ON THE STERILITY OF THE INTERRACIAL HYBRIDS IN DROSOPHILA PSEUDOOBSCURA

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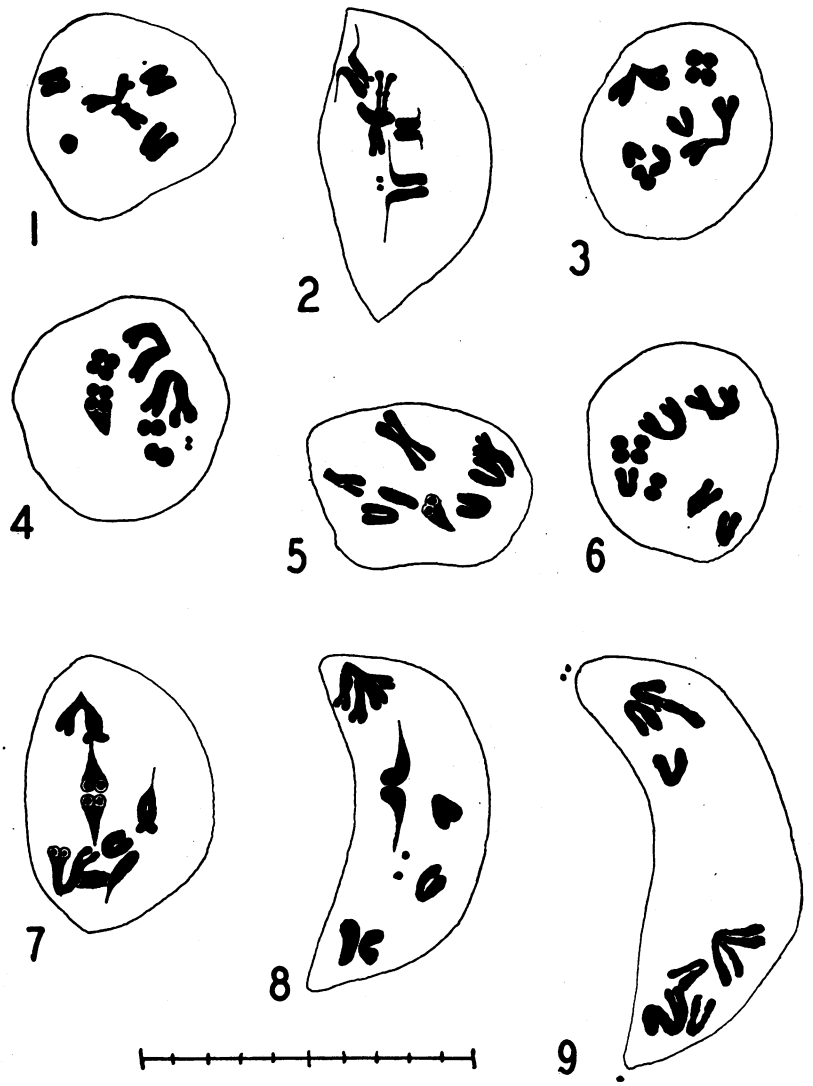
Offspring from interspecific crosses are frequently equal or superior to their parents in somatic vigor, and are, nevertheless, partially or completely sterile. The sterility is due to a disturbance in the process of gametogenesis usually involving a more or less complete lack of chromosome pairing at meiosis. The known instances of interspecific sterility fall into two groups. To the first group belong cases described by Karpechenko,[1] Clausen,[2] Tschermak and Bleier[3] and many others, who have found that the doubling of the chromosome complement of sterile hybrids results in the appearance of fertile allotetraploids showing a more or less complete chromosome pairing. To the second group belongs the case of the interracial hybrids in Drosophila pseudoobscura. As shown below, the doubling of the chromosomes does not influence here either the lack of chromosome pairing or sterility.

Lancefield[4] discovered that the species Drosophila psuedoobscura Frol.[5] is divided into two races or "physiological species." The two races, called race *A* and race *B* respectively, are indistinguishable in appearance. Both races possess five pairs of chromosomes, but the *Y*-chromosome is *J*-shaped in race *A* and *V*-shaped in race *B*. The progeny of the interracial crosses consists of partially fertile females and completely sterile males.

The writer has found that the sterility of the hybrid males is due to a profound disturbance of spermatogenesis, including failure of chromosome pairing at meiosis. The upper part of the testis in the $(A\,♀ \times B\,♂)F_1$ hybrid males[6] consists of spermatogonia and young first spermatocytes which are rather similar to those found in the corresponding part of the testis in normal males. At diakinesis the differences become apparent. In normal males all the chromosomes are paired at diakinesis, and appear as bivalents of the tetrad type (Fig. 1). Usually only four bivalents are observable since one of the autosomes is invisible at meiosis on account of its small size. The other autosomes pair with their homologues along their entire lengths, while the *X*- and *Y*-chromosomes are, as first shown by Metz,[7] paired only for a rather short distance in the region of the spindle fibre attachments.

