VARIATION IN THE NUMBER OF THE CHROMO-SOMES AND ITS RELATION TO THE TOTAL-ITY OF THE GENES

THE theory that the chromosomes are made up of independent self-perpetuating elements or genes that compose the entire hereditary complex of the race, and the implication contained in the theory that similar species have an immense number of genes in common, makes the numerical relation of the chromosomes in such species of unusual interest. This subject is one that could best be studied by intercrossing similar species with different numbers of chromosomes, but since this would yield significant results only in groups where the contents of the chromosomes involved were sufficiently known to follow their histories, and since as yet no such hybridizations have been made, we can only fall back on the cytological possibilities involved, and on the suggestive results that cytologists have already obtained along these lines.

A good deal of attention has been paid in recent years to the not uncommon fact that one species may have twice as many chromosomes as a closely related one. So frequent is this occurrence that it seems scarcely possible that it is due to chance. The implication is that the number of the original chromosomes has either become doubled, or else halved. If the number is simply doubled there would be at first four of each kind of chromosome from the point of view of genetic contents. This is what I understand by tetraploidy. There is some direct evidence that doubling may occur. If a new race or species is ever established in this way, we should anticipate that in the course of time changes might occur in the four identical chromosome groups so that they would come to differ

and form two different sets.[1]   Theoretically, the number of different genes in a species might in this way be increased. If changes in the same gene in the same direction sometimes occur, as the evidence indicates that they do, then identical new mutant genes, derived from the same kind of original ones, might later arise in different pairs.

There is, however, another way in which the number of chromosomes may be doubled without doubling the number of genes. If the chromosomes break in two, double the number will be produced. It is not easy to explain how this could occur in all of the chromosomes at the same time if the process is supposed to be accidental. If it be supposed that the break first occurred accidentally in one member of the pair, it is not clear why such a broken chromosome could establish itself on the theory of chance, for the intermediate condition of one broken and one intact chromosome would seem of no apparent advantage. The same reasoning applies to the converse process, *viz.*, the coming together of chromosomes end to end which would reduce the number by half.   Such a process would not increase the number of genes in the total complex. Until we know more about the physical or chemical forces that hold the genes in chains, and more about the way new genes arise, it is not worth while to speculate about the causes or probabilities of such occurrences.

What has just been said in regard to doubling and halving of the whole set of chromosomes applies also to doubling in one pair of chromosomes. If doubling occurred in one pair of a ten-chromosome type, a twelve-chromosome type would result; if in two pairs, a fourteen-chromosome type, etc.   Unless tetraploidy is the simpler procedure we should *a priori* suppose that increasing (or decreasing) in pairs would, on the theory of chance alone,

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[1] The question as to whether the four chromosomes involved would or would not mate at random introduces a difficulty (as shown in the primula case).

be the more common procedure. A few examples will illustrate what has been found out so far concerning some of these possibilities.

The evening primrose, *Œnothera lamarckiana,* has 14 chromosomes as its full or somatic number, and 7 as its reduced number (Fig. 58, *a*), and these numbers characterize most of the mutant types that De Vries found. But there is one mutant known as gigas, that has 28 chromosomes as its full number, and 14 as its reduced number (Fig. 58, *b*). Stomps estimates that gigas appears about 9 times in a million cases, *i.e.,* in 0.0009 per cent. Gigas is distinguished from *Lamarckiana* in many details of structure, but chiefly in its thick stem, etc., which is associated with larger cells.

Fig. 58.—Chromosome group of *Œnothera lamarckiana, a;* chromosome group of *O. gigas, b;* triploid group, *c.*

The type breeds true, *i.e.,* it does not revert to *Lamarckiana;* thus De Vries grew a family of 450 individuals from his original gigas, only one being a dwarf gigas, *viz.,* nanella. The way in which gigas originates has been much discussed, but no conclusion reached. De Vries suggested that it is produced by an egg with 14 chromosomes (diploid), being fertilized by a sperm with 14 chromosomes, both of these diploid cells originating by the suppression of a cytoplasmic division in the development of the gametes. It has also been suggested that a tetraploid condition might arise in a spore mother cell that developed without fertilization (by apospory). Gates pointed out that by suppression of the first division of the egg, *after fertilization,* the tetraploid condition would arise. The only objection to this last view, that *seems*

the simplest one since such suppressed division has been seen and can be induced in animal eggs, is that the following division might be expected to be into four parts owing to the doubling of the centres.

