A DESINAPTIC MUTANT IN RICE[1]

(A Preliminary Note)

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Occurrence

An attempt was made in 1958 to induce rice mutations through irradiations. Dry seeds of two varieties, Taichung No. 65 and Chainan No. 8, were irradiated with various doses of X-rays and thermal neutrons. Among the R_2 progenies of such irradiated materials one line, 210–4 (Chainan No. 8, irradiated with 3.99×10^{13} nth/cm^2 thermal neutrons), was noticed to segregate with normal and sterile plants as follows:

Class	Per cent of seed set per plant	No. of plants
Normal	71.1–88.5	27
Sterile	0.1– 0.9	7

Although the population is not large, segregation of normal and sterile plants into 3:1 ratio is indicated ($X^2=0.354$, $0.50<P>0.30$). Upon checking the microsporocytes of 8 normal and 3 sterile plants, it was found that while the 8 normal plants show invariable 12 bivalents at diakinesis and first meiotic metaphase, the sterile plants have about 8 bivalents and 8 univalents at these stages. Two sterile plants have been propagated vegetatively and a number of spikes have been picked from these plants and checked cytologically. Failure of pairing of a number of chromosomes at diakinesis and first meiotic metaphase was observed in all the spikes. Thus, the low fertility of the sterile plants is evidently caused by such abnormal meiotic division which is due to a monogenic recessive arisen as a mutant, since the sterile plants have the external morphology and coloration characteristics of their normal sibs.

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(1) The writers are grateful to Dr. Seymour Shapiro, Brookhaven National Laboratory for having supervised administration of the X-ray and thermal neutron treatment and to Prof. Y. L. Ku, agronomy Department, National Taiwan University, for having critically read the manuscript.

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Similar mutants have been found in a number of plants, such as maize (Beadle, 1930, 1933), *Rumex* (Yamamoto, 1934), *Datura* (Berger, Cartledge, and Blakeslee, 1934), *Nicotiana* (Goodspeed and Avery, 1939), common wheat (Li *et al*, 1945), *Tradescantia* (Celarier, 1955), *Sorghum* (Krishnaswamy and Meenakshi, 1957), and Andropogoneae (Celarier and Mehra, 1959). In describing such mutants, both asynapsis and desynapsis have been used by investigators. However, the majority of cases described under asynapsis has normal chromosomal pairing at early meiotic prophase. As it will be mentioned in the latter section, the mutant described in this note has normal chromosomal pairing at early meiotic stages of microsporogenesis and falling apart a part of homologous chromosomes occurred mostly at diplotene. It seems to the writers that the term "desynapsis" describes this mutant more properly and hence desynapsis is adopted in this note.

Meiosis in Desynaptic Plants

Cytological studies of the desynaptic plants were confined to the microsporocytes. The spikes were fixed in acetic alcohol and usual iron aceto-carmine smear method was employed throughout the entire study. Drawings were made under the microscope with the aid of a camera lucida at the magnification of ×2,000.

First Meiotic division: Little is known about the early meiotic prophase of rice due to smallness of its chromosomal size. However, in those spikes of the desynaptic plants showing a great number of univalents at diakinesis and first meiotic metaphase, normal pairing of chromosomes can be observed at pachytene stage. Separation of a part of the homologous chromosomes is found but the case is very rare. Thus, most chromosomes synapsize in a normal way at the early meiotic prophase. Falling apart of chromosomes occurs at diplotene and, as a result, varying number of univalents is observed at diakinesis and first meiotic metaphase. Similar phenomena have been observed in the asynaptic maize (Beadle, 1930, 1933), desynaptic common wheat (Li *et al*, 1945), and many other asynaptic or desynaptic mutants.

At diakinesis of the desynaptic plants, the number of univalents varies from cell to cell as indicated in Table I. It presents the frequency distribution of cells with varying number of univalents at diakinesis found in different spikes of the sterile plants. The average number of univalents per cell of a spike also shows variation among different spikes of the same plant but picked on different date. It is not certain whether or not such variation also exists among the different plants since only two sterile plants have been studied extensively.

