A NEW RACE OF *DROSOPHILA MIRANDA*

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(With Forty-three Text-figures)

Introduction

Drosophila miranda is a species closely related to *D. pseudoobscura*, and almost always produces sterile hybrids when crossed to the latter. The morphological, physiological, and cytological differences between the two species were described by Dobzhansky (1935*b*). *D. pseudoobscura* has, in both sexes, an even number of chromosomes, namely ten, and a regular X–Y sex-determining mechanism. In *D. miranda*, the male has nine and the female ten chromosomes; the male has one heteromorphic chromosome pair (X^1–Y) and one odd chromosome (X^2), while in the females there are two X^1 and two X^2.

Until recently the known geographical distribution of *D. miranda* was restricted to the Puget Sound region (Brinnon, Lake Quinault, Quilcene, Seattle in the State of Washington, and Cowichan Lake on Vancouver Island, British Columbia). In the summer of 1937, however, the species was found in a canyon on the eastern slope of Mount Whitney, Sierra Nevada, California (Dobzhansky & Koller, 1938). In the present paper evidence is presented to show that the population of Mount Whitney belongs to a race distinct from the population of the same species inhabiting the Puget Sound region. The two races will be referred to as "Whitney race" and "Olympic race" respectively.

Morphology

D. miranda differs from *D. pseudoobscura* in various morphological characters, such as size and coloration of the body. In both species the proximal sex comb (located on the first tarsal joint) is larger than the distal one (situated on the second tarsal joint). There are more teeth in the proximal sex comb of *D. miranda* than in that of *D. pseudoobscura*. The mean numbers of teeth in the sex combs of the different races of the two species are given in Table I.

The data show that males of Whitney race seem to have fewer teeth in the distal and proximal sex combs than do males of Olympic race, but

statistical analysis indicates that this difference is not significant, since the same kind of differences were observed between strains within each race. These variations, being present under controlled environmental conditions, are genetic in nature. The size of the sex comb is a quantitative character, and by analogy with other quantitative characters it is probably determined by multiple factors or modifiers. The range of variations in the size of the sex comb found in various strains may be due to the fact that populations of these strains are genetically heterogeneous.

TABLE I

Mean number of teeth in the sex combs

		Sex comb			
Species	Race	Distal	Proximal	*n*	Author
D. pseudoobscura	A	5·22 ±0·05	6·57 ±0·05	165	Dobzhansky (1936)
	B	4·81 ±0·06	6·77 ±0·06	88	Dobzhansky (1936)
D. miranda	Olympic	5·80 ±0·06	8·44 ±0·07	132	Dobzhansky (1936)
	Olympic	5·27 ±0·07	7·45 ±0·07	150	Koller (1938)
	Whitney	4·87 ±0·06	7·53 ±0·10	125	Koller (1938)

It was found, furthermore, that a decrease in the size (or number of teeth) of one sex comb is not accompanied by a simultaneous increase in the size of the other, i.e. the variations are independent.

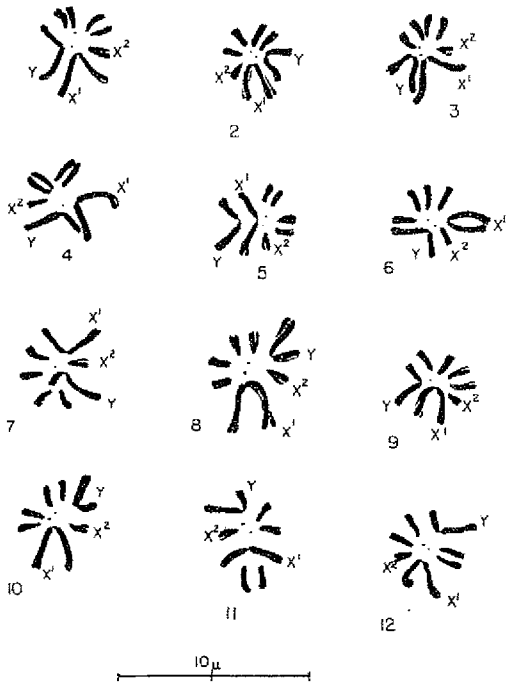
Various experiments were undertaken to determine the degree of sexual isolation between the two races of *D. miranda* (Dobzhansky & Koller, 1938). In one experiment ten females of each race were placed in a vial together with ten males, of either the same or the other race. After 4 days' exposure the intraracial matings were found to be more frequent than the interracial ones.

