POLYPLOID SERIES

IN recent years an ever increasing number of closely related wild and of cultivated types have been reported whose chromosome numbers are multiples of a basal haploid number. The polyploid series run in groups which suggest that members of the series with the higher numbers have come from the lower members by a continuous process of additions. Whether taxonomists will decide to give such forms as are stable specific rank is for them to decide.

It is probably significant that the polyploid series have been found in several groups that were known as polymorphic groups that had bewildered taxonomists owing to their variability and to their close resemblance to each other, to their failure in many cases to breed true from seeds, etc. All this accords with the cytological findings. In so far as the chromosome groups are balanced, the genetic expectation is that these plants would be very similar, except in so far as the increase in the size of the cells may introduce physical factors that affect the structure of the plant, and except in so far as the increased number of the genes may introduce chemical effects in the cytoplasm.

The Polyploid Wheats.

In the small grains, wheat, oats, rye, and barley, multiple chromosome groups have been found. The wheat series has been most extensively studied and the hybrid types produced by crossing them have been examined in a

number of cases. Of these, T. monococcum, has the fewest chromosomes, *viz.*, 14 (n=7). It belongs to the Einkorn group and can be traced back, according to Percival
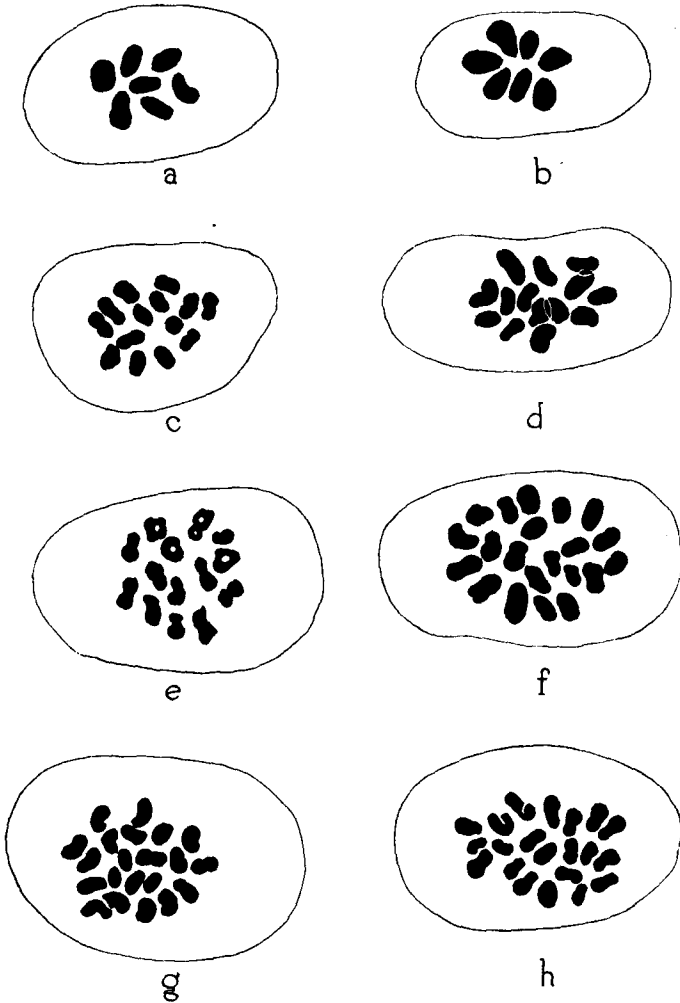

FIG. 88.

Reduced number of chromosomes of diploid, tetraploid, and hexaploid wheats. (After Kihara.)

(1921), to the Neolithic period in Europe. Another type, the Emmer group, with 28 chromosomes, was grown in Europe in prehistoric times, and in Egypt as early as 5400 B.C. It was later supplanted in the Graeco Roman period by wheat with 28 chromosomes, and by one with 42 chromosomes of the Vulgare group (Fig. 88). The number of varieties is greatest in the Emmer group, but there are more different "forms" in the Vulgare group.

The chromosomes have been studied by several investigators. The most recent work is that of Sakamura (1920) and Kihara (1919, 1924) and Sax (1922). The following account is taken largely from Kihara's monograph and to some extent also from Sax's papers. The next table gives the observed diploid number of chromosomes and the observed or estimated haploid number.

	Haploid	Diploid
Einkorn group, Triticum monococcum	7	14
Emmer group, Triticum dicoccum	14	28
Emmer group, Triticum polonicum	14	28
Emmer group, Triticum durum	14	28
Emmer group, Triticum turgidum	14	28
Vulgare group, Triticum Spelta	21	42
Vulgare group, Triticum compactum	21	42
Vulgare group, Triticum vulgare	21	42

The haploid groups are represented in Fig. 88a (monococcum), Fig. 88e (durum), and Fig. 88h (vulgare).

