CHAPTER IX

TRIPLOIDS

IN recent work a number of threefold, or triploid, types have also been recorded. Some of these triploids have arisen from known diploid types; others have been found in cultivated plants, while still others have been found in the wild state.

Gates and Anne Lutz described triploid plants of Oenothera (semi-gigas), with 21 chromosomes. Triploids of Oenothera have since been described by de Vries, van Overeem, and others. They are supposed to be produced by the union of a diploid with a haploid germ-cell.

The distribution of the chromosomes of triploids during maturation has been studied by Gates and Geerts and van Overeem. They find that while, in some cases, the chromosomes are rather regularly distributed at reduction, in other cases some of the chromosomes are lost and degenerate. Miss Lutz found in fact great variation in the kind of offspring produced by triploids. Gates records that, in one 21-chromosome plant, the two cells resulting from the first maturation division contained "almost invariably" 10 and 11 chromosomes respectively and only occasionally 9 and 12. Geerts found more numerous irregularities. He describes 7 of the chromosomes going regularly to each pole, while the remaining 7 that were unpaired were irregularly distributed to the poles. This account fits well with the view that 7 conjugate with 7, leaving the remaining 7 without partners. Van Overeem states that in Oenothera, when the triploid serves as the mother plant, the results show that most of the ovules are functional, regardless of the distribution of the unpaired chromosomes, or, in other words, all or most of the possible different groups of egg-cells survive and may be fertilized. The outcome is a varied assortment of forms with many different combinations of chromosomes. On the other hand, when the pollen of a triploid Oenothera

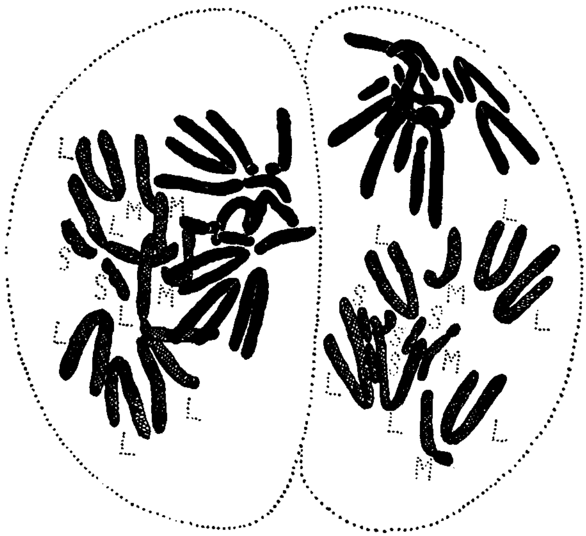
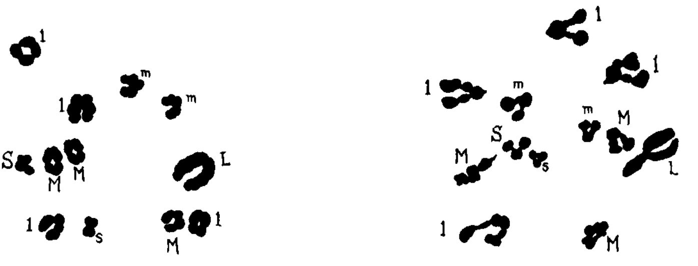


FIG. 80.

Triploid chromosome-group of the pollen mother cell of the Hyacinth. (After Belling.)

is used, the results show that only those carrying 7 or 14 chromosomes are functional. The pollen grains with intermediate numbers are, for the most part, not functional.

Triploid hyacinths have been found under cultivation by de Mol. He states that they are replacing the older types as a result of selection for commerce. Some of their derivatives, with chromosome numbers varying around the triploid, constitute a considerable part of modern cultivated types. Since hyacinths are usually reproduced by bulbs, any particular form can be perpetuated. De Mol has studied the maturation of the germ-cells, both of the normal and the triploid hyacinths (Fig. 80). The normal diploid type has 8 long, 4 medium, and 4 short chromosomes. The haploid germ-cell contains 4 long, 2 medium, and 2 short chromosomes. Both de Mol and Belling have pointed out that the "normal" may be already a tetraploid, since in the reduced group there are two chromosomes of each size. If so, the so-called triploid may possibly be a double triploid, since it has 12 long, 6 medium, and 6 small chromosomes.



a *b*

FIG. 81.

a, Reduced chromosome group of diploid Datura; *b*, reduced chromosome group of triploid Datura. (After Belling and Blakeslee.)

