# CYTOGENETIC STUDIES OF PRECOCIOUS MEIOTIC CENTROMERE DIVISION IN LYCOPERSICON ESCULENTUM MILL.[1]

CARL D. CLAYBERG

*Department of Genetics, Connecticut Agricultural Experiment Station, New Haven, Connecticut*

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IN the normal course of meiosis chromosome division is completed at the beginning of AII and the sister chromatids migrate to opposite poles. When division occurs earlier, it is regularly associated with the presence of unpaired chromosomes in late PI or at MI and is very likely stimulated by this lack of pairing. Rarely precocious division may take place in the absence of reduced pairing.

Unpaired meiotic chromosomes are present in organisms deviating from the diploid chromosome complement, in species hybrids with reduced chromosome homology, and in asynaptics. At AI in monosomics the univalent divides in almost all cells (OLMO 1936; SEARS 1952) or in about half of them (MORRISON 1953). The univalents of haploids usually segregate randomly to the poles during AI dividing rarely at this stage (BELLING 1927; IVANOV 1938; LEVAN 1942, 1945). In a few haploids the unpaired chromosomes divide frequently in AI (GAINES and AASE 1926; LESLEY and FROST 1928). The reduction of pairing in trisomics, polyploids, and species hybrids can lead to univalents at MI, but their behavior as to time of division is often quite irregular even in the same material (LESLEY 1928; MCCLINTOCK 1929; UPCOTT 1935).

Some univalents may lag and divide at AI or TI in partial and complete asynaptics, but this division usually does not occur until AII. There are, however, a few striking examples of precocious chromosome division associated with asynapsis. SMITH (1936) observed division of all univalents at AI in complete asynaptics segregating from the hybrid *Triticum monococcum* × *T. aegilopoides*. With the absence of bivalents at MI in partially asynaptic *Crepis capillaris*, all univalents sometimes divided during AI (RICHARDSON 1935). Regular division of all univalents took place at AI in asynaptic *Oenothera decipiens* regardless of their position on or off the metaphase plate (CATCHESIDE 1939). In contrast to Crepis the presence or absence of bivalents, which behaved normally, failed to influence this division.

Asynapsis in *Alopecurus myosuroides* (JOHNSSON 1944) represents a more extreme situation. Precocious division occurred at AI not only in all univalents but also in the bivalents, which sometimes had not yet completed chiasma separation. As with the previous case in Oenothera, a MII plate did not form and daughter univalents segregated randomly to the poles without dividing again.

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JOHNSSON (1944) believed that the aberrant behavior represented a true precocity rather than a retarded first division. He based this opinion on his study of chromosomes in other *A. myosuroides* mutants possessing retarded first division and concluded that in his asynaptic "the centromere division itself [distinct from the asynapsis] would seem to be subject to a genotypical variation." Here, as elsewhere used in the present account, "*centromere division*" refers to completion of chromosome division, for true centromere division may normally occur as early as AI (LIMA-DE-FARIA 1956).

In autotetraploid *Chrysanthemum atratum*, DOWRICK (1953) observed a high proportion of cells at MI having only bivalents. All the centromeres divided precociously during this stage in these cells, although sister chromatids did not fall apart until homologues had migrated to opposite poles at AI. Each daughter nucleus thus contained the unreduced chromosome number. The second division was completely suppressed in such cells. Normal microsporocytes in the same material had the chromosome associations and behavior typical of autotetraploids, the univalents dividing at AI. Reduced chromosome pairing and chiasma frequency and a delayed PI were associated with the centromere precocity.

LAMM (1944) has briefly reported a rare instance in which precocious chromosome division occurring in TI was apparently not caused either by asynapsis or by an unbalanced chromosome complement. A sterile mutant in *Lycopersicon esculentum* appeared in segregating progenies which suggested inheritance by a single recessive factor. Anthers examined from one of the sterile plants showed meiosis to be normal during diakinesis and MI, with homologous chromosomes segregating regularly to opposite poles at AI. Chromosomes at TI "arranged themselves at each pole into a plate, whereupon their centromeres divided." The resulting TI groups thus contained the somatic chromosome number. The daughter chromosomes became oriented on two plates at MII and segregated to the poles at random in AII without further division. Microspore quartets usually resulted despite irregular chromosome distribution. No fertile pollen was produced. Although the aberrant plant analyzed cytologically was also trisomic, later observations of diploid segregants indicated that the precocity was not due to the extra chromosome (LAMM, unpublished).