The normal maturation of a member of each of these groups is shown in Fig. 89 from Sax. In the Einkorn wheat the seven gemini (conjugated chromosomes) divide at the first division, seven going to each pole. There are no lagging chromosomes. At the second division of each daughter cell the seven chromosomes split into daughter halves. Seven go to each pole. In the Emmer type the 14 gemini divide at the first maturation stage. Fourteen chromosomes go to each pole. At the second division each

chromosome splits, and 14 daughter chromosomes move to each pole. In the Vulgare type the 21 gemini divide at the first maturation division. Twenty-one go to each pole. At the second division the daughter halves split and 21 move to each pole.

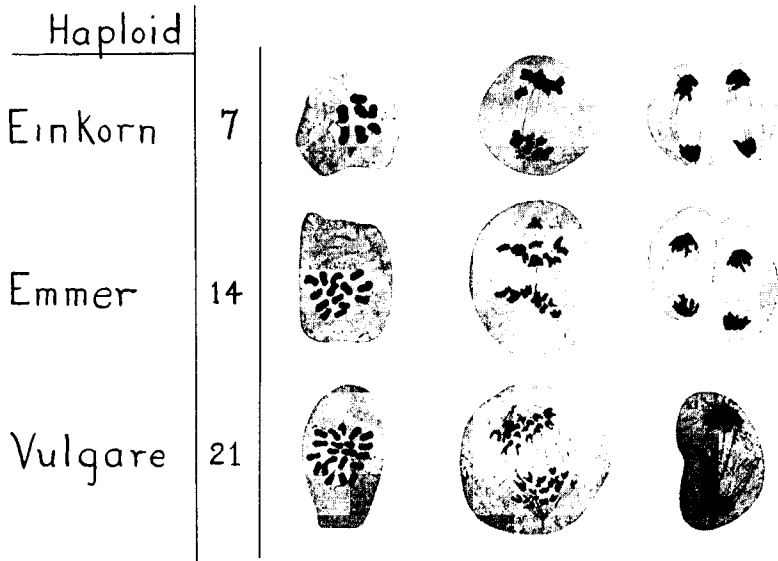| Haploid		
Einkorn	7	
Emmer	14	
Vulgare	21	

Fig. 89.

The first, or reduction, division of diploid, tetraploid, and hexaploid wheats. (After Sax.)

This series of types may be interpreted as diploid, tetraploid, and hexaploid. Each is balanced and each is stable.

Crosses have been made between several of these types with different chromosome numbers. Some of the combinations produce slightly fertile hybrids, others completely sterile ones. The behavior of the chromosomes in several of the combinations, where different parental

numbers are involved, brings out some interesting rela-
tions. A few examples will serve as illustrations.

Kihara examined the hybrid produced by crosses be-
tween an Emmer with 28 chromosomes (n=14) and a
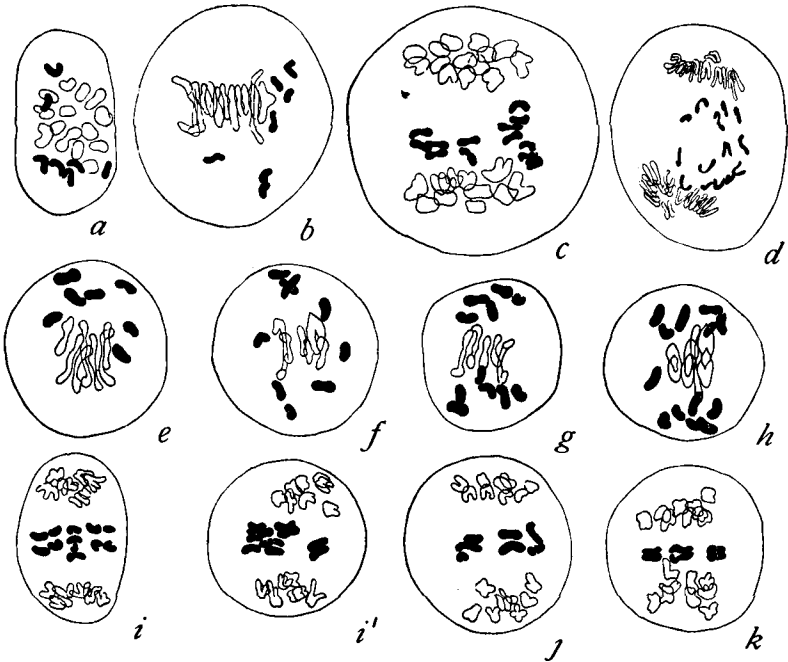Vulgare type with 42 chromosomes (n=21). The hybrid

FIG. 90.
Reduction division of hybrid wheats. (After Kihara.)

has 35 chromosomes. It is therefore a pentaploid hybrid.
In the maturation stages (Fig. 90a-d) there are 14
gemini and 7 single chromosomes. The former divide, 14
going to each pole; the latter, the single chromosomes,
are irregularly scattered on the spindle, where they lag
for some time after the "reduced" chromosomes have
reached the poles (Fig. 90d). Later these single chromo-

somes split lengthwise, and the daughter chromosomes move to the poles, not, however, with complete regularity. When the distribution is equal there will be 21 chromosomes at each pole.