Gregory has described two tetraploid races of *Primula sinensis*,[2] one of which arose from ordinary plants in the course of his experiments. Since known genetic factors were present an opportunity was given to examine into the relation between the members of the four chromosomes of a set. The possibilities involved are these: Assuming the parents to be AA', and aa', and that conjugation of chromosomes takes place in twos only, then if any one of the four (AA' aa') chromosomes of a set may mate with any other member, there will be six possible unions, *viz.*, AA', Aa, Aa', $A'a$, $A'a'$, aa'. If the two derived from the same parents were the only ones that can mate, only two combinations are possible, AA', aa', and if the two derived from the opposite parents were the only ones that mate only two (but different ones) could form, *viz.*, Aa, $A'a'$. The genetic expectation is somewhat different for each of the three cases, since the number of different kinds of gametes produced is different in each. The data obtained by Gregory are not sufficient to give convincing evidence in favor of any one of these possibilities, although as Muller has shown by an analysis of the evidence, they are more in favor of the first possibility, *viz.*, that of random assortment. Gregory, without committing himself to the chromosome view, follows the second possibility in his analysis of the case. There is, however, nothing in the chromosome theory that would support the view that restricts the conjugation of homologous chromosomes according to their parental origins.

There are two other species of primose, *Primula floribunda* and *P. verticillata,* each with 18 chromosomes that have, after crossing, produced tetraploid types. In a

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[2] Other giant races of *P. sinensis* examined by Keeble and by Gregory are diploid.

cross between these two, a hybrid called *P. kewensis* was produced, which Digby has shown has also 18 chromosomes. It produced only thrum flowers, and was therefore sterile. Five years later, after this plant had been multiplied by cuttings, one pin flower appeared which was pollinated by a thrum flower. It gave rise to the fertile race of *P. kewensis,* that had 36 chromosomes. What connection there may have been between the hybridization and the subsequent doubling, if there is any connection, is by no means clear. It may be noted that in the reciprocal cross between *P. verticillata* and *P. floribunda,* a hybrid, *P. kewensis,* with 36 chromosomes also appeared.

The most interesting results on tetraploidy are those of Elie and Emile Marchal on certain mosses, for they have been able to produce tetraploid types experimentally. It may be recalled that in mosses there is an alternation of generations. The diploid $(2N)$ generation is known as the sporophyte (Fig. 59) that develops out of and remains attached to the other haploid generation, the gametophyte or moss plant $(1N)$. The sporophyte produces a large number of spores, each containing the half number of chromosomes $(1N)$ as a result of reduction that has taken place in their formation, and from each spore a young moss plant develops, beginning as a protonema of loose threads. When the moss plant produces its heads or flowers the sexual organs appear—archegonia (♀) and antheridia (♂). Thus the "sexes" are here represented by the haploid generation.

The egg-cell, contained in the archegonium, is fertilized by a sperm-cell, the antherozooid. The fertilized egg-cell $(2N)$ develops *in situ* into the straight stalk imbedded at its lower end in the tissue of the moss plant, expanding at its upper end into the cup containing the spores. The mother-cells of the spores—like the tissue of the sporophyte itself—contain the $2N$ number of chromosomes, which, by two divisions (similar to these already described for the animal cells during reduction), reduces