The present study was initiated to determine the nature of another sterile tomato mutant whose infertility appeared to be unassociated with asynapsis or chromosome unbalance (CLAYBERG 1958a). Cytological analysis of later generations revealed that the sterility was caused by precocious centromere division begun late in the first meiotic division, mostly completed by PII, and resulting in irregular chromosome segregation at AII.

## MATERIAL

The mutant originated from a partially sterile plant found in 1953 by DR. CHARLES M. RICK of the University of California at Davis. This plant appeared in a commercial field of the tomato variety Earlypak.

*Inheritance*

A few seeds set by open pollination on the original plant gave rise to a family containing both fertile and pollen-sterile individuals. Some of the pollen-sterile plants were crossed with a highly inbred strain of Pearson, a variety quite similar in general habit to Earlypak. Pollen-sterile plants in the resulting progeny were backcrossed by Pearson. A probable simple trisomic (56L130–1) from this backcross and a fertile diploid (56L111–5) from the first cross with Pearson were progeny tested using open pollinated seed. Cytological studies initiated in these two test progenies revealed the presence of sterile diploids possessing the meiotic abnormality to be described.

Both of these test families were grown from seed of open pollinated fruit but may be regarded as selfed progenies. RICK (1948) has found that the rate of natural cross-pollination in male-sterile mutants at Davis is quite low, ranging from one to seven percent. In addition plant 56L130–1 was grown in an isolated male-sterile crossing plot where the only available pollen was the little the plant itself produced. The seed from this plant gave rise to family 57L501, containing 70 plants which were examined cytologically. Twenty-eight of these possessed the meiotic precocity and had 90–100 percent aborted pollen. Ten of the 28 were also simple trisomics. The 42 plants lacking the precocity included 13 trisomics. The extra chromosome in all cases probably was chromosome 4 on the basis of plant habit (RICK and BARTON 1954).

This family contributes little evidence for the inheritance of the precocity. The $\chi^2$ value calculated for monofactorial recessive determination of the aberrancy was 8.40 with $p = 0.006$. It does not appear that the trisomy is affecting the inheritance of the precocity, for a contingency test suggests no association between the two ($\chi^2 = 2.56$, $p = 0.11$).

Family 57L506 from the fertile diploid 56L111–5 provides more satisfactory information. Cytological examination showed that 14 of the 50 plants grown in this family were diploids with the precocious centromere division and 90–100 percent pollen abortion. The remaining 36 were normal fertile diploids. This ratio satisfactorily fits inheritance by a single recessive gene ($\chi^2 = 0.24$, $p = 0.64$).

Part of this family was grown in the greenhouse and not maintained after cytological identification. Open pollinated seed collected at Davis from the 27 fertile plants in the field grown portion of the family was planted in the summer of 1958 at Mt. Carmel, Connecticut.

The complete correlation in families 57L501 and 57L506 between the meiotic precocity and greater than 90 percent pollen abortion has already been mentioned. This correspondence permitted identification of aberrant plants in the 1958 plantings by acetocarmine pollen smears, using a minimum of three flowers per plant. Nine of the 27 families were nonsegregating, containing 18–20 fertile plants each. The observed proportion of segregating to nonsegregating families thus gives an exact fit to the 2:1 ratio expected. Table 1 shows the results for the 18 segregating families. The summation $\chi^2$ value of 24.24 ($p = 0.15$) is com-

patible with the assumption that all of these families are segregating in a 3:1 ratio.

On the basis of this evidence the symbol *pc* is proposed for the single recessive gene controlling the centromere division precocity. No expression of this gene was observed other than its action on meiosis.

## *Cytology*

Cytological analysis was confined to microsporocytes which were fixed in 1:3 acetic alcohol, mordanted in iron alum, and stained with acetocarmine as described by SOOST (1951). The technique was modified by briefly heating the stained material over a steam bath before smearing (BARTON 1950).