EMMER BY VULGARE
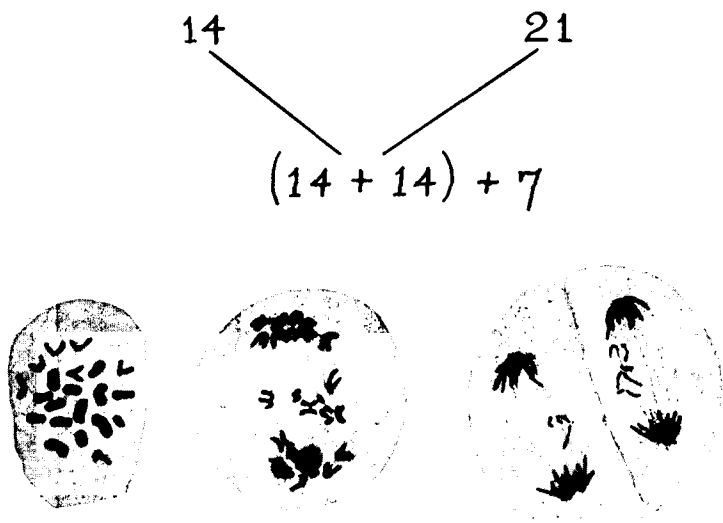
$$14 \qquad\qquad 21$$

$$(14 + 14) + 7$$

FIG. 91.

Reduction division of the hybrid between Emmer and Vulgare wheat. (After Sax.)

In passing it should be recorded that according to Sax's results for triploid wheat, the 7 single chromosomes do not divide at this time, but are distributed unequally to the poles, the more common distribution being 3 and 4 (Fig. 91).

At the second division, according to Kihara, 14 chromosomes that are split lengthwise appear and 7 chromosomes that are not split. The former divide, 14 going to

each pole, while the 7 singles are distributed at random—more often 3 going to one pole and 4 to the other. According to Sax, the 7 single as well as the 14 reduced chromosomes split at the second division.

Whichever interpretation holds for the single chromosomes (and there are in other forms precedents for either interpretation), one important fact is evident, *viz.,* that conjugation takes place only between 14 chromosomes. Whether this union is between the 14 chromosomes derived from the Emmer and 14 chromosomes derived from the Vulgare, or whether the 14 chromosomes of the Emmer unite to make 7 conjugants and 14 of the Vulgare unite to make 7 conjugants, leaving one set of 7 over, is not clear from the cytological evidence. A genetic study of these or similar combinations (this one gives a fertile hybrid) may furnish decisive evidence, but this is lacking at present.

Kihara also crossed Einkorn, having 14 chromosomes ($n=7$), with Emmer wheat, having 28 chromosomes ($n=14$). The hybrid, having 21 chromosomes, is a triploid. In the maturation of the germ-cells of the hybrid (pollen mother cells) there is much more irregularity than in the last case (Fig. 90e-k). The number of the conjugating chromosomes is variable and their union, when it occurs, is less complete. The number of the gemini varies as shown in the next table.

Somatic number	Gemini	Singles
21	7	7 (Fig. 90e)
21	6	9 (Fig. 90b)
21	5	11 (Fig. 90g)
21	4	13 (Fig. 90h)

At the first division the components of the gemini separate and pass to the poles. The splitting of the single chromosomes does not always take place before they have

moved to one or the other pole; some reach the poles un-
divided, others split and the halves move to the poles.
Not infrequently 7 single chromosomes are left in the
middle plane between the two polar groups (Fig. 90i).
Three counts are given in the following table:

Upper pole	Between the poles	Lower pole
8	6	7 (Fig. 90i)
9	4	8 (Fig. 90j)
9	3	9 (Fig. 90k)

At the second division 11 or 12 chromosomes are, as a
rule, present; some are doubles (split lengthwise), others
singles. The former divide normally, the daughter chro-
mosomes going to one or the other pole; the singles are
distributed without division to one or the other pole.

From this evidence it is not possible to determine
which chromosomes conjugate in the hybrids. Since the
number of gemini does not exceed 7, these may be inter-
preted as the result of union of the 14 chromosomes of
the Emmer parent, or as the result of the union of 7 of
the Einkorn with 7 of the Emmer chromosomes.

In a few crosses between Emmer and Vulgare, fertile
hybrids have been obtained. Kihara has studied the chro-
mosomes in the maturation division of some of the F_3, F_4,
and later generations. The chromosome numbers in the
plants vary and there are irregularities in the distribu-
tion of some of them during maturation, leading to fur-
ther irregularities, or to the reëstablishment of a stable
type like one of the original types, etc. These results,
important for the genetic study of the hybrids, are too
complex for our present purpose.

Kihara studied hybrids (one combination) between a
Vulgare wheat and a race of rye, the former having 42
chromosomes (n=21), the latter 14 chromosomes (n=
7). The hybrid (with 28 chromosomes) may be called a

tetraploid. This hybrid between these two widely different species is, according to earlier observations, sterile, but fertile according to other observers.