Chromosome homology

In order to determine whether structural differentiation has taken place in the chromosomal apparatus, chromosomes of the Olympic and Whitney races were compared (1) during the mitotic cycle, (2) in the salivary gland nuclei, and (3) during spermatogenesis in interracial hybrids.

(1) *Mitosis.* The chromosomes of *D. miranda* closely resemble those of *D. pseudoobscura*. In the female there are a pair of V-shaped *X* chromosomes, three pairs of rod and one pair of dot chromosomes. In the male besides the V-shaped *X* and *Y*, which differ in the ratio of the lengths of the two arms, there are only two pairs of rod chromosomes; the third rod is without a partner and hence it is designated as X^2 by Dobzhansky (1935*b*).

The only difference detected in the chromosome apparatus of the two races concerns the *Y* chromosome. It seems larger in the Whitney race (Figs. 1–3) than in the Olympic race (Figs. 7–9). The spindle attachment or centromere is submedian in both races, the chromosome having two arms. In Whitney the ratio is about 4 : 5, in Olympic race it is 3 : 5. The same difference was observed in the male sex of the reciprocal hybrids; a larger *Y* chromosome is present in the chromosome complement when a



Figs. 1–12. Camera lucida drawings of chromosomes in the male *Drosophila miranda*. Figs. 1–3. Whitney race. Figs. 4–6. Olympic ♀ × Whitney ♂ hybrid. Figs. 7–9. Olympic race. Figs. 10–12. Whitney ♀ × Olympic ♂ hybrid. × 2300.

Whitney male parent is used (Figs. 4–6), and a smaller *Y* when the male parent belongs to the Olympic race (Figs. 10–12). The other sex chromosomes X^1 and X^2 and the autosomes are apparently alike in both races with respect to their external morphology.

During metaphase of mitosis the homologous chromosomes usually lie side by side showing somatic pairing. The presence of an odd chromosome in the male does not interfere with the somatic pairing. The X^2 chromosome frequently lies next to the X^1 (Figs. 1–3, 5, 9, 12) or between X^1 and *Y* chromosomes (Figs. 6–8, 10, 11) and sometimes it was found

beside the Y (Fig. 4). According to Dobzhansky (1935*b*) the X^2 lies more frequently between the two autosomal pairs. The position of X^2 in 147 cells is analysed and is given in Table II.

The frequency of the expected position of X^2 was calculated on the assumption that it is at random. A comparison of the observed and expected frequencies, however, indicates that the position of X^2 is not due to chance alone; the juxtaposition of X^2 and X^1 may be an expression of a closer relationship. The frequency of those cells in which chromosomes show somatic pairing is about 70–75 % in the pure races. Somatic pairing is apparently not disturbed in the hybrids.

(2) *Salivary gland chromosomes.* In the nuclei of the salivary gland of *D. miranda* five long strands and a very short one are present. Two of the longer strands correspond to the two arms of the X, and the very short

TABLE II

The various position of X^2 *chromosome during mitotic metaphase*

	X^1X^2Y	YX^2A	X^1X^2A	AX^2A	Total
Whitney ♂	12	4	9	5	30
Olympic ♂	8	6	13	7	34
$\frac{\text{Whitney ♀}}{\text{Olympic ♂}}$ F_1 ♂	10	7	10	9	36
$\frac{\text{Olympic ♀}}{\text{Whitney ♂}}$ F_1 ♂	16	9	13	9	47
	46	26	45	30	147

	X^2X^1	X^2Y	X^2A	X^2A	Total
Observed	91	72	65·5	65·5	294
Expected	73·5	73·5	73·5	73·5	294

$\chi^2 = 6{\cdot}0278$. D.f. $= 3$. $P = 0{\cdot}20$–$0{\cdot}10$.

strand represents the small dot chromosome. In the male, three of the longer strands are single; two of them correspond to the arms of X^1 and the third to the X^2 chromosome.