the number to 1N. It is at this time, too, in mosses with separate sexes, that sex differentiation takes place, for as the Marchals have shown, each spore gives rise to a male
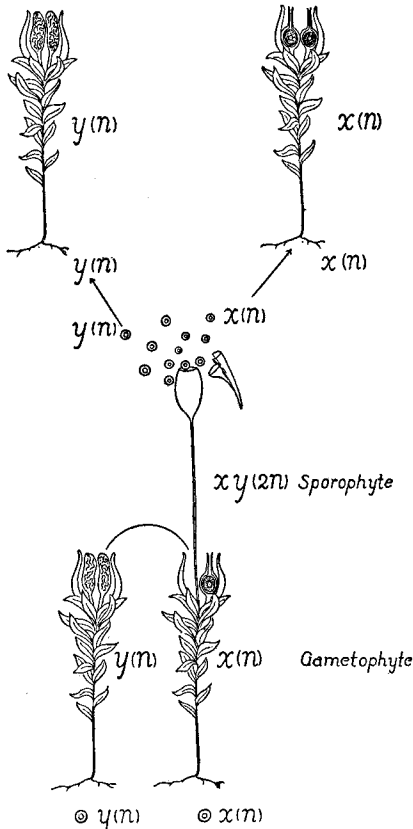

y (n)

x (n)

y (n)

x (n)

y (n)

x (n)

$x y$ $(2n)$ $Sporophyte$

y (n) x (n) $Gametophyte$

y (n) x (n)

Fig. 59.—Life cycle of moss. The mycelial thread and the moss plant constitute the $1n$, or gametophyte generation; and the stalk and capsule (with its contained spores), arising after fertilization out of the moss plant, constitutes the $2n$ or sporophyte generation.

or to a female thread that produces archegonia or else antheridia regardless of the condition under which the young plants are reared. Allen has recently shown in related plants—the liverworts—that during the reduction division (that gives rise to the spores) an unpaired sex-

chromosome is present that goes to half only of the spores. Presumably then in liverworts, and mosses, also, there is an internal mechanism for producing the two "sexes."

The Marchals have worked both with species having separate sexes and with hermaphrodites. We may con-
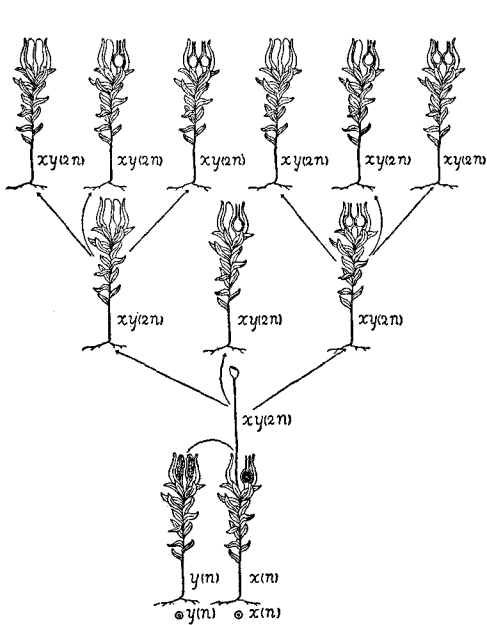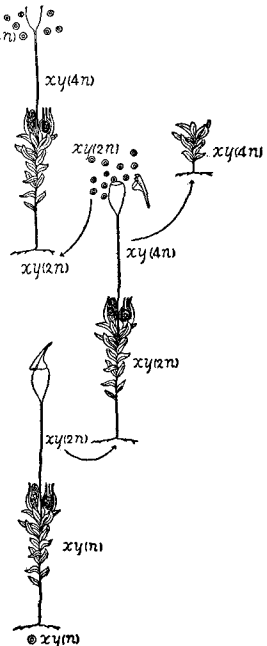

FIG. 60.

FIG. 61.

FIG. 60.—Diagram illustrating the formation of $2n$ individuals from the regeneration of the sporophyte in a diœcious species. (According to Marchal.)

