THE HOMOLOGIES OF THE CHROMOSOME ELEMENTS IN THE GENUS DROSOPHILA

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INTRODUCTION

IT IS becoming increasingly clear that certain elements in the chromosome complexes of the Drosophilas maintain their identity from species to species, though undergoing various changes in their relations to each other and in their internal structure (DONALD 1936; STURTEVANT and TAN 1937; STURTEVANT 1938a, 1940). The terminology for these various elements, however, is far from uniform, since several conflicting systems of lettering and numbering are in use. The most satisfactory general solution of the problem of nomenclature seems to be that suggested by MULLER (1940). According to this system the recognizable elements are lettered, in the sequence familiar in *melanogaster*. The X of that species becomes A; IIL, B; IIR, C; IIIL, D; IIIR, E; IV, F. It is not expected that this system will replace those established by long usage, as in *melanogaster*, but it is strongly recommended that it be applied in those cases where the change might more easily be made. Furthermore, arbitrary systems of numbering or lettering used to facilitate studies on the genetics and cytology of unexplored species should be selected with full appreciation of the ambiguities that may arise when the homologies of the various elements become known.

In those cases where species are so closely related that their salivary gland chromosomes show obvious similarities, or that their hybrids can be obtained, the task of homologizing the elements is greatly simplified; for all other species it is necessary to resort to a comparison of their mutant genes with those of species whose elements have been determined. (The term "element" seems the most appropriate one for this unit since chromosome, arm, and limb have all been used with other connotations.) Since only a fraction of the mutants can be regarded as "good" parallels, comparisons must be made with caution; on the other hand, the tendency to minimize otherwise good homologies which do not appear to be consistent with the scheme must be watched carefully.

It is our purpose in the present paper to extend these homologies as far as now seems possible, and to examine critically evidence contrary to the working hypothesis that the elements have remained essentially intact. The species to be so examined include, among others, *affinis*, *algonquin*, *ananassae*, *azteca*, *busckii*, *funebris*, *hydei*, *miranda*, *montium*, *pseudoobscura*, *simulans*, *virilis*, and *willistoni*.

TABLE 1

Compositions of the chromosomes in terms of the elements.

SPECIES	A	B	C	D	E	F	AUTHORITY
melanogaster	X	IIL	IIR	IIIL	IIIR	IV	
affinis	XL	IV	III	XR	II	V	STURTEVANT 1940
algonquin	XS	C	A	XL	B	D	MILLER 1939
ananassae	X part IV part	IIIR	IIIL	IIR	IIL	IV	KIKKAWA 1938
azteca	XS	C	A	XL	B	D	DOBZHANSKY and SOCOLOV 1939
miranda	XL	IV	X2	XR	II	V	DOBZHANSKY and TAN 1936
pseudoobscura	XL	IV	III	XR	II	V	LANCEFIELD 1922
simulans	X	IIL	IIR	IIIL	IIIR	IV	STURTEVANT 1922
virilis	I	VI	V	III	II	IV	METZ, MOSES and MASON 1923
virilis	V	II	IV	I	III		HEITZ 1934
virilis	X	IV	V	III	II	VI	CHINO 1936
virilis	X	D	E	C	B	M	HUGHES 1939

THE AFFINIS GROUP

The metaphase chromosome configurations of females in this group (*affinis*, *algonquin*, *athabasca*, *azteca*) contain a large pair of V-shaped X chromosomes, two pairs of V-shaped autosomes, a pair of rods, and a pair of microchromosomes (METZ 1916). The original account (DOBZHANSKY in STURTEVANT and DOBZHANSKY 1936) of the salivary gland chromosomes in the members of the *affinis* group has been confirmed and extended by MILLER (1939). The observations of DOBZHANSKY and SOCOLOV (1939) on *azteca* failed to include the longer salivary gland chromosome arm of their "C" chromosome, a circumstance that invalidates their conclusion that "Some genes found in *D. azteca* in a single linkage group must belong to different ones in *D. pseudoobscura;* conversely, some genes linked in *D. pseudoobscura* may be expected to be independent in *D. azteca.*"

The salivary gland chromosomes of the different members of the *affinis* group are sufficiently similar so that one familiar with any one of these species can recognize the homologous elements in any other. [Since there is considerable variation in gene sequence within each species, the salivary gland chromosomes of interspecific hybrids from strains taken at random tend to possess quite remotely related chromosomes. These need not be interpreted as interspecific differences, as they have been (BAUER and DOBZHANSKY 1937; DOBZHANSKY 1937), for it is possible that identical or simply related sequences exist within each species.] The homology of the *affinis* elements being known through a comparison of mutant types (STURTEVANT 1940), it was necessary only to correlate the genetic linkage groups with the salivary gland chromosomes of this species. XL of *pseudoobscura* agrees cytologically with the short arm of the X in *affinis* in having

an interstitial heterochromatic region near the base and identical banding at the tip. It follows that the longer arms of the X chromosomes of the two species, containing the same genetic material, are homologous. For the identification of the genetic autosomes with the arbitrarily lettered salivary chromosomes of *azteca* (DOBZHANSKY and SOCOLOV 1939) and of *algonquin* (MILLER 1939), a study was made of nine X-ray induced translocations in *affinis*, with the result shown in table 1. From this correlation it is evident that both elements B and E have median centromeres, yielding the V-shape obvious in two of the metaphase and salivary gland chromosomes.

D. ANANASSAE

The metaphase chromosome configuration of *ananassae* indicates that, while the two large autosomes are not unlike those of *melanogaster*, the centromere of the X chromosome has been shifted from a terminal to a median position and the dot chromosome has been transformed into a small V-shaped chromosome (METZ 1916). The nucleolus-forming region and the bobbed gene, ordinarily related to the sex chromosomes in other species, are associated with the small V-shaped fourth chromosome (KAUFMANN 1937; KIKKAWA 1938). This may have been achieved by a simple exchange of centromeres of the dot and X chromosomes, along with adjacent heterochromatin. If this be the case, the exchange must have occurred prior to the median shift in the centromere of the X; that this sequence is correct is borne out by the cytological observations of KIKKAWA (1936) on *montium*, a relative of *ananassae*, in which the V-shaped fourth chromosome is present, but the X chromosome retains its rod shape. There are other possible explanations, involving an exchange of the Y and fourth chromosome centromeres.

A number of mutants in *ananassae* furnish means for comparing its chromosomes with those of *melanogaster* and with the elements. A more complete discussion of these mutants and their linkage data can, in general, be obtained from the papers of MORIWAKI (1935, 1938) and KIKKAWA (1938). *Melanogaster* mutants with which those of *ananassae* are compared are followed by a symbol showing the limb in which they occur.

