Chapter 18
Variation in Function of Sex Chromosomes

The so-called “normal function” of the sex chromosomes was discussed in Chapter 5. As there are genetic factors that upset the normal function of the autosomes, there are naturally also those that upset the normal function of sex chromosomes. Since the sex chromosomes constitute a distinct group with a much specialized task of specific genetic expression their special treatment is warranted and is presented in this chapter.

18.1 Variation in Sex Ratio

The normal sex ratio is determined by the number of males vs. females at birth, which generally is 1:1 or close to it. Deviations from this ratio can be caused by several factors. Sturtevant and Dobzhansky (1936) discovered a sex ratio gene in *Drosophila pseudoobscura* and *D. persimilis*. This gene caused abnormal frequency of daughters (more than 90%) if it was present in the male parent of a cross. During the first meiotic division of the spermatocyte the X and Y chromosomes did not pair but the X chromosome split twice and separated mitotically (Fig. 18.1) during meiosis I so that each daughter cell received one X chromosome. The Y chromosome did not divide during meiosis I but passed to one of the first division poles, became enclosed in a vesicle, and degenerated. Since the X chromosome had split twice during meiosis I (probably two replications during premeiotic interphase), it could again separate in meiosis II, distributing one X chromosome to each sperm. Novitski et al. (1965) and Polansky and Ellison (1970) reinvestigated the sex ratio gene in *D. pseudoobscura* and found that the mechanism was different. During anaphase I the X and Y chromosomes regularly passed to opposite cell poles. Following meiosis I the Y chromosome degenerated leading to nonfunctional sperm formation. Consequently, each primary spermatocyte produced only two instead of four functional sperms. Thus, the X chromosome did not split twice as was suggested by Sturtevant and Dobzhansky.

Another case of the distortion of the sex ratio in favor of females was reported by Novitski and Hanks (1961) and Erickson and Hanks (1961). Males of *Drosophila melanogaster* containing the gene *Recovery Disrupter* [*RD(1)*, chrom. 1:62.9] may produce approximately 67% female progeny, due to a reduction in the recovery of the Y chromosome. The mechanism involved causes a fragmentation of the
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Fig. 18.1. Meiosis in a "sex ratio" male of Drosophila pseudoobscura. (A₁₋₄ = autosomes). According to an older concept, the X splits in both meiotic divisions. The Y is heteropycnotic and eventually disintegrates (Y₀). (From White, 1954. After Sturtevant and Dobzhansky, 1936. Redrawn by permission of the University Press, Cambridge).

Y chromosome during meiosis (Erickson, 1965). A second RD chromosome [RD(2)] has been discovered on chromosome 2, but the map location has not been determined (Wallace in Lindsley and Grell, 1968). This factor is thought to be another example of meiotic drive (see Section 17.5).

18.2 Different Sex Chromosome Systems

In Chapter 5 the basic form of sex determination in animals and in some plants was discussed. In the basic system, one sex has a pair of chromosomes that, microscopically, are similar (XX) and the other sex has visibly different chromosomes (XY). The closest deviation from this XY:XX system is the XO:XX system. The O in this formula merely indicates the absence of the Y chromosome. As mentioned, Henking in 1891 found the first one of such systems in the insect Pyrrhocoris apterus (Chapter 1). In meiosis I of such XO organisms, the X chromosome oriented itself in the metaphase plate without forming a bivalent. Usually, if autosomal univalents occur in meiosis, they do not line up on the metaphase I plate. Here, the X chromosome moves randomly to one of the two cell poles and later is recovered in 50% of the gametes. Autosomal univalents often lag behind in ana-