SPECIES CROSSING AND CHANGES IN CHROMOSOME NUMBER

SOME interesting relations have come to light as a result of crossing species having different chromosome numbers. One species may have exactly twice or three times as many chromosomes as the other; in other cases, the larger chromosome group may not be a multiple of the other.

FIG. 108.
Diploid and haploid groups of the sundew, Drosera rotundifolia.
(After Rosenberg.)

The classic case is that of the cross between two species of sundew by Rosenberg in 1903-1904.

One species of sundew, Drosera longifolia, has 40 chromosomes (n=20), another species, rotundifolia, has 20 chromosomes (n=10) (Fig. 108). The hybrid has 30 chromosomes (20+10). In the maturation of the germ-cells of the hybrid, there are 10 conjugating chromosomes, often called gemini or bivalents, and 10 singles (univalents). Rosenberg interpreted this condition to mean that 10 of the longifolia unite with 10 of the rotundifolia leaving 10 of the former without a mate. At the first maturation division of the germ-cell, the conjugants

separate, the members going to opposite poles; the 10 single chromosomes are distributed irregularly, without division, to the daughter cells. Unfortunately the hybrid is sterile, and cannot be used for further genetic work.

The cross between two species of tobacco, Nicotiana Tabacum and N. sylvestris, has been extensively studied by Goodspeed and Clausen. Only recently, however, has the chromosome number been determined; Tabacum has 24 ($n=12$) and sylvestris 48 ($n=24$) chromosomes. This difference in chromosome number has not as yet been correlated with the genetic results; and the behavior of the chromosomes in the maturation divisions has not been reported.

The hybrid from crossing these two species resembles in every particular the Tabacum parent, even when that parent is pure for factors that behave as recessives toward the normal factors of the type Tabacum (*i.e.,* in crosses with varieties or races of Tabacum). Goodspeed and Clausen interpret this result to mean that the Tabacum genes dominate as a group the sylvestris genes. They have expressed this by saying that the ''reaction system'' of Tabacum dominates the embryological processes of the hybrid; or ''the elements of the two systems must be largely mutually incompatable.''

The hybrids are highly sterile, but a few functional ovules are formed. As the breeding results show, these functional ovules are exclusively (or predominately) either pure Tabacum or pure sylvestris. It may seem, therefore, that in the hybrid only those (or largely only those) ovules that contain a complete set (or nearly complete set) of one or the other group of chromosomes are functional. This view is based on the following experiments.

When the hybrid is fertilized with the pollen of sylvestris, a variety of forms is produced, among which there

is a considerable proportion of plants that are pure syl-
vestris in all their characters. These plants are fertile
and breed true to sylvestris. They must be supposed to
have come from ovules with a sylvestris chromosome
group, fertilized by sylvestris pollen. There are also
plants that resemble sylvestris, but contain other ele-
ments, probably derived from the Tabacum group of
chromosomes. They are sterile.

Back-crossing to Tabacum was unsuccessful, but a few
hybrids have appeared in the field from open pollination
that are like Tabacum and have undoubtedly come from
Tabacum pollen. Some of them are fertile. Their descend-
ants never show sylvestris characters. They exhibit segre-
gation for whatever Tabacum genes were present. There
are also sterile forms in the series, and these resemble the
F_1 hybrids between Tabacum and sylvestris.

These remarkable results are important in another re-
spect. The F_1 hybrid may be obtained both ways; *i.e.*,
either species may be the ovule parent. It follows that
even with a sylvestris protoplasm the Tabacum group of
genes completely determines the character of the indi-
vidual. This is strong evidence in favor of the influence
of the genes in the determination of the character of the
individual, since this result is obtained when the proto-
plasm belongs to a widely different species.

The idea of a reaction system, proposed by Clausen
and Goodspeed, while novel, contains nothing in principle
that is opposed to the general interpretation of the gene.
It means only that the haploid set of genes of sylvestris,
when placed in opposition to the haploid set of genes of
Tabacum, is totally eclipsed and ineffectual. The sylves-
tris chromosomes, nevertheless, retain their identity.
They are not eliminated or injured, since from the hybrid
a set of functional sylvestris chromosomes may be re-
gained in back-crosses to a sylvestris parent.

An extensive series of crosses between species of Crepis have been carried out by Babcock and Collins. The chromosomes of these hybrids have also been studied by Miss Mann (1925).

Crosses between Crepis setosa with 8 chromosomes (n=4), and C. capillaris with 6 chromosomes (n=3) have been made by Collins and Mann. The hybrid has 7 chromosomes. At maturation some of the chromosomes conjugate and other chromosomes, without dividing, are scattered in the pollen mother cells, forming nuclei with from two to six chromosomes. At the second division all the chromosomes divide, at least, those in the larger groups, and pass to opposite poles. The cytoplasm usually divides into four cells, but sometimes into 2, 3, 5, or 6 microspores.