The X Chromosome

Yellow, scute, white, Notch, cut, singed, miniature, dusky, forked, and Beadex seem good homologies with the same sex-linked mutants of *melanogaster*. The terminology for singed and forked may be reversed, as in *pseudoobscura*, but their value is not thereby impaired, since both occur in the same element. The close linkage of yellow with scute and of miniature with dusky (also found in *melanogaster*, *pseudoobscura*, and *virilis*) adds weight to already good comparisons. Vermilion, ordinarily a good parallel

between the X chromosomes of two species, lacks the confirmation of a feeding or transplantation test.

Chromosome II

Cardinal in the left limb of this chromosome corresponds to cardinal (IIIR) and can be differentiated from its mimics, scarlet and cinnabar, by virtue of its striking change in color with age. Plexate probably represents Delta (IIIR), agreeing both in phenotype and in mutability. Off is much like Bare of *pseudoobscura* (element E), although its dominance, its effect of clipping and removing the bristles, and the occasional viability of the homozygote are not conclusive. Puffed has no homolog in *melanogaster.* but agrees with Puffed in *virilis*, which has small, reddish, and "inflamed" eyes (MORIWAKI 1938). This mutant is located on the second chromosome of *virilis*, which will be shown to correspond to element E. For this reason, we believe that the locus of this gene in *ananassae*, which has not been determined because of its association with an inversion, will prove to be in the left arm.

The right limb of this chromosome has no mutants suitable for homologies, but it may be concluded that it represents the element associated with E in *melanogaster*—that is, D—since elements B and C are both accounted for below.

Chromosome III

Plum, in the left limb of chromosome III, is like Plum (IIR) in *melanogaster* in having a dominant mottled eye color, a recessive lethal effect, and an association with an aberration involving heterochromatin (KIKKAWA 1938). Furthermore, it produces a mottled white eye color in combination with vermilion. This indicates its allelomorphism to brown.

Gap compares with gap (IIR) in weakening the fourth longitudinal vein and in giving the posterior crossvein an oblique direction. This is not conclusive in itself, but serves to confirm the identity of the left limb of the third chromosome of *ananassae* with the right limb of the second chromosome of *melanogaster.*

Only one mutant, plexus, has been found on the right limb of this chromosome. Since we would expect true plexus to occur in the same limb as Plum, we feel that this is in fact net (IIL), one of the most common mutant types in other species.

Chromosome IV

The fourth linkage group contains a dominant mutant, similar to Shaven. This dominant form is not known in *melanogaster*, but is in *simulans* (unpublished data). Haplo-IV individuals correspond quite closely to those of *melanogaster.* The linkage of bobbed with these two has already been discussed.

From the above homologies, it would seem that the nomenclature for the autosomal linkage groups has been reversed with respect to that found in *melanogaster* and, in each case, the significance of left and right as applied to the chromosome arms has also been reversed (table 1).

D. BUSCKII

The metaphase chromosome configuration here is essentially the same as in *melanogaster*, except for the dot chromosomes which are absent as such and may be attached to the X chromosomes as satellites (METZ 1916; KRIVSHENKO 1939). KRIVSHENKO has obtained a considerable number of mutants in this species after treatment with X-radiation. Forked, miniature, Notch, scute, singed, vermilion, white and yellow, all on the X chromosome, may be homologous to the sex-linked mutants in *melanogaster*. Autosomal dominants resulting from X-ray treatment, the most abundant type in KRIVSHENKO'S studies, are usually unsuitable for drawing comparisons, partly because of their non-specific effects and partly because of their frequent association with chromosomal aberrations which make linkage studies difficult. One exception in this case is Delta, which occurred seven times, once associated with a IIL–IIIL translocation and once with a IIL–IIR–IIIR translocation, in each case one of the break points occurring in the same region of IIL. This would point to the correspondence of IIL of *busckii* with element E.

D. FUNEBRIS

The mutants in *funebris* available for drawing comparisons are generally unsatisfactory, both because of their indefinite nature and of their unknown linkages, with the exception of a few sex-linked types. Notch corresponds closely to Notch (X) (STURTEVANT 1918). Forked may be either forked (X) or singed (X) (MORGAN, BRIDGES, and STURTEVANT 1925). The similarity of bobbed to bobbed (X, Y) has been pointed out by LUERS (1937). STUBBE and VOGT (1940), by transplantation of eye disks, have shown vermilion to be homologous to vermilion (X). They have also confirmed the identity of autosomal cinnabar with cinnabar (IIR) by the same technique. Radius incompletus bears some resemblances to radius incompletus (IIIL) (TIMOFÉEF-RESSOVSKY 1927) and cubitus incompletus to cubitus interruptus (IV); but any attempt to elaborate these and other possible autosomal homologies seems unprofitable in the absence of linkage data.

D. HYDEI

Notch, white, vermilion, and bobbed in the X chromosome of *hydei* (CLAUSEN 1923; SPENCER 1927) seem probable homologs of the same sex-linked mutants in *melanogaster*. For this species in particular and for many

others there remains unavailable a considerable body of unpublished information, which, as far as we are aware, is not in disharmony with the scheme of permanent elements but which, in a great many cases, furnishes additional evidence in its favor.

D. MIRANDA

The homologies of the salivary chromosomes of *miranda* with those of *pseudoobscura* have been deduced from studies of their hybrids (DOBZHANSKY and TAN 1936). Besides a large number of differences between homologous elements arising, presumably, from the effects of cumulative inversions, DOBZHANSKY and TAN conclude that at least five translocations (involving all the chromosomes) have become established between the two species. In view of MACKNIGHT'S criticism (1939) on cytological grounds, WRIGHT'S mathematical calculations (1940) for the incorporation of one such translocation (see below) and the absence of conclusive evidence to the contrary, we are forced to conclude that these cases very probably do not represent exceptions to the rule of the indivisibility of the elements.

D. MONTIUM

A number of mutants described by OSIMA (1940) provide means for drawing parallels between the linkage groups of montium and the elements. On the X chromosome, white, Notch, and vermilion compare favorably with the similar sex-linked mutants in other species.

Curled-b (left limb of II) simulates curled (IIIR) by curling the wings up and raising and crossing the posterior scutellar bristles. Confluent (left limb of II), obtained twice after X-ray treatment, would correspond to Delta (IIIR), one of the most frequent of mutants found after raying. Hairless, also on chromosome III, agrees with Hairless (IIIR) in its bristle and wing vein diminishing effect, in its dominance and in its lethality when homozygous. This mutant has not yet been allocated to a definite limb; it can be suggested here that it will prove to be on the left limb.

