CYTOGENETICAL STUDIES IN SESAMUM

Part I. Cytology of the Parents, *Sesamum orientale* Linn. and *Sesamum prostratum* Retz. and the Cytology of the Sterile Hybrid between them and of the Fertile Amphidiploid

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I. INTRODUCTION

PEDALINEÆ is a very small family of annual and perennial herbs, distributed mainly in the eastern tropics. Bentham and Hooker (1885) record only two genera in India, *Pedalium* and *Sesamum*. *Martynia* which is also included in this family is reported to be an American weed introduced into India.

The genus *Pedalium* is represented only by a single species, *Pedalium murex* Linn. which grows wild in waste lands of South India. The genus *Sesamum* is represented by both perennial and annual species. Bentham and Hooker (1885) have recorded only three Indian species of *Sesamum*,

Sesamum orientale Linn. and *Sesamum prostratum* Retz., and *Sesamum laciniatum* Klein. Among these *Sesamum orientale* is an annual whereas the other two species are perennials. *Sesamum prostratum* grows wild on the sand dunes near about the shores of Madras while *Sesamum laciniatum* thrives on the barren rocks of the Deccan hills.

Little cytological and cytogenetical data have been recorded for the two genera, *Pedalium* and *Sesamum*. The genera *Pedalium* and *Martynia* have been investigated cytologically and cytomorphologically in this laboratory as part of the extensive cytogenetical investigations in the family Pedalineæ (Srinivasan, A. R., 1942). The chromosome number of *Pedalium murex* Linn. was determined to be $2n$: 16 and its life-history was worked out with special reference to the development of the endosperm haustoria in the female gametophyte. The species *Martynia diandra* Glox, which grows wild in these parts, was also investigated and its diploid chromosome number was determined to be 32.

According to Schnarf (1931) the genus *Sesamum* has been investigated with reference to the occurrence of endosperm haustoria, by Balicka Iwanowska (1899).

Morinaga *et al.* (1929) determined the somatic number of *Sesamum orientale* ($2n$: 26). Nohara (1934), Richharia and Suguira (1936) have reported the meiotic number of the same species (*Sesamum orientale*) to be 13. The present cytological investigation goes to confirm the numbers previously recorded.

The perennial species *Sesamum prostratum* has never been investigated either cytologically or cytomorphologically till recently when its meiotic number was determined to be 16 by Ramanujam (1941). This number has been confirmed in the present investigation.

While cytogenetical investigation in this laboratory had proceeded more than half way through, a short note appeared in *Current Science* recording some data in respect of hybridisation between the cultivated and wild species of *Sesamum* (Ramanujam, 1942).

In the course of the present investigation the chromosome number of *Sesamum laciniatum* Klein, another wild species, was determined for the first time in this laboratory to be $2n$: 28 (Raghavan and Krishnamurthy, 1945).

Interspecific hybridisation between *Sesamum orientale* and *Sesamum prostratum* has been in progress for some years now in this laboratory and the sterile hybrid derived therefrom was made fertile artificially by the induction of amphidiploidy, through the application of Colchicine. The cytology

of the sterile hybrid, its meiotic irregularity and the ultimate formation of abnormal sporads are detailed in this paper. The regular meiosis of the fertile hybrid after the artificial induction of amphidiploidy has also been included.

II. Materials and Method

Crops of *Sesamum orientale* belonging to the local red-seeded strain were raised from time to time in the University Botanical Gardens, Annamalainagar. Seeds of *Sesamum prostratum* were collected from various localities, especially from Adyar beach, Madras and Coimbatore. Seeds were sown in small pots and were kept in a warm room where they germinated early. Root tips from *Sesamum orientale* were available within 60 hours after sowing whereas those of *Sesamum prostratum* could be obtained only after 5 or 6 days.

Good root tips of the parents and the hybrid could easily be obtained without injuring them since they were sown only on the upper layer, just below the soil. Various fixing fluids were used and fixing was done at various intervals of time. Maximum mitotic activity was observed at mid-day. The fixatives used were Karpechenko's modification of Nawaschin's chrome-acetic-formalin, Irene Manton's modification and Muntzing's formula. Of these fixatives, Irene Manton's modification proved to yield good results. Prefixation in Carnoy's fluid was done in all cases to aid proper fixation.

Flower buds were fixed at various hours of the day. Here also mid-day fixing showed good results. Irene Manton's formula was used. Materials were imbedded in paraffin of melting point 52° C. using chloroform as the paraffin solvent.

Sections were cut at thickness varying from 12 to 15 microns and stained in Newton's Iodine Gentian Violet and Haidenhain's Iron Alum Hæmatoxylin (Chamberlain, 1932). Right stages of anthers were determined before fixing by aceto-carmine examination. Drawings were made at table level using Abbe drawing apparatus and their respective magnifications are indicated.

III. Cytological Observations

(*a*) *Sesamum orientale* Linn.

Somatic chromosomes.—Fig. 1 shows a somatic metaphase plate of *Sesamum orientale* with 26 chromosomes thus confirming the previous record made by Morinaga *et al.* (1929). There is no disparity in the size of the chromosomes in the somatic complement. Almost all the chromosomes would appear to be characterised by terminal centromeres. An analysis

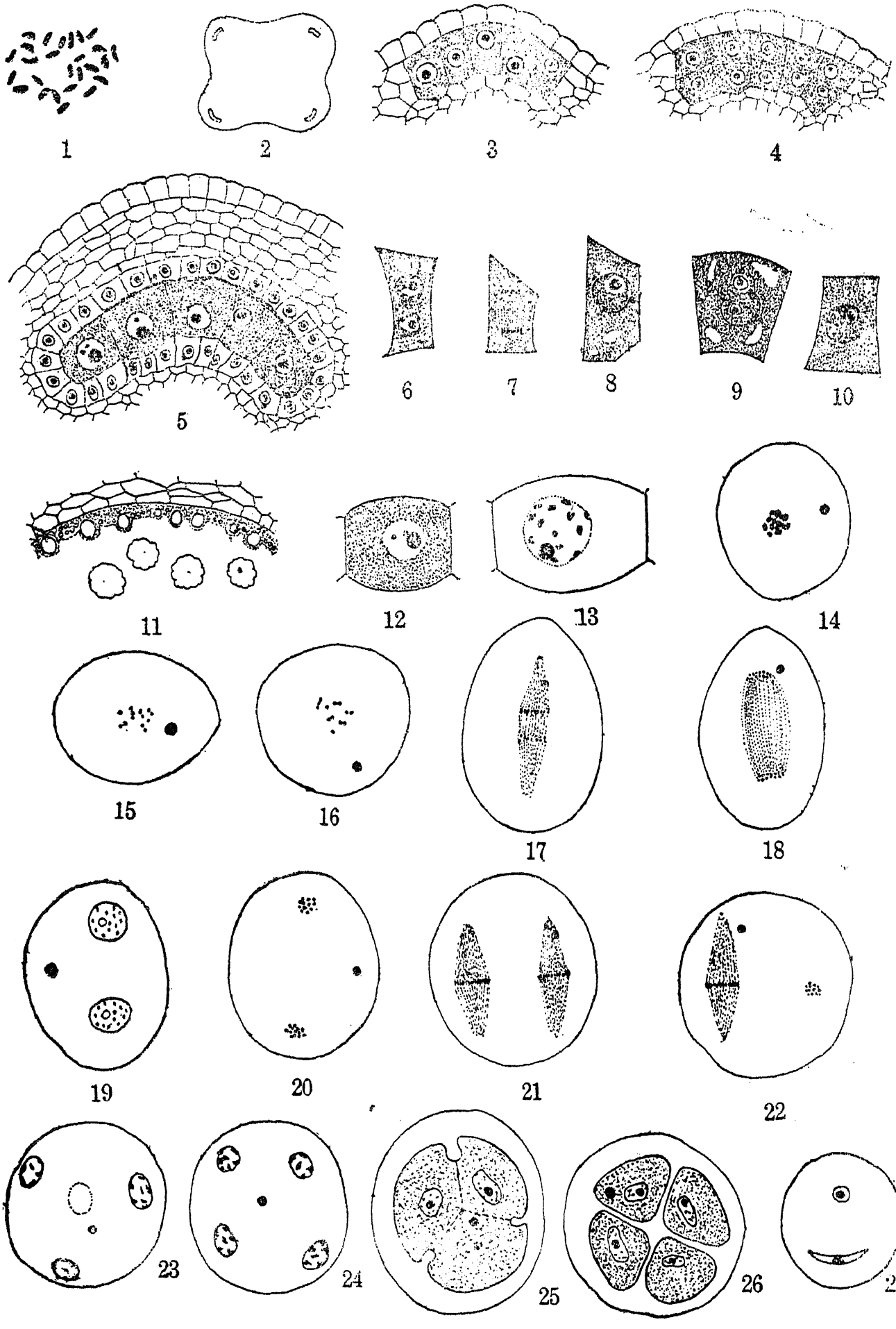
of the chromosome complement on the basis of their morphology was not therefore considered useful and hence not attempted.

Microsporangial development.—The archesporium of the anther consists of groups of 5 or 6 hypodermal cells in the four corners of the anther as seen in Fig. 2. Multicellular archesporia are by no means uncommon. In the closely related genus (*Pedalium*, such extensive archesporia have been recorded (Srinivasan, A. R., 1942). They have also been found in the genus *Nicotiana* (Raghavan and Srinivasan, A. R., 1941 *a*).

To begin with, the single row of archesporial cells (Fig. 3) divide periclinally resulting in the formation of two layers of cells, outer forming the primary parietal cells and the inner primary sporogenous cells (Fig. 4). In the mature anther, the parietal tissue consists of four or five layers, the innermost of which functions as the tapetum (Fig. 5).

It is interesting to note, in this connection, the behaviour of the tapetal nucleus. To start with, the tapetal cells are uninucleate and contain dense cytoplasm (Fig. 6). At a later stage, the nucleus of the tapetal cell shows signs of division resulting in the formation of two nuclei (Fig. 7). Division of the tapetal nucleus takes place even before the nucleus of the pollen-mother cells enters into the early stages of meiosis. After the division, two nuclei are formed within the same tapetal cell, which, after some time, come together. Fig. 8 shows two nuclei after division. In most cases, it has been observed that these two nuclei of the tapetal cells do not remain separate, but that they tend towards fusion. Fig. 9 shows a big binucleate tapetal cell showing the fusion of the two nuclei. There are stages when more than two nuclei are formed by repeated division and ultimately fuse with one another resulting in a tapetal cell with the nucleoli of all the nuclei so fused. Thus in Fig. 10 we find that there are 5 nucleoli within the single nucleus, indicating thereby that the nucleus of the tapetal cell has divided giving rise to 5 daughter nuclei all of which have fused together to form the five-nucleolated nucleus. Cooper (1933) recognises three types of tapetal cells: (1) in which the tapetal cells remain uninucleate, (2) in which they are binucleate and (3) in which they become plurinucleate. The present case in *Sesamum orientale* belongs to the third type described by Cooper. Such plurinucleate tapetal cells have been a common feature in many of the angiospermic genera investigated. In *Gynadropsis* (Raghavan, 1938), in *Chenopodium* (Bhargava, 1936), in *Portulaca* (Raghavan and Srinivasan, A. R., 1941*b*), in *Astercantha* (Rangaswamy, K., 1941) and in *Crescentia* (Venkatasubban, 1944) they have been observed to occur.

