MEMOIRS OF THE COLLEGE OF SCIENCE, KYOTO IMPERIAL UNIVERSITY, SERIES B.
VOL. IV, NO. 3, ARTICLE 8, 1929.

Karyological Studies of the Narcissus Plant.

I. Somatic Chromosome Numbers of Some Garden Varieties and Some Meiotic Phases of a Triploid Variety.

By

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With 40 Text-figures

(Received December 1, 1928)

INTRODUCTION.

There are many garden varieties of the narcissus plant known, having various chromosome numbers, such as 14 (diploid), 21 (triploid), 28 (tetraploid) and other heteroploid numbers in somatic cells, but with regard to these varieties no details are known about the behavior of chromosomes in the meiosis which may give a clue to the origin of these different numbers. In triploid plants, for example, we have hitherto found the following three main types of the chromosome behavior in the first maturation division:

1. Non-formation of bivalent chromosomes:—In this type there are as many unpaired or univalent chromosomes as the number of somatic chromosomes (*Hieracium laevigatum*, *H. lacerum*, ROSENBERG (1917)).

2. Co-existence of bivalent and univalent chromosomes (*Morus*, OSAWA (1920) or many other examples).

3. Formation of trivalent chromosomes (examples as listed in p. 185).

These differences in the behavior of chromosomes may be due to the intensity of affinity between three "homologous" chromosomes. If the intensity of affinity between these chromosomes is normal, they will behave like the third type, but if the intensity is below the normal, the behavior will be such as in the first case or in the second. In other words we may say that in the second case, one of the three chromosomes is a chromosome derived from a different origin. Thus in the strict sense, the chromosomes forming bivalents may not be said to be homologous with the unpaired chromosomes. In the third case, on the other hand, the three chromosomes which make up a trivalent complex are homologous with one another, because they may be taken to have been derived from the same origin.

If we find that three chromosomes in which the MENDELian factors in question are involved form a trivalent complex at the first division, we may say from this fact that there will be found the triploid segregation instead of normal MENDELian or diploid segregation. Good examples have been illustrated in a *Datura* mutant and the triplo-IV mutant of *Drosophila*[1].

Thus it is an important problem in cytological genetics, not only from its scientific interest but also from the point of view of breeding, to study polyploidal or multisomic states of homologous chromosomes, with special reference to their genetical relations as well as their origin.

The object of the present investigation is to learn the chromosome behavior and the origin of various chromosome numbers in various garden varieties of *Narcissus*. The investigation is now still in progress, and the present paper deals only with some results obtained from some of the garden varieties investigated since the autumn of 1927. These will be discussed in a later paper.

My thanks are due to Prof. Y. KUWADA for his valuable suggestions and constant guidance throughout the work and to Prof. H. KIHARA who showed me much kindness in allowing me the use of his libraries.

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1. MORGAN, 1926.

I am also indebted to Mr. O. MINOUCHI and Mr. T. MAEDA for their kind advice and help.

MATERIALS AND METHODS.

The materials used were taken from plants which had been cultivated in the experimental garden of our laboratory[1]. Root-tips of the material plants were fixed in the field at once in FLEMMING's strong solution. For pollen mother cells, NAWASCHIN's fixative[2] was found the best of the fixing fluids used, though this fixative may not be said to be a very good one. For staining, HEIDENHAIN's iron alum haematoxylin was exclusively employed in the case both of the root-tips and of the pollen mother cells.

THE SOMATIC CHROMOSOME NUMBERS.

The number of chromosomes of the narcissus plant was first reported by STOMPS (1919) and later by DE MOL (1922, 1925) and HEITZ (1926). The results (2n) reported by these authors are as follows:—

Narcissus poeticus var.		
Poetarum	14 or 16	STOMPS (1919)
Ornatus	14 or 16	,,
Glory of Lissy	16	,,
Albion	16	,,
Narcissus biflorus		
(*N. poeticus gigas* × *N. tazetta*)	24	,,
Narcissus Pseudonarcissus var.		
minor type	14	DE MOL (1922)[3]
minor cyclamineus	14	,,
nanus	14	,,

1. These materials were collected from nurseries by Mr. NISHIO, whose investigation was discontinued some years ago owing to a certain circumstance.—Y.K.

2. 1% Chromic acid 10 parts
40% Formalin 4 parts
Glacial acetic acid 1 part
Formalin was added immediately before use. For further information, *cf.* MAEDA, 1928.

3. Cited from GAIGER, 1926.

minimus	14	DE MOL (1922)
muticus	14	,,
capax plenus	14	,,
Teramonius plenus	14	,,
Johnstoni Queen of Spain	20	,,
Maximus	21	,,
Golden Spur	21	,,
Bicolor Victoria	22	,,
Buttonhole	22	,,
King Alfred	28	,,
Van Waveren's Giant	28	,,
N. poeticus × *N. Pseudonarcissus*		
Lucifer	14	DE MOL (1925)
Lucifer (bud variation)	ca. 28	,,
Fuselier	14	,,
Fuselier (bud variation)	ca 28	,,
Narcissus incomparabilis	14	HEITZ (1926)[1]
Narcissus Balbocodium	42	,,

The number of chromosomes that I have ascertained in root-tips are as follows[2] :—

Narcissus Pseudonarcissus var.		
" Victoria "	14	Fig. 1,*a*.
" Albicans "	14	Fig. 1,*b*.
" Empress "	22	Fig. 1,*c*.
" Grandee "	ca. 22	Fig. 1,*d*.
" Olympia "	28	Fig. 1,*e*.
" King Alfred "	28	Fig. 1,*f*.
" Golden Supr "	30	Fig. 1,*g*.

Narcissus incomparabilis var.

1. Cited from TISCHLER, 1927.
2. As to the knowledge of classification of garden varieties of this plant, I am much indebted to Dr. Y. HOSHINO and Dr. U. URAKAWA of Hokkaido Imperial University, Sapporo, to wohm I wish to take this opportunity of expressing my thanks for their kindness.

