Number and Behavior of Chromosomes in the Genus *Narcissus*[1]

By

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With 242 Figures

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1. Karyological studies of the narcissus plant III.

Introduction

Polyploidy is a subject of special interest in the field of genetico-cytology. While many plants have been used and closely studied in the investigation of this problem, the *Narcissus* plants have attracted the attention of only some few authors. STOMPS (1919) was the first to give some account of the chromosome numbers in these plants. This investigation was followed by those of DE MOL (1922[1], '25, '26, '27[2], '28[3]), HEITZ (1926), NAGAO (1929, '30) and FERNANDES (1931 a, b), and a polyploid condition was shown to exist in these plants. But most of the investigations have been made mainly with root-tip cells, and have taken no account of the behavior of the chromosomes in the reduction division, except in the case of some garden varieties of *Narcissus tazetta* and *N. poeticus* (NAGAO 1929, 1930).

In the present paper the results obtained from observation of the behavior of chromosomes in the reduction division in pollen mother cells in some of these and other species and garden varieties, as well as in some species which are taxonomically regarded as hybrids are

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1. Cited from GAISER (1926).
2, 3. Cited from GAISER (1930).

more fully given than in the previous papers and a discussion of the chromosome number, not only in its relation to the phylogenetical relationship between these species or varieties, but also with regard to its physiological and genetical significance viewed from both the scientific and the applied biology standpoint, is attempted.

It is my pleasant duty to record here a debt of gratitude to Prof. Y. KUWADA for his valuable suggestions and criticisms throughout the work.

Material and Method

According to ENGLER and GILG (1924) the genus *Narcissus* comprises thirty five species. In the present investigation, however, I had at my disposal only a restricted number of garden species known by the names *Narcissus Pseudonarcissus*, *N. incomparabilis*, *N. Jonquilla*, *N. Bulbocodium*, *N. intermedius*, *N. tazetta*, *N. odorus*, *N. biflorus* and *N. Barrii*, and some of their garden varieties. It was my intention to carry out crossing experiments, but this was unattainable owing to the high sterility of the plants which is found even in diploid forms, as I convinced myself in the attempts I have made every year for the past few years, and also to the fact that these plants take many years to reach maturity and flower. No hybrid forms experimentally raised were, therefore, investigated.

The material used for microscopical investigations was taken from plants collected from several nursery companies, and cultivated for several years in the experimental garden of the Botanical Institute of Kyoto Imperial University. Observations were made with root-tip cells for the somatic number of chromosomes and with pollen mother cells for the reduction division. Root-tips were fixed in FLEMMING's strong solution or the BONN modification of it. For pollen mother cells, NAWASCHIN's fixative (1 % chromic acid 10 parts; glacial acetic acid 1 part; 40 % formalin 4 parts[1]) was exclusively used. This fixative proved good, generally speaking, but gave somewhat varying results according to peculiarities of the species and varieties. To fix the material, the flower bud was taken out of a bulb by cutting it, and then each anther was carefully made free from the main body of the bud, and immediately fixed in the fixative.

The season in which the reduction division takes place in pollen mother cells is different in different species and in different garden

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varieties of the same species. The best seasons, I found from my observations of them in our garden in the past few years, are as follows :—

Narcissus tazetta : from the end of September to early November.

N. Pseudonarcissus and *N. incomparabilis* : from the middle of October to early November.

N. Jonquilla and *N. poeticus* : the middle of November.

N. intermedius : from the end of October to early December.

N. Bulbocodium and *N. biflorus* : from early December to the end of December.

Sections were cut 15 microns thick for root-tips, and 10 to 15 microns thick for pollen mother cells. They were exclusively stained with HEIDENHAIN's iron alum haematoxylin.

All the figures reproduced in the present paper were drawn by the aid of an ABBE's camera lucida with a ZEISS achromatic imm. 1/12 and compensation oculars K12 and K18.

Observation

I.   Cases where the cardinal number of chromosomes is 10

Narcissus tazetta L.[1]

A)   Diploid

a)   " Franklin "

External characteristics :—Leaves flat and obtuse, 1.5 cms. broad, 4 in number : flowers 11–15 in number, 3.5 cms. across ; crown yellow, segments cream white with yellow tint ; style more or less exceeding the anthers.

The somatic number of chromosomes is 20 in root-tip cells (Fig. 1). In pollen mother cells, 10 bivalent chromosomes or gemini are counted at diakinesis and metaphase in the heterotype division, and 10 univalents at metaphase in the homotype division (Figs. 2, 3, 4, 6). 6 gemini of the 10 are rod shaped and thicker than the remaining 4, which are round in shape (Figs. 3, 4). This difference in shape and size is so clear that we can easily distinguish these two types of chromosomes in every figure. The division figures are, practically speaking, all regular both in the heterotype and homotype divisions (Fig. 5). The pollen grains are mostly normal in appearance and the abortive ones amount to less than 10 % (Fig. 13).

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1.   A preliminary report on observations of some of the varieties of this plant was published in Japanese with an English summary (NAGAO 1930).
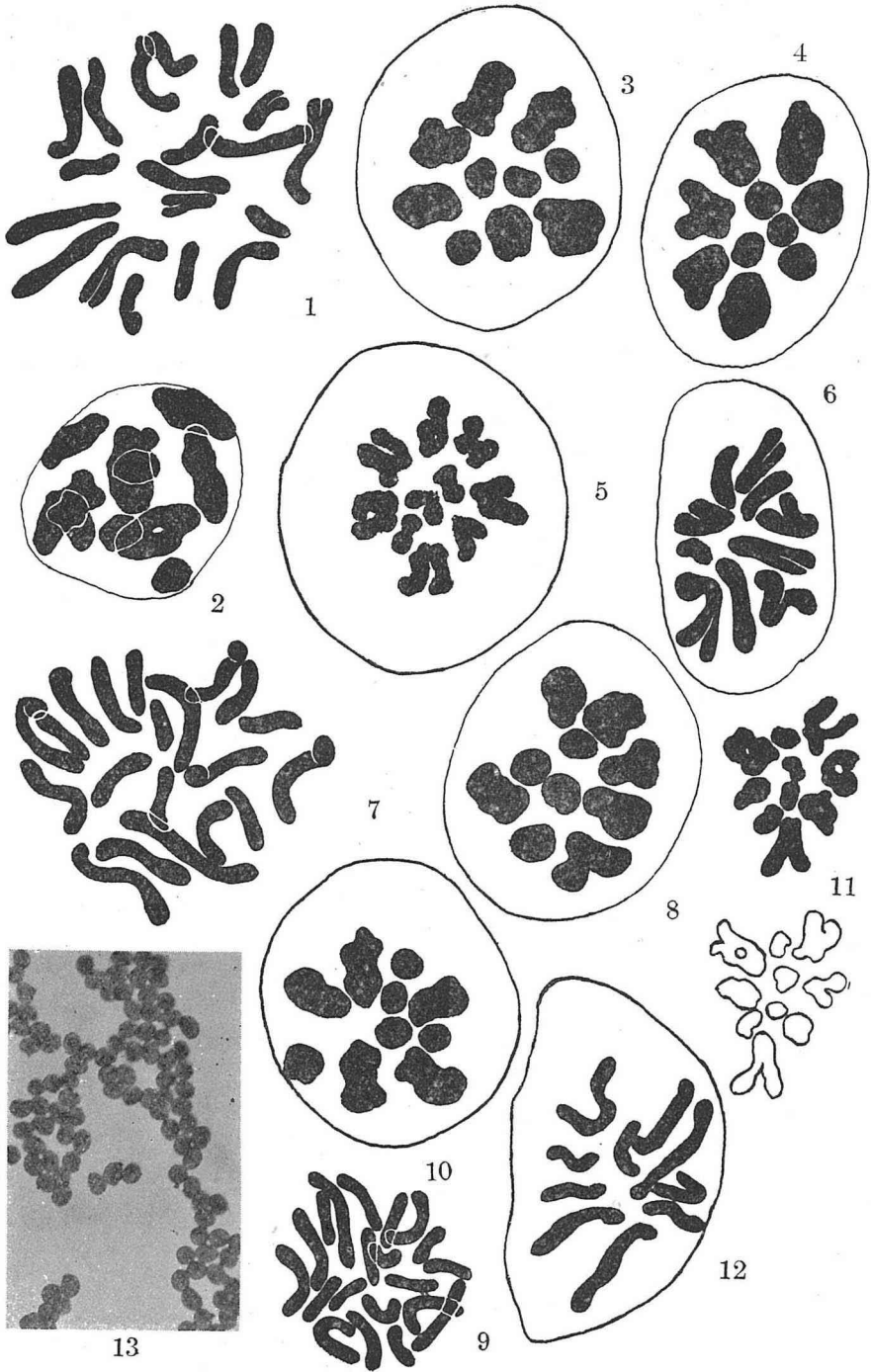
Figs. 1-6 *N. tazetta*, "Franklin" 1. Somatic nuclear plate, showing 20 chromosomes. ×2210; 2-6. Meiotic phases. Figs. 2-5 ×1710, Fig. 6 ×2210; 2. Diakinesis, showing 10 gemini; 3. Heterotype metaphase, showing 6 large and 4 small gemini; 4. The same. 2 small gemini occupy the inner position; 5. Heterotype anaphase; 6. Homotype metaphase, showing 10 chromosomes.

Figs. 7 and 8. *N. tazetta*, "L_{20}" 7. Somatic nuclear plate, showing 20 chromosomes. ×2210; 8. Heterotype metaphase, showing 6 large and 4 small gemini. ×1710.

Figs. 9-12. *N. tazetta*, "B_{20}" 9. Somatic nuclear plate, showing 20 chromosomes. ×2210; 10. Heterotype metaphase, showing 5 large and 5 small gemini. ×1710; 11. Heterotype anaphase. ×1710; 12. Homotype metaphase. ×1710.

Fig. 13. Pollen grains of *N. tazetta*, "Franklin" (Microphotograph).

b) Variety "L_{20}"[1]

External characteristics :—Leaves 4 in number : leaves and scape about 30 cms. long : flowers 7-8 in number, 3-3.5 cms. across ; crown, brownish yellow, segments, pale lemon yellow ; style not exceeding the anthers.

The somatic number of chromosomes is 20 as in the former variety (Fig. 7). The chromosomes found in the heterotype division are quite the same in size in relation to one another as well as in the numerical ratio between the large and small ones, this being 6 : 4 as in the variety "Franklin," as shown in Fig. 8.

c) Variety "B_{20}"

External characteristics :—Small : leaves and scape about 20 cms. long : flowers 7-8 in number ; crown, soft yellow, segments, cream white ; style more or le.s exceeding the anthers.

This variety shows 20 chromosomes in the root-tip cells (Fig. 9) and 10 bivalents or gemini in the heterotype metaphase. The size relation between these gemini is recognizable as the same as in the case of "Franklin," but the numerical ratio between the large and small ones is different from that found in "Franklin." In this variety it is 5 : 5 instead of 6 : 4 (Figs. 10, 11, 12). Nothing abnormal is found in the chromosome behavior in division. The phylogenetic significance of the difference between these two varieties in the ratio of chromosomes of different sizes will be considered later.

B) Triploid

a) "Yellow Prince"

External characteristics :— Small but strong : leaves flat and obtuse, 4-6 in number ; leaves and scape about 18-21 cms. long : flowers 5-8 in number, 3.5 cms. across ; crown, cadmium orange, segments, soft yellow ; style not exceeding the anthers.

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1. BAKER has classified the polyanthus narcissus into three groups, "bicolores," "albae" and "lutae" according to the difference in the color of the collora (BAILEY 1917, p. 2112). By "L_{20}" it is meant here that the plant is one belonging to the "lutae" type and has 20 chromosomes in its somatic cells. In like manner, the letters "A" and "B" in the following also indicate that the plants called by these letters belong to the groups, the name of which have those letters as initials, and the numbers attached to the letters signify the somatic numbers of the chromosomes which the plants carry.
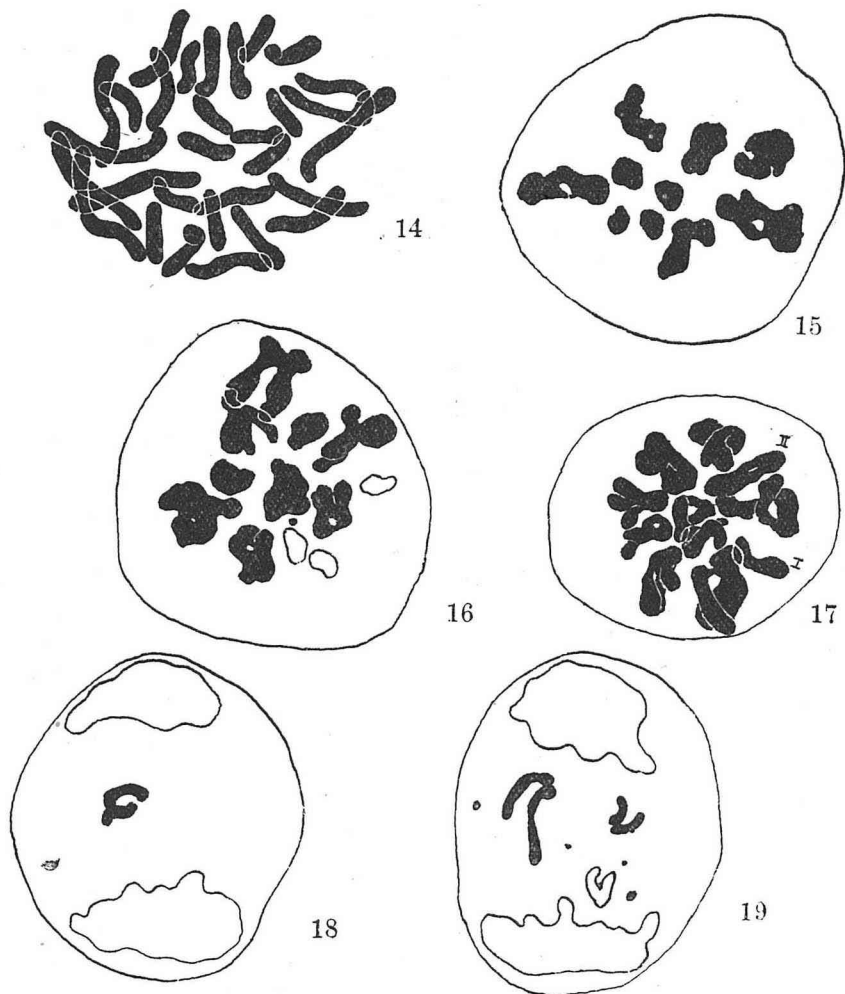
Figs. 14-19. *N. tazetta,* " Yellow Prince "   14. Somatic nuclear plate, sh wing 30 chromosomes. ×2210; 15—19. Meiotic phases. ×1710 ; 15. Heterotype metaphase, showing 10 chromosomal elements ; 16. The same, showing 9 trivalent and 3 univalent chromosomes ; 17. The same, showing 9 trivalent, 1 bivalent and 1 univalent chromosomes. 18. Heterotype anaphase. A triplet shown solid black split longitudinally   19. The same. 2 triplets shown solid black split longitudinally.

This is .a triploid variety of *tazetta* having 30 chromosomes in the somatic cells (Fig. 14). In the heterotype division, there is a strong tendency among the chromosomes to form trivalent complexes as in the case of triploid *Datura, Hyacinthus* (BELLING and BLAKESLEE 1922, BELLING 1925c) and some other triploid forms (Fig. 15). In a number

of cases, some of the chromosomes fail to unite into trivalents, so that more than 10 chromosomal elements, usually 11, 12 or 13, are countable in the heterotype metaphase. In Figs. 16 and 17, polar views of the metaphase are reproduced, where the chromosomal constitutions $9_{III} + 3_I$ and $9_{III} + 1_{II} + 1_I$ are recognizable respectively. In Table I the frequency of occurrence of these different numbers of chromosomal elements found in the heterotype metaphase in 57 pollen mother cells is given without reference to the valency of these elements.

Table I

Number of chromosomal elements	10	11	12	13	Total
Frequency	23	24	9	1	57

It is seen from this table that the occurrence of 12 and 13 elements is exceedingly rare, while the other cases, 10 and 11, occur about equally often. In attempting to determine microscopically the valency of these elements we often encounter almost insurmountable difficulty, but the determination is usually indirectly possible in so far as it is concerned merely with the question of how many chromosomal elements of certain valencies there are in a given nuclear plate. For example, if we have a nuclear plate composed of 11 elements, 9 of the elements must be trivalent, the remaining two being bivalent and univalent respectively, otherwise, the number 11 can not be maintained. The case where there are 8 trivalents ($8_{III} + 3_{II}$) may be considered, if the conjugation of non-homologous chromosomes is assumed, but this assumption is impossible in the present state of knowledge and accordingly the chromosomal constitution $9_{III} + 1_{II} + 1_I$ is the only reasonable constitution that we can consider for the case where the number of elements is 11. In Table II all the possible cases are given for each number of elements, including unreasonable constitutions, which are marked with an asterisk.

Table II

Number of chromosomal elements	10	11	12	13
Possible constitution[1]	10_{III}	$9_{III} + 1_{II} + 1_I$ $8_{III} + 3_{II}^*$	$9_{III} + 3_I$ $8_{III} + 2_{II} + 2_I$ $7_{III} + 4_{II} + 1_I^*$ $6_{III} + 6_{II}^*$	$7_{III} + 3_{II} + 3_I$ $6_{III} + 5_{II} + 1_I^*$ $5_{III} + 7_{II} + 1_I^*$ $4_{III} + 9_{II}^*$

1. The roman numerals attached to the figures indicate the valencies of chromosomes, their numbers being shown by those figures.

The results given in Table I being interpreted in the manner shown in Table II, we see that the fact that the cases of 10 and 11 elements most frequently occur shows that there is a strong affinity among every three chromosomes causing them to form a trivalent element, and we come to the conclusion that this variety is an auto-triploid plant,[1] having 10 as its basis[2,3] or cardinal number of chromosomes.

At anaphase one or two univalent chromosomes lag behind the others, and split longitudinally. Their halves separate from each other towards the poles after the other chromosomes of normal behavior have reached the poles (Figs. 18, 19). About 45 % of abortive pollen grains is found. The abortion seems to be due to the chromosome aberration in the meiotic divisions.

b) " Chinese Sacred Lily "

External characteristics :—Robust form : leaves flat, 4–6 in number : leaves and scape about 32 cms. long: flowers prominent, 4.5 cms. across ; crown primuline yellow, segments snow white ; style more or less exceeding the anthers.

Observations in root-tip cells show that this variety or form is also a triploid plant having 30 chromosomes in the somatic cells, as in the case of the variety " Yellow Prince " (Fig. 20). The chromosome behavior in the reduction division, however, is different in certain respects from what is found in that variety. In the heterotype meta-phase the number of chromosomal elements varies from 7 to 14. It is a peculiar fact that fewer than 10 chromosomal elements are found in such a plant as this variety which is regarded as a triploid carrying 30 somatic chromosomes. This peculiar phenomenon leads us to the logical conclusion that there must exist some number of chromosome complexes of a higher order than those in " Yellow Prince ", such as, for instance, some tetra- or pentapartite elements, instead of all being tripartite. Though the direct determination of the chromosomal constitution of these elements is very frequently hardly successful in this plant too, owing to their compactness of union, it is at least possible in certain cases to secure some idea about the constitution. The nuclear plate reproduced in Fig. 21 shows 8 chromosomal elements, of which one is probably of the pentapartite nature. Fig. 22 shows another nuclear plate with 10 chromosomal elements of which one is very large (probably multipartite) and some are much smaller (probably

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1. A terminology proposed by KIHARA and ONO (1926, p. 480).

2. A terminology introduced by BRIEGER (1928).

3. FERNANDES (1931 a, b) has reported that the number 10 is the diploid number of *Narcissus tazetta*. The cardinal number of this plant will be discussed in a later chapter.

univalent). In Fig. 23 a nuclear plate consisting of 14 chromosomal elements, probably of the constitution, $5_{III} + 6_{II} + 3_I$, is shown.

From these figures it is seen that there is no regularity in the constitution of the complexes, that is, that the constitution of the complexes or elements may be different in different elements. Primarily the constitution must have been such as that we have seen in " Yellow Prince", but in the variety in question a secondary union or association, due to certain peculiar characteristics of the chromosomes, must have taken place among the primary complexes, so that chromosome complexes of higher orders than triple must result. A similar phenomenon has been reported by KIHARA and NISHIYAMA (1930), occasionally observed in one of the triploid species hybrids of *Triticum*, and by NISHIYAMA (1929) in a triploid hybrid of *Avena*. According to these authors, the tetrapartite complexes which are often observed in these triploid *Triticum* and *Avena* hybrids must have originated in the union of two independent bivalents, and therefore, they are not tetravalents ; a tetrasomic complex can not be expected to exist in a triploid plant. The multipartite state or multiple association of chromosomes has also been found in diploid and triploid varieties of *Pyrus* (DARLINGTON and MOFFETT 1930) and in some species of *Pomoideae* such as *Crataegus monogyna* and *Pyrus minima* (MOFFETT 1931). In the case of *Pyrus*, the association of four, five, six, seven, eight and even nine chromosomes has been reported. DARLINGTON and MOFFETT (DARLINGTON and MOFFETT 1930, MOFFETT 1931) have concluded from these results of observation that the *Pyrus* plants are, though functionally diploid, historically quadruply tetrasomic and trebly hexasomic. LAWRENCE (1931a, b) has also reported a similar result of observation in *Dahlia,* and expresses the view that the formation of the chromosome complexes is due to the " secondary association " which takes place secondarily between primary pairs of chromosomes.

The frequency of occurrence of different numbers of chromosomal elements obtained from observation of 64 pollen mother cells is shown in Table III.

Table III

Number of chromosomal elements	7	8	9	10	11	12	13	14	Total
Frequency	3	24	12	11	6	4	1	3	64

If the chromosomal elements are 9 or less than 9 in number, there must exist some multipartite chromosomes, though such a chromo-
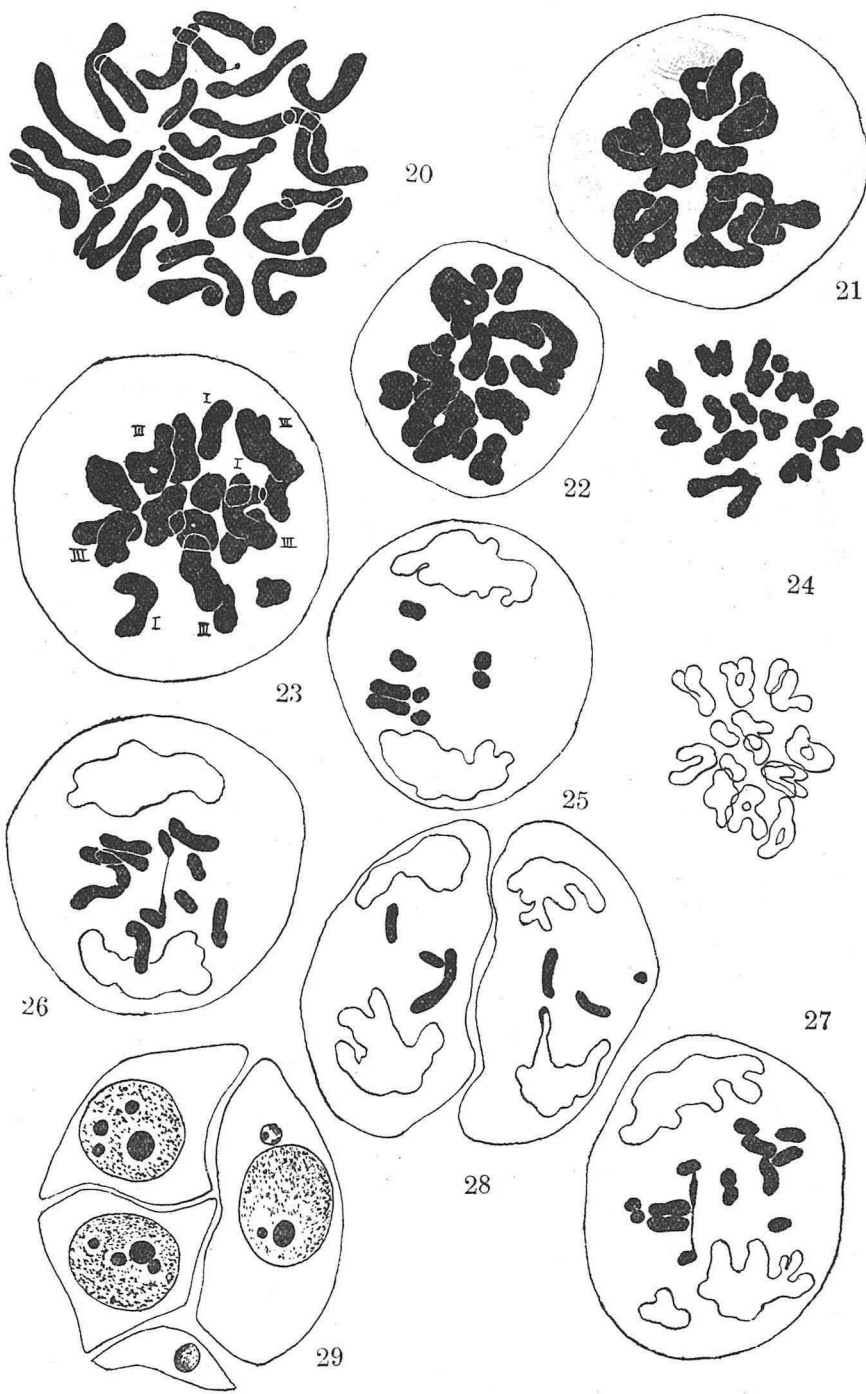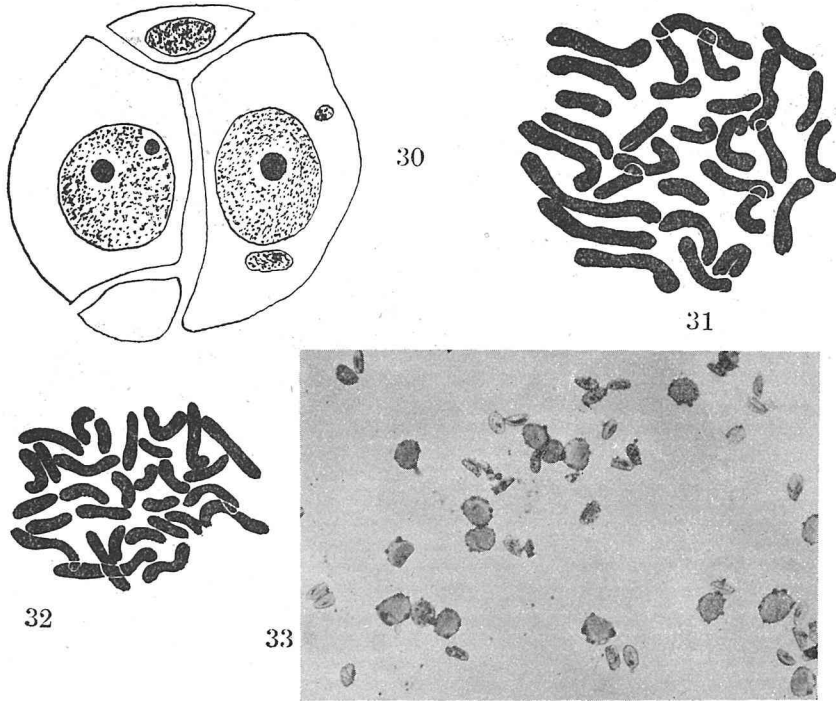
Figs. 20-30. *N. tazetta*, "Chinese Sacred Lily". 20. Somatic nuclear plate, showing 30
chromosomes. ×2210. 21-30. Meiotic phases. ×1710; 21. Heterotype metaphase. 8
chromosomal elements, one of which is probably pentapartite, are shown; 22. The same,
showing 10 chromosomal elements; 23. The same, showing 14 chromosomal elements
probably of $5_{III}+6_{II}+3_{I}$; 24. Heterotype anaphase, showing 15 chromosomes in each pole;
25-27. The same. 4, 5, 6 chromosomes shown solid black respectively split longitudinally;
28. Homotype anaphase; 29 and 30. Irregular pollen tetrads.
Fig. 31. *N. tazetta*, "Soleil d'Or". Somatic nuclear plate, showing 30 chromosomes. ×2210.
Fig. 32. The wild growing species. Somatic nuclear plate showing 30 chromosomes. ×2210.
Fig. 33. Pollen grains of *N. tazetta*, "ChineseS acred Lily" (Microphotograph).

some or chromosomes may also exist in those cases where 10 or more
than 10 elements are counted, as is shown in Fig. 22. According to
our data, the number of chromosomal elements is less than 10 in 39
cases out of 64. This fact must mean that the multiple association
of chromosomes is of common occurrence in this variety.

In anaphase the chromosomes may be distributed in equal numbers
to both poles, as is shown in Fig. 24. Irregularities in division are,
however, rather commonly observed. In Figs. 25, 26 and 27 where
anaphase figures in the heterotype division are reproduced it is shown

that 4, 6 and 7 chromosomes respectively lag behind the others, all or some of them (as shown in the latter two figures) having split longitudinally. Lagging chromosomes are also found in the homotype division, as is shown in Fig. 28. Through these and other irregularities in the meiotic divisions, besides the normal pollen tetrads, abnormal tetrads with or without a dwarf-nucleus or -nuclei as well as diads and triads are produced (Figs. 29, 30). The presence of dwarf nuclei in the abnormal tetrads suggests that in the homotype division some chromosomes fail to take part in the formation of the tetrad nuclei. Despite these irregularities in the behavior of the chromosomes in division, polyspory is of rare occurrence in this garden form. A similar phenomenon has been reported in *Raphanus-Brassica* hybrids (PIECH and MOLDENHAWER 1927, p. 32). About 70 % of the pollen grains are empty in this *Narcissus* form (Fig. 33).

The root-tips of two other plants, " Soleil d'Or " (Fig. 31) and a wild plant known taxonomically under the name *Narcissus tazetta* L. var. *chinensis* ROEM , growing on the sea-shore in the temperate regions of Japan (Fig. 32) were investigated, and both were found to carry 30 chromosomes. This suggests that they are triploid, but the behavior of the chromosomes in meiosis was not investigated. The wild *Narcissus* at my disposal was that belonging to the bicolored type with double flowers. Owing to this double-flowered condition investigation of the meiosis was impossible.

Triploidy is known in garden plants in fairly numerous cases, but in wild plants it is known only in a restricted number of cases. To mention some examples hitherto known in wild plants, we have : *Hemerocallis fulva* (BELLING 1925 b, TAKENAKA 1929), *Lycoris radiata* (NISHIYAMA 1928, INARIYAMA 1931), *Lycoris squamigera* (TAKENAKA 1930, INARIYAMA 1931), *Iris japonica* (KAZAO 1928, 1929). In nature, only in those plants in which a vegetative method of propagation is habitual can the condition of triploidy be maintained ; in those plants in which amphimixis is the only method of propagation this condition is broken up by the process of meiosis, and only a new chance of producing diploid gametes and another new chance for them to unite with normal haploid gametes, or a new chance for a triple fusion of normal gametes can bring forth the triploid condition again. The case of triploid maize found by RANDOLPH, for instance, belongs to this latter case (*cf.* SHARP 1926, p. 398), and this is the reason why we can find triploid plants

in only a relatively limited number of cases as compared with the rather frequent occurrence of tetraploids in nature.

C) Heteroploid[1]

a) Variety " B_{21} "

External characteristics :—Leaves flat, 1.2 cms. broad, 4–5 in number : leaves and scape 15 cms. long : flowers 10–18 in number ; crown, light cadmium, segments, cream white ; style not exceeding the anthers.

21 chromosomes are counted in root-tip cells (Fig. 34). In diakinesis and metaphase in the heterotype division 10 bivalent chromosomes and 1 extra chromosome which is univalent are observable (Figs. 35, 36 and 37). The bivalents can be divided into two classes according to their sizes ; the chromosomes of the first class, which are 6 in number, are larger than the 4 chromosomes of the other, as in " Franklin " and " L_{20}". In Fig. 38, the extra chromosome is found on the equatorial plate while in Fig. 39 it lies in the achromatic figure outside of the plate. The behavior of the chromosomes in disjunction is regular in general except for this extra univalent (Fig. 40). In Fig. 41, a division figure in a stage slightly later than that reproduced in Fig. 39 is shown. Here the extra chromosome has already taken up its position at the pole in advance of the bivalents. In Fig. 42, an abnormal anaphasic figure is shown in which 11 chromosomes are found near the upper pole and the remaining 9 near the lower, the extra chromosome being found in the equatorial region. Fig. 43 shows one of the sister groups of chromosomes at a later anaphase consisting of 11 chromosomes from the bivalents and one extra chromosome. This excess in the chromosome number must be a result of the non-disjunction which is illustrated in Fig. 42. If in the heterotype division the bivalents disjoin normally, the number of chromosomes to be found in the homotype metaphase will be 10 in one of the sister cells and 11 ($=$10+the extra chromosome) in the other. This is often the case, as is shown in Figs. 44 and 45. Generally speaking, the meiotic process proceeds regularly except for non-disjunction, though there are some other minor irregularities.

The behavior of the chromosomes just described shows that this variety " B_{21}" is a hyperdiploid plant in which the cardinal number of chromosomes is 10, and not a triploid, though the number of

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1. The term " heteroploid " is used here in the sense of WINKLER (1916) corresponding to the term " aneuploid " introduced by TÄCKHOLM (1922) and " aploid " proposed by JÖRGENSEN (1928).