All counts and photographs are from temporary slides ringed with approximately equal parts of paraffin and anhydrous lanolin. These, being miscible, may be kept melted in a test tube in the steam bath and applied to the margins of the cover slip with a small brush.

The course of meiosis in normal material has already been characterized by HUMPHREY (1934). Both the fertile and aberrant diploids used for the following photographs come from families 57L501 and 57L506.

*Prophase and metaphase I*: Throughout these stages chromosome behavior appears to correspond in all respects to that of fertile plants. Initiation of pairing during zygotene seems in no way affected, and pachytene pairing is complete

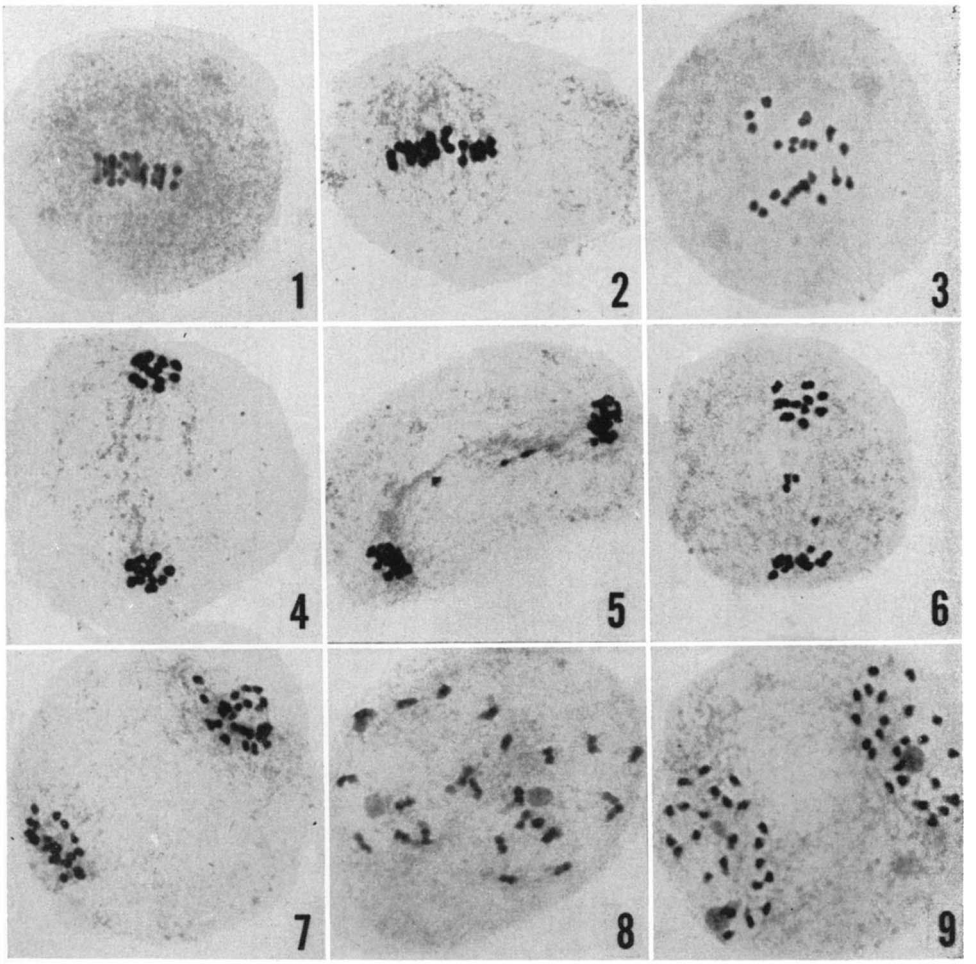
TABLE 1

*Frequency of plants with precocious centromere* (pc) *division in segregating $F_3$ progenies from family 57L506*