Table I. Frequency of Cells with Stated Number of Univalents at Diakinesis

Plant and spike No.	No. of univalents													No. of observed cells	Av. No. of univalents per cell
	0	2	4	6	8	10	12	14	16	18	20	22	24		
210-4-3-1		2	2	8	5	4	3	1						25	7.60
-2			1	1	3	4	2	2	5	8	2	1		29	14.21
-3	1		1	2	9	3	5	4	6	4	3		2	40	12.75
-4		1	2	2	6	2	7	2	3	3	3	1		32	12.06
-5	9	10	5	2	2									28	2.43
Total	10	13	11	15	25	13	17	9	14	15	8	2	2	154	10.17
210-4-34-1	1	3	3	1	2	1	3	2	1	1				18	8.22
-2		5	4	3	1	2	9	2	1					27	8.30
-3					1	1	6	3	2	1	1			15	13.47
Total	1	8	7	4	4	4	18	7	4	2	1			60	9.57

Table II presents the frequency distribution of univalents at first meiotic metaphase counted from the spikes from which the frequencies of univalents at diakinesis were also determined (Table I). By close examination of these two tables, it is interesting to note that within the same spike, the average number of univalents per cell is decidedly lower at mataphase than at diakinesis. Only in two spikes the reverse is true. But in these two spikes the number of univalents is small. Should separation of chromosomes commence at first meiotic prophase and proceed onward, the number of univalents at first meiotic metaphase would be greater than that at diakinesis or at least this number would be similar at these two stages.

Table II. Frequency of Cells with Stated Number of Univalents at Metaphase I

Plant and spike No.	No. of univalents													No. of observed cells	Av. No. of univalents per cell
	0	2	4	6	8	10	12	14	16	18	20	22	24		
210-4-3-1	2		8	3	7	3	2							25	6.40
-2			2	4	10	10	1	1						28	8.50
-3		4	3	13	10	11	6		2					49	8.00
-4	2	8	5	13	7	10	5	1						51	6.74
-5	7	5	7	4	3	2								28	3.78
Total	11	17	25	37	37	36	14	2	2					181	6.85
210-4-34-1	2	9	2	7	6	5	4	2						37	6.54
-2		4	2	1	2	3		1	1					14	7.00
-3	1	6	3	6	6	3	4							29	6.41
Total	3	19	7	14	14	11	8	3	1					80	6.57

Sakai (1940), in his study of unusual asynaptic division of microsporocytes of three varieties of rice which he attributed to the effect of unusual weather, found that the number of asynaptic cells was high at diakinesis and decreased at first meiotic metaphase. He explained this phenomenon as due to strong repulsion at diakinesis that pushed apart the homologous chromosomes. After this, force diminished at metaphase and attraction between homologous chromosomes caused reunion of some bivalents. The discrepancy of univalent frequencies between diakinesis and first meiotic metaphase of the same spikes found in this experiment may be explained by the same theory as Sakai proposed. Diakinesis is the stage of greatest contraction of chromosomes. Strong repulsion may break some connections between homologous chromosomes even in the normal organisms, especially this is true in those with small chromosomes (Darlington, 1937). It seems probable that in the desynaptic plants, the repulsion at diakinesis might break all the connections of those bivalents which are already in poor association. Such repulsion will eventually lead to a great number of separated chromosomes or of chromosomes connected only at the terminal part by fine threads hardly visible under microscope. In fact, difficulties are encountered in determining the number of univalents at diakinesis since it is observed that the two homologous chromosomes may lie far apart but with a very fine thread connected at the terminal portion of such univalents. For this reason, errors involved in the diakinesis determination may be relatively large. However, there is no doubt that the number of univalents is greater at diakinesis than at first metaphase in the majority of spikes studied. As meiosis proceeds from diakinesis to first metaphases the repulsion diminishes and attraction between homologous chromosomes causes some chromosomes to pair again. The number of univalents becomes greater at diakinesis than at first meiotic metaphase, and the same is true even in the number of chiasmata formed. This case has been observed by Beadle (1933) in maize, the chromosomes of which are suitable for such analysis. Beadle found that in the asynaptic maize plants the average number of chiasmata per bivalent is 1.1 at diakinesis in contrast to 1.4 at first meiotic metaphase. No definite explanation has been made by him on this point.