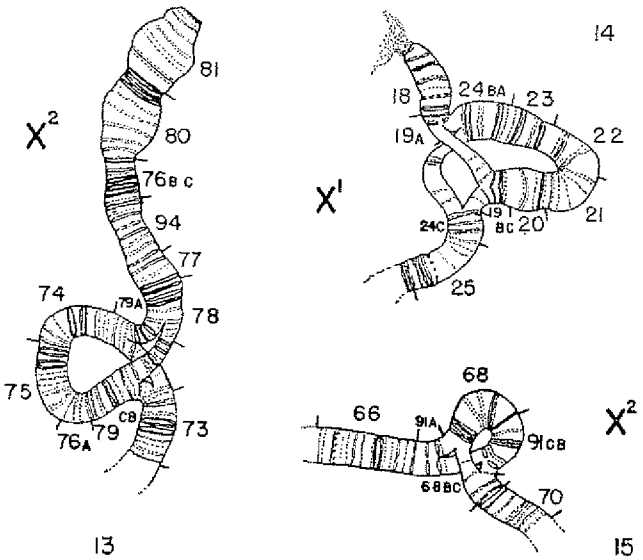
The analysis of the salivary gland chromosomes in the *D. miranda* and *D. pseudoobscura* hybrids has shown that the third chromosome of the latter corresponds to the X^2 of *miranda* (Dobzhansky & Tan, 1936). Besides numerous inversions, two translocations were identified as being responsible for the profound modification of the disk patterns and for the failure of chromosome pairing in the salivary gland cells. The gene arrangement in the distal region of the X^2 of Olympic race is inverted as compared with that in the third chromosome of *pseudoobscura*. The proximal breakage point is in the segment designated as 76, the distal lies between sections 79 and 80. (The numbers refer to the sections of the third chromosome of *D. pseudoobscura* in the salivary gland nucleus

numbered by Dobzhansky & Tan, 1936.) Thus, the standard gene arrangement in *D. pseudoobscura* and of Olympic *miranda* are as follows:

D. pseudoobscura ...73, 74, 75, 76 ABC, 77, 78, 79 ABC, 80, 81.
D. miranda (Olympic)...73, 74, 75, 76 A/79 CBA, 78, 77, 94, 76 CB/80, 81.

The inverted region includes also the small translocated portion of the segment 94 from the fourth chromosome of *D. pseudoobscura*.

The gene arrangement of X^2 in Whitney race differs from that of Olympic race by still another inversion, which extends from segment 74 to 79 A. The two inversions are overlapping in the short segment



Figs. 13–15. Inversions in X^2 and X^1 chromosomes.

79 CB. The gene arrangement in the X^2 of Whitney race is, therefore, as follows:

73/79 BC, 76 A, 75, 74, 79 A/78, 77, 94, 76 CB, 80, 81.

The other inversion (Fig. 15) is located near to the proximal end of X^2, and involves only parts of two sections, one of which sections is identified as 91 of the fourth chromosome. The gene arrangement in the two races is represented as follows:

Olympic ...66, 91 ABC, 68 ABC, 70.
Whitney ...66, 91 A/68 A, 91 CB/68 BC, 70.

In the Whitney population of *D. miranda* both the Olympic and the Whitney gene arrangements were observed in the X^2 chromosome.

While some larvae were heterozygous for both inversions, others were homozygous for one and heterozygous for the other, which indicates that crossing-over occurs between these two inversions. So far only a few individuals of the Whitney race have been tested and it is not improbable that more inversions may be found in X^2, in view of the fact that seventeen different gene arrangements were found by Dobzhansky & Sturtevant (1938) in the third chromosome of *pseudoobscura*.

A third inversion present only in the interracial hybrids was found in the right arm of X^1. The portion of the chromosome which lies between the chromocentre and the proximal breakage point is very small. The gene arrangement in the two races is as follows:

Olympic ...18, 19 ABC, 20, 21, 22, 23, 24 ABC, 25.
Whitney ...18, 19 A/24 BA, 23, 22, 21, 20, 19 CB/24 C, 25.

In the material at our disposal no other differences were detected between the gene arrangements of the two races.