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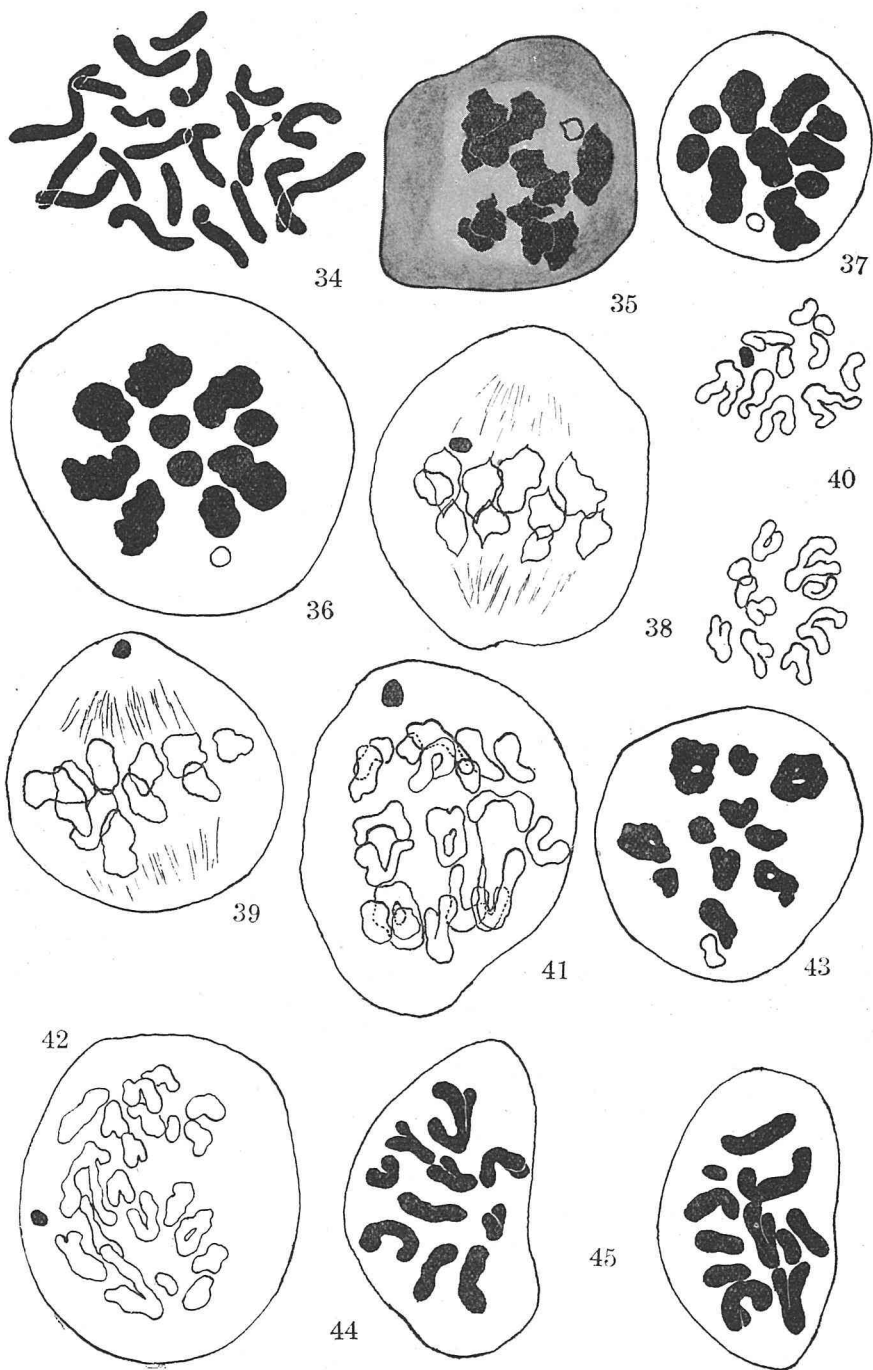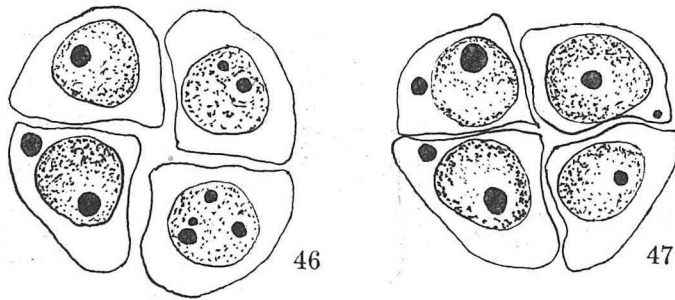
Figs. 34–47. *N. tazetta*, " B_{21} ". 34. Somatic nuclear plate showing 21 chromosomes. ×2210. 35–47. Meiotic phases. Figs. 35–40 and 46–47 ×1710, 41–43 ×2210; 35. Diakinesis, showing 10 bivalent and 1 extra (univalent) chromosomes; 36–37. Heterotype metaphase in polar view; 38. The same in side view; 39. The same. An extra chromosome is found in the achromatic figure; 40. Later anaphase, showing 11 chromosomes at the upper pole and 10 chromosomes at the lower; 41. The same. An extra chromosome at the pole in advance of the bivalents; 42. The same. 11 chromosomes are found near the upper pole and 9 chromosomes near the lower, 1 extra chromosome lying in the equatorial region; 43. One of the sister groups of chromosomes at the later anaphase, showing 11 and 1 extra chromosomes; 44–45. Homotype metaphase, showing 10 and 11 chromosomes respectively; 46–47. Pollen tetrads with deeply stained bodies.

chromosomes in the somatic cells is the same as that of a triploid variety of another *Narcissus* species whose cardinal number of chromosomes is 7, such as *N. poeticus*, for example (*cf.* Nagao 1929).

Sometimes there are found some small bodies, strongly stained, in the cytoplasm in pollen tetrad cells. They vary in number and size, and are found in only one of the tetrad cells in some cases and in two or three of them in some others (Figs. 46 and 47). Tschermak and Bleier (1926) have observed similar small bodies in the cytoplasm of tetrad cells in the hybrid between *Aegilops* and *Triticum*. They are of the view that this may be an extruded chromosome. Longley and Sando (1930) approve this view saying : " It seems quite probable that what appeared to Tschermak and Bleier as strongly stained bodies in the cytoplasm of the cells of the tetrads in their hybrids may have been similar to the micronuclei or extruded chromosomes observed by the writers in their material."

In the case of the variety " B_{21} ", the distribution of chromosomes towards the poles is generally regular in both heterotype and homotype divisions, and, hence, it seems unreasonable to take these bodies for an extruded chromosome or chromosomes which have failed to reach the pole in the telophase, or for micronuclei resulting from

alveolization of these chromosomes. I am inclined at present to take these stained bodies in this variety as extranuclear nucleoli, though their origin and fate have not yet been investigated.

　b)　Variety " A_{22} " (Probably " Paper White " ?)

External characteristics:—Slender and graceful, early blooming: leaves and scape 24–25 cms. long: leaves 4-6, mostly 4 in number: flowers small, 5–9, mostly 7 in number; both segments and crown snow white; style not exceeding the anthers.

This variety has 22 chromosomes in the root-tip cells (Fig. 48). The investigation of the meiotic phases in this variety gives some interesting results which suggest the origin and process of the hyper-diploid chromosome number deviation in some varieties of *Narcissus tazetta*. Figs. 57 and 58 show a nucleus in diakinesis and a division figure in the heterotype metaphase respectively; in both of them 11 gemini or bivalents are counted. Four bivalents among them are rod-shaped and larger than the remaining 7 which are round in shape. In many cases (386 cases out of 450), however, fusion of two smaller gemini into a tetrapartite complex of the size of the larger ones takes place, so that the total number of chromosomal elements is 10 instead of 11 (Figs. 56 and 59). As a consequence of this fusion of chromosomes into a complex, the numerical ratio between the numbers of small and large chromosomes becomes altered, it being now 5 : 5 instead of 4 : 7 (Figs. 55, 56, 59 and 60). This ratio is the same as that found in the variety " B_2 ". In the variety in question both types of pollen mother cells with and without the fusion of chromosomes are found in the same loculus of the anther. It would, then, not be un-reasonable to assume that the number 11 has been derived from 10 by the cross segmentation of a chromosome of the larger size, because, as will be discussed later, the latter number is the cardinal number in *Narcissus tazetta*. This secondary number is fixed in the somatic cells, but is liable to reversion into the primary number in the pollen mother cells. While the tetrapartite nature of the chromosome is clearly observable in a late prophase or diakinesis (Figs. 49–54), it is generally obscure in the metaphase, especially in polar view, complete coalescence into one taking place so intensely that no sign of the tetrapartite nature is discernible. Fig. 61 shows an exceptional case where one of the chromosomes occupying the central position in the arrangement clearly shows its tetrapartite nature. In Fig. 49 a tetra-partite chromosome taken out of a cell in a late prophase before diakinesis is shown. This chromosome corresponds to the tetrapartite chromosomes in diakinesis, reproduced in Figs. 52 and 53, in which the fourfold character is evident. In the tetrapartite complex shown

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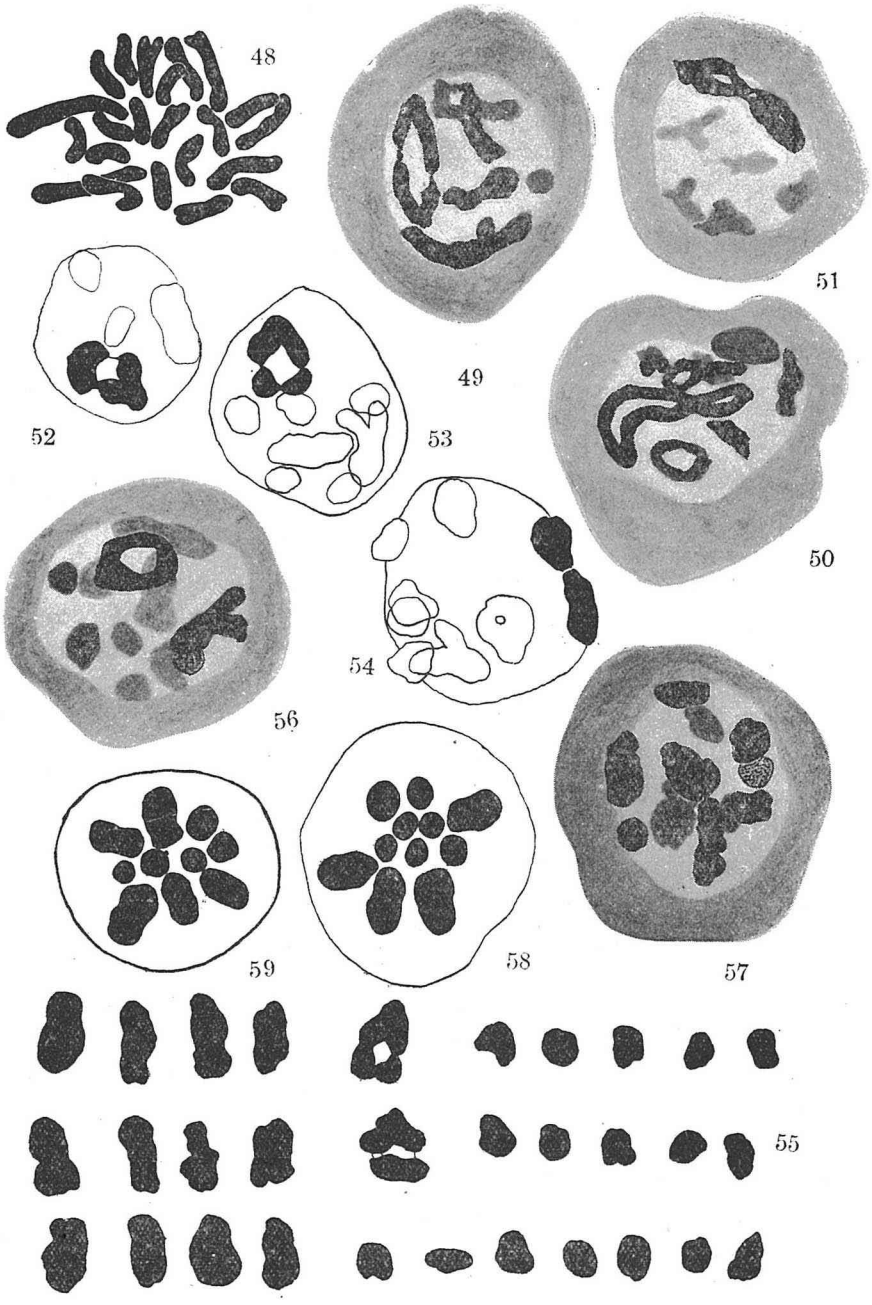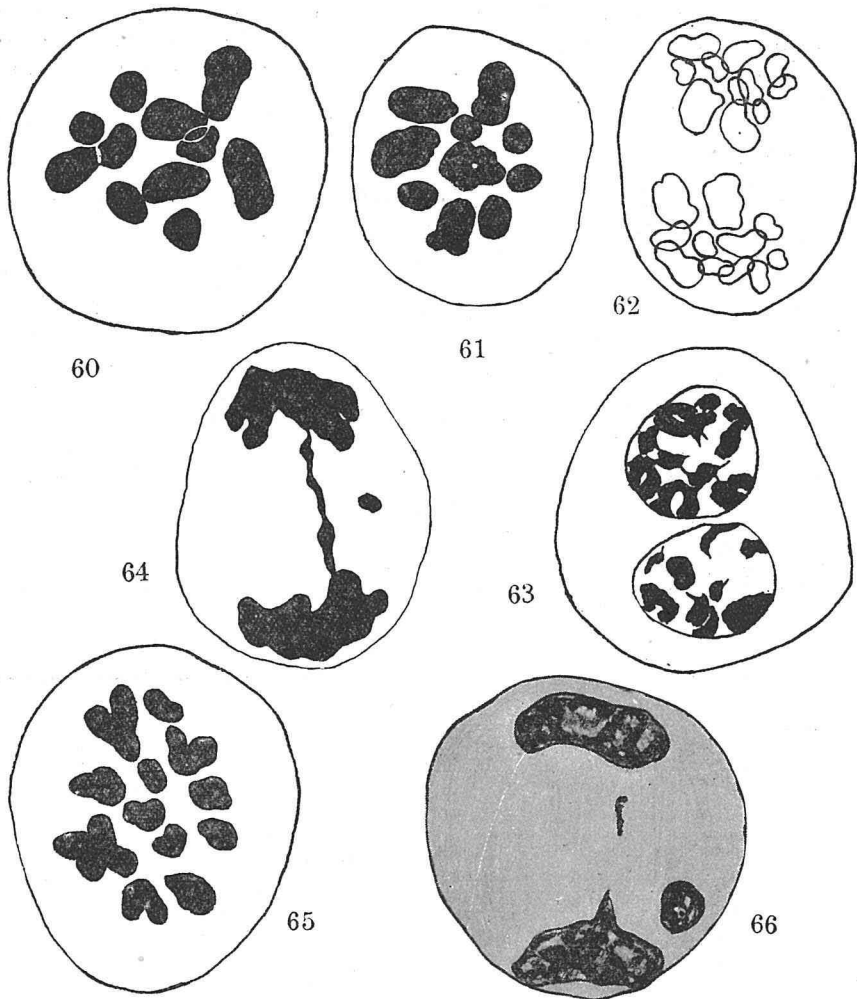
Figs. 48-66. *N. tazetta*, "A_{22}". 48. Somatic nuclear plate, showing 22 chromosomes. ×2210. 49-66. Meiotic phases. ×1710; 49. A late prophase: In one chromosome the tetrapartite nature is clearly shown; 50 and 51. The same, showing a large, tetrapartite chromosomal element; 52. Diakinesis. The four-fold nature is seen in a chromosomal element drawn solid black; 53. The same. A chromosomal element drawn solid black is separating into two halves; 54. The same. In a chromosomal element drawn solid black a constriction is seen; 55. Two sets of chromosomes taken out of diakinesis nuclei with and without cross segmentation of a chromosome, arranged in lines according to size and length; 56. Diakinesis, showing 9 bivalents, 1 tetrapartite ring chromosome and a nucleolus; 57. The same, showing 11 bivalent chromosomes and a nucleolus; 58. Heterotype metaphase in polar view, showing 4 large and 7 small chromosomes; 59. The same, showing 5 large and 5 small chromosomes; 60. The same, showing a constriction in one of the large chromosomes; 61. The same, having a tetrapartite ring complex occupying the central position; 62. Heterotype anaphase, showing 11 chromosomes at each pole;

63. Heterotype telophase. In the upper nucleus 11 chromatin bodies are seen; 64. Early telophase, showing the chromosome bridge and a chromatin granule; 65. Heterotype anaphase, showing 12 chromosomes; 66. Heterotype telophase showing a dwarf nucleus besides the two large nuclei.

in Fig 52, the component chromosomes are almost separated into two distinct double members. In some cases, in diakinesis as well as metaphase, a constricted, achromatic portion is found in a large chromosome. This constriction seems to suggest that this chromosome is of the tetrapartite nature. Figs. 54 and 60 show such chromosomes in diakinesis and metaphase. They may be compared with the large, prophasic chromosomes with the tetrapartite appearance which are reproduced in Figs. 50 and 51. In the anaphase, segregation of mating chromosomes towards the poles is regular in most cases (Fig. 62). In Fig. 63, in which a cell in the telophase is shown, 11 chromosomes are counted in the upper nucleus. Fig. 65 probably shows a case of non-disjunction. In Table IV the numbers of chromosomes counted in 64 pollen mother cells in the anaphase are given.

<div align="center">Table IV</div>

Anther loculus	Chromosome number				Total
	9	10	11	12	
A	0	8	34	1	43
B	1	1	18	1	21
Total	1	9	52	2	64

Besides non-disjunction, the so-called "chromosome bridge" and extra small nuclei are sometimes found (Figs. 64 and 66). With the exception of these abnormalities the division proceeds regularly in many cases. About 43 % of empty pollen grains is found in this variety.

The most interesting feature in the chromosome behavior described above in this variety is the occurrence of the cross segmentation of one special chromosome of the haploid set. Strasburger (1905) drew attention to the fact that in *Funkia* (*Hosta*) a number of small chromosomes is found in the heterotype nuclear plate among others which are much larger, and concluded that the smaller ones must have originated in the cross segmentation of the larger ones. This interpretation

was followed by MIYAKE (1905) and SYKES (1908), and STRASBURGER (1910) came to the same interpretation for similar cases in *Yucca* and *Galtonia*.

In his study of chromosomes of *Zea Mays* KUWADA (1911, 1915, 1919) has found 10 gemini in starch corn races and 12 in some sugar corn races. The correlation between the number and size of the chromosomes has been clearly demonstrated, as in the case of *Narcissus*. He says · " Wenn 10 Gemini vorhanden sind, so findet man unten ihnen immer zwei Grössere, wenn 11 Gemini gefunden, so nur ein Grösser und wenn 12 aufgewiessen, so kein Grösserer und die allen Gemini sind beinahe gleich in der Grösse " (KUWADA 1915, p. 86). Thus he has concluded that the variation in the number of chromosomes in *Zea Mays* is due to the cross segmentation of certain chromosomes.

GOTOH (1924) has found two kinds of individuals in *Secale cereale* which show 7 and 8 gemini in pollen mother cells respectively, and has concluded that the latter number has been derived from the former by the cross segmentation of a chromosome. This fact was confirmed later by BELLING (1925a) in the same plant and by EMME (1928) in *Secale montanum*[1] and *S. fragile*.

Some other examples of the cross segmentation of chromosomes have been given in *Oenothera scintillance* (HANCE 1918), *Crepis tectorum* (NAWASCHIN 1926), *Scirpus palustris* (HÅKANSSON 1929b) and others. In the animal kingdom, SEILER's investigation (1922, 1925) in *Solenobia* and *Phragmatobia* into this subject are well known. In *Bombyx mori*, too, KAWAGUCHI (1928) has come to the conclusion that the 28 chromosomes in this species have been derived through the cross segmentation of a chromosome from the set of 27 chromosomes which *B. mandarina* carries. In his studies of chromosomes in *Lepidoptera*, BELIAJEFF (1930) has mentioned the fact that in species with large numbers of chromosomes, such as *Pieris rapae* (n = 25), for example, the chromosomes are smaller in size than those of species with a smaller number, such as in *P. brassicae* (n = 15), while the chromosomes may be of nearly the same size even in different species, when the numbers are nearly equal, as is exemplified by *Smerinthus populi* (n = 21) and *S. ocellata* (n = 28). From these facts he concluded that the larger number of chromosomes in a species must have been derived from the smaller number of chromosomes in the original species by cross segmentation during its evolutional history.

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[1]. STOLZE (1925) has reported a reverse case in this species in which the haploid number 7 is reduced to 6 by the constant fusion of 2 chromosomes.

From the instances enumerated above it seems that the pheno-
menon of cross segmentation of the chromosome is not of infrequent
occurrence in both the animal and plant kingdoms, and that it may
play an important rôle in the production of a seeming hyperploidal
chromosome number.   Its bearing upon the study of phylogeny as
well as its significance in genetics have been discussed in detail by
several authors (KUWADA 1919, SEILER 1922, BÉLAŔ 1928, DELAUNEY
1922 and others).

The correlation between the size and the number of chromosomes
which is recognizable from comparison of the 22 chromosomes in the
variety " A_{22} " of *Narcissus tazetta* with the euploidal chromosomes
in the other varieties of that species described above, shows, beyond
doubt, that this variety represents a new case of increase of the
chromosome number by cross segmentation of a chromosome.

c)   Variety " B_{31} "

External characteristics :—Robust form : leaves flat, 2 cms. broad ; 4–5 in number :
leaves and scape 27–32 cms. long ; flowers 9–15 in number ; crown pale lemon yellow, segments
snow white ; style not exceeding the anthers.

In this variety the somatic number of chromosomes is 31 (Fig.
67).   In the heterotype division 10 bivalent and 11 univalent chromo-
somes are clearly observed (Figs. 68 and 69), and only in rare cases
both univalents and bivalents are 10 in number respectively (Fig. 70).
This co-existence of bivalents and univalents indicates that this variety
is of a hybrid origin.   The bivalent chromosomes or gemini are of
different sizes, and the size relation is just like that found between
those in " Franklin ".   The supernumerarity in the univalent chromo-
somes is considered to have originated in the cross segmentation of
a chromosome as in the variety " A_{22} ".   If this is actually so, the case
shown in Fig. 70, where the number of univalents is 10, can be taken
as representing the state in which the cross segmentation of a chromo-
some is suspended, or reunion has taken place between the segments.
Thus it would not be unreasonable to assume that this variety is a
hybrid produced by the union of a diploid gamete having chromosomes
of the " Franklin " type and a haploid gamete with chromosomes of
the " A_{22} " type.   Then, according to BRIEGER's terminology (1928),
this variety may be called a " haplo-diploid " plant, and it is a hetero-
genomous tribasic plant with two genomes each homologous to that
of " Franklin " or of " L_{20} " and capable of forming bivalents between
each other, and another genome, homologous to that of " A_{22} " variety,
or a genome probably derived through cross segmentation from that
of " B_{20} ".

76

77

78

79a

79b

80b

80a

81a

81b

82
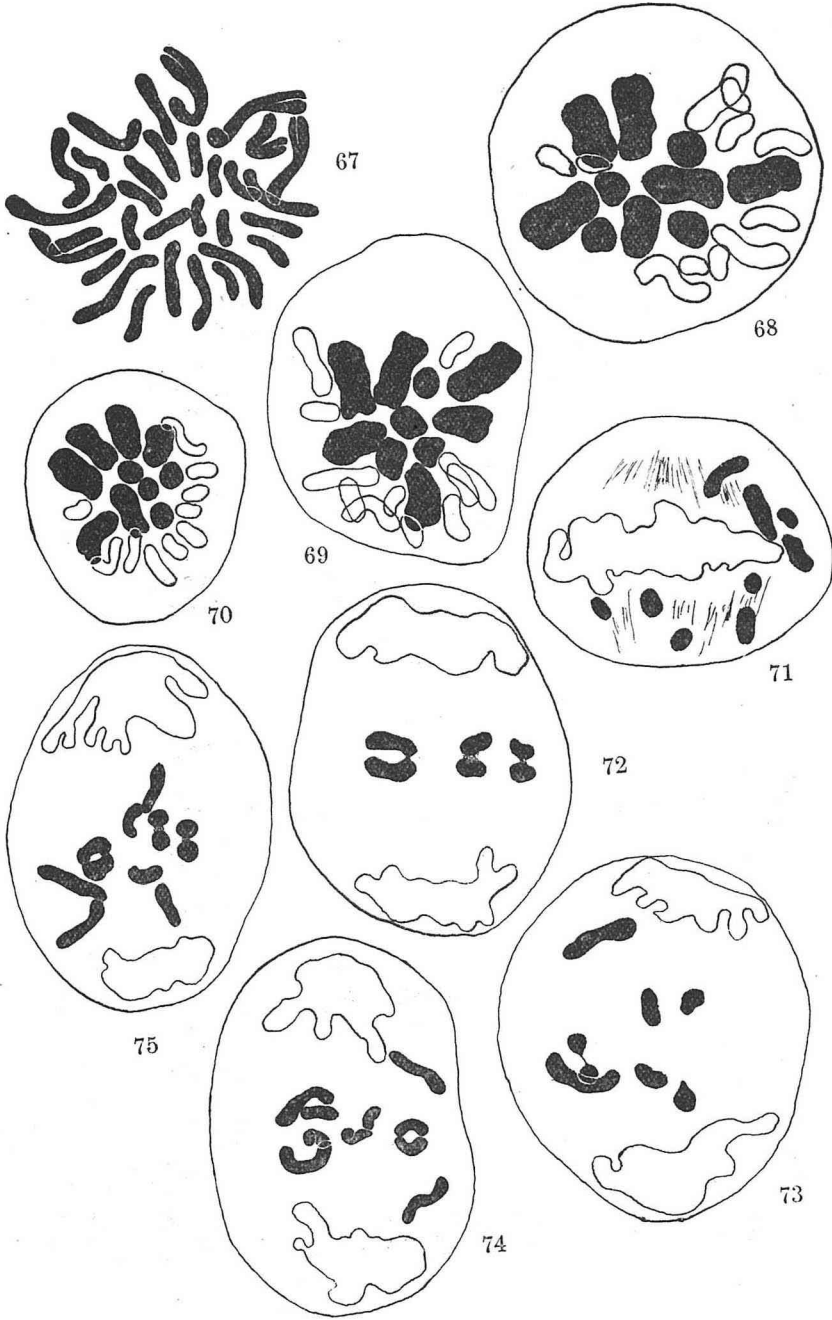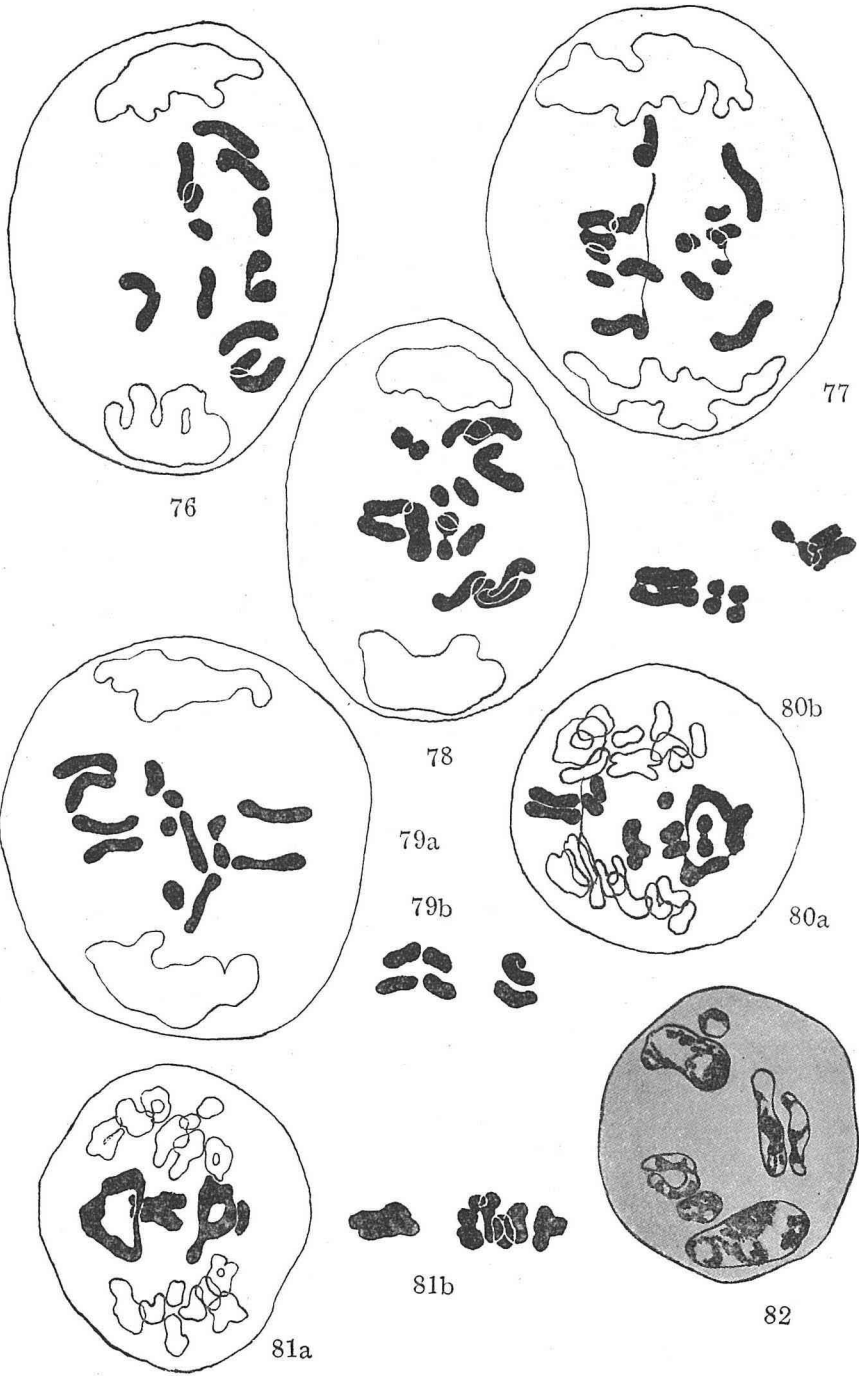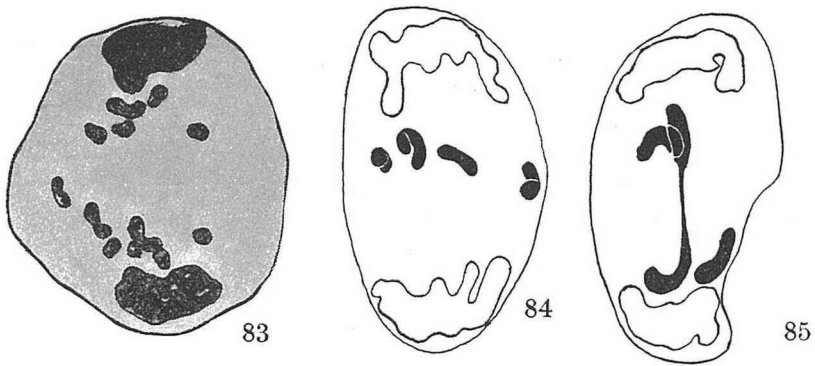
Figs. 67-85. *N. tazetta*, "B₃₁". 67. Somatic nuclear plate, showing 31 chromosomes. ×2210. 68-85. Meiotic phases; 68. Heterotype metaphase in polar view, showing 10 bivalents (drawn solid black) and 11 univalents (drawn in outline only). ×2210; 69. The same. ×2210; 70. The same, showing 10 bivalents (solid black) and 10 univalents (outline). ×1710; 71. Heterotype metaphase in side view, showing some univalent chromosomes (solid black) scattered irregularly in the cytoplasm. ×2210; 72. Heterotype anaphase, showing 3 pairs of divided lagging univalent chromosomes (solid black) in the equatorial region. ×2210; 73-78. The same. The longitudinal division is seen in 4, 5, 6, 7, 8 and 9 univalent chromosomes respectively, shown solid black. ×2210; 79a-b. The same, showing longitudinal division in 10 univalent chromosomes drawn solid black. ×2210. 3 of them are drawn, being taken out of their original positions to avoid complication of the figure; 80 a-b. The same, showing 31 chromosomal elements in all, of which 9 chromosomes lie at the upper pole, 8 at the lower, 1 tripartite and 11 univalent chromosomes between the poles. ×1710. 5 univalent chromosomes out of the 11 between the poles are drawn separated from the others; 81 a-b. The same, showing 31 chromosomal elements in all, of which 8 chromosomes lie in each pole, 2 tripartite and 9 univalents between the poles, 5 univalents out of the 9 being drawn separated from the others. ×1710; 82 and 83. Heterotype telophase, showing many dwarf nuclei. ×1710; 84. Homotype anaphase, showing 4 lagging monad chromosomes. ×1710; 85. The same, showing diad chromosomes which are separating into monads. ×1710.

The univalent chromosomes are usually found outside the nuclear plate which consists of the bivalents, but it not infrequently happens that some of the univalents occupy a position in the nuclear plate, and sometimes even all the univalents take part in the formation of the plate (Fig. 70).

In the anaphase the bivalents or double chromosomes disjoin into single chromosomes which pass to the poles with some of the unpaired, univalent chromosomes. The remaining univalents, 3–10 in number, lag behind on the equatorial plane, being longitudinally divided, and each half migrates towards the poles after the other chromosomes have reached there. In Figs. 72–79, division figures in this stage are

reproduced. This type of chromosome behavior belongs to the *Piro-sella* type of KIHARA (1924, p. 133). Sometimes some interesting figures are met with, in which one or two tripartite chromosomes, probably produced by the secondary association, are found. In Figs. 80 and 81, one or two tripartite chromosomes are shown in the achromatic area with several univalents which lag behind the others. This shows, that not only univalent chromosomes but also tripartite chromosomes may lag behind the others in division. The frequency of occurrence of the various numbers of lagging univalents which split longitudinally is recorded in Table V.

Table V

Number of lagging chromosomes	1	2	3	4	5	6	7	8	9	10	11	Total
Frequency	0	0	6	6	6	17	13	14	11	6	1	80

From this table it is seen that the cases where the number of lagging chromosomes is 6–8 are of the most frequent occurrence.

From the irregular behavior of the chromosomes mentioned above, it is to be expected that the number of chromosomes may be different in the sister anaphasic chromosome groups. Two examples are shown in Figs. 80 and 81. In Fig. 80, 9 chromosomes are found at the upper pole and 8 at the lower, and 1 tripartite and 11 univalents between the poles lagging behind the others; in Fig. 81, there are 8 chromosomes at each pole, and 2 tripartite and 9 univalents between the poles. Frequently the lagging chromosomes have great difficulty in migrating to the poles. In this case, even all of these are found left in the cytoplasm in the telophase, forming many dwarf nuclei (Figs. 82, 83). When tetrads are formed, there are, however, found, contary to expectation, only a few tetrad cells which are polynucleate. This is probably due to the possibility of the dwarf nuclei taking part in the formation of the nucleus proper during the homotype division. From the behavior of the chromosomes in the heterotype division it is also to be expected that a number of lagging chromosomes may appear in the homotype division too. In Figs. 84 and 85 such lagging chromosomes are shown. In the former figure they are 4 in number and all are monads not showing the longitudinal split. They are regarded as having originated in the longitudinal halves of the lagging chromosomes in the heterotype division. In the latter figure the lagging chromosomes are 2 in number, and both have been longitudinally divided, the halves being separated from each other to a considerable

extent in one of them. These chromosomes in the latter figure are regarded as having originated in those univalents which did not undergo the longitudinal division in the heterotype division.