FIG. 61.—Diagram illustrating the formation of $2n$ individuals from the regeneration of the sporophyte in a hermaphroditic species. (According to Marchal.)

sider the former first. If the sporophyte is removed and cut across, its cells regenerate a tangle of threads (protonema), which is the beginning of a new moss plant (Fig. 60). Since the sporophyte had the double number $(2N)$ of chromosomes, it is to be expected that the young moss plant that regenerates from its tissue (sporophyte) will also have the double number, and such proves to be the

case. The new moss-plant is therefore 2N (or diploid) instead of being 1N, as in the normal mode of propagation. Since no reduction has taken place into male- and female-producing individuals, it would seem possible that such a plant might produce either or both sexes. Such is the case, for when the 2N moss plant produces its "flowers" some contain archegonia, others spermatogonia (with their contained germ-cells) and other flowers contain both. The hermaphroditism here produced would seem to be the sum of both the contrasted elements. The expectation from such a 2N plant would be that its germ-cells (2N) would produce a 4N sporophyte—unfortunately the plants proved sterile. Imperfect germ-cells were present incapable of fertilizing or of being fertilized, so that it was not possible to perpetuate the 2N plant by sexual reproduction.

The results with the 2N plants derived from the regenerating sporophyte of the hermaphroditic species (Fig. 61) is different in one important respect. When, as before, a diploid (2N) plant is obtained by regeneration from the sporophyte it produces hermaphroditic flowers, *i.e.*, flowers containing both oögonia and spermatogonia, and these are fertile. The sporophyte that they produce is tetraploid (4N), due to the union of a diploid antherozooid with diploid egg. Regeneration from the tetraploid sporophyte (4N) should produce fertile gametes, which might give rise by their union to an octoploid sporophyte (8N). So far the Marchals have not been able to produce such plants, for although in a few cases the 4N sporophyte regenerated it failed to produce flowers.

The difference then between the results from mosses with separate sexes and mosses that are hermaphrodite is that the 2N plant of a race with separate sexes does not form normal gametes, while a 2N plant of hermaphroditic races forms fertile gametes. It may appear more or less plausible that the failure of the former is due to failure in the reduction of the spores into two alternative types,

while in the latter case, since there are presumably no such types found, there is no conflict. Some other difference would have to be appealed to to explain why the octoploid forms fail to develop.

A triploid condition ($3N$) has been found to occur in certain types of the evening primrose (Stomps, Lutz, Gates). De Vries has found in crosses in which *Lamarckiana* was the mother and some other species (muricata, cruciata, etc.), the father, that triploid types appear three times in 1000 cases. He interprets the results to mean that three in 1000 times the egg-cell of *Lamarckiana* has the double number of chromosomes (14), which being fertilized by a normal pollen grain with seven chromosomes, gives the triploid number, *viz.,* twenty-one chromosomes. The same result would be reached if a diploid pollen grain fertilized a normal egg. That such pollen grains appear is as probable *a priori* as that diploid eggs occur. It may be recalled that one explanation of the tetraploid evening primrose (gigas) is that it arises from a $2N$ pollen grain meeting a $2N$ egg-cell. How reduction takes place in the triploid œnotheras is uncertain, since the accounts of the process are different. Geerts states that, as a rule, only seven chromosomes conjugate ($7 + 7$), while the remaining seven chromosomes are irregularly distributed in the dividing germ-cells. On the other hand, Gates finds in a 21-chromosome type that the chromosomes separate into groups of 10 and 11, or occasionally into 9 and 12. The former account fits in better with results of the same kind obtained by others, and is more easily understood from a general point of view, because seven homologous pairs would correspond to the normal conjugation, while the seven chromosomes left over would have no mates and fail to divide at the reduction division, hence their erratic distribution.

It has also been shown in *Œnothera* that there are three 15-chromosome types. If the 15th chromosome is

sometimes one, sometimes another chromosome, there may be genetically several types, but as yet evidence on this point is lacking.

