaster* seems to include material that is in the X of every species of *Drosophila* yet studied, while the presence of the sex-ratio gene had previously indicated that the XR of *affinis* agrees with that of *pseudoobscura*. The composition of the fifth chromosome is also the expected one. With respect to the three large autosomes there was no satisfactory basis for a prediction of the constitution of *affinis*. The present data are themselves not sufficient to furnish a final solution here, especially since the position of the centromeres on the maps remains unknown, and the number of parallels is still small. It is still possible that the parallel genes in one or two of the *affinis* autosomes are all in one arm, so that the homology given is not certainly applicable to the entire chromosomes. Nevertheless, the absence of any parallels in disagreement with the suggested correspondence is striking, and may be taken as raising a strong presumption that each autosome of *affinis* contains essentially the same material as does one of those of *pseudoobscura*.

The implications of this result will be discussed below.

#### THE SUBGENUS SOPHOPHORA

The subgenus *Sophophora* falls naturally into four species groups, as follows:

1. Dark species; long fine ventral receptacle; long spiral testes; one or

two opaque heavily chitinized areas on the fifth abdominal tergite of the female; skipping larvae; no sex combs; filaments of eggs much expanded at apices. Found in tropical America. *D. saltans* and six undescribed species.

2. Yellow species; long fine ventral receptacle; medium long spiral testes; no opaque areas on tergites; larvae do not skip; no sex-combs; egg filaments much expanded at apices. Found in tropical America. *D. willistoni* and *nebulosa*.

3. Yellow species; rather long ventral receptacle; medium long spiral testes; no opaque areas on tergites; larvae do not skip; sex-combs present. Found in Old World tropics (the first three also in America, where they appear to be introduced). *D. melanogaster*, *simulans*, *ananassae*, *takahashii*, *montium*, *auraria*, *bipectinata*, etc. *D. miki*, from Austria, probably also belongs here.

4. Dark species; short ventral receptacle; testes elliptical or somewhat elongate, scarcely spiral; no opaque areas on tergites; larvae do not skip; sex-combs present; preapical bristles on anterior tibiae unusually long. Found in the north temperate zone (*azteca* and *pseudoobscura* reach Guatemala, but only in the mountainous temperate regions). *D. obscura*, *subobscura*, *pseudoobscura*, *miranda*, *affinis*, *algonquin*, *azteca*, *athabasca*, *narragansett*, etc.

At first glance, the relationships between these four groups appear to be those indicated by the sequence given, that is, the second group is intermediate between the first and third, the third between the second and fourth, and the first and fourth most distinct.

The chromosome configurations shown by these species are diverse. *D. willistoni* (group 2) has a V-shaped X, a V-shaped autosome, and a rod-shaped autosome (LANCEFELD and METZ 1921), as shown in figure 1. *D. saltans* is described as having the *melanogaster* oögonial configuration, which differs only in having a small dot, though the similarity is misleading, since in *melanogaster* the rod, rather than one of the V's, is the X. MR. E. NOVITSKI, in this laboratory, reports that the three *saltans* relatives he has studied have no dot; they may be supposed to have the same complex as *willistoni*. *D. earlei* (from Cuba) was described by METZ (1916b) as having the *willistoni* oögonial configuration; the species is evidently related to the *saltans* group, though it cannot be determined whether it should be placed with the first or the second group here defined (the larvae were not observed to skip, and in the available pinned material it is not possible to be certain whether an opaque area is present on the abdominal tergite). *D. nebulosa* is also listed as having the *melanogaster* oögonial configuration; but examination of the published figures (METZ 1916a) shows that no dots were found. It seems probable that the *willistoni* complex is characteristic of both the first and the second species groups.

Both the third and the fourth groups have a variety of configurations. The *melanogaster* type is found in *simulans*, and is recorded by KIKKAWA and PENG (1938) for *auraria*, *lutea*, *rufa*, and *takahashii*, with *ficuspbila* and *suzukii* probably the same but without a positive identification of the X. All these forms apparently belong to the third group of species. (In the cases of *lutea*, *rufa*, *ficuspbila*, and *suzukii* this reference is based on the published descriptions, since I have seen no material.) Also in this group