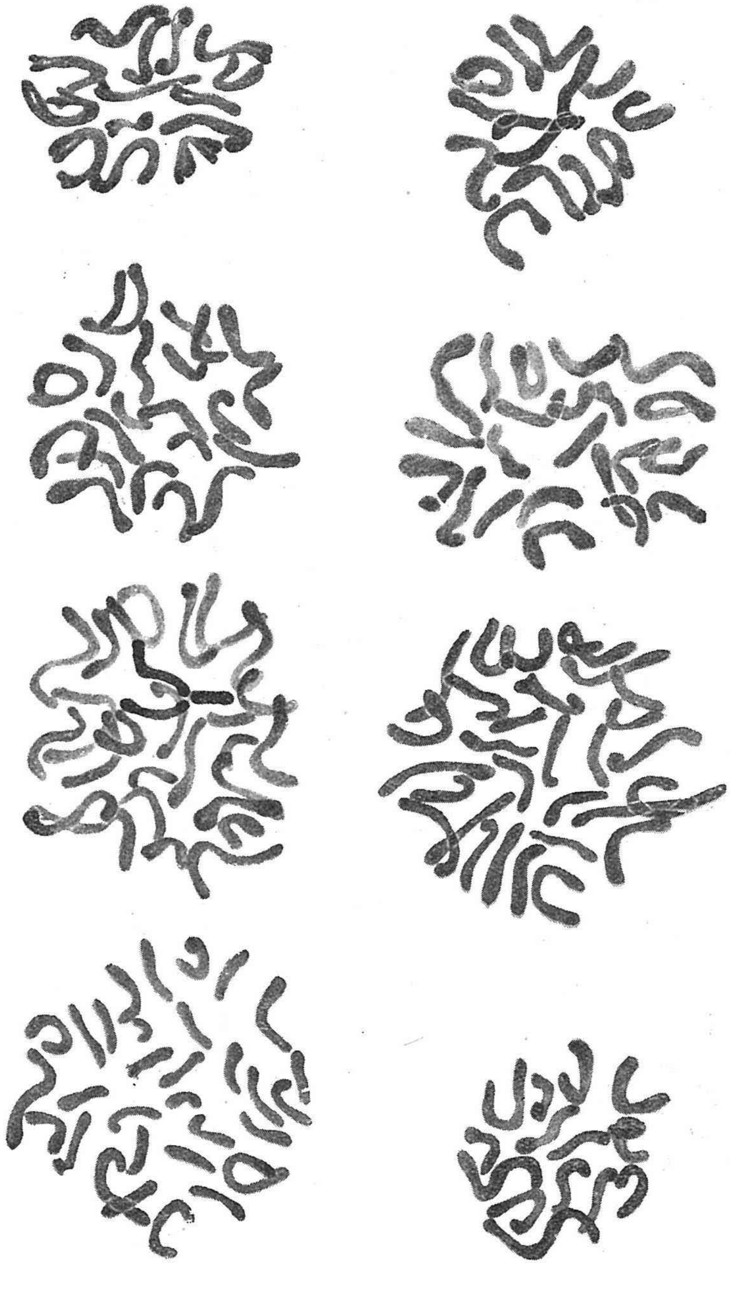


Fig. 1 *a–h*.

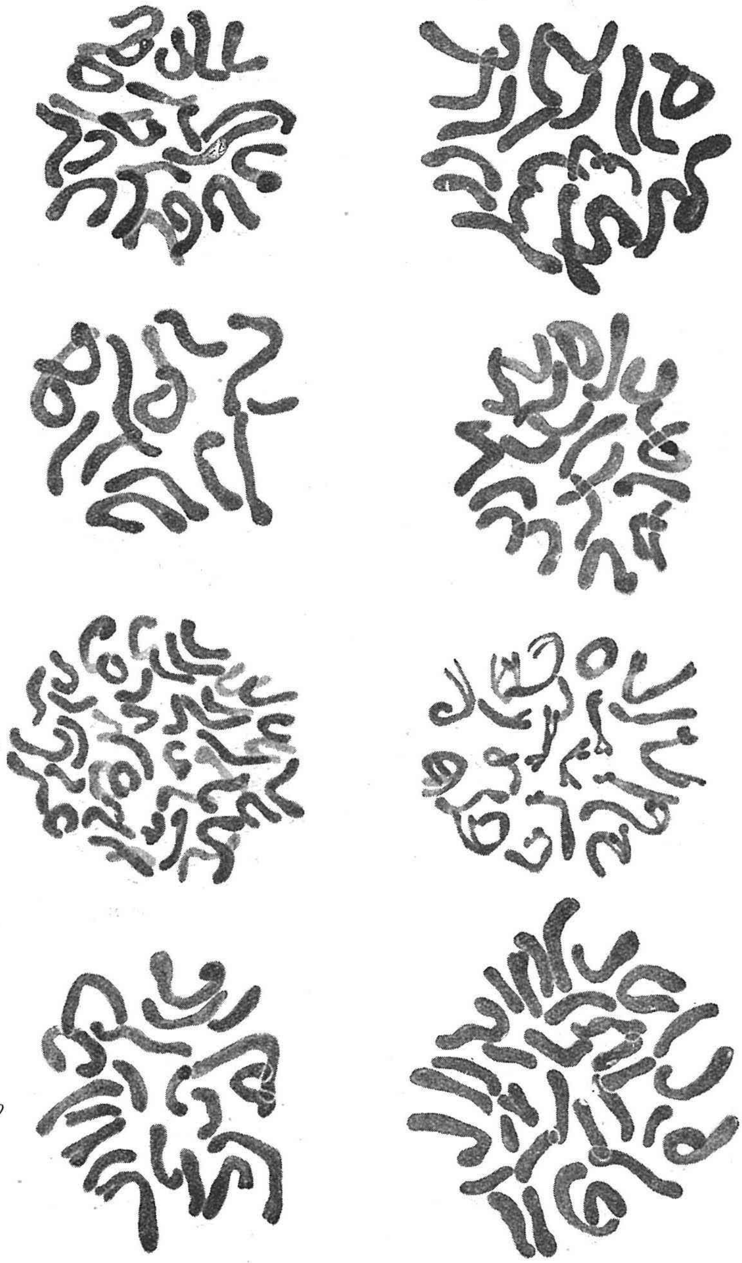
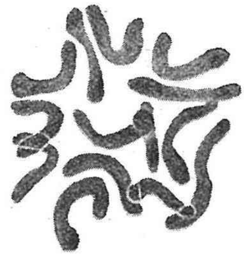


Fig. 1 *i–o* & *q*.

p 

 s

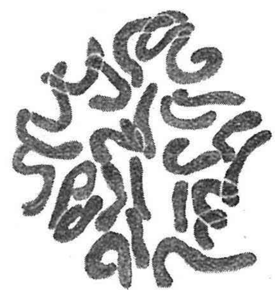
r 

Fig. 1 *a–s*.