| Family | *pc* | Total | $\chi^2$(3:1) |
|---|---|---|---|
| 58L52 | 3 | 20 | 1.07 |
| 58L54 | 6 | 18 | 0.67 |
| 58L55 | 2 | 18 | 1.85 |
| 58L56 | 8 | 20 | 2.40 |
| 58L57 | 3 | 19 | 0.85 |
| 58L58 | 3 | 20 | 1.07 |
| 58L63 | 1 | 20 | 4.27 |
| 58L64 | 4 | 20 | 0.27 |
| 58L65 | 1 | 20 | 4.27 |
| 58L67 | 3 | 20 | 1.07 |
| 58L69 | 5 | 20 | 0.00 |
| 58L70 | 6 | 19 | 0.44 |
| 58L71 | 3 | 20 | 1.07 |
| 58L73 | 5 | 16 | 0.33 |
| 58L74 | 5 | 19 | 0.01 |
| 58L75 | 5 | 18 | 0.08 |
| 58L76 | 8 | 20 | 2.40 |
| 58L77 | 2 | 19 | 2.12 |
| | | | $\chi^2_s = 24.24$ |
| | d.f. = 18 | p = 0.15 | |

with normal bivalent configurations maintained through MI (Figures 1 and 2). It is quite possible, however, that chiasma frequency could be reduced somewhat without altering bivalent associations. To verify this chiasma counts might be taken at diakinesis, since diplotene in tomato is unfavorable for observation (Soost 1951).

The presence of both trisomic and diploid *pc* plants in family 57L501 makes possible an alternative and simpler technique. If *pc* reduces chiasma frequency




FIGURES 1–9.—First metaphase to second prophase 740×. FIGURE 1.—First metaphase from a normal plant. FIGURE 2.—First metaphase from mutant *pc*. FIGURE 3.—First anaphase in a normal plant. FIGURE 4.—First telophase in a normal plant. FIGURE 5.—First telophase from *pc* with a lagging and dividing daughter bivalent and another lagging chromosome. FIGURE 6.—First telophase in *pc* with lagging chromosomes and showing undivided chromosomes in the upper nucleus. FIGURE 7.—First telophase in *pc* showing some division of daughter bivalents in the two nuclei. FIGURE 8.—Second prophase from a normal plant. FIGURE 9.—Second prophase in *pc* having 24 chromosomes in each daughter nucleus.

slightly, there should be a higher proportion of bivalent-univalent associations, instead of trivalents, in a trisomic homozygous for this gene than in an otherwise normal trisomic.

The results in Table 2 suggest that *pc* might have a slight effect in this direction, but the contingency $\chi^2$ value for the data is 0.34 ($p = 0.58$). This indicates that no significant differences exist between trivalent frequency in *pc* and non-*pc* plants and consequently that chiasma frequencies are quite likely the same in the two types.

*Anaphase and telophase I*: The chromosomes of the mutant first deviate from normal behavior at late anaphase. Although bivalents separate regularly, some of the resulting half-bivalents frequently lag and may divide (Figures 5 and 6). Figure 10 shows a cell at PII in which such a chromosome appears to have lagged and divided at AI with one of the sister chromatids being included in a telophase nucleus and the other remaining in the cytoplasm. Further observations on the frequency of lagging and division of half-bivalents at AI will be included in the description of PII.

It is not entirely clear when the centromeres begin their precocious division, aside from those that have split subsequent to chromosome lagging. The chromosomes in the upper group of the cell in Figure 6 have not divided by early telophase. But one or more chromosomes at the poles are divided in the telophase cell of Figure 7. These chromosomes may have lagged, divided, and finally reached the poles; or they may have completed migration before dividing. In any case the centromeres of most chromosomes have divided by PII in all cells observed. Much of this division very likely occurs during interkinesis.

The chromosomes do not form a plate at TI and then divide, as reported by LAMM (1944) for a similar mutant in tomato.

*Prophase II*: Cells in this stage (Figures 9 and 10) differ markedly from those of normal material (Figure 8), for most of the centromeres are clearly divided. Even when a few sister chromatids are conjoined, their points of attachment seem more attenuated than in chromosomes at the same stage in fertile plants (cf. Figures 8 and 10). The separated chromosomes have some tendency to be grouped two-by-two. This may be due to failure of movement following division, or forces of attraction may be acting to keep the chromosomes so oriented. The associations probably involve homologues, but verification of this has not been possible.