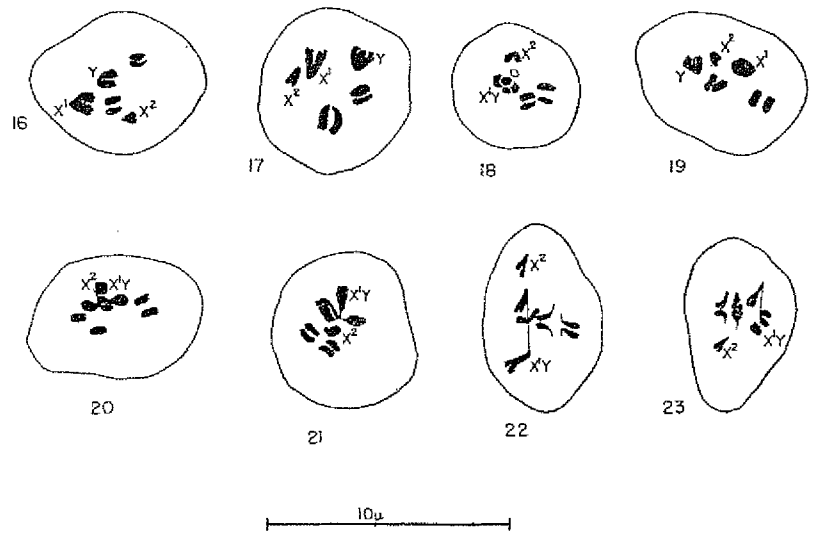
(3) *Chromosome behaviour during meiosis*. The chromosome behaviour during spermatogenesis in the Whitney race is similar to that found in the Olympic race by Dobzhansky (1935*b*). The chromosomes are clearly visible at late diakinesis, as bivalents, except the X^2, which is frequently represented as a single chromosome. The autosomes have four chromatids equally paired throughout their length without chiasmata. According to Darlington (1934) this condition is brought about by exaggerated somatic pairing. The X^1 and Y chromosomes, on the other hand, are associated by two reciprocal chiasmata which are formed on either side of the centromere. During diakinesis four clumps or bodies can be distinguished in the nuclei (Fig. 21); the largest of them, which is frequently cruciform, represents the X^1–Y bivalent, whereas the others correspond to the two autosomal bivalents, and the single X^2 chromosome. The dot-like chromosomes, owing to their small size, were seen at meiosis only in a few preparations.

During metaphase, the sex and autosomal bivalents are arranged in an equatorial plate (Figs. 22, 23). The position of the single X^2 varies within the spindle. Dobzhansky found that in Olympic race X^2 commonly lies off the equatorial plate. In some primary spermatocytes X^2 chromosome was identified lying even near to one pole. In Whitney race X^2 also lies off the equator, but it has been found not infrequently amongst the autosomal bivalents.

At anaphase, the members of bivalents disjoin and segregate to the opposite poles. Morphologically the X^1 and Y chromosomes are so much alike that it is difficult to distinguish them at this stage. Indirect

evidence was presented, however, by Dobzhansky to show that X^2 almost always passes together with X^1 to the same pole and that both chromosomes are included in the telophase group of four chromosomes. The Y chromosome, on the other hand, moves to the opposite pole, which consequently receives three chromosomes. The result of this "determinate segregation" is that only two kinds of gametes are formed in *D. miranda* during spermatogenesis, namely X^1X^2 and Y gametes.

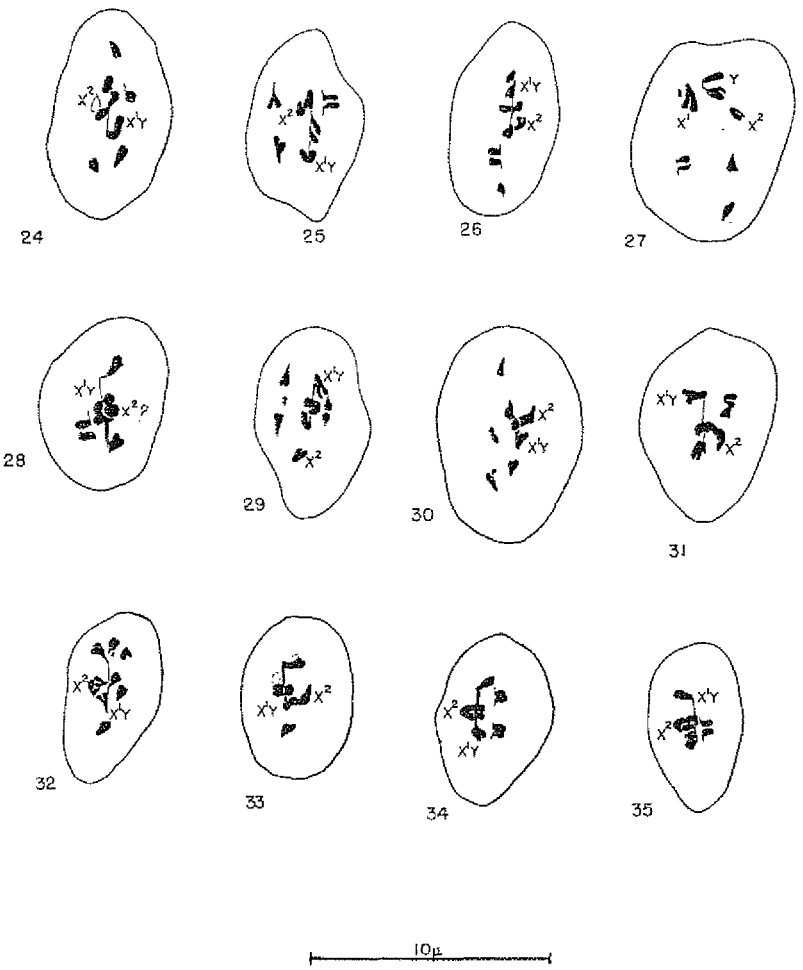
The above description fits the spermatogenesis in the pure races as well as that of the hybrids at 18–20° C. When, however, the hybrid larvae are reared at 24–26° C. chromosome behaviour is greatly affected.