The division of the tapetal cells has been found to be mitotic in this species (Fig. 7). It was at one time believed that the division of the tapetals



FIGS. 1–27

TEXT-FIGS. 1–27. *Meiosis in Sesamum orientale Linn.*—Fig. 1. Somatic complement of *Sesamum orientale* showing 26 chromosomes. Fig. 2. Section of a very young anther showing the hypodermal band of archesporium. ×150. Fig. 3. A band of primary archesporial cells. ×150. Fig. 4. Division of the archesporial cells × primary wall cells and primary sporogenous layer. ×150. Fig. 5. Mature anther showing five wall layers, the innermost forming the tapetum. ×150. Figs. 6–10. Tapetal cells showing stages of nuclear division and fusion. ×400. Fig. 6. Binucleate tapetal cell. Fig. 7. Mitotic division of the nucleus. Fig. 8. Uninucleate tapetum. Fig. 9. Fusion of the two nuclei in a single cell. Fig. 10. Cell showing 5 nucleoli within a single nucleus. Fig. 11. Degeneration of the tapetal layer at the pollen grain stage. Fig. 12. Resting nucleus of pollen mother cells showing the budding off of spherical bodies. ×1000. Fig. 13. Diakinesis showing 13 bivalents. ×1000. Fig. 14. Prometaphase. The persistent nucleolus is towards the one side of the cell. ×3,000. Figs. 15 and 16. Metaphase groups showing 13 bivalents in secondary association 1_3, 4_2 and 2_1. The persistent nucleolus is away from the equatorial region. ×3,000. Figs. 17 and 18. Anaphase separation with the persistent nucleolus going ahead of the chromosomes. Fig. 19. Interphase nuclei with the persistent nucleolus towards one side. Fig. 20. Metaphase II showing 13 chromosomes and the separately lying persistent nucleolus. Fig. 21. Spindles of Anaphase II stage lying parallel. Fig. 22. Spindles of Anaphase II stage lying at right angles. Fig. 23. Pollen mother cell showing 3 of telophase nuclei lying in one focus and the fourth in another. Fig. 24. Pollen mother cell showing 4 telophase nuclei all lying in one plane. The persistent nucleolus is in the middle. Fig. 25. Tetrahedral type of tetrad on the process of furrowing. The persistent nucleolus is included in one of the tetra cells. Fig. 26. Isobilateral tetrad cells arranged in one plane. Fig. 27. Two-celled pollen grain at the time of shedding. All figures have been drawn at a magnification of *Ca.* 3,000, unless otherwise stated.

nucleus is amitotic Rocen (1927), in *Portulaca*, and O'Neill (1920), in *Datura*. But that it is through ordinary mitosis has been observed critically and confirmed by Raghavan (1938) in connection with his investigations on *Gynandropsis*. In several other genera investigated in this laboratory, mitosis was found to be the rule. It would thus appear safe to generalise that tapetal nuclear division is through mitosis.

Meiosis.—The microsporangial tissue consists of a single row of five or six microspore mother cells (Fig. 5).

In the resting condition of the nucleus of some of the pollen mother cells, in addition to the big darkly stained nucleolus, small bodies similarly stained but smaller than the nucleolus have been found to occur (Fig. 12). In one and the same loculus of the anther, some pollen mother cells show these bodies while in others they are conspicuous by their absence. Similar bodies have been recorded in the pollen mother cells of various genera, *viz.*, in *Oryza* (Nandi, 1937), in *Hibiscus mutabilis* (Majumdar and Datta, *et al.*, 1934), in *Cicer arietinum* (Iyengar, N. K., 1939) and in *Oenothera rubrinervis* (Gates, 1908). Most of them regard these spherical bodies as extrusions from the nucleoli and consider them to be intermediate stages during the transference of chromatin material from the nucleoli to the chromosomes.

These bodies persist throughout the stages of meiosis right up to the tetrad stage and they have been observed to be included in one of the tetrad cells (Fig. 26).

The possibility of these bodies being chromosomes or their fragments is ruled out for the following reasons, namely, (1) they do not take up any particular position with respect to the cell and are apparently not attracted by forces of attraction or repulsion which are presumed to be responsible for the chromosome movements observed during nuclear division; (2) they are perfectly spherical in shape and homogeneous in structure; (3) they do not undergo any change in their shape or size during meiosis; (4) they are larger than the bivalents or chromosomes at any stage during meiosis, though they are smaller than the prophase nucleolus. That these bodies are nucleolar in origin has been confirmed by positive evidence also. The spherical bodies get stained to the same extent as the nucleolus itself. These bodies seem to bud off from the big prophase nucleolus (Fig. 12) and at various stages, the connection of these bodies with the big nucleolus has been observed clearly. Kumar and Abraham (1942) on their observation in *Sesamum*, call these bodies secondary nucleoli, a name suggestive of their origin.

The behaviour of these spherical bodies during meiosis is indicated at the different stages thereof. In some cases, these bodies were not to be found in the tetrad cells. It is believed that they disappear in the cytoplasm of the pollen mother cells when the tetrads are forming. Probably in most cases they disappear from the scene failing which they are included in one of the tetrad cells.

At diakinesis, the 26 chromosomes of the somatic complement are seen to form 13 bivalents (Fig. 13). These 13 bivalents are mostly of the rod type. They are distributed on the periphery of the nucleus. All the pairs are dispersed at equal distance from each other. This equidistant spacing of the bivalents, according to Lawrence (1931), is due to a repulsion phase which begins at early diakinesis and continues till mid-diakinesis.

The converging movement of the bivalents begins at mid-diakinesis and continues until the bivalents are in close association in the centre of the nucleus. The main nucleolus disappears though the nucleolar bit persists in the form of a spherical body, a little away from the clumped mass of bivalents (Fig. 14).

First metaphase follows prometaphase. The 13 bivalents are arranged on the equatorial plate and are evenly distributed unlike in the case of the sterile hybrid where they are scattered. The bivalents exhibit secondary association, frequently resulting in a number of groups. The maximum

association observed is 1_3, 4_2 and 2_1, thus bringing the total number of groups to 7. Probably this would suggest that the original basic number of the genus is 7. Based on this suggested basic number, the possible origin of the cultivated species has been discussed at the end of the paper. Figs. 15 and 16 show the metaphase plate exhibiting the phenomenon of secondary association. It may be noticed that the persistent nucleolus now takes up a position away from the dividing bivalents. This would naturally indicate that it does not get itself involved in the division of the bivalents and this rules out the possibility of its being chromosomal in nature.

After the metaphase stage, the chromosomes are subjected to anaphasic separation. Anaphase, in this case, is quite normal and the chromosomes disjoin with marked uniformity. The persistent nucleolar body, which is lying away from the equatorial plate during metaphase, is now to be seen at one of the poles. Presumably it has already gone ahead of the chromosomes towards the poles. Figs. 17 and 18 represent the normal anaphase separation and the persistent nucleolus lying at one of the poles.

At each pole, after anaphase, the chromosomes arrange themselves in groups and organize themselves into the interphase nuclei (Fig. 19). Now the nucleolus makes its appearance at both of the interphase nuclei. The chromosomes are more or less uniformly spaced. Such uniform spacing of the chromosomes in the first telophase nucleus has been recorded in *Angelonia* (Raghavan and Srinivasan, V. K., 1940), in *Oenothera* (Gates, 1909) and in *Gynandropsis* (Raghavan, 1938). Gates attributed the uniform spacing of the chromosomes at interkinesis to a mutual repulsion, and the clumping at early telophase, due to attraction. But the "medium in which bodies float frequently change their qualities of attraction and repulsion and it appears that the repulsion first develops after the appearance of the karyolymph in which the chromosomes float". No partition wall is formed between the daughter nuclei nor is the resting stage reached by the interkinesis nuclei (Fig. 19). The persistent nucleolus in some of the cells at this stage occupies a place towards the side of the pollen mother cell while in some cases they were found near one of the telophase groups (Fig. 19).

When second metaphase sets in, the interphase nuclei at either pole lose their nuclear membrane and their nucleoli. The persistent nucleolar body is not involved in it (Fig. 20). At this stage the 13 haploid chromosomes are seen arranged uniformly at the poles.

The second metaphase chromosomes undergo normal disjunction and they reach the poles without exhibiting any irregular phenomenon like bridge formation or fragmentation. Figs. 21 and 22 show the second ana-

phase stage and the persistent nucleolus may be seen on the spindle fibres of one of the anaphase sets. Here also there is an indication by its mere position at the poles that it precedes the chromosomes. The possible causes for the migration of the nucleolus to the poles ahead of the chromosomes have been discussed further below.

The organisation of the spindle during anaphase separation may take place in two ways. In some cells, the spindles lie parallel to each other as in Fig. 21. In others, they lie at right angles to each other so that in one focus, one anaphase group will show the side view of the chromosomes while the other will show the polar view as in Fig. 22. The nature of the tetrads will obviously depend upon the position of the spindles during anaphase. If the spindles are parallel then the four telophase nuclei lie in the same plane (Fig. 24) leading to the formation of iso-bilateral tetrads (Fig. 26). If they are at right angles as in Fig. 22 and 23 then the arrangement is tetrahedral (Fig. 25). Both the types of tetrad arrangement have been noticed in *Sesamum orientale*. The persistent body at this stage is found to be included in one of the tetrad cells (Figs. 25 and 26). Simultaneous furrowing takes place during the formation of the tetrad from the periphery towards the centre. Fig. 25 shows a stage in the process of furrowing. Due to the simultaneous furrowing all the four tetrads are organised simultaneously.

The pollen grain at the shedding stage shows a crescent-shaped generative cell and a small tube cell (Fig. 27). The pollen grains are uniform in size and their wall shows ridges and furrows. All the grains are viable and germinate rapidly in sugar agar cultures. Plate I, Fig. 1, shows a microphotograph of the pollen grains of *Sesamum orientale*.

(*b*) *Sesamum prostratum* Retz

The somatic complement is made up of 32 chromosomes (Fig. 28). They are uniform showing no disparity in size or morphology. All the chromosomes of the somatic complement show terminal constriction.

The microsporangial development and the general outline of meiosis conform to the details already described for *Sesamum orientale*. The tapetal nucleus and its behaviour is also similar to that of *Sesamum orientale*. Fig. 29 shows three tapetal cells in the process of division. In the first cell, anaphase has just set in. In the second cell, the chromosomes have separated and are reaching the poles. In the third cell, two nuclei have ready formed. These figures confirm the mitotic nature of the division of the tapetal cell.

Almost all the pollen mother cells, in their resting condition, show the peculiar phenomenon of nucleolar budding (Figs. 30 *a* to *f*). The nucleolar

buds so formed vary in number and it is found that within a pollen mother cell, in some cases, as many as 7 buds were seen (Fig. 30*f*). But these buds have not been found to persist as in the previous species through meiosis.

Further meiotic stages are normal. Fig. 31 shows first metaphase plate showing 16 bivalents.

(*c*) *Sterile Hybrid*

The diploid complement of the F_1 hybrid shows 29 chromosomes (Fig. 32). Somatic cells of the root tips and of flower buds were examined for purposes of confirmation. Of the 29 chromosomes 16 are derived from the *prostratum* parent and 13 from the *orientale* parent. Since the parental complements showed no morphological disparity among themselves no morphological distinction between these two sets of chromosomes could be recognised in the hydrid complement.

Meiosis: The origin and development of the microsporangium, tapetal behaviour, etc., present no deviation worth any special mention. There is also the same nucleolar budding which was a characteristic feature of both the parents. As many as seven bodies could be seen in the P.M.C. of the resting stage. It is, however, worthy of note that these bodies persist no further. In this respect the hybrid seems to resemble the *prostratum* parent for, in *orientale*, these bodies persist right up to the end. It seems probable that persistence of the nucleolus is a Mendelian recessive. The hybrid shows in some characters, resemblance to the *prostratum* parent a Mendelian dominance. Non-persistence would appear to be dominant to persistence. Hence we find the hybrid showing non-persistence. Full details regarding inheritance of characters by the hybrid are given in a separate paper.

During diakinesis only a few chromosomes pair while the others remain as univalents. The bivalents and the univalents are arranged peripherally around the nucleolus (Fig. 33). The most frequent number of bivalents met with based on an examination of a large number of pollen mother cells is eight.

After diakinesis, the prophase stage sets in when the bivalents and univalents appear clumped at the centre of the cell (Fig. 34). The nuclear membrane disappears at this stage and along with it the nucleolus. This stage comes to an end when the spindle fibres make their appearance.