In those microsporocytes having few univalents, their metaphase bivalents are comparable to those of the normal sibs in shape and size, and in orientation as to the regularity of distribution on equatorial plane (Fig. 2). While in those cells with a greater number of univalents the bivalents are mostly open type, i.e. the homologous chromosomes are connected by terminal chiasmata. Bivalents under such cases are often not orderly arranged in the spindle. Multivalents have been observed (Fig. 5) in some cases.

At first meiotic metaphase, the univalents are scattered all over the spindle.

Their distribution is very irregular. Groups of 2, sometimes 3 or more, univalents in close proximity are often observed (Figs. 3, 4). Judging from their shape and size, 2 univalents lying in close proximity are mostly homologous chromosomes.

At anaphase I, the distribution of chromosomes to the poles shows all the combinations like 1+23, 2+22, and so on to 12+12. The univalents may lag behind and form micronuclei at later stages or may divide (Figs. 7, 15) simultaneously with the bivalents. As a result of these irregular divisions, 2 unequal-sized cells are formed in many microsporocytes.

Second meiotic division: Second meiotic division from metaphase onward has been observed in a great number of cells of the desynaptic plants. The behavior of second meiotic metaphase is much more regular than the first one. However, as a result of irregular distribution of chromosomes in the first meiotic division, cells with varying number of chromosomes are observed. In rare instances, present the all 24 chromosomes in a single cell (Fig. 10). Since such cells have the shape and form comparable to that of the microsporocytes, they probably resulted from the failure of first meiotic division. Lagging chromosomes are found in some cells at anaphase II. Groups of 2 or 3 chromosomes are also noticed in some cells at this stage.

Fragmentation: The diminutive chromosomes described by Beadle (1930) in the asynaptic maize are noticed in this mutant at several stages of both first and second meiotic divisions (Figs. 8, 11). They may arise through the fragmentation of chromosomes or chromatids and are eventually lost during the course of meiosis.

Tetrads of spores: As a result of many irregularities of microsporogenesis in the desynaptic plants, tetrads formed are mostly aberrant types. Each tetrad contains from one to six cells as indicated in Table III. Although tetrads with 4 cells are greatest in number, yet even in such tetrads the cells are often unequal in size. The microspores soon degenerate and the mature anthers contain mostly aborted pollen grains (Fig. 17).

Table III. Frequency of Spores Per Sporocyte

Plant No.	No. of cells per tetrad					
	1	2	3	4	5	6
210-4-3	1	30	75	241	6	1
Per cent	0.3	8.5	21.1	68.1	1.7	0.3
210-4-34	26	99	146	246	15	2
Per cent	4.9	18.5	27.3	46.1	2.8	0.4

Progenies of the desynaptic plants

Before the desynaptic behaviour was all determined, a few seeds harvested from the sterile plants were planted. Three plants survived and cytological examinations of which has revealed that they all have 24 chromosomes. Normal meiosis has been observed in two plants while the third one shows desynapsis and is completely sterile. The normal progenies might have been arisen from the fertilization of haploid egg of the desynaptic plant with haploid sperm from outside source. The desynaptic plant could have come from zygote through the fusion of 2 haploid gametes of the desynaptic parent.

Discussion

Asynapsis or desynapsis has been observed in a number of plant genera since the pioneer work of Beadle in maize. In most of these cases, it is due to a monogenic recessive. However, such abnormal meiosis has also been observed in some plants grown under unusual conditions. Thus, Matsuura (1937) observed both asynapsis and desynapsis in the pollen mother cells of *Trillium* after being treated with high temperature. Sakai (1940) noticed partial asynapsis in 3 rice varieties planted at Sappora in 1933. He attributed such abnormal meiosis to the unusual weather prevailing in that year.

Asynaptic mutant in rice was first reported by Ramanujam and Parthasarathy in 1935. They observed an asynaptic mutant plant in the seed multiplication block of the strain No. 4. The chromosomes of this plant exhibited normal synapsis at early meiotic prophase but all fell apart at diakinesis. As a result, no bivalents were seen at first meiotic division. Jones and Longley (1941) in their study of sterility and aberrant chromosome number in Caloro and other varieties of rice, briefly mentioned 4 partial asynaptic plants, two of which had no normal anthers.