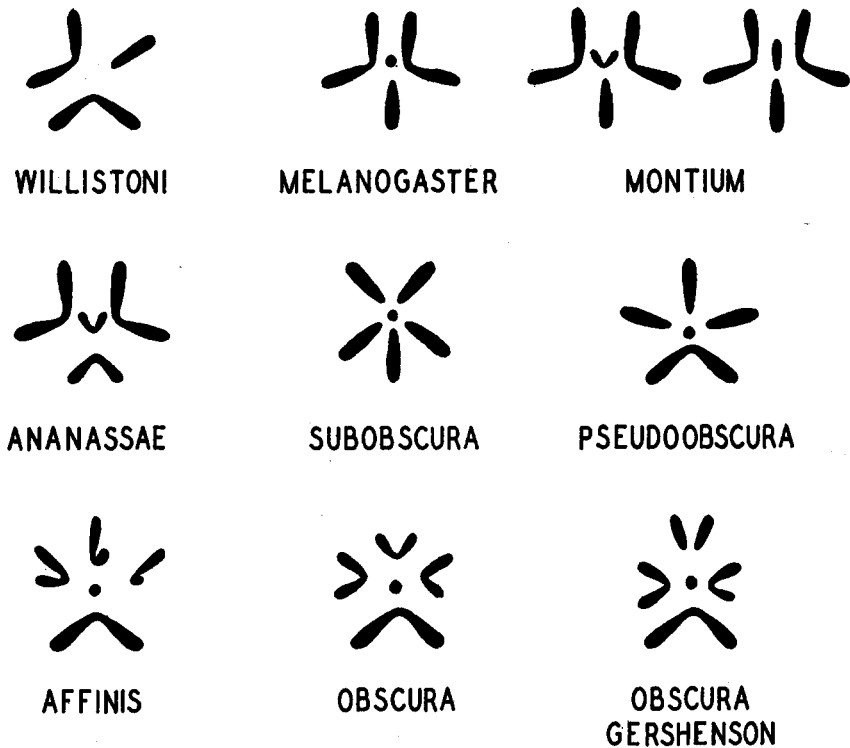


FIGURE 1.—Diagrammatic representation of the chromosome configurations known in the subgenus *Sophophora*. Haploid groups are shown. In every case the lowermost chromosome is the X; the Y, which is variable even within some of the species, is not shown.

are *montium* and *ananassae*, with the configurations shown in figure 1. *Bipectinata* resembles *ananassae* (KIKKAWA and PENG 1938), though the X has not been identified. KIKKAWA'S (1937, 1938) studies show that *ananassae* has the *melanogaster* arrangement with two modifications: the basal portion of X, including much of its heterochromatin, the nucleolus, and the gene bobbed, has become attached to the dot; and the remaining portion of X has acquired a median centromere. The configurations found in *montium* presumably represent the first of these changes (or one similar

to it—there is no evidence to show how much of X has been transferred to the dot), without the second one. The third group of species is thus characterized by the *melanogaster* configuration or relatively slight modifications of it.

The fourth group of species includes the last five types shown in the figure. Of these, the *affinis* and *obscura* arrangements (found also in *algonquin*, *azteca*, and *athabasca*) are essentially the same, differing only in the relative lengths of the arms of the autosomes. The “*obscura* Gershenson” configuration differs in that one of the autosomes is represented by two rods (see FROLOWA and ASTAUROFF 1929 for the two *obscura* types). *Pseudoobscura* and *miranda* differ from the *affinis* type in that the three J-shaped autosomes have all become rods, and that at least two of them appear to be shorter than in *affinis* or *obscura*. Finally, *subobscura* differs from *pseudoobscura* in having one arm of the X now present as an additional autosome.

The comparison of mutant genes in *melanogaster*, *simulans*, *willistoni*, *pseudoobscura*, and *miranda* shows that in these species the separate arms maintain their identities (see discussion by STURTEVANT and TAN 1937). The X of *melanogaster* and *simulans* remains as one arm of X in the other three species, and the other arm of X in these three species is the equivalent of 3L of *melanogaster* or *simulans*. The present account confirms the suggestion of STURTEVANT and DOBZHANSKY (1936) that the X of *affinis* has the same composition as that of *pseudoobscura*. The work of KIKKAWA (1937, 1938) shows that the X of *ananassae* is the same as that of *melanogaster*, except that the bobbed end has been removed and attached to the dot, while the centromere of the remaining portion has become median. The composition of the X is thus fairly clear throughout the subgenus.

With respect to the autosomes there are two chief problems: (1) where is the dot material in the *saltans* and *willistoni* configuration; (2) what is the content of the J-shaped autosomes of *affinis* and *obscura*? The first question cannot be answered from the available evidence; the second is answered in part by the data presented in this paper. It is probable that each autosome of *affinis* corresponds largely or entirely to one autosome of *pseudoobscura* or to one autosomal arm of *melanogaster*. The changes involved have, then, apparently been merely in the position of the centromeres and associated heterochromatin. This interpretation must be accepted with caution, however, as pointed out above.