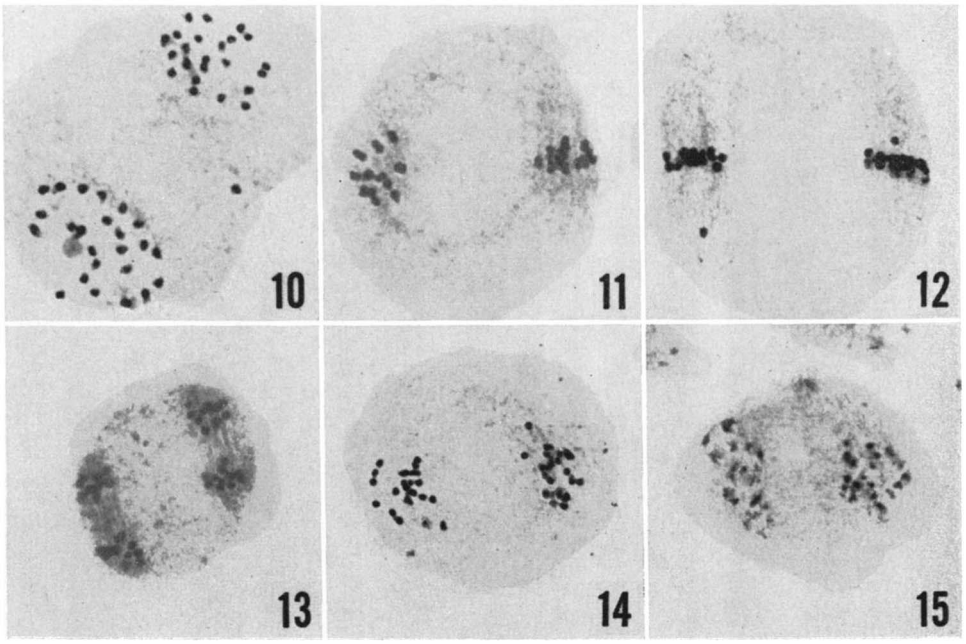
Table 3 records the frequency of various chromosome distributions at PII. No record was made of occasional incompletely separated sister chromatids, because

TABLE 2

*Chromosome associations in trisomics with and without precocious centromere division*

| | Number of cells counted | | | |
|---|---|---|---|---|
| | III | II–I | 3I | Total |
| 57L501–7 (*pc*) | 56 | 44 | 0 | 100 |
| 57L501–9 ($pc^+$) | 60 | 40 | 0 | 100 |

doubt existed as to whether they represented failure of division or chance contact in smearing. The proportion of cells with chromosomes excluded from the second prophase nuclei is 53 percent. A more extensive count of 411 cells in PII and MII on the same slide indicated that 41.3 percent contained micronuclei.




FIGURES 10–15.—Second prophase to second telophase 740×. FIGURE 10.—Second prophase in *pc* showing 24 chromosomes in one nucleus, 23 in the other, and one chromosome in the cytoplasm. Some of the chromosomes are not completely separated. FIGURE 11.—Second metaphase from a normal plant. FIGURE 12.—Second metaphase in *pc* with two chromosomes off the plates but in the spindles. FIGURE 13.—Second anaphase from a normal plant. FIGURE 14.—Second anaphase in *pc* showing much chromosome lagging. FIGURE 15.—Double restitution nucleus formation in *pc* plus a micronucleus.

TABLE 3

*Chromosome distributions at second prophase in microsporocytes of a diploid* pc *plant (57L501–68)*

| Number of daughter chromosomes excluded from prophase nuclei | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | | 1 | | 2 | | 3 | | 4 | | 7 | |
| Nuc. counts* | F. | Nuc. counts | F. | Nuc. counts | F. | Nuc. counts | F. | Nuc. counts | F. | Nuc. counts | F. |
| 24–24 | 10 | 23–24 | 6 | 23–23 | 2 | 22–23 | 1 | 21–23 | 1 | 20–21 | 2 |
| 23–25 | 1 | 22–25 | 1 | 22–24 | 1 | | | 20–24 | 1 | | |
| 22–26 | 2 | 20–27 | 1 | | | | | | | | |
| 20–28 | 1 | | | | | | | | | | |
| Total | 14 | | 8 | | 3 | | 1 | | 2 | | 2 |

Total number of cells = 30

Cells having excluded chromosomes = 53 percent

* Nuc. counts = Nuclear counts.
F = frequency.