The desynaptic mutant reported in this note shows monogenic recessive segregation even in a small population. Its desynaptic behavior has been confirmed in its progenies. This mutant resembles that reported by Ramanujam and Parthasarathy with regard to the normal synapsis at early meiotic prophase but differs from that which did not form bivalents at diakinesis and first meiotic metaphase and did not have diminutive chromosomes at any stage. Prakken (1943) classified the asynaptics or desynaptics into 3 types, namely (1) weak, (2) medium strong, and (3) complete. Thus the asynaptic mutant reported by Ramanujam and Parthasarathy may be described as complete while the mutant reported in this note may belong to the medium strong type.

A number of reports has indicated that medium strong desynapsis or asynapsis shows considerable variation in accordance with the environmental factors. Thus, in an asynaptic mutant in *Nicotiana sylvestris*, Goodspeed and Avery (1939) found that high temperature and low humidity promote a large number of asynapsis while high humidity and low temperature induce little or no asynapsis. Li *et al* (1945), in their extensive study of the desynaptic mutant in common wheat found that the mean frequency of bivalents of the desynaptic plants may show variation in relation to temperature.

The desynaptic mutant described in this note also shows variation in univalent frequency among different spikes of the same plants, especially at diakinesis. Experiment has been carried out to grow the desynaptic plants in the temperature-controlled rooms and investigated their behaviour in meiosis. No detailed data are available. Further studies would be necessary before a definite conclusion can be reached.

Summary

A desynaptic mutant of rice occurring in the thermal neutron-treated progenies is described in this note. It is evidently controlled by a monogenic recessive.

Meiosis in the desynaptic plants is characterized by normal synapsis of the homologous chromosomes at early meiotic prophase and falling apart a part of chromosomes at diplotene. According to Prakken's classification of asynaptics or desynaptics, this mutant belongs to the medium-strong class and shows variation in univalent frequency.

Greater number of univalents per cell at diakinesis than at first meiotic metaphase within the same spikes is explained by repulsion at diakinesis and attraction of homologous but unpaired univalent chromosomes at first meiotic metaphase.

As a result of irregular meiotic divisions of the desynaptic plants, ovules and pollen grains formed are mostly aberrant types.

水稻 Desynapsis 突變型之研究

趙傳纓　李恩澤　胡慧琳

兩水稻品種之種子，經X光線與中子處理後，R_2 之一系（嘉南 8 號，經 3.99×10^{13} nth/cm^2 中子之處理），有 3 正常：1不孕之分離發生。正常植株之結實率爲71.1—88.5%，不孕者 0.1—0.9%。

經用洋紅塗片法檢查 8 正常植株，3 不孕植株之花粉母細胞，發現前者減數分裂正常，而後者雖在早前期染色體有正常之配對，但至肥厚期 (Diakinesis) 與第一中期 (First Metaphase) 有 0—24 個單價體，故分裂不正常，因此植株爲高度不孕。由上述分離情形，以及不孕植株後裔之繼續有單價體存在，知 Desynapsis 是由於一隱性突變因子之故。

同一稻穗，肥厚期之單價體往往比第一中期爲多。此可能因水稻之染色體小，在此隱性突變因子之純接合體內，肥厚期同型染色體間之相拒力 (Repulsion force)，使部分染色體分開，進入中期後，此力消失，同型染色體可能相吸而有少數能重新結合之故。

單價體數隨採集之時日而有變動，此可能與外界環境因子，如溫度等有關，將植株栽培於不同溫度之室內，而觀察減數分裂之試驗正進行中。(摘要)

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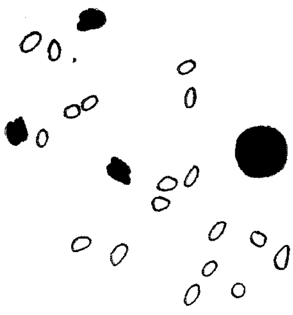
Plate I. Meiotic chromesomes in desynaptic plants

1. Diakinesis: 3 bivalents and 18 univalents.
2. Metaphase I: 11 bivalents and 2 univalents.
3. Metaphase I: 5 bivalents and 14 univalents.
4. Metaphase I: 6 bivalents and 12 univalents; notice 2 or 3 univalents in groups
5. Metaphase I: 4 bivalents, 11 univalents, and 1 multivalent.
6. Anaphase I: 2 or 3 chromosomes in groups.



