

Cytogenetics of *Verbena Tenera* Spreng

(with Plate XXIV)

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CYTOGENETICS OF *VERBENA TENERA* SPRENG.

by

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(with Plate XXIV)

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For cytogenetical study, genus *Verbena* for a long time past has been regarded as one of the most convenient materials (BEALE, 1940). Genetical investigation reveals that most of the interspecific and intraspecific differences in other genera owe their origin to gene mutation. The cytogenetical study of the inheritance of interspecific and intraspecific differences, which in many cases become notoriously complicated by sterility of hybrids, absence of clear segregation of the various characters etc. can be carried out more easily in this genus; because, according to BEALE (1940) in *Verbena*, «some hundred years have elapsed since the initial crosses were made, and selection has led to the production of comparatively fertile and true breeding strains. There is an added advantage with *Verbena* that the diploid chromosome number is always 10, so that the complications due to polyploidy do not arise (as, for example, they do in New World cottons). Moreover the small number of chromosomes makes the determination of linkage less laborious ».

According to DE CANDOLLE (1847), the genus *Verbena* is divided into two sections, *Verbenaca* and *Glandularia*. Section *Verbenaca* contains 55 species and is again subdivided into 5 groups, while the section *Glandularia* consists of 30 species without any further subdivision. The basic number of the *Glandularia* section (chromosome number of only four species of which has been determined; JUNELL, 1934; BEALE, 1940; NOACK, 1930) and of all the members of the *Nabiles* group of the *Verbenaca* section (DERMAN, 1936) is $b = 5$. In the members of *Glandularia* section the diploid number has been found to be $2n = 10$, excepting *Verbena tenera* in which the diploid number was determined by BEALE (1940) as $2n = 30$. But the present investigation with the same species reveals quite contradictory results and the

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diploid number has been found to be $2n = 10$, as in other species of the section.

Different varieties of the species *V. tenera* Spreng. with different flower colours are cultivated in gardens for ornamental purposes.

It is commonly distributed in Brazil and Argentina, especially in South Brazil, La Plata region, Montevideo and Sello. It is also enormously cultivated in France and in different places over the whole world (JACHSON, 1885; ENGLER & PRANTLE, 1932).

No critical cytological study has yet been made on any of the species of the section *Glandularia*. The present investigation was undertaken with a view to make a comparative study of the meiotic behaviour and the karyotype of its different varieties and, if possible to study the chromosome behaviour of intervarietal hybrids, if raised. In the present investigation a report on the karyotype and chromosome behaviour of the scarlet-magenta variety is given.

MATERIALS AND METHODS

The plant is grown in the Calcutta University's Botanical Garden located in the Science College. For the study of somatic chromosomes root tips were collected from cuttings transplanted in a pot containing saw dust and sand during summer and fixed in Platinic Chloride Formalin mixture (1:2) which was found to give the best result after a series of trials with different fixatives. In the other fixatives, though the constriction regions do appear, excessive clumping of chromosomes render their study difficult.

Similarly, for the study of meiosis, flower buds were tried in different fixatives of which only Flemming's medium solution gave satisfactory results. Prefixation treatment with Semmen's Carnoy's fluid was followed in case of flower buds.

The maximum frequency of divisions both somatic and meiotic has been found to be between 9-30 to 10-30 A.M.

After fixation of material both, root tips and flower buds, were washed and dehydrated and cleared in alcohol-chloroform grades and finally embedded in paraffin in the usual way. Paraffin sections of both root tips and flower buds were cut at 18μ to 20μ thickness.

For the study of both somatic and meiotic chromosomes, the sections were stained with the Crystal Violet Iodine technique. Bleaching in a solution containing H_2O_2 and 95 % alcohol (1:1) overnight, hydrolysis in normal HCl for 15 minutes and an overnight premordanting in 1 % chromic

acid have been found to be essential to bring out good results with Crystal Violet technique.

Observations were made with Leitz microscope with a compensating eye piece $\times 10$ and an apochromatic objective of 1.3 N.A. Drawings were made with Zeiss Abbe camera lucida using 1.3 N.A. apochromatic objective with a compensating eye piece $\times 18$ giving a total magnification of $\times 3600$ approximately.