Belling has also studied the maturation divisions of a triploid variety of Canna. The chromosomes of each type conjugate in threes. When the chromosomes separate two of each triplet pass as a rule to one pole and one to the other pole, but since the distribution for different triplets is at random only rarely will a diploid and a haploid sister cell result.

A triploid Datura has been reported by Blakeslee, Belling, and Farnham. It arose from a tetraploid fertilized by a normal. The normal diploid type has 24 chromosomes (n=12) (Fig. 81a). The triploid has 36 chromosomes (Fig. 81b). The haploid group is composed of 1 extra large (L), 4 large (l), 3 large medium (M), 2 small medium (m), 1 small (S), and 1 extra small (s) chromosomes. The diploid group is therefore 2 (L+4l+3M+2m+1S+1s) and the triploid has three of each kind.

The maturation divisions have been studied by Belling and Blakeslee. The reduced groups consist of 12 sets of three each, united as in Fig. 81b. These trivalents have the same size relations as have the bivalents in the diploid group, *i.e.*, they are formed by the union of like chromosomes only, which are united in various ways as seen in the figures. Two may be united at both ends and the third joined on at one end only, etc.

At the first division two of each triplo-set pass to one pole and one to the other pole of the spindle (Fig. 75, third column), and since the assortment takes place at random in the different triplets several combinations of chromosomes are realized. The numbers found in one count of 84 pollen mother cells are recorded below in Table I. The results are in close agreement with the expectation for random assortment.

TABLE I

ASSORTMENT OF CHROMOSOMES IN 84 POLLEN MOTHER CELLS OF TRIPLOID DATURA, 19729(1)

Metaphase of Second Division.

Assortment of Chromosomes	12 + 24	13 + 23	14 + 22	15 + 21	16 + 20	17 + 19	18 + 18
Nos. of double groups	1	1	6	13	17	26	20
Calculated on random orientation of trivalents	0.04	0.5	2.7	9.0	20.3	32.5	19.0

Rarely the first division of the triploid may be omitted. This is favored by transient cold. At the second division an equatorial division of the chromosomes takes place, giving two giant cells with 36 chromosomes each.

As a rule very few functional pollen grains are formed in the triploid, but apparently the egg-cells are more often functional. For instance, when a triploid is pollinated by a normal plant, the number of normal offspring (2n) produced is much beyond expectation on the assumption that the chromosomes of the egg are freely assorted.

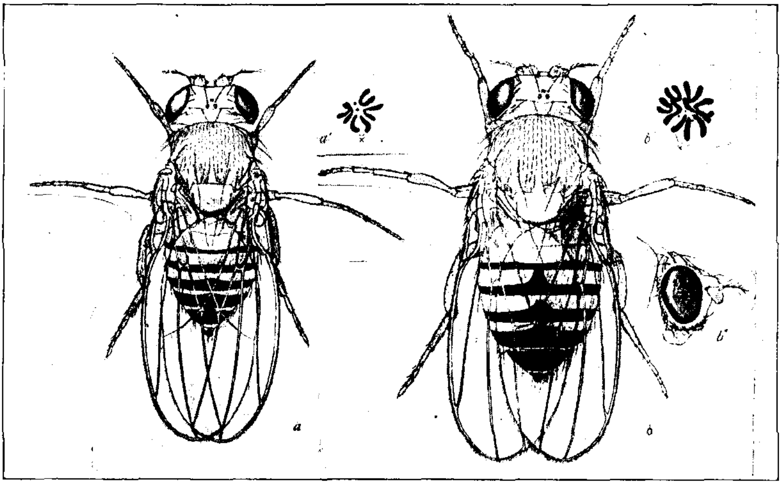


FIG. 82.

a, Normal or diploid female, and *b*, triploid of Drosophila melanogaster.

