CHROMOSOME COMPLEMENTS OF SOME SOUTH-BRAZILIAN SPECIES OF DROSOPHILIA

By TH. DOBZHANSKY*' AND C. PAVAN

COLUMBIA UNIVERSITY, NEW YORK, AND UNIVERSITY OF SÃO PAULO, BRAZIL

Communicated August 28, 1943

For the last several months the writers have been engaged in making a preliminary survey of species of Drosophila which inhabit the states of São Paulo and Rio de Janeiro in Brazil. Among the rather numerous species examined, at least two proved to possess chromosomal complements of unusual interest. The purpose of the present note is to put on record an account of the chromosomes in these two as well as in some related species.

We have collected at Bertioga (state of São Paulo) and at Jacarepagua (Federal District) some females of a species apparently identical with *Drosophila prosaltans* Duda.[1] This species breeds well in the laboratory, and strains have been established without difficulty. Acetic orcein smear preparations of nerve cells of larval ganglia and of larval salivary glands have been made. The nerve cell metaphases show two pairs of V-shaped and one pair of rod-like chromosomes (Fig. 1, *A–E*). The V-shaped chromosomes appear equal-armed, one pair being perhaps slightly larger than the other. The centromere constrictions are usually well pronounced; in some cells (Fig. 1, *C, D*) one arm of one of the V's shows a secondary constriction at about the middle of its length, while the other V may show a secondary constriction in one limb in a submedian position. The rod-like chromosomes are about as long as an arm of the V-shaped ones, and have distinctly subterminal centromeres (Fig. 1, *A, B, E*). Metaphase plates in female and male larvae are indistinguishable; this indicates that the *X*- and *Y*-chromosomes are of about the same size and shape. The salivary gland cells show five long chromosome strands radiating from a well-developed chromocenter. In male larvae two of the five strands are paler than the remaining three. The paler strands represent the *X*-chromosome; the *Y*-chromosome is evidently heterochromatic, and the *X*-strands have no paring mates in male cells.

Cells in which the chromocenter has been crushed by the pressure of the cover slip have been examined in order to determine the correspondence between the salivary and the metaphase chromosomes. In such cells the strands corresponding to a V-shaped chromosome frequently remain connected through the portion of the chromocenter formed by their heterochromatic regions. If a sufficient number of cells are examined this "vital artefact" gives data that are conclusive. In *D. prosaltans* most of the chromocentral mass goes with the two strands denoted in figure 2 as *A* and *B*. These two strands are alike in female and male larvae; therefore, they represent a V-shaped autosome. In some larvae of the Bertioga cultures the *B*-strand showed two inversions separated by an uninverted section (see Fig. 2). Two other strands (*C* and X^2 in Fig. 2) remain connected through a small fragment of the chromocenter. Very surprisingly, one of these strands (X^2) proved to be much paler in male than in female larvae, while the other strand (*C*) is similar in either sex. This difference has been seen in many cells, and it is frequently quite striking. One of the V-shaped metaphase chromosomes consists, therefore, of an autosomal and an *X*-chromosome limb. The fifth strand (X^1 in Fig. 2) is also paler in male than in female larvae; in cells with a fragmented chromocenter the X^1 strand lies frequently isolated from other chromosomes, the base having a small amount of heterochromatin. The X^1 strand corresponds to the rod-like chromosome of metaphase plates (Fig. 3).