In hybrid males chromosomes are mostly unpaired at diakinesis, although a variable number of bivalents is present in some cells (Figs. 3–6). Whether a given chromosome visible at diakinesis represents a univalent



FIGURES 1–9

Figure 1, diakinesis in a normal male (race *A*, four bivalents and the nucleolus); Figure 2, first division in a normal male (race *A*); Figures 3–6, diakinesis in hybrid males; Figures 7–9, first division in hybrid males. The scale for figures 1–17 represents 10 micra.

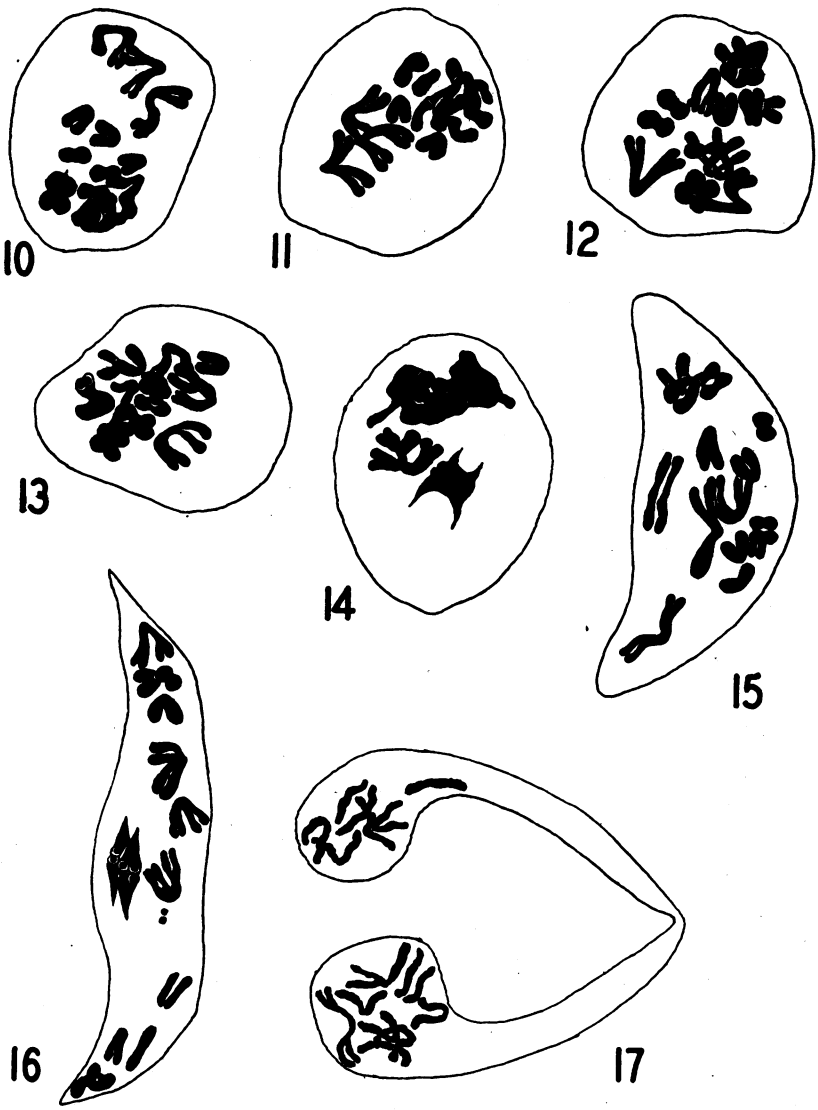
or a bivalent usually can be determined with accuracy. An autosomal bivalent seen in a side view appears as two closely paired rods, the space between which is, however, clearly visible (Fig. 1). In top view autosomal bivalents reveal their tetrad structure (one bivalent in the upper part of Fig. 3, two bivalents in the left part of Fig. 4). The autosomal univalents are split equationally, and appear as dyads. The sister chromatids diverge at their free ends, but are held together at the spindle fibre, which in these autosomes is terminal. Consequently, autosomal univalents appear in side view as more or less short *V*'s (Figs. 3, 5, 6), and in top view as dumb-bell-shaped bodies (lower part of Figs. 3 and 4, left part of Fig. 6). In the *X*- and the *Y*-chromosomes the spindle fibre attachments are median or submedian. Consequently, the *X*-*Y* bivalents appear as cross-shaped or branched bodies (Figs. 1 and 2). The unpaired *X*'s and *Y*'s are *V*-shaped chromosomes both limbs of which show the equational split (Figs. 3–6).