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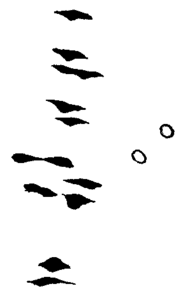

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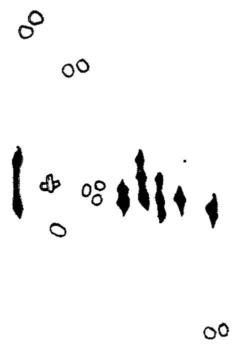

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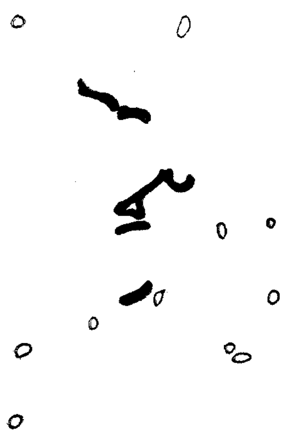

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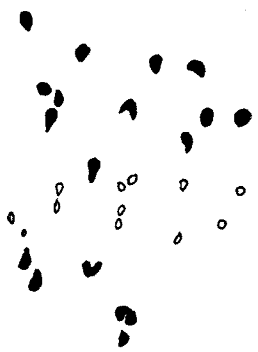
Plate II. Meiotic chromosomes in desynaptic plants

7. Anaphase I: division of univalents.
8. Telophase I: showing fragments.
9. Metaphase II: 1 single chromosome in one darghter cell, 23 in other cell.
10. Metaphase II: 24 chromosomes in a single cell.
11. Metaphase II: showing diminutive chromosomes.
12. Telophase II: showing laggards.

Plate II



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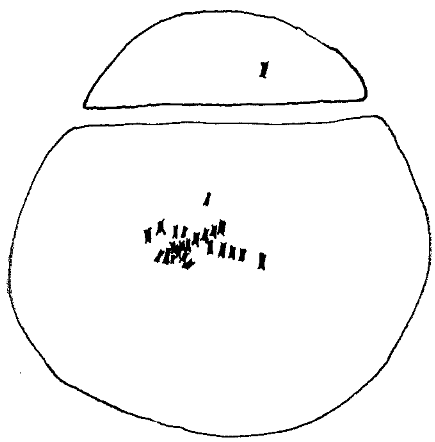

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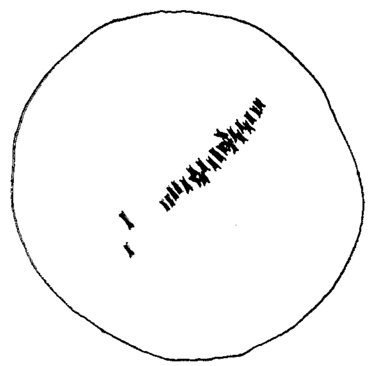

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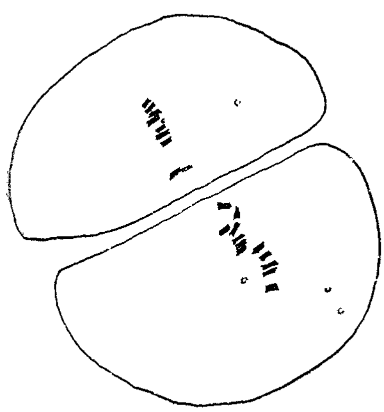

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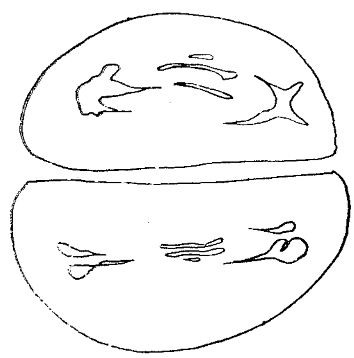