OBSERVATION

The present investigation reveals, that the morphology of the somatic chromosomes of the species involves several complexities. High number of secondary constrictions and satellites, has been found in all the chromosomes. Total number of nucleolar constrictions is as high as 28 while the diploid chromosome number is only 10. Such a high number has also been reported by BHADURI & BOSE (1947) and CHAKRAVARTI (1948) but in the present case the number of constrictions is higher in proportion to the low number of chromosomes.

The abnormal behaviour of chromosomes during meiosis is much more frequent than the normal behaviour, though the abnormalities observed are not of various types. The high percentage of irregularities may be correlated with the high percentage of pollen sterility, which has been found to be near about 43 %.

Karyotype analysis:

Diploid number of chromosomes in this species has been found to be $2n=10$ (Fig. 1), as has commonly been found in the other species of the section *Glandularia* of *Verbena*. BEALE (1940) has reported, however, the chromosome number to be $2n=30$, from an Italian variety of *V. tenera*. It is quite likely that the plant examined by BEALE (1940) was a polyploid one.

The karyotype of this species consists of medium sized chromosomes, ranging from 2.20μ to 2.79μ in length. In order of length, the chromosomes of the complement may be divided into two types, mainly long and short. If the morphology of the chromosomes in relation to the position of primary constriction and position and number of secondary constrictions and satellites is taken as the criteria of classification, the five pairs of chromosomes may be classified into five distinct following types. (Fig. 2).

Long chromosomes:

Type A: - (2.79 μ appx.) A pair of long chromosomes with a submedian primary constriction, the longer arm possessing a secondary constriction and a satellite. The shorter arm has also one secondary constriction making the total number of constrictions in each member, leaving the primary one, to be three. (Fig. 2, A).

Type B: - (2.70 μ appx.) A pair of long chromosomes with a more or less median constriction, both the arms possessing a terminal satellite. One of the arms has an additional secondary constriction. (Fig. 2, B).

Short chromosomes:

Type C: - A pair of short chromosomes (2.32 μ appx.) with a pronounced submedian primary constriction. The shorter arm has got a secondary constriction. The longer arm possesses a secondary constriction near the primary one and an additional secondary constriction. (Fig. 2, C).

Type D: - (2.32 μ appx.). It is a short chromosome pair with a more or less median primary constriction; one arm possess one secondary constriction and a terminal satellite and the other arm a secondary constriction only. (Fig. 2, D).

Type E: - (2.20 μ appx.). A pair of short chromosomes with a submedian primary constriction. The longer arm possesses a secondary constriction and the shorter arm a terminal satellite (Fig. 2, E).

Meiosis:

During meiosis in normal cases of division, five bivalents showed usual condensation along with terminalization of chiasmata (Fig. 3). Multivalent formations of different types were observed to occur in a few buds in this variety. Cases with two trivalents, one trivalent and one univalent were also met with (Figs. 4 & 5).

In metaphase I, five bivalents were observed showing different configurations (Fig. 6). All the bivalents in the same equatorial plane were found together only in rare cases, which gives an explanation of high percentage of nondisjunctions found in the later stages.

In the early anaphase, in some of the P. M. Cs, nondisjunctions of more than one bivalent and early separation of some bivalents were also often met with (Fig. 7).

In addition to normal dyads (Fig. 9), formation of micronuclei in the dyad stage was also observed in different cases (Fig. 8).

Tetrad formation is of the simultaneous type. Pollen grains are generally triangular. Percentage of pollen sterility in this variety has been counted to be 43 %.

DISCUSSION

1. - *Chromosome number and its relation to Ecology:*

BEALE (1940) first reports the chromosome number of *Verbena tenera* along with other species of the section *Glandularia* to be $2n = 30$. All the other species of the section, so far reported by other previous authors (JUNELL, 1934; NOACK, 1930) as well as by himself (BEALE, 1940) exhibit their somatic complement to be an ordinary diploid one having $2n = 10$ chromosomes. The report of a species of the same section with 30 chromosomes in the body cell complement demonstrates an abrupt lift isolated from the related members, where ten is the common number of chromosomes in the body cells.

The present investigation however, with an Indian *V. tenera* reveals that the material investigated is an ordinary diploid one possessing $2n = 10$ chromosomes. It can be suggested that the previous report of sudden increase in the number of chromosomes of the same species is due to the increase in the number of genomes, probably as a consequence of some external inducement.