Curled (left limb of III) and jaunty (IIL) seem good parallels; plexus (right limb) would consequently suggest plexus (IIR) rather than net (IIL) since it falls on the anticipated element. On this basis, Plexate, located in the middle of chromosome III, would correspond to Plexate (IIR) and would be expected to occur on the right limb along with plexus. The centromere, therefore, might be expected to fall to the left of Plexate.

The metaphase chromosomes, reported by KIKKAWA and PENG (1938), suggest that this species may be like *ananassae*, but with a terminal instead of a median centromere in the X. The genetic data do not help in checking this supposition.

D. PSEUDOOBSCURA

The metaphase chromosomes of a *pseudoobscura* female consist of a pair of V-shaped X chromosomes, three pairs of autosomal rods, and a pair of dot chromosomes. LANCEFIELD (1922) suggested that a portion of the V-shaped X chromosome of *pseudoobscura* might exist in other species as autosomal material. CREW and LAMY (1935) pointed out, among other comparisons, that certain mutants in the right arm of the X chromosome could be homologized with similar mutants in IIIL of *melanogaster*, although this was not immediately obvious from this paper because of the authors' peculiar terminology. The argument that the elements have remained essentially intact in *pseudoobscura* as compared with *melanogaster* was applied by DONALD (1936) who studied more mutants and implied the necessary corrections to the work of CREW and LAMY. STURTEVANT and TAN (1937) confirmed and extended the main conclusions, leaving no doubt of the identity of the elements in the two species (see table 1). Two additions (STURTEVANT and TAN, unpublished) may be made to the information published in this latter paper: The order of the loci on the X chromosome in the neighborhood of 72 has been shown to be forked, dusky, and bobbed, not dusky, forked, and bobbed as surmised before; also the distance between compressed and sepia is 30 units rather than the indicated 7, thereby increasing all loci from sepia to the right end inclusive by about 25 units.

TAN (1935) correlated the salivary gland chromosomes with the genetic linkage groups in this species.

D. SIMULANS

Since *simulans* hybridizes with *melanogaster*, suspected homologies can be tested directly by mating the corresponding mutants. Thus ordinarily insecure comparisons become unquestionable. The genetic evidence (STURTEVANT 1921a, 1921b, 1929) indicates a close agreement between the limbs of the *simulans* chromosomes and those of *melanogaster* (table 1). The hybrid salivary gland chromosome analyses by PÄTAU (1935) and by KERKIS (1936) confirmed the homologies of the chromosomes and verified the existence of an inverted sequence of genes in the third chromosome, the first inversion to be found in Drosophila (STURTEVANT 1921c). The more detailed examination by HORTON (1939) revealed that as many as 23 additional intra-chromosomal differences, all very small, may exist between the two species.

Six unpublished corresponding mutant types of *simulans* may be noted here: scute (X, 0), ocelliless (X, 24), javelin (III, 0), radius incompletus (III, 58), recessive hairless (III, 61), and dominant Shaven (IV). The sex-

linked parallel vermilion (X, 31.8) was reported by STURTEVANT (1932), without its locus. All of these have been shown to be allelic to the *melanogaster* types whose names they bear and which they closely resemble.

DROSOPHILA VIRILIS

D. virilis remains the only species in the subgenus Drosophila (STURTEVANT 1939) with a sufficient array of mutants to make possible homologizing all the linkage groups with the elements. The six linkage groups agree with the metaphase configuration of five pairs of rods and one pair of microchromosomes. METZ, MOSES, and MASON (1923) and CHINO (1929, 1936) have drawn many comparisons of *virilis* mutants with those of *melanogaster*. *Melanogaster* mutants are followed by a notation of the chromosome limb in which they occur, all others being *virilis* types. We will attempt to evaluate these and, in some cases, make additional suggestions.

X Chromosome

Convincing parallels have been drawn in the cases of yellow, forked, singed, glazed (METZ, et al.), of crossveinless (WEINSTEIN 1920), of scute, white, Notch, miniature, dusky, rudimentary, Beadex, and bobbed (CHINO) with the identically-named mutants (except lozenge for glazed) in the X chromosome of *melanogaster*. HOWLAND, GLANCY, and SONNENBLICK (1937) have established the identity of vermilion of *virilis* with vermilion (X) by the transplantation of eye disks.

The comparisons of echinus with echinus (X), magenta with ruby (X), vesiculated with vesiculated (X), ragged with cut (X), decline with wavy (X), apricot with garnet (X), and small bristle with tiny (X) (CHINO) are open to doubt, but they do serve as corroborative evidence that the composition of the X chromosome of *virilis* and *melanogaster* is essentially the same.

Chromosome II

Confluent is very probably homologous to Delta (IIIR) (CHINO), although the weaker alleles described by METZ et al. show some discrepancies. Concave and crumpled (IIIR) constitute one of the most striking cases of homology (METZ et al.); the case is strengthened by the occurrence of similar types in element E of *affinis* and *pseudoobscura*. Our examination of varnished indicates that it is a good parallel to glass (IIIR).

It has been suggested that ebony corresponds to ebony (IIIR), brick to claret (IIIR), and broken to crossveinless-b (IIIR) or to crossveinless-c (IIIR) (CHINO). These are not diagnostic mutants and may be questioned, although they do fall in the proper limb.

Radius incompletus (IIIL) has been compared to both incomplete and

detached of virilis (CHINO). From the published figures, it would seem that incomplete is quite like radius incompletus (IIIL), but this homology loses its force since it is not in the expected element. A similar situation is found in the case of lanceolate (see below).

Thus chromosome II of *virilis* corresponds to IIIR of *melanogaster*, or element E.

Chromosome III

Short veins suggest veinlet (IIIL) (CHINO) but the comparisons of rose with rose (IIIL), spread with dihedral (IIIL), and rolled with rolled (IIIL) (CHINO) are less convincing.

The striking resemblance of hunch to ascute (IIIL) has been pointed out (METZ et al.) but was discarded as a possible homology because a similar mutant was sex-linked in *D. pseudoobscura*. Since it is now known that the limb of the X chromosome of *pseudoobscura* in which this mutant is located corresponds to IIIL of *melanogaster* (DONALD 1936), this can be considered a convincing parallel. Telescoped has no homolog in *melanogaster*, but agrees closely with deformed and its allele serrate in *willistoni* (LANCEFIELD and METZ 1922) and to compressed in *pseudoobscura* where it is located in element D (STURTEVANT and TAN 1937). Garnet, like Henna (IIIL), is a dominant dark eye color; the only other possible homology would be Plum (IIR), which may be eliminated because of its mottling effect and allelism to brown (see eosinoid below).