Many tetrads present the normal appearance, but in a few, each cell is polynucleate containing, besides the nucleus proper, a dwarf-nucleus or -nuclei in it. Polyspory is of rather rare occurrence in this variety. About 60 % of the pollen grains are empty.

d) " Luna "

External characteristics :—Leaves mostly 6 in number : flowers 5 in number ; crown light yellow, segments snow white ; style not exceeding the anthers.

In this variety 32 chromosomes are counted in the root-tip cells (Fig. 86). The material at my disposal for the study of the meiotic phase was so insufficient that it was hardly possible thoroughly to trace out all the meiotic phases, but the results so far obtained will be mentioned below. The meiotic division is very irregular in this variety, and it is not easy to determine exactly the number of gemini or chromosome complexes nor to analyse their chromosomal constitution. In many cases the number is 16 in the metaphase, but may vary from 16 to 20. This variation in number seems due to the possibility of some chromosomes sometimes remaining unpaired, and sometimes fusing into tripartite chromosomes. In Fig. 91 such tripartite chromosomes are shown.

It is very curious that in this variety no diakinesis stage is found. Since, in this plant, the reduction division proceeds regularly in acropetal succession from the pollen mother cells at the bottom of the pollen sac to those on upper levels, it is not very difficult to trace each stage in the division one after another, and yet no diakinesis is found. After shortening and thickening, the strepsitene spiremes group together in the central region of the nucleus (Fig. 87), and without passing through the typical diakinesis, they proceed directly into the metaphase, in which the chromosomes are very irregularly distributed. In Figs. 88–90, 16, 17 and 20 chromosomes are countable respectively. Clumping of some chromosomes is frequently observed as shown in Fig. 92. It hardly ever happens that all the chromosomal elements are regularly arranged in the equatorial plane, and as shown in Fig. 93, the migration is very irregular, the chromosomes mostly failing to travel towards the poles. This often results in the formation of a giant nucleus of a considerably irregular shape—the restitution nucleus. In Fig. 95 a tetranucleate cell having nuclei of different sizes is shown, and in Figs. 94 and 96, large restitution nuclei. The giant nucleus may be accompanied by a number of dwarf nuclei as in the case shown in

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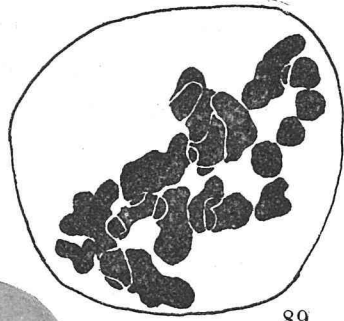
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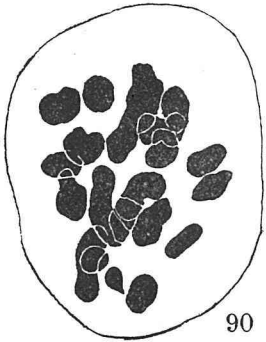
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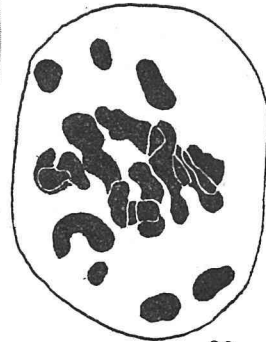
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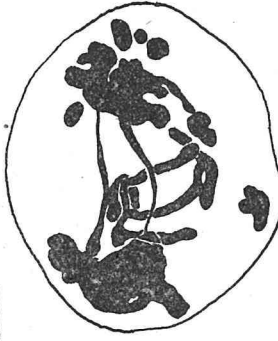
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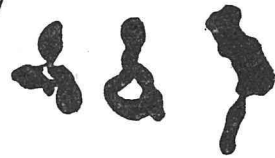
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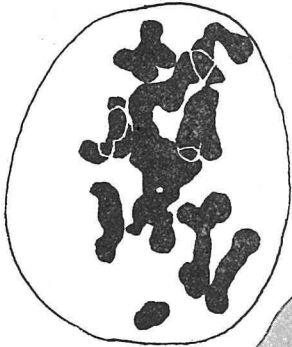
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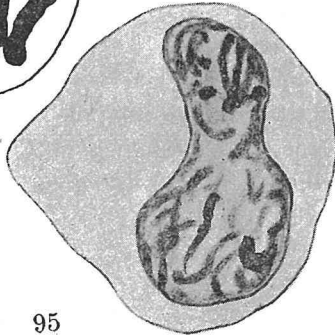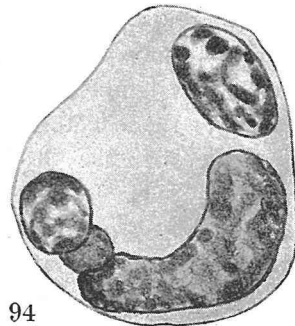
95   94
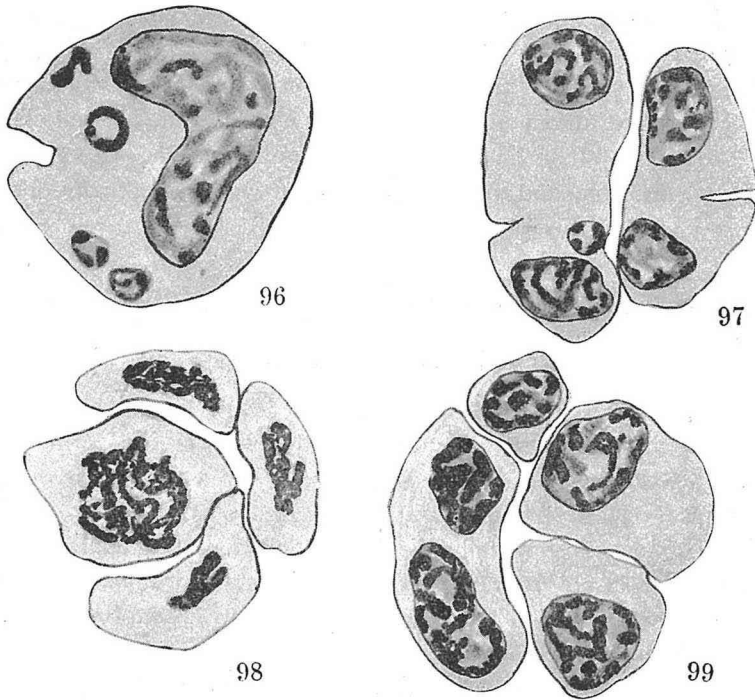
Figs. 86-99. *N. tazetta*, "Luna". 86. Somatic nuclear plate showing 32 chromosomes. ×2210. 87-99. Meiotic phases. ×1710; 87. A late prophase showing chromatin elements grouped together in the nucleus; 88. Heterotype metaphase showing irregular arrangements of chromosomes, scattered about the cytoplasm. 16 chromosomal elements can be counted; 89. The same. About 17 chromosomal elements can be counted; 90. The same showing 20 chromosomal elements; 91. Tripartite chromosomes in the heterotype metaphase; 92. Heterotype anaphase showing a clump of chromosomes; 93. The same showing an irregular distribution of chromosomes; 94-96. Heterotype telophase showing nuclei of various sizes and shapes; 97. Homotype telophase. A dwarf nucleus is seen; 98 and 99. Irregular pollen tetrads.

Fig. 96. Though actual observation is lacking, it is highly probable that these restitution nuclei divide further. Through these irregularities, various abnormal types of tetrad cells are produced. Some of them are shown in Figs. 97-99.

It seems possible to consider that this variety is of a hybrid origin and the irregularities in the chromosome behavior mentioned above are principally due to this hybrid nature. FERNANDES (1931 a, b) reports that he has found 12 chromosomes in the somatic cells in certain *Narcissus* species (*cf.* p. 168). If an interspecific fertilization happens

to take place between abnormally produced diploid gametes from a diploid form of *N. tazetta* and those from a species whose somatic number of chromosomes is 12, we may expect that the resulting hybrid plant should carry $2n = 32$ $(20 + 12)$ chromosomes. If, furthermore, it is assumed that autosyndesis takes place within each parental chromosome group, we shall have as many gemini as 16 $(10 + 6)$ in the heterotype division, and this number is what we have actually observed in many cases in this plant.

II. Cases where the cardinal number of chromosomes is 7

1. *Narcissus Jonquilla* L.

The somatic number of chromosomes is 14 in this species (Fig. 100). This number is also found in the double flowered forms of this species (NAGAO 1929), and the same number has been reported by FERNANDES (1931 a, b) in *Narcissus Jonquilla* L. var. *jonquilloides* (WK). The chromosome behavior in the pollen mother cells is on the whole regular in this species. The number of chromosome pairs or gemini is found in most cases to be 7 at diakinesis and metaphase in the heterotype as well as the homotype division (Figs. 101–105). This number " 7 " is also found in *N. Pseudonarcissus*, *N. incomparabilis*, and some other species (*cf.* later chapter), and thus we can provisionally say that there exist at least two cardinal numbers in the genus *Narcissus*, 7 and 10, the latter of which we have already mentioned above.[1] 2 gemini of the 7 are, in *N. Jonquilla*, slightly smaller than the remaining 5, but this difference in size is not so distinct as that found between the chromosomes in *N. tazetta*. In some cases, in 1 or 2 gemini the component chromosomes are very loosely associated, or even quite separated from each other, so that more than 7 chromosomal elements are counted in the heterotype nuclear plate. Even in this latter case the separated or disjoined chromosomes are found in the neighbourhood of each other, very often occupying a position in the outer ring of the chromosome arrangement (Figs. 106 and 107). This peculiar behavior of chromosomes in disjunction may be compared with that observed by ICHIJIMA (1930) in the 7-chromosome species of *Fragaria*, in which, according to him, a pair of chromosomes disjoin and move towards the poles in advance of the other chromosome

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1. FERNANDES (1931 a, b) reports that he has found another haploid number, 6, in some species. This number may be regarded as another cardinal number in the genus *Narcissus*, though, so far as I am aware, this is the only report hitherto made.
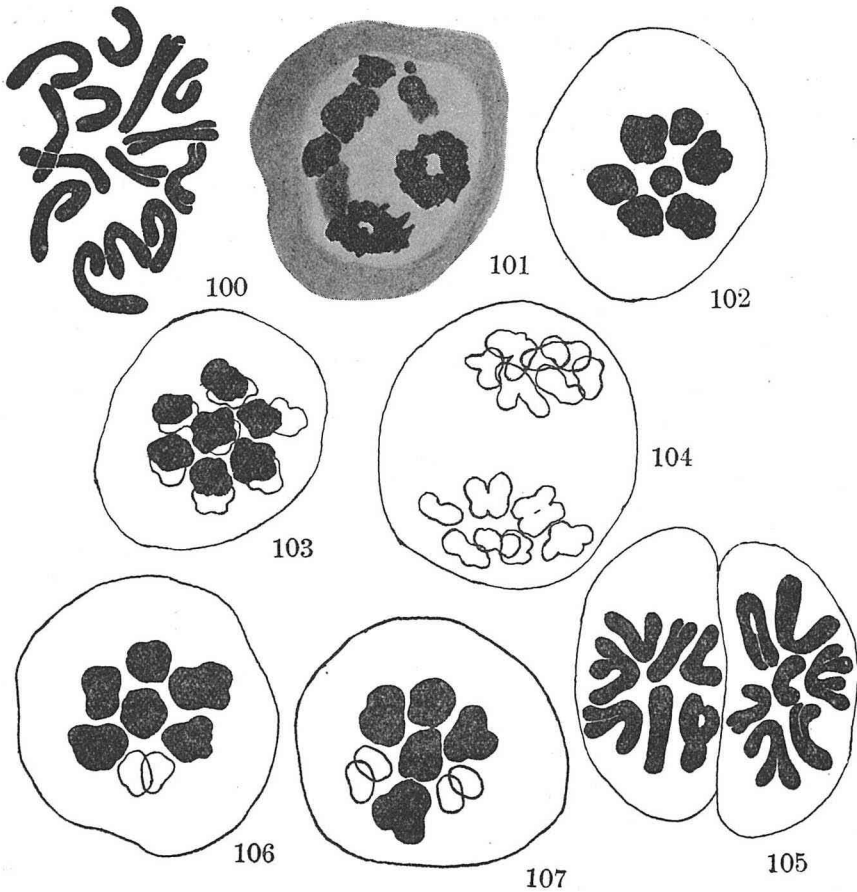
Figs. 100–107. *N. Jonquilla.* 100. Somatic nuclear plate showing 14 chromosomes. ×2210; 101. Diakinesis. Showing 7 gemini and 2 nucleoli. ×1710; 102. Heterotype metaphase in polar view showing 7 bivalent chromosomes. ×1710; 103. Heterotype anaphase in polar view showing 7 chromosomes at each pole. ×1710; 104. Heterotype anaphase in side view showing 7 chromosomes in each pole. ×1710; 105. Homotype metaphase showing 7 chromosomes in each sister cell. ×2210; 106. Heterotype metaphase showing 6 bivalents and 2 univalents (shown in outline). ×1710; 107. The same showing 5 bivalents and 4 univalents (shown in outline). ×1710.

pairs. To this peculiar pair of chromosomes he has given the name "precursory chromosomes". In *Narcissus Jonquilla,* such a precursory movement has not yet been observed, but failure of conjugation is of quite frequent occurrence in one or two pairs of chromosomes in the meiotic division of pollen mother cells, as is also the case in ICHIJIMA's *Fragaria.*

In the second division the metaphase plates are very regular (Fig.
105). The two plates are disposed at right angles or parallel to each
other. In Fig. 105, 7 chromosomes are clearly counted in both sister
cells. About 37 % of empty pollen grains is found in this species.

2. *Narcissus Pseudonarcissus* L.

A) Diploid

The diploid number of chromosomes is 14 in the garden varieties
of this species, " Victoria," " Albicans " and " Princeps Maxim " (Fig.
108). In these varieties, owing to the lack of sufficient material, the
behavior of chromosomes in the meiotic division was not observed,
but it is inferred from this diploid number that the reduced number
is 7 in these varieties as in the case of the other species investigated
such as *Narcissus Jonquilla* and *N. incomparabilis*, and according to
DE MOL this is actually the reduced number in this species (DE MOL
1928).

B) Triploid

" Emperor "

External characteristics :—Strong stout : leaves flat, 2-2.5 cms. broad, 4-6, mostly 4 in
number : scape 30-32 cms. long : flowers horizontal, golden yellow ; trumpet more or less
frilled.

The somatic number of chromosomes is 21 in this variety (Fig.
109). In the metaphase in the heterotype division there are found 7
trivalent elements, each of which consists of three component chromo-
somes (Fig. 110). These component chromosomes must be homologous
with one other, and this variety is regarded as an autotriploid form.
Sometimes, however, we find among the trivalent elements one or
more single or univalent, and double or bivalent chromosomes which
fail to form the trivalent complex with their partners, so that a some-
what larger number of chromosomal elements than 7, usually 8 or 9,
and sometimes still more, may be counted in the nuclear plate (Figs.
111-113).

The frequency of occurrence of these different numbers of chromo-
somal elements in the metaphasic plates, obtained from observations
of 94 pollen mother cells, is given in Table VI with all possible sets
of chromosomal elements of different constitutions or valencies for each
observed number of the elements.

In this table possible but improbable sets are marked with an
asterisk to distinguish them from those which probably occur. If it
is assumed that the latter sets have an equal chance of occurring, it

Table VI

Number of chromosomal elements	7	8	9	10	11
Observed frequency	6	16	13	20	13
Possible constitutions of chromosomal elements	7_{III}	$6_{III}+1_{II}+1_{I}$	$6_{III}+3_{I}$ $5_{III}+2_{II}+2_{I}$ $4_{III}+1_{II}+4_{I}$ $3_{III}+6_{II}{}^*$	$5_{III}+1_{II}+4_{I}$ $4_{III}+3_{II}+3_{I}$ $3_{III}+5_{II}+2_{I}{}^*$ $2_{III}+7_{II}+1_{I}{}^*$ $1_{III}+9_{II}{}^*$	$5_{III}+6_{I}$ $4_{III}+2_{II}+5_{I}$ $3_{III}+4_{II}+4_{I}$ $2_{III}+6_{II}+3_{I}{}^*$ $1_{III}+8_{II}+2_{I}{}^*$ $10_{II}+1_{I}{}^*$

Number of chromosomal elements	12	13	14	15
Observed frequency	17	4	4	1
Possible constitutions of chromosomal elements	$4_{III}+1_{II}+7_{I}$ $3_{III}+3_{II}+6_{I}$ $2_{III}+5_{II}+5_{I}$ $1_{III}+7_{II}+4_{I}{}^*$ $9_{II}+3_{I}{}^*$	$4_{III}+9_{I}$ $3_{III}+2_{II}+8_{I}$ $2_{III}+4_{II}+7_{I}$ $1_{III}+6_{II}+6_{I}$ $8_{II}+5_{I}{}^*$	$3_{III}+1_{II}+10_{I}$ $2_{III}+3_{II}+9_{I}$ $1_{III}+5_{II}+8_{I}$ $7_{II}+7_{I}$	$3_{III}+12_{I}$ $2_{III}+2_{II}+11_{I}$ $1_{III}+4_{II}+10_{I}$ $6_{II}+9_{I}$

will result from this table that the frequency of occurrence of the various numbers of trivalent chromosome complexes in the sets will be as shown in Table VII.

Table VII

Number of trivalent chromosomes in a set	Frequency	Per cent.
7_{III}	6	6.38
6_{III}	$16+\dfrac{13}{3}$	21.63
5_{III}	$\dfrac{13}{3}+\dfrac{20}{2}+\dfrac{13}{3}$	19.86
4_{III}	$\dfrac{13}{3}+\dfrac{20}{2}+\dfrac{13}{3}+\dfrac{17}{3}+\dfrac{4}{4}$	26.95
3_{III}	$\dfrac{13}{3}+\dfrac{17}{3}+\dfrac{4}{4}+\dfrac{4}{4}+\dfrac{1}{4}$	13.03
2_{III}	$\dfrac{17}{3}+\dfrac{4}{4}+\dfrac{4}{4}+\dfrac{1}{4}$	8.43
1_{III}	$\dfrac{4}{4}+\dfrac{4}{4}+\dfrac{1}{4}$	2.39
0_{III}	$\dfrac{4}{4}+\dfrac{1}{4}$	1.33
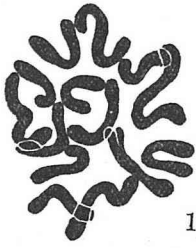
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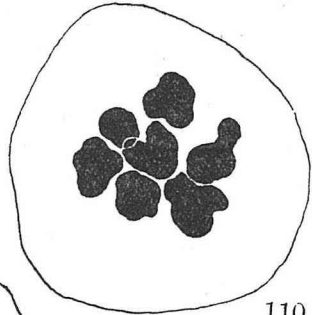
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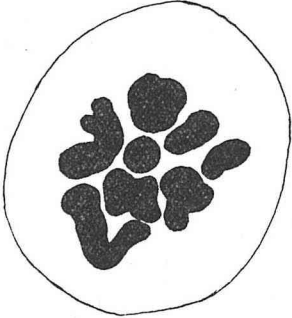
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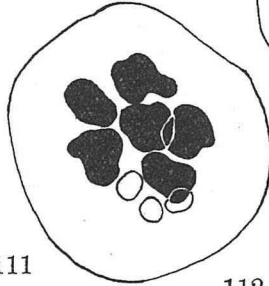
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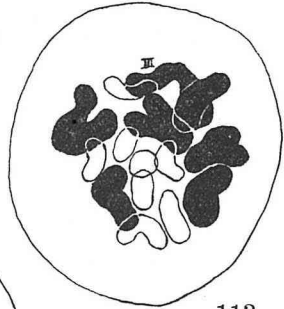
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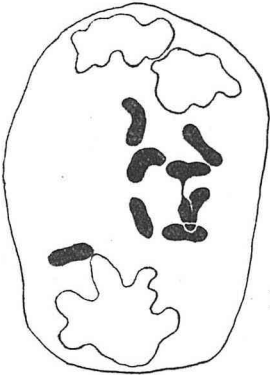
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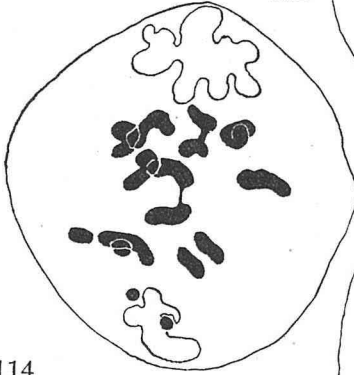
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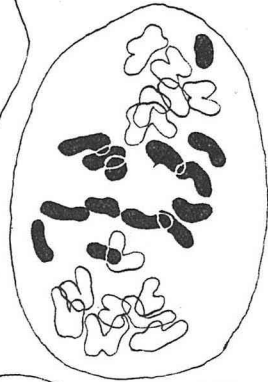
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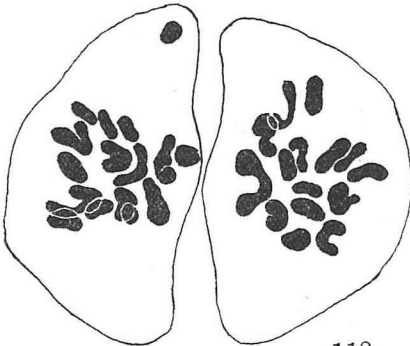
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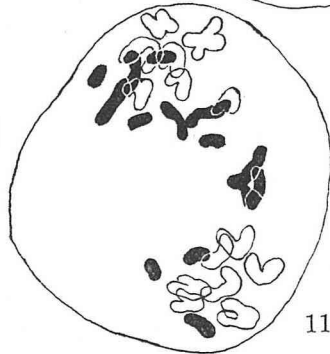
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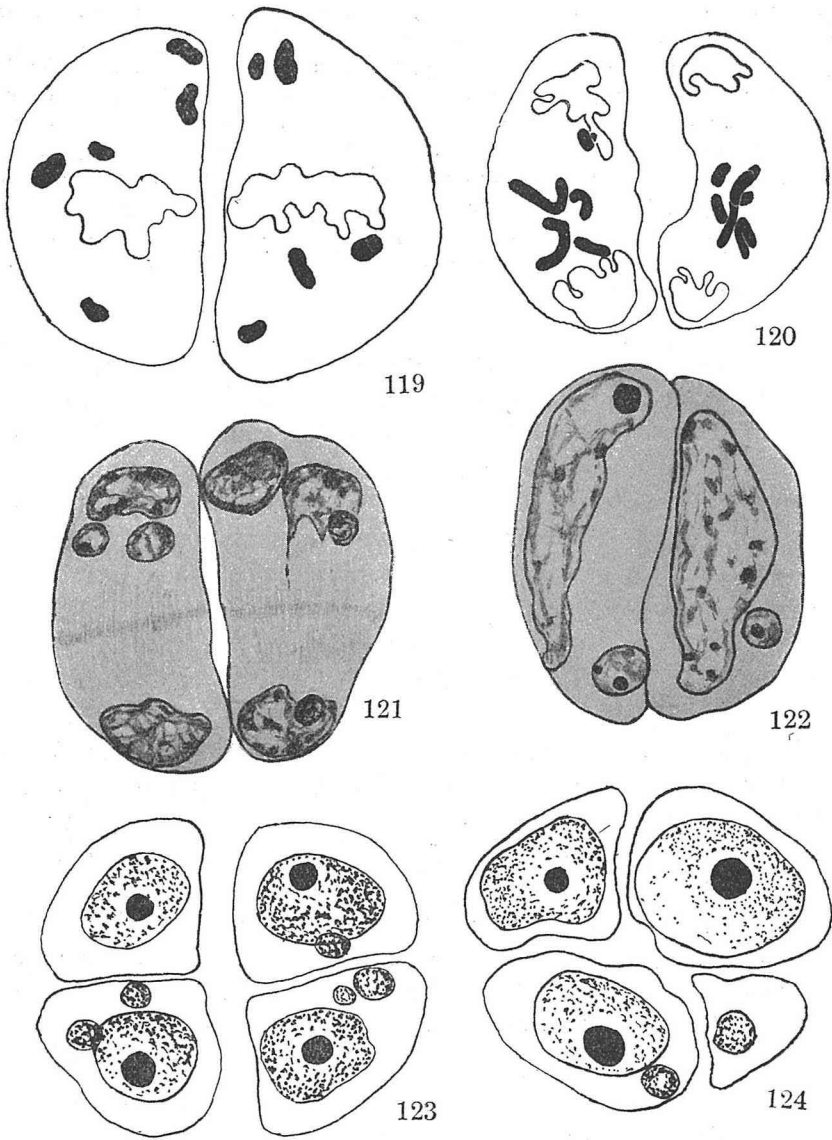
Figs. 108-124. Diploid and triploid trumpet daffodils. 108. " Princeps Maxim ". Somatic nuclear plate showing 14 chromosomes. ×2210; 109. " Emperor ". The same showing 21 chromosomes. ×2210.

Figs. 110–124. " Emperor " (triploid). Meiotic phases. Figs. 110-118 and 120-124 ×1710, Fig. 119 ×2210. 110. Heterotype metaphase showing 7 trivalent chromosomes; 111. The same in polar view showing 8 chromosomal elements; 112. The same showing 9 chromosomal elements (6 trivalents and 3 univalents); 113. The same showing 14 chromosomal elements, probably consisted of 1 triple, 5 double and 8 single chromosomes; 114

and 115. Heterotype anaphase showing longitudinal division in the third triplet (shown solid black) ; 116. The same showing 21 chromosomes in all, of which 6 lie at the upper pole and 8 at the lower, and the remaining 7 (shown solid black) split longitudinally ; 117. The same showing 21 chromosomes in all, of which 7 lie at each pole, the remaining 7 (shown solid black) being split longitudinally ; 118. Homotype metaphase showing about 15–16 chromosomal elements ; 119. Homotype metaphase in side view. 5 monad chromosomes (shown solid black) are found scattered in the cytoplasm ; 120. Homotype anaphase showing 5 monad chromosomes lagging behind the others in the equatorial region ; 121. Homotype telophase showing polynucleate sister cells ; 122. The same. A dwarf nucleus and a giant elongated nucleus are seen in each sister cell ; 123 and 124. Pollen tetrads with or without dwarf nuclei.

It is seen from the table that the case where the trivalent chromosomes are 4 in number is most numerous, the percentage frequency being 26.95, and the cases where they are 6 and 5 in number come next in the order named, the frequencies being 21.63 % and 19.86 % respectively, while the case where all the elements are trivalent occurs only in 6.38 % of the cases. A case where there is a set of 6 trivalents and 3 univalents which have failed to form a complex is shown in Fig. 112, and in Fig. 113, a case where we have a set of 14 chromosomal elements, probably of the constitution $1_{\mathrm{III}} + 5_{\mathrm{II}} + 8_{\mathrm{I}}$.

In the heterotype anaphase, while every two of the triplets of the trivalent complexes regularly pass to opposite poles, some of the third lag behind, and undergo the longitudinal splitting which is followed by the separation of the halves towards the poles that takes place after the other chromosomes have reached the poles as observed in the case of a triploid variety of *Narcissus poeticus* (NAGAO 1929). The number of lagging chromosomes ranges from 1 to 7. In Figs. 114 and 115 respectively, 4 and 7 lagging chromosomes in the anaphase which split longitudinally are shown. In Fig. 115, two chromosome fragments (?) are seen at the lower pole. In Figs. 116 and 117, the numbers of the chromosomes at the two poles are different from each other, a fact which may be expected from the abnormal behavior of the chromosomos just mentioned above.

A similar behavior of chromosomes has been observed in triploids of *Tulipa* (NEWTON and DARLINGTON 1929), *Salix* (HÅKANSSON 1929), *Zea* (McCLINTOCK 1929) and *Allium* (LEVAN 1931), while in most other triploids where also the formation of trivalent chromosome complexes prevails, the chromosome distribution to the two poles is hap-hazard, and neither lagging nor longitudinal splitting of triplets occurs at all (for example, *Canna, Datura, Hyacinthus* ; BELLING ; 1921, 1925 ; BELLING and BLAKESLEE 1922).

In Figs. 118–124, some kinds of abnormality in the second division are illustrated. Sometimes, the number of chromosomes comprising the two sister nuclear plates is larger than that in the somatic cell (Fig. 118). This supernumerarity seems due to the separation from each other of the longitudinally split halves of some chromosomes in the heterotype division. Frequently, in the metaphase, a number of monad chromosomes which must represent these separated halves of the chromosomes are found in the achromatic area (Fig. 119), and in the anaphase they are found lagging behind the others (Fig. 120). It is interesting to note in connection with these irregularities that in most cases some dwarf nuclei are found besides a large proper nucleus. It seems that they are formed as the result of failure of some chromosomes to take part with the others in the formation of the proper, normal nucleus. It is a characteristic feature in this variety that each individual cell of the pollen tetrads contains one or more dwarf nuclei besides a large one. In his study of *Ribes Gordonianum*, MEURMAN (1928) says: " My observations show that the cells with supernumerary nuclei are at least as common as those without." (p. 325).

Other irregularities in pollen-tetrads are shown in Figs. 121–124. In Fig. 121, a figure of the homotype telophase where both sister cells are polynucleate is reproduced, the nuclei being of different sizes. In Fig. 122, a dwarf nucleus and a giant, elongated nucleus are found in each sister cell. The origin of the elongated form is to be found in the irregular distribution of chromosomes from pole to pole. In Fig. 123, all the cells of the pollen tetrad except the one on the upper left side carry a dwarf nucleus or -nuclei besides a large one, and in Fig. 124, one of the cells is devoid of contents except a dwarf nucleus. Polyspory is observed only in rare cases.

C) Tetraploid

a) " King Alfred "

External characteristics :—Tall and vigorous: leaves broad and flat, 3-4 in number: flowers ascended, golden yellow, not frilled ; the expanded trumpet 4 cms. in diameter.

In this variety the number of chromosomes in the root-tip cells is 28, a number which is twice as large as that found in the diploid forms (Fig. 125). In the heterotype division in pollen mother cells, there are often found 7 tetravalent complexes of chromosomes in the metaphase (Fig. 129), a feature which is characteristic of autotetraploid plants. More frequently, however, in some of the complexes, the association of chromosomes into the tetravalent complex is incomplete, so that 8–15 chromosomal elements are counted in nuclear plates (Figs.

130–136). The configuration taken up by the complexes is manifold. The figure of eight is that which is most commonly found, but figures such as an open or an oval ring are also found (Figs. 126-128). The frequency of occurrence of the various numbers of chromosomal elements counted in the metaphase in 273 pollen mother cells is given in Table VIII, together with the chromosome constitutions (valencies) of the elements which it is possible for each number to assume in the metaphasic plate.

Table VIII

Number of chromosomal elements	7	8	9	10	11
Possible constitutions of chromosomal elements (Improbable constitutions which are marked with an asterisk being also given)	7_{IV}	$6_{IV}+2_{II}$ $6_{IV}+1_{III}+1_{I}$ $5_{IV}+2_{III}+1_{II}*$	$5_{IV}+4_{II}$ $6_{IV}+1_{III}+2_{I}$	$4_{IV}+6_{II}$ $5_{IV}+3_{II}+2_{I}$ $6_{IV}+4_{I}$	$3_{IV}+8_{II}$ $4_{IV}+5_{II}+2_{I}$ $5_{IV}+2_{II}+4_{I}$
Frequency	23 (Fig. 129)	54	72	71 (Fig. 130)	28 (Fig. 131)

Number of chromosomal elements	12	13	14	15	Total
Possible constitutions of chromosomal elements (Improbable constitutions which are marked with an asterisk being also given)	$2_{IV}+10_{II}$ $3_{IV}+7_{II}+2_{I}$ $4_{IV}+4_{II}+4_{I}$ $5_{IV}+1_{II}+6_{I}$	$1_{IV}+12_{II}$ $2_{IV}+9_{II}+2_{I}$ $3_{IV}+6_{II}+4_{I}$ $4_{IV}+3_{II}+6_{I}$ $5_{IV}+8_{I}$	$1_{IV}+12_{II}+1_{I}$ $2_{III}+10_{II}+2_{I}$ $3_{III}+8_{II}+3_{I}$ $4_{III}+6_{II}+4_{I}$ $5_{III}+4_{II}+5_{I}$ $6_{III}+2_{II}+6_{I}$ $7_{III}+7_{I}$ 14_{II}	$1_{III}+11_{II}+3_{I}$ $2_{III}+9_{II}+4_{I}$ $3_{III}+7_{II}+5_{I}$ $4_{III}+5_{II}+6_{I}$ $5_{III}+3_{II}+7_{I}$ $6_{III}+1_{II}+8_{I}$ $13_{II}+2_{I}$	
Frequency	17 (Fig. 132)	3 (Figs. 133, 134)	3 (Fig. 135)	2 (Fig. 136)	273

If we assume that those sets of the elements of different constitutions given in the table have an equal chance of occurring, we shall obtain from this table the frequency of occurrence of the various numbers of tetravalent complexes in the metaphasic plates. These frequencies are shown in Table IX.

