

AN ASYNAPTIC MUTANT IN RICE (*ORYZA SATIVA*).

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Received June 18, 1935.

(Communicated by Mr. K. Ramiah, M.Sc., Dip. Agri. (cantab.), L.Ag.)

1. Occurrence and Description.

IN the seed multiplication block of one of the Coimbatore strains, Co. 4, a sterile plant was noticed in the season of 1932-33. It looked slightly more erect and shorter than the others with non-emergent panicles and continued to grow and produce fresh tillers when the rest had stopped growth and ripened their ears. The flower opening was not normal in this plant and the anthers were considerably reduced and non-dehiscent. The pollen was found to be all aborted (Plate IV). The ovaries for all external appearance looked normal but would not set seed even when pollinated with normal *diploid* pollen. The plant was propagated vegetatively over two or three seasons and nearly a thousand ovaries had been cross-pollinated without any success. It would appear that ovule sterility is nearly as complete as pollen sterility. The plant resembled the parents in all its pigment and morphological characters and should evidently have arisen as a mutant.

This plant closely resembled another mutant designated 'male sterile' in external characters but differed from it in its cytological behaviour (Ramanujam, 1935). The sterility in the case of the present mutant has been found to be due to lack of pairing of homologous chromosomes at meiosis.

Similar asynaptic plants have been noted in Maize (Beadle, 1930), *Nicotiana* (Clausen, 1931) and *Datura* (Bergner, Cartledge and Blakeslee, 1934). In these cases the mutations appeared as heterozygotes which on breeding showed the mutant character to be a simple recessive to the normal. In Maize, it was further possible to confirm the inheritance by artificial crosses, as about 10% of the ovules set seed on being crossed with normal pollen. In rice, artificial crossing, to study the inheritance of this character has been unsuccessful, and heterozygous individuals occurring spontaneously have not been met with so far. The meiotic behaviour of this mutant described in this note, closely resembles that of the other asynaptic plants

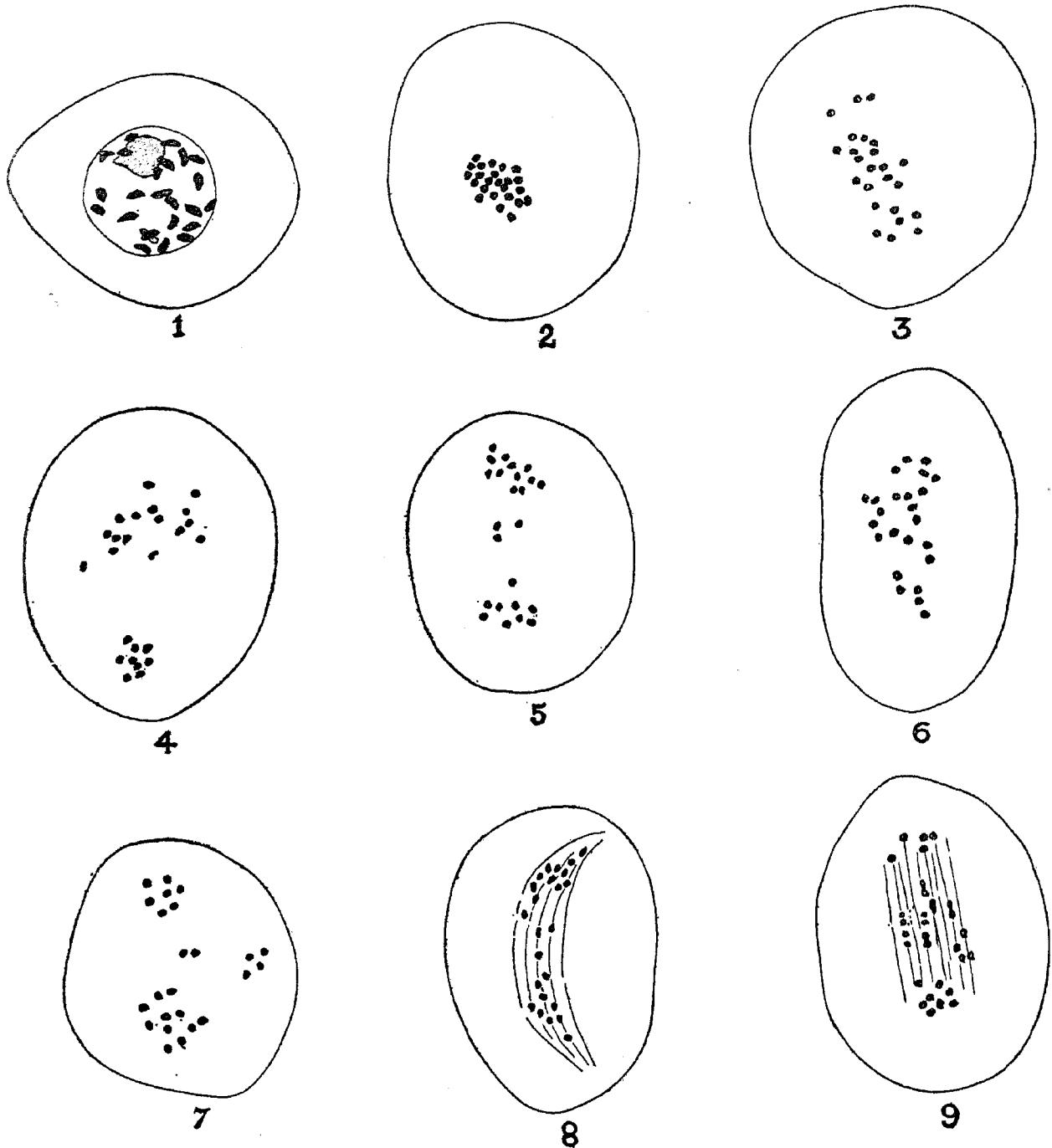
and this would appear to confirm the presumption that this mutant is genetically similar to those reported in other genera.