The evidence favors the correspondence of *virilis* chromosome III with *melanogaster* IIIL or element D. On this basis, it may be safely predicted that cinnabar, after appropriate tests, will prove to be scarlet (IIIL) and not cinnabar (IIR).

Chromosome IV

Dachsous and dachsous (IIL), Star and Star (IIL) and reduced and reduced (IIL) seem good comparisons (CHINO). Clipped probably represents one of the truncate alleles of dumpy (IIL) (CHINO).

However, CHINO's identification of rough-4a with roughish (IIL), black with black (IIL), Squat with Squat (IIL) and flipper with pupal (IIL) are less convincing. Since the suggested homologs lie in the proper arm, they do tend to confirm the correspondence of these limbs. His figure of veinlet indicates that it is not veinlet (IIIL), as he suggests (see short vein, above)

Plexus might correspond to either net (IIL) or plexus (IIR). We would favor the first alternative since it falls in the proper limb. Lanceolate has been compared to lanceolate (IIR). This is one case where a mutant suitable for homologizing does not have an equally good or better comparison in the anticipated element. The force of this discrepancy is diminished by DONALD'S observation (1936) that a similar mutant is found in element D

in *pseudoobscura*, in addition to that found later in element C (STURTEVANT and TAN 1937). Also, KIKKAWA (1938) lists two such mutants, lance and lanceolate, one on the second, the other on the third chromosome of *ananassae*.

The bulk of the evidence favors the view that the third chromosome is element B.

Chromosome V

Eosinoid agrees with brown (IIR) in giving a white eye color in combination with scarlet or cinnabar (MORI 1937). Vestigial and vestigial (IIR) and straw and straw (IIR) seem excellent homologies (CHINO). Comparisons of ruffled with intwined (IIIL), fat with fat (IIL), dachsoid with four-jointed (IIL), mahogany with clot (IIL) and with sepia (IIIL), Beaded with Beaded (IIIR) and morula with morula (IIR) (CHINO) are questionable. Beaded may be compared with Jagged (C) of *pseudoobscura*.

Branched might be either net (IIL) or plexus (IIR); the latter seems more likely on the basis of the other homologs. For the same reason, we believe that scarlet corresponds to cinnabar (IIR) and not to scarlet (IIIR) (see cinnabar above).

Chromosome VI

The comparison of abdomen rotatum with abdomen rotatum (IV) (CHINO) is convincing; Gap, which shortens the fifth longitudinal vein, may be questioned as a homolog to cubitus interruptus. To these may be added the parallel of stubby with shaven (IV). Thus the dot chromosomes of both species are apparently the same.

As far as the above data can show, the elements have remained essentially intact. We are therefore reluctant to accept in its entirety CHINO's conclusion that "it seems to be justified to assume that in the evolutional course of Drosophila there occurred many inversions, mutual translocations, and attachments or fragmentations of all chromosomes."

FUJII (1936), by means of four translocations and an inversion, has correlated the salivary gland chromosomes with the linkage groups, as indicated in table 1.

SPENCER (1940) has described a native American subspecies, *virilis americana*, in which elements D and E are united to form a V; elements A and B are also fused, the additional B necessary to the diploid complement of the male being present as a single rod (HUGHES 1939; STALKER 1940; PATTERSON, STONE, and GRIFFEN 1940). In another subspecies, *virilis texana*, elements B and D have a single centromere (PATTERSON, STONE and GRIFFEN 1940). In each case the remaining elements are present as rods.

D. WILLISTONI

The X chromosome of this species is V-shaped, as in *pseudoobscura*, while the autosomes are comprised of one V and one rod (LANCEFIELD and METZ 1921). From the metaphase chromosome length relationships, it is clear that one of the elements that is autosomal in most species is part of the X in *willistoni*. The homologies of the sex-linked mutants here are consequently of considerable interest.

Yellow has been compared to yellow (X), scute to scute (X), vermilion to vermilion (X), stubby to forked (X), triple to bifid (X), forked to singed (X) (LANCEFIELD and METZ 1922; FERRY, LANCEFIELD, and METZ 1923). In addition, square agrees with rudimentary (X); unpublished data show that a newly arisen vermilion (locus in X unknown) lacks the v^+ substance, as determined by the feeding technique. Deformed and its allele serrate correspond quite closely to telescope of *virilis* (element D) and to compressed of *pseudoobscura* (element D) (STURTEVANT and TAN 1937); stump compares favorably with radius incompletus (IIIL), and short and veinlet (IIIL) seem good parallels.

The evidence thus indicates that elements A and D have fused to form the X in *willistoni*, as in *pseudoobscura*. This conclusion is strengthened by the distribution of the mutants homologized: all those paralleling element A mutants are found on one half of the X (34.5 to 84) while all those paralleling element D mutants are on the other half (0 to 34). The genetic locus of the centromere on this basis would be between 34 and 34.5. Low interference values for this region, as deduced from the crossing over data of LANCEFIELD and METZ (1922) support this hypothesis.

The autosomal mutants do not yield a satisfactory account of the composition of the V and rod-shaped autosomes. Balloon (chromosome II) has been homologized with balloon (IIR) (FERRY, LANCEFIELD, and METZ 1923). Apterous (chromosome II) agrees well with apterous (IIR); both remove the wings, reduce the balancers, diminish the number of posterior scutellar bristles, deform the thorax, and sterilize both sexes. Clipped and Scalloped, both on chromosome II, probably represent the dominant vestigial deficiencies (IIR). Approximated and dachs (IIL) are close parallels. These homologies indicate that the second chromosome of *willistoni* includes elements B and C, as in *melanogaster*. The location of Knot, which bears some resemblances to Delta (IIIR), on the second chromosome casts doubt on this conclusion. In either case, however, chromosome II must be the autosomal V; this is supported by the slightly greater number of mutants in II than in III (11 in II as compared to 8 in III).

Neither the genetic nor the cytological evidence gives a clue as to the location of element F in *willistoni*, but it is to be noted that the salivary

gland chromosomes have not yet been studied in this species. The most likely place to look for F would appear to be as a short arm on the apparently rod-shaped chromosome (III, element E?).

HOMOLOGOUS GENES IN THE VARIOUS SPECIES

Table 6 lists the homologous genes in the species discussed, to which some previously unpublished cases have been added. Unpublished data of other workers, available particularly in Drosophila Information Service, tend to strengthen the suggested homologies given in the table.