Tetraploid forms, since they were first found in *Oenothera* by DE VRIES, have increasingly been reported in various plants, such as, for instance: *Solanum* (WINKLER 1916, JÖRGENSEN 1928, LESLEY, M. M. and LESLEY, J. M. 1930, LONGLEY and CLARK 1930, LINDSTORM and

Table IX

Number of tetravalent chromosomes in a metaph. plate	Frequency	Per cent.
7_{IV}	23	8.42
6_{IV}	$54+\dfrac{72}{2}+\dfrac{71}{3}$	41.64
5_{IV}	$\dfrac{72}{2}+\dfrac{71}{3}+\dfrac{28}{3}+\dfrac{17}{4}+\dfrac{3}{5}$	27.05
4_{IV}	$\dfrac{71}{3}+\dfrac{28}{3}+\dfrac{17}{4}+\dfrac{3}{5}$	13.86
3_{IV}	$\dfrac{28}{3}+\dfrac{17}{4}+\dfrac{3}{5}$	5.20
2_{IV}	$\dfrac{17}{4}+\dfrac{3}{5}$	1.78
1_{IV}	$\dfrac{3}{5}$	0.22
0_{IV}	5	1.83

Koos 1931), *Euchlaena* (LONGLEY 1924), *Datura* (BELLING and BLAKE-SLEE 1924), *Galeopsis* (MÜNTZING 1930 a, b), *Petunia* (KOSTOFF 1930 b, KOSTOFF and KENDALL 1931 b), *Primula* (SÖMME 1930, DARLINGTON 1931 a), *Allium* (LEVAN 1931) and others. We have, however, only a few reports in which the formation of the tetravalent complexes is recorded, as in the case of *Datura* (BELLING and BLAKESLEE 1924), *Primula* (DARLINGTON 1931),[1] and *Solanum* (LESLEY, M. M. and LESLEY, J. M. 1930, LINDSTORM and KOOS 1931).[2]

The chromosome distribution to the poles is generally quite regular in this variety, but sometimes a few exceptional cases are observed. In this latter case, generally 1 or 2, but exceedingly rarely 3 or 4, lagging chromosomes which split longitudinally are found in the equatorial plane. In Figs. 137–140 some of these examples are illustrated. In connection with the view that the tetraploids may be regarded as plants which are balanced and stable (MORGAN 1926), it is interesting to note that in this variety, contrary to the cases of triploids and heteroploids, there are found only as few lagging chromosomes as 1 or 2, or rarely (in so low a frequency as less than 1 %) 3 or 4 of these, and that no case where there are more than 5 of these is found at all. Fig. 141 shows a pair of anaphasic chromosome groups in polar

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1. According to SÖMME (1930), in the tetraploid *Primula sinensis* (2n=48), the elements are not all tetravalent in most of the pollen mother cells, but as a rule only one or a few, the others being bivalent.

2. According to JÖRGENSEN, 24 bivalent chromosomes are generally found in this plant.

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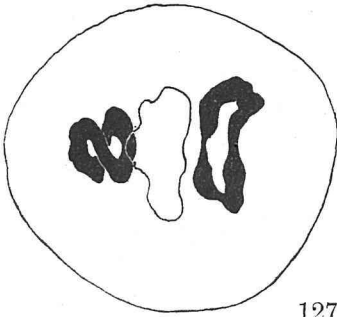
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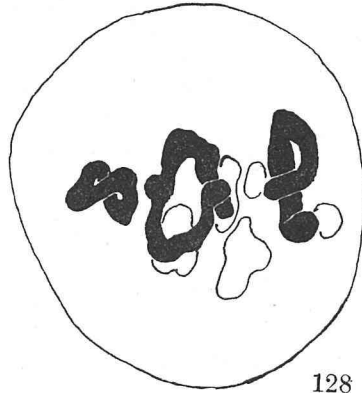
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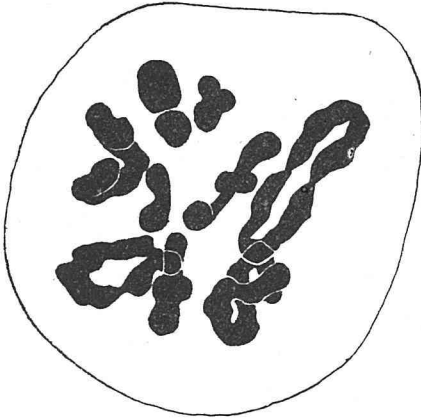
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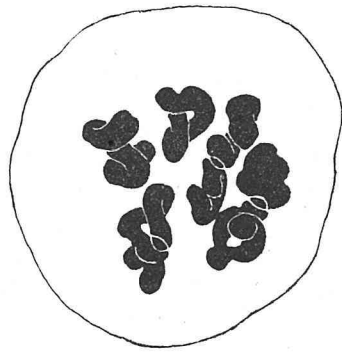
129

Figs. 125-147. *N. Pseudonarcissus*, "King Alfred". 125. Somatic nuclear plate showing 28 chromosomes. ×2210. 126—147. Meiotic phases. Figs. 126–140 and 144–147 ×1710; 126. Diakinesis. Showing some of the tetravalent chromosomes; 127-128. Heterotype metaphase in side view, showing types of tetravalent chromosomes; 129. Heterotype metaphase in polar view showing 7 tetravalent chromosomes; 130. The same showing 10 chromosomal elements, probably $4_{IV} + 10_{II}$.

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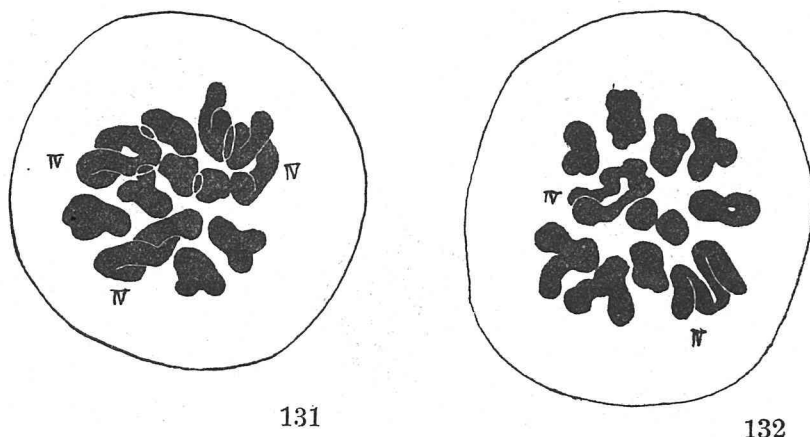
Figs. 131—132. " King Alfred ". 131. Heterotype metaphase showing 11 chromosomal elements, probably $3_{IV}+8_{II}$; 132. The same showing 12 chromosomal elements, probably $2_{IV}+10_{II}$.

view. In each of these groups 14 chromosomes are counted, a fact which tells that the division is regular.

Figs. 142-147 show the homotype metaphase, anaphase and pollen tetrads. In Fig. 142, there are shown 14 chromosomes, which are very distinct from one another in each sister cell. In Fig. 143, 15 chromosomes are counted in one of the sister cells, and 13 in the other. Lagging chromosomes are also found in the homotype division, as is shown in Figs. 144 and 145. In Fig. 146, a pollen tetrad which must have been produced through an irregular division is shown. A normal pollen tetrad and healthy pollen grains are reproduced in Figs. 147 and 225. Abortive pollen grains amount to less than 10 %. The seeds are set, though not in all individuals, by natural pollination in the field. This natural seed production seems not to be the case with the diploid, triploid, and heteroploid varieties of this species.

b) " Olympia "

External characteristics :—Like " King Alfred ", but trumpet handsome yellow and frilled. Flowers horizontal.

This variety is also a tetraploid having 28 chromosomes in its somatic cells (Fig. 148). No essential difference is found between this variety and the former one in the process of meiosis. Figs. 149–151 show heterotype metaphase figures with varying numbers of tetra-, bi- and univalent chromosomes. The total number of chromosomal elements is accordingly variable. The frequency of occurrence of these numbers of chromosomal elements is given in Table X.

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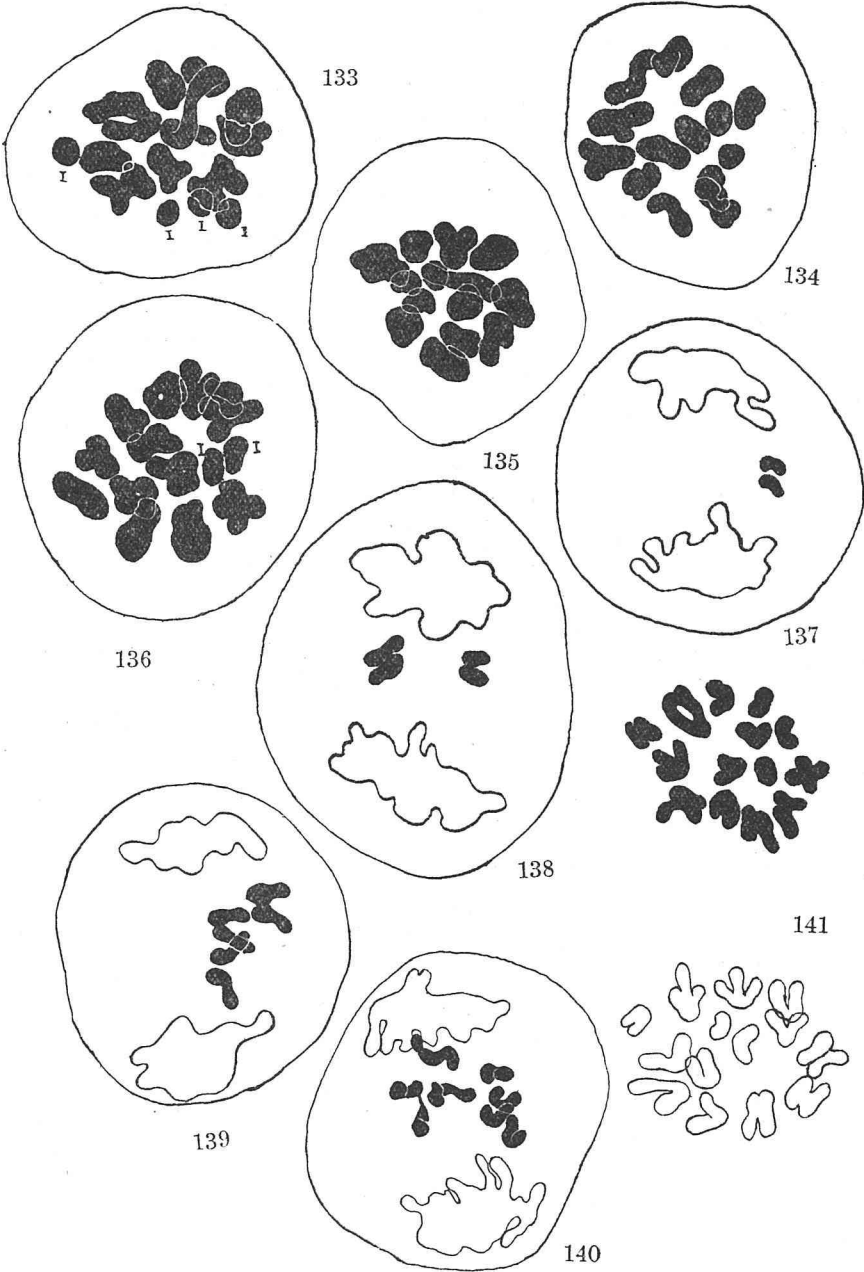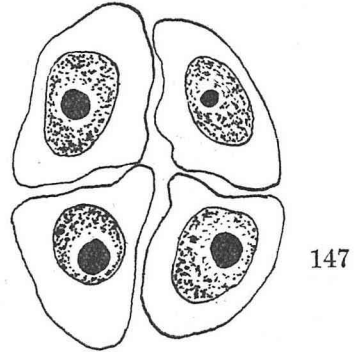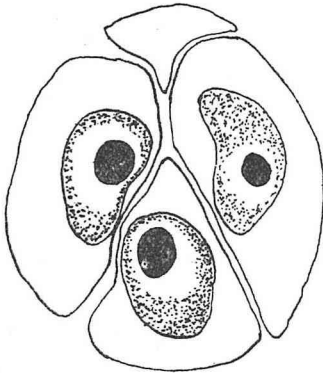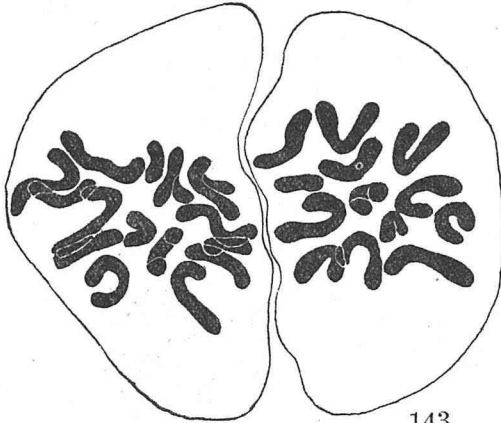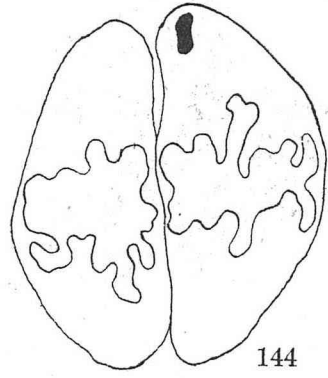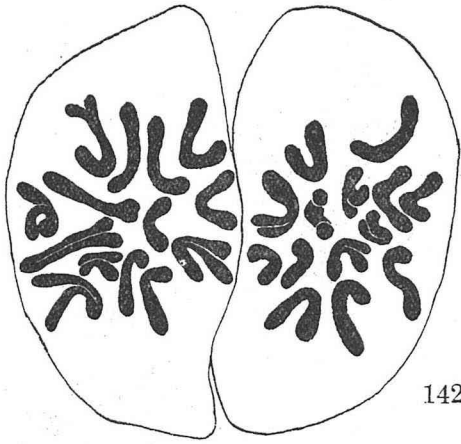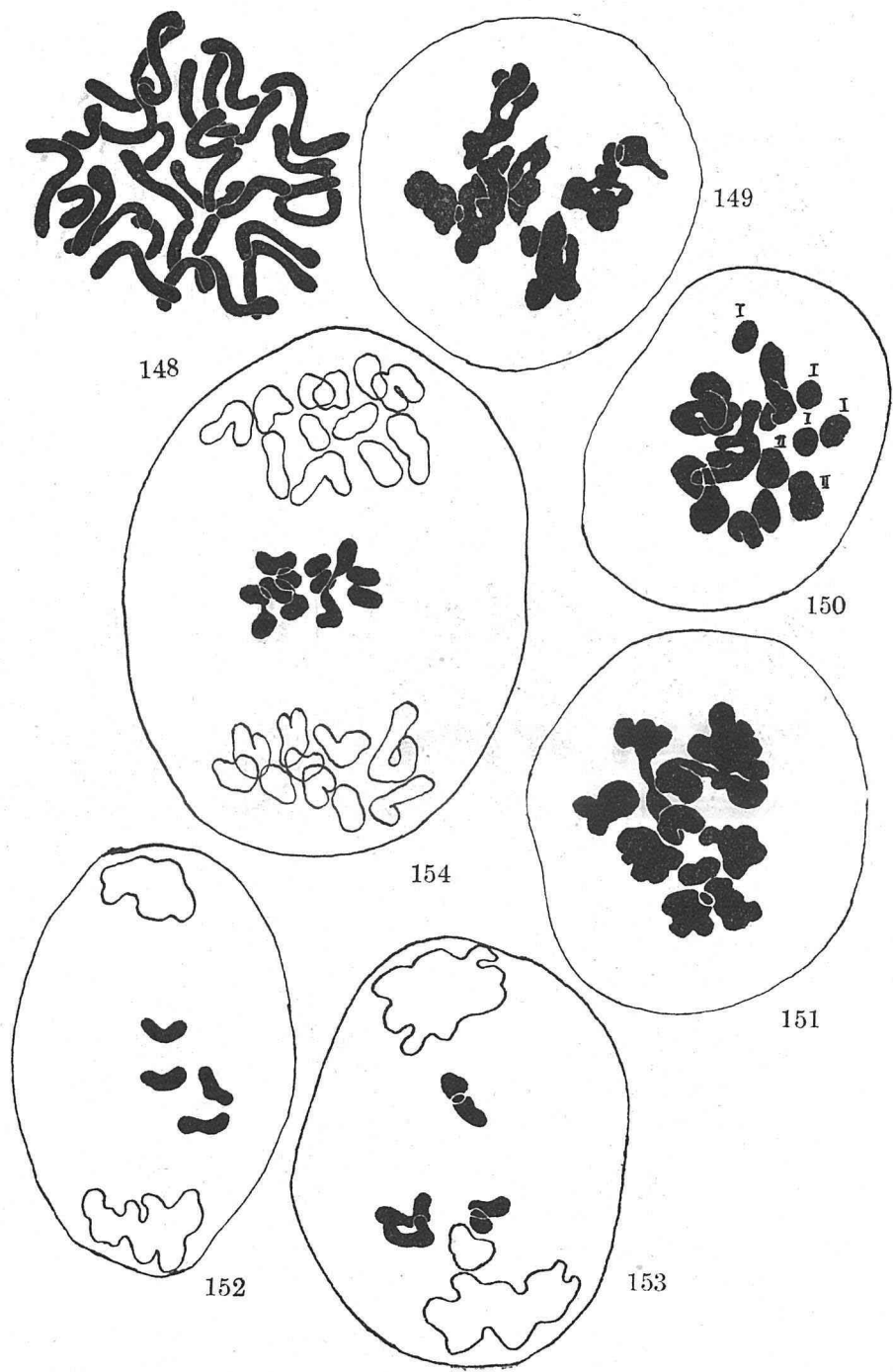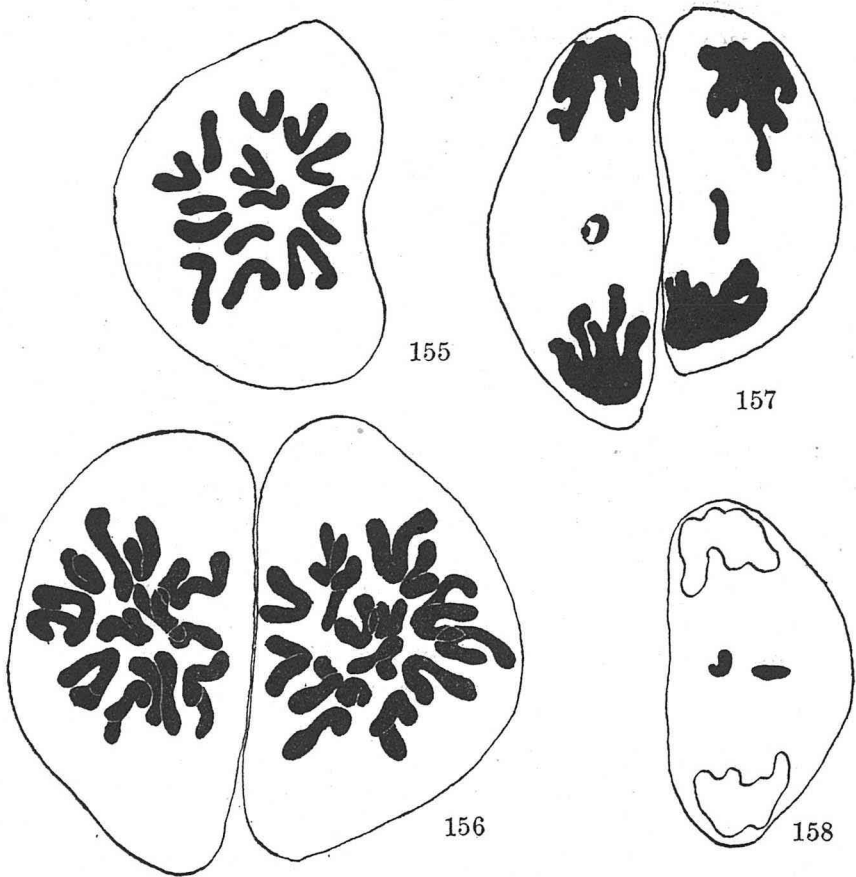
Figs. 133—147. "King Alfred". 133. Heterotype metaphase showing 13 chromosomal elements; 134. The same showing 1$_{IV}$+12$_{II}$; 135. The same showing 14 chromosomal elements; 136. The same showing 15 chromosomal elements; 137-140. Lagging chromosomes (shown solid black) in anaphase; 141. Heterotype anaphase showing 14 chromosomes in each pole. ×2210: 142. Homotype metaphase in polar view showing 14 chromosomes in each sister cells. ×2210; 143. The same showing 13 chromosomes in the cell on the right hand side and 15 in the other. ×2210; 144. Homotype metaphase in side view. One monad chromosome is seen. 145. Homotype anaphase showing 2 lagging chromosomes at the equatorial region; 146. Pollen triad: 147. Pollen tetrad.
Figs. 148-158. *N. Pseudonarcissus*, "Olympia". 148. Somatic nuclear plate showing 28 chromosomes. ×2210. 149—158. Meiotic phases; 149. Heterotype metaphase in polar view. 7 tetravalent chromosomes are seen. ×1710; 150. The same showing 11 chromosomal elements. ×1710; 151. The same showing 9 chromosomal elements. ×1710; 152 and 153. Heterotype anaphase. Lagging chromosomes (shown solid black) divide longitudinally. ×1710; 154. The same showing 28 chromosomes in all, of which 12 chromosomes are found at the upper pole, 10 at the lower and 6 longitudinally split between the poles. ×2210: 155. Homotype metaphase showing 14 chromosomes. ×2210; 156. The same

showing 16 chromosomes in the cell on the right hand side and 12 in that on the left
×2210; 157 and 158. Homotype anaphase showing lagging chromosomes between the
poles. ×1710.

Table X

Number of chromosomal elements	7	8	9	10	11	12	13	14
Frequency	1	12	9	5	1	1	2	0

Some univalent chromosomes split longitudinally in the anaphase
of the heterotype division as in the case of the variety " King Alfred ",
but the number of these univalents is greater than in that case.
Generally 2 or 3 of them split longitudinally and lag behind the others
in the equatorial region (Figs. 152 and 153), while in some cases there
may be as many as 6 (Fig. 154). Figs. 155 and 156 show metaphase
figures in the homotype division. In Fig. 155, 14 chromosomes are
counted in the cell, and in Fig. 156, 12 in one of the sister cells and
16 in the other. This inequality in the number of chromosomes in
the two sister cells must be due to the abnormal chromosome distri-
bution which has taken place in the previous division. Lagging chromo-
somes are also observed in this division (Figs. 157 and 158).

No case is met with in this variety where seeds are raised. This
probably depends on the irregular chromosome distribution in the
meiotic division which is largely connected with the intensity of the
affinity between homologous chromosomes.

D)   Heteroploid

a)   " Grandee "

The number of chromosomes in the root-tip cells is 22 in this
variety (Fig. 159). This number is the same as that found in the
variety " A_{22} " of *Narcissus tazetta* as mentioned already. Investigation
into the meiosis shows, however, that this similarity is only an apparent
and numerical coincidence. While in the variety " A_{22} ", the nuclear
plate in the heterotype division consists of 11 bivalents, it consists in
this variety of 7 trivalents and 1 univalent as a rule (Fig. 160), show-
ing the hypertriploid condition ($3n + 1$) in which 7 is the basis, or the
cardinal number. Not infrequently some of single or univalent chromo-
somes may appear which fail to form trivalent complexes. Some
lagging chromosomes which split longitudinally are also found in the
anaphase as in the case of the other varieties of this species mentioned
above. Figs. 161–163 show these lagging chromosomes, split or un-
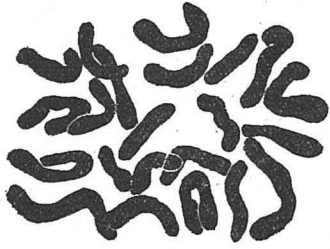
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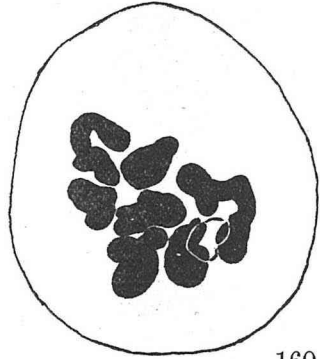
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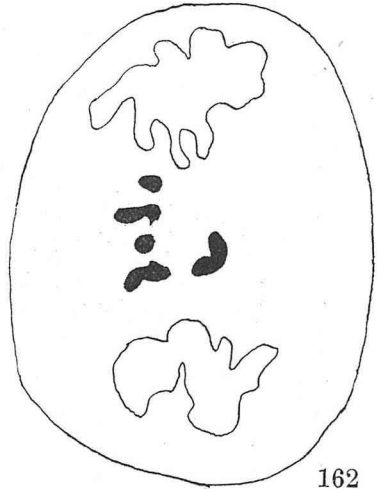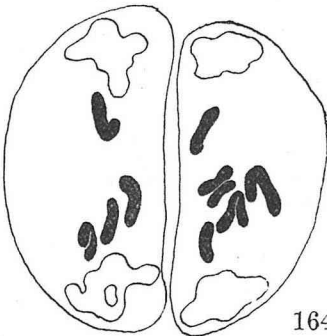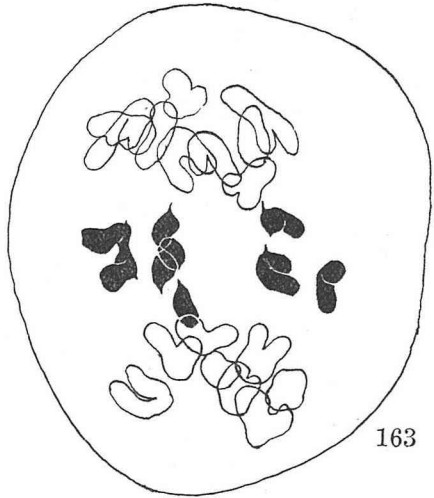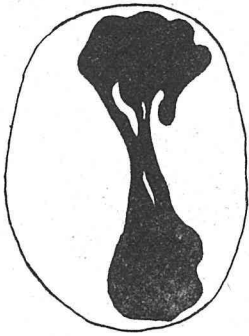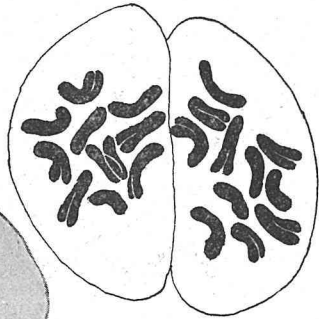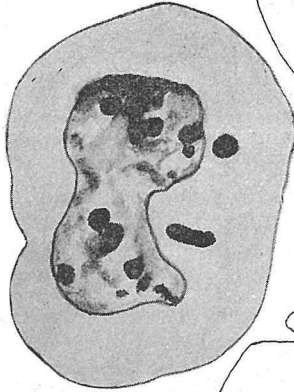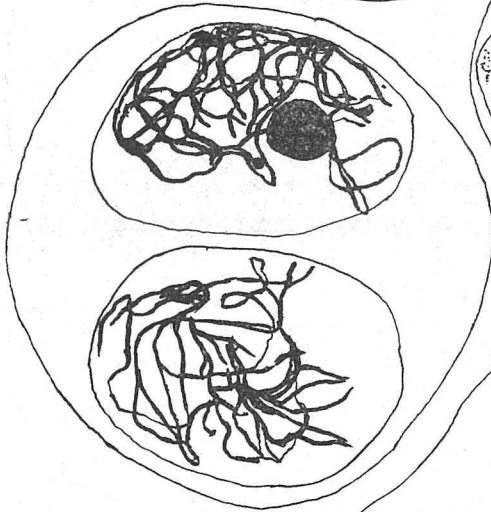
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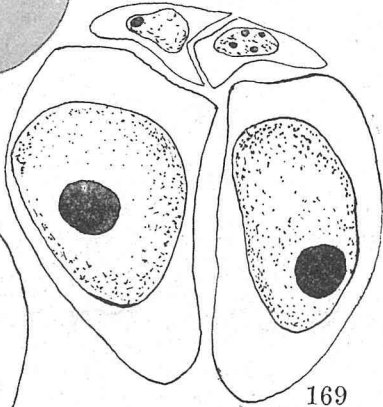
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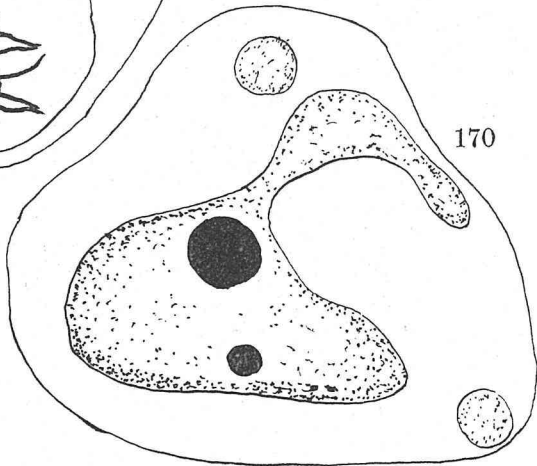
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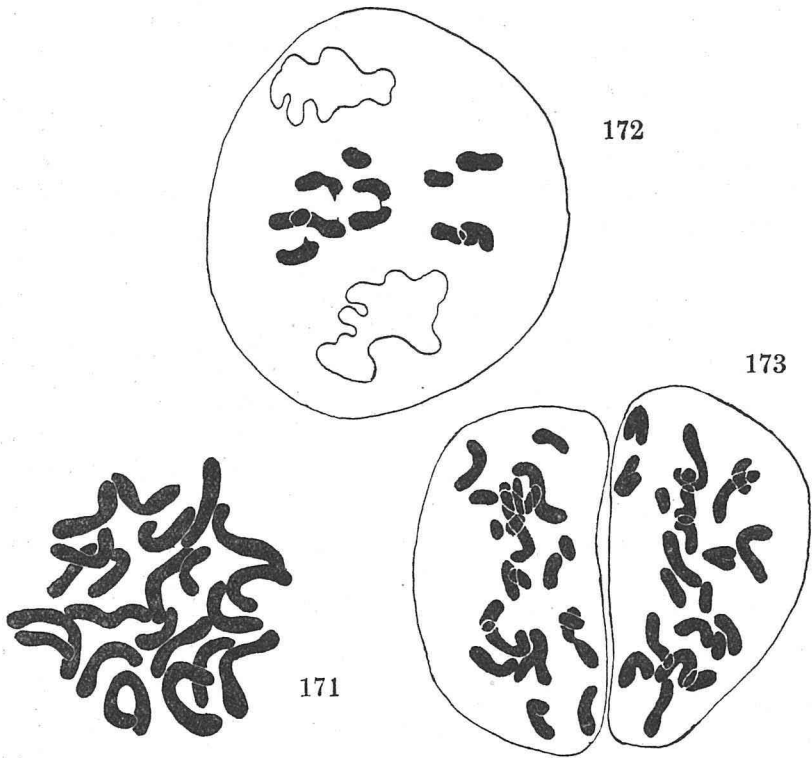
Figs. 159-170. *N. Pseudonarcissus*, "Grandee". 159. Somatic nuclear plate, showing 22 chromosomes. ×2210. 160—170. Meiotic phases; 160. Heterotype metaphase showing 7 trivalent (solid black) and 1 univalent chromosomes. ×1710; 161. Heterotype anaphase. Longitudinal division is seen in 3 chromosomes shown solid black. ×2210; 162. The same showing 3 lagging chromosomes, of which 2 are split longitudinally. ×2210; 163. The same showing 9 chromosomes at the upper pole, 8 at the lower, 5 between the poles, amounting to 22 in all. ×2210; 164. Homotype anaphase showing random distribution of monad chromosomes. ×1710; 165. Homotype metaphase showing 11 chromosomes in each sister cell. ×1710; 166. Chromosome clumping in heterotype anaphase. ×1710; 167. Restitution nucleus. ×1710; 168. A large binucleate cell with nuclei in prophase. ×1710; 169. Irregular tetrad. ×1710; 170. Giant monad cell, including one large and two small nuclei. ×1710.

Figs. 171-173. *N. Pseudonarcissus*, "Empress". 171. Somatic nuclear plate showing 22 chromosomes. ×2210; 172. Heterotype anaphase showing 6 lagging chromosomes, of which 5 are dividing longitudinally. ×1710; 173. Homotype meta-anaphase showing about 22 chromosomes in each sister cell. ×1710.

split, in the anaphase. In Figs. 162 and 163, we find one unsplit chromosome and two pairs (Fig. 162) or four pairs (Fig. 163) of split or divided chromosomes. Both the split and unsplit chromosomes are

probably those univalent chromosomes which have failed to form the
trivalent complexes in the metaphase. It seems highly probable that
the unsplit chromosomes are destined to be divided in the homotype
division. In the cell on the right hand side in Fig. 164, in which a
pair of sister cells in the homotype anaphase is shown, one longitudinal-
ly split chromosome (diad) is observable besides four monad chromo-
somes which are found in both the cells. The fact that the monad
chromosomes are found in equal numbers in the two sister cells, while
the diad is found only in one of them, points to the conclusion that
the diad must be that chromosome which is unpaired and unsplit, and
undergoes a chance distribution to one of the poles in the heterotype
division, and the monad chromosomes must be those which are longi-
tudinally divided and numerically equally distributed to both poles.
In some rare cases the number of chromosomes in the homotype
metaphase is equal in both sister cells (Fig. 165). This fact must
show that in this case all the chromosomes have been equally distributed
in the heterotype division.