Previous investigation with different angiospermous species, viz. *Tradescantia virginiana*, *Biscutella*, the Scandinavian polyploid types of *Ericaceae* and other species and genera, as well as the survey of the angiosperm flora of Schleswing-Holstein and other different floras have clearly demonstrated that (a) the percentage of polyploid types is twice as great among northern species as among southern ones, (b) diploids predominate on lime-poor soils while the polyploids constitute 95 p. c. of the species found on the lime-rich soils, and (c) polyploidy may be induced by severe cold as well as by the influence of extremely hot and dry habitats.

Verbena tenera which is mainly distributed in tropical South America and enormously cultivated all over the world, may in every possibility be a species of tropical origin with ten chromosomes in the somatic set, as has been reported here from a material belonging to tropical regions. It is very likely that owing to an extensive cultivation in temperate regions, from where $2n = 30$ has been reported, hexaploidy arose in at least some of the varieties of the species as a consequence of some environmental sudden changes.

Of course, unless a thorough search as to the chromosome number of the species and varieties growing in different localities is carried out, it would not be possible to arrive at a definite conclusion about the origin of the species.

Anyhow the study of the meiotic behaviour of chromosomes of the species, in the present investigation gives sufficient proof of its truly diploid nature with $b = 5$ chromosomes, and any deviation from this number must be regarded as being due to derivation from this original number caused as a result of some sort of influences.

2. - *Nondisjunction of chromosomes:*

Different modes of irregular segregations including mainly nondisjunctions in the microsporogenesis studied here suggest the possibility of origin of an aneuploid series of plants in nature, e. g. monosomic ($2n - 1$), trisomic ($2n + 1$), tetrasomic ($2n + 2$) etc., depending on the number of chromosomes contained in the uniting gametes.

A thorough search is highly desirable in *V. tenera*, taking into consideration the minute phenotypic differences.

The high number of pollen sterility (43 %) may be the result of meiotic irregularities observed in the species. But the percentage of irregularities observed are much too high in proportion to the percentage of pollen sterility, occurring in the species.

It probably suggest that pollens with only one extra chromosome or deficient in only one chromosome, retain their viability, maintaining also their more or less normal morphology.

3. - *Numerically normal diploid plants with abnormal genomic constitution.*

If such types of irregularities, as has been observed during microsporogenesis, occur during macrosporogenesis too, then we may expect plants occurring in nature, produced by the combination of gametes, one having one chromosome extra and the other one less, and such plants may have the chance of having 10 chromosomes but with one chromosome deficient and another duplicated in the complement.

The origin of such plants, having normal number but abnormal constitution is only possible when the gametes deficient in one chromosome, is deficient in that particular chromosome which is not in duplicate in the other gamete. To explain further, the gametic constitution of the uniting pair producing such a plant would be ABCDEE and ABCE respectively (if the chromosome type of *Verbena* be represented as ABCDE). Such plants would have a complement of 10 chromosomes, where E chromosome is represented thrice and D only once.

Multivalent and univalent formations are expected during meiosis of such plants. As has been mentioned in the text, it has already been noted

in some of the buds of *V. tenera*. It is quite likely that if a thorough search is made, karyotypes of these plants would reveal the presence of one chromosome represented thrice, the other only once. This would be the cause of the origin of plants having normal chromosome number but with abnormal genomic constitution.

On the basis of this hypothesis, the formation of multivalents in this species which is evidently a diploid one, may easily be explained without assuming translocations. Such types of phenomena have also been met with and thus accounted for by BHADURI and SHARMA (1946) in *Datura fastuosa* with the normal diploid chromosome number $2n = 24$.

4. - Increase in number of nucleoli:

An unusually high number of secondary constrictions (28) in the species with a very low number of chromosomes in the diploid set ($2n = 10$) has been reported for the first time in the present paper. BHADURI and BOSE (1947) counted as many as 26 nucleolar constrictions in the male plants of *Trichosanthes dioica* ($2n = 24$). CHAKRAVARTI (1948) reports 30 nucleolar constrictions in *Musa superba* ($2n = 18$), and as many as 50 in a tetraploid variety, Amritsagar, of *M. paradisiaca* ($3n = 33$). The corresponding number of nucleoli in telophase has also been counted.