Chromosomes in nuclear plate from root-tips of various garden varieties. Explanation in the text. *a–l* & *n–o*, × 2210. m. × 2990.

"Nelson Major"	14	Fig. 1, *h.*
"Gloria Mundi"	21	Fig. 1, *i.*
"Sir Watkin"	21	Fig. 1, *j.*
Narcissus Balbocodium var.		
"Common Hooped Petticoat" (double flowered)	14	Fig. 1, *k.*
"Conspicuous"*	21	Fig. 1, *l.*
"Androecium of Balbocodium"	42	Fig. 1, *m.*
Narcissus poeticus var.		
"Poetarum"	21	Fig. 1, *n.*
Narcissus tazetta var.		
a variety ("bicolores" type)	20	Fig. 1, *o.*
a variety ("albae" type)	22	Fig. 1, *p.*
"Luna"	ca. 32	Fig. 1, *q.*
Narcissus poetaz var.		
"Elvira" ?	25	Fig. 1, *r.*
Narcissus Jonquilla (double flowered)	14	Fig. 1, *s.*

As will be seen from the results of the previous authors and of

* This named variety is classified by some authors as some other species.

myself, the narcissus plant consists of polyploidal groups (diploid, triploid, tetraploid and hexaploid) having 7 as the cardinal number, and of some heteroploid varieties which are furnished with a number of chromosomes, such as 20, 22, 25, 30 or 32. Among 19 garden varieties of the narcissus plant I have observed, there are 5 diploid, 4 triploid, 2 tetraploid, 1 hexaploid and 7 heteroploid varieties having the chromosome numbers as just listed above.

It is to be noted here that there are in some varieties such as "Golden Spur", "Poetarum", certain differences between the chromosome numbers obtained by myself and those given by the previous authors, while in others an exact coincidence is seen. According to DE MOL, "Golden Spur" has 21 chromosomes and according to STOMPS, "Poetarum" has 14 or 16 chromosomes; but according to my results, the former has 30 chromosomes and the latter 21 chromosomes. It may not be impossible to suppose that the difference in locality may bring about these changes in chromosome number, but we have no means to identify these plants with those investigated by other authors. The same results as those of the previous authors were obtained, on the other hand, in some varieties, such as "King Alfred" and others. The number of chromosomes of this named variety has been found to be 28 by both DE MOL and myself. According to HEITZ, *N. Balbocodium* and *N. incomparabilis* have 42 and 14 chromosomes respectively. My results show that some of the varieties in these species have these chromosome numbers.

In the heteroploid forms I have found varieties with 25, 30, and 32 chromosomes besides those with 20 and 22 chromosomes which were observed by DE MOL. But varieties having 16 or 24 chromosomes such as were reported by STOMPS have not been found so far as the present investigations go.

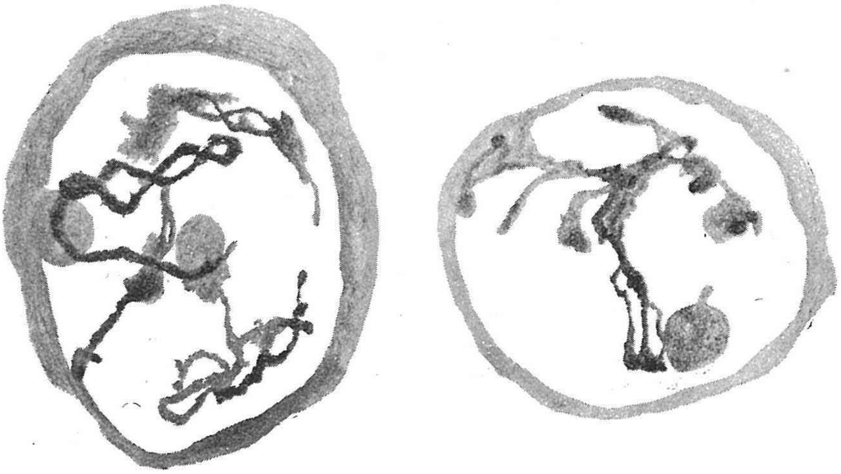
Through what processes these heteroploid forms have arisen is an interesting question. Several possible processes are to be considered. Investigations on the meiotic phases of these plants, which are now going on, may cast some light on the problem.

MEIOTIC PHASES OF A TRIPLOID VARIETY,

Narcissus poeticus var. ***poetarum.***

"Poetarum" (=*N. poeticus* var. *poetarum*) is a triploid variety with 21 chromosomes in somatic cells.

Heterotype Division. The synaptic threads are so fine and so slender that it is quite impossible to recognize whether or not the three homologous chromosomal threads conjugate three by three to form trivalent elements. According to M. M. LESLEY (1926), in triploid tomatoes the spirem is longitudinally double in some parts and single in others.



2 3

Figs. 2–40. Meiotic phase of pollen mother cells of triploid variety "Poetarum".

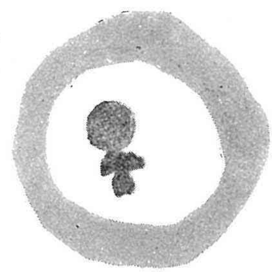
Fig. 2. Late pachinema or early strepsinema, showing spirem threads in side by side arrangement having the third element joined end-to-end. × 2210.

Fig. 3. The same, showing three spirem threads all in side by side arrangement. × 2210.

In a later stage where the segmentation of the spirem occurs, there can clearly be seen not infrequently the triple arrangement of the chromosomal threads. Sometimes the three components are so arranged that one component is conjoined end-to-end to the other two which run paralell to each other (Fig. 2), and sometimes all three come together side by side to be longitudinally triple (Fig. 3).

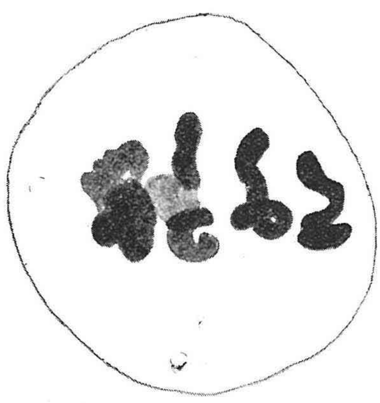
Both in diakinesis and metaphase there are found 7 (=" basis " or

4 *a*



4 *b*

5



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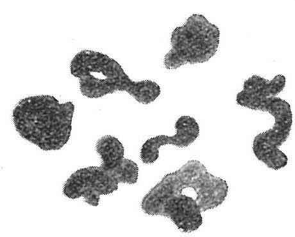

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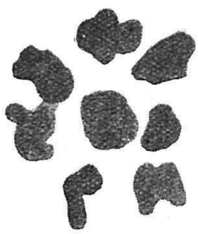
Fig. 4, *a–b*. Two consecutive sections. Diakinesis showing 7 trivalent chromosomes and one nucleolus. ×1710.