Generally speaking, the distribution of the chromosomes is more
irregular in this variety than in all the cases of other varieties described
above. The formation of restitution nuclei is of frequent occurrence
(Figs. 166 and 167). A binucleate pollen mother cell is also found
as another peculiarity (Fig. 168). This occurrence of binucleate pollen
mother cells has been reported by GATES and REES (1921) in *Lactuca*,
by RANDOLPH and McCLINTOCK (1926) in *Zea Mays*, by KARPECHENKO
(1927) in *Raphanus-Brassica* hybrid, by INARIYAMA (1929) in *Iris* and
by ICHIJIMA (1930) in *Fragaria*. As suggested by these authors, this
binucleate condition seems to have its origin in the suppression of cell
wall formation in the premeiotic phase. Many irregularities are found
in pollen tetrads also (Fig. 169). A case is shown in Fig. 170, where
the cell division into the tetrad has not taken place and the cell con-
tains a giant nucleus of irregular shape and some smaller nuclei.
About 63 % out of 284 pollen grains appear to be abortive.

   b) " Empress "

In this variety, too, 22 chromosomes are found in the root-tip
cells as in the variety " Grandee " (Fig. 171). The constitution or
valency of the chromosomal elements in the heterotype metaphase has
not yet fully been worked out, but, so far as my investigation goes,
there are, besides trivalents, some univalents and bivalents, as in the
case of " Grandee ". Fig. 172 shows a figure of the heterotype
anaphase with 6 lagging chromosomes, of which 5 have been divided

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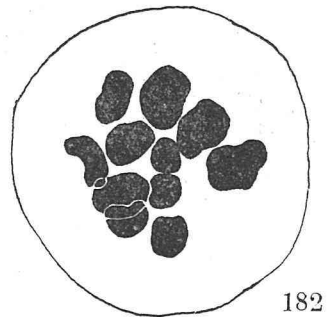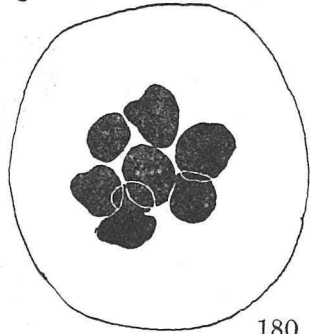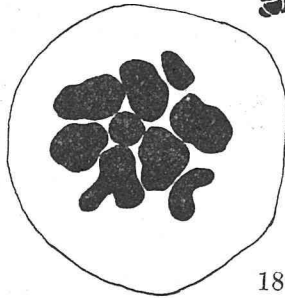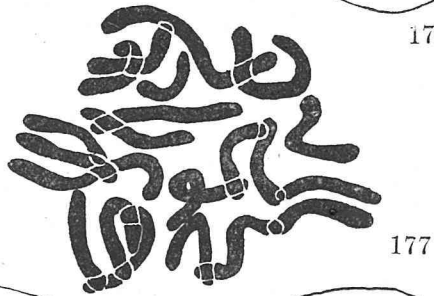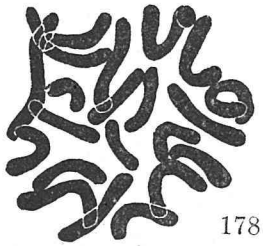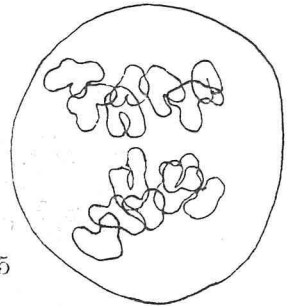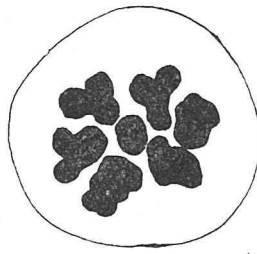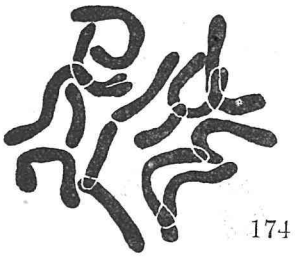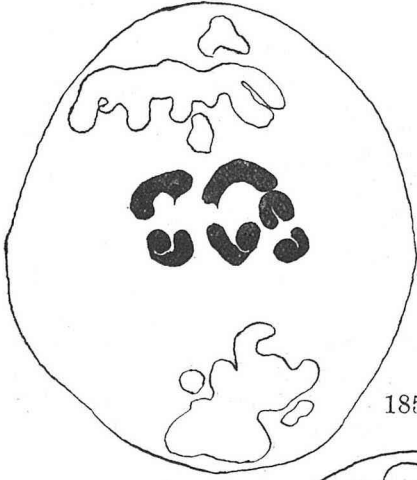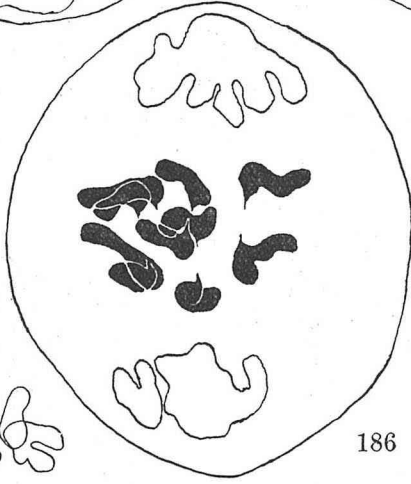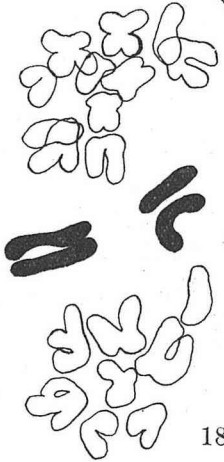
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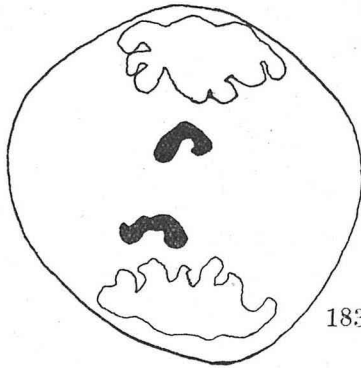
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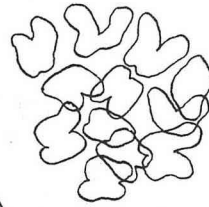
Figs. 174-176. *N. incomparabilis.* "Nelson Major" 174. Somatic nuclear plate showing
14 chromosomes. ×2210; 175 and 176. Heterotype meta- and anaphase. ×1710.
Fig. 177. "*Aurantus*", showing 21 somatic chromosomes. ×2210.
Fig. 178. "Gloria Mundi", showing 21 somatic chromosomes. ×2210; 179-188. Meiotic
phases; 179. Diakinesis showing 7 trivalent chromosomes and 1 nucleolus. ×1710; 180.
Heterotype metaphase showing 7 trivalent chromosomes. ×1710; 181 and 182. The same
showing 9 and 11 chromosomal elements respectively. ×1710; 183-186. Heterotype
anaphase showing 1, 2, 3 and 5 lagging chromosomes longitudinally divided respectively.
×2210; 187. Heterotype anaphase showing 9 chromosomes at the upper pole, 12 chromo-
somes at the lower. ×1710; 188. The same showing 11 chromosomes at the upper pole,
8 chromosomes at the lower, 2 chromosomes between the poles, amounting to 21 in all.
×1710.

and 1 remains single. In Fig. 173, about 22 chromosomes are counted
in each sister cell. This must be the result of abnormality in which
equation division takes the place of the reduction division.

3. *Narcissus incomparabilis* MILL.

The diploid number of chromosomes in this species is 14 as in
the case of *N. Pseudonarcissus.* This number is found in both bicolored
and single colored yellow varieties. Figs. 174–176 are drawings from
the yellow flowered variety "Nelson Major", showing respectively a
somatic nuclear plate, heterotype metaphase, and anaphase in pollen
mother cells. In this variety the chromosome pairing is regular and
a large percentage of pollen tetrads are normal in appearance. The
triploid number of chromosomes, 21, is found in some yellow-flowered
varieties, "Gloria Mundi" and "Sir Watkin" (Fig. 178), and "*aurantus*"
(Fig. 177) in the latter of which the trumpet is orange at the top.
Some details of the meiotic phase observed in "Gloria Mundi" only
will be mentioned below.

"Gloria Mundi" (Triploid)

The behavior of the chromosomes in the meiotic division is similar
to that observed in the other triploid varieties already described. Figs.
179 and 180 are pollen mother cells in diakinesis and heterotype
metaphase respectively, showing 7 trivalent chromosome elements each.
Failure to form trivalent complexes is also observed in some of the
elements, resulting in the total number of elements being different.
In Fig. 181, 9 chromosomal elements are counted, and in Fig. 182,
11. Some lagging chromosomes which have been longitudinally divided
are also found in the anaphase, as is shown in Figs. 183–186. In
Fig. 187, a figure of the heterotype anaphase is reproduced in which
9 chromosomes (drawn solid black) are counted in one group and 12
(outline only) in the other. In Fig. 188, 8 chromosomes are found

at the lower pole and 11 at the upper and 2 lagging chromosomes which have been longitudinally divided, on the equator.

4. *Narcissus Bulbocodium* L.

In this species the somatic number of chromosomes has been reported to be 14 in some varieties (NAGAO 1929, FERNANDES 1931 a, b), and 21 and 42 in others (HEITZ 1926, NAGAO 1929). The results so far obtained from the plant with 42 chromosomes in the root-tip cells (Fig. 189) will be mentioned below, although the observations are not yet complete owing to the lack of material.

In the diakinesis and the succeeding metaphase in pollen mother cells, the chromosomes pair, in most cases, two by two to form 21 bivalents (Fig. 192) instead of 7 sexivalents, in contradiction to our expectation from the somatic number of the chromosomes, 42 ($=7 \times 6$). Sometimes, however, there are cases where one or more than one multivalent chromosomes are found in the diakinesis as well as the metaphase. Figs. 190 and 191 show nuclei in the diakinesis stages ; 2 tetravalents are found in the former figure and 1 sexivalent in the latter. Fig. 193 shows a polar view of the heterotype metaphase where 1 tetravalent is found besides the other 19 bivalents. In the anaphase, the distribution of chromosomes to the two poles is regular in some cases, but irregular in others. In the latter case, which occurs not infrequently, some elements, commonly bivalents, remain somewhere in the cytoplasm, while the other elements are disjoining regularly. These aberrant elements disjoin later on, too, as will be seen from Fig. 194 where three of these disjoined chromosomes are found near each group of chromosomes having reached the pole in advance. In Fig. 195 are shown four of these aberrant chromosomes which are disjoining in the region of the equatorial plane. So far as my observations go, these lagging chromosomes form no dwarf nuclei at all, but take part in the formation of daughter nuclei with the chromosomes of normal behavior (*cf.* DARLINGTON and MOFFETT 1930). Further stages have not been observed, but the fact that a large percentage of pollen grains of good appearance are found in the anther (Fig. 226) seems to indicate that regularity prevails more in the homotype division than in the heterotype division.
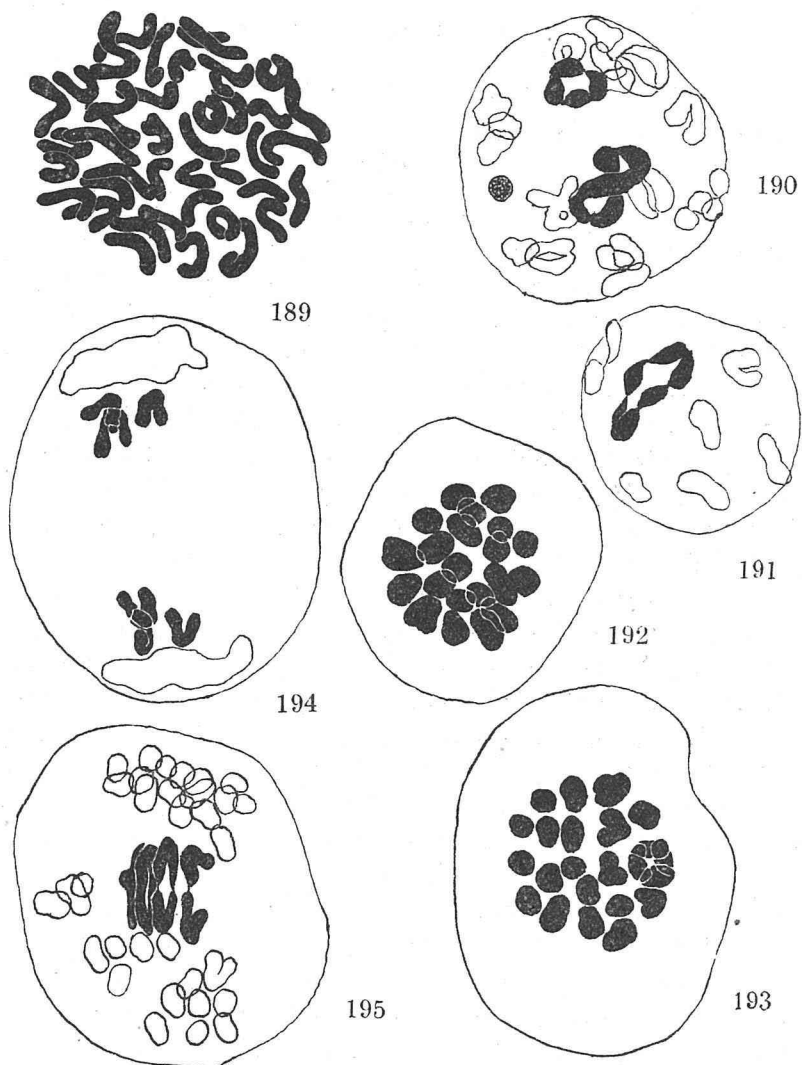
Figs. 189–195. *N. Bulbocodium*. 189. Somatic nuclear plate showing 42 chromosomes. ×2990. 190—195. Meiotic phases. ×1710; 190. Diakinesis. Showing 2 tetravalents, 17 bivalents and 1 nucleolus; 191. The same showing 1 hexavalent chromosome; 192. Heterotype metaphase showing 21 chromosomes; 193. The same showing 1 tetravalent and 19 bivalent chromosomes; 194. Heterotype anaphase showing 3 chromosomes near the pole lagging behind the others: 195. The same showing 4 bivalent chromosomes disjoining in the region of the equatorial plane.

III. Cases of species hybrids

1. *Narcissus intermedius* LOIS.

External characteristics :—Slender : leaves green and narrow, deep channeled, a charac-
teristic by which this form may be distinguished from *N. tazetta*, 4 in number : leaves and
scape 17–20 cms. long : flowers 2–7, mostly 4 in number, ca. 3.5 cms. across ; segments narrow,
bright yellow, crown darker than the segments ; style more or less exceeding the anthers.

This horticultural species has 17 chromosomes in the somatic cells
(Fig. 196). This number and other cytological features which will be
mentioned below, indicate that this plant must be a species hybrid in
its origin, probably being raised by hybridization between a diploid
variety of *N. tazetta* and some other *Narcissus* species with 7 chromo-
somes in the haploid phase. According to BAILEY, this species has
taxonomically been considered by some authors to be a hybrid between
N. tazetta and *N. Jonquilla* (BAILEY 1917), a view which is in accord
with the conclusion we can draw from the cytological point of view.

With the same fixation and manipulation as in the case of the
other species and varieties investigated, many pollen mother cells in
the first maturation division are frequently found shrunk and distorted
in this plant. This peculiarity seems largely due to fixation. ERLANSON
(1929) has noted a similar phenomenon in a hybrid rose, *Rosa blanda*,
var. *glandulosa*, and HÅKANSSON (1929) in a *Salix* hybrid. According
to the latter author, the difficulty of fixing pollen mother cells in
diakinesis is greater in the hybrid form than in the pure stock. The
reason why there is such a difference between the results of fixation
in the pure and hybrid forms is obscure, but it seems certain, at least
in some cases, that it is due to a special feature which is connected
with hybridity. It may probably with justice be assumed that the
reaction of the protoplasm to fixing reagents may not be the same
in hybrid and in pure plants, and conversely that the difference in the
results of fixation is a visible expression of this difference in the re-
action of the protoplasm. The question is interesting from the physio-
logical point of view, with which, however, we need not here deal
further. In some cases, the cells are fairly well fixed, and the chromo-
some behavior can be somewhat clearly traced. In the first maturation
division, 17 univalent chromosomes, that is, as many chromosomes as
those in the somatic cells, are found, forming the equatorial plate.
Among them no trace of a tendency towards pairing is observed (Fig.
197). This must mean that there is not a pair of chromosomes which
are homologous with each other. This type of the heterotype division
is called by ROSENBERG (1917) " halbheterotypie" or " semiheterotypie",
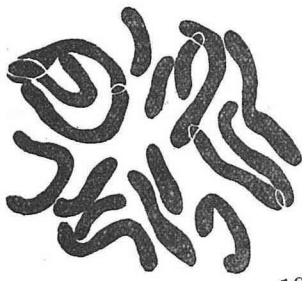
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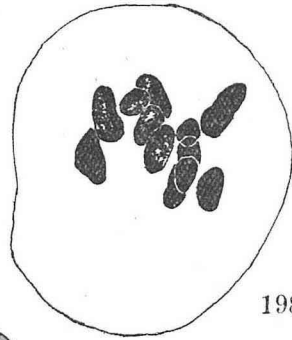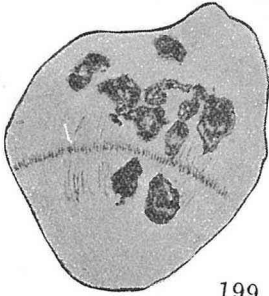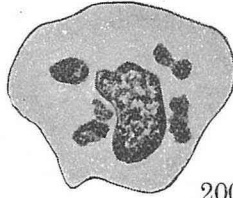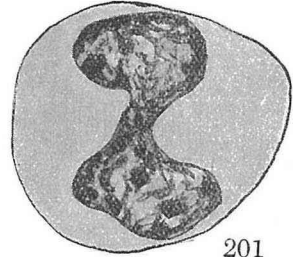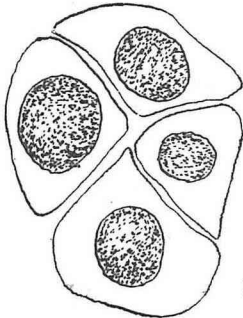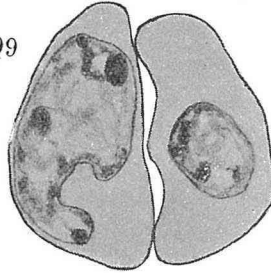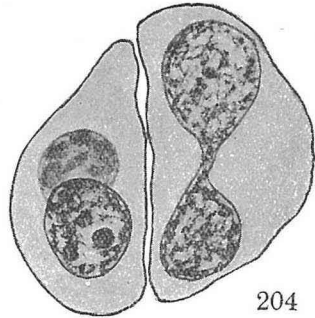
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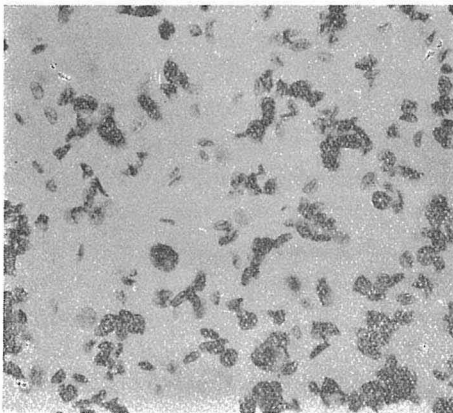
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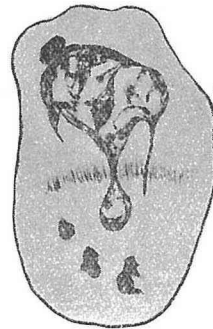
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Figs. 196-206. *N. intermedius.* 196. Somatic nuclear plate showing 17 chromosomes. ×2210. 197-205. Meiotic phases. ×1710; 197. Heterotype metaphase in polar view showing 17 univalent chromosomes; 198. Heterotype chromosomes showing sign of vacuolization; 199-202. Heterotype telophase showing several small and large nuclei of various sizes and shapes; 203. Two sister cells whose nuclei are of different sizes; 204. Homotype telophase. In one of the sister cells the nucleus is very large and dumb-bell shaped; 205. Pollen tetrad; 206. A microphotograph showing a large amount of empty pollen grains.

which he first observed in *Hieracium lacerum* and *H. levigatum* (p. 186). To designate such a lack of affinity between the parental chromosomes BRIEGER (1928) has proposed the term "asyndesis".

A number of instances of asyndesis have been reported in plants. To enumerate some of them, we have : *Taraxacum albidum* (OSAWA 1913), *Digitalis lutea* × *D. purpurea* (HAASE-BESSELL 1916), *Crepis setosa* × *C. capillaris* (COLLINS and MANN 1923), *Aegilops ovata* × *Triticum dicoccum* (PERCIVAL 1926, SAX 1928), *Aegilops cylindrica* × *Triticum turgidum* (GAINES and AASE 1926), *Crepis capillaris* × *C. aspera* (NAWASCHIN 1927), *Raphanus sativus* × *Brassica oleracea* (KARPECHENKO 1924, 1927), *Aegilops cylindrica* × *Triticum durum* (BLEIER 1928), *Triticum dicoccoides* × *Secale montanum*, *T. vulgare* × *S. cereale* (LONGLEY and SANDO 1930), *Fragaria* (*virginiana* × *glauca*) × *F. collina* (ICHIJIMA 1930), *Nicotiana sylvestris* × *N. Rusbyi* (KOSTOFF 1930 a), *Triticum dicoccoides* × *Aegilops ovata* (KIHARA and KATAYAMA 1931) and others.

In *Narcissus intermedius*, all the chromosomes are generally arranged on the equatorial plane, and sometimes a few are scattered in the cytoplasm. The longitudinal splitting or division of the chromosomes in the anaphase is not observed. The migration of the chromosomes takes place very irregularly ; they may move towards the poles too slowly, and some begin to be vacuolized in the metaphase (Fig. 198) and form dwarf nuclei without taking up the polar localization. Fig. 199 shows these dwarf nuclei which have been divided into two groups by the formation of the cell wall. Other irregularities are shown in Figs. 200–202 in which a large nucleus of an irregular shape which reminds us of amitosis, a restitution nucleus, or a nucleus of smaller size accompanied by some supernumerary nuclei or vacuolated chromosomes is found. No such a figure is observed as that in which a chance distribution of chromosomes at the poles into two groups is recognizable.

These abnormalities in the behavior of chromosomes should further result in many types of irregularities in the second division, and conse-

quently in the production of abnormal tetrads. From Fig. 206 it seems that this is probably the case, because in this figure it is seen that hardly any healthy-looking pollen grains can be found in the anther, though, as shown in Fig. 205, tetrads, the four cells of which are of about equal size, are rarely observed. Figs. 203 and 204 show some irregularities in the homotype division. In Fig. 203, the nuclei in the sister cells are unequal in size, and in Fig. 204, the nucleus in one of the sister cells is large and dumb-bell shaped, while in the other there are found two spherical nuclei.

2. *Narcissus biflorus* CURT.
(*N. poeticus-tazetta* hybrid)

This species, *N. biflorus*, is regarded by some authors as a hybrid between *N. tazetta* and *N. poeticus* (BAILEY 1917). The form raised originally in Holland in 1885 by crossing *N. poeticus* var. *ornatus* with *N. tazetta*, is called the poetaz narcissus, or *Narcissus poetaz* (BAILEY 1924). Both *N. biflorus* and *N. poetaz* have 24 chromosomes in the somatic cells (Figs. 207 and 208). In my previous paper it was reported that in the form " Elvira "? of *N. poetaz* the somatic chromosome number is 25. A re-examination has shown, however, that this number is incorrect, and the correct number is 24 in this form too.

The form of *N. biflorus*, in which the meiotic processes in pollen mother cells were investigated, has the following characteristics : leaves 3–5, mostly 4 in number: leaves and scape 27–35 cms. long : flowers 1 or 2 in number ; crown yellow, segments white ; flowering season from April to May.

In this form, observation is somewhat difficult owing to the scantiness of pollen mother cells in the pollen sacs and the extraordinary irregularity in the orientation of the chromosomal elements. In some clear figures of diakinesis and metaphase which can be picked out from those not suitable for observation, it can be determined with certainty that the chromosome set in the metaphase consists of 7 bivalents and 10 univalents (Figs. 209–211). This constitution of the set must show that this plant is a hybrid produced by the union of a gamete carrying twice as many chromosomes as the cardinal number, 7, and a gamete carrying a haploid number of chromosomes in which the cardinal number is 10. If this interpretation is correct, the cytological results we obtained are in harmony with the view that this species is a hybrid between *N. poeticus* and *N. tazetta*.

The normal distribution figures of chromosomes in the heterotype anaphase are not observed ; but all the figures indicate that the division
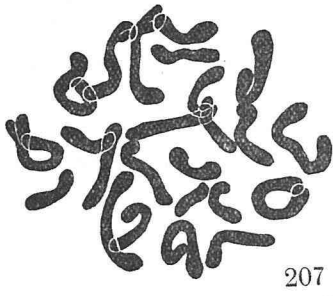
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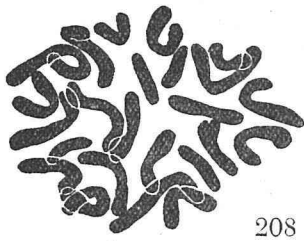
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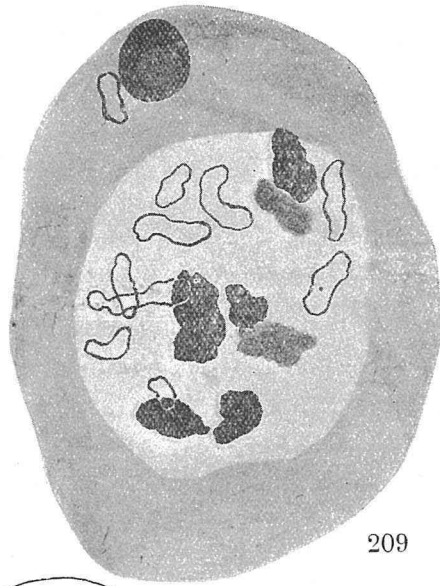
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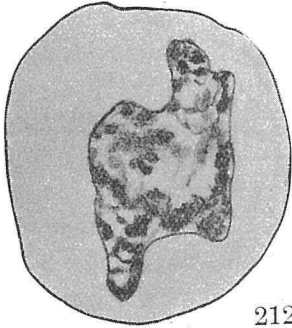
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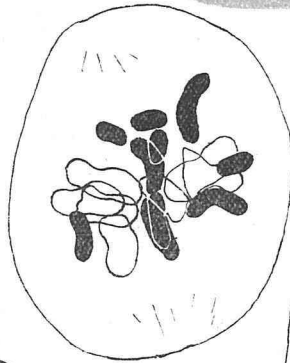
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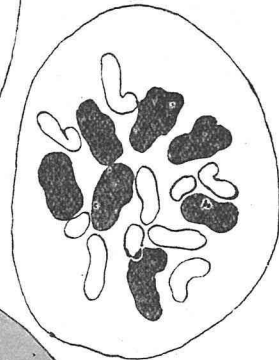
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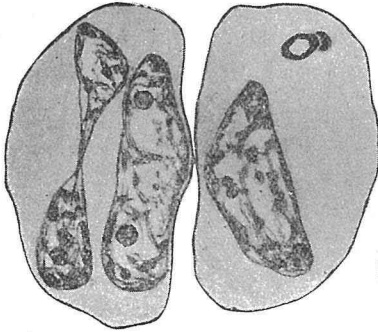
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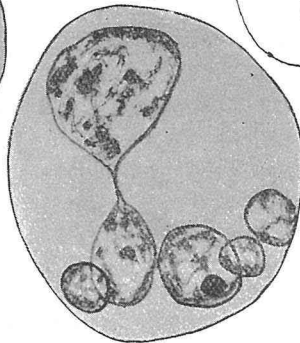
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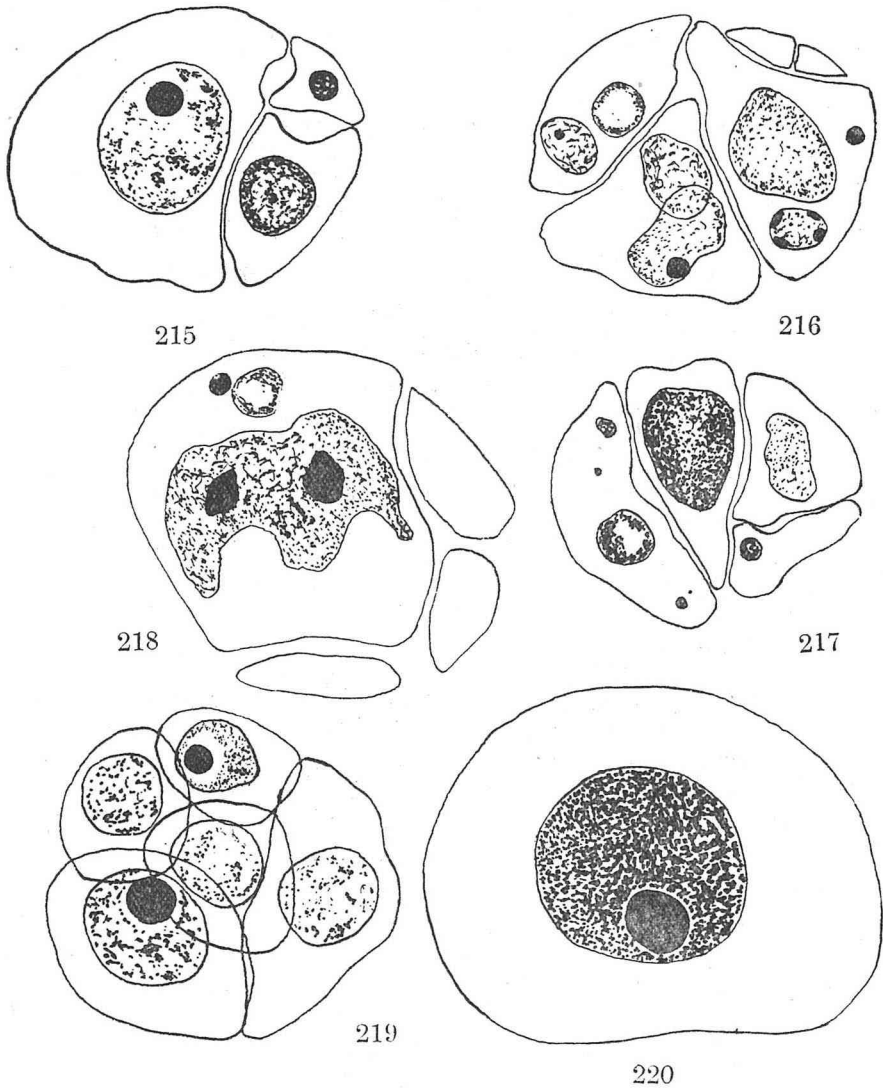
Figs. 207–221. *N. biflorus.* 207. Somatic nuclear plate showing 24 chromosomes. ×2210; 208. "Elvira?" Showing 24 somatic chromosomes. ×2210. 197–205. Meiotic phases. Figs. 210–220 ×1710; 209. Diakinesis. Showing 7 bivalents, 10 univalents and a nucleolus. ×2210; 210. Heterotype metaphase in polar view showing 7 bivalents (drawn solid black) and 10 univalents (drawn in outline); 211. The same in side view. Bivalent chromosomes are drawn in outline and univalents solid black; 212. Heterotype telophase showing a restitution nucleus; 213. The same showing five nuclei in various sizes; 214. Homotype telophase showing two large elongated nuclei in the cell on the left hand side, and a large and two small ones in that on the right; 215–220. Irregular pollen "tetrads"; 221. A microphotograph showing a large mass of periplasmodium.

Fig. 222. *N. Barrii*. Showing 14 somatic chromosomes. ×2210.
Fig. 223. *N. odorus*. Somatic nuclear plate showing 14 chromosomes. ×2210.
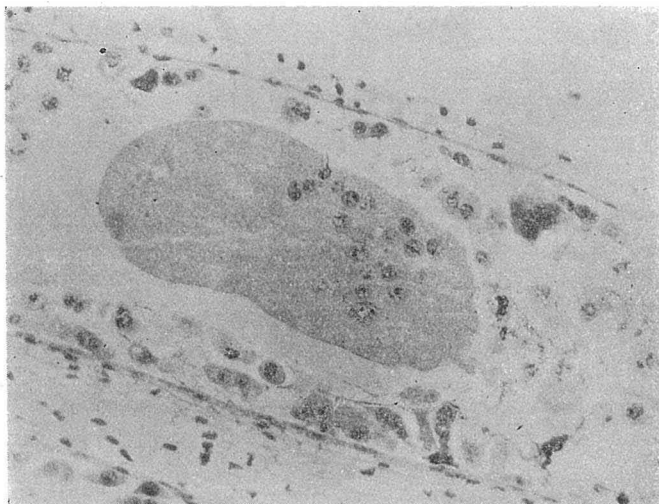
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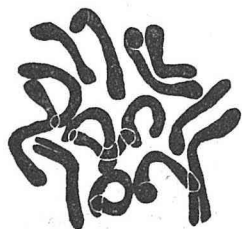
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process is generally of a very irregular nature in the pollen mother
cells. In Fig. 212, a cell containing a giant restitution nucleus of a
very irregular shape is shown, and in Fig. 213, another one in which
a number of nuclei of different sizes are distributed irregularly. Some-
times an enormously large mass of periplasmodium is observed (Fig.
221); this has never been found with such prominence in the other
species or varieties of *Narcissus,* so far as my observations are con-
cerned. In Fig. 214, an irregular homotype telophase is illustrated;
in the cell on the right hand side, one large and two smaller nuclei
are shown and in that on the left, two large, elongated nuclei. As
a consequence of these irregularities, the resulting pollen tetrads are
very abnormal (Figs. 215–220); some are not tetrads, but triads (Fig.
215) or pentads (Fig. 219), and in an extreme case they may be single

cells (Fig. 220). Binucleate pollen tetrad cells are also of very frequent occurrence (Fig. 216). Pollen grains which are set free from their tetrad union are greatly shrivelled or are empty of their contents, and are few in number.

3. *Narcissus Barrii* (or *N. Leedsii*) HORT.

This is also a horticultural species, regarded as a hybrid between *Narcissus poeticus* and *N. Pseudonarcissus*. I have examined a variety of this species and found that the somatic number of the chromosomes is 14 (Fig. 222).

4. *Narcissus odorus* L.

FERNANDES (1931 a, b) has reported that the diploid number of chromosomes in this species is 10. My observations, however, show that the chromosome number in the root-tip cells is clearly 14 as shown in Fig. 223. It is obscure at present to what reason this difference in the chromosome number between the results of FERNANDES and my own is due, and consequently we have no idea which number is the correct one, but I wish to emphasize the fact that the result I obtained is in accord with the view of some authors[1] that this horticultural species is a hybrid between *Narcissus Jonquilla* and *N. Pseudonarcissus* in both of which the cardinal number of chromosomes is 7.

Relation of the Chromosome Number to the Size of the Cell

It has been assumed by many earlier workers that the nucleo-plasmic ratio has an essential bearing on the normal or healthy co-operation of the nucleus and cytoplasm. That in this relation the nuclear volume may be expressed in terms of the chromosome number has been shown in many cases. Beautiful examples have been given by BOVERI (1904) in his "Ergebnisse", and in connection with the plant kingdom the following works may be cited : GATES (1909), GATES and GOODWIN (1930) in *Oenothera,* TISCHLER (1910) in *Musa,* WINKLER (1916) in *Solanum,* OSAWA (1920) in *Morus,* BREMER (1923) in sugar cane, TOKUGAWA and KUWADA (1924) in *Canna,* WETTSTEIN (1924, 1927) in the moss, CLAUSEN and GOODSPEED (1925) in *Nicotiana,* KIHARA and ONO (1926) in *Rumex,* MÜNTZING (1927–'28) in *Galeopsis,* KAGAWA

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1. BAILEY (1917, p. 2111).