These 7-chromosome hybrids do not give functional pollen, but some of the ovules are functional. When the hybrid was used as pistil parent and fertilized by pollen from one of the parents, five plants were obtained with 8 and 7 chromosomes. The maturation stage of one with 8 chromosomes was examined. It had 4 bivalents, which divided normally. The plant resembles C. setosa in its characters and has the same type of chromosomes. One of the parental types has been recovered.

Another cross was made between Crepis biennis with 40 chromosomes (n=20) and C. setosa with 8 chromosomes (n=4) (Fig. 109). The hybrid has 24 chromosomes (20+4). In the maturation of the hybrid, at least 10 bivalents are present, and a few univalents. It follows that some of the biennis chromosomes must conjugate with each other, since setosa contributes only 4 chromosomes. At the ensuing division 2 to 4 chromosomes lag behind the rest, but finally pass, in most cases, to one or the other nucleus.

The hybrids are fertile. They produce (F_2) plants hav-

ing 24 or 25 chromosomes. There seems to be a chance
here of producing new stable types with a new chromo-
some number that may contain one or more pairs of chro-
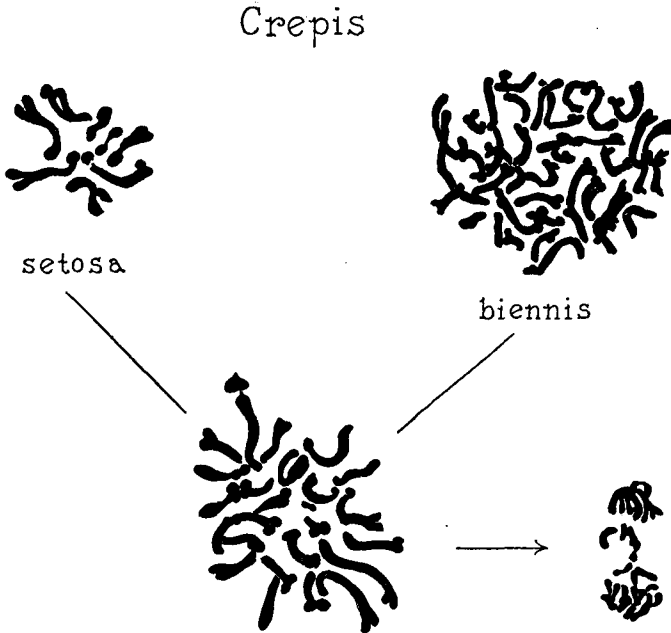mosomes derived from the species contributing the

Crepis

setosa

biennis

Fig. 109.

Chromosome groups of Crepis setosa and C. biennis. (After Collins
and Mann.)

smaller number. The presence of 10 conjugants in the
hybrid suggests that Crepis biennis is a polyploid, pos-
sibly an octoploid. In the hybrid the like chromosomes
unite in pairs. This F_1 hybrid, with half the full number
of biennis chromosomes, is an annual, while biennis itself
is biennial. The reduction in the number of its chromo-
somes has caused a change in its habits. It reaches matu-
rity in half the time necessary for biennis.

Two types of Mexican teosinte have been described by Longley, one, mexicana, an annual type with 20 chromosomes (n=10), the other, perennis, a perennial with 40 chromosomes (n=20). Both plants have normal reduction divisions. When the diploid teosinte (n=10) is crossed to Indian corn (n=10), the hybrid has 20 chromosomes. At maturation, there are 10 bivalents in the hybrid's germ-cells. This would ordinarily be interpreted to mean that 10 chromosomes of teosinte have united with 10 of Indian corn.
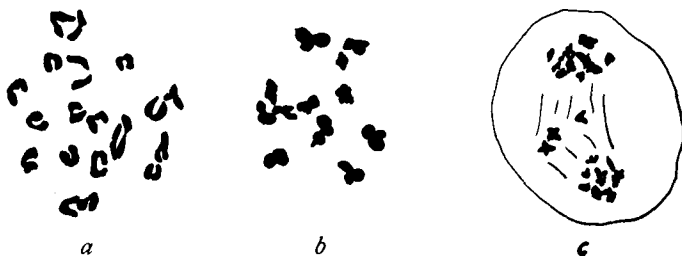

a   b   c

FIG. 110.

Reduced chromosome group, *a*, of perennial teosinte; *b*, of hybrid with maize; *c*, reduction division of last. (After Longley.)