Fig. 5. Heterotype metaphase, showing 7 trivalent chromosomes. Polar view. ×1710.

Fig. 6. The same showing trivalent nature of chromosomes very clearly. Polar view. ×1710.

Fig. 7. The same. Side view, showing 7 trivalent chromosomes. Trivalent nature is very clearly shown. × 1710.

cardinal number) trivalent elements, each consisting of three component chromosomes (Figs. 4–7). In Figs. 4, 6 and 7, the trivalent nature can



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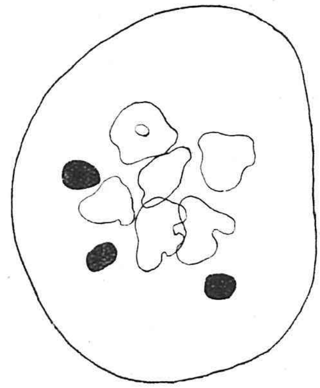

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Fig. 8. Heterotype metaphase showing 6 triple, 1 double and 1 single chromosomes. Polar view. ×1710.

Fig. 9. The same, showing 6 triple and 3 single chromosomes. Polar view. ×1710.

Fig. 10. The same, showing 10 chromosomal elements. Polar view. ×1710.

clearly be seen. Sometimes we find from one to several single or univalent chromosomes among the trivalent chromosomes, so that 8, 9 or 10 chromosomal elements may be counted in the nuclear plate, as shown in Figs. 8, 9 and 10.

Since trivalent chromosomes were reported as having been found in *Canna* by BELLING (1921)[1], the same constitution of heterotype chromosomes has been found by several investigators in several triploid plants listed below :—

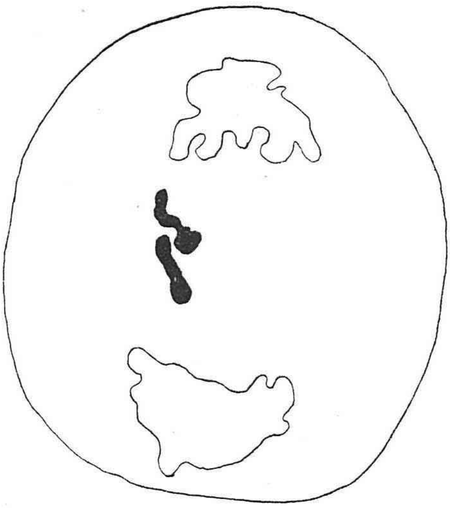
Canna (BELLING, 1921), *Datura* (BELLING and BLAKESLEE, 1922), hybrid between perennial teosinte and Indian corn (LONGLEY, 1924)[2], *Hyacinthus* (BELLING 1925), *Hemerocallis* (BELLING, 1925), Tomato (M. M. LESLEY, 1926), *Zea* (RANDOLF and McCLINTOCK, 1926), *Campanula* hybrid (GAIRDNER, 1926)[3], *Oenothera* (HÅKANSSON, 1926–'27), *Prunus* (OKABE, 1927), *Primula* (ONO, 1927), *Iris* (KAZAO, 1928), *Lycoris* (NISHIYAMA, 1928), triploid intersexual plant of *Rumex Acetosa* (ONO, 1928).

1. Cited from WILSON, 1925.
2. Cited from MORGAN, 1926. Trivalent chromosomes are found here in varying numbers, such as 1, 2, 4.
3. Cited from HÅKANSSON, 1926–'27.

Narcissus now adds another example to this list. Recent researches on *Triticum* hybrid by KIHARA and NISHIYAMA (1928) also show that in the triploid hybrid of *Triticum*, chromosome combinations with some trivalent chromosomes varying in number from 0 to 3 are met with besides the normal ($7_{II}+7_{I}$) combination in which no trivalent chromosomes are found but bivalents and univalents only. Recently BRIEGER (1928) has also found in two back-crossed individuals of a certain *Nicotiana* hybrid varying numbers of trivalent chromosomes together with corresponding numbers of bivalents and univalents besides 12 bivalents which are constantly found in these individuals.

In *Canna* and *Datura* (BELLING, 1921; BELLING & BLAKESLEE, 1922), when the chromosome distribution to the poles takes place, two triplets of the trivalent chromosomes separate from each other towards the poles, the remaining one ranging itself at random with any one of the separating triplets, and thus several different combinations results in the number of chromosomes in *Datura*, for example, such as 12 : 24, 13 : 23, 14 : 22 etc. up to 18 : 18.

In *Narcissus*, the behavior of the unpaired triplet is sometimes the same as in *Canna* or *Datura*, but is not always so. It can be not infrequently observed that during the distribution of two triplets towards the poles, some of the third triplets lag behind the other chromosomes, but longitudinally split, and their halves separate towards the poles after the other chromosomes have reached the poles. Similar behavior of chromosomes has also been observed recently by KARPECHENKO (1928) in the F_2 hybrid with triploid number of chromosomes, produced from the crossing of *Raphanus* and *Brassica*. The number of this kind of triplets in one pollen mother cell varies from 0 to 7 (Figs. 11–17). The frequency of these numbers observed in 112 pollen mother cells is recorded in the following table.