(1928) in *Aegilops,* DERMEN (1931) in *Petunia,* SCHMIDT (1931) in *Physcomitrium* and so forth. In *Oenothera* it is well known that in association with the chromosome number doubling pollen grains become 4-lobed (*Oenothera gigas* (GATES 1915) and *Oe. gigantea* (HÅKANSSON 1924)), while they are 3-lobed in the diploid *Oenotheras,* a fact which GATES (1915) interprets as meaning that " the extra lobe probably represents an adjustment to the increase in the size of nucleus which contains 14 chromosomes instead of seven, permitting a proportional increase in the cytoplasm."

In *Narcissus,* measurements were attempted with pollen grains and epidermis cells in the scale leaves of the bulb.

I. Pollen grain

The shape of the pollen grains in *Narcissus* is, practically speaking, ellipsoid or ovoid. The relative length and width were measured with fresh ripe pollen grains stained with acetocarmine, by means of an ocular micrometer under a magnification of about 1050 times. For each variety and species 100 pollen grains were measured. The results obtained are given in Tables XI–XXIII, in which the relative lengths and widths are shown by the numbers of divisions in the micrometer covering the lengths and widths of the pollen grains. In the tables the following abbreviations are used :—

 L : Length of pollen grains.
 W : Width of the same.
 T : Total number of pollen grains measured.
 s n : Somatic number of chromosomes.

The mean length and width, standard deviation, and coefficient of variability which were obtained for each variety and species from the data given in these tables, and the volume of pollen grains obtained, by the formulae[1] :

Mean, $M = \dfrac{\Sigma\, Cf}{n}$

Standard deviation, $\sigma = \pm \sqrt{\dfrac{\Sigma\, D^2 f}{n}}$

Coefficient of variability, $CV = \dfrac{\sigma}{M} \times 100$

Volume of pollen grains, $V = \dfrac{1}{6} ab^2\pi$

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1. JOHANNSEN 1926.

where,

$\quad$ C = Class value

$\quad$ f = Frequency

$\quad$ D = Mean—Class value (deviation)

$\quad$ n = Total number of pollen grains measured

$\quad$ a = Length of pollen grain

$\quad$ b = Width of pollen grain,

are shown in Table XXIV, where the following abbreviations are used :

$\quad$ M_l, M_w $\quad$: $\quad$ Mean length and width of pollen grains respectively.

$\quad$ σ_l, σ_w $\quad$: $\quad$ Standard deviation of the mean length and width respectively.

$\quad$ CV_l, CV_w : $\quad$ Coefficient of variability of the mean length and width respectively.

Table XI

N. Jonquilla (sn=14 : diploid)

W \ L	12	13	14	15	16	17	18	T
9	•	1	•	•	•	•	•	1
10	•	•	•	•	•	•	•	0
11	1	•	1	5	4	2	•	13
12	2	3	4	10	29	11	•	59
13	•	•	•	4	10	9	1	24
14	•	•	•	•	2	•	1	3
T	3	4	5	19	45	22	2	100

Table XII

"Victoria" (sn=14 : diploid)

W \ L	14	15	16	17	18	19	20	T
11	•	•	1	1	•	•	•	2
12	•	2	2	3	•	•	•	7
13	•	3	3	18	7	1	•	32
14	1	•	2	13	12	6	•	34
15	•	•	1	3	3	6	3	16
16	•	•	•	•	1	2	4	7
17	•	•	•	•	•	1	1	2
T	1	5	9	38	23	16	8	100

Table XIII

"Emperor" (sn=21 : triploid)

W\L	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	T
15	1	1	1	1	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	6
16	1	·	3	4	4	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	13
17	·	·	1	5	3	5	4	2	1	·	·	·	·	·	·	·	·	·	·	·	·	21
18	·	·	2	2	8	6	5	·	·	·	·	·	·	·	·	·	·	·	·	·	·	23
19	·	·	·	·	2	2	4	1	1	1	·	·	·	·	·	·	·	·	·	·	·	11
20	·	1	·	·	1	1	2	·	2	3	·	·	·	·	·	·	·	·	·	·	·	10
21	·	·	·	·	·	·	1	2	·	·	·	·	·	·	·	·	·	·	·	·	·	3
22	·	·	·	·	·	·	·	·	3	·	1	·	·	·	·	·	·	·	·	·	·	4
23	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	1
24	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
25	·	·	·	·	·	·	·	·	·	·	1	·	·	·	1	·	·	·	·	·	·	2
26	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	1
27	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	1
28	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	1	2
29	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
30	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
31	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
32	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1
33	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
34	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1
T	2	2	7	12	19	16	16	5	7	5	3	0	1	1	1	0	0	0	0	0	3	100

Table XIV

"Gloria Mundi" (sn=21 : triploid)

W\L	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	T
10	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	1
11	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
12	1	·	·	·	1	1	1	·	·	·	·	·	·	·	·	4
13	·	·	·	·	·	4	1	3	·	·	·	·	·	·	·	8
14	·	·	·	·	1	·	6	9	·	·	·	·	·	·	·	16
15	·	·	·	·	·	·	2	11	4	2	·	·	·	·	·	19
16	·	·	·	·	·	·	·	11	7	3	2	·	·	·	1	24
17	·	·	·	·	·	·	1	1	5	7	1	·	·	·	·	15
18	·	·	·	·	·	·	·	·	1	3	·	·	·	·	·	4
19	·	·	·	·	·	·	·	1	1	1	1	·	·	·	·	4
20	·	·	·	·	·	·	·	·	·	1	1	·	·	·	·	2
21	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	2
22	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	1
T	1	0	0	0	3	5	11	36	18	17	5	1	1	1	1	100

Table XV

"Grandee" (sn=22: hypertriploid)

W\L	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	T
14	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
15	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
16	.	.	2	2	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
17	1	1	.	3	11	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20
18	.	.	.	1	5	6	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16
19	.	.	.	1	.	4	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
20	.	.	.	.	1	1	4	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	13
21	.	.	.	.	.	.	1	3	2	1	2	.	.	.	.	.	.	.	.	.	.	.	9
22	.	.	.	.	.	.	2	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	5
23	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	3
24	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
27	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	2
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1
30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
32	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
T	2	2	3	8	21	18	15	11	6	3	6	0	0	1	1	1	1	0	0	0	0	1	100

Table XVI

"King Alfred" (sn=28: tetraploid)

W\L	20	21	22	23	24	25	26	T
13	.	1	.	.	.	.	.	1
14	1	.	.	.	.	.	.	1
15	1	1	3	1	2	.	.	8
16	1	1	9	28	10	2	.	51
17	.	.	6	16	7	5	.	34
18	.	.	.	1	1	1	1	4
19	.	.	.	.	.	1	.	1
T	3	3	18	46	20	9	1	100

Table XVII

N. Bulbocodium (sn=42: hexaploid)

W\L	23	24	25	26	27	28	29	T
16	1	.	1	2	.	.	.	4
17	.	.	10	2	1	1	.	14
18	.	5	8	9	3	.	.	25
19	.	2	8	10	10	3	1	34
20	.	1	4	5	10	2	.	22
21	.	.	.	.	.	1	.	1
T	1	8	31	28	24	7	1	100

Table XVIII

"L_{20}" (sn=20: diploid)

W \ L	14	15	16	17	18	19	20	21	T
12	1	2	2	.	.	.	.	1	6
13	.	15	9	3	.	.	.	.	27
14	.	3	15	22	.	.	.	1	41
15	.	1	6	11	4	.	.	.	22
16	.	.	.	.	3	.	.	.	3
17	.	.	.	.	.	.	.	.	0
18	.	1	.	.	.	.	.	.	1
T	1	22	32	36	7	0	0	2	100

Table XIX

"B_{21}" (sn=21: hyperdiploid)

W \ L	12	13	14	15	16	17	T
10	.	.	.	1	.	.	1
11	.	1	2	7	1	.	11
12	2	8	11	25	10	3	59
13	.	3	7	10	9	.	29
T	2	12	20	43	20	3	100

Table XX

"A_{22}" (sn=22: hyperdiploid)

W \ L	12	13	14	15	16	17	T
8	3	1	.	.	.	.	4
9	.	.	.	.	.	.	0
10	.	.	.	.	.	.	0
11	2	2	.	3	.	.	7
12	1	8	3	24	16	1	53
13	.	.	2	6	18	4	30
14	.	.	.	.	2	3	5
15	.	.	.	.	.	1	1
T	6	11	5	33	36	9	100

Table XXI

"Yellow Prince" (sn=30: triploid)

W\L	13	14	15	16	17	18	19	20	21	22	23	24	T
13	1	•	•	•	•	2	•	•	•	•	•	•	3
14	•	•	1	•	2	4	5	1	•	•	•	•	13
15	•	•	•	1	3	2	6	11	•	•	•	•	23
16	•	•	•	•	•	3	3	8	4	•	•	•	18
17	•	•	•	•	•	•	1	3	15	3	•	•	22
18	•	•	•	•	•	•	•	1	6	3	2	1	13
19	•	•	•	•	•	•	•	•	3	2	•	•	5
20	•	•	•	•	•	•	•	•	•	2	1	•	3
T	1	0	1	1	5	11	15	24	28	10	3	1	100

Table XXII

"Chinese Sacred Lily" (sn=30: triploid)

W\L	14	15	16	17	18	19	20	21	22	23	24	T
10	•	•	•	2	•	•	•	•	•	•	•	2
11	1	2	3	2	•	•	•	•	•	•	•	8
12	1	3	7	12	2	1	1	•	•	•	•	27
13	1	•	1	8	14	1	•	•	•	•	•	25
14	•	1	1	8	4	2	1	•	•	•	•	17
15	•	•	•	2	4	2	•	•	•	•	•	8
16	•	•	•	•	2	4	2	•	•	•	•	8
17	•	•	•	•	•	•	1	•	•	•	•	1
18	•	•	•	•	1	•	1	•	•	•	•	2
19	•	•	•	•	•	•	•	•	•	•	•	0
20	•	•	•	•	•	•	•	•	•	•	2	2
T	3	6	12	34	27	10	6	0	0	0	2	100

Table XXIII

"B$_{31}$" (sn=31: hypertriploid)

W\L	13	14	15	16	17	18	19	20	21	22	23	T
11	•	•	1	•	•	•	•	•	•	•	•	1
12	•	•	•	2	2	•	•	•	•	•	•	4
13	1	•	•	2	12	7	2	•	•	•	•	24
14	•	•	2	3	7	11	3	1	•	•	•	27
15	•	•	•	1	3	11	4	1	•	•	•	20
16	•	•	•	•	•	6	3	7	1	•	•	17
17	•	•	•	•	•	•	•	2	•	1	•	3
18	•	•	•	•	•	1	•	•	1	•	•	2
19	•	•	1	•	•	•	•	•	•	•	•	1
20	•	•	•	•	•	•	•	•	•	•	1	1
T	1	0	4	8	24	36	12	11	2	1	1	100

Table XXIV

Plants in 7-cardinal chromosome number class

Plant name	sn	M_l	M_w	σ_l
N. Jonquilla	14	15.73±0.08	12.14±0.05	±1.207±0.06
Victoria	14	17.54±0.09	13.84±0.08	±1.282±0.06
Emperor	21	21.59±0.24	18.77±0.23	±3.589±0.17
Gloria Mundi	21	20.52±0.12	15.62±0.14	±1.836±0.09
Grandee	22	22.48±0.22	18.99±0.21	±3.216±0.16
King Alfred	28	23.08±0.07	16.32±0.05	±1.101±0.05
N. Bulbocodium	42	25.41±0.08	18.57±0.08	±1.253±0.06

Plant name	σ_w	CV_l	CV_w	Volume	Volume in ratio
N. Jonquilla	±0.749±0.03	7.67±0.36	6.17±0.30	386.35 π	0.69
Victoria	±1.172±0.05	7.31±0.35	8.49±0.40	559.93 π	1.
Emperor	±3.405±0.15	16.62±0.79	18.14±0.86	1267.72 π	2.26
Gloria Mundi	±2.063±0.10	6.76±0.30	10.05±0.48	834.41 π	1.49
Grandee	±3.163±0.15	14.31±0.68	16.66±0.77	1351.12 π	2.41
King Alfred	±0.835±0.04	4.77±0.23	5.12±0.24	1024.52 π	1.83
N. Bulbocodium	±1.123±0.05	4.93±0.24	6.05±0.30	1460.39 π	2.61

Plants in the 10-cardinal chromosome number class

Plant name	sn	M_l	M_w	σ_l
L_{20}	20	16.36±0.08	13.94±0.07	±1.127±0.05
B_{21}	21	14.76±0.07	12.16±0.04	±1.059±0.53
A_{22}	22	15.09±0.09	12.20±0.08	±1.314±0.06
Chinese Sacred Lily	30	17.46±0.11	13.36±0.12	±1.615±0.07
Yellow Prince	30	19.93±0.12	16.17±0.11	±1.745±0.08
B_{31}	31	17.92±0.10	14.47±0.10	±1.521±0.07

Plant name	σ_w	CV_l	CV_w	Volume	Volume in ratio
L_{20}	±1.004±0.05	6.89±0.33	7.20±0.34	529.84 π	1.
B_{21}	±0.647±0.31	7.17±0.34	5.32±0.26	363.73 π	0.69
A_{22}	±1.122±0.05	8.71±0.42	9.20±0.44	374.33 π	0.71
Chinese Sacred Lily	±1.868±0.09	9.25±0.44	13.98±0.67	519.37 π	0.98
Yellow Prince	±1.631±0.80	8.76±0.42	10.09±0.48	868.48 π	1.64
B_{31}	±1.532±0.07	8.48±0.40	10.59±0.50	625.34 π	1.84

The conclusions which may be drawn from these statistical results are as follows :

a) Cases where the cardinal number of chromosomes is 7.

1. The length of the pollen grains increases in correspondence with the increase in the number of haploid chromosome sets or genomes ; the mean length is shortest in the diploid, intermediate in the triploid, hypertriploid and tetraploid, being longer in the order named, and longest in the hexaploid.

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2. The mean width also shows a similar increment corresponding to that of the number of chromosome sets, except for the cases of a triploid, " Emperor " and a hypertriploid " Grandee ", where, contrary to our expectation, it is broader than that of any of the other investigated varieties of the 7-cardinal number class, it being 18.77 in " Emperor " and 18.99 in " Grandee ".

3. The cell volume of the pollen grains in the varieties " Emperor " and " Grandee " is much larger than expected. In this connection it is interesting to note that in these varieties the chromosome behavior in the course of meiotic division is far more irregular than in the other varieties with which the volumes have been compared. In the other cases excepting these two varieties, there is a recognizable relationship between the volume of pollen cells and the number of chromosome sets (*cf.* Figs. 224–226).

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b) Cases where the cardinal number of chromosomes is 10.

The conclusion just drawn in the case of plants of the 7-cardinal number class is applicable on the whole to this case of plants of the 10-cardinal number class. But some remarks may be made here. In the varieties "A_{22}" and "B_{21}" the mean length is shorter than that in the variety "L_{20}" notwithstanding the

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Figs. 224–226. Microphotographs of pollen grains in *N. Pseudonarcissus* and *N. Bulbocodium* in the same magnification ; 224. *N. Pseudonarcissus*, "Victoria " (diploid) ; 225. The same, "King Alfred " (tetraploid) ; 226. *N. Bulbocodium* (hexaploid).

fact that the chromosome number is greater in these varieties than in the latter. With regard to the variety "A_{22}", this may be interpreted as due to the difference between the genomes in these two varieties, as suggested by the morphological characteristics of the chromosomes, while, with regard to "B_{21}", we find no other plausible explanation than that it is due to inaccuracy in the method of measurement, since the morphological features of the chromosomes suggest that the constitution of the genome must be the same in the two varieties "B_{21}" and "L_{20}", except that the former variety carries an extra chromosome. A similar relation is also found between a triploid variety " Yellow Prince " and a hypertriploid form "B_{31}", where the mean length is shorter in the latter than in the former. It seems, however, worth while pointing out here that the latter variety is heterogenomous, while the former is autotriploid, as is seen from the chromosome behavior in the heterotype division in these varieties.

II. Epidermis cells in the scale leaves of the bulb

No selection being made, parts of the epidermis were drawn carefully by means of an ABBE's camera on paper under a magnification of about 300 times. The length and width of the cells thus drawn were measured. The results obtained are given in Tables XXV–XXXV, and the mean lengths and mean widths are given in Table XXXVI. In these tables the following abbreviations are used:

L : Relative length.

W : Relative width.

M_l, M_w : Mean relative length and width of the cell.

$M_{l \times w}$: Average of L × W.

Table XXV

N. Jonquilla (sn=14)

No.	L	W	L × W
1	52	9	468
2	35	9	315
3	58	9	522
4	40	6	240
5	40	9	360
6	25	7	175
7	58	9	522
8	45	9	405
9	59	9	531
10	28	9	252
Average	44.0	8.5	379.0

Table XXVI

"Princeps Maxim" (sn=14)

No.	L	W	L × W
1	31	9	279
2	28	10	280
3	39	9	351
4	46	10	460
5	32	8	256
6	43	9	387
7	40	8	320
8	33	9	297
9	30	10	300
10	30	10	300
Average	35.2	9.2	323.0

Table XXVII

"Emperor" (sn=21)

No.	L	W	L × W
1	53	12	636
2	34	11	374
3	54	10	540
4	48	9	432
5	56	10	560
6	40	10	400
7	55	11	605
8	68	10	680
9	50	12	600
10	40	12	480
11	40	12	480
12	43	14	602
13	40	12	480
14	43	10	430
15	74	10	740
Average	49.2	11.0	535.9

Table XXVIII

"Empress" (sn=22)

No.	L	W	L × W
1	49	10	490
2	75	11	825
3	59	10	590
4	55	10	550
5	43	10	430
6	58	10	580
7	52	9	468
8	48	10	480
9	57	11	627
10	42	10	420
Average	53.8	10.1	546.0

Table XXIX

"King Alfred" (sn=28)

No.	L	W	L × W
1	58	19	1102
2	85	19	1615
3	70	13	910
4	80	14	1120
5	64	14	896
6	72	12	864
7	100	15	1500
8	70	15	1050
9	63	16	1008
10	77	18	1386
11	70	18	1260
12	73	22	1606
13	70	13	910
14	101	14	1414
15	78	13	1014
Average	75.9	15.7	1177.0

Table XXX

N. Bulbocodium (sn=42)

No.	L	W	L × W
1	100	12	1200
2	50	12	600
3	56	13	728
4	59	15	885
5	70	11	770
6	62	13	806
7	71	10	710
8	60	13	780
9	74	11	814
10	46	10	460
Average	64.8	12.0	775.3

Table XXXI

"Franklin" (sn=20)

No.	L	W	L × W
1	60	12	720
2	56	11	616
3	70	11	770
4	65	11	715
5	92	11	1012
6	72	11	792
7	70	9	630
8	50	12	600
9	50	10	500
10	56	11	616
Average	64.1	10.9	697.1

Table XXXII

" Chinese Sacred Lily " (sn=30)

No.	L	W	L × W
1	89	15	1335
2	70	15	1050
3	76	15	1140
4	91	15	1365
5	100	18	1800
6	86	16	1376
7	50	15	750
8	57	18	1026
9	82	12	984
10	80	13	1040
Average	78.1	15.2	1186.6

Table XXXIII

" B_{31} " (sn=31)

No.	L	W	L × W
1	108	9	972
2	80	9	720
3	135	9	1215
4	63	10	630
5	90	10	900
6	104	8	832
7	112	8	892
8	127	9	1143
9	85	8	680
10	102	8	816
Average	100.6	8.8	880.4

Table XXXIV

N. intermedius (sn=24)

No.	L	W	L × W
1	60	16	960
2	60	18	1080
3	61	28	1708
4	30	30	900
5	65	14	910
6	65	16	1040
7	46	27	1702
8	59	23	1357
9	46	33	1518
10	75	15	1125
Average	60.7	22.0	1230.0

Table XXXV

N. biflorus (sn=24)

No.	L	W	L × W
1	43	7	301
2	50	7	350
3	56	6	336
4	40	7	280
5	58	7	406
6	61	9	549
7	38	7	266
8	84	8	672
9	52	5	260
10	70	6	420
Average	55.2	6.9	384.0

Table XXXVI

Plant name		s n	M_l	M_w	$M_{l \times w}$	$M_{l \times w}$ in ratio	Remarks on $M_{l \times w}$ in ratio
N. Jonquilla		14	44.0	8.5	379.0	1.17	
N. Pseudonarcissus	Princeps Maxim	14	35.2	9.2	323.0	1.0	Princeps Maxim ta..en as unit.
	Emperor	21	49.2	11.0	535.9	1.66	
	Empress	22	53.8	10.1	546.0	1.69	
	King Alfred	28	75.9	15.7	1177.0	3.64	
N. Bulbocodium		42	64.8	12.0	775.3	2.40	
N. tazetta	Franklin	20	64.1	10.9	697.1	1.0	Franklin taken as unit.
	Chinese Sacred Lily	30	78.1	15.2	1186.6	1.70	
	B₃₁	31	100.6	8.8	880.4	1.26	
N. biflorus		24	55.2	6.9	384.0	0.54	See text.
N. intermedius		17	60.7	22.0	1230.0	2.29	

From Table XXXVI the following conclusion may be drawn (*cf.* Figs. 227–231).

a) Cases where the cardinal number of chromosomes is 7.

1. In this series of plants, the correlation between the length of the cell and the number of chromosome sets is recognized, except in the case of *N. Bulbocodium* (hexaploid), in which the mean relative length of the cell lies between those of the tetraploid and triploid varieties.

2. The mean relative width is narrowest in the diploid varieties and broadest in the tetraploid variety, that of the hexaploid variety
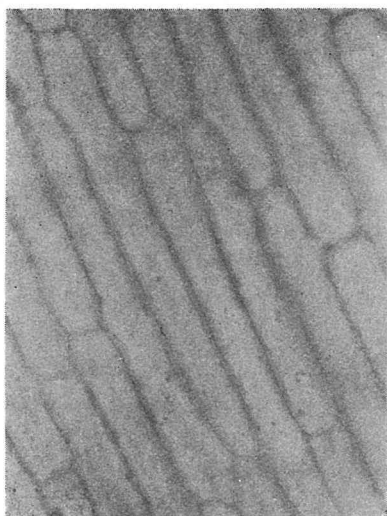
227

228
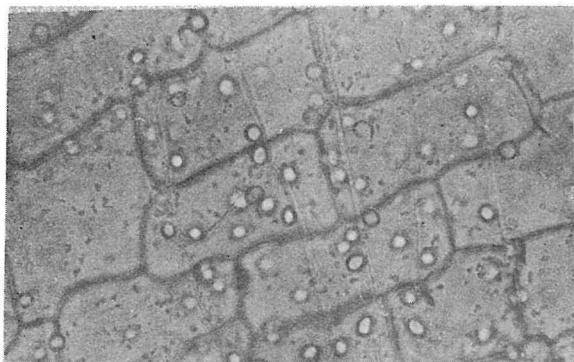
229

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231

Figs. 227–231. Microphotographs of epidermal cells of the scale leaves of bulbs in the same magnification; 227. *N. tazetta*, "Franklin" (diploid); 228. The same, "Chinese Sacred Lily" (triploid); 229. *N. Pseudonarcissus* "Princeps Maxim" (diploid); 230. The same, "Empress" (hypertriploid); 231. The same, "King Alfred" (tetraploid).

lying between those of the tetraploid and triploid as in the case of the mean relative length.

b) Cases where the cardinal number of chromosomes is 10.

In this series too, the mean relative length of the cell increases, as the chromosome number is greater. While the same is true of the width in the cases of diploid and triploid, it is exceedingly narrower in the hypertriploid variety (" 2n "$=31$) than expected. Accordingly the mean relative area occupied by the cell on paper is larger in the triploid variety than in the hypertriploid, and is smallest in the diploid.

c) Cases of species hybrids.

Narcissus biflorus. In this species the nucleus contains three genomes, of which two consist of 7 chromosomes each and the third of 10 chromosomes. We have already data of the size of cells in which the chromosome number is 2×7 and of cells in which it is 2×10. If the same nucleo-plasmic ratio as in these plants holds for the hybrid forms too, we may obtain from these data the relative size or area on paper of the cell in *N. biflorus* by calculating with the formula $1/2\,(2S_7 + S_{10})$, where S_7 and S_{10} represent the relative areas of diploid cells in which the haploid numbers of chromosomes are 7 and 10 respectively. The relative area thus obtained by calculation is 671.55, the figures 323.0 found for S_7 in the variety "Princeps Maxim", and 697.1 found for S_{10} in the variety "Franklin" being used. The actual number obtained by measuring in *N. biflorus* is, however, 384. This is about one half of the number 671.55 obtained by calculation on the assumption that the same nucleo-plasmic ratio as in those plants in which the cardinal numbers of chromosomes are 7 and 10 respectively holds for the hybrids between these two kinds of plants.

N. intermedius. The relative area of the cell in this hybrid obtained by using the formula $1/2\,(S_7 + S_{10})$ which is directly derived from its genomic constitution is 538.1, the number obtained by measurement for the relative size of the cell in *N. Jonquilla*, a known parent, and that obtained in the case of "Franklin" being used for S_7 and S_{10} respectively. This number is less than one half of the number 1230.0 actually obtained by measurement.

According to Tischler (1908, 1925) the degeneration in pollen grains in *Mirabilis* hybrid becomes apparent only after the course of

the reduction has normally proceeded, and he regards it as due to the abnormal nucleo-plasmic ratio which he found in young pollen grains. The nucleo-plasmic ratio may also be altered by external agencies, as was found by Goodspeed (1929) in the palisade cells of the leaves of a *Nicotiana* variant, the alteration in this case being induced by X-raying in the seedling stage. He says : " Cell number, form and arrangement is the same in treated and control but increase in cell volumes in the former (X-rayed plants)[1] accounts for the abnormal

232

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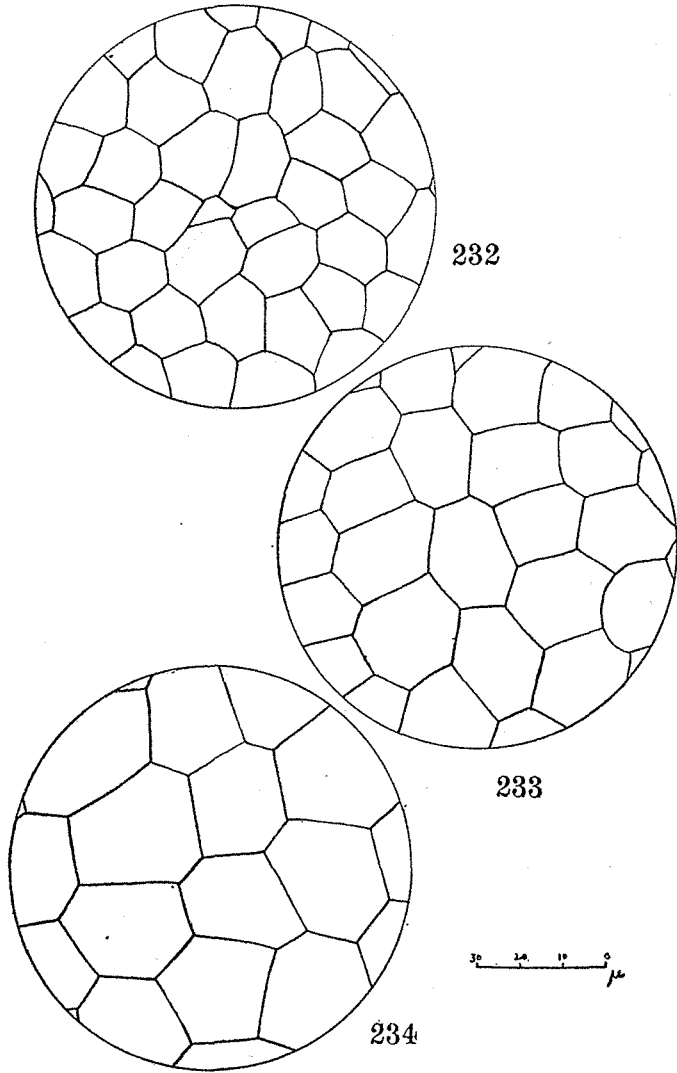
1. The words in brackets were inserted by me.
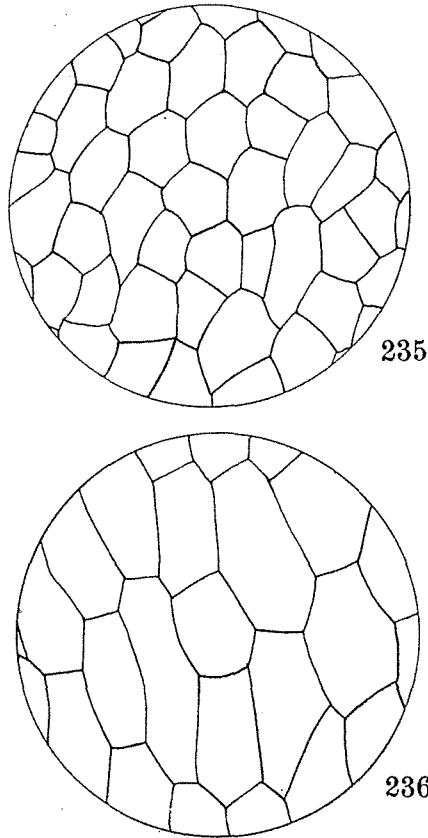
Figs. 232-236. Cells in petal epidermis. 232-234. *N. Pseudonarcissus*; 232. "Victoria" (diploid); 233. "Grandee" (hypertriploid); 234. "King Alfred" (tetraploid); 235-236. *N. tazetta*; 235. "Franklin" (diploid); 236. "Chinese Sacred Lily" (triploid).

leaf thickness. On the other hand, so far as could be determined, there was no distinction in nuclear volume. The nucleo-cytoplasmic ratio has apparently been altered, perhaps as a result of some induced inhibition of mitosis without decrease in the growth capacity of the protoplast." (p. 254).

From these facts it may be said that the change in the normal nucleo-plasmic ratio may be caused by an internal factor as well as an external. In the case of *N. biflorus* and *N. intermedius*, it seems that the abnormal nucleo-plasmic ratios are caused by an internal factor due to hybridity. The case of *N. intermedius* belongs to the ordinary category in which the volume of cytoplasm surpasses that in the case where the normal nucleo-plasmic ratio is found, but *N.*

biflorus is a case where it is greatly reduced below the normal volume. It is interesting to note, however, that this reduced volume is approximately the same as that of the cell carrying 2×7 chromosomes. If in this hybrid a parent plant whose cardinal number of chromosomes is 7 was the mother plant, this fact must be very significant.

Parts of the petal epidermis are reproduced in Figs. 232–236 under the same magnification to give a clear impression at a glance as to how the size of the cell and the chromosome number are correlated in *Narcissus*.

Discussion

I. Cardinal number of chromosomes in the genus *Narcissus*

In this genus several different numbers of chromosomes which may be regarded as representing diploid, triploid, tetraploid, hexaploid and some heteroploid numbers have been reported by STOMPS, DE MOL and some other authors (*cf.* pp. 167–169). So far as the results of my investigation are concerned, there are two different cardinal numbers of chromosomes in this genus, namely 7 and 10 (*cf.* p. 110). Species or varieties in which the chromosome number is a multiple of 7 are : *Narcissus Pseudonarcissus*, *N. incomparabilis*, *N. poeticus*, *N. Jonquilla*, *N. Bulbocodium*, *N. odorus*, *N. minor*, *N. reflexus* and *N. Barrii* (or *Leedsii*). In *N. Pseudonarcissus*, *N. poeticus* and *N. incomparabilis* some varieties are diploid (2n=14) and others triploid (21). The tetraploid number (28) is found in *N. Pseudonarcissus* and the hexaploid (42) in *N. Bulbocodium*.

In *N. tazetta*, on the other hand, all the chromosome numbers hitherto found in various varieties of this species are multiples of 10, or its heteroploid numbers, the somatic numbers of chromosomes being 20 (diploid) or 30 (triploid) in the former and 21, 22, 31 or 32 in the latter. Observation of the meiotic division in pollen mother cells has proved that the number 10 is the basis of these numbers. No chromosome number in which the basis is 7 has as yet been found in the varieties belonging to *N. tazetta* and none in which it is 10 has been found with certainty in the species or varieties other than those belonging to *N. tazetta*. In the case of hyperploid plants such as the variety " Grandee " (p. 126) in which the somatic number of the chromosomes is 22, the somatic number alone can suggest nothing about the cardinal

number, but investigation into the behavior of the chromosomes in meiosis can reveal what it is. In the variety named it shows that it is 7, and hence the plant is a hypertriploid. It has been reported by DE MOL (1922) and NAGAO (1929) that in two varieties not belonging to *N. tazetta*, the somatic numbers of the chromosomes are 20 and 30 respectively. Both these numbers are multiples of 10, but it may be expected that they will be found to be 7-chromosomic hypotriploid and hypertetraploid numbers respectively, although in these varieties the behavior of the chromosomes in meiosis has not yet been observed.

FERNANDES (1931 a, b) has reported other chromosome numbers, which I have not found in any of the species and varieties at my disposal. According to him, in *Narcissus tazetta* and *N. odorus* the somatic number is 10, and in *N. rupicola*, *N. scaberulus*, *N. calcicola* and *N. gaditanus* it is 12, and in some others it is 14. From the results of his observations he has concluded as follows :

" 1. Les espèces (au sens de LINNÉ) du genre *Narcissus*, peuvent être identifiées par le nombre et la forme de leurs chromosomes.

2. Les espèces portugaises de ce genre peuvent être distribuées en 3 groupes, respectivement caractérisés par le nombre des chromosomes : 5, 6 et 7.

3. Dans le genre *Narcissus*, on observe fréquemment des chromosomes du type Lk et kk, avec moins de fréquence les types li et lk et rarement les types LL, Ll et ll." (FERNANDES 1931 a, p. 7).