In the maturation stages of the germ-cells, few or even no conjugating chromosomes were observed, as shown in the next table:

Gemini	Singles
0	28
1	26
2	24
3	22

The distribution of the chromosomes to the poles is very irregular; few if any of the singles divide before reaching the poles; some of them are left scattered in the cell. In the second division many of the chromosomes split, but those that divided in the first division lag and pass slowly to the pole; the number that lag is, however, much less than in the first division.

The almost complete absence of conjugating chromosomes in the cross between wheat and rye is the most interesting feature of the cross. The resulting irregularity in the distribution of the chromosomes will probably account for the generally observed sterility of the hybrid. There is a possibility that all the chromosomes (or most of them) belonging to one species might, as a rare event, pass to one pole. This might lead to the formation of a functional pollen grain.

The Polyploid Roses.

Since the time of Linnaeus the classification of many of the roses has baffled the skill of taxonomists. The recent discoveries of a Swedish botanist, Täckholm, and of three English botanists, Harrison and Blackburn in collaboration, and Hurst, a rose expert and geneticist,

have shown that certain groups of roses, especially those belonging to the family of canina rose, are polyploid types. Their differences are not only due to polyploidy, but combined with this there is evidence of extensive hybridization.
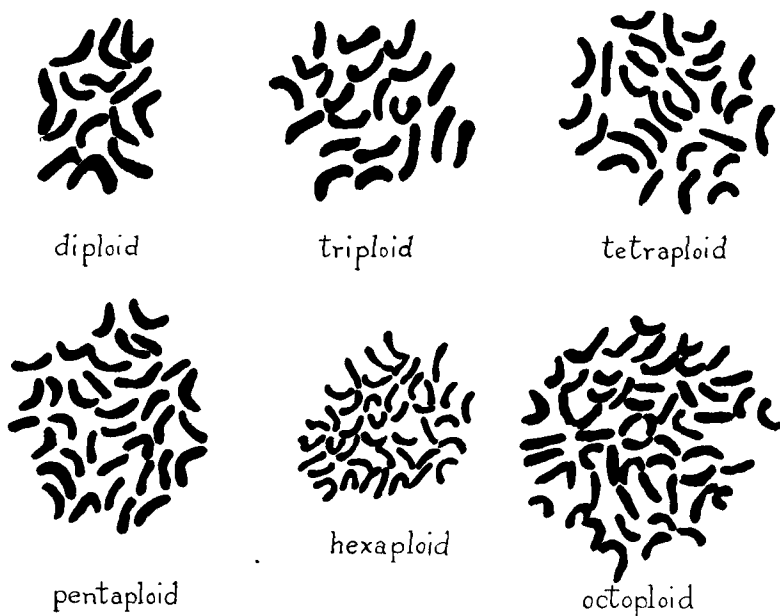

Fig. 92.
Polyploid series of roses. (After Täckholm.)

Täckholm has recently made an elaborate study of these roses. His account may first be followed. The species with 14 chromosomes ($n=7$) have the smallest number, and may be taken as the basal type. There are triploids (3 times 7), tetraploids with 28 chromosomes (4 times 7), pentaploids (5 times 7), hexaploids with 42 (6 times 7), and octoploids with 56 (8 times 7). See Fig. 92. In the maturation division of some of these polyploids

that are balanced, all the chromosomes are united in pairs (gemini), while in those polyploids with odd numbers and even in some of those with even numbers (taken to be hybrids) only 7 (or 14) gemini are present, the rest of the chromosomes being single in the first maturation division. In other words, when there are four, six, or eight chromosomes of each of seven kinds they conjugate in twos, as though these types were diploid. Whatever their origin may have been, the chromosomes never conjugate in fours, sixes, or eights. In these polyploids, the conjugants separate at the first maturation division, half going to each pole. At the second division each chromosome divides, and half of each goes to one or the other pole. The germ-cells, whether pollen or ovules, thus come to contain half the original number of chromosomes. Hence, if they propagate sexually, the characteristic number is maintained.

Another group of roses is regarded as hybrid by Täckholm, because the changes that take place in their germ-cells show them to be unstable forms. Some of these have 21 chromosomes, hence are triploids. In the early maturation stages of the pollen mother cells there are 7 bivalents (gemini) and 7 single chromosomes. At the first division the 7 bivalents divide and 7 go to each pole; the 7 single chromosomes do not divide and are distributed at random to the poles. Hence several combinations are possible. The type is unstable in this respect. At the second maturation division, all the single chromosomes divide, whether they come from the earlier bivalents or from single chromosomes. Many of the resulting cells degenerate.

In other hybrids there are 28 chromosomes (4 times 7), but these are not classified as true tetraploids by Täckholm, because the behavior of the chromosomes at the time of conjugation indicates that there are not four of

each kind. Only 7 bivalents appear and 14 single chromo-
somes. At the first division the 7 bivalents split, the 14
singles do not divide and are distributed irregularly.