Irregularities in the germ-cells of *Œnothera* have been observed by Gates of such a kind that one cell gets 6, the
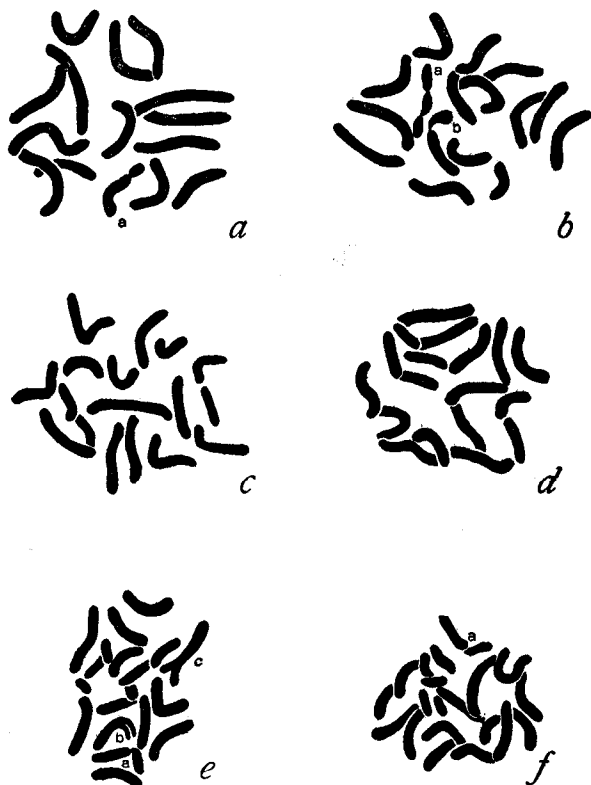

Fig. 62.—Somatic chromosome groups of *Œnothera scintillans*, showing variable numbers of chromosomes. (After Hance.)

other 8 chromosomes. A pollen grain with 8 chromosomes fertilizing an egg with 7 would give a 15-chromosome type. When such a 15-chromosome plant forms its egg-cells the supernumerary chromosome having no mate may go to either pole of the spindle, hence eggs of two

sorts would result, *viz.*, 7- and 8-chromosome cells.[3]   Such a plant if crossed to a normal plant should give half normal (14), half 15-chromosome types.   Such plants have been shown, in fact, to be produced (Lutz).   Other combinations that would give 22, 23, 27, 29 chromosomes have been reported.

A variation in the number of the chromosomes of a somewhat different kind has been described by Hance for *Œnothera scintillans,* one of the 15-chromosome types of *O. Lamarckiana.*   No variation in number was found in the germ-tract of the same individuals that consistently gave two types of pollen grains, one with 7 and the other with 8 chromosomes.   The number of chromosomes in the somatic cells was found to vary from 15 to 21.   Some of the groups are shown in Fig. 62.   When the 15 chromosomes of the type-group are measured, it is found that they can be arranged in respect to length in 7 pairs, with one odd one (marked *a* in the figures).   There is also found a constant length difference between the pairs.   In those cases where there are more than 15 chromosomes in a cell, measurements show that the pieces can be assigned to particular chromosomes.   When this is done, Fig. 63, the lengths of the chromosomes come out as in the typical cells.   There can be no doubt that the extra chromosomes in these cases represent pieces that have broken off from typical chromosomes.   This process of fragmentation does not destroy the "individuality of the chromosomes" since the increase in this way of the number of chromosomes would not lead to any immediate change in the number of the genes.   The peculiarity of the mutant *O. scintillans* is not connected with the increase in the number of its chromosome bodies, but rather to the presence of a 15th chromosome.

Bridges has called attention to a peculiar case in *Drosophila* (1917) in which an individual behaves as

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[3] No pollen is produced by most of the lata plants.

though a piece of the X-chromosome (recognizable from its genes that normally lie in the middle of the chromosome) had become attached to one end of the other X-chromosome. Owing to this piece (including the region that contains the normal allelomorphs of vermilion and sable) the individuals give unexpected results in relation to dominance or recessiveness of certain factors. For example,
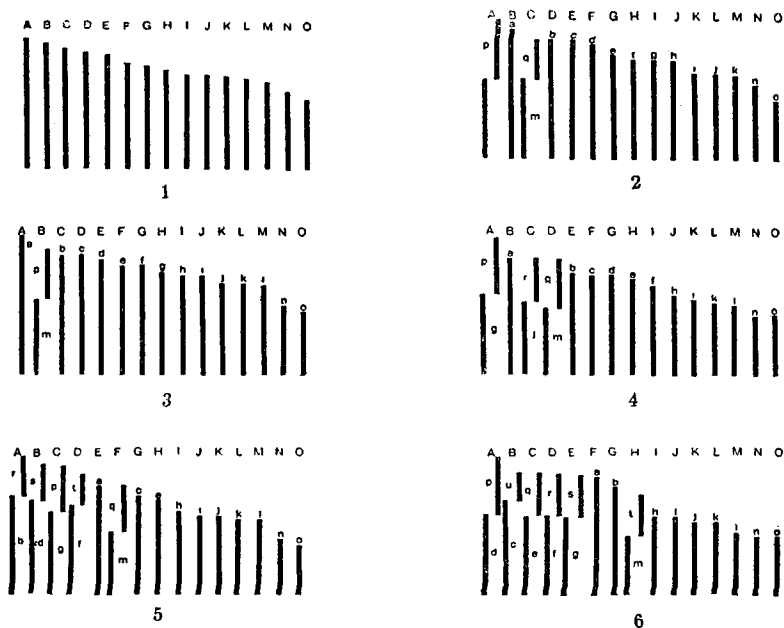