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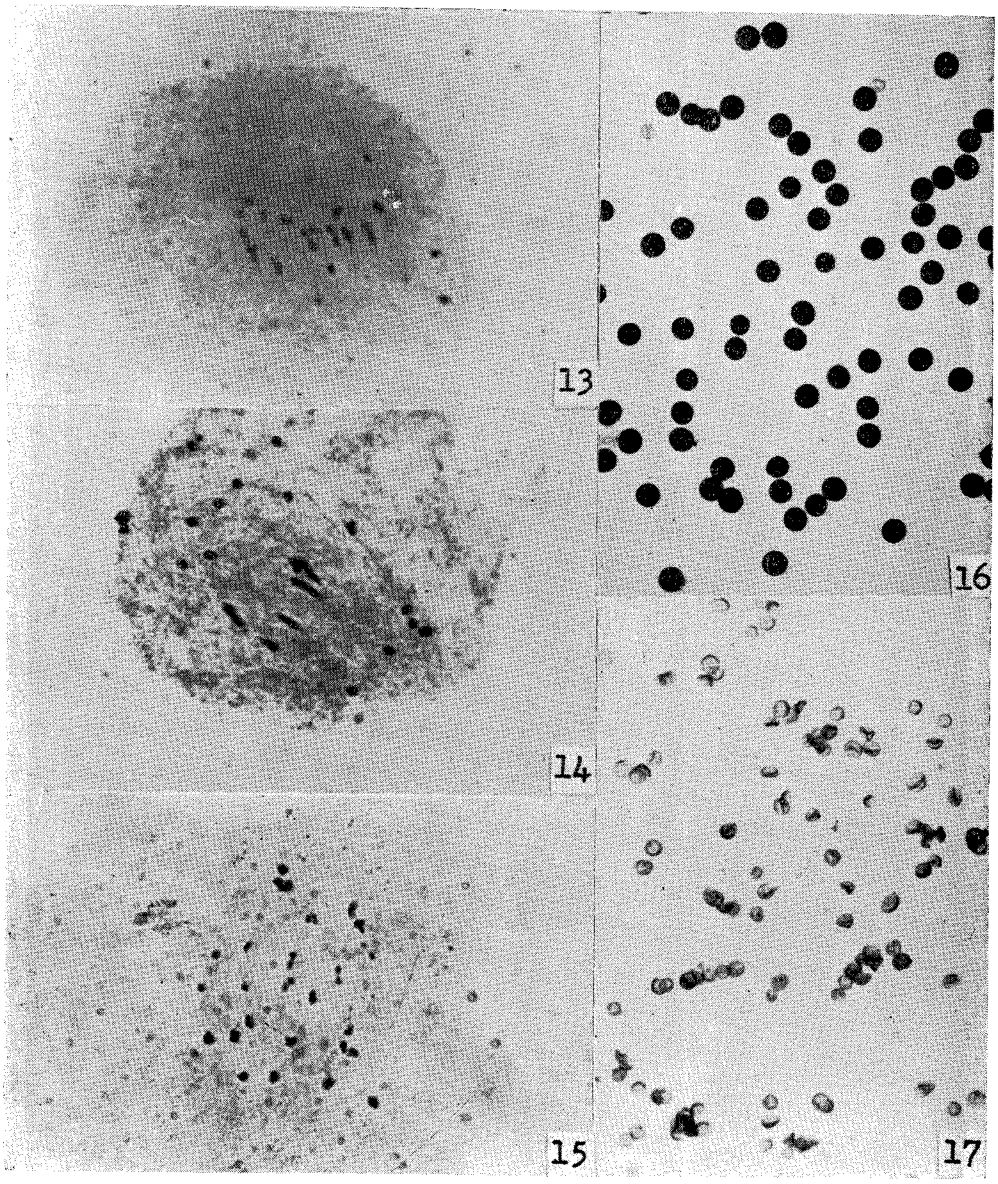
Plate III. Photomicrographs of the meiotic chromosomes and pollen grains in desynaptic plants

13. Metaphase I: 5 bivalents and 14 univalents.
14. Metaphase I: 4 bivalents and 16 univalents.
15. Anaphase I: division of univalents.
16. Pollen grains of its normal sib.
17. Pollen grains of the desynaptic plant.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