When the perennial teosinte (n=20) is crossed to Indian corn (n=10) the hybrid has 30 chromosomes. At the first maturation division of the pollen mother cells there were found some trivalent groups loosely held together, some bivalents, and some single chromosomes in varying numbers, thus as 4:6:6; or as 1:9:9; or as 2:10:4, etc.; see Fig. 110b. At the first division the bivalents divide and the partners move to opposite poles; the trivalents divide, two going to one pole, one to the other; the singles lag and are distributed (without division) irregularly to the two poles (Fig. 110c). A very unequal distribution results.
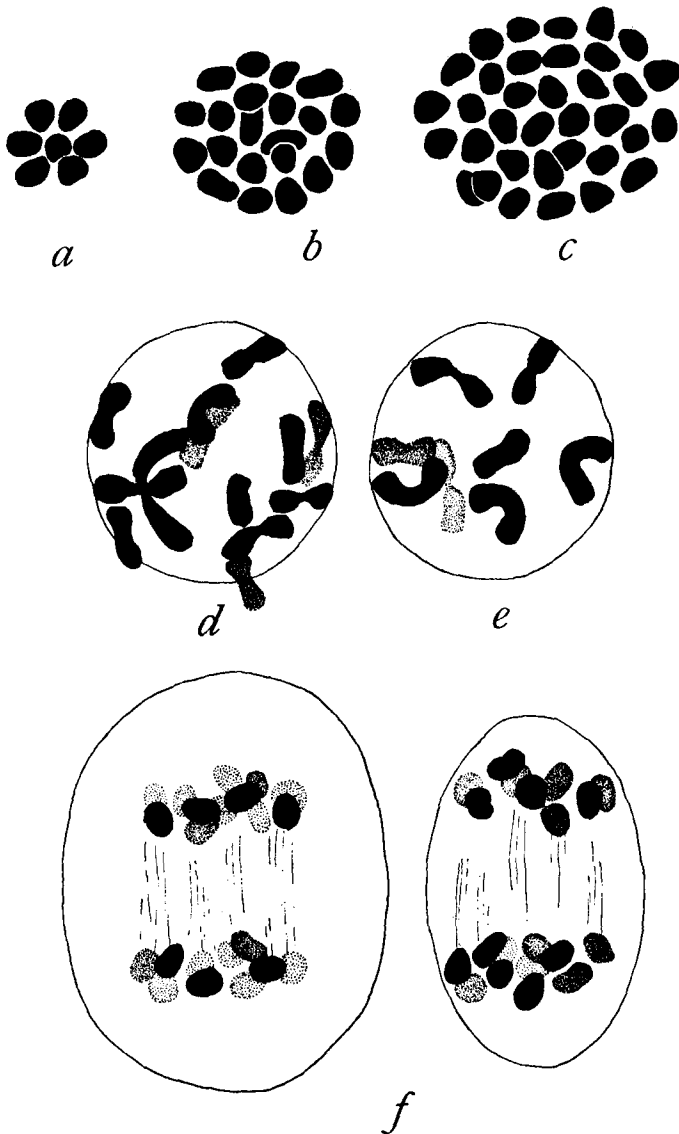
Quite recently a case has been described in which a

FIG. 111.

Cross between two species of poppies, one, *a*, Papaver nudicaule, having 14 chromosomes (n=7) and the other, *c*, P. striatocarpum having 70 chromosomes (n=35). The hybrid, *b*, has 42 (n=21). *d-e*, embryo mother cell of hybrid. *f*, first maturation division of hybrid, anaphase. (After Ljungdahl.)

new stable hybrid that is fertile has been produced by crossing two species with widely different chromosome numbers. Ljungdahl (1924) crossed Papaver nudicaule, having 14 chromosomes (n=7), with P. striatocarpum, with 70 chromosomes (n=35) (Fig. 111). The hybrid has 42 chromosomes. At maturation of the hybrid germ-cells there are 21 bivalents (Fig. 111, b, c-e). These divide, 21 going to each pole. No single chromosomes are present, and none lag on the spindle. The result must be interpreted to mean that the 7 chromosomes of nudicaule have mated with 7 chromosomes of striatocarpum, and that the remaining 28 chromosomes of striatocarpum have conjugated in twos to give 14 bivalents. This gives a total of 21 bivalents, the number observed. It seems natural to assume that the form striatocarpum, with 70 chromosomes (n=35), is probably a decaploid type, *i.e.*, a type with ten times each kind of chromosome.

The new type (F_1) produces germ-cells with 21 chromosomes. It is balanced and stable. It is also fertile and may be expected to produce a new stable type. From it still other stable types are theoretically possible. If back-crossed to nudicaule it should give rise to a tetraploid type (21+7=28). Back-crossed with striatocarpum it should produce an octoploid type (21+35=46). Here, through hybridization of a diploid and a decaploid type, there may be produced in subsequent generations tetraploids, hexaploids, and octoploid types that are stable.

Federley's experiment (Chapter IX) with species of moths of the genus Pygaera illustrate a very different relation. Owing to the failure of the chromosomes to conjugate in the germ-cells of the hybrid the double number is retained. By back-crossing the double number may be continued, but as the hybrids are very sterile nothing permanent could result from these combinations under natural conditions.