FIG. 63.—Scheme showing the probable relation between the extra chromosome pieces of Fig. 62, and the normal 15 chromosomes of this mutant. (After Hance.)

a male that contains the recessive genes for vermilion and for sable, normally located, and having attached to this chromosome the duplicated piece (containing the normal allelomorphs of vermilion and sable) is in appearance a wild-type fly, instead of being vermilion sable as it would otherwise be without the piece. On the other hand, a female having one such chromosome and a normal vermilion sable chromosome is in appearance not wild type

(as might have been expected), but shows vermilion and sable, because in this case the two recessive genes for vermilion and for sable dominate the single normal allelomorphs. But a female having two such duplicated chromosomes (*i.e.*, tetraploid for the genes of certain regions of the sex-chromosome) is now wild type in appearance, because the two dominants dominate the two recessives. Such a female crossed to a vermilion sable male gives wild-type sons and vermilion sable daughters, which is criss-cross inheritance in an opposite sense from that ordinarily met with in *Drosophila*.

A second instance discovered by Bridges, but not yet reported, seems best explained on the assumption that a piece taken from the second chromosome has become attached to the middle of the third chromosome. This condition makes possible the linkage of mutant characters to genes in both the second and the third chromosome at the same time. The second chromosome that lost a piece, and the third chromosome that gained the piece (both were of course in the same cell), have been easily kept together in the same stock ever since, because in those cases where they become separated through assortment every zygote that receives the deficient (2nd) chromosome dies unless the same zygote has received the third chromosome with the duplicate piece.

The preceding results show that chromosomes may not only gain genes by the attachment of pieces (duplication), but also that chromosomes may lose pieces (deficiency).

Other instances of deficiency have been reported by Bridges which can be explained either as total losses of certain regions, or due to their inactivation. Unless the lost pieces happen to have been retained as in the last case, the distinction between these possibilities is difficult. A study of one case has shown that no crossing over takes place in the region of deficiency, although the rest of the chromosome was little or not at all affected. As a result

the chromosome is "shortened" by an amount correspond-
ing to the "length" of the deficient region.

It is not without interest to notice that in the first
case the duplicating piece is attached to that end of the
first chromosome where the spindle fibre is attached. In
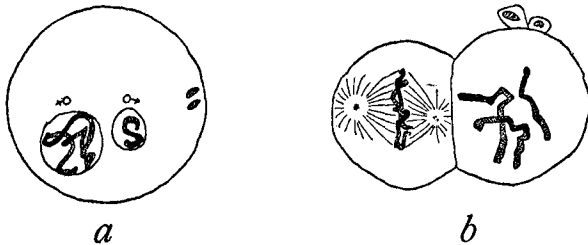the other case the duplicating piece is attached to the

a   b

Fig. 64.—An egg of *Ascaris bivalens* fertilized by sperm of *A. univalens, a;* later stage
of same, *b.*

middle of the third chromosome, and in this chromosome
the spindle fibre is attached to the middle.