The first meiotic division in normal males has been described by Metz.[7] At anaphase the autosomal bivalents separate first at their spindle fibre ends, the opposite ends remaining associated until late anaphase (Fig. 2). Mitochondria assemble on the surface of the spindle making its outline very clearly visible. The telophase proceeds normally, two second spermatocytes are formed, whose nuclei, after a rather brief interphase during which the chromosomes do not pass into a resting stage, undergo the second division, giving rise to young spermatids.

In hybrid males the first division is highly abnormal. The univalents form no equatorial plate but are scattered on the spindle (Fig. 7). At anaphase the univalents move toward the poles, but their distribution is frequently unequal, so that more chromosomes go to one pole than to the other (Fig. 7). The homologous univalents frequently go to the same pole (see the *X*- and the *Y*-chromosomes at the same pole in Figs. 8 and 9). The bivalents, if any are present in the nucleus, stay on the equator of the spindle longer than do the univalents (Figs. 7 and 8), and disjoin normally.

Already at early anaphase the spindle in hybrids shows signs of an abnormal elongation. Soon the poles of the spindle approach the periphery of the cell, and, since the elongation continues, the spindle begins to bend (Fig. 9). Further enormous elongation of the spindle causes the poles to slide toward each other, the spindle becoming a nearly closed ring (Fig. 17). The daughter nuclei are then formed, but the cytoplasm fails to divide. The second division is absent. The binucleate spermatids transform into giant worm-like bodies somewhat resembling the atypical spermatozoa of certain Prosobranchia. This behavior of the spindle is interesting in connection with Belar's[8] views on the mechanism of mitosis.

Islands of tetraploid tissue are not infrequently met with in the testes



FIGURES 10–17

Figures 10–13, diakinesis in tetraploid spermatocytes in hybrid males; Figure 14, same, early anaphase; Figures 15–16, same, late anaphase; Figure 17, late telophase.

of hybrid males (in about one out of every four testes examined), but so far have not been seen in the testes of normal males. The origin of the tetraploid tissue is due to spermatogonial mitoses not followed by fission of the cytoplasm. Binucleate spermatogonia are thus formed. The two nuclei in such spermatogonia divide again, the two mitotic spindles lying side by side in the same cell. It is, presumably, at the telophase of such divisions that the pairs of daughter nuclei fuse with each other with the consequent formation of tetraploid spermatogonia. The tetraploid spermatogonia, recognizable by their large size, divide further and transform into tetraploid spermatocytes. Meiosis can be observed in the tetraploid spermatocytes.

Figures 10–13 show diakinesis in tetraploid cells. On account of the large number of chromosomes the figures are not as clear as the corresponding figures in the diploid cells. It is, however, easy to see that most chromosomes are unpaired and appear as univalents (dyads). In each of the figures three or four *V*-shaped chromosomes showing the equational split in one or in both arms are present. These chromosomes are unquestionably the unpaired *X*'s and *Y*-chromosomes. In each of the figures one can see also a large number of dyads which are the autosomal univalents. Like the diploid cells, the tetraploid spermatocytes show a varying number of bivalents. In figure 10 at least one bivalent is visible (in the lower left); no bivalents are evident in figure 11; in figure 12 there is at least one bivalent (see the lower part of the figure, under the left arm of the *V*-shaped chromosome); in figure 13 at least two bivalents are present. Some of the figures observed even suggest the possibility of the formation of multivalents. Figure 14 represents an early anaphase. This figure is, on the whole, unclear, but a distinct bivalent may be seen in its upper part, and in its lower part one sees a body with four spindle fibre attachments which are directed two by two in the opposite directions. This body is best interpreted as a quadrivalent (octad).

The course of the first meiotic division in the tetraploid spermatocytes is similar to that observed in the diploid ones. Figure 15 represents an early anaphase. The univalent chromosomes are scattered on the spindle; no bivalents seem to be present. Figure 16 shows a late anaphase. The univalents are going toward the poles, the spindle begins to bend. In the region of the equator of the spindle two clear autosomal bivalents are visible; their spindle fibre ends have already disjoined, the other ends are still associated.

The telophase of the first division in the tetraploid cells shows the same enormous elongation of the spindle which has been observed in the diploid cells. The poles of the spindle converge, and giant binucleate cells are formed. The second division being absent, the binucleate cells transform directly into abnormal octoploid worm-like spermatids.

The doubling of the chromosome complement in the interracial hybrids in Drosophila pseudoobscura does not lead to an increase in the frequency of chromosome pairing at meiosis, nor to restoration of fertility. These hybrids are, therefore, fundamentally different from the allotetraploids described in many species of plants.