Figs. 16–23. Diakinesis and metaphase of meiosis. The sex chromosomes are marked.

Unpaired chromosomes are present during diakinesis in varying numbers. At this stage the nucleus of primary spermatocytes being large, the number of bodies within it can easily be counted. When their number is greater than four, some univalent chromosomes must be present. Besides the increased number, the size of the bodies also may suggest that they are single chromosomes. Several spermatocytes were encountered in which only the X^1, X^2 and Y chromosomes are left unpaired (Figs. 16, 17, 19), while the other chromosomes are associated into pairs. Other instances were observed in which X^1 and Y form a bivalent but the autosomes are present as single chromosomes (Fig. 20). In some spermatocytes single autosomes have been seen to lie adjacent to each other (Figs. 19, 20). They may represent the two homologues and the adjacent

position may be due to chance alone. However, in view of several observations made in *Lilium* hybrids (Ribbands, 1938), in asynaptic *Crepis* (Richardson, 1935), maize (Beadle, 1933) and *Pisum* (Koller, 1938) it may be permissible to make the following suggestion. Since



Figs. 24–35. The first meiotic metaphase in Olympic ♀ × Whitney ♂ hybrids. Several unpaired chromosomes and a few "tripartite" sex-chromosome complexes are shown.

in these plants the juxtaposition of homologous chromosomes was taken as an indication of their previous association, which failed to persist to the end of metaphase as it does normally, it is possible that in *D. miranda* hybrids the juxtaposition of single chromosomes is similarly due to a precocious separation of the two homologues that constituted a

bivalent. If this is the case, then the distance between the corresponding chromosomes may indicate the duration of the time which has elapsed between the termination of association and the stage in which the cell was fixed. Thus chromosomes seen lying far apart may have been separated earlier than those which lie in close juxtaposition.

During metaphase the number of single or "univalent" chromosomes can easily be counted. Frequently they are found at the poles while the bivalents occupy the equator (Figs. 24, 30, 32). Fig. 27 shows a primary spermatocyte with three single sex chromosomes grouped together; the equatorial plate is apparently absent, and the spindle is irregular, and bivalents, if they are formed, may lie excentrically (Figs. 25, 26). A symmetrical position of two univalents as they lie oriented towards opposite poles is seen in some spermatocytes (Figs. 24, 25, 27, 29, 30). A similar chromosome arrangement was found in *D. pseudoobscura* (Darlington, 1934) and in pure races of *D. miranda*. However, spermatocytes showing univalents which are scattered at random are more frequent in the *D. miranda* hybrids (Figs. 24, 26, 30, 31, 33).

TABLE III

The frequency of normal and irregular primary spermatocytes during diakinesis and metaphase in hybrid males at 24° C.