During Metaphase I the chromosomes separate and unlike in normal meiosis, the chromosomes fail to arrange on the equatorial plate. The bivalents and the univalents are scattered on the spindle. The most frequent arrangement is for the bivalents to occur at the equator and for

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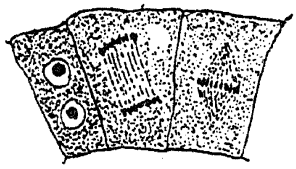

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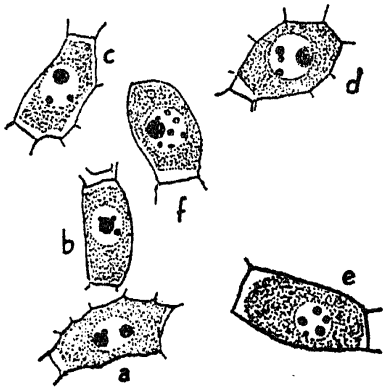

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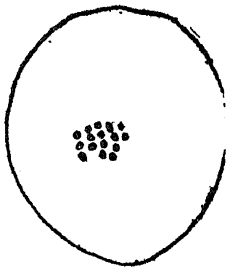

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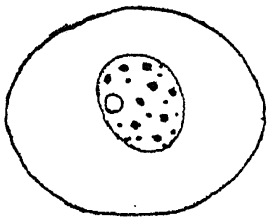

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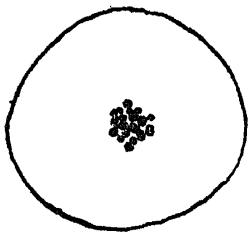

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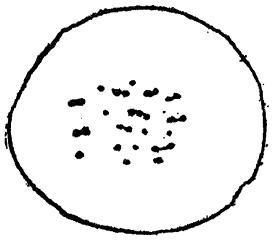

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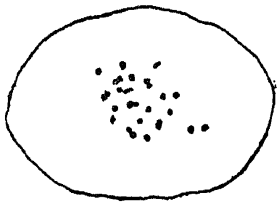

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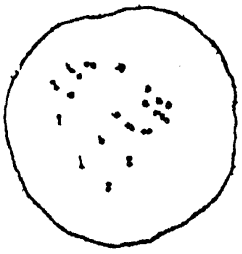

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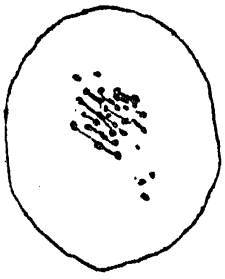

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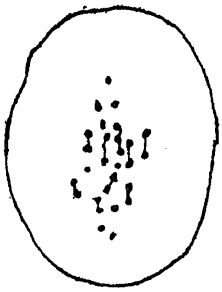

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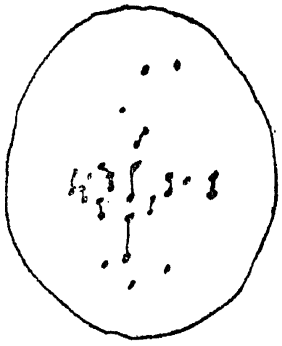

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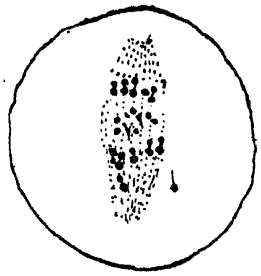

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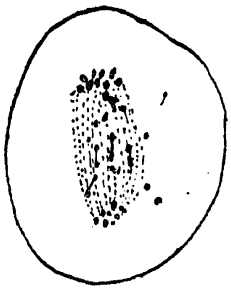

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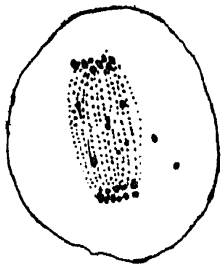

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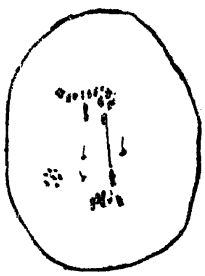

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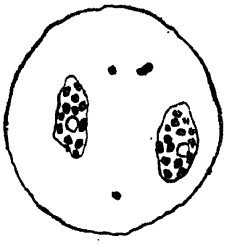

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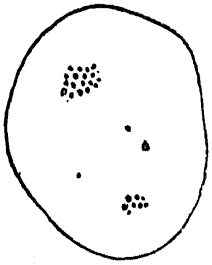

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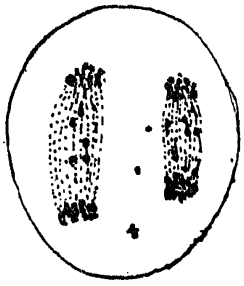

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FIGS. 28–47

TEXT-FIGS. 28–47.—Figs. 28–31. *Meiosis in Sesamum prostratum.* Fig. 28. Somatic plate of *Sesamum prostratum* showing 32 chromosomes. Fig. 29. Three tapetal cells showing mitotic division. ×400. Fig. 30. Resting nucleus of the P.M.C. showing nucleolar budding in various degrees. ×400. Fig. 31. Metaphase I polar view showing 16 bivalents. Figs. 32–47. *Meiosis in the sterile hybrid.* Fig. 32. Somatic complement showing 29 chromosomes. Fig. 33. Diakinesis showing bivalents and univalents. Fig. 34. Prometaphase showing clumped chromosomes. Figs. 35–38. Metaphase I showing bivalents and the univalents scattered. The bivalents are at the equatorial region while the univalents are nearer the poles. Fig. 39. Metaphase I showing 8 bivalents, 1 trivalent and 10 univalents. Fig. 40. Metaphase I showing 9 bivalents, 1 trivalent and the rest univalents. Fig. 41. Anaphase I. Irregular disjunction of the chromosomes. Figs. 42 and 43. Univalents and bivalents lagging in the spindle during anaphase. Fig. 44. Formation of chromosome bridges during anaphase I. Fig. 45. Interphase nuclei showing two cells having unequal number of chromosomes with the left out univalents in the cytoplasm of the P.M.C. Fig. 46. Metaphase II with unequal number of chromosomes. Fig. 47. Anaphase II with the usual lagging chromosomes. All figures have been drawn at a magnification of *Ca.* 3,000, unless otherwise stated.

the univalents to be scattered at the poles (Figs. 35, 36, 37 and 38). Fig. 39 shows 8 bivalents, 1 trivalent and 10 univalents. Fig. 40 shows the metaphase side-view representing 9 bivalents, 1 trivalent and the rest univalents.

There seems to be some relationship between the degree of synapsis and the arrangement of chromosomes in the equatorial region. In all cases where weak pairing is exhibited by the chromosomes this scattered condition prevails. Many cases of haploidy have been cited to show that asynapsis and absence of a regular equatorial plate at Metaphase I, go together. Haplonts of *Nicotiana Tabacum* (Chipman and Goodspeed, 1927) and *Nicotiana glutinosa* (Goodspeed and Avery, 1929) were observed to show this feature. Catcheside (1932) recorded such a behaviour in a haploid *Oenothera* and states in that connection that " many of the chromosomes have never been at the equator of the spindle, but have a definite bias towards one or the other end of the poles ever since diakinesis ". Humphry (1934) has reported such cases in haploid tomatoes. Many examples of interspecific hybrids in the genus *Nicotiana* may be cited to show this prevailing condition of scattered arrangement of the chromosomes, *Nicotiana sylvestris* × *Nicotiana tomentosa* (Goodspeed and Clausen, 1928), *Nicotiana bigelovii* × *Nicotiana solanifolia* and *Nicotiana Tabacum* × *Nicotiana rustica* (Goodspeed, 1934), *Nicotiana glutinosa* × *Nicotiana Tabacum* (Raghavan and Srinivasan, A. R., 1941 *a*).

Thus during first metaphase stage the chromosomes are scattered along the whole length of the pollen mother cell. Their weak pairing during diakinesis and the consequent scattered arrangement of the chromosomes during metaphase constitute cytological basis for the sterility of the hybrid.

The metaphase stage which is characterised by random distribution of the bivalents and the univalents is followed by anaphase which is equally irregular. In normal pollen mother cell, anaphase is characterised by uniform disjunction of the bivalents which results in an equal distribution of chromosomes. But in the case of the hybrid, the bivalents and the univalents during their disjunction exhibit various irregularities.

Fig. 41 shows the migration of the bivalents and the univalents to the poles. Some univalents are seen left out of the spindle and they seem to divide. These divided bits of univalents either reach the poles along with the separating bivalents or they are left out in the cytoplasm where they remain to the last without being included in any of the daughter nuclei.

Frequently bivalents and univalents are seen to lag on a spindle (Figs. 42 and 43). These laggards also get included in one of the daughter nuclei or they remain in the cytoplasm during the interphase stage. These organize themselves into groups and finally form a membrane around them to form the micronuclei (Fig. 50). Sometimes they are found in the plasma in the succeeding stages. In some cases they are included in one of the daughter nuclei. Similar cases of laggards have been recorded in many hybrids. In *Nicotiana* hybrids, *N. glutinosa* × *N. Tabacum* (Raghavan and Srinivasan, A. R., 1941 *a*), in *Brassica* hybrids (Morinaga, 1929) (Ramanujam, 1943), laggards of a similar kind have been found frequently.

Sometimes due to unequal disjunction, the separating chromosomes are connected by long chromatin thread, forming chromatin bridges (Fig. 44). The exact nature of these bridges and the reason for their formation could not be studied in detail.

After the complete separation of the chromosomes, interphase sets in. The two chromosome groups organise into two nuclei at the poles. It is observed that one of the poles contains a larger number of chromosomes than the opposite pole (Fig. 45). This is due to the unequal separation that takes place during anaphase. Further some of the chromosomes have been left out as laggards in the plasma itself. Hence the disparity in number of chromosomes between the two interphase nuclei. No wall is formed between them. Wall formation after the first division is not a common feature of the dicotyledons. But in *Nicotiana* hybrids, between *Nicotiana glutinosa* and *Nicotiana Tabacum* (Raghavan and Srinivasan, A. R., 1941 *a*), wall formation has been recorded.

Second metaphase plate shows two groups of chromosomes distributed with unequal numbers. Some of the laggards are also seen in the cytoplasm. These laggards remain as such and are not included in the second metaphase plate (Fig. 46).