One may surmise that the failure of chromosome pairing and the consequent sterility observed in interspecific hybrids may be due to either of two different causes. First, rearrangements of the chromosomal material, such as translocations and inversions, may lead to the chromosomes of one species or race finding no complete homologues among the chromosomes of another species or race. The consequent conflict of the attraction forces (Dobzhansky,[9] Darlington[10]) results in a failure of chromosome pairing in the hybrids. The doubling of the chromosome complement furnishes an exact homologue to every chromosome. Chromosomes pair normally at meiosis, and the sterility is eliminated. Second, the failure of chromosome pairing in the hybrids may be due to the action of complementary genetic factors contributed by the parent species or races involved in the cross. In this case the doubling of the chromosome number should produce no change in the course of meiosis, and the hybrid sterility should be preserved.

The sterility of the hybrids giving fertile allotetraploids is probably due to the factors of the first type. The factors of the second type seem to be responsible for the sterility of the interracial hybrids in Drosophila pseudoobscura (cf. Dobzhansky and Boche[11]), and probably also for the sterility of the hybrids between Drosophila melanogaster and Drosophila simulans (Schultz and Dobzhansky[12]).

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[2] Clausen, R. E., "Interspecific Hybridization in Nizotiana. 7. The Cytology of Hybrids of the Synthetic Species, Digluta, with Its Parents, Glutinosa and Tabacum," *Univ. Calif. Publ. Botany*, **11**, 177–211 (1928).

[3] Tschermak, E., and Bleier, H., "Über fruchtbare Aegilops-Weizenbastarde," *Ber. Deut. Botan. Ges.*, **48**, 110–132 (1926).

[4] Lancefield, D. E., "A Genetic Study of Two Races or Physiological Species in Drosophila Obscura," *Zeit. ind. Abst. Vererbgsl.*, **52**, 287–317 (1929).

[5] The American species Drosophila pseudoobscura Frol. is frequently confused with the European species Drosophila obscura Fall. Frolova and Astaurow (*Zeit. Zellf. mikr. Anat.*, **10** (1929)) have shown that these two forms are unquestionably specifically different.

[6] The present paper is devoted to the description of the spermatogenesis in the $(A\,♀ \times B\,♂)F_1$ hybrid males only. Spermatogenesis in the $(B\,♀ \times A\,♂)F_1$ hybrid males is different in many important details, and will be described elsewhere. In both cases the failure of chromosome pairing at meiosis is, however, observed.

[7] Metz, C. W., "Observations on Spermatogenesis in Drosophila," *Zeit. Zellf. mikr. Anat.*, **4**, 1–28 (1926).

[8] Belar, K., "Beiträge zur Kausalanalyse der Mitose. 2. Untersuchungen an den Spermatocyten von Chorthippus (Stenobotrus) lineatus Panz," *Roux Arch. Entwmech.*, **118**, 359–484 (1929).

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[10] Darlington, C. D., *Recent Advances in Cytology*, Philadelphia, Blakiston's, 559 pp. (1932).

[11] Dobzhansky, Th., and Boche, R. D., "Intersterile Races of Drosophila pseudoobscura," *Biol. Zbl.*, in press.

[12] Schultz, J., and Dobzhansky, Th., "Triploid Hybrids between Drosophila melanogaster and Drosophila simulans," *J. Exptl. Zoöl.*, in press.

A FURTHER STUDY OF BLOOD GROUPS OF THE RABBIT

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It has been shown in previous publications that, by means of immune sera, domestic rabbits may be separated into four groups characterized by the presence or absence from the blood of two different hæmagglutinogens, which we have called H_1 and H_2.[1] These agglutinogens are inherited as Mendelian dominant characters. The constitution of the four groups as regards the agglutinogens is as follows. Rabbits of one group (the double dominant) possess both agglutinogens. We may refer to them as H_1H_2 animals. Rabbits of a second group (the double recessive) possess neither agglutinogen. They may be called the *O* group. Rabbits of the other two groups are single dominant animals, possessing, respectively, either H_1 or H_2 alone. The genes for H_1 and H_2 are borne on the same chromosome, an unidentified autosome, since the inheritance is not sex-linked. These two genes are either allelomorphs or closely linked, more probably allelomorphs.

We are able to confirm the generally accepted view that such hæmagglutinogens as these are borne in or on the red blood-corpuscles. For upon injection of *washed* blood-corpuscles from a rabbit possessing an agglutinogen into the body of a rabbit *not* possessing it, a specific antibody (agglutinin) for that same agglutinogen makes its appearance in the serum of the recipient. Thus (*a*) if blood from an H_1 rabbit is injected repeatedly into an H_2 rabbit or a *O* rabbit, the serum of the recipient will later be found to contain an antibody (agglutinin) which will