In other hybrids there are 35 chromosomes (7 times 5).
At maturation there are 7 bivalents and 21 single chro-
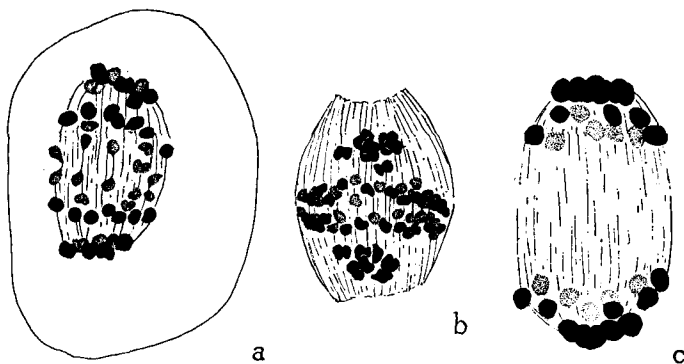mosomes (Fig. 93). Both behave as in the last case.

FIG. 93.

First maturation division of a thirty-five chromosome heterotypic
rose. (After Täckholm.)

In a fourth type of hybrid there are 42 chromosomes
(7 times 6). At maturation there are again only 7 biva-
lents, and, here, 28 single chromosomes. The behavior of
the chromosomes at maturation is the same as before.

These four types of "hybrid roses" are classified
below in tabular form in regard to their pollen formation.

7 bivalent and 7 single chromosomes. Whole number 21
7 bivalent and 14 single chromosomes. Whole number 28
7 bivalent and 21 single chromosomes. Whole number 35
7 bivalent and 28 single chromosomes. Whole number 42

The unique behavior of these hybrids consists in the
conjugation of only 14 chromosomes to give the 7 biva-
lents. These chromosomes, we must suppose, are identi-

cal, or so nearly alike that they conjugate. It is not obvious why the other sets do not conjugate, unless, as Täckholm suggests, each set of 7 has come from a different wild species by crossing. The additional chromosomes arising in this way are sufficiently different from the original set and from each other to interfere with conjugation.
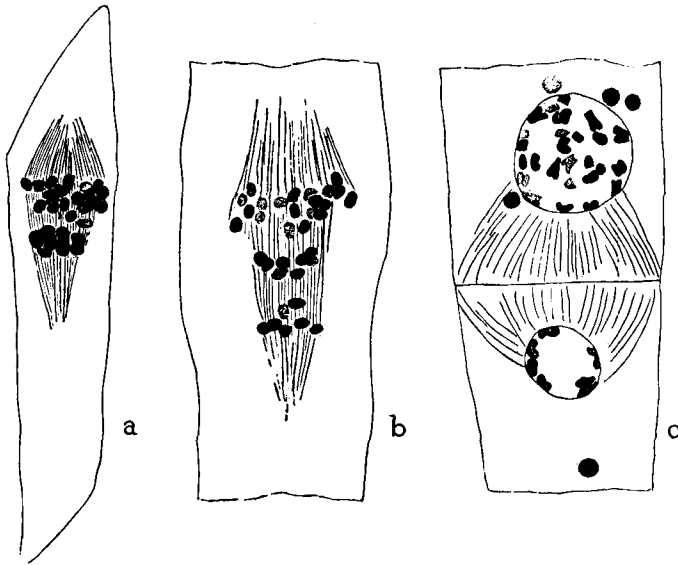

FIG. 94.

Maturation division of egg-cell of rose. All the single chromosomes move to one pole where they are joined by half of the conjugants. (After Täckholm.)

Two other hybrid forms may be mentioned; in both there are 14 bivalents and 7 single chromosomes. In these there are twice as many conjugating chromosomes as in the former hybrids.

In only a few hybrids of the canina group is the history of the chromosomes in the embryo mother sac (where the egg develops) described (Fig. 94). There are 7 bivalents

lying in the equator of the spindle, while all the single chromosomes are collected at one pole. The bivalents separate, half of each going to one pole, half to the other. One of the resulting daughter nuclei contains 7 chromosomes (derived from the bivalents) and all of the 21 single chromosomes, while its sister cell contains only 7 chromosomes. The egg-cell is derived from the former group. If the egg develops, as appears to be the case, from the (7+21) chromosome cell, and is fertilized by a sperm with 7 chromosomes (the other pollen grains assumed to be non-functional), the fertilized egg will contain 35 chromosomes, *the original number of such a type.*

The reproductive processes in these polyploid hybrid roses has not been fully worked out. In so far as they reproduce by stolons they will maintain whatever number of chromosomes may result from fertilization. Those that form seeds by parthenogenesis may also maintain a definite somatic number. It seems probable that, as a result of the irregularities in the formation of the pollen and egg-cells many different combinations may be established. Without a knowledge of the chromosome interrelations of these types the hereditary processes would have been very baffling. Even with this advance in our knowledge there still remains a great deal to make clear the composition of these hybrid roses.

Hurst, who has studied species of Rosa, both wild and cultivated, thinks that the wild diploid species consist of five primary groups *that may be designated* AA, BB, CC, DD, EE, Fig. 95, a-d, e-h, i-l, m-p, q-t. Many combinations of these five fundamental types are recognizable. Thus, one tetraploid is designated BB, CC; another, BB, DD; one hexaploid is AA, DD, EE; another hexaploid is AA, BB, EE; an octoploid is BB, CC, DD, EE.