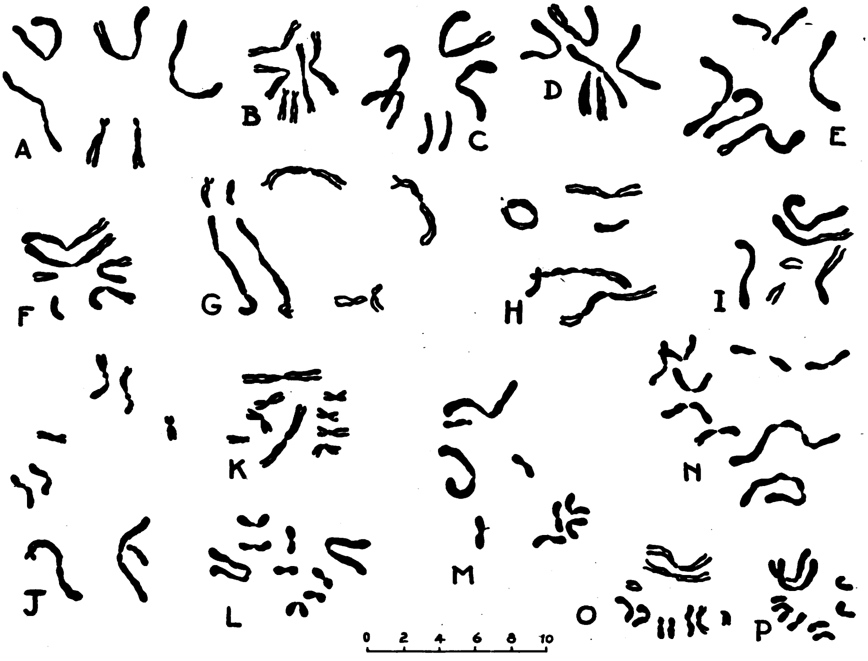

FIGURE 1

Nerve cell metaphases in *Drosophila prosaltans* (*A–E*), *D. sturtevanti* (*F–I*) and *D. annulimana* (*J–P*). The scale below represents 10 micra.

We are forced to conclude that in *D. prosaltans* there are two *X*- and two *Y*-chromosomes: one rod-like and free (X^1–Y^1) and the other attached to an autosomal rod, forming with the latter a V-shaped complex (AX^2–

AY^2). The formula of the female is, consequently, $X^1X^1AX^2AX^2$, and of the male $X^1Y^1AX^2AY^2$. Such a chromosomal structure (Fig. 3) is unique in Drosophila; it must lead to a number of genetic complications. If, during the spermatogenesis, the X^1–Y^1 and the AX^2–AY^2 bivalents disjoin independently, four classes of spermatozoa, X^1AX^2, Y^1AY^2, X^1AY^2, Y^1AX^2, must be formed. The two last classes would give rise to inviable zygotes.

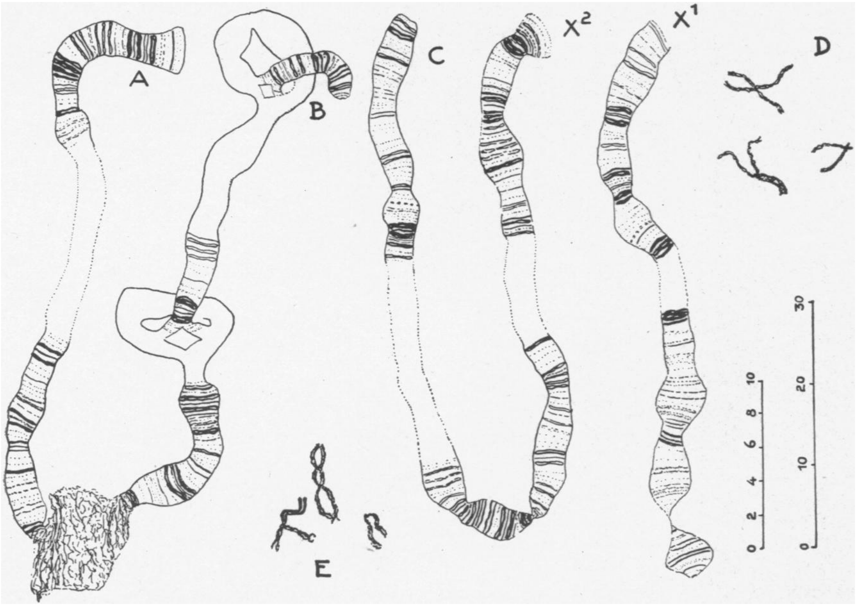

FIGURE 2

Salivary gland chromosomes (A, B, C, X^1 and X^2) and diakinesis configurations (D and E) in *Drosophila prosaltans*. The disc patterns are represented only in the basal and the terminal portions of the salivary gland chromosomes; the relative lengths of these chromosomes are not reflected in the drawings. The 30 micra scale applies to figures A, B, C, X^1 and X^2, the 10 micra scale to D and E.