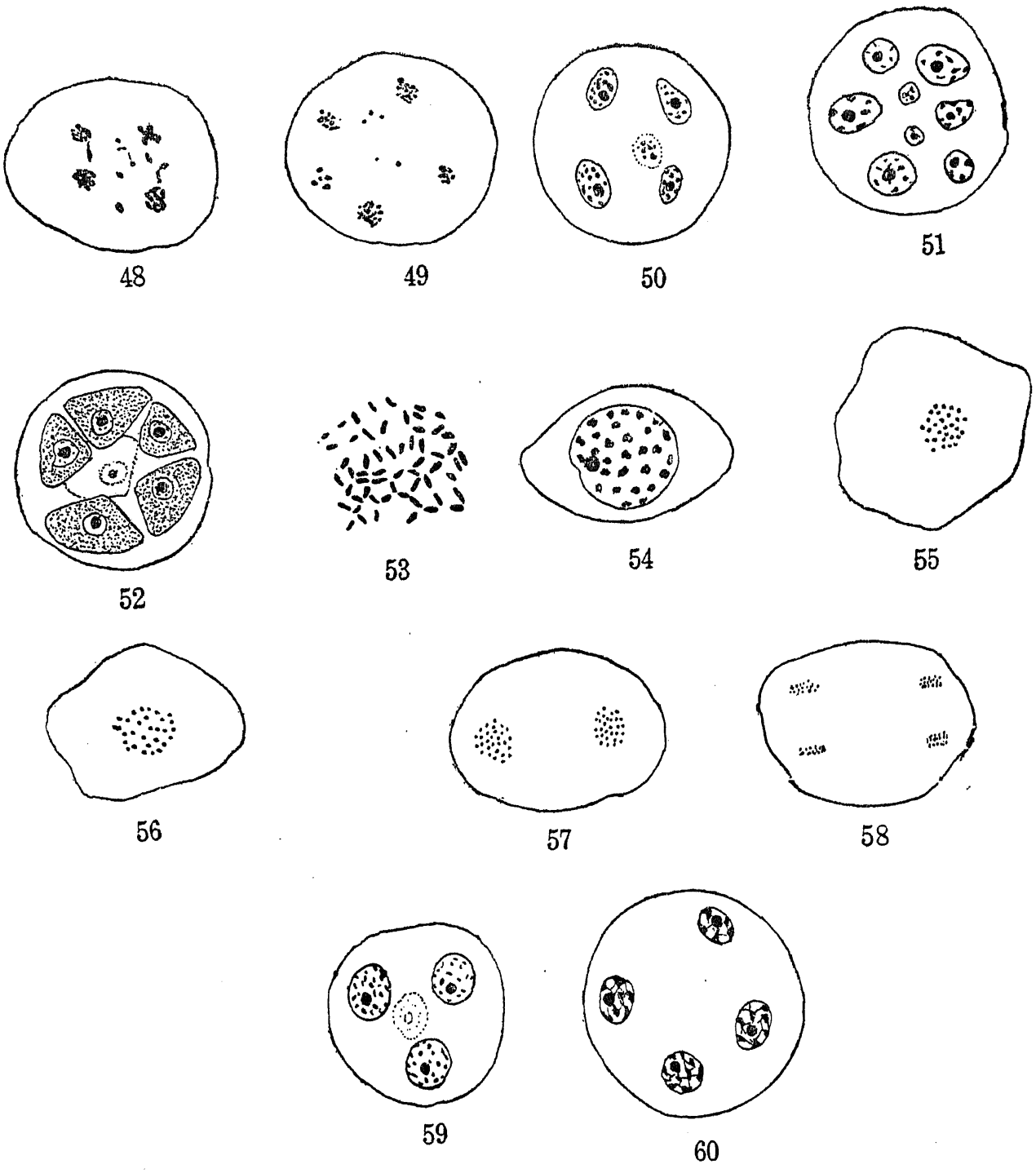
During the succeeding second Anaphase also the chromosomes separate exhibiting irregularities of the kind occurring during first anaphase (Fig. 47). Some chromosomes are left behind on the spindle. Some remain out of the spindle and assemble together. As in first anaphase equal number of chromosomes do not go to each pole. As a result of these, groups having varying numbers of chromosomes are formed and the four daughter nuclei are organised around each one of these groups (Figs. 48 and 49). A few laggards are also seen in the cytoplasm which are not included in any of the telophase nuclei. The discrepancy in the number of chromosomes in the telophase groups is responsible for the formation of the daughter cells of unequal size which ultimately results in tetrads and pentads, big and small. Fig. 51 shows daughter cells of unequal size being formed. Since the chromosomes of the haploid complement are not evenly distributed among the four telophase nuclei, the grains that result from them are non-viable, leading to the sterility of the hybrid. In some cases, some of the laggards that were left out of the spindle arrange themselves in small groups and form micronuclei (Fig. 50). Thus instead of regular tetrads being formed, pentads and hexads result out of the irregularities of meiosis in the hybrids (Figs. 51 and 52). Hence grains exhibit various sizes and shapes resulting in their polymorphic nature. Plate XII, Fig. 3 is a microphotograph of the pollen grains of the sterile hybrid, to show the polymorphic grains. Only 5 to 10% of the pollen grains reached the size of the pollen grains of the parents.

The pollen grains are highly non-viable. They do not germinate even in sugar agar cultures. The pollen grains were deposited on the stigma of both the parents, *Sesamum orientale* and *Sesamum prostratum.* In both the cases, the grains did not germinate. Pollen grains were deposited on the stigma of the sterile hybrid itself. Even then the result proved negative.

Thus it is evident from the above observations that the sterility of the hybrid is the outcome of the irregularity of meiosis.

(*d*) *The Amphidiploid*

Weak pairing between the parental chromosomes in the hybrid indicates that there is no homology between the chromosomes of *Sesamum orientale* and *Sesamum prostratum.* Presumably the parental chromosome sets exhibit structural disparity, hence there is little possibility of their coming together in pairs. This absence of pairing due to the weak homology between the chromosomes could be overcome by supplying these two sets of chromosome complements, each with another homologous set. Thus 13 *orientale* chromosomes may be supplied with another 13 of its own so that both the



TEXT-FIGS. 48–60.—Figs. 48–52. *Meiosis of the sterile hybrid.* Figs. 48 and 49. Anaphase groups of chromosomes containing varied number of chromosomes and also a few left out laggards. Fig. 50. Formation of 4 telophase nuclei and organisation of the micronucleus by the lagging chromosomes. Fig. 51. P.M.C. containing 8 telophase nuclei of different sizes. Fig. 52. P.M.C. containing 6 daughter cells as a result of irregular meiosis. Figs. 53–60. *Meiosis in the Fertile Hybrid* (the amphidiploid) : Fig. 53. Somatic complement showing 58 chromosomes. Fig. 54. Diakinesis showing 29 bivalents. Figs. 55 and 56. Metaphase I showing 29 bivalents at the equator. Fig. 57. Metaphase II showing the equatorial plates containing 29 chromosomes each. Fig. 58. Anaphase II showing normal disjunction. Fig. 59. Telophase nuclei arranged three in one plane and one below. Fig. 60. Telophase nuclei, all the four in one plane. All figures have been drawn at a magnification of *Ca.* 3,000 unless otherwise stated.

sets may pair among themselves. Similarly for *Sesamum prostratum* another set of 16 chromosomes may be made available so that pairing may take place between the two sets of 16 chromosomes. This has been made possible recently by colchicine application by which doubling of genes is brought about.

In the present investigation the 29 chromosomes of the sterile hybrid have been doubled ($2n$: 58). That is, the 13 chromosomes of *orientale* have been duplicated as also the 16 chromosomes of *prostratum*. The result is, the hybrid proves to be completely fertile unlike its sterile predecessor. The cytological explanation of the fertility is the regularity with which meiosis takes place.

Fig. 53 shows a somatic plate containing 58 chromosomes which is double the number of the sterile hybrid ($2n$: 29). But a distinction could not be made between the two parental sets of chromosomes since they were identical in their morphology.

Meiosis.—Microsporangial development is of the normal type as described for *Sesamum orientale.*

Meiosis is regular. At diakinensis there is regular pairing and 29 bivalents are formed (Fig. 54). Metaphase I (Figs. 55 and 56) shows the 29 bivalents arranged in the form of a flat plate in the equator. Obviously pairing has taken place among the duplicated parental genomes, that is, 16 *prostratum* with 16 *prostratum* and 13 *orientale* with 13 *orientale* chromosomes.

First Anaphase is normal and the chromosomes disjoin without exhibiting any irregularity. Fig. 57 shows the metaphase plates during Metaphase II. Second anaphase also is regular (Fig. 58). Equal numbers of chromosomes go to the respective poles. As a result of regular meiosis, the four telophase nuclei are organised with equal number of chromosomes and tetrads are organised in the normal way (Figs. 59 and 60).

The pollen grains that are formed are of uniform shape and size without showing any polymorphism. They are however bigger in size than those of the parents. Plate XII, Fig. 4, is a microphotograph of the pollen grains of the fertile hybrid.

The pollen grains are highly viable as evidenced by the formation of a large number of fruits in the fertile hybrid. Also experiments on germination of the pollen grains in agar culture have shown the rapidity with which the grains germinate. Consequently the fertility of the hybrid has increased the yield of an individual plant by 6 times its parent, *Sesamum orientale*,

The ovary is fertile as revealed by the presence of a large number of seeds which in each fruit amounts to about 50. The amphidiploid thus derived is breeding true and the meiosis in all the subsequent generations have been found to be quite regular. This fertile hybrid may be regarded as a stable true-breeding species, deserving an independent position along with the parents, *Sesamum orientale* and *Sesamum prostratum.*

IV. Discussion

(*a*) *Nucleolus—its behaviour and persistence*

In angiosperms normally the nucleolus appears at the telophase stage and remains till the onset of metaphase, after which it disappears along with the disappearance of the nuclear membrane. However, cases where the nucleolus persists even after the metaphase stage are not uncommon. In *Polanisia trachysperma* persistence upto metaphase in somatic mitosis was recorded by Raghavan (1938). But the nucleolar persistence throughout meiotic stages such as was seen in *Sesamum orientale* is comparatively rare. The behaviour of these nucleolar bodies is varied.

The persistent nucleolus arises as a spherical bud from the nucleolus of the resting nucleus. Many such buds are formed, most of them disappearing during diakinesis stage except one which persists with the same size neither diminishing nor dividing until finally incorporated in the tetrad cells. There are also cases where this body after remaining for most of the stages of meiosis, disappears into the cytoplasm.

The possibility of these bodies being chromosomes or their fragments is ruled out by the fact that they are bigger than the chromosomes and perfectly spherical in shape. They take the stain to the same extent as the nucleolus does. During meiotic stages they do not play any part. Thus it may be seen that by their origin from the margin of the big nucleolus and by their taking up the stain to the same extent, these bodies are nucleolar in nature.

The persistent nucleolus in the pollen mother cells of *Sesamum orientale* is observed to exhibit varied movements. During the earlier stages of meiosis it either remains in the equator or lies apart. If it remains in the equator it migrates to the pole when anaphase separation sets in; or in some cases it disappears altogether. If they persist they get incorporated into one of the tetrad cells. Thus it stands to reason that some force has been acting upon these persistent nucleolar bodies to enable them to execute such movements.

The factors which are responsible for such a movement have not been clearly established. They are presumably acted upon by the same forces

which are responsible for chromosome movements, like the contraction of spindle fibres, electromagnetic repulsion or attraction set up by cytoplasmic currents in the spindle region. Mensinkai (1939) regards the division and migration of the persistent nucleolus as being due to the stretching of these spindle fibres. But since the persistent nucleolus has been found to have no connection with the spindle fibre, it is unlikely that the contraction of the spindle brings about the movement of the nucleolus. The other alternative is the magnetic attraction set up by the cytoplasmic current. The fact that sometimes the persistent nucleolus remains at the equator while at other times it moves towards the poles would suggest that these movements may be due to the above cause. Further the spindle region would appear to be one of localised forces and when a body lies in that region it is carried away provided it is not attached to any thing like the spindle fibre. The persistent nucleolus by its position at the border of the spindle fibres and also by its migration to the poles ahead of the chromosomes, it would appear that the movement of the nucleolus might be controlled by the localised forces that have been referred to above.

During metaphase the chromosomes are attached to the spindle fibres and since contraction of the fibres takes place only a little later, the chromosomes are prevented from being carried away by the forces at the spindle area, while the nucleolus lies unattached to the spindle fibres so that it is free to move and hence it is found to reach the poles ahead of the chromosomes. Movements of this kind may perhaps be explained by the electromagnetic theory of nuclear division (Kuwada and Sugimoto, 1928). According to this theory, the persistent nucleolus, because of the presence of plastin, which it has retained instead of giving to the chromatin, becomes highly electropositive, while the poles remain oppositely charged. As a result of this the persistent nucleolus is attracted towards the pole and hence the movement. It is further explained that in the normal cases where there is no persistent nucleolus, the chromosomes change their electric charge due to the transference of the plastin from the nucleolus. A similar explanation for the differential movement of the persistent nucleoli and the chromosomes would seem probable in the present instance also.

(*b*) *Interspecific hybridisation—a guide to ancestral homology.*

Interspecific and intergeneric hybridisations and the study of the behaviour of such hybrids have long been engaging the attention of many cytologists, since the results of the observation serve as valuable clues to determine the relationship between the various species. The mode of origin of new species can be inferred with the help of hybridisation results as disclosed by cytological data.