Triploid Drosophilas have been found by Bridges (Fig. 82). They are females because they have three X-chromosomes balanced against three of each kind of autosome. This is the same balance that produces the normal female. Since genetic factors in all the chromosomes are known, it has been possible to study the behavior of the chromosomes at maturation by means of the character-distribution in the progeny. It has also been possible to study the crossing-over, and to determine that the chromosomes mate in threes.

In true triploid Drosophilas there are three sets of ordinary chromosomes and three X-chromosomes also. If, on the other hand, there are only two X-chromosomes present the individual is an intersex. If only one X is present the individual is a supermale. These relations are as follows:

3a+3X=triploid female
3a+2X=intersex
3a+1X=supermale

In bisexual animals another triploid is known in an embryonic stage. Females of the bivalens variety of the threadworm Ascaris have been reported whose ripe eggs with two chromosomes have been fertilized each by a spermatozoön of a univalens variety with one chromosome. These eggs produce embryos with three chromosomes in each cell. Since the embryos escape before their own germ-cells mature, the most significant feature of their chromosome behavior, namely, union during conjugation, has not been observed, for as yet no adult triploids of Ascaris have been reported.

Triploids have been produced by crossing diploid species and back-crossing the hybrid (that has diploid germ-cells owing to the failure of conjugation and reduction) to one of the parental stocks. The experiment was carried out by Federley with three species of moths with the following chromosome numbers.

	Diploid	*Haploid*
Pygaera anachoreta	60	30
Pygaera curtula	58	29
Pygaera pigra	46	23

The hybrid between the first two species has 59 chromosomes (30+29). When the germ-cells of the hybrid reaches the maturation stages no union takes place between the chromosomes. At the first maturation division, each of the 59 chromosomes splits into daughter halves. Each daughter cell receives this number. At the second maturation division many irregularities occur. The chromosomes split again, but the halves often fail to separate. Nevertheless, the male is partially fertile and, as the result shows, some of his germ-cells contain the full number (59) chromosomes. The F_1 female is sterile.

If the F_1 male is back-crossed to a female of one of the parent species, to anachoreta, for example, whose ripe eggs contain 30 chromosomes, the second hybrid has 89 chromosomes (59+30), and is therefore a hybrid triploid. These F_2 hybrids resemble closely the F_1 hybrids. They have two sets of anachoreta chromosomes and one set of curtula chromosomes. They are, in a sense, permanent hybrids, although in each generation only half of their chromosomes conjugate. For instance, in the ripening of the germ-cells of these 89 chromosome hybrids the double set of anachoreta chromosomes (30+30) conjugates, the 29 curtula chromosomes remain single. The former separate at the first division, the latter divide, giving 59 to each cell. At the second division all 59 chromosomes divide. The germ-cells contain, therefore, 59 chromosomes and are diploid. As long as back-crossing continues it should be possible to produce triploid individuals. While under controlled conditions it might be possible to maintain a triploid line in this way, it is not probable, owing to the sterility of the offspring resulting from irregularities in the spermatogenesis of the hybrid, that under natural conditions a permanent triploid race could be established.[1]

[1] The account in the text has been intentionally somewhat simplified. In

The embryonic development of triploid individuals is expected to be normal because of the balanced condition of the genes. The only inharmonious factor that may enter into the situation is the relation between three sets of chromosomes and the inherited quantity of cytoplasm. How far auto-regulation takes place is not definitely known, but it may be surmised that in plants at least the cells of the triploid are larger than those of the normal type.

Other triploid types that have arisen or have been produced by crossing wild species, one of which has twice as many chromosomes as the other, will be described in a later chapter.

the F_1 hybrid one or more of the chromosomes appear to conjugate at times. Probably reduction follows for this pair, which would change by one or more the actual number of chromosomes in the germ-cells of the F_2 individuals.