The occurrence of "sex-ratio" in *melanica*, a member of the subgenus Drosophila, seems worthy of special mention. It has been previously noted only in the subgenus Sophophora (*obscura*, *pseudoobscura*, *affinis*, *athabasca*, and *azteca*) and in those cases analyzed, is located in element D, which is part of the X chromosome. It seems likely, then, that the X of *melanica* is a V, one arm of which is element D. The cytological observations of METZ (1916) indicate that a V-shaped chromosome of the required size is present, although no identification of the X has been made.

LENGTHS OF THE ELEMENTS IN THE SALIVARY GLAND NUCLEI

The percentage each element comprises of the total euchromatic length of the salivary gland chromosomes is listed in table 2. These values have been derived from the published lengths for *ananassae*, *melanogaster*, and *virilis*, from measurements of the published drawings for *algonquin* and *azteca*, and from a combination of two sets of drawings plus our estimate for element D for *pseudoobscura*. The figure given for element B of *azteca* has been obtained by assuming that it bears the same ratio to the other autosomal elements as do the homologous elements in *algonquin*.

TABLE 2

Relative lengths of the elements in the salivary gland nuclei.

	A	B	C	D	E	AUTHORITY
algonquin	16.4	18.5	19.7	20.0	25.4	MILLER 1939
ananassae	19.3	19.1	18.0	18.4	25.1	KIKKAWA 1938
azteca	15.1	18.8	19.0	21.4	25.8	DOBZHANSKY and SOCOLOV 1939
melanogaster	18.9	18.5	21.0	18.0	23.6	BRIDGES 1935
pseudoobscura	14.0	19.9	16.3	24.0	25.8	TAN 1936; DOBZHANSKY and TAN 1939
virilis	19.3	19.3	19.5	18.3	23.5	FUJII 1936
virilis	19.3	20.1	19.0	18.2	23.4	HUGHES 1939

Since these lengths are a function of both the elasticity of the chromosomes and the personal equation of the observer, the comparative lengths of the homologous elements are quite variable, with one striking exception: in every case element E is considerably longer than any of the others. This

identification of the longest salivary gland element with element E may be of practical value in those instances where the correlation may be impracticable for other reasons. SLIZYNSKA and SLIZYNSKI (1941) report that in *funebris*, one of the elements is considerably longer than any of the others; it therefore probably corresponds to element E.

It is also to be noted that element D is about the same length as A when it is autosomal, but is distinctly longer in the three species in which it is part of the X. It seems clear from the table that the lengths of element A and D tend to show a negative correlation with each other. Numerous speculations are suggested by these relations, but they can scarcely be profitably discussed without more information than is now available.

SEQUENCE OF CORRESPONDING GENES IN DIFFERENT SPECIES

In general there is little similarity in the sequence of corresponding loci within each element, except when such closely related species as *melanogaster* and *simulans* are compared. In discussing *melanogaster* and *pseudoobscura*, STURTEVANT and TAN (1937) state: "The mathematical properties of series of letters subjected to the operation of successive inversions do not appear to have been worked out, so that we are so far unable to present a detailed analysis. It does appear, however, that the five arms (taken together) are definitely more alike in the two species than could result from chance alone." These statements now require some modification.

With the help of PROF. MORGAN WARD, a beginning has been made in the study of the mathematical consequences of successive inversions. Complete catalogs have been prepared, showing all the possible different arrangements of 2, 3, 4, 5, and 6 loci, respectively, together with the minimum number of successive inversions required to change each arrangement into a single arbitrarily chosen one. Actually, numbers were used, and the required arbitrary sequence was the ordinal one (1, 2, 3, 4, etc.). Table 3 shows the mean number of inversions required, together with the standard deviations for the respective populations.

TABLE 3

Mean number of inversions required to transform random arrangements of numbers into ordinal series.

NUMBER OF LOCI	MEAN	STANDARD DEVIATION
1	0	0
2	.500	.50
3	1.167	.69
4	1.750	.66
5	2.392	.70
6	3.036	.71
8	4.367 ± .092	.71 ± .06
9	4.975 ± .13	.82 ± .09

In the cases where more than six loci were involved, it became impracticable to make complete catalogs. Accordingly, for the two rows shown (eight and nine loci), random series of numbers (60 and 40 sequences, respectively) were chosen, and for each such sequence there was determined the minimum number of successive inversions required to reduce it to the ordinal sequence chosen as "standard." For numbers of loci above nine the determination of this minimum number proved too laborious, and too uncertain, to be carried out.

The table as it stands, however, gives a solution that seems safe to use for any numbers of corresponding loci likely to be encountered in such studies as these, since a plot of the values shows that there is an approximately linear relation between the number of loci considered and the average number of inversions required to reduce to ordinal sequence. For each additional locus considered, there is an increase of about .64 in the average number of inversions required. The curve is more irregular near its point of origin; and the values are exact up to six loci. Accordingly, for values above six it seems safest to start with the value 3.036 (for 6) and add to it $.64(n-6)$, where n is the number of loci concerned.

The standard deviations shown in the table give a less regular curve when plotted, but it is clear that they are increasing only slowly. It may probably be assumed that σ will not be greater than 1 for values up to $n=15$—beyond which it is unlikely that the present problem will require a solution for many years. This means that the spread is not great—in other words, that any random sequence is unlikely to require a number of inversions much different from the calculated one. If a number much less is in fact encountered, it may be concluded that there is a significant degree of resemblance. This method has been applied to the sequence differences between *melanogaster* and *pseudoobscura*, with the result shown in table 4. Evidently the two species are not more alike than could easily result from chance alone.

TABLE 4

Comparison of the required and calculated numbers of inversions to change the melanogaster into the pseudoobscura sequences.

ELEMENT	A	B	C	D	E	TOTAL
Loci	13	6	6	6	7	
Inversions required	7	2	4	3	3	19
Inversions calculated	7.6	3.0	3.0	3.0	3.7	20.3

In any series of successive loci, each locus has two neighbors, and each of these may be either "right" or "wrong"—that is, may or may not be one that lies adjacent to the given locus in the arbitrarily chosen standard

ordinal sequence. For a terminal locus there is only one adjacent locus, but the terminal position itself may be taken as constituting a "connection" and then may be treated in the same way, a "right connection" here meaning that the terminal locus is not only terminal in the chosen standard sequence but also lies at the same end (proximal or distal). There are then n+1 "connections" in any sequence of n loci. It may be shown that in any series of random arrangements the average number of "right" connections is two, regardless of the value of n. It is also evident that any single inversion changes two and only two connections, since it has two ends, each of which must fall in a connection. These two relations are very helpful in working out the consequences of successive inversions. The conception of "right connections," however, is responsible for the incorrect conclusion drawn by STURTEVANT and TAN. One of the right connections appearing in their comparison has now disappeared, as a result of the revision of the *pseudoobscura* sequence recorded above (it may be noted that this revision does not change the number of inversions required to transform one sequence into the other). The result now is that there are 13 "right" connections (that is, identical in the two species) where ten are expected (two in each of the five elements) on chance alone. The difference is probably not a significant one.