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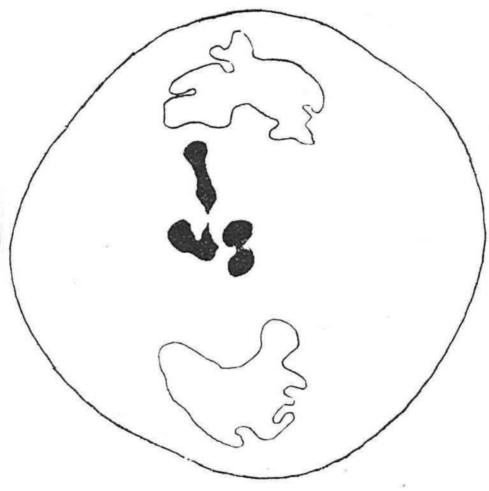

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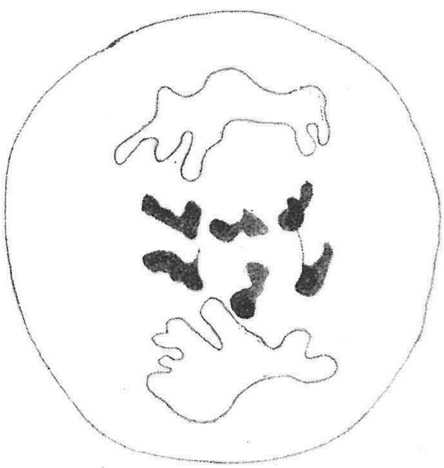

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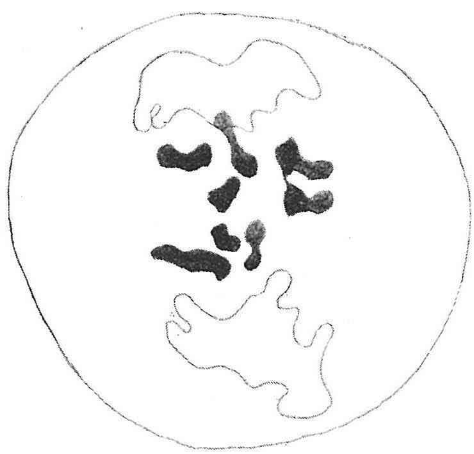

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Figs. 11—17. Showing longitudinal division taking place in some of the third triplets during the distribution of the other two triplets to the poles. ×2210.

Fig. 11. Longitudinal division is seen in one triplet shown solid black.

Fig. 12. " " " in two triplets " " "

Fig. 13. " " " in three triplets " " "

Fig. 14. " " " in four triplets " " "

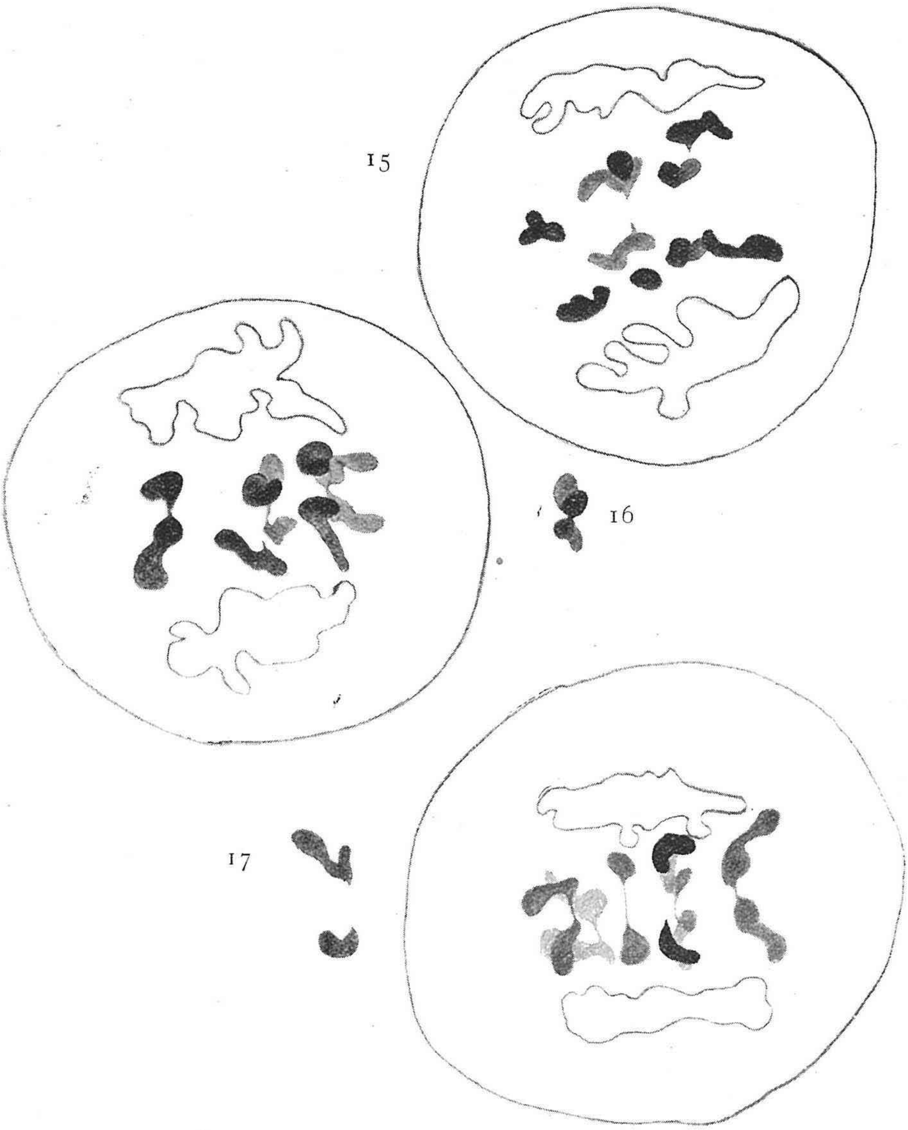


Fig. 15. Longitudinal division is seen in five triplets shown solid black.

Fig. 16. " " " in six triplets. One chromosome is drawn separated from its original position to avoid complication in the figure.

Fig. 17. Longitudinal divison is seen in seven triplets. One chromosome is drawn separated from its original position for the same purpose as in Fig. 16.

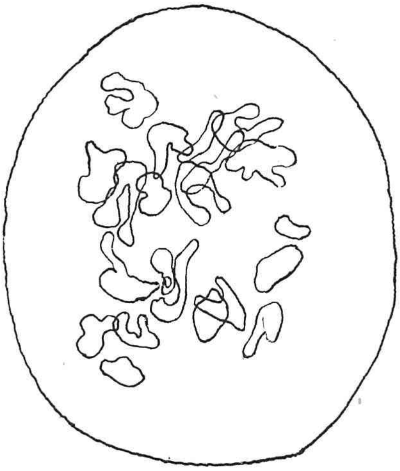
Number of lagging chromosomes	0	1	2	3	4	5	6	7	Total
Frequency	9	18	28	26	17	8	4	2	112

As will be seen from this table, the extreme case where 6 or 7 lagging chromosomes are formed is exceedingly rare, being only 3.6% in the former case and 1.8% in the latter. This fact means that there is little chance for the taking place of the equational division in all or the majority of the third triplets. On the other hand, cases where the equational division takes place only in 2 or 3 third triplets are of far more frequent occurrence, their frequency being 25 and 23% respectively. This shows that there is a higher possibility for cases where the lagging chromosomes are two or three in number. Cases where one or four triplets lag behind the other chromosomes are intermediate in frequency between the two extremes, and cases where there are no or five lagging triplets come next in frequency.