Species having the same number of chromosomes when crossed with each other will give either fertile hybrids or hybrids of partial or completely sterile nature. Such fertile hybrids are met with in the following cases. *Viola* (Clausen, 1931), *Nicotiana* (Goodspeed, 1934) and *Triticum* (Aase, 1930). Clausen (1931) crossed *Viola tricolour* (n: 13) with *Viola alpestris* (n: 13) and got a hybrid which was fertile ($2n$: 26). During meiosis, he observed that 13 chromosomes of *Viola alpestris* paired completely with 13 chromosomes of *Viola tricolour* thus resulting in a fertile hybrid. The complete synapsis in this case indicates the complete homology of the two sets of chromosomes. Hence these two species, though taxonomically distinct may be regarded as having had a common origin on the basis of this piece of cytological evidence.

In the case of sterile hybrids, some show partial pairing with varying number of bivalents and univalents during meiosis. In such cases the greater the number of bivalents formed, the greater has been the fertility of the hybrids. For instance, Clausen (1931) crossed *Viola nana* (n: 24) with *Viola lutea* (n: 24). The hybrid was found to be partially fertile; meiotic stages showed the presence of only a few bivalents 6 to 8. In the normal case if there is complete pairing there should be 24 bivalents formed. But as there were only a few bivalents, the hybrid was partially sterile; correspondingly in the hybrids between *Viola orphinidis* (n: 11) and *Viola cornuta alba* (n: 11) he found a greater number of bivalents amounting to 9 or 10. The hybrid was almost completely fertile. Thus it would appear that the degree of hybrid fertility is directly proportional to the number of bivalents formed during the meiotic stages of the hybrids.

In the case of some hybrids, pairing is totally absent and consequently the hybrids are completely sterile. Karpechenko (1927 *a*, 1927 *b*) got a hybrid which was completely sterile, by an intergeneric cross between *Raphanus sativus* (n: 9) and *Brassica oleracea* (n: 9). This complete sterility was attributed to the total absence of synapsis or pairing of parental chromosomes during meiosis. This only confirms the previous inference that the degree of synapsis is a measure of the degree of hybrid fertility.

Thus it is noticeable that though the two parental chromosomes of hybrids are equal in number, yet they vary in their degree of affinity indicating thereby that the pairing of chrmosomes does not depend upon the numerical identity of the chromosomes but on their structural and morphological homology. This homology between chromosomes of two gametic sets will be nearer if both the parents have had a common origin. Thus the cytological behaviour of species hybrid indicates not only the extent of homology between the species but also the ancestry of the parental forms.

In the case of hybrids derived out of parents having different chromosome numbers, the behaviour of hybrids exhibits complication which is nonetheless interesting.

The behaviour and the extent of affinity of the chromosomes in such hybrids as disclosed by their behaviour at meiosis has been classified by Tackholm (1922) into three groups. They are (1) *Drosera* scheme of pairing where there is strong affinity between parental chromosomes; (2) *Hieracium Boreale* type where there is a weak affinity; and (3) the *Pygrarea* type where there is no affinity. It was Rosenberg (1909) who first observed this phenomenon of pairing in *Drosera* hybrids. He crossed *Drosera rotundifolia* (2*n*: 20) with *Drosera longifolia* (2*n*: 40). As a result he got a hybrid containing 30 chromosomes, 10 from the *rotundifolia* parent and 20 from the *longifolia* parent. During synapsis only 10 bivalents were formed and 10 chromosomes remained as univalents. Rosenberg concluded that the 10 chromosomes of *rotundifolia* paired with 10 of *longifolia*, leaving the other 10 of *longifolia* unpaired. Such a type of pairing between two sets of chromosomes belonging to two different parental species which may or may not have equal number of chromosomes is known as Allosyndesis. Here 10 chromosomes of *rotundifolia* and 10 chromosomes of *longifolia* paired allosyndetically. Similar cases of allosyndesis have been recorded in *Triticum* hybrids (*n*: 35) resulting from a cross between *Triticum Emmer* (*n*: 14) and *Triticum Vulgare* (*n*: 21). 14 synaptic pairs were formed. 14 chromosomes of *Triticum Emmer* paired with 14 of *Triticum Vulgare* while the remaining 7 chromosomes of *Vulgare* parent were left in an unpaired condition (Kihara, 1919; Sax, 1922). In *Nicotiana* hybrids between *Nicotiana Tabacum* (*n*: 12) and *Nicotiana sylvestris* (*n*: 24) (Goodspeed and Clausen, 1927) there was an arrangement of 12 bivalents and 12 univalents indicating allosyndesis between 12 chromosomes of *Nicotiana Tabacum* and 12 chromosomes of *Nicotiana sylvestris* (*n*: 24).

There are also cases where in addition to allosyndesis there is also autosyndesis. Autosyndesis indicates the pairing among the chromosomes of a single set. Thus in *Digitalis* hybrids (2*n*: 72), between *D. lutea* (*n* : 48) and *D. micrantha* (n: 24) 72 chromosomes were found in the somatic complement, and during meiosis, they organised into 36 gemini (Haase-Bessel, 1916) indicating that all the chromosomes have paired. It means that 24 chromosomes of *D. micrantha* have paired with 24 chromosomes of *D. lutea* to form 24 bivalents. The remaining 24 chromosomes of *D. lutea* have paired among themselves to form 12 more bivalents, thus bringing the total to 36 bivalents. In such a case as this, there is not only pairing between the members of the gametic complements of the two different species, namely,

D. lutea and *D. micrantha* (allosyndesis) but also among the remaining chromosomes of the same gametic complement, namely *D. lutea* (autosyndesis).

Similarly in *Papaver* hybrids (Ljundahl, 1924), *viz.*, *Papaver nudicaule* (n: 7) and *Papaver radicatum* (n: 35) there are 21 gemini formed which may be explained on the same basis. 7 chromosomes of *nudicaule* have paired with 7 of *radicatum* and the 28 chromosomes of *radicatum* have paired among themselves to form 14 gemini. Thus there is allosyndesis between 7 of *radicatum* and 7 of *nudicaule* and autosyndesis between the 28 chromosomes of *radicatum* themselves. This revealed that though the two parental complements differ in number yet there is a marked affinity between the two sets. Allosyndesis and Autosyndesis would thus indicate the extent to which there exists homology between the two parents.

In hybrids exhibiting weak pairing among the chromosomes of the parents, varying degrees of synapsis and in some cases asynapsis also occur in the meiotic cycle of the hybrid and consequently it becomes sterile. Raghavan and Srinivasan, A. R. (1941 *a*) record such weak pairing among the chromosomes in the hybrids between *Nicotiana glutinosa* ($2n$: 24) and *Nicotiana Tabacum* ($2n$: 48). They observed varying degrees of synapsis and also in certain cases complete asynapsis. This would indicate distant homology. This hybrid has been classified by them under the *Hieracium Boreale* type. Hybrids belonging to the last scheme, namely, showing no affinity between the members of the two complements have been recorded in many cases. *Crepis* (Collins and Mann, 1923), *Digitalis* (Haase-Bessel, 1921) and *Nicotiana* (Goodspeed, 1934).

In the present investigation the meiosis of the sterile hybrid was studied in detail with a view to find out the degree of affinity that existed between the two sets of gametic complements. The sterile hybrid ($2n$: 29) of the cross between *Sesamum orientale* (n: 13) and *Sesamum prostratum* (n: 16) shows irregular meiosis with varying numbers of bivalents. It is also found that in the majority of cases 8 bivalents are formed with the rest scattered as univalents. The somatic number 29 of the hybrid should contain 13 of *orientale* chromosomes and 16 of the *prostratum* parent. If it conforms to the *Drosera* scheme of pairing, then 13 of *orientale* chromosomes should pair with 13 of *prostratum*, leaving the three *prostratum* chromosomes unpaired. But such a maximum pairing has never been observed to take place as most of the pollen mother cells show 8 and very occasionally 10 bivalents. This can be interpreted in two ways: (1) That the 8 chromosomes of *orientale* pair with a corresponding number of *prostratum* chromosomes leaving the others

unpaired. This means that it is a case of allosyndetic pairing. (2) That the *prostratum* chromosomes might pair among themselves to form 8 bivalents, leaving the 13 *orientale* chromosomes in an unpaired condition. This suggests autosyndesis among *prostratum* chromosomes. Either of these interpretations would indicate only a weak homology between the chromosomes of *Sesamum prostratum* and *Sesamum orientale*. It is therefore reasonable to infer that we have to look to some other source for the origin of the cultivated til (*Sesamum orientale*) than from *prostratum*. It is not likely that they could have had a common origin on account of their distant homology as revealed by the behaviour of their chromosomes in the hybrid. This would appear to be supported also by the fact that even though they belong to the same genus, they are different in their habit. The one is erect whereas the other is prostrate. *Sesamum orientale* is an annual herb whereas *Sesamum prostratum* is perennial almost a shrub. It may be that future explorations into the Indian wilds may show the presence of ancestral forms of the domesticated til. In this connection, we have also to remember the American tropics. Only one wild species has been reported from Argentina, which is *Sesamum radiatum* ($2n$: 64) (John and Rao, 1941). Its number suggests tetraploidy from *Sesamum prostratum*. Whether there are any more forms which could throw light upon the origin of the cultivated til, future exploration alone can reveal.

(*c*) *Artificial synthesis of a new species*

The genes on the chromosomes govern plant characters. Any alteration of the genes either in their position or in their number would consequently affect the configuration of a plant. Gene mutations thus bring about mutations of plant characters. Generally gene mutations involve a rearrangement of the genes such as inversion, reciprocal translocation, etc. These lead to mitotic and meiotic aberrations resulting in external morphological mutations of several kinds. A more common and fruitful way in which changes in plant configurations occur is through the duplication of genes of certain chromosome sets or the duplication of the entire genic complement. That is, all the members of the chromosome complement undergo reduplication and this is known as Polyploidy. The phenomenon of polyploidy may be of two kinds, Autopolyploidy and Allopolyploidy. In the former there is a duplication of the chromosomes derived from the same parent (as in self-pollinated plants) or from parents belonging to the same species as in cross-pollinated plants. In the latter two sets of chromosomes from two different parents are involved. This may happen in interspecific hybrids and very rarely in intergeneric hybrids.

Autopolyploids arise either spontaneously in nature or are artificially induced. Allopolyploidy on the other hand indicates hybridisation, whether interspecific or intergeneric. Autopolyploids may be stable species breeding true. In most cases where there is induced polyploidy sterility of the autopolyploid is quite common as in *Cosmos* (Earl Newcomer, 1941). Allopolyploids as aforesaid arise out of hybridisation. The hybrid so derived may be sterile or fertile. If the hybrids prove fertile, then the allopolyploids breed true and establish themselves as stable species. Allopolyploids which are sterile due to hybridisation may be made fertile by artificial induction of amphidiploidy about which a detailed mention is made further below.

The most common form of autopolyploids occurring in nature are the tetraploids. Tetraploids arise as a result of the duplication of the diploid chromosomal set. Many causes are in evidence for the duplication of chromosomes in the plant cell. Cytomyxis, occurring in the pollen mother cells, is considered by some to be one among them. This phenomenon was first observed by Gates (1911) in the pollen mother cells of *Oenothera gigas*. He described the process as a migration of the chromatic material from the one pollen mother cell into the adjacent cell. But he contended that the chromatic material disappeared into the cytoplasm of the recipient cell and that the chromatic material of the recipient cell was not increased by the addition of extruded chromatic material from the adjacent cell. Thus according to him, cytomyxis does not bring about chromosome duplication. Binucleate pollen mother cells arisen from cytomyxis, have been recorded in *Tridax* (Raghavan and Venkatasubban, 1941) where the two nuclei enter independently into successive division stages and ultimately it was observed that this phenomenon was responsible for the degeneration of the pollen mother cells and the significant sterility in the species was attributed to cytomyxis. Nandi (1937) also describes such cases of binucleate pollen mother cell formation from cytomyxis at diakinesis in *Oryza*. Particularly in the case of hybrids both interspecific and intergeneric this abnormal phenomenon seems to be quite common. Kattermann (1933) in *Triticum* × *Secale* hybrids, Percival (1930) in hybrids between *Aegilops* × *Triticum* species and Raghavan and Srinivasan, A. R. (1941 *a*) in *Nicotiana glutinosa* × *Nicotiana Tabacum* hybrids. From this and from the evidence of Church (1929) who found the occurrence of this phenomenon in the hybrids of *Phalaris*, we may infer that it is more probable that this phenomenon is associated with hybrids than being an artifact as Sinoto (1922) regarded. It cannot however be said with any amount of certainty whether the formation of additional nuclei through cytomyxis is a certain method of origin of polyploidy.