A somewhat analogous situation is observed in *D. miranda*, where the male is X^1YX^2, but where only two types of sperms are produced; the X^1 and X^2 always go to the same pole, and the Y-chromosome goes to the opposite pole.[2] The Y-chromosome of *D. miranda* contains, however, some material homologous to that contained in the X^1 as well as to that in X^2.[3] How many classes of spermatozoa are formed in *D. prosaltans* is unknown. However, a species producing 50% of inviable eggs could hardly survive in nature; it is extremely likely that X^1AY^2 and Y^1AX^2 spermatozoa are either not formed or are not functional. Unfortunately, *D. prosaltans*, like most other species of Drosophila having highly spiralized testes, is unfavorable for examination of spermatogenesis. A few smear preparations of the testes of young males have been made, but in none of them have good meta- and anaphases of the first meiotic division been encountered. Some cells showed stages of early diakinesis; three separate bivalents may be distinguished (Fig. 2, *D*, *E*). One of the bivalents consists of two rod-like chromosomes, invariably associated at one end only. The bivalents formed by the V-shaped chromosomes show a variety of structures, in some cases suggesting chiasmata, although this may be only a false appearance. The problem of chromosome disjunction in *D. prosaltans* is, evidently, an open one. Another open problem concerns the behavior of the genes carried in the autosomal pair associated with the X^2–Y^2 chromosomes. The genes in this autosome should show all gradations between the normal autosomal inheritance and inheritance of sex-linked genes having alleles in the *Y*-chromosome (such as bobbed in *D. melanogaster*). The evolutionary fate of the genes located close to the centromere in the autosome associated with the *Y*-chromosome constitutes a still other interesting problem. Finally, a fourth problem which suggests itself is the origin of the unique heterochromosome mechanism of *D. prosaltans*. Fortunately, this problem can be somewhat clarified by comparison with a related species, namely, *D. sturtevanti* Duda.

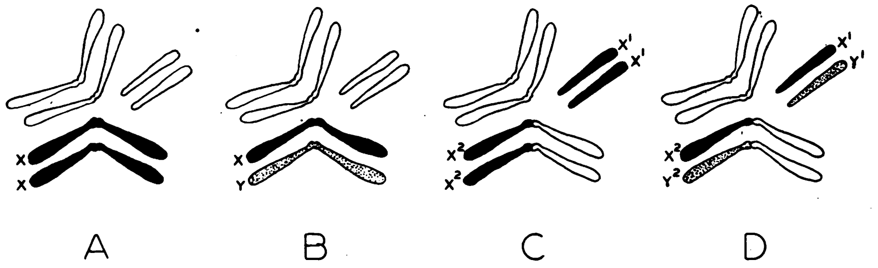

FIGURE 3

A scheme of the chromosome structure in *Drosophila sturtevanti* females (*A*) and males (*B*), and *D. prosaltans* females (*C*) and males (*D*). White—autosomes; black—*X*-chromosomes; stippled—*Y*-chromosomes.