An interesting case of triploidy has been reported in
the threadworm *Ascaris* (Boveri). Two varieties occur,
one with four chromosomes (haploid two), and one with
two (haploid one). Rarely a female of one variety is

a

a

Fig. 65.—Diploid and haploid groups of the sundew *Drosera.*   (After Rosenberg.)

found that has mated with a male of the other variety.
The fertilized eggs have each three chromosomes (Fig.
64). As yet no triploid adults have been met with, so that
the method of conjugation of the chromosomes in the
triploid types is not known.

Rosenberg crossed two species of sundew, *Drosera
longifolia,* with 40 chromosomes (haploid 20), and *D.
rotundifolia,* with 20 chromosomes (haploid 10), Fig. 65.

The hybrid had 30 chromosomes (20+10). He found that when this hybrid produces its germ-cells they show, after reduction, 20 chromosomes, which he interprets as due to 10 of the rotundifolia conjugating with 10 of the longifolia. This leaves 10 without mates. At the following maturation division Rosenberg describes the 10 paired chromosomes as reducing, sending one member of each dyad to one pole, the other member to the other; but the
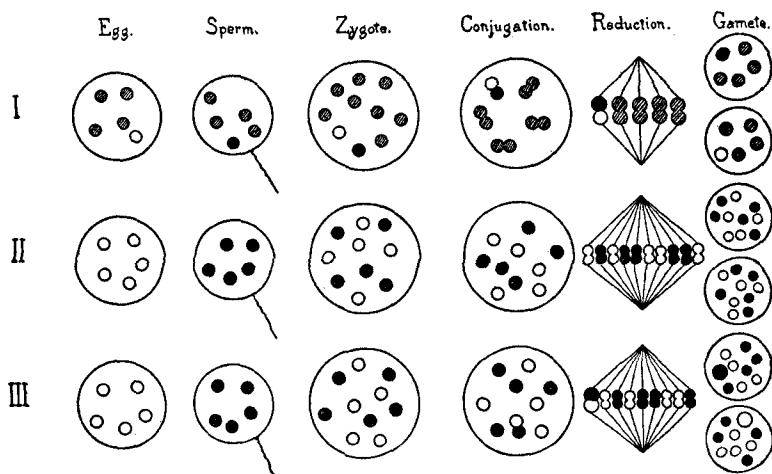

FIG. 66.—A scheme illustrating the fertilization of the egg of one species of moth by the sperm of another, with reduction in I, with no reduction in II, and with partial reduction in III.

10 unpaired chromosomes are irregularly distributed at this division. If the account is confirmed, the situation is peculiar, for if the 20 (haploid) chromosomes of longifolia correspond to the 10 (haploid) of rotundifolia it is not obvious why all 20 might not find a place alongside of the 10, unless chance or some difference of length, etc., makes this impossible. This assumes, however, that longifolia is not tetraploid—if it is, then a further question arises as to which chromosomes of each set of three would be the ones most likely to conjugate, etc.

Crosses between three species of the moth *Pygœra,*

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having different chromosomes, were made by Federley. The hybrids showed intermixed characters of both parents, and their chromosome number was the sum of the haploid numbers of their parents (Fig. 66).

No reduction in number of the chromosomes takes place in the hybrid at the synaptic stage (except perhaps for one or two small ones), so that the 1st spermatocytes contain nearly the sum of the haploid number of the

Egg.   Sperm.   Zygote.   Conjugation.   Reduction.   Gamete.
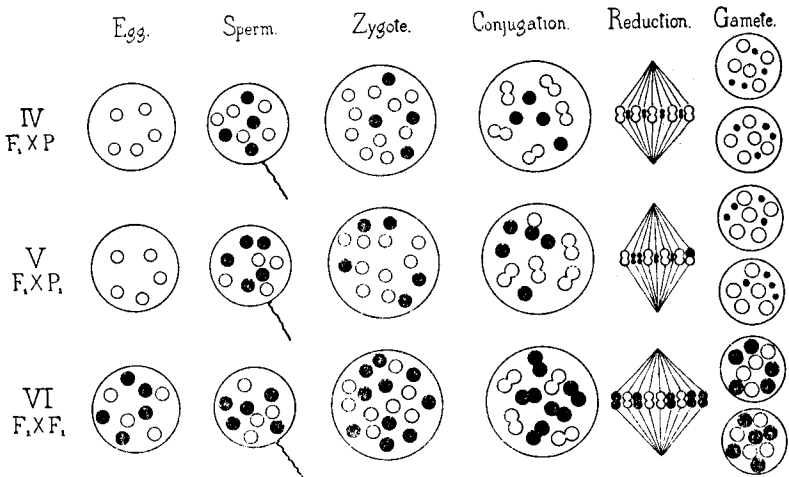
IV
F. X P

V
F. X P.