Tetraploidy may also arise from fusion of unreduced gametes having the diploid number of chromosomes. They are formed due to absence of cross-wall formation after the heterotypic division. When an unreduced gamete fertilises a gamete with the haploid number, then a triploid results. If it fertilises another unreduced gamete, a tetraploid is formed. Such instances of tetraploidy are common in *Datura*, and Tobacco. In *Brassica* hybrids it was observed by Ramanujam and Srinivasachar (1943).

Experimental tetraploids have been obtained in a number of species. As early as 1914 Gregory described a tetraploid strain in *Primula sinensis*, containing 48 chromosomes. It has been shown that in the chromosome sets of diploids there are chromosomes of different kinds, each of which is represented twice, one of the two being derived from egg and the other from the pollen. In the tetraploids with 48 chromosomes, it was found that the chromosomes often came together in fours at reduction division. It was found that the 48 chromosomes of the tetraploid united into 12 groups of four. Winkler (1916) induced polyploidy in *Solanum* by grafting together the species *Solanum lycopersicum* and *Solanum nigrum*. The adventitious shoots arose at the grafting point were in some cases tetraploid. Decapitation is another means of bringing about tetraploidy. Terminal buds of tomato, tobacco have been decapitated and callus allowed to form which produced adventitious buds from which arose tetraploids (Beadle, 1940).

Certain drugs, particularly the alkaloid, Colchicine, extracted from *Colchicum autumnale* have been known to produce characteristic disturbances in the cell division. Blakeslee and Avery (1937) showed that treating seeds with an appropriate solution of colchicine produces tetraploid tissues from which tetraploid strains may be derived. Their work has been subsequently confirmed and employed by many investigators (Nebel and Ruttle, 1938), (Levan, 1938, 1939 and 1940 *a*) and many others.

An important property of Autopolyploids concerns the behaviour of their chromosomes at meiosis. In a diploid organism, every chromosome has its homologous partner. Of the two homologous sets one is from the male cell and the other belongs to the female sexual cell. A number of bivalents equal to the haploid chromosome number is formed and the disjunction at meiosis gives rise to gametes all of which contain haploid sets of the chromosomes. In an autopolyploid every chromosome has more than one homologue so that opportunity presents itself for the formation of trivalents, quadrivalents and higher associations. The disjunction at meiosis is frequently abnormal, different numbers of chromosomes going to two poles of the division spindle. In order to breed true, an autotetraploid

must produce gametes all of which have the same complements of chromosomes. Since loss or addition of chromosomes usually reduces the viability of the offspring, the reproductive cells of polyploids are frequently non-functional. But there are a number of cases of tetraploids which are normal and consequently breed true and have established themselves as stable forms, *e.g.*, *Tradescantia* (Anderson and Sax, 1936).

Apart from their existence in nature, due to natural hybridisation, allopolyploids have been produced experimentally. The intergeneric hybrids between radish (*Raphanus sativus*, n: 9) and cabbage (*Brassica oleracea*, n: 9) serve as an illustration of the results obtained when the chromosome complement is reduplicated in crosses of taxonomically remote forms (Karpechenko, 1927 *a* and *b*). Both parents have the diploid number 18. Cross succeeded fairly easily. The hybrids had 18 chromosomes, 9 from the radish and 9 from the cabbage parent. No chromosome pairing took place and the 18 chromosomes remained as univalents at metaphase of the first division and were distributed at random to the poles. At the second division the univalents split, giving rise to cells with a varying number of chromosomes, mostly from 6 to 12. In some of the pollen mother cells however, the first division was abortive and nuclei were formed that included all the 18 univalents. The second division then gave rise to two diploid spores. Two pollen grains containing the diploid complements were organised. The F_1 hybrids mostly were sterile but few seeds were produced. Cytological examination showed that most of the F_2 hybrids derived from the seeds had 36 chromosomes in their somatic cell. The origin of such plants was in all probability due to the union of the few diploid gametes produced in the F_1 hybrid. The F_2 plants therefore contained 18 radish and 18 cabbage chromosomes; in other words, the diploid complement of the chromosomes of each parental species. Such F_2 hybrids were allotetraploids. The meiotic divisions were very regular in striking contrast with the abnormalities observed at meiosis in the F_1 hybrids. In the tetraploids, 18 bivalents were formed, disjunction was normal and the resulting cells contained 18 chromosomes each. It is practically certain that 18 bivalents that appeared at meiosis were due to the pairing of 9 radish chromosomes with their 9 radish homologues. Thus the pairing was between similar chromosomes of the same parent (Autosyndesis) rather than between the chromosomes of different species (Allosyndesis). The tetraploid plants were fertile and bred true. This true breeding type was assigned the name *Raphano-Brassica* because it arose out of the two genera, *Raphanus* and *Brassica*, after hybridisation.

Raphano-Brassica is by no means the only new species which has arisen through allopolyploidy in experimental cultures. *Primula Kewensis* (n: 18

and $2n$: 36) is another allotetraploid which arose as a bud sport among population of *Primula floribunda* and *Primula verticillata*, both having haploid number 9. *Primula Kewensis*, the diploid hybrid of *Primula floribunda* and *Primula verticillata*, was observed to set seed on three occasions since its first production in 1900 (Newton and Pellew, 1929). Each time its seed gave rise to fertile plants with the tetraploid number of chromosomes, $2n$: 36. In the vegetative cells of one of the fertile inflorescences, tetraploid number of chromosomes was found, showing that the doubling process took place in the somatic division. It was the only case known of a sterile (diploid) hybrid giving rise to a fertile tetraploid by somatic doubling of chromosomes. In the meiotic division of the diploid hybrid of *P. Kewensis* (n: 18) 9 pairs of chromosomes were formed which may be indicated as F1 V1, F2 V2 and so on. The resulting gamete would contain all possible combinations of chromosomes. Most of these gametes were non-viable; a few however were viable and these while they bore many *P. floribunda* characters also showed traces of *P. verticillata*. But in the tetraploid hybrid each chromosome was represented twice and if 18 pairs were formed in meiosis, they might either be pairs of identical chromosomes (F1 F1, V1 V1) or of corresponding *floribunda* and *verticillata* chromosomes (interspecific pairing) as in the diploid hybrid. In the last case, the number of possible combinations would be much greater than in the diploid. In the former case, F1 F1, V1 V1 or identical chromosomes separate and the gamete will each contain a complete set of *floribunda* or *verticillata* chromosomes which on fertilisation will give a uniform progeny. Thus the hypothesis of pairing of identical chromosomes (intraspecific) gives a satisfactory explanation of a perfectly constant tetraploid hybrid. This hypothesis was put forward by Winge (1917) in discussing the possible origin of tetraploids from hybrids. He considered that doubling of chromosomes might result in failure to conjugate at meiosis, followed by splitting and subsequent pairing of the identical halves.

The case of *Crepis* is somewhat different from that of *Primula Kewensis*. Poole (1931) showed that in the diploid hybrid of *Crepis*, *Crepis rubra* (n: 5) × *Crepis fœtida* (n: 5) there was complete pairing of the chromosomes. They behaved as though they were from the same parents. Consequently, the hybrid was fertile and the tetraploid derived from it behaved almost like an autotetraploid. Quadrivalent formation was very common. In the F_1 hybrid R (rubra) and F (fœtida) chromosomes paired (RF). In the tetraploid form duplication of the chromosomes took place, resulting in RR and FF. Because of the complete homology of R and F chromosomes, these four chromosomes formed one quadrivalent (RRFF). But in the case of

Primula Kewensis tetraploid (FFVV) there were no quadrivalents formed. Instead F and F paired and V and V paired forming 18 bivalents. It might be that even though F and V were somewhat related, they were not completely homologous so as to induce quadrivalent formation. Presumably VV and FF bivalents may exhibit secondary association indicating their ancestral relationship.

Experimentally-produced allopolyploids of the kind described above happen to be identical to wild Linnæn species already existing in nature. The classical example of such an allotetraploid is that of *Galeopsis Tetrahit*, an existing Linnæan species which was experimentally synthesised from its putative ancestors. In his monograph on the genus *Galeopsis*, Muntzing (1930, 1932 and 1937) showed that six out of the eight species investigated had the haploid number of chromosomes 8 and the two remaining ones had n: 16. Among the former were the species of *Galeopsis pubescens* (n: 8) and *Galeopsis speciosa* (n: 8) and among the latter was *Galeopsis Tetrahit* (n: 16). The crosses between *G. pubescens* and *G. speciosa* succeeded easily when *G. pubescens* was used as the female parent. At meiosis varying numbers of bivalents and univalents were formed. The anther of the flowers of this hybrid contained only 8 to 20% of good pollen grains. A few good ovules however were produced. In the F_2 progeny raised by the few seeds obtained, a single plant was found that proved to be a triploid ($3n$: 24). Its origin is probably due to the union of a gamete containing the somatic complement of the hybrid (8 chromosomes of *G. pubescens* and 8 chromosomes of *G. speciosa*) with a gamete carrying 8 chromosomes. This triploid was backcrossed to pure *G. pubescens*. A single seed resulted from the backcross. It gave rise to a plant which proved to be a tetraploid ($4n$: 32). This tetraploid was fertile and became the progenitor of a strain which was named " artificial Tetrahit".

This ' artificial Tetrahit ' was like the real *Galeopsis Tetrahit* described by Linnæus, in possessing 32 chromosomes in somatic cells and 16 bivalents at meiosis. The irregular meiosis characteristic of the F_1 hybrids ceased to exist in the artificial Tetrahit. In short, the artificial *G. Tetrahit* and the natural species are similar not only in their morphology but also in their genetical and cytological behaviour.

Spartina Townsendii ($2n$: 56) is another example of an experimental allotetraploid. *Spartina stricta* (n: 28) and *Spartina alternifolia* (n: 35) were crossed (Huskins, 1931). The tetraploid form of the hybrid was found to contain 126 chromosomes. *Spartina Townsendii* showed a diploid number of 126 chromosomes and with morphological and cytological evidences,

Huskins proved that *Spartina Townsendii* was an allotetraploid derivative of the hybrid between *Spartina stricta* and *Spartina alternifolia.*

Since the discovery of colchicine as an agent for the doubling of chromosomes, several experiments have been conducted to confirm the origin of existing species by artificially repeating the supposed event that led upto their formation. Thus existing polyploid species have been artificially synthesised from their putative ancestors, in *Nicotiana* (Greenleaf, 1941), in *Gossypium* (Harland, 1940) and in *Triticum* (Thompson, Britten and Harding, 1943). Recently *Brassica juncea* was artificially synthesised and its origin was traced with the help of cytological and cytogenetical evidences (Ramanujam and Srinivasachar, 1943). According to Morinaga (1934) *Brassica juncea* ($2n$: 36) is an allotetraploid composed of the genomes of *Brassica campestris* (n: 10) and *Brassica nigra* (n: 8).

Two evidences were adduced to the allotetraploid origin of *Brassica juncea.* Firstly in a cross between *Brassica juncea* (n: 18) and *Raphanus sativus* (n: 9) there was complete absence of pairing among the *B. juncea* chromosomes themselves in the F_1 hybrid. Secondly, when crosses were made on the one hand between *B. juncea* and *B. campestris* and on the other between *B. juncea* and *B. nigra*, the Drosera scheme of pairing was observed. That is in the F_1 hybrids (*B. juncea* × *B. campestris*) and (*B. juncea* × *B. nigra*) the configuration of 10 bivalents and 8 univalents and 8 bivalents and 10 univalents occurred respectively. In *B. juncea* × *B. campestris* 10 chromosomes of *B. campestris* paired with 10 of *B. juncea*, leaving the 8 chromosomes of *B. juncea* as univalents.