We have laboratory strains of *D. sturtevanti*[4] derived from females collected at Bertioga (state of São Paulo) and at Rio de Janeiro (the latter collected by Professor Hugo Souza Lopes). As in *D. prosaltans*, the nerve cell metaphases of *D. sturtevanti* show two pairs of V-shaped and a pair of rod-like chromosomes (Fig. 1, *F*–*I*). A close examination discloses, however, differences between these two species. In *D. sturtevanti* one of the V-shaped pairs is clearly longer than the other; in favorable cells it can be seen that one of the arms of the smaller V is appreciably longer than the other. The rod-like chromosome is much shorter than either limb of at least the larger V; in contrast to *D. prosaltans*, the centromere constriction in the rod is not clearly subterminal. Very fortunately, the disc patterns in salivary gland chromosomes of *D. sturtevanti* proved to be sufficiently similar to those of *D. prosaltans*, so that the identification of the corresponding strands can be made without difficulty. In cells with a crushed chromocenter it can be seen that the *A*- and *B*-strands of *D. sturtevanti* are associated through a large chromocentral mass, forming, consequently, a V-shaped complex, like they do in *D. prosaltans*. In contrast to *D. prosaltans*, the *C*-strand of *D. sturtevanti* is frequently isolated

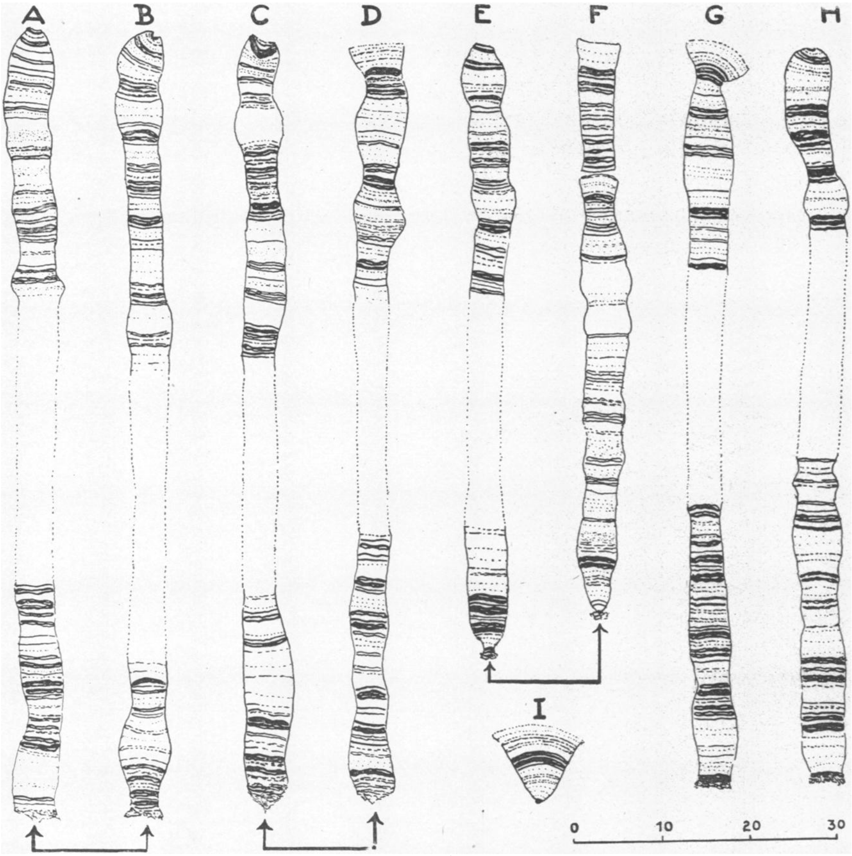

FIGURE 4

Salivary gland chromosomes of *Drosophila annulimana*. Except in the *F*- and *I*-chromosomes the disc patterns are shown only in the basal and the terminal portions; the relative lengths of the chromosomes are not reflected in the drawings. The scale below represents 30 micra.

from the other strands, while the X^1 and X^2 strands are connected with each other through a small heterochromatic segment. As in *D. prosaltans*, the X^1 and X^2 strands in male cells of *D. sturtevanti* are paler than the other strands.