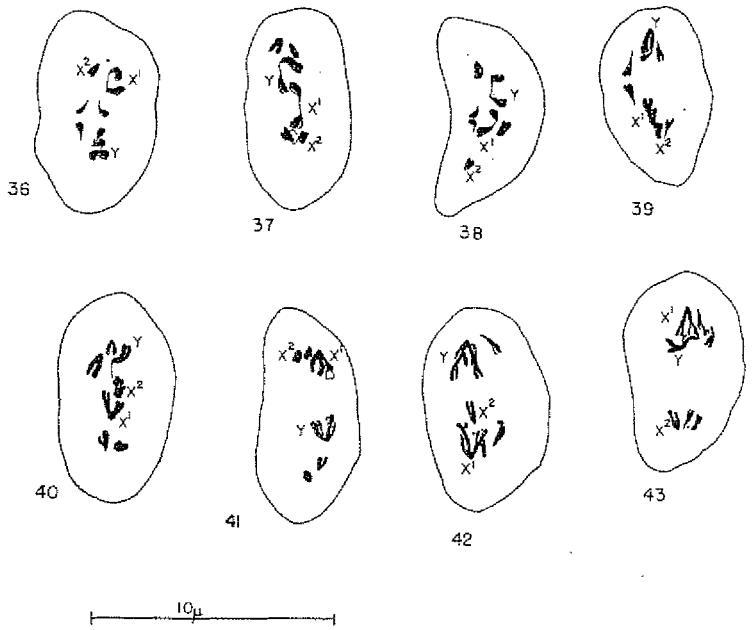
Stages of meiosis	No. of spermatocytes: Normal*	Irregular	*N*
Diakinesis	17 (18·28)	76 (81·72)	93
Metaphase	40 (29·85)	94 (70·15)	134
	Total 57 (25·11)	170 (74·89)	227

* Percentage is given in brackets.

A few of the spermatocytes were found to contain an even number of single chromosomes. Such cases naturally suggest the possible association of the X^2 with the sex chromosomes and the formation of a "trivalent" chromosome group. In these spermatocytes the structure of the sex-chromosome complex was carefully analysed and X^2 appeared to be associated with the X^1Y bivalent to form a tripartite structure. Whether the association is a real one or is due only to the fact that X^2 accidentally lies near to the X^1Y complex is very difficult to ascertain, since the chromosomes are too small to allow a critical study (Figs. 28, 30–35). Instances when X^2 lies close to XY complex are none too rare in the spermatocytes of pure races.

It is often impossible to draw a sharp distinction between metaphase and anaphase, since metaphase plates with several univalents distributed

within the spindle may look like anaphase, while on the other hand, bivalents may be present at early anaphase (Figs. 27, 30). During late anaphase, however, a definite grouping of chromosomes can be seen, the spindle attachment regions of four chromosomes being directed towards one pole, those of the three others towards the opposite pole (Figs. 36, 38–40). When the number of chromosomes at the poles at telophase was counted in a sample of cells, the counts indicated a normal segregation in



Figs. 36–43. Anaphase of the first meiotic division in the interracial hybrid showing normal segregation of chromosomes.

most cases. The number of spermatocytes showing normal and irregular chromosome behaviour during metaphase and telophase is given in Table IV.

A statistical analysis of the above data shows that (1) different individuals are alike in respect of chromosome behaviour, (2) there is no difference between reciprocal hybrids, and (3) the sex chromosomes (X^1 and Y) do not form bivalents as frequently as do the autosomes.

Only six spermatocytes were found which did not show the regular 3 : 4 chromosome distribution at early anaphase; two spermatocytes have 1 : 5 at the opposite poles. One spermatocyte was encountered showing non-disjunction of the X^1 and Y chromosomes at telophase (Fig. 43). In

some instances only one chromosome was seen to be lagging at anaphase (Figs. 40, 42).

The number of spermatocytes which are expected to have unbalanced chromosome number at telophase was calculated on the basis of the data showing the frequency of the bivalents and the univalents at metaphase, assuming that any two univalents are as likely to pass to the same pole as to the opposite poles (Table V).

TABLE IV

The number of spermatocytes showing normal and irregular chromosome behaviour during metaphase and telophase in hybrid males at 24° C.