This analysis does not take into account the distances concerned—a connection may be assumed to be like in two elements regardless of the amount of crossing over shown. Thus, in element B, jaunty and hook are adjacent in the series of corresponding genes both in *melanogaster* and in *pseudoobscura;* but the crossover values are 5.2 and 23.1, respectively. In such a case, it is probable that further corresponding loci will show that the sequence resemblance is an accidental one. For certain pairs of loci that lie quite close together, the situation is different, as may now be shown.

Yellow and scute are quite near each other in *melanogaster, simulans, pseudoobscura, virilis, ananassae,* and *willistoni;* they are separated by other loci in *affinis.* (Unpublished data of DR. W. P. SPENCER indicate that they are also separated in *hydei.*) Notch and white are from one to four units apart in *melanogaster, simulans* (Notch is not known here, but facet serves to identify its locus), *ananassae, montium, hydei, virilis,* and *pseudoobscura.* Miniature and dusky give few if any crossovers in *melanogaster, ananassae, pseudoobscura,* and *virilis.* It may be noted that these are all short distances, not only in terms of crossing over, but also in terms of the salivary gland chromosome maps of *melanogaster,* which is the only species for which element A is adequately known in the salivary glands.

It may be concluded that inversions with end-points falling within these short sections have not become established during the differentiation of

these species, except for those between yellow and scute in *affinis* and in *hydei*. It may be observed that all three sections appear to exist intact in both of the subgenera studied, since *virilis* and *hydei* belong to Drosophila while all the other forms named are members of the subgenus Sophophora. Evidently, then, these sections represent associations of loci that have been in their present conditions for a very long period of time.

DISCUSSION

The essential argument showing the improbability of the incorporation of a translocation into a population has been published a number of times and has been prevalent in genetic thought since an earlier date; nevertheless, it seems opportune to recapitulate it briefly here, with specific reference to the Drosophilas.

Translocations have been observed to occur spontaneously under laboratory conditions (all the Drosophila translocations discovered prior to the advent of the X-ray technique fall in this category) and, in the few cases mentioned below, have been found in natural populations. It seems not unreasonable to assume therefore that they continually arise in nature with some very low frequency. Once having arisen, such a translocation would exist in the heterozygous state and thereafter chiefly in the heterozygous rather than homozygous state. The extensive studies on such rearrangements in Drosophila have amply demonstrated the selective disadvantage which their heterozygotes must suffer as a consequence of their production of unbalanced gametes. Thus a certain number of translocated chromosomes along with a number of normal chromosomes is lost in every generation; the percentage loss of the former may be considerable because of its low total frequency, whereas the percentage loss of the latter is usually insignificant. In this way selection discriminates against the less prevalent arrangement, progressively decreasing its frequency until it is wiped out.

It follows that the sole opportunity for a translocation to become established lies in its attaining a percentage frequency sufficiently great so that the discrimination of selection is not adequately expressed before chance changes the ratio of the frequencies in favor of the newer arrangement, whereupon the original is eliminated. A high percentage frequency can be reached only when the total number of chromosomes is low—that is, when the population size (N) is small. Furthermore, the population size must be small for chance to upset the ratio of the two arrangements in favor of the newer type.

For reciprocal translocations in which only the completely balanced types survive, WRIGHT (1940) has shown that fixation is difficult unless N is very low. Certain types of translocations might be expected not to

encounter such drastic adverse selection, by virtue of the viability and fertility of individuals possessing an unbalanced (that is, heterozygous for a duplication or a deficiency or both) complement of chromosomes (STURTEVANT 1938b). The effect of this condition is to decrease the selection against the new arrangement and so to increase the maximum population size into which it might be incorporated. PROFESSOR WRIGHT has given us his kind permission to present here some more exact probabilities which he has calculated as an extension to his previous statements (WRIGHT 1940). For a translocation whose unbalanced products are completely inviable, the probabilities of fixation are of the order of 10^{-3} if $N=10$, 2×10^{-6} if $N=20$, and 3×10^{-14} if $N=50$. In the most favorable case, when the heterozygous unbalanced products are both viable and fertile (only the homozygous deficiencies being eliminated), the probabilities are roughly 3×10^{-3} in populations of 20, 4×10^{-6} in populations of 50, and 3×10^{-10} in populations of 100. For the case of a small insertional translocation whose homozygous duplication product is not always accompanied by a homozygous deficiency and consequently may be viable and fertile, the probabilities must be somewhat greater than those given for the last case. Nevertheless, they are still very small and cannot greatly increase the maximum values indicated for N in the last case.

The various factors involved in the incorporation of a translocation into a population may be summarized as follows:

1. The translocation must occur in at least one of the individuals of a subpopulation. As N becomes smaller, the probability of this event becomes smaller, the relation being an approximately linear one.

2. The translocation must become incorporated into the whole subpopulation. N must be very small (see figures above); as N increases, the probability decreases rapidly.

3. The subpopulation must not become extinct. As the value of N increases, the probability that the subpopulation will survive increases.

4. The translocation must maintain itself in the descendants of the subpopulation, in competition with normal chromosomes that may be introduced by interbreeding with other subpopulations. As N increases, this probability also increases, since each introduced chromosome has a smaller effect on the composition of the subpopulation.

The third factor might be omitted, since it could be treated merely as decreasing the total number of subpopulations concerned. It is included here to emphasize the point that, if there is variability in the size of the subpopulations, the smaller ones are more likely to become extinct than the larger ones.

The final probability of the establishment of a translocation is the product of the four probabilities just enumerated. The first, third, and

fourth components increase with an increase in N, the second decreases very rapidly with an increase in N. The result is that the product of the four must always be very small. The only situation in which the establishment of a translocation seems likely to occur with any considerable frequency—even if a long period of time be assumed—is that in which hermaphroditic individuals frequently self-fertilize—that is, when there are many subpopulations in which N = 1. It would thus seem desirable to have suspected cases of translocation in Drosophila supported by more conclusive evidence than has been considered necessary in the past.