Thus FERNANDES adds two new cardinal numbers 5 and 6 to those given above. The number 5 as a cardinal number may put the conclusion that the number 10 is the cardinal number in *Narcissus tazetta* open to doubt. If, then, the latter conclusion is wrong and the former number is correct, those varieties of *N. tazetta* in which the somatic number of chromosomes is 20 must be regarded as tetraploids and those in which it is 30 must be looked upon hexaploid varieties (*cf.* FERNANDES 1931 b, p. 75). But it seems that this is not the case, because, if the varieties which we take for diploids and triploids are really tetraploids and hexaploids respectively, such chromosome behavior as we have described for these varieties in the foregoing chapter is not to be expected. We have, moreover, other facts which substantiate the view that the number 10 is at least a, even if not the, cardinal number in *N. tazetta*, namely : 1) while in the varieties " Franklin " and " L_{20} " six gemini of the 10 are large, and four small, in " B_{20} " and " A_{22} " five are larger and five small. If in these cases the cardinal number is 5, these sets of chromosomes must

consist of two similar sets each. This is assumable in the former case, but not in the latter. 2) In *N. intermedius*, a chromosome hybrid between 7 and 10, the two groups of chromosomes are shown to represent independent genomes, no affinity is shown between chromosomes of the 7 and those of the 10. They are found to be all univalent in the heterotype metaphase, and no two chromosomes are a mating pair. In *N. biflorus*, a *poeticus-tazetta* hybrid, the 10 *tazetta* chromosomes also remain as univalents having no mates at all in the heterotype division. These facts show that the 10 univalent chromosomes from the parent *tazetta* have no mating chromosomes not only in the group of chromosomes from the other parent, but also among chromosomes in their own group. To put it into other words, this group of 10 chromosomes in *tazetta* is a haploid set which composes a genome. The number 10 must, therefore, be a cardinal number of this species.

According to TISCHLER (1928), JARETZKY has observed that in *Polygonum aviculare* the haploid number of chromosomes is 10 " in einer selten Varietät ", while it is 20 " in weitaus den häufigsten Rassen " (pp. 323–324). It would not be improbable to assume, then, though speculative, that FERNANDES might unconsciously have carried out his observation with a special form (haploid in this case) just as happened to JARETZKY in his observation of *Polygonum aviculare*. A decided answer is, of course, to be given only by a future investigation into the behavior of the chromosomes in meiosis in that form, investigated by FERNANDES. But I wish to point out here that according to the result I obtained, the somatic number of chromosomes in *N. odorus* which FERNANDES investigated is 14 instead of 10.

The general conclusions which we can draw at present are, therefore, as follows :—

1. In the present state of knowledge we must admit that in the genus *Narcissus* there are three cardinal numbers 6, 7 and 10.

2. It must be left for future researches to decide whether the number 5 represents one of the cardinal numbers in *Narcissus* as considered by FERNANDES.

Advantage may be taken of this opportunity to give here the unpublished results obtained by Mr. STOW[1] in his observation of a white flowered variety of *Narcissus tazetta*, which he kindly conveyed me

in a letter. According to him, in this variety the somatic number of chromosomes is 34 or 35, the former probably being the right number.[1] In diakinesis in pollen mother cells there are found both bivalents and univalents in the cell. In the heterotype metaphase, 16–20 of these elements, mostly 20, are counted. In the stages from anaphase to telophase, 4–10 (mostly 6) univalent elements each of which clearly shows the longitudinal splitting, lag behind the other chromosomes (Figs. 238–242).
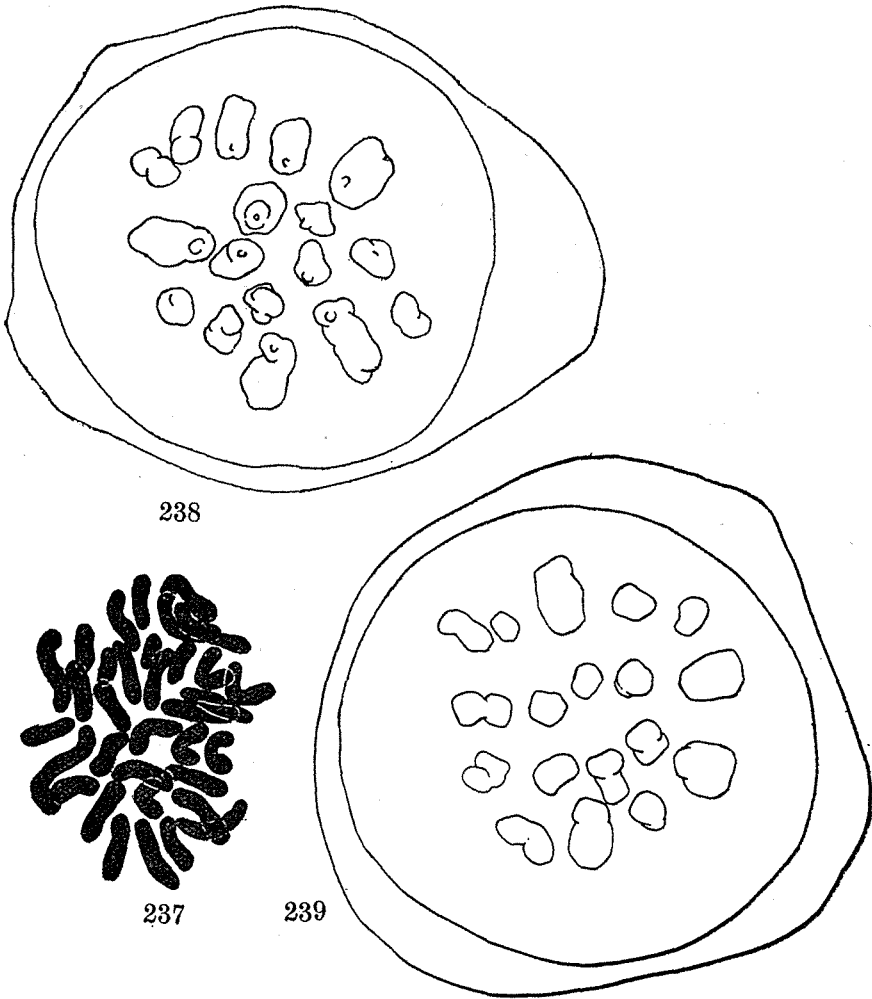
238

237   239

240

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242
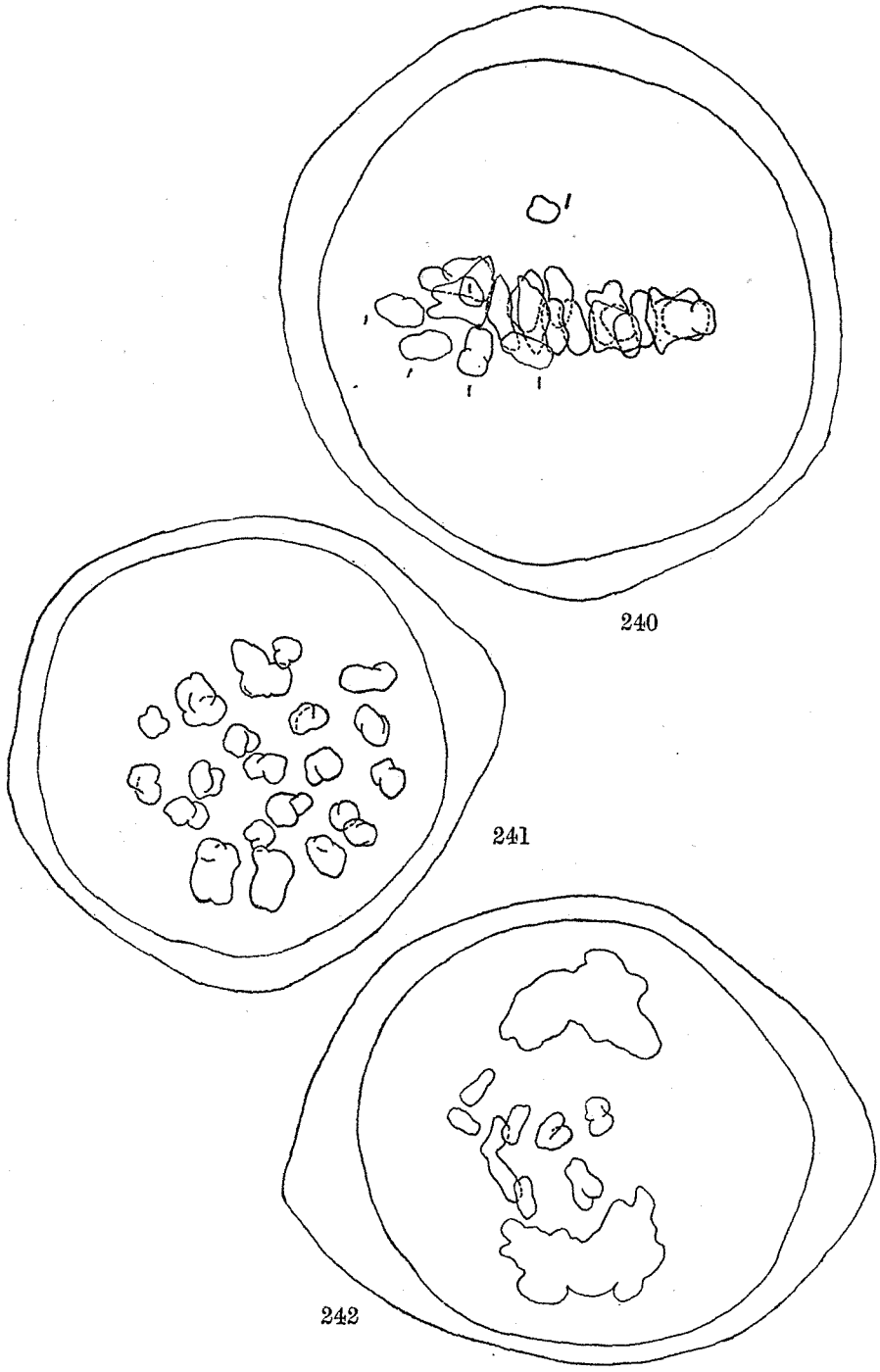
Figs. 237–242. Mr. STOW's drawings except 237. *N. tazetta*. 237. Somatic nuclear plate showing 34 chromosomes. 238–242. Meiotic phases ; 238. Heterotype metaphase showing 17 chromosomal elements ; 239. The same showing 18 chromosomal elements ; 240. The same in side view showing $14_{II}+6_I$ chromosomal elements ; 241. The same in polar view showing 21 chromosomal elements ; 242. Heterotype anaphase showing 5 lagging chromosomes which are split longitudinally in the equatorial region.

This information leads us to two different views in regard to the origin of this variety. As one of the alternatives, we may assume that this plant is a hybrid raised by the union of a tetraploid gamete from a plant in which the cardinal number of chromosomes is 7 and a haploid gamete from such a plant as that found by FERNANDES in which the cardinal number of chromosomes is 6. If the plant in question is really a hybrid of such an origin, we should have in the heterotype metaphase 20 chromosomal elements of which 14 are bivalent and 6 are univalent. The fact that the number of chromosomal elements which is most frequently found is 20 is in accord with this view.

As already mentioned above, however, in *Narcissus tazetta* neither euploids nor heteroploids in which the cardinal number is 7 are found. It is impossible to assume, therefore, that a variety carrying no 10-chromosome set, or no *tazetta* genome can present *tazetta* characteristics, and we are led to the second alternative in which we assume that the variety in question is a hybrid raised by the union of two diploid gametes, the cardinal number of chromosomes of which is 10 in the one and 7 in the other. If this is actually the case and autosyndesis takes place in this hybrid, it may be expected that the number of chromosomal elements in the heterotype metaphase will be 17 (10_{II} $+ 7_{II}$). In Fig. 238, an actual case where 17 chromosomal elements are counted is shown. The occurrence of more than 17 chromosomal elements may be interpreted by assuming that an accidental failure to pair may take place between homologous chromosomes, as is frequently found in the other forms of *Narcissus*. Although in this interpretation, we find no reasonable explanation as to the reason why in this plant the number of chromosomal elements that occurs most frequently is 20, nevertheless, this latter interpretation seems to be by far better than the first in which it must be assumed that *tazetta* characteristics can come forth in the absence of the *tazetta* genome.

The chromosome numbers hitherto investigated in the genus *Narcissus* will be enumerated in the following list. In this list the numbers which are reported for the first time in the present paper are marked with an asterisk, and the numbers which occur with other numbers of lesser occurrence, or those which are theoretically expected are marked with two asterisks.

	n	" 2n "[1]	
Narcissus tazetta			
		10	FERNANDES (1931 a, b)
" Franklin "	10	20	NAGAO (1930)
" L_{20} "	10	20	„*
" B_{20} "	10	20	„ (1929, 1930)
" B_{21} "	$10_{II}+1_{I}$	21	„* (1930)
" A_{22} " (Paper White ?)	11	22	„ (1929, 1930)
" Yellow Prince "	10_{III}	30	„ (1930)
" Chinese Sacred Lily "	7 — 14	30	„* (1930)
" Soleil d'Or "		30	„ (1930)
Wild growing form		30	„*
" B_{31} "	$10_{II}+1_{I}$	31	„* (1930)
" Luna "	$10_{II}+6_{II}$**	32	„* (1929, 1930)
a variety (albae type)	$10_{II}+7_{II}$**	34	STOW*
Narcissus Pseudonarcissus			
minor type		14	DE MOL (1922)
minor cyclamineus		14	„ (1922)
nanus		14	„ (1922)
minimus		14	„ (1922)
muticus		14	„ (1922)
capax plenus		14	„ (1922)
Teramonius plenus		14	„ (1922)
	7	14	„ (1928)
" Victoria "		14	NAGAO (1929)
" Albicans "		14	„ (1929)
" Princeps Maxim "		14	„ (1929)
Johnstoni Queen of Spain		20	DE MOL (1922)
Maximus		21	„ (1922)
" Golden Spur "		21	„ (1922)
„		30	NAGAO (1929)
" Emperor "	7_{III}	21	„*
" Bicolor Victoria "		22	DE MOL (1922)
" Buttonhole "		22	„ (1922)
" Empress "		22	NAGAO (1929)
" Grandee "	$7_{III}+1_{I}$	22	„* (1929, 1930)
" King Alfred "		28	DE MOL (1922)
„	7_{IV}	28	NAGAO* (1929)
" Van Waveren's Giant "		28	DE MOL (1922)

1. By " 2n " is here meant the somatic number of chromosomes, not the diploid number, and in the latter sense the notation is used without the quotation marks. In all the following instances the two different forms are used in these different senses.

	n	" 2n "	
" Olympia "	7IV	28	NAGAO* (1929)
var. *bicolor*		28	FERNANDES (1931 a, b)
Narcissus minor		14	FERNANDES (1931 a, b)
Narcissus incomparabilis			
		14	HEITZ (1926)
" Nelson Major "	7	14	NAGAO* (1929)
" Sir Watkin "		21	„ (1929)
" Gloria Mundi "	7III	21	„* (1929)
var. *aurantus*		21	„*
Narcissus Jonquilla	7	14	„* (1929)
var. *jonquilloides*		14	FERNANDES (1931 a, b)
Narcissus poeticus			
var. *poetarum*		14 or 16	STOMPS (1919)
„	7III	21	NAGAO (1929)
var. *ornatus*		14 or 16	STOMPS (1919)
" Glory of Lisse "		14 or 16	„ (1919)
var. *Glorie van Lisse*	7		DE MOL (1928)
" Albion "		14 or 16	STOMPS (1919)
	7	14	DE MOL (1928)
Narcissus Bulbocodium			
		42	HEITZ (1926)
		14	NAGAO (1929)
" Conspicuous "		21	„ (1929)
	21	42	„* (1929)
var. *genuinus*		14	FERNANDES (1931 a, b)
var. *nivalis*		14	„ (1931 a, b)
Narcissus Barrii (or *Leedsii*)			
a variety		14	NAGAO*
Narcissus biflorus (*N. poeticus-tazetta*)			
(*N. poeticus gigas* × *N. tazetta*)		24	STOMPS (1919)
a variety	7II+10I	24	NAGAO*
" Elvira ? "		24	„ *
Narcissus multiflorus " Ideal "		32	HEITZ (1926)
Narcissus odorus		10	FERNANDES (1931 a, b)
„		14	NAGAO*
Narcissus triandrus		14	FERNANDES (1931 a, b)
Narcissus reflexus		14	„ (1931 a, b)
Narcissus rupicola		12	„ (1931 a, b)
Narcissus calcicola		12	„ (1931 a, b)
Narcissus gaditanus var. *minutiflorus*		12	„ (1931 a, b)
Narcissus scaberulus		12	„ (1931 a, b)
N. Pseudonarcissus × *N. poeticus*		28	DE MOL (1926)

	n	" 2n "	
N. Pseudonarcissus × *N. poeticus*		14	DE. MOL (1927)
N. poeticus × *N. Pseudonarcissus*			
" Lucifer "		14	DE. MOL (1925)
" Lucifer " (bud variation)		ca. 28	„ (1925)
" Fuselier "		14	„ (1925)
" Fuselier " (bud variation)		ca. 28	„ (1925)

II. Genomes in the genus *Narcissus*

In polyploidy it is necessary to make a distinction between two cases, one where the plant is homogenomous, or carries homologous genomes and the other where it is heterogenomous, or carries bastard genomes. KIHARA and ONO (1926) have proposed the term " autopolyploidy " for the former case and " allopolyploidy " for the latter. They say : " unter Autopolyploidie versteht man die Verdoppelung desselben Chromosomensatzes ; unter Allopolyploidie die durch das Zusammenkommen verschiedener Chromosomensätze auf dem Wege der Bastardierung erfolgte Chromosomenvermehrung." (p. 480).

Whether a plant in question is homogenomous or heterogenomous can be determined from the karyological and genetical point of view by the following methods :

1.   The comparative morphological study of individual chromosomes.   It is generally accepted that in plants within a certain restricted circle of affinity the number of chromosomes as well as their size and form can serve as a criterion for the determination of the homology between the genomes in one plant and another.   The analysis of the phylogenetical relation between plants by this method of investigation has been attempted by HEILBORN (1924) in *Carex*, by KAGAWA (1929) in some cereals, by GOTOH and STOW (1929–'30) in *Trillium* and *Paris*, and by others in some other plants.

2.   The examination of the intensity of the affinity between chromosomes, or the behavior of the chromosomes in meiosis.   In hybrids the following three main types of chromosome behavior are known :—

a)   Formation of bivalent chromosomes by pairing taking place between chromosomes from different parents—allosyndesis.   This type is usually found in fertile hybrids raised between plants which have the same number of chromosomes, as, for example, in the cases of *Fragaria americana alba* × *F. vesca* var. *rosea* (ICHIJIMA 1930), *Secale cereale* × *S. montanum* (LONGLEY and SANDO 1930) and others.

b) Formation of bivalent chromosomes by pairing taking place
between chromosomes from the same parent—autosyndesis. In this
case we expect theoretically that both or one of the parents must
primarily be tetraploid at least, so that the reduced number of chromo-
somes in such a parent is diploid, and therefore that the number of
chromosomes contributed by gametes from this parent must be an
even number. If, therefore, autosyndesis takes place between every
two chromosomes from each of the parents, the number of chromo-
some pairs must be one half of the sum of the parental chromosomes,
an example of which we find in the case of the tetraploid hybrid of
Solanum nigrum × *S. luteum* (JÖRGENSEN 1928), for instance.

c) Non-formation of bivalent chromosomes, or complete lack of
affinity between chromosomes—asyndesis. In this type there are as
many unpaired, or univalent chromosomes as there are somatic chromo-
somes, or the sum of the reduced numbers of both parent chromo-
somes. Examples have been listed on p. 138. The chromosome be-
havior in *Narcissus intermedius* belongs to this type.

These types are also found combined with one another or with
the normal type of syndesis in some way or other. d) The formation
of polyvalent chromosomes such as is found in the case of triploid
and tetraploid forms of *Datura*, *Narcissus* and others[1] is autosyndesis
combined with the normal type of syndesis, and e) the case known
as the *Drosera* scheme where both bivalents and univalents co-exist
is a combination of allosyndesis and asyndesis as in *Nicotiana* hybrid
investigated by BRIEGER (1928), or a combination of autosyndesis and
asyndesis. The latter case is, to use RENNER's term, " ungesättigte
Autosyndese ", which he describes as : " die Glieder des grösseren Satzes
gepaart, die des kleineren univalent " (RENNER 1929, p. 108). A
beautiful example for this case is found in the hybrid between *Crepis
setosa* (n＝4) and *Crepis biennis* (n＝20). According to COLLINS and
MANN (1923) this hybrid shows 24 chromosomes in the somatic division,
and 10 bivalent and 4 univalent chromosomes in meiosis. This fact
shows, as is pointed out by the authors, that autosyndesis has taken
place between chromosomes from *biennis*. DARLINGTON's case of a

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1. For autotriploid cases, we may mention : *Canna* (BELLING 1921, 1925 b), *Hyacinthus*
(BELLING 1925 c), tomato (M. M. LESLEY 1926), *Oenothera* HÅKANSSON 1926–'27), *Prunus*
(OKABE 1927, DARLINGTON· 1928), *Rumex* (ONO 1928), *Zea* (RANDOLPH and McCLINTOCK
1926), *Lilium tigrinum* (TAKENAKA and NAGAMATSU 1930), and others, and for autotetraploid :
Datura (BELLING and BLAKESLEE 1924), tomato (LESLEY, M. M. and LESLEY, J. M. 1930),
and others.

cross between the hexaploid *Prunus domestica* (n = 24) and the diploid *P. cerasifera* (n = 8) may be taken as an example of another combined type. He has found 16 bivalent chromosomes in this hybrid (DARLINGTON 1927[1]), and it seems highly probable that in this case both autosyndesis and allosyndesis must have taken place in combination. To use RENNER's term, this is a case of " gesättigte Allo-Autosyndese ", and this combined type is also known in *Digitalis lutea × D. micrantha* (HAASE-BESSELL 1921), *Papaver nudicaule × P. radicatum* and *P. nudicaule × P. striatocarpum* (LJUNGDAHL 1924) and some others.

The difference in the behavior of chromosomes is generally regarded as due to the intensity of the affinity between chromosomes. If the intensity is normal between parental chromosomes, they will behave as in case *a*, *b* or *d*, but if it is below that, the behavior will commonly be such as in *c*. In the former the pairing, or complexforming chromosomes are homologous, and in the latter no chromosomes are homologous with others. In case *e*, none of the unpaired, univalent chromosomes is homologous with any of those chromosomes that form bivalents.

In *Narcissus*, the results of my investigation are not complete enough to enable me fully to discuss this problem of the genomes, but some considerations on the problem may be entered into so far as these results are concerned. As already mentioned, we have in *Narcissus* three different cardinal numbers 6, 7 and 10. It is of course a matter of difficulty to make clear how these numbers arose, but it is certain from the results of my observation that they are quite independent from one another, no affinity being shown between them. In *N. intermedius* which is taken by some authors for a hybrid between *N. tazetta* and *N. Jonquilla*, the pollen mother cells show 17 univalent chromosomes of extraordinarily irregular behavior in the meiosis. This number of univalents is the same as the number of chromosomes in the somatic cells, and it seems not unreasonable to assume that 10 chromosomes of the 17 are those contributed from *N. tazetta* and 7 those from *N. Jonquilla*. The fact that there is no pairing at all between these two chromosome groups, 10 and 7, makes it reasonable to regard them as representing different genomes. If we call the genome consisting of the 10 chromosomes A, and that of the 7 chromosomes B, *Narcissus intermedius* will be represented by the formula A + B. In the same way *N. biflorus*, the *poeticus-tazetta* hybrid, may be represented by the formula A + BB, since it is beyond doubt that

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1. Cited from DARLINGTON 1928.

in this plant 7 bivalents and 10 univalents are formed in meiosis out of 24 chromosomes.

In the diploid form of *N. tazetta* in which the cardinal number is 10, there are two types of chromosome groups. In the one it consists of 6 large and 4 small chromosomes, and in the other, of 5 large and 5 small. The first type of chromosome group or genome is that which has just been called A and the second type is now called A'. In the diploid varieties " Franklin " and " L_{20} " the genome is AA and in " B_{20} " it is A'A'. In " B_{21} " the chromosome constitution in the heterotype metaphasic plate is $10_{II} + 1_I$, and hence the genome formula may be written $AA + 1$. In the variety " A_{22} " the formula is A'A', since the chromosome constitution is essentially the same as that of " B_{20}", though in this variety the total number of chromosomes has numerically been increased by the cross segmentation of a large chromosome to 11 in the haploid set, and consequently the number of the large chromosomes has been reduced from 5 to 4.

In the triploid variety " Yellow Prince ", the chromosome constitution is of the A form, and this variety is an autotriploid, and therefore the formula will be AAA. Another triploid form, " Chinese Sacred Lily ", is also an autotriploid, but it has not been determined whether its chromosome constitution belongs to A or A' (see p. 89), and consequently it is left undetermined whether the formula is AAA or A'A'A'.

The chromosome behavior in the variety of *N. tazetta*, " Luna ", suggests that in this variety the genome formula must be AA (or A'A' ?) + CC, where the latter genome, C, represents the set of 6 chromosomes which FERNANDES (1931 a, b) has found to be one of the cardinal numbers in *Narcissus*.

Though it is as yet premature to draw a conclusion as to the genetical relationship between the genomes A and A', the behavior of the chromosomes in " B_{31} " seems to show that there exists only a weak affinity, if any, between these genomes, because in this variety the heterotype metaphasic plate consists of 10 bivalents of type A, and 11 univalents of type A'. The genome formula will, therefore, be $AA + A'$ in this variety.

In the species or varieties in which the cardinal number of chromosomes is 7, the genomes may all be called B, because all the polyploid forms have so far been found to be autopolyploid. Thus the triploid and tetraploid forms can be represented by the formulae BBB and BBBB respectively.

The genome formulae of the species and varieties in *Narcissus* which I investigated are shown in the following list:

Plant name	Genomes
Narcissus tazetta	
" Franklin "	AA
" L$_{20}$ "	AA
" Yellow Prince "	AAA
" B$_{20}$ "	A'A'
" A$_{22}$ "	A'A'
" B$_{21}$ "	AA+1
" Chinese Sacred Lily "	AAA (or A'A'A' ?)
" B$_{31}$ "	AA+A'
" Luna "	AA (or A'A' ?)+CC
Narcissus Pseudonarcissus	
diploid	BB
triploid	BBB
hypertriploid	BBB+1
tetraploid	BBBB
Narcissus incomparabilis	
diploid	BB
triploid	BBB
Narcissus Jonquilla	BB
Narcissus Bulbocodium	(BBBBBB ?)
Narcissus intermedius	A+B
Narcissus biflorus	A+BB
Narcissus Barrii	BB
Narcissus odorus	BB

III.   Origin of polyploidy

The number of chromosomes in allied species in the plant and animal kingdom may be classified into two categories, polyploid and non-polyploid or heteroploid.[1]   Useful lists of chromosome numbers in plants have been given by ISHIKAWA (1916), TISCHLER (1921–'22, 1927) and GAISER (1926, 1930), and of those in animals by HARVEY (1920), BRESSLAU-HARNISH (1927) and others.   In the study of chromosome numbers belonging to the first category the pioneer was TAHARA (1921) who found in *Chrysanthemum* plants a series of haploid numbers of chromosomes: 9, 18, 27, 36 and 45, or numbers which are multiples of 9, the cardinal number.   Other beautiful examples have been found in the genus *Rosa* where the series consists of the numbers: 14 (2n), 21, 28, 35, 42 and 56 (octoploid) (TÄCKHOLM 1922, BLACKBURN and

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1. A high degree of polyploidy appears to be more commonly found in plants than in animals as pointed out by GATES (1924) and MULLER (1925).

HARRISON 1924, HURST 1925, ERLANSON 1929), and in *Senecio* (AFZELIUS 1924) where it consists of 5, 10, 20, 25, 30 and 90. Recently KIHARA and ONO (1926) have added another beautiful example found in *Rumex*, the series of numbers consisting of 10 (n), 20, 30, 40, 50, 60 and 100. In the genus *Narcissus* too, this polyploid relation is found to exist, as already mentioned above.

While various problems in polyploidy have hitherto been discussed by many authors, the fundamental one is, by what cause and through what process it is brought about. SAKAMURA (1920) has pointed out the following probable modes by which the doubling of chromosome numbers may be realized. To quote it in his original words:

" I. Vor der Befruchtung.

a) Durch die früher erwähnten Teilungsabnormitäten in den Urmutterzellen oder in den Gonotokonten entstehen die diploiden Gameten.

b) Durch die ungewöhnlichen Zustände in der Interkinese spalten sich die Chromosomen wiederholt längsweise, und dies gibt so Anlass zur Entstehung von diploiden Gameten.

II. Dispermatische Befruchtung.

III. Nach der Befruchtung. Durch die früher erwähnten Teilungs- abnormitäten in befruchteten Eiern entstehen die tetraploiden Proembryo- nen."

BRIEGER (1928) has given the processes, putting them in the follow- ing words:

" Fall I. Vermehrung durch ungleichmässige Verteilung der Chromosomen.

Fall II. Vermehrung der Chromosomenzahl durch Verschmelzung der beiden Spindeln der zweiten Reifeteilung.

Fall III. Vermehrung der Chromosomenzahl durch eine vorzeitige zweite Reifeteilung, die eine Aequationsteilung ist.

Fall IV. Ausbleiben der Reduktion.

Fall V. Verschmelzung zweier Metaphasen der ersten Reife- teilung."

Recently DARLINGTON (1930) has described the processes in the following terms:

" I. The nullification of the first or second division.

II. The double division of the chromosomes.

III. Syndiploidy or the formation of binuclear germ-mother cells.

IV. The complete suppression of the first division."

While SAKAMURA considers all possible cases, BRIEGER and

DARLINGTON deal only with those cases "before fertilization" which have been brought to light by the recent, rapidly increasing progress in this branch of cytology. Since this problem is directly connected with the interpretation of the origin of some hybrid forms of *Narcissus* such as, for instance, *N. biflorus*, and *N. tazetta* "Luna", the problem will be discussed in the following paragraphs in the light of the results of recent investigations on a larger scale than it was by BRIEGER and DARLINGTON.

I. An essential phenomenon for the arisal of polyploid individuals is that it is preceded by the arisal of gametes which carry a corresponding number of the haploid sets of chromosomes. It has been shown by many investigators that in haploids and triploids as well as in many hybrids an irregular distribution of chromosomes commonly takes place in the reduction division. This kind of irregularity is also of common occurrence in *Narcissus*, especially in its triploid and heteroploid forms. This irregularity appears to give rise to the formation of gametes which carry aberrant numbers of chromosomes, and it appears that it plays a great rôle in the arisal of individuals with different numbers of choromosomes. But we have facts that go to prove that most of the tetrad cells produced through such an irregular meiotic process can not function owing to illegitimate combinations of chromosomes. In the haploid mutant of *Datura*, BELLING (1926) has found that in meiosis the distribution of the 12 chromosomes to the poles takes place by chance, resulting in pairs of chromosome groups: $11 : 1$, $10 : 2...6 : 6$, and according to BLAKESLEE and CARTLEDGE (1926, 1927) 80 % of the pollen grains are empty in this haploid. In a haploid mutant of *Oenothera franciscana* DAVIS and KULKARNI (1930) have found that such pollen grains amount to 60–90 %, and according to GATES and GOODWIN (1930), in another *Oenothera* haploid produced from *Oe. rubricalyx* by pollination with *Oe. eriensis*, a large amount of the pollen grains are shrivelled and no attempt at germination is successful with seeds, which are sometimes produced though very few in number, by open pollination in this hybrid. Examples are also found in triploid and heteroploid varieties of *Narcissus*. In these plants, 45–70 % of the pollen grains are empty, and in the extreme case which is exemplified by *N. intermedius* almost all of them are empty.

Even in these cases, however, progeny may rarely be produced. In the haploid *Datura*, it may be obtained by self-pollination, but it is diploid in all cases (BELLING 1926). This shows that only gametes which carry the complete haploid set of chromosomes are viable, while

others are not. In his study of *Raphanus-Brassica* hybrid, KARPECHEN-
KO (1927) emphasizes the fact that "only the gametes possessing the
entire haploid sets of both parents or even twice their number appear
among our hybrids to be able to produce offspring." (p. 355). He
has also mentioned that in the progeny of the F_1 of this hybrid no
hypotri- nor hypotetraploid individuals are found, while individuals
which are tetraploid, hypertriploid, hypertetraploid or hypohexaploid
are produced. According to him, the F_1-pollen tetrad cells which have
fewer than 18 chromosomes are all non-functioning, and even if some
of these cells are vital, they "are not able to compete in fertilization
with the diploid and tetraploid sexual cells" (KARPECHENKO 1928, p.
13). In triploids too, it has been shown by ONO (1928), LESLEY
(1926) and others that gametes with the complete set or sets of
chromosomes are produced, although they are of very rare occurrence.
These examples show that functioning gametes or those with the
complete haploid set or sets of chomosomes may be produced even in
the cases where random assortment or unequal distribution of chromo-
somes is of customary occurrence, but there is only a small chance
of this.

II. Retardation or suppression of the reduction division may be
mentioned as a noteworthy phenomenon which is one of the causes
of the formation of diploid gametes. This phenomenon has been ob-
served in several plants and in *Narcissus*, too. ROSENBERG (1917, 1926–
'27) has pointed out the following two types of the peculiarity which
he found in the parthenogenetic *Euhieracium* species.

a. At the heterotype metaphase or anapase the process of divi-
sion does not proceed further, but is arrested by the premature
homotype division, whereby the restitution nucleus—as it is called by
him—is formed.

b. In the second type, the prophase nucleus in the heterotype
division contracts markedly together with the cytoplasm surrounding
it, this being followed by a stage in which the nucleus shows the
characteristic feature in the interkinesis that every chromosome is split
longitudinally.

In both types the final results is the same, this being the forma-
tion of the pollen dyad. ROSENBERG regards this peculiarity as an
important process in the doubling of the chromosome number in organ-
isms. He says: "Die diploiden Pollenzellen wurden genau nach
demselben Schema wie in dem eben genannten *Hieracium*-Beispiel
gebildet. Die gestörte heterotypische Teilung hat die Bildung von

Restitutionskernen ausgelöst. Es werden Dyadenzellen gebildet mit der diploiden Chromosomenzahl. Findet derselbe Vorgang bei der Embryosackbildung statt, so ist dadurch eine befriedigende Erklärung der Bildung von tetraploiden F_2-Pflanzen gegeben. Die Triploiden sind natürlich durch Vereinigung von haploiden und diploiden Gameten entstanden." (ROSENBERG 1928, p. 338). And he mentions the result of CARANO's investigation in *Erigeron* as an example for the case of the formation of restitution nuclei in embryosac mother cells, and thus of diploid egg cells. According to KUWADA (1928) the formation of restitution nuclei also takes place in embryosac mother cells in *Balanophora japonica*, known as a plant of somatic apogamy.