The chromosome behavior in this type of division is analogous to the behavior of chromosomes found by KIHARA (1924) in the triploid hybrid of *Triticum*, which have been summarized under the "*Triticum* × *Secale* type" (his paper, pp. 113–137), except that affinity between homologous chromosomes is stronger in the case of *Narcissus* than in the *Triticum* hybrid.

From the irregular distributions of chromosomes mentioned above, different numbers of chromosomes may be expected to be found in both anaphasic chromosome groups. Some examples are shown in the following table based on the data obtained from those pollen mother cells drawn in Figs. 18–22.

	Fig. 18	Fig. 19	Fig. 20	Fig. 21	Fig. 22
Upper pole	10	11	10	7	7
Between the poles	0	3	3	4	7
Lower pole	11	7	8	10	7



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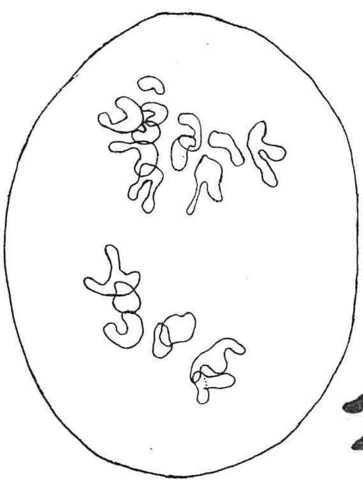
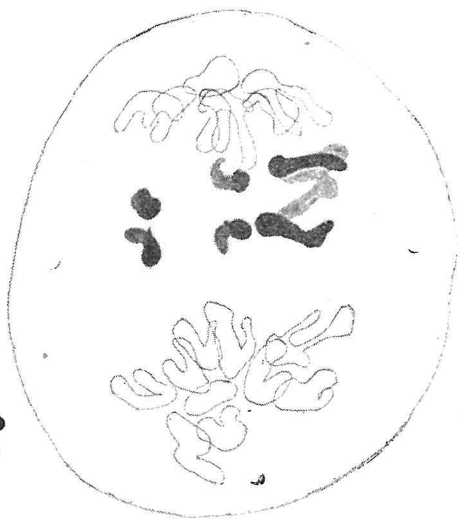


19 *a*

19 *b*



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Figs. 18—22. Heterotype anaphase. ×2210.

Fig. 18. 10 chromosomes at the upper pole, 11 at the lower, being 21 in all.

Fig. 19, *a–b*. 11 at upper pole, 7 at the lower, 3 between the poles, 21 chromosomes in all. 3 chromosomes between the poles are drawn separated from their original positions to avoid complicating the figure (*b*).

Fig. 20. 10 at the upper pole, 8 at the lower, 3 between the poles, the total being 21.

Fig. 21. 7 at the upper pole, 10 at the lower, 4 between the poles, the total being 21 chromosomes.

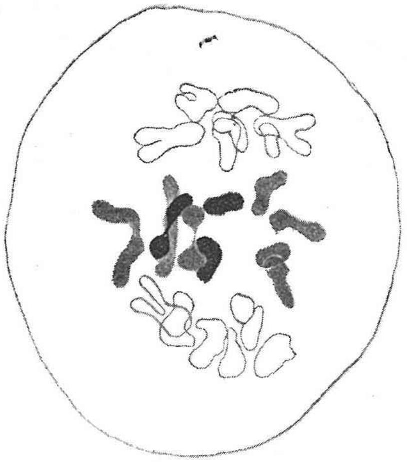

Fig. 22.

7 at the upper pole, 7 at the lower, 7 between the poles, the total being 21 chromosomes.

Occasionally the nuclear membrane is formed before some of the lagging chromosomes can reach the pole. These chromosomes are left in the cytoplasm and form micronuclei (Figs. 23–25). The number of the micronuclei is mostly one or two.

Before the completion of the chromosome distribution to the poles, there is sometimes formed a large nucleus (Figs. 26, 27). ROSENBERG (1926–'27) has observed this type of nuclear formation (" Restitutionskerne ") in parthenogenetic *Euhieracium*, and pointed out that it may play an important rôle in the doubling of chromosome numbers in organisms. KUWADA (1928) recently published a paper on an occurrence of the restitution nucleus in *Baranophola japonica*, and states that " an internal tendency to respond to external or environmental conditions may be strong in one plant and weaker in another. In plants where it is very strong, such peculiarities as what is called the restitution nuclei would be almost of normal occurrence, because in such plants a slight change in temperature &c will cause the peculiarities." (p. 126). It may not be impossible to consider that a triploid plant is in an unbalanced[1] condition and thus it is more sensible to the external environmental

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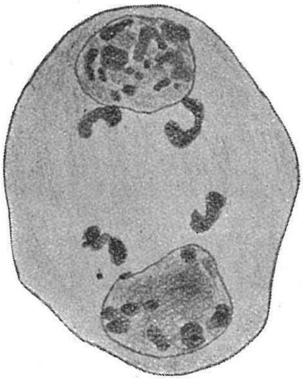
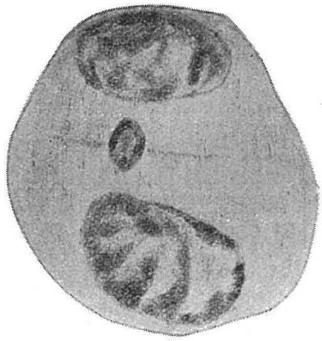
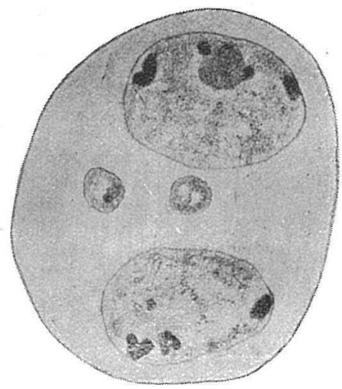
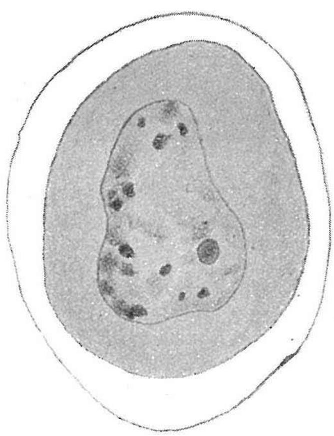
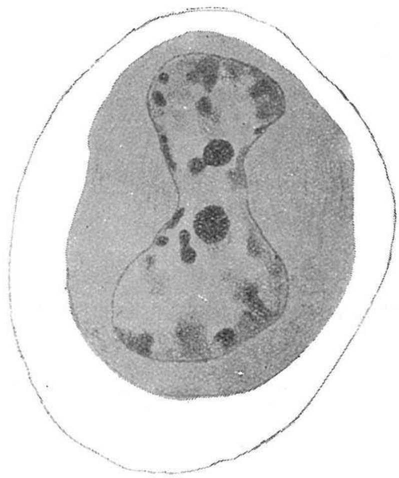
1. By " balanced " is meant, according to MORGAN, that the numerical relations of the genes is the same as that in the diploid or normal type (MORGAN, 1926, p. 124).