It is now well-established that there is a direct correlation existing between the maximum number of nucleoli present in a species and the total number of secondary constrictions in the chromosome complement (GATES, 1942; BHADURI, 1940, 1941, 1942 *a,b,c*, 1944; BHADURI and SHARMA, 1946; SHARMA, 1947; BHADURI and BOSE, 1947; DATTA, 1952, 1953). The high number of secondary constrictions which in *V. tenera* is 28, suggests possibly the presence of a high number of nucleoli in the somatic complement. Unfortunately, however, the nucleolar observations could not be carried out in the present case, due to the unavailability of suitable quality of reagents.

DE MOL (1928) first suggested that the number of nucleoli generally represents the number of genomes present in a species. In *Hyacinthus* spp. he found that haploid cells have one, diploid two and triploid three nucleoli. Later the work was further elaborated by GATES and his collaborators (1939, 1942). Apart from this simple process of increase in the number of nucleoli through polyploidy, there are records of more complicated processes by which an increase in the number of nucleoli may be brought about. Thus secondarily balanced polyploids which were originally known to be diploids, were found to possess more than two nucleoli (NANDI, 1936, RAMANUJAN, 1938; GATES, 1939; IYENGAR, 1939; SIKKA, 1940; PATHAK, 1940 *a* & *b*). There are other cases also where the presence of more than two nu-

cleoli and correspondingly more than two nucleolar constrictions could not be explained even on the basis of secondary polyploidy (McCLINTOCK, 1934; WOODS, 1937; SINOTO, 1938; MATSUURA, 1938; BHADURI 1942 *a, b* & *c*). Some of these anomalous cases have since been explained as due to their structural hybrid nature produced as a result of reciprocal translocation between nucleolar and non-nucleolar chromosomes. (McCLINTOCK, 1934; BHADURI, 1942 *a, b*, & *c*; BHADURI and BOSE, 1947). CHAKRAVARTI (1948) put forward several proofs and arguments in support of the view that the fragmentation of chromosomes like several other means of increase in the maximum number of nucleoli, may as well bring about an increase in the number of nucleoli and that the number will be increased by the number of loci that have undergone breaks.

The meiotic behaviour of *V. tenera* as well as its chromosomes' number which is too low suggests its true diploid nature, beyond all doubts. Therefore it is absurd to think that this twenty eight secondary constrictions which if nucleolar, and in each probability which it is, could by any chance be brought about by 28-ploidy of the species. So, the other two alternatives would be (1) that these have come about through nonhomologous interchanges involving nucleolar chromosomes; or (2) a high number of secondary constrictions was already present in the basic complement.

As to the first alternative, though the presence of supernumerary constrictions suggests its origin through structural changes of chromosomes still no evidence of ring formation, a definitive clue to structural hybridity has been encountered during meiosis. It is quite likely, however, that the different varieties of *V. tenera* occurring in nature may differ in the number of their nucleolar constrictions, if we assume that such translocations play an important role in the evolutionary process of the varieties of *V. tenera*. In that case the occurrence of ring chromosomes allowing the homologous segments to pair with each other is expected in such intervarietal hybrids the parents of which are all supposed to be homozygous for translocation. Thus, extensive hybridization in different strains of *V. tenera* may provide a good material for the identification and classification of chromosome ends of *Verbena* as been done in case of *Datura* by BERGNAR (1943), *Zea* by Mc CLINTOCK (1934), *Tradescantia* & *Rhoeo* by BHADURI (1942 *a* & *b*), BARLEY by TJIO & HAGBERG (1951). But unless conclusive data are obtained in this direction it would be a premature decision to designate *V. tenera* as originating through the union of such gametes containing translocation.

As regards the second alternative, it is worth mentioning here that the original concept of DE MOL that a genome must have one nucleolus and

one nucleolar constriction has already been questioned by BHADURI and BOSE (1947) and CHAKRAVARTI (1948). It has been suggested that a genome may have more than one nucleolus and even supernumerary constrictions (cf. BHADURI and BOSE in *Curcubita*; 1947). If the above suggestion be proved to be correct, then it is possible to visualize such a high number of nucleolar constrictions to be originally present in the basic complement of *Verbena tenera*.