Hurst states that each member of the five primary series has at least 50 diagnostic characters. These can be
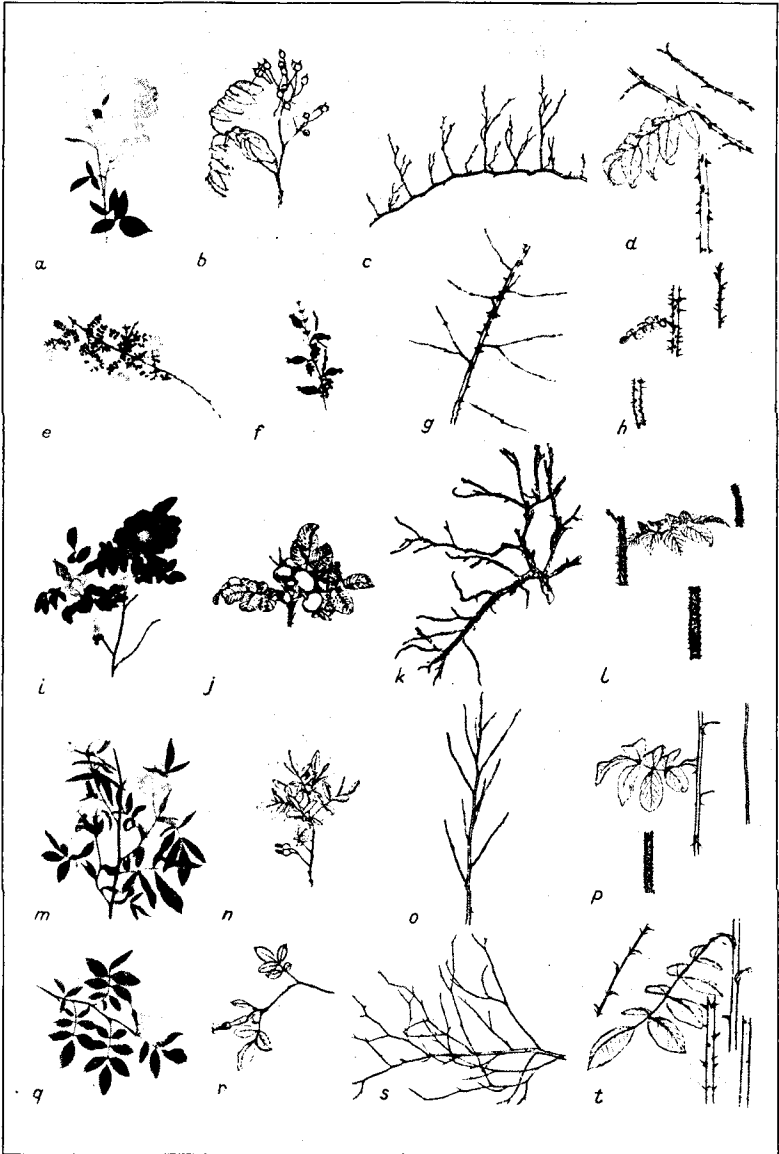
FIG. 95.

The five types of canina roses, *viz.*, a-d, e-h, i-l, m-p, q-t. The characteristics of each type are indicated in the same horizontal line including flower, seed capsule, method of branching, spines, and leaf insertion. (After Hurst.)

recognized in combinations in the hybrids. The environmental conditions may alternately favor the expression of one or the other set of characters. Hurst believes that a classification of the species of the genus is possible on the basis of these interrelations.

Other Polyploid Series.

In addition to the types that have just been described, there are a number of other groups in which multiple chromosome varieties and species have been reported.

The genus Hieracium is known to contain some species that reproduce by sexual methods, and other species that reproduce by parthenogenesis, even although stamens are sometimes present in them that may contain some normal pollen grains. Rosenberg has studied the development of the pollen of several species that produce pollen. He has also examined hybrids between different species. In the latter he has studied the maturation divisions of the pollen cells of the hybrid between H. auricula with 18 chromosomes ($n=9$) and H. aurantiacum with 36 ($n=18$). In the hybrid there are 9 gemini and 9 single chromosomes in the first maturation division but some exceptional cases are found, due perhaps to aberrant numbers of chromosomes in the pollen of one of the parents, *viz.*, H. aurantiacum. At the first division the gemini separate, and most of the single chromosomes divide.