Cross	Individuals	Metaphase* no. of single chromosomes						Telophase†	
		0‡	1	2	3	4	5	7	3–4	2–5
Olympic ♀ × Whitney ♂	A	2	6	2	8 (2)	1	4 (1)	4 (4)	20	1
	B	1§	4	1§	3	—	1	1 (1)	8	1
	C	—	4	1	4	—	1	—	16	—
	D	2	3	2	8 (1)	1§	3	—	3	—
	Total	5	17	6	23 (3)	2	9 (1)	5 (5)	47	2
Whitney ♀ × Olympic ♂	A	—	3	1	4	—	—	1 (1)	7	—
	B	2	1	—	9 (1)	—	4	—	7	—
	C	—	1	—	5 (1)	—	2 (1)	—	6	1
	D	2	3	1§	6 (1)	—	2 (1)	—	9	1
	E	1	5	1	9 (1)	—	6 (1)	1 (1)	12	—
	Total	5	13	2	33 (4)	—	14 (3)	2 (2)	41	2

* Numbers in brackets indicate sex chromosomes.
† Chromosome number in the two telophasic groups is given.
‡ X^2 chromosome is amongst the autosomes.
§ X^2 is associated with X^1Y bivalents, case analysed.

TABLE V

The observed and expected frequency of the normal and irregular distribution of chromosomes at telophase

	No. of chromosomes at opposite poles		
	3–4	2–5 or 1–6	Total
Observed	88	6	94
Expected	74·7528	19·2472	94

$a^2/m = 103{\cdot}595 \pm 1{\cdot}871$. $\chi^2 = 11{\cdot}4660$. $P = 0{\cdot}01$. D.f. $= 1$.

The difference between the observed and expected frequency is very significant; the segregation as seen at telophase proves to be considerably more normal, at least numerically, than might have been expected on the basis of metaphase data. It may be conjectured that segregation following irregular diakinesis and metaphase is only numerically normal, and that a great number of gametes are unbalanced owing to non-disjunction of homologous chromosomes. This assumption, however, requires itself an explanation because it gives no idea as to how a quantitatively regular

segregation is brought about. In order to prove that segregation is not only quantitatively, but also qualitatively regular, hybrid males, reared at 24–26° C., were mated to females of either race and the egg mortality was recorded. It is assumed that zygotes derived from gametes with abnormal chromosome balance are inviable. The data obtained in these experiments were as follows:

	No. of eggs laid	No. of larvae hatched	Percentage of hatching
Olympic × Olympic	500	471	94·2
Whitney × Whitney	177	155	87·5
Whitney × W. ♀/O. ♂	145	127	87·6
Olympic × O. ♀/W. ♂	254	231	91·0

The figures show that segregation is normal not only quantitatively but also qualitatively, and that functioning gametes are produced.

Another possibility which must be taken into consideration is the elimination of the unbalanced secondary spermatocytes and spermatids through cell degeneration. From the observed number of metaphases showing unpaired chromosomes we should expect at least 40–60 % of the secondary spermatocytes to contain unbalanced chromosome sets and therefore to degenerate. No indication of such a process of degeneration was observed in the testes of hybrids, which indicates that spermatogenesis after the first telophase is normal and leads to the formation of viable gametes.

Discussion

The differences found to exist between the two races of *D. miranda* are (1) genic, and (2) chromosomal. The first are manifested in the sexual isolation, and may be considered of great importance because they can lead to further diversification. The chromosomal differentiation is inferred from (*a*) the size of the *Y* chromosome and (*b*) the presence of inversion in the right arm of the X^1 in interracial hybrid.

The *Y* chromosome of Olympic race is apparently smaller than that of *D. pseudoobscura* designated as type I by Dobzhansky (1935*a*). It is characteristic of race B found on Vancouver Island, British Columbia, and in the State of Washington, the territory where Olympic race of *D. miranda* was discovered. The *Y* chromosome of Whitney race corresponds completely to type I of *D. pseudoobscura* race B. Its distribution extends to Sequoia Park, California, which is adjacent to the habitat of Whitney race. The morphological and physiological properties of the various strains of *D. pseudoobscura* and of the two races of *D. miranda* are not affected by the type of *Y* chromosome. These facts suggest that the

differentiation of the *Y* chromosome in the two races may be considered not to be of primary importance.

While there are gross differences between the chromosome apparatus of *pseudoobscura* and *miranda*, the two races of *miranda* differ in respect of only a small region of the right arm of the X^1 chromosome, for this chromosome in the salivary gland nuclei of the hybrids was always found to be heterozygous for the X^1 inversion.