From all the above evidences, it is quite clear that unless a thorough search into cytogenetics of different varieties of *V. tenera* is made, it is not all possible to claim confidently any way as to the origin of such a high number of secondary constrictions in the diploid species, *V. tenera*.

SUMMARY

1. - Chromosome number of an Indian strain of *Verbena tenera* Spreng. ($2n = 10$) has been determined, both from the study of somatic and meiotic chromosomes. The report is in contrast to that of BEALE (1940), where the chromosome number has been claimed to be $2n = 30$ in an Italian variety of the species.

V. tenera is mainly distributed in Tropical America. So, it has been suggested that probably the plant is tropical originally with 5 chromosomes in the basic set, and the variety studied by BEALE is a hexaploid one, the number of genomes being increased as a result of some environmental disbalance.

2. - In course of a study of the microsporogenesis, different types of meiotic irregularities, including nondisjunctions, have been met with. Taking all these into account, as well as from a study of pollen sterility, it has been suggested that plants with aneuploid series are expected in nature.

3. - Occurrence of multivalents in some plants with $2n = 10$ chromosomes, has been explained as due to the production of plants resulting from a combination of two abnormal gametes, one deficient in one chromosome the other having an extra one, the extra chromosome being not of the same type, which is absent in the other.

Without assuming translocation, this provides a means of the origin of plants with normal diploid chromosome number, the genomic constitution of which is different from the normal.

4. - An unusually high number of secondary constriction which has been found to be 28 in plants having such low number of chromosomes is for the first time reported in the present paper. It has been suggested that the high number of nucleolar constrictions was either present in the original

set or it has come about through nonhomologous interchanges involving nucleolar chromosomes.

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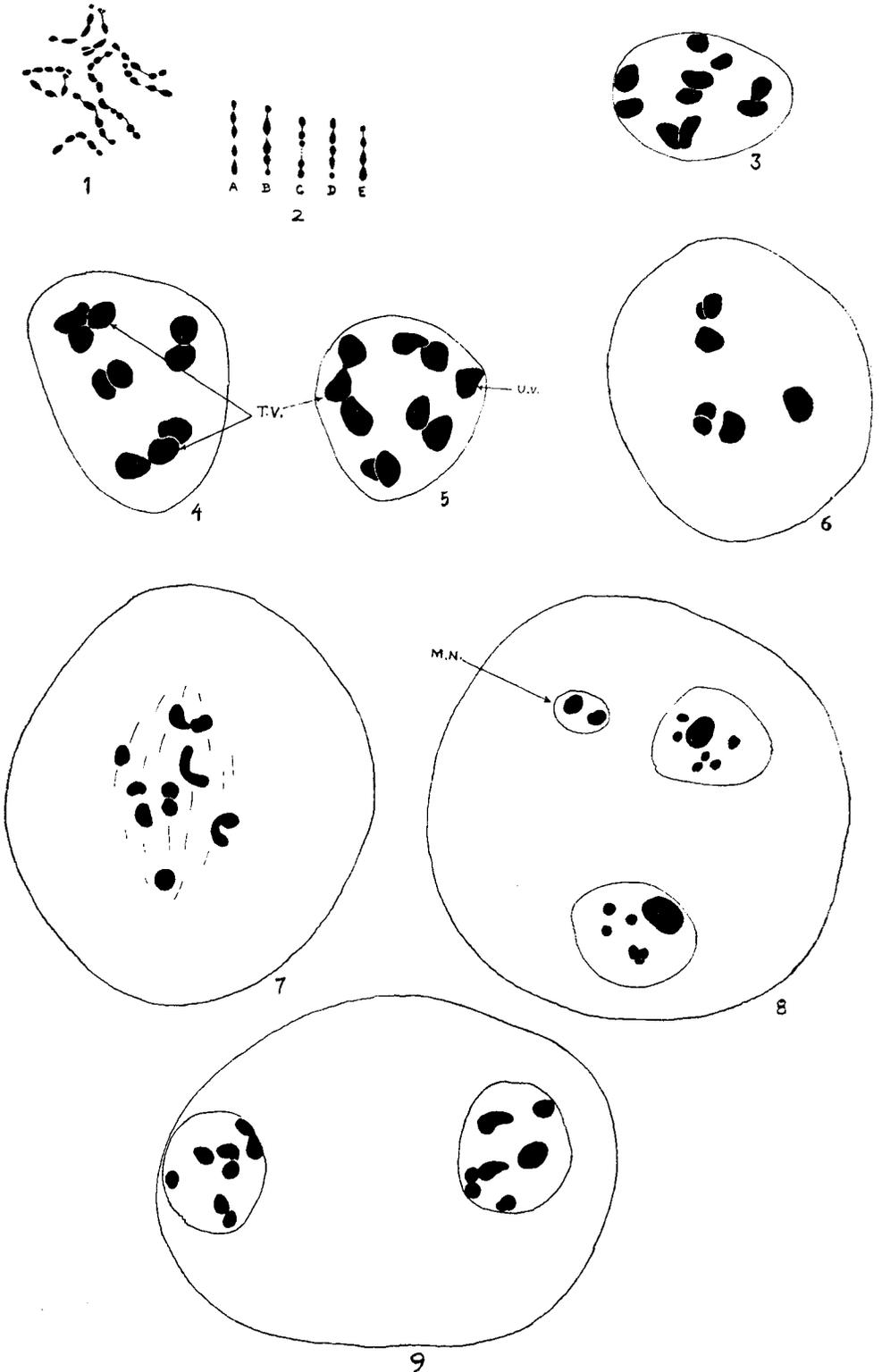
In conclusion, I wish to express my sincerest gratitude to Dr. P. N. BHADURI, under whose guidance the work was originally started and to Mr. A. K. SHARMA, for kind guidance since Dr. BHADURI's departure from the department. My thanks are also due to Dr. A. K. CHAKRAVARTI for his kind help and to Prof. P. C. SARBADHIKARI for the facilities provided.