Rosenberg has also studied the maturation division of F_1 hybrids between two tetraploid or 36 chromosome types, *viz.*, H. pilosella and H. aurantiacum. The somatic cells of the hybrid have 38 to 40 chromosomes. In two cases 18 gemini were present and 4 single chromosomes. In another cross between H. excellens, with 36 or 42 chromosomes ($n=21$), and H. aurantiacum, with 36 ($n=18$), there were in one case 18 gemini. It is probable that the H. excellens parent had 36 chromosomes. In another

similar cross, in which the pollen in F_1 was largely abortive, there were large numbers of *gemini* present and many single chromosomes. Results similar to these were
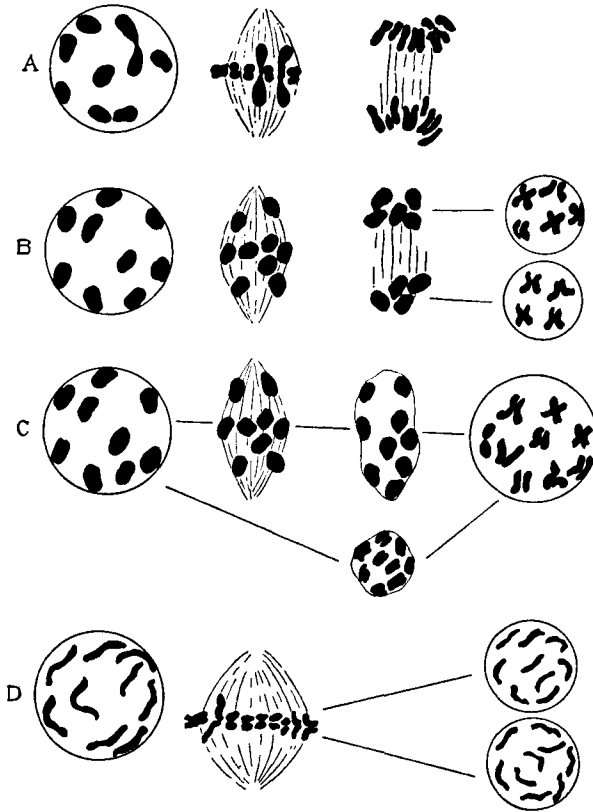

FIG. 96.

Maturation stages of several types of apogamous species of Hieracium. (After Rosenberg.)

found in two other tetraploid crosses. In general, the result with tetraploids shows that like chromosomes are present in these different species that conjugate with each other, or at least it seems more probable that the

gemini are formed in this way rather than that they are formed by the union of the like chromosomes within each species group.

Rosenberg has also studied the maturation of the pollen in species of Archieracium, in which species both sexual and parthenogenetic methods of reproduction occur, the latter being the more common method. There is no reduction division in the parthenogenetic types in
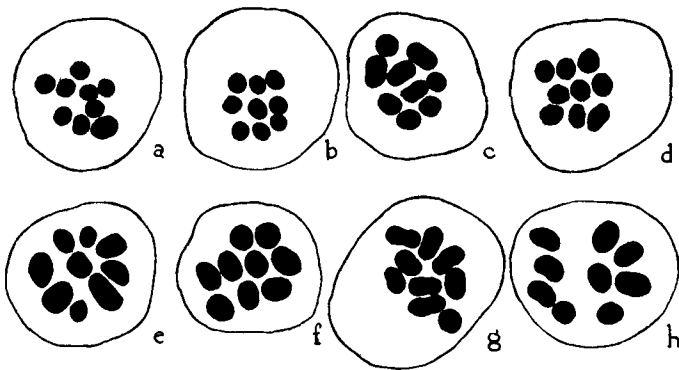

FIG. 97.

Types of chromosomes of eight varieties of chrysanthemums, each having the reduced number of nine chromosomes. (After Tahara.)

the embryo sac, but the diploid number of chromosomes is retained. The pollen development is much altered and good pollen is seldom present. The reduction divisions in the pollen mother cells are very irregular. Rosenberg has described the maturation stages of several apogamous species of Hieracium in which the pollen is scarcely ever functional (Fig. 96). He interprets the changes as, in part, due to their tetraploid origin (bivalent and single chromosomes appear in most types) and in part due to a progressive loss of all conjugation between the chromosomes, accompanied by a suppression of one of the matu-
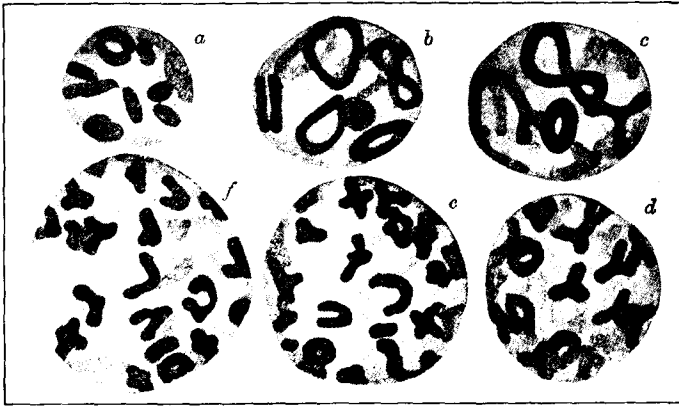
FIG. 98.