The historical interpretation suggested by these configurations is indicated in the accompanying diagram. It should be emphasized that the names in the diagram refer to chromosome configurations as shown in figure 1, not to the species themselves. .



*melanogaster* type—in *Chymomyza amoena*, *Scaptomyza graminum*, and (with doubt as to which chromosome is the X) in *Mycodrosophila dimidiata*, *Chymomyza procnemis*, *Chaetopsis fulvifrons*, and the following species of *Drosophila* (all of uncertain subgeneric reference, but probably neither *Sophophora* nor subgenus *Drosophila*): *bromeliae*, *florae*, *coracina*. *Quinaria* and *robusta*, of the subgenus *Drosophila*, have been referred here, but *robusta* is certainly different, and the published figures for *quinaria* show no dot and do not indicate which is X.

*subobscura* type—in *ramsdeni*, *virilis*, *similis*, *cardini*, *mulleri*, *phalerata*, *transversa*, all belonging to the subgenus *Drosophila*. Essentially the same arrangement, with differences only in amount and distribution of heterochromatin, occurs also in the following members of the subgenus *Drosophila*: *funnebris*, *histrion*, *hydei*, *repleta*.

*pseudoobscura* type—in *virilis americana* (HUGHES 1939), where it is evidently a secondary derivative of the *subobscura* type.

*affinis* type—in *duncani* (DOBZHANSKY, unpublished), which is the type of an unnamed subgenus (referred by STURTEVANT (1939) to *Dasydrosophila* Duda, but not in reasonable agreement with the type of that subgenus).

This comparison thus suggests that species-group 3 is related to *Chymomyza* and *Scaptomyza* and less certainly to *Chaetopsis* (of the very remote family Ulidiidae), *Mycodrosophila*, and two little-understood subgenera of *Drosophila*; and that species-group 4 is related to the subgenus *Drosophila* and to *duncani*. There is no indication that groups 1 and 2 are connected directly with any other form that has been studied.

The method of comparing resemblances in many different characters (STURTEVANT 1939) is in general agreement with this. The closest resemblance of any species of *Sophophora* with any of the other species examined is that between the *affinis* forms and an undescribed member of the subgenus *Drosophila* from the mountains of California. It should be pointed out that none of the forms listed above as having the *melanogaster* group is included in these latter comparisons. An undescribed American species that is close to *coracina* is included; it does not have the *melanogaster* chromosome group, and does not appear to be closely related to *duncani* or to any of the species of *Sophophora* or *Drosophila* that have been examined.

Another method of approach is through examination of the characteristics of each species group, to determine which seem most likely to be special and recently arisen peculiarities. In this category of characters are to be placed the opaque areas on the tergites (group 1), and sex-combs

(groups 3 and 4). It is also rather probable that relatively short ventral receptacles and testes (group 4, and group 3 to a lesser degree) are primitive. This method may be taken as agreeing with the others in indicating that group 1 is not the point of origin for *Sophophora*, and in suggesting group 4 as the more primitive—though group 2 is also to be considered as a possibility.

The most obvious inter-subgeneric relationship is that between group 4 and the subgenus *Drosophila*. It should be pointed out that *Drosophila* is a more complex subgenus than *Sophophora*, including more species groups, whose interrelationships and geographical distribution are more difficult to describe. It seems likely, therefore, that *Drosophila* is at least as old as *Sophophora*—again suggesting group 4 as the most ancient one in *Sophophora*.

#### SUMMARY

1. Forty-seven mutant types of *Drosophila affinis* are described, dependent on mutant genes in 40 different loci. Of these, 13 are in the X chromosome, 15 in the second, 5 in the third, 4 in the fourth, and 3 in the fifth.

2. Twenty-eight of these types resemble ones previously known in *D. melanogaster* or *D. pseudoobscura*. Their distribution among the chromosomes indicates the following homologies:

<i>affinis</i>	XL	XR	2	3	4	5
<i>pseudoobscura</i>	XL	XR	2	3	4	5
<i>melanogaster</i>	X	3L	3R	2R	2L	4

3. There are no probable parallels in disagreement with these homologies.

4. The subgenus *Sophophora* falls into four species-groups. A discussion of the morphology and cytology of the available representatives of each of these groups leads to a tentative phylogeny. The species-group that includes *pseudoobscura* and *affinis* is perhaps nearer the ancestral type than are the other three. This leads to the supposition that the *melanogaster* chromosome group was derived from the *pseudoobscura-affinis* arrangement.

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