23 24 25

26 27

Figs. 23—25. Heterotype telophase. ×1710.

Fig. 23. Showing lagging chromosomes left in cytoplasm.

Fig. 24. Showing one micronucleus.

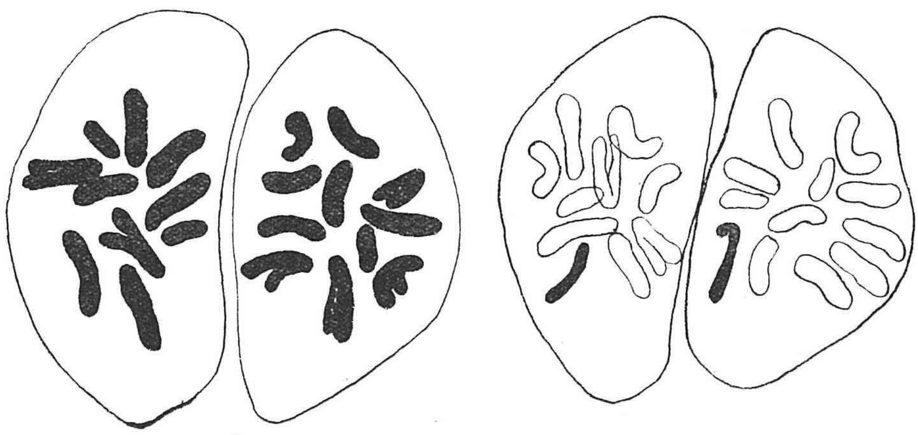
Fig. 25. Showing two micronuclei.

Fig. 26. An early stage in the nuclear membrane formation of a large nucleus ("restitution nucleus"). ×1710.

Fig. 27. The same. Phlagmoplast is seen. ×1710.

influence than a diploid one. According to BELLING and BLAKESLEE in triploid *Datura*, the first nuclear division is entirely omitted and only two nuclei, each with 36 chromosomes, are formed in the second division. They hold the view that these cases of non-reduction may be greatly increased in number by transient cold. This fact seems to support our view that a triploid plant may be more sensible to the external environmental influences than a diploid one. KARPECHENKO (1928) also has observed the same "ommission" of first division in triploid F_2 hybrid of *Raphanus* × *Brassica*. It is an interesting fact indeed from the view point just mentioned, that in triploid *Narcissus* there are some phenomena similar to the restitution nucleus. Though details are left for future researches, I can say at present with certainty that in this plant too, there are found many diad pollen cells in the homotype telophase.

Homotype Division. The observation of homotype division is not yet fully completed, but the results so far obtained will be mentioned here. The chromosome numbers in the nuclear plate of both sister cells



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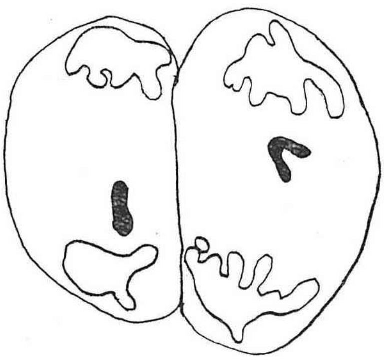
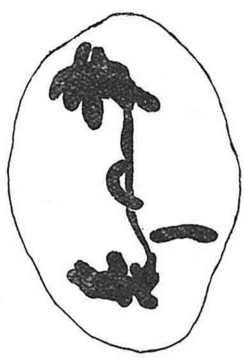
Figs. 28—29. Homotype metaphase. Polar view. ×2210.
Fig. 28. 11 : 10 chromosomes.
Fig. 29. 9 diads + 1 monad : 11 diads + 1 monad, the total number of chromosomes being 21.

are 10 : 11, 10 : 12 as is to be expected from the behavior of the chromosomes in the first division (Figs. 28, 29). In Fig. 28, 10 : 11 chromosomes are seen amounting to 21 in all, and in Fig. 29, 9 diads + 1 monad : 11 diads + 1 monad, the total being 21 chromosomes.

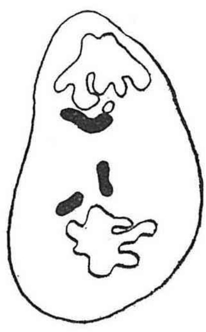
It is highly probable that the equational division may take place in the chromosomes that have undergone chance distribution or a random assortment in the first division, but not in those chromosomes that have already split longitudinally in the first division. These latter chromosomes



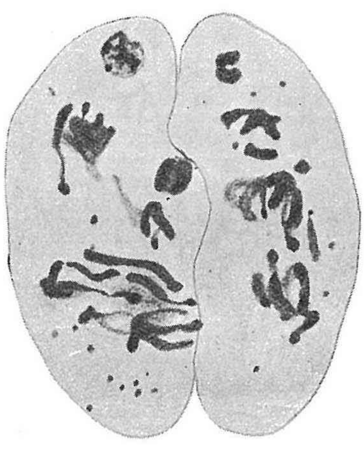
30



31



32



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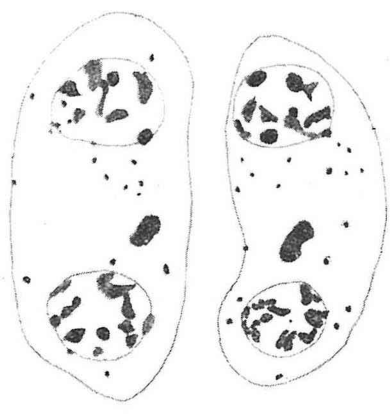

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Figs. 30—33. Homotype anaphase. Side view. ×1710.