It is clear from the regular formation of bivalents in these hybrids that the haploid set of *B. juncea* chromosomes is equivalent to the haploid set of the two species, *B. nigra* and *B. campestris* and that by doubling the chromosomes of the F_1 hybrid got between them, plants resembling *B. juncea* could be produced.

Recently such an origin of *Brassica juncea* as an allotetraploid from *B. campestris* and *B. nigra* parents has been confirmed by the more direct evidence of synthesising the species by successfully effecting crosses between the two parents and subsequently inducing amphidiploidy by the application of colchicine (Ramanujam and Srinivasachar, 1943). Additional confirmation was obtained from the fact that there was uniform pairing between synthetic *B. juncea* and natural *B. juncea* when they were crossed. They crossed *B. campestris* and *B. nigra* and the F_1 hybrid that resulted out of this cross possessed $2n$: 18 and these appeared as bivalents and univalents during meiosis. Occasional cases of quadrivalent formation were also met

with. Anaphase I and II were characterised by bridge formation. Fruit setting was very poor and only a few seeds could be available. The first generation of Amphidiploid was produced as a chimeral branch on F_1 hybrid of the above cross. Two branches were treated with ·4% colchicine in 50% glycerine. The branches treated showed fertility and an A_2 generation of plants were raised from the seeds available in the fruits of the treated branches. The A_2 generation possessed diploid set of 36 chromosomes and resembled in all respects those belonging to the species *B. juncea.* This amphidiploid crossed easily with the natural *B. juncea.* Pairing was complete thereby indicating that the haploid set of the amphidiploid was homologous to the haploid set of *B. juncea.* Indirect evidences as adduced by Morinaga (1934) stand confirmed by this direct evidence through artificial synthesis.

In a manner similar to the above mentioned cases, hybridisation and artificial induction of amphidiploidy led to the establishment of a true breeding species of *Sesamum* in this laboratory. The amphidiploid, details of whose characters are given in another paper, proved to be a stable true-breeding type and deserves an independent place along with the parental species, namely, *Sesamum orientale* and *Sesamum prostratum. Sesamum orientale* ($2n$: 26) and *Sesamum prostratum* ($2n$: 32) were crossed reciprocally. This resulted in a hybrid having $2n$: 29. Meiosis was found to be irregular because neither complete autosyndesis nor complete allosyndesis was observed. The result was that the hybrid proved to be sterile. A duplication of the chromosomes means the duplication of the parental chromosome sets. Then during meiosis there would be autosyndesis which would result in regular meiosis. Thus with this object in view the sterile hybrid was treated with colchicine and amphidiploidy was successfully induced.

Colchicine solution in tap water of strength ·4% was applied in the form of drops at the terminal bud of young seedlings of the hybrid. The treatment was given twice a day on three alternate days. A cotton wool was placed at the region of application to prevent excessive evaporation of the chemical. The colchicine effect was revealed in the hybrid by its stunted growth and deformed leaves. Flowers were formed which were almost twice as big as those of the sterile hybrids. Viable pollen grains were formed and the treated seedlings yielded fruits with good seeds. Thus fertility was induced through amphidiploidy.

The cause of the fertility may be inferred as follows: The 29 chromosomes of the hybrid plant would have been doubled to 58 by the action of colchicine so that the somatic complement instead of having 16 chromosomes

of *prostratum* and 13 chromosomes of *orientale* would have 32 chromosomes of *prostratum* and 26 chromosomes of *orientale*. During meiosis no irregularity was noticed because the 32 chromosomes of *Sesamum prostratum* paired autosyndetically, to form 16 bivalents and the 26 chromosomes of *Sesamum orientale* parent paired autosyndetically among themselves to form 13 bivalents, thus resulting in autosyndesis or intraspecific pairing in both the parents. The 29 bivalents observed in meiosis of the amphidiploid must be the total number of bivalents of both the parents. This amphidiploid has been established as a stable true breeding type evolving out of interspecific hybridisation followed by amphidiploidy.

The true breeding fertile hybrid resembles the *prostratum* parent more than the *orientale* including the perennial habit. Even the sterile hybrid shows greater resemblance to *Sesamum prostratum*. The cytological explanation for this may lie in the fact that both in the sterile and fertile hybrids there is a greater number of *prostratum* chromosomes. The F_1 hybrid is only an annual whereas the amphidiploid is a perennial. Possibly the presence of a very large number of *prostratum* chromosomes, 32 in a complement of 58, is responsible for incorporating this parental feature also in the amphidiploid. Thus cytological investigations of many of the existing species, wild and cultivated, may well show that, in speciation, amphidiploidy has played an important role. Many of the existing forms may be proved to be amphidiploids, provided their parental ancestors are discovered. Thus in evolution of new species, allopolyploidy has played an important part.

(*d*) *The possible origin of the cultivated Til, Sesamum orientale* Linn.

From the cytological data gathered through interspecific hybridisation, it is safe to infer, in an empirical way, the possible origin of the cultivated Til. If, in the interspecific hybrid between *Sesamum orientale* Linn. and *Sesamum prostratum* Retz., there was exhibited Drosera scheme of pairing, then it would have meant that the genome of *Sesamum prostratum* contained within it the genome of *Sesamum orientale* and consequently the two would be related ancestrally. But that is ruled out.

The frequent occurrence of 8 bivalents can be regarded as autosyndetic pairing amongst the 16 *prostratum* chromosomes, leaving the 13 chromosomes of *orientale* unpaired.

Or it may be that the 8 chromosomes of *prostratum* have paired with 8 chromosomes of *orientale* to form the bivalents. In this case 8 chromosomes of *prostratum* and 5 chromosomes of *orientale* are left out unpaired. This means allosyndetic pairing between 8 chromosomes of *prostratum* with 8 of *orientale*.

If it was allosyndetic, then all the 13 chromosomes of *orientale* must have paired with 13 *prostratum* chromosomes (Drosera scheme). It cannot be that 8 alone of *orientale* chromosomes could be homologous with 8 chromosomes of *prostratum* and the rest did not show any homology. So it is likely that the 8 bivalents frequently met with are the result of autosyndetic pairing among the *prostratum* chromosomes. This means that there is no pairing at all between *prostratum* and *orientale* chromosomes.

From the above two suggestions, two things are evident. (1) That the haploid sets of *orientale* chromosomes are not sufficiently homologous with one another to pair among themselves. So Til might have arisen through allopolyploidy. (2) An absence of pairing between the two parental chromosomes sets indicates the lack of homology between the chromosomes of *prostratum* and *orientale* and hence they could not have had a common origin.

This absence of homology as indicated by absence of autosyndesis amongst the *orientale* chromosomes must be due to either of two causes: (1) That the basic number of Til is 13 and that polyploidy has not played a part in the evolution and that the 13 gametic chromosomes, even though they may not show wide disparity in their morphology, are none the less structurally different from one another which results in their non-pairing. (2) The second alternative is that it should have arisen from a lower chromosome-numbered ancestor through the operation of polyploidy. If so, the absence of autosyndesis indicates that allopolyploidy has been the operating factor. Of these two alternative possibilities the latter seems the more likely.

In the previous investigation as well as in the present, the phenomenon of secondary association has been frequently met with and on the basis of maximum association, it has been suggested that 7 is the basic number of the species—meaning thereby that Til must have arisen from an ancestral form with a set of 7 haploid chromosomes. How this 26 chromosomed Til could have been evolved from such a basic number, through the operation of allopolyploidy, can be explained as follows:—

Supposing there were 2 ancestral species P_1 and P_2 each having 7 haploid chromosomes, one parent from P_1 would have gametic genome A, B, C, D, E, F and G, whereas the other parental form P_2 possibly arisen through gene mutations, not involving numerical change, would have a genome of the same number of chromosomes (7), A_1, B_1, C_1, D_1, E_1, F_1 and G_1. Then the parents are:

P_1	A	P_2	A_1	Gametic genomes. n: 7.
	B		B_1	
	C		C_1	
	D		D_1	
	E		E_1	
	F		F_1	
	G		G_1	

A natural cross between the two forms P_1 and P_2 would result in a hybrid P_3 having:

P_3	A	A_1	$2n$: 14. Sterile hybrid.
	B	B_1	
	C	C_1	
	D	D_1	
	E	E_1	
	F	F_1	
	G	G_1	

The hybrid P_3 is presumably sterile because chromosomes A and A_1 from parents P_1 and P_2 are not homologous and so do not pair.

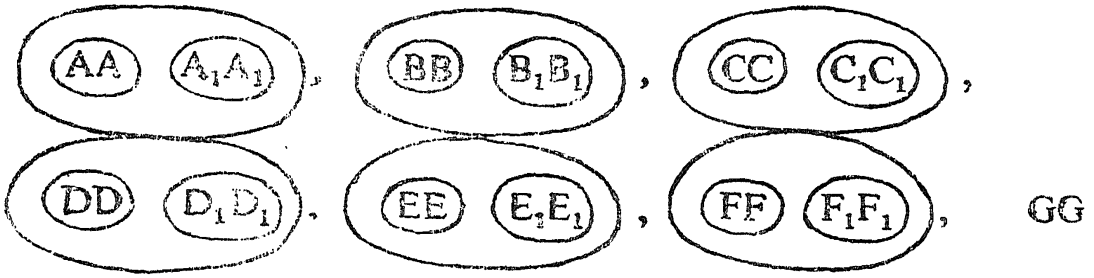
Somatic doubling takes place by some means, say, fusion of unreduced gametes. Then the chromosome sets in P_3 will be doubled resulting in P_4 having $2n$: 28.

P_4	AAA_1A_1
	BBB_1B_1
	CCC_1C_1
	DDD_1D_1
	EEE_1E_1
	FFF_1F_1
	GG (G_1G_1) Deletion.

Deletion of one pair of duplicated chromosomes in P_4 results in the disappearance of one of the chromosome pairs say (G_1G_1). Now P_5 resulting after the deletion of one pair would contain $2n$: 26 only (= *S. orientale*).

P_5	AA	A_1A_1	$2n$: 26
	BB	B_1B_1	
	CC	C_1C_1	
	DD	D_1D_1	
	EE	E_1E_1	
	FF	F_1F_1	
	GG	—	

Meiosis in P_5.—13 pairs are formed in 7 groups. Because of distant homology of A and A_1 chromosomes AA bivalents is secondarily associated with A_1A_1. Thus we get 6 groups of secondarily associated bivalents, *viz.*,



GG remains unassociated, G_1G_1 having been deleted during separation.

During the disjunction in P_5

A	is separated from	A	A_1	is separated from	A_1
B	,,	B	B_1	,,	B_1
C	,,	C	C_1	,,	C_1
D	,,	D	D_1	,,	D_1
E	,,	E	E_1	,,	E_1
F	,,	F	F_1	,,	F_1
G	,,	G			

So the gametic genome consists of:

A and A_1, B and B_1, C and C_1, D and D_1, E and E_1, F and F_1, & G. Since A and A_1, B and B_1, C and C_1, D and D_1, E and E_1, F and F_1 are not homologous enough to pair, as evidenced in the non-pairing in P_3 leading to its sterility, they do not show autosyndesis in the meiosis of the sterile hybrid ($2n$: 29)—*Sesamum orientale* (13) × *Sesamum prostratum* (16).

The fact that these remained unpaired without any autosyndesis therefore implies an allopolyploid origin of Til in the manner suggested above.

So far no species of *Sesamum* having n: 7 has been recorded. It is reasonable to expect such wild forms to be putative ancestors to the cultivated form. Only an extensive search for the wild ancestors of cultivated forms, such as organised by the Soviet, can throw light upon the problem.

(*e*) *The possible origin of Sesamum prostratum* Retz.