III. BELLING has added another type of diploid pollen formation observed in *Datura*, which, according to him, occurs frequently in the haploid, " much more frequently than in the diploid or even in the triploid." " Two groups of 12 unsplit chromosomes each are formed at the anaphase. There is no further division, and only two pollen grains result. In non-reduction in haploids (as in diploids, triploids, and tetraploids) the chromosomes at the first metaphase become 4-lobed and show the split while still in the equatorial plate." The first maturation division is entirely omitted in this haploid—the " non-reduction "—and therefore, the formation of dyads occurs instead of tetrads. A similar behavior has also been observed in *Raphanus-Brassica* hybrid by KARPECHENKO (1927, 1928). In this hybrid plant, in the first division the 18 (9 *Raphanus* + 9 *Brassica*) univalent chromosomes do not move towards the pole in the usual manner, but each is divided longitudinally, so that the number of chromosomes counted at the anaphase is 36 in all. The result is the formation of a dyad, which develops directly into pollen grains without undergoing a further division.

IV. In hybrid plants it is often observed that the division of unpaired, univalent chromosomes, all or some, is equational in either one of the two divisions, heterotype or homotype, and in the other division, i. e. homotype or heterotype, the distribution is merely random. In the *Narcissus*, the equational or longitudinal division takes place in the heterotype division, and the random distribution in the homotype division. While these are of common occurrence, it is known in some few cases that the division is equational in both heterotype and homotype divisions (*Viola hyperchromatica*, CLAUSEN 1926-'27 ; *Rhoeo discolor*, SAX 1931). BRIEGER and DARLINGTON regard this type of division as one of the probable processes of polyploid formation. This type of chromosome doubling has not actually been observed in *Narcissus*

in any of its processes. But in a heteroploid variety of *N. Pseudonar-cissus*, the " Empress ", a pair of sister cells in the homotype metaphase was observed in each of which the number of chromosomes was nearly the same as that of the somatic chromosomes. This seems to show that in this case the double equational division had probably taken place as in those cases which BRIEGER and DARLINGTON call " Fall IV " and " case II " respectively.

V. The fusion of the homotype spindles is also an important phenomenon in regard to the doubling of the chromosome numbers in gametes. This case has been observed by several authors in several plants, such as LJUNGDAHL (1922) in *Papaver*, GOODSPEED (1923) and BRIEGER (1928) in *Nicotiana*, AFZELIUS (1924) in *Senecio*, MATSUDA (1927) in *Petunia*, KARPECHENKO (1927) in *Raphanus* × *Brassica*, FUKUDA (1927) in the potato, HÅKANSSON (1929a) in *Salix*, MÜNTZING (1930) in *Galeopsis*. This mode of chromosome doubling is not found in *Narcissus*, since in this plant the cell wall formation takes place successively after each division in meiosis.

VI. In the variety " Grandee " of *Narcissus Pseudonarcissus* there are sometimes found pollen mother cells containing two nuclei instead of one, a fact which may be regarded as another process of chromosome doubling in gametes. This fact has been observed by GATES and REES (1921) in *Lactuca*, by KARPECHENKO (1927) in *Raphanus* × *Brassica*, by INARIYAMA (1929) in *Iris*, by RANDOLPH and McCLINTOCK (1926) in *Rea* and by ICHIJIMA (1930) in *Fragaria*. As pointed out by KARPECHENKO (1927), a premeiotic nuclear division must have taken place without being accompanied by cell division, resulting in the formation of binucleate pollen mother cells. If these nuclei fuse together during the process of meiotic division, giant diploid pollen grains will be produced.

VII. Several plants are known to have cells carrying the di-diploid number of chromosomes in somatic tissues. Examples are found in *Spinacia* and *Cannabis* (DE LITARDIÈRE 1923, 1925), *Acacia* (GHIMPU 1929), the tomato (M. M. LESLEY 1925, LINDSTORM and KOOS 1931), *Viola* (CLAUSEN 1930) and some others. Experimentally JÖRGENSEN (1928), and LINDSTORM and KOOS (1931) have obtained diploid and tetraploid plants from the haploid and diploid ones respectively by the method of decapitation of young sprouts. JÖRGENSEN says : " the majority of polyploid forms, ..., in my opinion owe their origin to the doubling process (" endo-duplication ") in the somatic tissue. Considering the widespread occurrence of binucleate cells in the soma

and the continuous somatic development of most plants, it is only natural that endo-duplication must be an important factor in the formation of polyploid plants." (p. 201)[1]. LINDSTORM and KOOS have also found many binucleate cells in the callus formed in the decapitated haploid tomato.

VIII.   Dispermy or triple fusion of the egg nucleus with two male nuclei has been observed by NĚMEC (1912)[2] in *Gagea lutea*, and a similar phenomenon by ISHIKAWA (1918) in *Oenothera nutans* × *Oe. pycnocarpa*.   It seems not improbable that there may be triploid individuals in *Narcissus* through this process of triple fusion as a consequence of ab rrant behavior of the second male nucleus, which GUIGNARD (1900)[3] observed in this plant normally to fuse with the polar nuclei, though no evidence supporting this view has yet been observed in *Narcissus*.

We may, then, summarize probable and possible cases where the abnormalities may result in the multiplication of the chromosome number in germ cells as follows :

Case I.   Abnormalities in the meiotic division.
> *a.*   Unequal distribution of chromosomes in the heterotype division (Paragraph I).
> *b.*   Formation of restitution nucleus (Paragraph II).
> *c.*   Equational division instead of reduction division (Paragraph III, IV).
> *d.*   Fusion of the two homotype spindles in the second division (Paragraph V).

Case II.   Formation of binucleate cells in the premeiotic stage (Paragraph VI).

Case III.   Formation of di-diploid or syndiploid nuclei in somatic cells (Paragraph VII).

Case IV.   Dispermy or triple fusion of the egg nucleus with two male nuclei (Paragraph VIII).

In the case of *Narcissus*, Case I, *a* and *b,* and Case II take place, Case I *a* being of most frequent occurrence.

In the next place, we shall consider external and internal factors that could induce the mitotic or meiotic irregularities which give rise

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1.   By " endo-duplication " JÖRGENSEN means the union of two spindles in a binucleate cell into a giant spindle.   The chromosome doubling in the egg by fertilization has been called by him " exo-duplication ".

2.   Cited from ISHIKAWA 1918.

3.   Cited from SCHÜRHOFF 1926.

to the multiplication of chromosome numbers in germ cells. Many anaesthetics, unusually high or low temperature, and other physical agencies such as irradiation with ultra-violet rays, X-rays and radium, and other stimuli may be enumerated as external factors. A certain definite dose or strength of these agencies may, if applied to pollen mother cells, give rise to the formation of pollen monads, pollen dyads, pollen triads, and pollen tetrads of cells of unequal size. A high percentage of them are usually abortive, but some are viable. In the latter, the chromosome number may occasionally be some multiple of the basic number such as 3n and 4n. In the somatic cells too, this multiplication or doubling of the chromosome number may take place as in the case of pollen mother cells. To mention examples : NĚMEC (1904) and SAKAMURA (1920) produced this in root-tips of *Vicia* and *Pisum* by chloralization ; MICHAELIS (1926, 1928) in *Epilobium* and *Oenothera*, BORGENSTAM (1922) in *Syringa*, SHIMOTOMAI (1927) in *Liriope* and *Scilla*, BLEIER (1930) in *Triticum*, by subjecting pollen mother cells to cold ; KOSHUCHOW (1925) in *Cucumis* and *Zea*, SAKAMURA and STOW (1926) in *Gagea*, STOW (1927) in the potato, TAKAGI (1928) in *Lychnis*, BLEIER (1930) in *Triticum*, HEILBORN (1930) in the apple, by subjecting somatic or pollen mother cells to an unusually high temperature ; GOODSPEED (1929) in *Nicotiana* by exposing the plant to X-rays and radium rays ; WINKLER (1916) and SANSOME (1930) in *Solanum*, UFER (1927, 1929) in *Cleome*, KOSTOFF (1930 c) in *Nicotiana*, by grafting ; JÖRGENSEN (1928), LINDSTORM and KOOS (1931) in *Solanum* by decapitation of young sprouts ; KOSTOFF and KENDALL (1931a) in *Nicotiana* by physical stimuli such as needle puncture of floral buds.

In the natural condition, not only the influence of temperature (*cf.* BELLING and BLAKESLEE 1922, BLAKESLEE and CARTLEDGE 1925, SAX 1931, LEVAN 1931, HAGERUP 1932), but also an attack by animal parasites (KOSTOFF and KENDALL 1929) may cause the production of offspring of abnormal chromosome types. According to BELLING and BLAKESLEE (1922), in *Datura* " non-reduction may be greatly increased by transient cold ". This conclusion has been shown by KOSTOFF and KENDALL (1931b) also to hold for the case of the tetraploid *Petunia*.

These examples are all cases where external factors play a prominent rôle, but the internal factor which may be induced by hybridization is more important in this respect of chromosome doubling in nature.

The hybridization hypothesis, first proposed by WINGE (1917), is

receiving increasing experimental verification. Prominent examples have been shown by BREMER (1923) in F_1 of *Saccharum officinarum* ($n=40$) $\times$ *S. spontaneum* ($n=56$), in which the chromosome number in somatic cells is $2 \times 40 + 56 = 136$, by BLACKBURN and HARRISON (1924) in a tetraploid plant ($n=21$) from *Rosa pinpinellifolia* ($n=14$) $\times$ *R. tomentosa* ($n=7$), by CLAUSEN and GOODSPEED (1925) in a hybrid ($n=36$) from *Nicotiana glutinosa* ($n=12$) $\times$ *N. tabacum* ($n=24$), by ICHIJIMA (1926) in that ($n=14$) from *Fragaria bracteata* ($n=7$) $\times$ *F. Helleri* ($n=7$), by CLAUSEN (1926) in *Viola hyperchromatica* ($n=2 \times 17 + 13$) obtained by crossing *Viola tricolor* ($n=13$) with *V. arvensis* ($n=17$), by TAHARA and SHIMOTOMAI (1927) in F_1 of *Chrysanthemum marginatum* ($n=45$) $\times$ *Ch. lavandulaefolium* ($n=9$) which carries as many chromosomes as $72 \ (=\overline{36 + 9 \times 2} + 9 \times 2)$ in root-tip cells, by BRIEGER (1928) in a *Nicotiana* hybrid ($2n = 24 + \overline{24 + 12}$) obtained by back crossing one of the F_1 plants of *N. tabacum* $\times$ *N. Rusbyi* with *N. tabacum*, and by FRANDSEN and WINGE (1932) in *Brassica napocampestris* ($n=28$), a species hybrid between *Brassica napus* ($n=18$) and *B. campestris* ($n=10$).

Amphidiploid hybrids have also been obtained by the union of diploid gametes: the tetraploid *Aegilotricum* was produced by TSCHERMAK and BLEIER (1926) by crossing *Aegilops ovata* with *Triticum durum* and *T. dicoccoides*; a constant tetraploid hybrid, *Raphanobrassica*, by KARPECHENKO (1927–'28) from *Raphanus sativus* $\times$ *Brassica oleracea*, and by TERASAWA (1932) from the F_4 hybrid of *Brassica chinensis* $\times$ *B. sativus*. MÜNTZING (1930b) has obtained a tetraploid plant by back crossing a triploid F_1 plant of *Galeopsis pubescens* $\times$ *G. speciosa* with *G. pubescens*. KIHARA and KATAYAMA have also reported a constant octoploid *Aegilotricum* raised from the F_2 individual of *Triticum dicoccoides* $\times$ *Aegilops ovata* (KIHARA 1931).

In the genus *Narcissus* the various numbers of chromosomes must have been derived from the cardinal numbers as the result of intra- or interspecific crossing, or the result of cross segmentation or non-disjunction of certain chromosomes. It may be emphasized here that in the hybrid forms of *Narcissus*, the chromosomal constitution found in pollen mother cells show that they are haplo-diploid or diplo-diploid with only one exception —*Narcissus intermedius*— so far as my investigations are concerned. To put it in other words, in these hybrids the number or numbers of the chromosomes from one or both of the parental plants have been doubled, namely :

Narcissus tazetta " B_{31} "............" $2n$ " $= 31 (= 2 \times 10 + 11)$

Narcissus tazetta "Luna"............" 2n "$= 32 (= 2 \times 10 + 2 \times 6)$

Narcissus biflorus ...." 2n "$= 24 (= 2 \times 7 + 10)$

It is natural to consider that these plants are raised by an inter-specific fertilization which happens to take place between a haploid gamete and an abnormally produced diploid gamete, or between such diploid gametes. But they may also be looked upon as substantiating WINGE's hypothesis of "pathozygoty". So far as my own work is concerned, experimental proof of this view is lacking, but DE MOL (1925) shows by his experiments that it is probable. He has reported that he obtained a tetraploid variety (" 2n "$= 28$) from a cross between *Narcissus Pseudonarcissus* ($2n = 14$) and *N. poeticus* ($2n = 14$).

In this latter case of chromosome number doubling where hybridization plays a prominent rôle, it must be essential that the internal factor or a change in the protoplasmic activity induced by hybridization should result in an increase of sensibility, or a decrease of power of resistance to external factors (*cf.* KUWADA 1928, NAGAO 1929). Pure species are those which have sufficient power of adaptation to natural changes in the milieu. It is, therefore, natural to conclude, and this is actually the case, that in nature the doubling of the chromosome number must be connected with hybridization, through which alone a plant can be brought to a sensibility high enough to induce chromosome doubling within the range of the natural change in the environmental conditions.

Before concluding this chapter some remarks may be given about non-disjunction, cross segmentation and fusion of chromosomes, phenomena which are intimately connected with the hyperploidic increase and hypoploidic decrease of the chromosome number.

Non-disjunction, a term which has become familiar to us since BRIDGES' work on the sex chromosomes of *Drosophila*, is of very frequent occurrence in those forms in which the parental chromosomes form a ring or chain instead of the usual pairwise association in the heterotype division, as in *Oenothera*. The first observation of this phenomenon in *Oenothera* was made by GATES (1908) in *Oenothera rubrinervis*[1]. In other cases also, where the usual pairwise association is the case, the phenomenon is of not infrequent occurrence. ICHIJIMA (1930) has reported that in *Fragaria* the frequency of occurrence of non-disjunction is as high as 9.21 % in an individual, the average being 6.60 %. In *Datura*, the origin of the trisomic as well as other

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1.   Cited from GATES 1915, p. 175.

abnormal types of the plant has been sought in this phenomenon of non-disjunction (BLAKESLEE and BELLING 1924), and BLAKESLEE and CARTLEDGE (1927) express the opinion that cold may increase the frequency of occurrence of abnormal chromosome types of plantes which may be looked upon as originating in non-disjunction.

The cross segmentation of a chromosome into two mero-chromosomes is another process by which hyperploidic increase of the chromosome number may be brought about (*cf*. p. 187). This has been reported in *Zea Mays*, *Secale* sp. and some other plants and insects (*cf*. p. 101), and it is also the case with *Narcissus*.

The reduction of the chromosome number due to the fusion of two or more chromosomes into one has been found in some plants. In *Lactuca* the haploid number of chromosomes is 9, and it has been found by GATES and REES (1921) that " a striking feature of the heterotypic metaphase is the frequent coalescence (more or less complete) of two or four of the chromosome bivalents, so that only eight or seven bodies appear on the heterotypic spindle." (p. 376). STOLZE (1925) has found a similar case in *Secale montanum* in which the somatic chromosome number is 14. According to him, in pollen mother cells, only 6 chromosomal elements are " einwandfrei " counted in both heterotype and homotype metaphase as the result of fusion of two peculiar chromosomes, while in diakinesis 7 gemini are always counted as expected. JARETZKY (1928) has observed in *Rumex roseus* that while in many cases the number of chromosomes in the heterotype division of pollen mother cells is 9, it is 10 in eight cases, where two chromosomes out of the 10 are smaller. He is of the opinion that the number 9 must have been derived from the 10 by the fusion of two chromosomes, since in a closely allied species, *R. scutatus*, the haploid number of chromosomes is 10. WETZEL (1929) gives 11 for the haploid number of various *Quercus* species, but JARETZKY (1930) believes from the data he obtained that the haploid number of chromosomes in the species of this genus is 12, and that if a smaller number than 12, such as that given by WETZEL is counted, it is the result of reduction due to the fusion of some chromosomes.

IV. Significance of the chromosome number from the biological and practical point of view

The increasing knowledge as to the nature of chromosomes from both sides of investigation, karyological and genetical, has pointed to the conclusion that the chromosomes are the carriers of the hereditary

genes, and this conclusion is forming the basis of the new method of
plant breeding. Since it may now be looked upon as an established
fact that the chromosomes are the bearers of the hereditary genes, it
may readily be seen that an addition or loss of certain chromosomes
in an individual will necessarily result in a change in quality or quantity
in the characters of that individual. KUWADA (1919) has classified the
possible cases of the chromosome number increasing in organisms from
the physiological and biological point of view into the following three
cases :

     1. Qualitative increase.

     2. Quantitative increase.

     3. Numerical increase.

 In the first category he has discussed the case of hybridity. We
may expect in hybrid plants a new combination of the genes carried
by the parent plants. The chracteristics of the hybrids may be inter-
mediate between those of the parents, or one-sided under the complete
control of the law of dominancy, or may sometimes be new ones brought
about through the complementary effect of the two parent genes.
Among the physiological changes may also be mentioned here sterility,
heterosis, and so on, which are especially often found in crosses be-
tween plants standing in a relatively remote relationship, such as intra-
or intergeneric crosses. The karyological data alone are of course not
complete enough to explain these phenomena, but they provide a
fundamental basis for the study of the problem. KIHARA (1924) has
found that in the progeny of a pentaploid hybrid of *Triticum*, the
degree of sterility depends upon the kinds of the combinations of the
chromosomes. In the constant raddish-cabbage hybrid, *Raphanobrassica*,
KARPECHENKO and SHCHAVINSKAIA (1929) have found a sexual incom-
patibility with their parent plants. This " is evidently in connection
with their doubled chromosome complex, as the diploid F_1 hybrids of *Ra-
phanus × Brassica* are readily crossed, at least, with one of the parents
—— *Raphanus*." According to NOHARA, in the F_1 hybrid between
Quamoclit pennata (vulgaris) and *Q. coccinea*, no seeds are set (IKENO
1927, p. 100, 241), and according to KAGAWA and NAKAJIMA (1930),
and to NAKAJIMA (1931) the somatic number of chromosomes is 30 in
the former species and 28 in the latter. This latter fact seems to
serve as the basis for the interpretation of the former phenomenon.
The phenomenon of sterility is of general occurrence in the crosses
between remotely related plants and may be regarded as due to the
unbalanced and unstable state of the hybrid, conditioned by the union

of less harmonious parental genomes. According to MORGAN (1926), "balanced" means that "the numerical relation of the genes is the same as that in the diploid or normal type", and "stable", that "the mechanism of maturation is such that the type, once established, perpetuates itself." (p. 124).

Crossing experiments show that the sterility or inferior fertility of a hybrid is not necessarily accompanied by vegetative inferiority to the normal type, but may even be accompanied by a superior vigorousness. This phenomenon, heterosis or hybrid vigor, is known rather widely to occur in those crosses which are made between plants with chromosomes equal to or different from each other in number, as has been found in the cases of the rye-wheat hybrid (THOMPSON 1926), the radish-cabbage hybrid (GRAVATT 1914, KARPECHENKO 1924), the cotton hybrid (NAKATOMI 1931) and many others. This phenomenon has been interpreted by JONES by the linked dominant factor hypothesis.

While sterility is a negative phenomenon, so to speak, hybrid vigor is a positive phenomenon, and may have an important bearing upon breeding, but the formation of constant fertile hybrids carrying all the parental chromosomes may be even more important and interesting in both the scientific and the practical sense than hybrid vigor. This had been merely an imaginary conception without a cytological basis, before, so far as I am aware, FEDERLEY's paper on some *Pygaera* hybrids appeared (*cf.* JOHANNSEN 1926, pp. 593-598). We have now, however, some of these plants realized, among which are those mentioned above, i. e. *Aegilotricum*, *Raphanobrassica*, and a *Fragaria* hybrid obtained by ICHIJIMA (*cf.* p. 181). Besides these, the constant intermediate hybrid of rye-wheat has been obtained by LEVITZKY and BENETZKAIA (1929), and *Crepis artificialis*, another constant fertile hybrid carrying 10 pairs of chromosomes from one of the parents, *C. biennis*, and 2 pairs of those from the other parent, *C. setosa*, has been found by COLLINS, HOLLINGSHEAD and AVERY (1929) among F_4 plants of the cross. Recently KOSTOFF (1931) has also succeeded in producing a fertile triple hybrid, *Nicotiana tabacum* × (*N. sylvestris* × *N. Rusbyi*). This is the first instance of a fertile triple hybrid composed of complete chromosome contributions from the three different species. These instances seem to prove the possibility that this method of producing new individuals which breed true may be applied to the art of plant breeding.

There is a phenomenon which may appear in some cases to be analogous to the hybrid vigor, but is quite different in its nature from hybrid vigor. This is the case of quantitative increase, which is due

to the cumulative effect and is of frequent occurrence in autopolyploid plants.

It is well known that in triploids and tetraploids, the cells and nuclei are larger than those of diploid forms, generally giving rise to vegetative vigorousness of the plants. This relation between the chromosome number and the size of the cells holds to some extent for the case of *Narcissus* too. Although in this genome multiplication no marked qualitative change is to be found as a rule, but only a quantitative change which is due to the cumulative effect of genes already present, nevertheless it must have an important significance in plant breeding if the genes in question are concerned in the development of economically valuable characters such as increased longevity, greater hardiness, better viability, resistance to disease and insect injury and so on, especially in case the vegetative method of propagation is available (*cf.* DE MOL 1932). In cultivated economic plants, triploid forms have been reported by OSAWA (1920) in *Morus*, by NEBEL (1929), CRANE and LAWRENCE (1930) in apples. LONGLEY and CLARK (1930) have reported that except for only three yellow-fleshed, diploid form of the potato from South America ($n=12$), in all the others out of forty cultivated varieties investigated the gametic chromosome number is 24, a number which shows the tetraploid condition of the plants. It seems to be a noteworthy fact that plants under cultivation frequently show a large number of chromosomes as compared with that of the wild type, as is found in *Triticum, Avena, Fragaria* and the potato. In view of this fact that many cultivated forms of plants are characterized by the largeness of the chromosome number, an attempt at breeding aiming at multiplication of the genome is a matter not only of mere scientific interest but also of practical importance. It has been reported that in Java the sugar industry has been greatly improved by the successful breeding of better forms of sugar cane by this method of breeding. (*cf.* TERAO 1931).

The hyperploidic increase is another important case of the quantitative increase. The hypoploidic decrease of the chromosome number is, on the other hand, a case of loss, a phenomenon diagonally opposite to the former, but we find it convenient to discuss these two phenomena together. MORGAN (1926, p. 301) states: "the addition of a single chromosome or of two members of the same pair, or of two or more members of different pairs to the group, or the loss of a whole chromosome from the group, may be expected to produce more evident effects on the individual." Illustrations for this view may be found in *Datura*

in which BLAKESLEE and BELLING (1924) have found 12 distinct trisomic types. Since there are just 12 pairs of chromosomes in the normal type of this plant, 12 different simple trisomic types may be expected, and these have actually been found. Similar trisomic types have also been found in *Oenothera* (DE VRIES and BOEDYN 1923). In these instances the physiological equilibrium is kept undisturbed, so that the plant can live. The case of the triplo-IV's mutant of *Drosophila* is another instance of this balanced type of chromosome multiplication, and the case of the haplo-IV's mutant of *Drosophila* is an instance of the balanced type of chromosome subtraction. While these grow up, we have another type of mutants which can not live. The tetra-IV's and nullo-IV type of the fly are of this type, and it is seen from this fact that the complete absence of the IV-chromosome or its four-fold presence upsets the physiological balance to such an extent that these individuals can no longer live. The flies which are triple with regard to the X-chromosome or chromosomes II or III can not live either (MORGAN 1926, pp. 174–177).

It has also been shown in *Datura* that types with extra-chromosomes are of low fertility (BLAKESLEE and CARTILEDGE 1926). From the high percentage (63%) of empty pollen grains found in the varieties, " Empress " and " Grandee ", in *Narcissus* it is also seen that illegitimate sets of chromosomes give rise to pollen sterility.

The phenomena of cross segmentation and fusion of chromosomes are cases of numerical increase and decrease, and hence the hereditary units may thereby remain unchanged not only in number but also in other respects, but these phenomena are of a special interest in connection with the genetical phenomena of the inversion and translocation of genes, which have recently been discovered and fully investigated in *Drosophila* (MORGAN, BRIDGES and STURTEVANT 1925, MULLER 1928, DOBZHANSKY 1930, RHOADES 1930, and others). It has been shown by parallel investigations performed cytologically and genetically that these genetical phenomena are the necessary consequence of the cytological phenomena of cross segmentation and refusion (PAINTER and MULLER 1929). The latter phenomena attract our attention to " segmental interchange ", a hypothesis put forward by BELLING and BLAKESLEE (BELLING and BLAKESLEE 1926, BELLING 1927) and supported by many advocates such as DARLINGTON (1929), CLELAND and BLAKESLEE (1930, 1931), BLAKESLEE and CLELAND (1930), MEURMAN (1929) and others. DARLINGTON has found in the meiosis in several species in *Tradescantiae* several types of chromosome

association (*cf.* DARLINGTON 1929, p. 271) which are according to him not intelligible directly in terms of diploid or polyploid pairing of homologous whole chromosomes, but intelligible if it is assumed that there occur translocation of segments from one chromosome to another, segmental interchange between non-homologous chromosomes, inversion of segments and a process of terminalization of chiasma taking place between diplotene and diakinesis. He is of the opinion that the occurrence of these various abnormal types of chromosome association is connected with the condition found in structural hybridity. By structural hybrid he means " a zygote derived from the union of gametes dissimilar in respect of the structure of their chromosomes (i. e. in respect of arrangement rather than of quality or quantity). Whether this condition arises as a result of structural change in its immediate parents or in its remote ancesters (i. e. whether by internal or external hydridization in LOTSY's sense) does not concern us at present." (DARLINGTON 1931b, p. 240).

To put shortly what we have discussed above, both modes of chromosome number increase, qualitative and quantitative, bring about genotypical changes in organisms, and may, therefore, cause pheno-typical changes as well, while the mode of numerical increase has no direct bearing upon these changes. The principle implied in the quali-tative increase of the chromosome number is virtually a new *combi-nation* of chromosomes, or in terms of genetics, of hereditary genes. This principle has been applied to the method of plant breeding since the rediscovery of the MENDELian laws of heredity. This is the hybridi-zation method, and in this method it is fundamental that we have to select out species or races in which the characters in question are of better quality from the breeding point of view. The method, therefore, consists of selection and combination, and this in no sense implies the idea of *producing* or *inducing* new characters artificially. The recent progress in cytology, especially in the field of experimental investigation is, however, opening up to us another method of breeding, though its establishment into a form capable of practical use seems at present to be beyond reach. This is the method by which we can artificially induce characters, new or better, at least in the quantitative sense, than those carried by the species or races we have in nature. The cytological data which offer the basis of this method are chiefly polyploidal or hyperploidal multiplication of chromosomes — the quanti-tative increase — which can be induced by artificial means, such as cold or unusual temperature, many anaesthetics, X–rays and radium,

grafting and so on (e. g. GOODSPEED 1929, SAPÈHIN 1930, KOSTOFF 1930 c, and others). The mutation thus induced is the so-called " chromosome mutation ", and gene mutation, which we do not intend to deal under this heading, may also be induced by these artificial means (*cf.* BUCHHOLZ and BLAKESLEE 1930, KOSTOFF 1930 c).

Although the artificially induced mutants or variants hitherto obtained are mostly those which carry characters of no practical or economic significance, such as dwarfishness, chlorophyll deformation, or other defects (GOODSPEED, STADLER), and although plants carrying characters of economic value are, as pointed out by STADLER (1930), more likely to be found out among plants cultivated under control in the usual manner than among the progeny of experimentally or artificially treated plants, it seems, nevertheless, important from the view point, not only of scientific interest, but also of practical necessity in breeding, to carry out further studies of this artificial inducement. STADLER states : " There are, however, certain special cases in which incuced mutation, even in the present state of knowledge, offers a fair possibility of successful application. These are in general cases in which hybridization is not feasible or in which a character dependent on a single gene-change is particularly important." (STADLER 1930, p. 18).

Summary

1. The plants which were used as material in the present investigation are those known as, or garden varieties and forms belonging to : *N. Pseudonarcissus, N. incomparabilis, N. Jonquilla, N. Bulbocodium, N. odorus, N. tazetta, N. intermedius, N. biflorus* and *N. Barrii.*

2. They can be classified into two groups with regard to the cardinal number of chromosomes which they carry, namely, the 7-chromosomic and 10–chromosomic groups.

3. So far as my investigation is concerned all the garden varieties of *N. tazetta* belong to the 10–chromosomic group, the chromosome numbers shown by these varieties in the somatic cells being 20 (diploid), 30 (triploid), 21, 22, 31 and 32 (heteroploids).

4. In pollen mother cells in the diploid varieties of *N. tazetta*, there are found 10 bivalent chromosomes in the heterotype metaphase. In the varieties " Franklin " and " L_{20} ", 6 gemini are large and 4 small, and in the variety " P_{21} ", 5 are large and 5 small.

5.　In the triploid variety " Yellow Prince ", trivalent chromosomes are found (autotriploid). The number of the trivalents is 10, or less than 10.　In the latter case the corrseponding number of bivalents and univalents are found with the trivalents.

6.　In another triploid variety, " Chinese Sacred Lily ", a secondary association of chromosomes frequently takes place, so that complexes of a higher order than triple are formed, the number of chromosomal elements being correspondingly reduced.

7.　In the veriety with 21 chromosomes, 10 bivalents and 1 univalent are found in the heterotype metaphase.　This variety is, therefore, a hyperdiploid.

8.　In the variety with 22 chromosomes, 11 gemini are found in the heterotype division.　Of them 4 are large, and 7 are small.　From the result obtained in " B_{20} " it is concluded that two of the small ones must have been derived from one of the large ones by cross segmentation.　Thus the variety in question is essentially diploid, though it is numerically a hyperdiploid.

9.　In the variety with 31 chromosomes, the number of chromosomal elements in the heterotype division is 21, of which 10 are bivalent and 11 univalent.　This fact shows that this veriety is a heterogenomous tribasic plant, consisting of two genomes homologous to those of " Franklin " as is indicated by the corresponding ratio between the numbers of large and small gemini, and a genome homologous to that of the 22-chromosome variety.

10.　In the variety " Luna " with 32 chromosomes the behavior of the chromosomes in meiosis shows that this variety must have been raised by the union of a diploid gamete abnormally produced in a certain diploid form of *N. tazetta* and one produced in such a species as that investigated by FERNANDES in which the haploid number of chromosomes is 6.

11.　The wild growing form of the narcissus plant, known taxonomically as *N. tazetta* var. *chinensis*, is a triploid having 30 chromosomes in the somatic cells.

12.　*N. Pseudonarcissus*, *N. incomparabilis*, *N. Jonquilla*, *N. poeticus* and *N. Bulbocodium* belong to the 7-chromosomic group.

13.　In some varieties of *N. Pseudonarcissus*, *N. incomparabilis* and *N. poeticus* the number of chromosomes in the somatic cells is 21. In the heterotype metaphase, 7 trivalent chromosome complexes are found, a feature which is characteristic of autotriploid plants. Frequently, however, in some of the complexes, the association into the trivalent

complex is incomplete, so that as many chromosomal elements as 8, 9, 10, etc. may be counted.

14. In the varieties of *N. Pseudonarcissus*, " King Alfred " and " Olympia ", with 28 chromosomes each, the chromosomes form 7 tetravalent complexes in the heterotype metaphase. In some cases some of the chromosomes fail to conjugate with their homologues, so that more than 7 chromosomal elements may be counted.

15. In two varieties of *N. Pseudonarcissus* with 22 chromosomes each, the behavior of the chromosomes in meiosis shows that they are hypertriploid plants ($7_{\mathrm{III}} + 1_{\mathrm{I}}$).

16. The hexaploid number 42 is found in a form of *N. Bulbocodium*. In diakinesis and metaphase in the heterotype division, the chromosomes pair two by two resulting in 21 bivalents in most cases, but in some cases one or more than one multivalent (tetra- or sexivalent) chromosome is also found with the corresponding reduction of the number of chromosomal elements.

17. Such irregularities in the meiotic division as the longitudinal splitting of some univalent chromosomes in the heterotype division, lagging of some unsplit univalents behind the others in the anaphase, the formation of giant restitution nuclei or dwarf mero-nuclei, etc. are found to a greater or less extent in the tri- and tetraploid as well as heteroploid varieties.

18. *N. intermedius*, the species hybrid between *N. tazetta* and *N. Jonquilla*, shows 17 chromosomes in the somatic mitosis. In the heterotype division these chromosomes show no tendency at all to pairing between any two of them.

19. *N. biflorus*, the species hybrid between *N. tazetta* and *N. poeticus*, shows 24 chromosomes in the somatic mitosis, and 7 bivalent and 10 univalent chromosomes in the heterotype division.

20. In these species hybrids, the process of meiosis is extraordinarily irregular, and all the pollen grains appear abortive.

21. 14 chromosomes are found in the somatic cells in *N. Barrii* and *N. odorus* which are regarded by some authors as the species hybrids between *N. poeticus* and *N. Pseudonarcissus*, and between *N. Jonquilla* and *N. Pseudonarcissus* respectively.

22. So far as my investigation is concerned, there is no evidence to show that there is the cardinal number 5 in the genus *Narcissus* as believed by FERNANDES. My conclusion is that there are three cardinal numbers known with certainty at present in this genus, namely 6, 7, and 10.

23. Measurements were attempted with pollen grains and epidermis cells in the scale leaves of the bulb to see whether there is a correlation between the chromosome number and the cell size.

a) In pollen grains ; the length increases in correspondence with the increase in the number of haploid chromosome sets or genomes. The width increases similarly except in the cases of a triploid and a hypertriploid in both of which it is broader than in tetraploid varieties. From these results it is seen that except for the cases of these triploid and hypertriploid plants there is a certain correlation between the size of pollen cells and the number of chromosome sets.

b) In epidermis cells, the same correlation between the cell size and the number of chromosome sets is also recognizable, at least to some extent, in the case of the plants carrying as many chromosomes as multiples of 7 as well as those where the cardinal number is 10, while this relation does not hold for the cases of species hybrids between these two cardinal numbers, *N. intermedius* and *N. biflorus*.

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