Fig. 30. Showing two triplets that have been longitudinally split in the first division. One goes to the lower pole in one of the sister cells, while the other goes to the upper in the other cell.

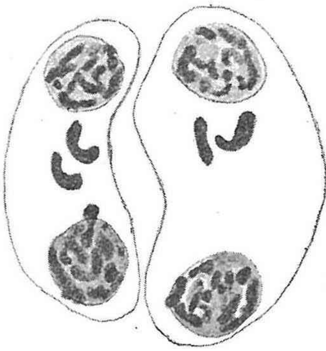
Fig. 31. Showing two lagging chromosomes and a chromosome bridge between the poles.

Fig. 32. Showing three lagging chromosomes.

Fig. 33. Irregular behavior of chromosomes, showing larger or smaller chromatin granules found here and there in cytoplasm.

Fig. 34. Homotype telophase, showing one lagging chromosome left in cytoplasm. ×1710.

should undergo chance distribution in the second division. Observations have shown that this is actually the case. Figs. 30–32 show these lagging chromosomes in the homotype anaphase. In Fig. 30, in one of



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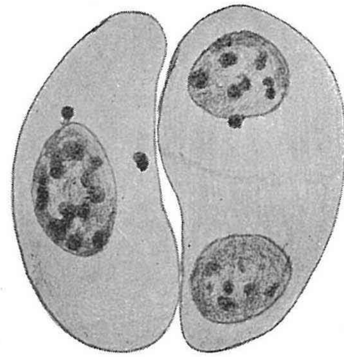

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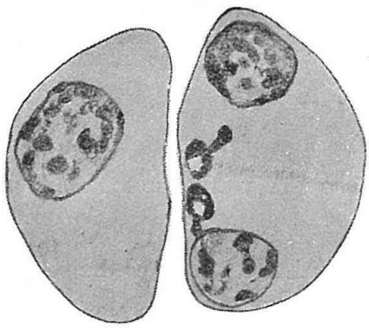

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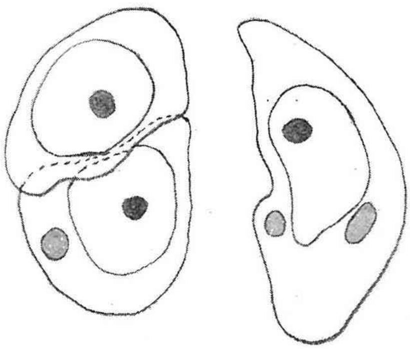

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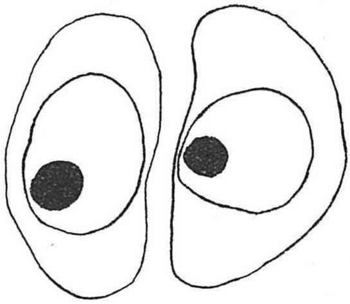

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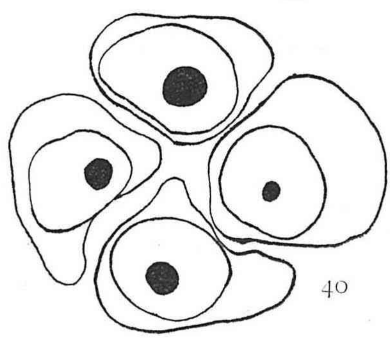

40

Fig. 35. The same showing two lagging chromosomes left in cytoplasm. ×1710.
Fig. 36. Homotype telophase, showing a triad state of nucleus. ×1710.
Fig. 37. The same with micronuclei. ×1710.
Fig. 38. Pollen triad. ×1710.
Fig. 39. Pollen diad. ×1710.
Fig. 40. Pollen tetrad. ×1710.

the cells a lagging chromosome goes upwards, in another, one goes downwards. In Figs. 31 and 32 we can see again such lagging chromosomes in the homotype anaphase, two in the former figure and three in the latter. In Fig. 31 a chromatin connection or a chromosome bridge between the poles is also observable.

Anomalous behavior of chromosomes such as is met with on treating tissues or cells with some narcotics (SAKAMURA, 1920) is also frequently observable. In Fig. 33, the regular distribution of chromosomes is entirely disturbed, some number of chromatin granules of varying sizes being found in the cytoplasm here and there. Figs. 34 and 35 show that one or two lagging chromosomes are still found free in the cytoplasm after the nuclear membrane has been formed around the chromosomes which are regularly distributed at the poles. This shows that micronuclei may be formed in the homotype division also just as in the heterotype division.

The resulting pollen tetrads are regular in form and size in general (Fig. 40). Not infrequently, however, diads or triads are also found (Figs. 36–39). Fig. 38 shows a triad with micronuclei within the cells and Fig. 39 a diad. Figs. 36 and 37 are figures of the telophase of the second division which suggest the formation of triads. The diad formation may provisionally be explained as a direct consequence of the formation of a restitution nucleus, which is highly likely to take place in *Narcissus*.

SUMMARY.

1. The somatic number of chromosomes in some garden varieties of the narcissus plant was determined in root-tips. There are 5 diploid, 4 triploid, 2 tetraploid, 1 hexaploid and 7 heteroploid plants so far as the present investigations are concerned.

2. The meiotic phases of a triploid variety, *N. poeticus poetarum* were observed.

3. In diakinesis and metaphase, there can be seen 7 trivalent chromosomes, the number of which is equal to the "basis" or cardinal number.

4. It was observed that while the two triplets of a trivalent element are separated regularly to the poles, the third triplet undergoes a random distribution. This third one lags sometimes behind the others, being left near the equatorial plate showing a clear longitudinal split. This behavior results in different combinations and different numbers of chromosomes at the poles.

5. The chromosome numbers in homotype division are 10 : 11, 10 : 12, etc. as is to be expected from the behavior of chromosomes in the first division.

6. Micronuclei are frequently formed as a result of the heterotype as well as the homotype division.

7. Certain abnormalities which remind us of the restitution nucleus can be seen.

8. Diad or triad pollen cells are also seen besides normal tetrad pollen cells.

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