For a translocation to be observed in a natural population, it must be found in the relatively short interval between its origin and its elimination. It seems significant that, despite the extensive genetic and cytological analyses of natural populations of Drosophila, not one translocation has been reported.

In the grasshopper Trimerotropis, CAROTHERS (1931) found a single individual heterozygous for a translocation among fifteen specimens from one locality. A more substantial case from the population standpoint is that reported by WHITE (1940). In 1934 he found a specimen of the grasshopper Metrioptera heterozygous for a translocation and in 1937 recognized the same translocation in some more individuals from the same locality. We are not familiar with the genetic properties of this translocation, with the statistical data for this case, or with the population mechanics of this genus; it therefore seems unwise to discuss the situation further.

Among hermaphroditic plants there are many instances of translocations that have become established. Here, however, the population size may frequently reach the theoretical minimum value of one and remain essentially that for several generations.

A class of "neutral" translocations which might be expected to give non-random segregation in the heterozygote includes those found in *virilis americana* and *virilis texana*, where two elements, ordinarily separate, have fused near the centromere. Such a fusion would seem likely to result, in the heterozygote, in almost completely regular disjunction of the individual rods from their attached homologs. If, in this particular case, there is some slight irregularity in disjunction, it would seem to be more than compensated for by the small sizes of the populations in which these two subspecies are found (PATTERSON, STONE, and GRIFFEN 1940).

RHOADES (1940) has demonstrated the instability inherent in a telocentric chromosome in maize; both the X and fourth chromosomes of *melanogaster*, once considered to have terminal centromeres, have been shown to have two arms (KAUFMANN 1934; GRIFFEN and STONE 1939, 1940). The view of NAWASCHIN (1916) and LEWITSKY (1931) that telo-

centric chromosomes do not exist is considerably strengthened. On this basis, apparent rods in Drosophila have a minute heterochromatic second arm. This arm would then serve as an anchor on which another element, less its centromere, could become attached by translocation, forming a V.

The reverse change, the formation of two rods from a V, demands an additional centromere. STURTEVANT and TAN (1937) suggest that "perhaps the spindle attachment of the Y chromosome is somehow utilized, since the properties of this chromosome allow it to be present as an extra or a fragment without damage to the organism." Means are thus provided for increasing the chromosome number. The one clear instance where such an increase has occurred, in *obscura* Gershenson, involves the breakage of a V-shaped element into two rods.

From the genetic data and metaphase chromosome configurations in *melanogaster, willistoni, immigrans, virilis,* and *pseudoobscura,* it is apparent that they all differ in the associations of their elements. Regardless of the metaphase chromosome configuration that may be assumed ancestral to that of all the Drosophilas, both fusion and fragmentation must have taken place. Although not in complete agreement with the systematic relationships, perhaps the simplest interpretation is that the ancestral type corresponded to the *virilis* configuration, five pairs of rods and a pair of dots. With slight modifications, mostly in the distribution of heterochromatin, this is the most common in the subgenus Drosophila. All other types can be derived by simple fusions of elements and changes in the positions of the centromeres within the elements by inversions, with the exception of *obscura* Gershenson and *ananassae,* as noted above. Within *virilis* itself, a single translocation of this kind has evidently given rise to the configuration found in subspecies *texana;* and two translocations from the *texana* arrangement have produced that of subspecies *americana.* The sequences found within the elements are in agreement with this conclusion (PATTERSON, STONE, and GRIFFEN 1940).

It seems clear that, in general, decrease in chromosome number is more easily brought about than is increase. Accordingly lower chromosome numbers may be regarded as probably (though not necessarily in every case) more recent than higher numbers. This conclusion will hold, however, only in forms—such as Drosophila—in which chromosomes frequently have nearly terminal centromeres, with one arm made up of heterochromatin.

A NOTE ON THE RELATIONS BETWEEN THE SPECIES GROUPS OF SOPHOPHORA

It was suggested by STURTEVANT (1940) that the *willistoni* (AD, BC, EF) and *melanogaster* (A, BC, DE, F) chromosome configurations have been derived from the type now found in *pseudoobscura* (AD, B, C, E, F).

If this be so, the first event was probably the union of elements B and C, to give a hypothetical arrangement AD, BC, E, F. From this, a union of E and F presumably gave the *willistoni* type, while a translocation between AD and E gave the *melanogaster* one.

The hypothetical arrangement, which seems likely to have existed even if the sequence of events was different from that outlined above, has not been reported. In the absence of the identification of the X, it would be listed as the *melanogaster* type; accordingly we have been led to examine the descriptions of the phenotypic characters of the few Sophophoras for which such a report exists. One of them, *D. suzukii*, turns out in fact to be intermediate between the *melanogaster* and *obscura* species groups, as shown in table 5. We are inclined to surmise that this species (recorded by KIKKAWA and PENG (1938) from Japan and China) will be found to have the hypothetical configuration.

TABLE 5

Comparison of some phenotypic characters of the melanogaster and obscura species groups and D. suzukii.

	COLOR	COSTAL INDEX	4TH VEIN INDEX	SECOND ORAL	MIDDLE ORBITAL
melanogaster group	yellow	1.2–2.2	2.2–2.7	long	short
suzukii	yellow	4.0*	2.2	long	long
obscura group	black	2.7–3.0	1.7–2.1	short	long

* The description given by KIKKAWA and PENG lists the costal index as 4.0; their illustration (Plate 32) suggests that this is perhaps a misprint for 3.0, which would make *suzukii* fall within the range of variation of the *obscura* species group.

THE EFFECT OF PERICENTRIC INVERSION ON THE ELEMENTS

None of the changes discussed above interferes with the integrity of the elements. There remains, however, one mechanism which may exchange genic material from one element to another. If two elements are united to form a V, an inversion across the centromere (pericentric) will shift genes from one to the other, and *vice versa*. Heterozygotes for this type of inversion are at a selective disadvantage because single crossovers within the inverted section produce inviable duplication-deficiency zygotes, thus leading to a situation similar to that of translocations. However, if crossing over be hampered, either by the nature of the inversion or by the presence of a crossover suppressor, the new arrangement may become established in the population. The products of a subsequent separation of these two limbs will simulate the effects of a reciprocal translocation.

MILLER (1939) has recorded such an inversion in *algonquin*, occurring with a high frequency in eight out of nine localities studied between Quebec, Canada, and Wooster, Ohio. In this case, only one element (E) was

TABLE 6

Summary of the corresponding mutant types in the different species.