2. Cytology.

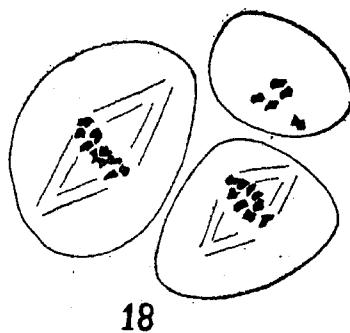
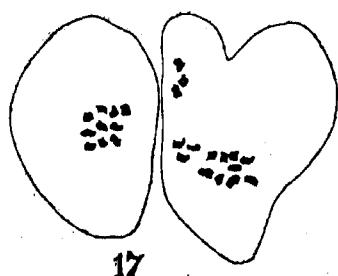
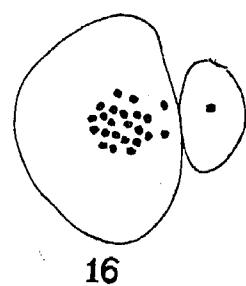
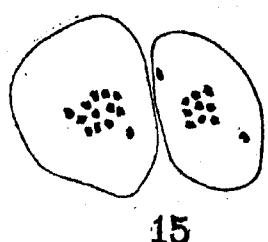
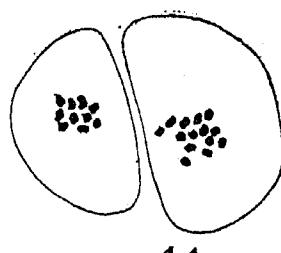
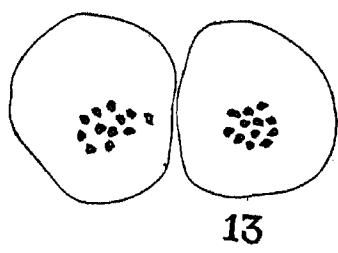
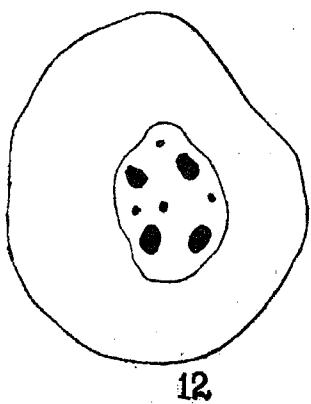
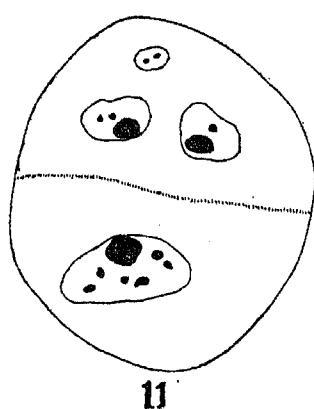
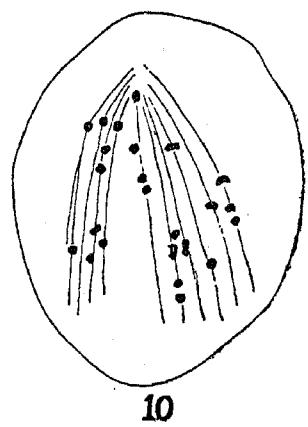
(a) *Materials and Methods.*—Studies of meiosis in the asynaptic plant were largely confined to microsporogenesis as it was difficult to get suitable preparations for a study of megasporogenesis. Aceto-carmine smears of pollen mother cells and material sectioned in paraffin and stained with Iron-Alum-Hæmatoxylin and Iodine-Gentian-Violet were largely used for the study and drawings were made with the aid of a camera lucida at 2,000 and 600 diameters and reduced to $\frac{1}{4}$ the size in reproduction.