It is interesting to note that while one set of parental chromosomes (*Sesamum orientale*) do not pair among themselves, the other set of parental chromosomes (*Sesamum prostratum*) pair autosyndetically. The cause for the non-pairing among the *orientale* chromosomes is likely to be its origin as an allopolyploid in the manner previously described.

On similar lines, it may be supposed that autosyndetic pairing of *Sesamum prostratum* chromosomes in the sterile hybrid might be due to its origin as an autopolyploid from an ancestral form having haploid chromosome number

8. If that be the case then the ancestral form will have the somatic constitution as

AA, BB, CC, DD, EE, FF, GG, HH — $2n$: 16

Supposing doubling of chromosomes takes place then the zygote will contain $2n$: 32

AAAA, BBBB, CCCC, DDDD, EEEE, FFFF, GGGG, HHHH — $2n$: 32

Presumably no quadrivalent formation takes place and 16 bivalents are formed during the meiosis in *Sesamum prostratum.*

Since A and A are homologous, they pair and hence when they are in a new surrounding, namely, with *orientale chromosomes* in the sterile hybrid, they pair among themselves. They do not pair with *orientale* chromosomes because they are structurally different from them. This means that *Sesamum orientale* and *Sesamum prostratum* could not have arisen from a common ancestor. For, if that were so, the *Drosera*-scheme of pairing would have been exhibited in the hybrid meiosis. If the frequent occurrence of 8 bivalents could mean autosyndetic pairing of 16 chromosomes of *prostratum* chromosomes, then it is likely that *Sesamum prostratum* has arisen as an autotetraploid from a parent having 8 haploid chromosomes in the manner described above.

In the meiosis of *Sesamum prostratum* there has been observed a regular absence of multivalents. Normally in autotetraploids, any four chromosomes ordinarily tend to form a quadrivalent group in meiosis. Often the synaptic association is such as to group the four members into two bivalents. Thus tetraploid sporocytes may sometimes exhibit the diploid number of bivalents "the double diploid" (Sharp, 1934).

According to Crane and Lawrence (1934) it seems that competition in pairing at prophase meiosis in an autotetraploid may give rise to univalent chromosomes instead of multivalents.

Autotetraploids may change the pairing habit of their chromosomes and the number of chiasmata may be reduced to one for each chromosome so that no quadrivalent formation can be formed (Darlington, 1939). In *Tulipa* tetraploids this is found to happen to a varying degree (Margaret Upcott, 1939). It is observed that the chiasma frequency of the tetraploids is low, are sexually reproducing, and have been subjected to selection because of their origin from diploid ancestors. They have been selected for fertility and hence the absence of multivalents.

Many species have been found to include a series of polyploid forms. In some cases these are indistinguishable from one another except by distribution. It is plausible to assume that these forms have arisen as autopolyploids with free pairing amongst their homologous chromosomes. This condition is still found in certain forms which have presumably remained unaltered since their origin.

However, in most cases of autotetraploids low fertility or complete sterility has been the rule. This is due to the irregular meiosis. Formation of multivalents is very common and their disjunction is unequal. Hence polymorphic grains are formed which are non-viable. So in speciation, autopolyploidy has not played as important a part as allopolyploidy. There are however cases where autotetraploids have established themselves as stable species. They show regular meiosis and bivalents have been found instead of multivalents. Upcott (1939) has recorded tetraploids showing no multivalent formation in *Tulipa*-species. The autopolyploids of *Tradescantia* (Anderson and Sax, 1936) is another instance in point. The above authors have reported the occurrence of an entire group of vigorous autopolyploids in the genus *Tradescantia*. These unlike the usual autopolyploids were found to reproduce themselves by seeds.

Sesamum prostratum may well be included under such autotetraploids. The perennial habit, the luxuriant growth and the high yield mingled with the non-susceptibility to any disease, either fungal or insect, may be an additional advantage acquired by *Sesamum prostratum* through autotetraploidy. According to Erlanson (1938) polyploid forms are better fitted to withstand Arctic or Alpine conditions while the diploids will simply perish. Navaschin (1929) has pointed out that " through changes in the rate of development, a polyploid individual may acquire the ability of withstanding different climatic conditions, and as a consequence, penetrate into new territory ". Hagerup (1933) also has stated that " polyploid forms may be ecologically changed so as to grow in other climates and formations where the diploid forms will not thrive".

If *prostratum* could have arisen through autopolyploidy and established itself as a stable form, then the presence of other wild forms like *Sesamum radiatum* Shum and Thonn (*n*: 32), *Sesamum laciniatum* Klein (*n*: 14) may be explained as a series of polyploid forms arising out of the putative ancestor having *n*: 8. Then *Sesamum radiatum* (*n*: 32) will be an octoploid whereas *Sesamum laciniatum* (*n*: 14) will be a tetraploid, having lost a pair of chromosomes in its meiotic complement (from *n*: 16 to 14). Morphological evidences also may add proof to the inclusion of these two wild forms in the scale of polyploidy. *Sesamum laciniatum* and *Sesamum radiatum* have been found to grow luxuriantly maintaining at the same time the perennial habit. So, it might be that these forms, along with *Sesamum prostratum*, have arisen from an ancestor having a basic number of chromosomes *n*: 8, as autopolyploids.

V. Summary

Interspecific crosses between *Sesamum orientale* Linn. and *Sesamum prostratum* Retz. were effected reciprocally and the sterile hybrid was made fertile by artificial induction of amphidiploidy through colchicine. The cytology of the parents and the hybrids was studied in detail.

Details of meiosis of *Sesamum orientale*, one of the parents employed have been worked out. The peculiar persistence of the nucleus and its movements during the meiotic cycle are recorded. The other parent *Sesamum prostratum* has also been cytologically studied.

The irregular meiosis of the sterile hybrid and the occurrence of scattered bivalents and univalents in the metaphase plate, leading to the ultimate formation of abnormal sporads have been described fully.

The regular meiosis of the fertile amphidiploid is compared with the irregular meiosis of the sterile hybrid and the cause of this regularity is explained.

The nucleolus with behaviour of the special regard to its persistence and movements is discussed.

Interspecific hybridisation as a guide to ancestral homology and the artificial synthesis of a new species are discussed in the light of cytological data gathered in the present investigation.

The origin of the cultivated Til *Sesamum orientale* Linn. from a putative ancestor having haploid number 7 through allopolyploidy is traced with the help of cytological details obtained in the hybrid meiosis.

The origin of the wild *Sesamum prostratum* Retz. is also traced to an ancestral form possessing haploid number of 8 chromosomes through autopolyploidy.

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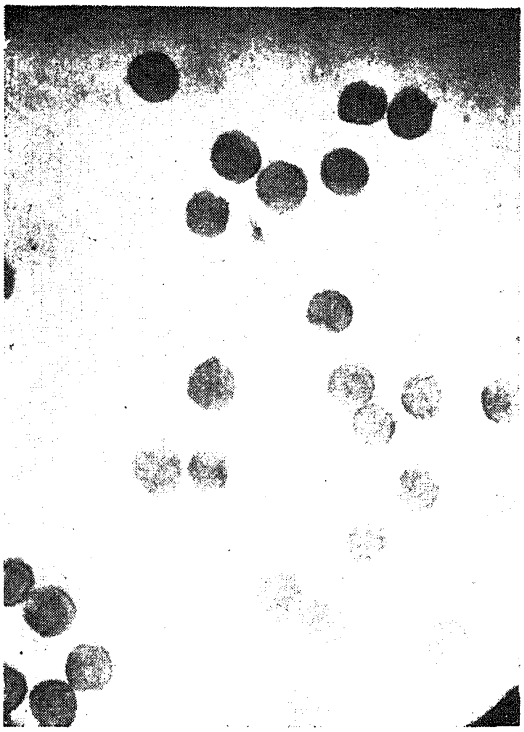

FIG. 1

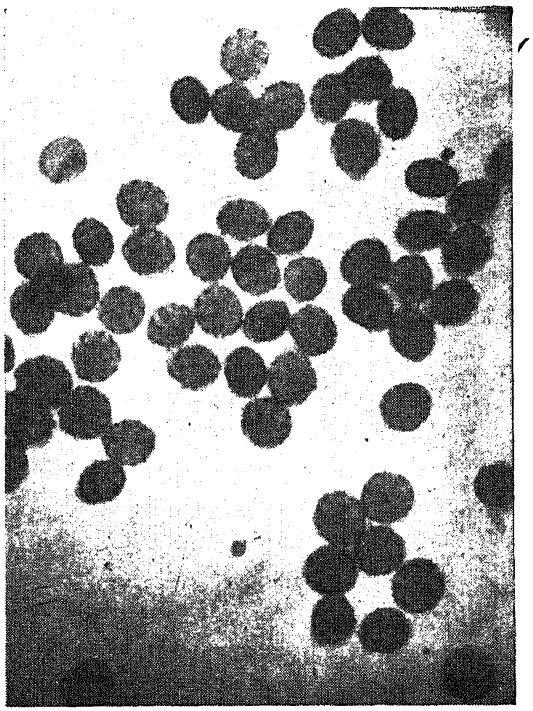

FIG. 2

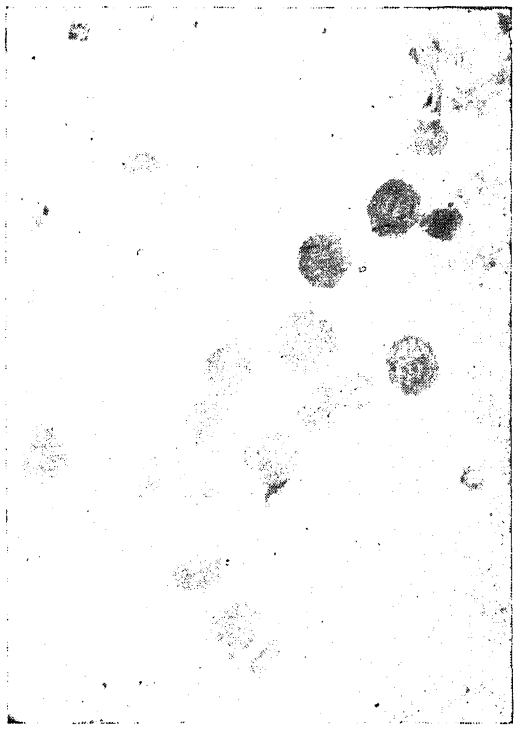

FIG. 3

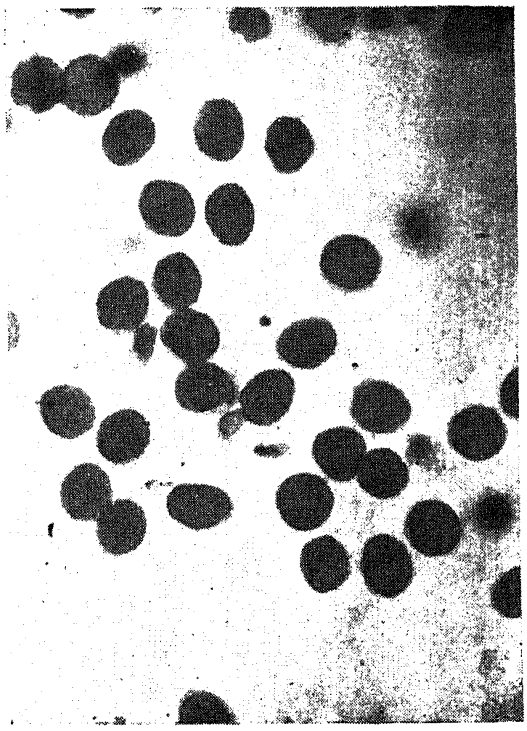

FIG. 4

Microphotographs of pollen grains of the parents and hybrids

FIG. 1. *Sesamum orientale* Linn. Uniform
FIG. 2. *Sesamum prostratum* Retz. Uniform
FIG. 3. Grains of the sterile hybrid. Polymorphic
FIG. 4. Grains of the Fertile amphidiploid. Big and uniform

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