Explanation of Plate XXIV.

Figs. 1-9. *Verbena tenera* Spreng.: 1 & 2, Somatic metaphase plate and idiogram respectively. 3, Normal diakinesis stage. 4 & 5, Diakinesis stages showing a univalent (U. V.) and trivalents (T.V.). 6, Normal meiotic metaphase stage. 7, Meiotic anaphase stage showing non-disjunction and early separation of bivalents. 8, Dyad stage showing a micronucleus (M. N.). 9, Normal dyad stage.

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RIASSUNTO

1 - Il numero dei cromosomi di un ceppo indiano di *Verbena tenera* Spreng. è risultato $2n = 10$, e il reperto di questo numero, determinato sia nelle mitosi somatiche sia durante la meiosi, è in contrasto con il reperto del BAELE (1940) che su una varietà italiana della specie trovò $2n = 30$.

Siccome *V. tenera* è diffusa anche nell'America tropicale, è stata avanzata l'ipotesi che la pianta sia di origine tropicale con un corredo base di 5 cromosomi, cosicchè la varietà studiata dal BAELE sia esaploide, e che l'aumento del numero dei genomi sia l'effetto di uno squilibrio ambientale.

2 - Durante lo studio della microsporogenesi sono state riscontrate irregolarità meiotiche di tipo diverso, compresa la non disgiunzione. Tale reperto, in aggiunta a quello della sterilità pollinica, permette di prevedere la presenza in natura di piante aneuploidi.

3 - La presenza di multivalenti in alcune piante con $2n = 10$ cromosomi è spiegata come dovuta alla produzione di piante generate dalla combinazione di due gameti anormali, uno deficiente di un cromosoma, l'altro avente un cromosoma supplementare di tipo diverso da quello deficiente nel primo.

Senza dover ricorrere all'ipotesi di traslocazioni cromosomiche, è questo un meccanismo di produzione di piante con numero diploide normale, la cui costituzione genomica sia differente da quella normale.

4 - E' riportato per la prima volta in questa memoria il reperto di un numero straordinariamente elevato di costrizioni secondarie, che sono state riscontrate ascendere a ben 28, in piante con un così basso numero di cromosomi. Si pensa che l'alto numero di costrizioni nucleolari fosse presente anche nel corredo originario, oppure che esso sia sorto per mezzo di scambi tra cromosomi non omologhi in cui siano stati coinvolti i cromosomi nucleolari.