(b) *First Meiotic Division.*—The youngest microsporocytes of the asynaptic plant exhibited 'synizesis' and resembled those of the normal. When however, the synizetic knot unloosened and the chromatin threads condensed to form the diakinetic chromosomes, no pairing was visible and later instead of the twelve bivalent chromosomes characteristic of normal plants, twenty-four univalents appeared at the stage corresponding to diakinesis (Fig. 1). At metaphase (Fig. 2) no closed bivalents were seen but chromosomes were sometimes noticed loosely attached at one end only. A true reduction division was absent and the twenty-four univalent chromosomes were irregularly distributed in the pollen mother cells at first anaphase (Figs. 3 to 7). At this stage the behaviour of the chromosomes, in several respects, resembled that of the rice *haploid* (Ramiah, Parthasarathy and Ramanujam, 1933). The chromosomes were distributed to the poles in all combinations like 1+23, 2+22 and so on to 12+12. In many cases the distribution of the chromosomes was either throughout the cell or on the spindles only. The spindles were of different sizes, shapes and number and these probably determine the distribution of the chromosomes at first anaphase. Such a connection between the spindles and chromosome distribution has already been suggested by Bergner and others in *Datura*. Some spindles were short and broad and these evidently determined such distributions as 0+24, 1+23 and 2+22. Others were long and they extended either lengthwise (Fig. 9) or in a crescent-shaped manner (Fig. 8) from pole to pole. In such cases, the chromosomes lagged at the plate and formed a third group more easily than when the spindles were short. Although one bipolar spindle was formed in most cases, tripolar and occasionally *supernumerary* and even split spindles (Fig. 10) were noted causing diverse distribution of the chromosomes at first division. Sometimes the chromosomes strayed into the cytoplasm and failing to be included in the daughter nuclei formed independent nuclei (Fig. 11). As a result of these irregular

distributions, instead of two equal cells associated with the end of first division in normal plants, two cells, more often unequal than equal, and even three cells were formed. Occasionally a portion only of the cell was



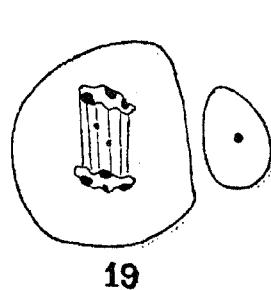
pinched off while all the chromosomes collected together in a single nucleus in the pollen mother cell amounting to non-reduction. In rare instances,



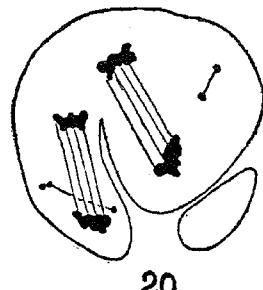
failure of reduction and formation of a single nucleus at the end of the first division was also noticed (Fig. 12). Additional nuclei in daughter cells were common at this stage. Very occasionally the cells resulting from the first division included nuclei that appeared to be degenerating. This phenomenon has been noticed by Beadle in Maize. Splitting of univalents so characteristic of inter-specific and inter-generic hybrids was occasionally observed in some cells (Fig. 9). Such cases have also been noticed in the asynaptic plants of Maize and Datura. Similar phenomenon has also been observed in the rice *haploid* and *triploid* (Ramiah, Parthasarathy and Ramanujam, 1933). Giant cells, the result of coalescence of a number of pollen mother cells, with a large number of chromosomes assorting on several spindles, were noticed in aceto-carmine smears examined in 1932-33 season. But these, however, were not noted in 1933-34. It is possible that the season has some influence, as has been noticed with regard to the fertility of pollen in *tetraploids* (Ramiah, Parthasarathy and Ramanujam, 1935). Such plasmoidal masses have been recorded by Beadle and McClintock (1929) in maize and Gaines and Aase (1926) in wheat.