In hybrids bred at 24–26° C., the chromosomes during meiosis show properties which are characteristic of chromosome behaviour commonly found in species hybrids. Single chromosomes or "univalents" are present in varying numbers during diakinesis and metaphase. The remarkable fact is, however, that while in species hybrids such disturbances in chromosome association during the meiotic prophase are usually followed by partial or complete sterility, in *D. miranda* hybrids this is not the case. Secondary spermatocytes with haploid chromosome number, indicating normal segregation, are formed. Such a peculiar chromosome behaviour is apparently unique in the *D. miranda* hybrid; as shown by a special control experiment, in males of the pure races bred at 24–26° C., the meiotic processes are entirely normal.

Several instances are known when environmental changes affected chromosome behaviour in the hybrid. Hollingshead (1932) reported that in *Triticum* hybrids the percentage of pollen mother cells with univalents increased in plants kept in a greenhouse in comparison to those in the field. In *Kniphofia* (Moffett, 1932), *Saccharum* (Bremer, 1923), *Allium* (Modilewski, 1930) and in *Papaver* hybrids (Yasui, 1937), similar changes were observed and attributed to the seasonal variation in temperature. How a temperature change exerts its influence upon meiotic prophase and interferes with chromosome pairing is not known.

The lack of metaphase pairing in the hybrid is followed by a "non-random" distribution of the single chromosomes. A determinate segregation operates during anaphase, causing homologous chromosomes to proceed towards opposite poles, though they might have been unpaired at metaphase. This results in the production of viable gametes which, as we have seen, are qualitatively as well as quantitatively balanced. Apparently the only plausible explanation of this otherwise highly paradoxical situation is to suppose that the bivalents are normally formed at prophase, but the chromosomes composing them fall apart previous to diakinesis and are gradually repelled from each other towards opposite poles. Their drifting apart is not hindered and frequently they are found already at the poles at metaphase, while bivalents are still

seen lying on the equator. The movements of the univalents are directed; they do not merely drift apart, but move towards the poles.

Several cases of determinate segregation of homologous chromosomes without previous association at metaphase are known to occur in various organisms (cf. Wilson, 1928). Recently Klingstedt (1933) found that though the sex chromosomes of some Neuroptera are unpaired during meiotic prophase they always lie at the opposite poles during metaphase.

In view of these facts (including the specific chromosome behaviour in the interracial hybrid of *D. miranda*) the general validity of the assumption that "normal segregation depends on metaphase pairing of the homologous chromosomes" may be questioned. In such cases normal segregation may be assumed to depend upon a prophase pairing which is followed immediately by a drifting of the partners towards opposite poles. Hence the apparent lack of pairing at metaphase does not disturb the normal segregation. It is not improbable that we are confronted in the behaviour of the single chromosomes in the interracial hybrid and in that of the X^2 of the pure races essentially with the same phenomenon. The relation of the X^2 with X^1 and Y and the reason for its orientated segregation to the same pole as X^1 is a matter for future investigation.

Summary

1. A new race of *Drosophila miranda*, designated as the Whitney race, was found on the eastern slope of Mount Whitney, Sierra Nevada, California. Hitherto *D. miranda* was known only in the Puget Sound region (Olympic race).

2. The chromosomes of the two races are similar, except the Y, which is larger in the Whitney race.

3. The position of X^2 chromosome on the equatorial plate during mitosis is apparently not at random; it lies more often adjacent to the other sex chromosomes.

4. Two intraracial inversions in X^2 of the Whitney race and one interracial inversion in the right arm of X^1 chromosome were detected.

5. Spermatogenesis is normal in the interracial hybrids when they are bred at 19–22° C.; X^1 and Y and the autosomes form bivalents during meiosis. X^2 chromosome is apparently independent of the X^1Y bivalent, but always goes to the same pole as X^1.

6. If the hybrids are bred at 24–26° C., several single or univalent chromosomes are present during the meiotic prophase and metaphase. The univalents occasionally lie in juxtaposition.

7. In a few instances chromosome configurations suggesting the association of the X^1Y bivalent with X^2 were observed in the hybrid. The "tripartite" structure of X^1Y and X^2 complex may, however, be due to the fact that X^2 accidentally lies beside X^1Y.

8. The numbers of chromosomes at the opposite poles during telophase of the first meiotic division indicate that the segregation of univalents is not at random. The low percentage of zygotic mortality also suggests that the gametes contain balanced chromosome complements. Hence it is assumed that segregation is normal qualitatively as well as quantitatively.

9. It is suggested that the determinate segregation of univalents may be due to prophase pairing, followed immediately by an early separation of the homologous chromosomes, which then drift gradually towards opposite poles.

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