It is evident, therefore, that one of the V-shaped chromosomes of *D. sturtevanti* is an *X*-chromosome (or, in the male, an *Y*-chromosome), while the other V and the rod are autosomes (Fig. 3). The type of chromosome complement found in *D. sturtevanti* is "orthodox," and is, virtually certainly, ancestral to the aberrant type of *D. prosaltans*. The origin of the latter form from the former can be visualized only as taking place through reciprocal translocations between the *X*- and *Y*- chromosomes on one hand and an autosomal pair on the other (Fig. 3). V-shaped *X*- and *Y*-chromosomes exchange major portions of one of their limbs for most of a rod-like autosome (*sturtevanti*), giving rise to rod-like *X*- and *Y*-chromosomes and to a V-shaped pair consisting of autosomal and heterochromosomal limbs (*prosaltans*). This change must have involved some situations which, theoretically, might be discriminated against in natural populations. Indeed, the exchange of segments between the autosome and the *X*- and *Y*-chromosomes must have occurred in a species with *sturtevanti*-like chromosomes. At least for a time, translocation heterozygotes of a rather complex kind must have existed, for example, individuals with one V-shaped *X*, one rod-like *X*, one rod-like autosome and one V-shaped autosome-*X*-chromosome complex (and similar heterozygotes for the *Y*-chromosome-autosome translocation). With the disjunction mechanism now present in *D. prosaltans* as yet imperfect, the fertility of such translocation heterozygotes should have been below normal.

It is well known that, in Drosophila, individuals of a race, races of a species and species of the genus frequently differ in inversions of chromosome segments. A great majority of the inversions are paracentric (involving breaks on one side of a centromere), rather than pericentric (involving breaks on two sides of a centromere). The predominance of paracentric inversions in the phylogeny is understandable; paracentric inversion heterozygotes produce few, and pericentric inversion heterozygotes produce relatively many aneuploid gametes. Yet, it can be demonstrated that evolutionary changes sometimes take place through formation of pericentric inversions.[5] In this respect, the chromosome complement of *D. annulimana* Duda is of interest. We possess some cultures of this very large species derived from females collected at Bombas, near Iporanga, state of São Paulo. The nerve cell metaphases in the females show (Fig. 1, *J–P*) ten chromosomes, including a pair of large V's, three pairs of much smaller V's and a pair of Y-shaped or rod-like bodies. The centromere constrictions are so strong that in some cells the two arms of a V appear as two separate chromosomes; the long V and one of the short V's may show also very strong secondary constrictions in one limb (Fig. 1, *N*). Male cells show nine chromosomes: a pair of large and three pairs of small V's and an unpaired Y or a rod (Fig. 1, *I–M*). *D. annulimana* is, consequently, *XX* in the female and *XO* in the male; this is the second known case of an *XO* species of Drosophila, the first being *D. orbospiracula* Patterson and Wheeler.[6]

The salivary gland cells of *D. annulimana* are very favorable for study. Eight relatively long and one very short chromosome strands can be counted without much difficulty. The disc patterns in the distal and the proximal portions of each strand are shown in Fig. 4, the middle portions being omitted except in shorter strands. The relatively long *A*- and *B*-strands are frequently associated in their proximal parts; they very likely represent the large V-shaped pair of metaphase chromosomes. The *C*-strand is almost always associated with *D*, and *E* with *F*; they probably correspond to two of the smaller V-shaped pairs of the metaphase plates. The *G*-strand is the *X*-chromosomes; *H* and the very small *I* probably belong together, although this has not been established by direct observation.

A majority of species of Drosophila so far cytologically investigated have five long and one very short chromosomal strands in their salivary gland cells, corresponding to the five variously associated or free rods and one dot-like chromosome of metaphase plates. Five free rods and a dot is the most likely ancestral condition of the chromosomal apparatus in the genus Drosophila, and it occurs frequently in species of the repleta group,[6] of which *D. annulimana* is an aberrant member.[7] The minimum of changes which have to be assumed to derive the chromosome complement of *D. annulimana* from the ancestral complement are as follows: (1) junction of two rods to form the large V of *annulimana*; (2) pericentric inversions in two rods with subterminal centromeres; (3) translocation of enough material from one of the rods onto the dot to transform the latter into a small V.