(c) *Second Meiotic Division*.—The second division was generally normal. But the cells were, however, commonly aberrant as a result of irregularities in the first division. Some of the cells in second metaphase are figured in Figs. 13 to 18 which show the irregular distribution of chromosomes at first division. Although cells with varying number of chromosomes were to be seen at this stage, those with $11+13$, $12+12$ and $14+10$ were the most common. Supernumerary spindles and lagging chromosomes were sometimes also observed at the second division (Figs. 19 and 20). Occasionally, single cells with twenty-four unsynapsed chromosomes in the stage corresponding to diakinesis, were noted in anthers in which the majority of cells were undergoing second division. These probably are the result of ameiosis (suggested by Beadle for maize) which leads to the formation of unreduced spores. That unreduced spores also result from failure of first division and the splitting of univalents at second division was apparent in rare cases. Diminutive chromosomes recorded in maize were not noticed in rice.

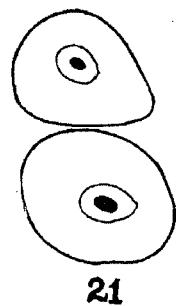
(d) *Tetrad of Spores*.—Normally a microsporocyte is divided into a quartet of cells, the nucleus of each containing a set of twelve chromosomes. Here, as a result of the two irregular divisions, very few pollen mother cells showed a tetrad of equal sized spores characteristic of normals. Microspores and microcytes of varying size and number were formed (Figs. 21 to 26). The spores soon degenerated and a mature anther contained only shrivelled and apparently empty pollen grains.



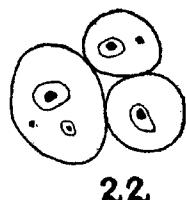
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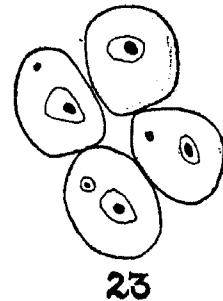
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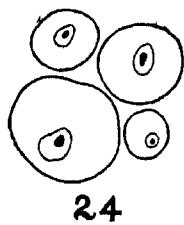
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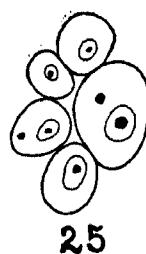
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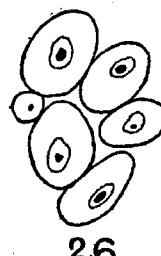
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3. Discussion.

In general meiotic behaviour this mutant resembles those where a single recessive gene has been found to cause asynapsis at metaphase in Maize, Datura and Nicotiana. With regard to lack of bivalents at metaphase, the rice mutant resembles Datura but it differs from Nicotiana and Maize where varying number of bivalents has been noted to occur. While the asynaptic

plants of Datura, Nicotiana and Maize have given rise to some progeny either through their pollen or ovule, that of rice has not set any seed so far. Pollen of asynaptic plants of Datura used on the ovaries of $4n$ plants have given rise to *tetraploids* while normal pollen on maize asynaptic plants have yielded *triploids*. The pale steriles in Nicotiana have given rise to *trisomics* and *monosomics* when pollinated with normal pollen. Thus it is seen that such genetic factors as the one responsible for asynapsis afford an additional mechanism, besides many others already known, for the formation of *auto-polyhaploids* and *polysomics*. It is possible that such forms may arise from the asynaptic plant of rice which is being continually propagated vegetatively and crossed with normal plants reciprocally.

4. Summary.

An asynaptic mutant occurring in the bulk crop of one of the Coimbatore strains, Co. 4, is described and observations of its meiosis reported.

This plant closely resembles another mutant of rice designated 'male sterile' in external appearance, but differs from it in its cytological behaviour.

Meiosis in the microsporocytes of the asynaptic plant is characterised by complete failure of synapsis at metaphase and the presence of univalents leading to irregular distribution of chromosomes at first division. Splitting of univalents, presence of lagging chromosomes and supernumerary spindles are some of the other irregularities of this division.

Second division is comparatively more regular but is not free from irregularities like the presence of multiple spindles and lagging chromosomes.