VI
F. X F.

FIG. 67.—Scheme illustrating the history of the chromosomes, and the back-cross between a hybrid male and one or the other parent; also between two such hybrid F₁ individuals.

parents (A and B) after division of each chromosome (Fig. 67). A second maturation division follows in which each chromosome again divides. As a result each sperm contains the full number of chromosomes, half paternal, half maternal (A and B). The hybrid female is sterile, but the male is fertile. If he is back-crossed to a female of the A race his sperm, carrying both sets of chromosomes, will produce a $3N$ individual, $A + B + A$. It will have two sets of the A genes to one set of B. In appearance the moth is practically the same as the F_1 hybrid, because both contain both sets of chromosomes—the

double set AA with B not producing any striking differ-
ence from the single set $A+B$. When this second hybrid
($3N$) matures its germ-cells, the two homologous series
($A + A$) mate with each other, and then segregate at the
first division, while the unmated B-series simply divides.
At the second division both the A- and the B-series divide,
thus giving to each sperm a haploid set of chromosomes
($A + B$). The sperm then is the same as the sperm of
the first hybrid. So long as the back-crossing continues
the outcome is expected to be the same.

If, instead of back-crossing the first hybrid to parent
A, it is back-crossed to parent B, the same result as
before takes place, except that the second hybrid is now
$A + B + B$. When it matures its germ-cells, the B's
unite and then separate, giving AB sperm as before.

Here then we find a kind of inheritance that super-
ficially appears to contradict the generality of Mendel's
law of segregation.   On the contrary, a knowledge of the
chromosomal behavior shows that the results are different
because the mechanism of conjugation of the chromosomes
is changed, and changed moreover in such a way that on
the chromosome theory itself the results are what are to
be expected.

These crosses are so important that some further
details may be added. The whole ($2N$) and half ($1N$)
number of chromosomes of the three species studied by
Federley are as follows:

	Whole	Half
Pygaera anachoreta	60	30
Pygaera curtula	58	29
Pygaera pigra	46	23

In the hybrid between the first two species the number of
spermatocyte chromosomes was found to be 59 ($30 + 29$).
No union between any of the maternal and paternal chro-
mosomes could have taken place. But in the hybrid
formed by the union of the two more nearly related spe-
cies, curtula and pigra, the number of spermatocyte chro-

mosomes was found to be as a rule somewhat smaller than the sum of the parental haploid numbers, indicating that one or more had conjugated.   To the extent to which such union, and the consequent reduction, takes place, the characters of the second hybrid generation may differ from those of the first—at least if the conjugating pairs have different factors in them.

A similar behavior of the chromosomes has been described by Doncaster and Harrison for two species of moth of the genus Biston (Fig. 24).   The hybrids were sterile, and no further generations were raised.

Federley later made similar crosses with three other moths.   A cross between *Smerinthus ocellata* (with 27 chromosomes as the haploid number) and *Dilina tiliæ* (with 29) he regards as a cross between genera.   A cross between *S. ocellata* and *S. populi* (with 28) he regards as a species cross.   A cross between *S. ocellata* and *S. ocellata* var. *planus* he regards as a racial, or varietal, cross. As before the spermatocytes of the hybrid have the sum of the two parental numbers of chromosomes (or a few less at most).   In other words, conjugation of the chromosomes does not take place.   The most unexpected result in these combinations is that the types that are so alike as to be classified as varieties behave as regards conjugation like the other two combinations.   The results suggest that ordinary conjugation may not be due to the similarity of the sets of genes carried by the chromosomes so much as to other peculiarities of the combination.