Multiple chromosome groups of different varieties of chrysanthe-
mums; a, with 9; b, with 9; c, with 18; d, with 21; e, with 36;
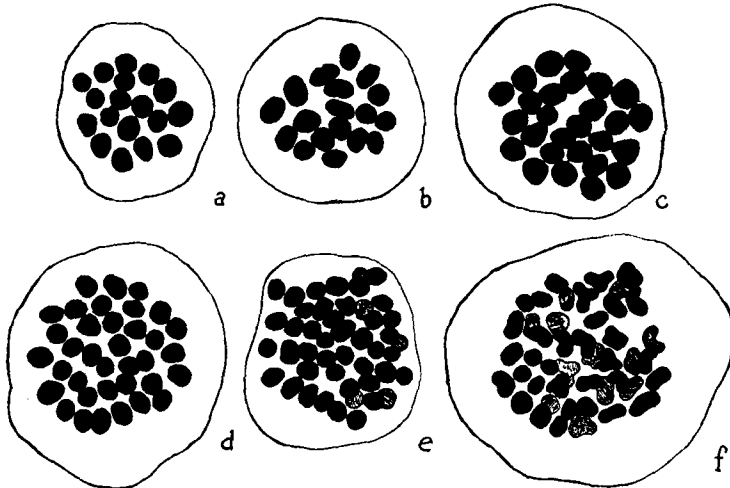f, with 45 chromosomes. (After Tahara.)

FIG. 99.

Nuclei in the diakinetic stage of several varieties of chrysanthe-
mums, a and b with 18 chromosomes; c with 27; d with 36; e with
45; f with 45 chromosomes. (After Tahara.)

ration divisions. It is suggested that a comparable series of changes may exist in the egg mother cells and lead to the retention of all the chromosomes in the parthenogenetic egg-cells.

In the cultivated varieties of chrysanthemum, Tahara has found a polyploid series. In ten varieties (Fig. 97) nine haploid chromosomes are present, but the chromosomes themselves have different sizes, and, more important still, the relative size of the chromosomes may be different in different species (Fig. 98). This point will be considered later. It is also significant that the nuclear size may be different in some of these cases where the total number of chromosomes is the same. Other species of chrysanthemum have multiples of nine (Fig. 99); two species have 18, two have 27, one has 36, two have 45. The following table gives the relation between chromosome number and nuclear size.

Name	Chromosome number	Nuclear diameter	Radius³
Ch. lavanduloefolium	9	5.1	17.6
Ch. roseum	9	5.4	19.7
Ch. japonicum	9	6.0	29.0
Ch. nipponicum	9	6.0	27.0
Ch. coronarium	9	7.0	43.1
Ch. carinatum	9	7.0	43.1
Ch. Leucanthemum	18	7.3	50.7
Ch. morifolium	21	7.8	57.3
Ch. Decaisneanum	36	8.8	85.4
Ch. arcticum	45	9.9	125.0

Triploid varieties of the mulberry (Morus) have been reported by Osawa. Of the 85 varieties studied, 40 are triploids. The diploid number of chromosomes is 28 ($n=14$) and the triploid 42 (3×14). The diploid plants are fertile, while the maturation divisions of the triploid show irregularities (univalent chromosomes) and have abortive pollen grains and embryo sacs. In the first matu-

ration division of the triploid, both in the pollen and in the megaspore mother cell, there are 28 bivalents and 14 univalents. The latter pass to the poles at random. They all divide at the second division.

In the maples (Acer) there appears to be a possible polyploid species. Taylor reported two species with 26 (n=13), two with 52 (n=26), and others with approximately 144 (n=72), or 108 (n=54), or 72 (n=36). Other species with different numbers were also found.

In the sugar cane (Saccharum) Tischler found races with the haploid numbers 8, 16, and 24 (bivalent) chromosomes. Bremer reports about 40 haploid chromosomes in another variety and 56 in a third. Other numbers have also been reported. Some of the combinations may be due to hybridization, but little is known at present to what extent the observed differences in number have arisen in this way. Bremer has also studied maturation divisions of a few hybrids.

In the genus Carex, Heilborn states that the chromosome numbers are quite different and that no apparent polyploid series exists in this genus. "It is of importance now to define somewhat more clearly the meaning of the word polyploid. It appears from the list of chromosome numbers in Chap. II that there are several numbers that constitute, apparently, a series of multiples with 3 as the fundamental number (9, 15, 24, 27, 33, 36, and 42), others, again, that form a series with 4 as fundamental number (16, 24, 28, 32, 36, 40, and 56), others with 7 (28, 35, 42, and 56) and so on, but, according to the author's opinion, these merely arithmetical relations cannot be regarded as cases of polyploidy. The chromosome group of a polyploid species must necessarily contain a certain number of complete haploid chromosome sets and it must have arisen through addition of such sets. We know, however, that, for instance, C. pilulifera does not contain 3 sets of

3 chromosomes, but 3 long, 4 medium, and 2 short chromosomes; that C. ericetorum does not contain 5 such sets, but 1 medium and 14 short chromosomes, and that, consequently, the chromosome groups in these two species have not arisen through an addition of such sets but in some other way." More problematical polyploid series are reported in Rumex, Papaver, Callitriche, Viola, Campanula, Lactuca. Two numbers, one of which is double or triple the other, have been found in Plantago (6, 12), Atriplex (9, 18), Drosera (10, 20), Platanthera (21, 63). It has also been recently reported by Longley that hawthorns and raspberries, known to be complex polymorphic species, show extensive polyploidy.