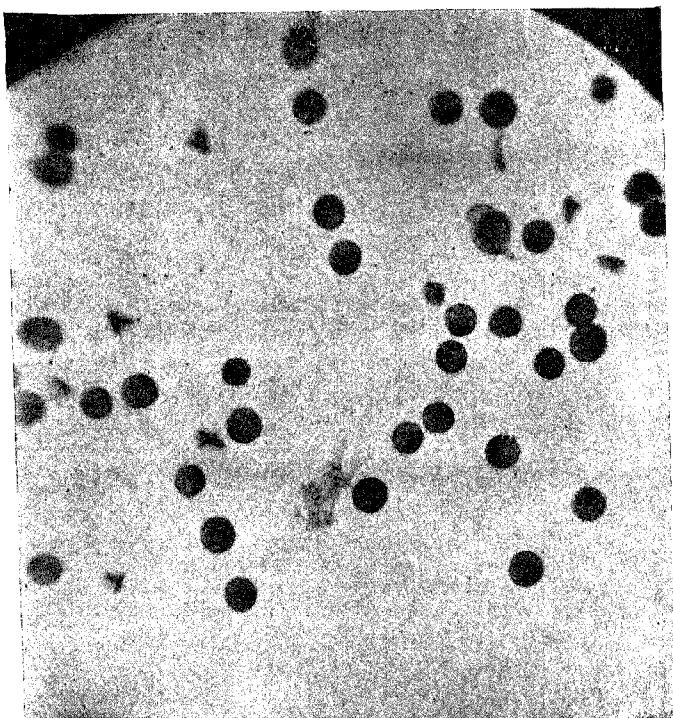
Microspores of different numbers and sizes are formed in each pollen mother cell, as a result of the irregular divisions and these soon degenerate into shrivelled pollen grains.

Acknowledgments.

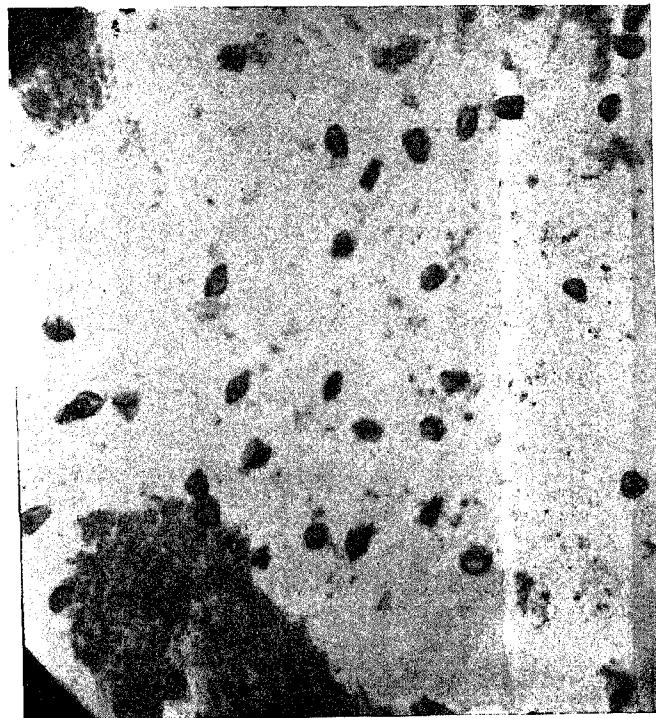
We are deeply indebted to Mr. K. Ramiah, Paddy Specialist, for kind encouragement and guidance in the investigation and preparation of this article.

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b

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EXPLANATION OF PLATE AND FIGURES.

PLATE I.—Pollen of normal (a) and asynaptic (b) plants (Aceto-carmine smears. \times 150).

FIG. 1.—Stage corresponding to Diakinesis in the asynaptic plant (Gentian violet. \times 2000).

FIG. 2.—Metaphase (Gentian violet.).

Figs. 3-7.—First anaphase showing irregular distribution of chromosomes (Gentian violet.).

FIG. 8.—Crescent-shaped spindle at first division (Gentian violet.).

FIG. 9.—A straight spindle with univalents splitting (Gentian violet.).

FIG. 10.—A split spindle (Gentian violet. \times 2000).

FIG. 11.—Pollen mother cell after first division showing additional nuclei (Gentian violet. \times 2000).

FIG. 12.—Pollen mother cell where, after the first division, a single nucleus is formed (Gentian violet. \times 2000).

Figs. 13-18.—Second metaphase showing irregular distribution of chromosomes in the two cells (Gentian violet. \times 2000).

FIG. 19.—Second anaphase with lagging chromosomes (Gentian violet. \times 2000).

FIG. 20.—Second anaphase showing supernumerary spindles (Gentian violet. \times 2000).

Figs. 21-26.—Different kinds of microspore groups (Aceto-carmine smears. \times 600).