ELEMENT A

melanogaster	*simulans*	*pseudoobscura*	*affinis*	*virilis*	*ananassae*	other species
yellow	yellow	yellow	yellow	yellow	yellow	*busckii, willistoni*
scute	scute	scutellar	scute	scute	scute	*busckii, takahashii, willistoni*
prune	prune					
white	white	white	white	white	white	*busckii, hydei, montium*
facet	facet					
Notch		Notch		Notch	Notch	*busckii, funebris, hydei,*
echinus		echinus		echinus?		[*montium*
bifid						*willistoni* (triple)
ruby	ruby			magenta?		
crossveinless	crossveinless			crossveinless		
vesiculated	vesiculated			vesiculated?		
cut	cut	beaded	cut	ragged?	cut	
singed	singed	forked		singed	singed?	*busckii, willistoni* (forked)
ocelliless	ocelliless					
lozenge	lozenge	glazed		glazed, rugose		[*montium? willistoni*
vermilion	vermilion	vermilion	vermilion	vermilion	vermilion?	*busckii? funebris, hydei?*
miniature		miniature	miniature	miniature	miniature	*busckii, takahaskii*
dusky	dusky	dusky		dusky	dusky	*algonquin*
garnet	garnet			apricot?		
rudimentary	rudimentary			rudimentary		*willistoni* (square)
forked	forked	singed		forked	forked?	*busckii, funebris? willistoni*
Beadex		Pointed		Beadex	Beadex	[(stubby)
fused	fused					
bobbed	bobbed	bobbed	bobbed	bobbed	on chrom. IV	*hydei, funebris*

ELEMENT B

melanogaster	*simulans*	*pseudoobscura*	*affinis*	*virilis*	*ananassae*	other species
dachsous				dachsous		
net		tangled	net	plexus	plexus	
Star		Rough		Star		
Curly		Curly				
dumpy	Truncate		truncate	Clipped		
dachs						*willistoni* (approximated)
abrupt		incomplete				
black	black			black?		
jaunty		jaunty	jaunty			*montium* (curled)
reduced				reduced		
hook		hook				

ELEMENT C

melanogaster	*simulans*	*pseudoobscura*	*affinis*	*virilis*	*ananassae*	other species
straw	straw		straw	straw		
apterous						*willistoni*
cinnabar		orange	cinnabar	scarlet?		*athabasca, algonquin, funebris*
vestigial	vestigial-nick	Jagged		vestigial		*willistoni* (Clipped, Scalloped)
gap					gap	
curved		curved				
arc	arc					
plexus		plexus		branched?		*montium*
brown		purple		eosinoid		
Plum					Plum	
lanceolate		narrow	narrow			
	polychaete	polychaete, Scute				

ELEMENT D

melanogaster	*simulans*	*pseudoobscura*	*affinis*	*virilis*	*ananassae*	other species
veinlet		short	veinlet	short veins		*willistoni* (short)
javelin	javelin	slender				
Henna				Garnet		
sepia	sepia	sepia				
hairy			hairy			
tilt		tilt	tilt			
scarlet	scarlet	scarlet	scarlet	cinnabar?		
ascute		ascute	ascute	hunch		
r. incompletus	r. incompletus	snapt				*willistoni* (stump)
		compressed		telescoped		*willistoni* (deformed, serrate)
		sex-ratio	sex-ratio			*athabasca, azteca, melanica, obscura*

ELEMENT E

melanogaster	*simulans*	*pseudoobscura*	*affinis*	*virilis*	*ananassae*	other species
pink	peach	pink, claret?	pinkish, claret?			
curled		upturned				*montium* (curled-b)
Stubble		Stubble				
bithorax		bithorax	bithorax			*athabasca*
aristapedia	aristapedia	aristapedia				
glass		glass		varnished		
Delta	Delta	Smoky	Delta	Confluent, Delta	Plexate	*busckii, montium* (Confluent)
Hairless	hairless					*funebris, montium*
cardinal		cinnabar			cardinal	*azteca*
crumpled		crumpled	crumpled	concave		
claret	claret	claret, pink?	pinkish, claret?	brick?		
		Bare			Off?	
		pauciseta	pauciseta			
				Puffed	Puffed	

ELEMENT F

melanogaster	*simulans*	*pseudoobscura*	*affinis*	*virilis*	*ananassae*	other species
abdomen rotatum			abdomen rotatum	abdomen rotatum		
grooveless		grooveless				
shaven	Shaven		reduced?	stubby	Shaven	
Minute-4	Minute-4					

involved (this element being a V in this species), and another associated inversion acted as a crossover suppressor. The fact that this inversion has been found to have a high frequency makes more probable the occurrence of similar inversions in other species where a V is composed of two different elements.

It is self-evident that the scheme of the integrity of the elements must break down for the more distantly related species of the Diptera. Where this will first happen is not clear. The common metaphase chromosome configuration among the higher Diptera has six chromosomes; whether these are the Drosophila elements with a few alterations or whether they represent quite different gene combinations can be answered only after a more thorough analysis of their genetics is made.

SUMMARY

The six chromosome arms of *D. melanogaster* (X, IIL, IIR, IIIL, IIIR, IV) retain their essential identity among the species of Drosophila so far studied. They are here called "elements" and are designated by the letters A to F in the order just stated.

The corresponding mutant genes on which this conclusion is based are summarized in table 6 of this paper; and the relation of the letter designations to the various chromosome terminologies previously used is summarized in table 1.

Element E is consistently the longest of the six, when studied in the salivary gland chromosomes; element F is always very short. The others are so nearly the same in size that their lengths are not diagnostic.

Analysis of the mathematical properties of sequences subjected to repeated inversions indicates that, in the specific case of *melanogaster* and *pseudoobscura*, the sequences are not significantly more alike than might result from chance.

Three pairs of loci—yellow and scute, Notch and white, miniature and dusky—apparently represent sections which have remained intact over a long period, since the two members of each pair are associated in numerous species and in representatives of both subgenera studied. Yellow and scute are separated, however, in *affinis* and in *hydei*.

The conclusion that the elements remain intact within the group means that few or no translocations have become established in the history of these two subgenera. Analysis of the conditions necessary for such establishment leads to the conclusion that the supposed instances of its occurrence as between species are not adequately established—with the exception of the attachment of part of element A to element F in *ananassae*.

The various ways in which the elements are attached to each other may be supposed to result from a special type of translocation in which both breaks occur in heterochromatin near the centromeres. Under the conditions found in most Drosophila species, this type of translocation more easily decreases chromosome number than increases it. It may be surmised that the configuration found in *virilis* (where all six elements are separate) is the most primitive one among those yet analyzed in Drosophila.

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