---

* Visiting Professor at the University of São Paulo, working under the auspices of the Committee for Interamerican Artistic and Intellectual Relations.

[1] Duda (*Arch. f. Naturgesch.*, **91,** 164 (1925)) has described "*Drosophila prosaltans* new species or variety of *saltans* Sturtevant"; the description is based on a single museum specimen from Hohenau, Paraguay. Sturtevant (*Univ. Texas Publ.*, **4213,** 39 (1942)) gave the name *Drosophila sellata* to a species from Guatemala and Mexico which is very close to *D. prosaltans* Duda. Sturtevant's own comment is: "The chief reason for not applying that name (*prosaltans*) to it (*sellata*) is the distribution, plus the fact that I have not seen Duda's material." Our flies fit the description of *D. prosaltans* and differ only slightly from that of *D. sellata*.

[2] Dobzhansky, Th., *Jour. Genetics*, **34,** 135–151 (1937).

[3] Mac Knight, R. H., *Genetics*, **24,** 180–201 (1939).

[4] Described by Duda (*Arch. f. Naturgesch.*, **91**, 167 (1925)) from a single Museum specimen from Mapiri, Bolivia. A very close, possibly identical, species has been named *Drosophila biopaca* by Sturtevant (*Univ. Texas Publ.*, **4213**, 37 (1942)).

[5] Miller, D. D., *Genetics*, **24**, 699–708 (1939).

[6] Patterson, J. T., and Wheeler, M. R., *Univ. Texas Publ.*, **4213**, 67–109 (1942).

[7] *Drosophila annulimana* is described by Duda (*Arch. f. Naturgesch.*, **91**, 117 (1925)) as a member of his subgenus Paradrosophila. As delimited by Duda, this subgenus is not a natural group; it includes most diverse forms having in common only a single character, namely, prescutellar bristles. *Paradrosophila annulimana* is much closer to species of the repleta group of the subgenus Drosophila than to such representatives of Paradrosophila as *bromeliae* Sturtevant. A new species close to *bromeliae* is found in São Paulo. It has three pairs of about equally long V-shaped chromosomes.

A TYPE OF UNIVERSAL ARITHMETICAL FORMS

By E. T. Bell

Department of Mathematics, California Institute of Technology

Communicated, November 8, 1943

1. By a few obvious changes in the wording, all that follows may be restated for any unique factorization domain. The type of forms considered is defined in §§2, 3.

If the integer $n \neq 0$ is expressible in the form $x^a y^b \ldots w^c$, where all the letters denote integers, $a, b, \ldots, c$ are constants and (without loss of generality) are all different, we shall say that n has the *index* $[a, b, \ldots, c]$, and write

$$I(n) = [a, b, \ldots, c].$$

The order of $a, b, \ldots, c$ within the bracket is immaterial.

The set of all integers having the index $[a, b, \ldots, c]$ will be written $I^{-1}[a, b, \ldots, c]$. Hence if at least one of $a, b, \ldots, c$ is 1, $I^{-1}[a, b, \ldots, c]$ is $I^{-1}[1]$, the set of all integers except zero.

Let $p_1, \ldots, p_s$ be the distinct positive prime divisors of $n > 1$, and let

$$t = \prod_{i=1}^{s} p_i^{t_i}, \qquad t = x^a y^b \ldots w^c,$$

be the prime decomposition of t and a representation of t with index $[a, b, \ldots, c]$ and $x, y, \ldots, w > 0$. Denote by $L(t;\ a, b, \ldots, c)$ the number of such representations. Then, on replacing $x, y, \ldots, w$ by their prime decompositions, it is evident that

$$L(t;\ a, b, \ldots, c) = \prod_{i=1}^{s} (t_i;\ a, b, \ldots, c),$$