Those cells in Table 3 having one or both nuclei with odd numbers of daughter chromosomes may be used to estimate the minimum frequency of precocious chromosome division in AI. The data indicate that this event occurs in at least one chromosome for every two cells.

*Metaphase II*: All chromosomes are *regularly* oriented on the metaphase plates (Figure 12). Frequently one to several chromosomes are in the spindles but off the plates. These chromosomes may have failed to migrate to the plates, or they may have precociously initiated poleward movement. Chromosomes excluded from the TI daughter nuclei appear to remain out of the MII spindles.

At this stage the chromosomes are associated two-by-two, as they are during PII. This continued association therefore seems to eliminate failure of chromosome movement as an explanation for the association in PII. Although in lateral view (Figure 12) plates superficially resemble those of normal material, the chromosomes are clearly divided when the plates are viewed in polar position.

*Anaphase and telophase II*: Chromosome segregation to the poles is random without further division (Figure 14). Many of the chromosomes tend to lag in the center of the spindle. As a consequence restitution nuclei frequently form from one or both spindle groups (Figure 15). Table 4 gives "quartet" counts for two diploid *pc* plants.

Unquestionably a significant difference exists between them: 57L501–68 has a mean of 2.36 spores per group while the mean for 57L501–69 is 3.67.

Family 57L501, as mentioned earlier, resulted from two consecutive crosses of Earlypak by Pearson. Although these varieties are similar in general plant habit, they differ sufficiently for a number of genes to be segregating in backcross progenies. Some of these genes might reasonably be expected to modify the frequency with which second division restitution nuclei occur in different plants homozygous for *pc*.

*Fertility*: The proportion of stainable pollen in all examined *pc* plants varied from zero to ten percent. Some stainable pollen is probably functional, since tetraploids appeared in the progeny of the original partially sterile accession. Furthermore, cytological examination of one of these tetraploids proved it to be *pc*.

The difference in restitution nucleus formation between plants 57L501–68 and 57L501–69 does not seem to affect appreciably the proportion of stainable pollen grains they produce. Examinations were made of a total of six flowers for each plant collected over a period of four months, and a minimum of 500 grains per flower were counted. The amount of stainable pollen for 57L501–68 ranged from 0.00 to 4.94 percent and for 57L501–69 from 0.19 to 3.23 percent.

TABLE 4

*Distribution of "quartet" types in diploid plants with precocious centromere division*

| | Number of spores per "quartet" | | | | | | Total "quartets" |
|---|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | 6 | 7 | |
| 57L501–68 | 234 | 89 | 11 | 3 | | | 337 |
| 57L501–69 | 39 | 136 | 167 | 56 | 8 | 2 | 408 |

Since diploid grains should be functional, one possible explanation of the high pollen sterility in 57L501–68 might be unfavorable action of *pc* on the mitotic division of the microspore. The strongly granular nature of the cytoplasm at this stage in tomato discourages investigation of this possibility. In view of the high proportion of chromosomes excluded from the daughter nuclei, as indicated in Table 3, it seems more probable that the abortion of these "diploid" spores is due to degeneration resulting from chromosome unbalance.

Ovule fertility is also reduced. Twenty-one backcross pollinations of 57L501–68 and 57L501–69 by normal Earlypak all yielded fruit, 17 being parthenocarpic. The remaining four fruits contained a total of 14 seeds, only one of which germinated. The resulting plant, 57L521–1, was triploid and non-*pc*. Presumably it developed from the union of an unreduced egg from the *pc* parent, 57L501–68, and a normal haploid sperm of Earlypak.

Megasporogenesis was not studied cytologically in *pc* plants. But their apparent formation of diploid megaspores, as indicated by the triploid 57L521–1 and the tetraploids previously mentioned, plus their high ovule infertility imply that meiosis proceeds similarly in both megasporocytes and microsporocytes. Simple and multiple trisomics identified in the Pearson backcross progenies demonstrated that *pc* mutants can also produce functional hyperploid megaspores. The chromosome unbalance probably is a consequence of irregular segregation at either the first or the second meiotic division.

## DISCUSSION

The observed meiotic aberrancies of *pc* mutants may all be attributed to a division precocity of the chromosome regions normally holding sister chromatids together until AII. LIMA-DE-FARIA's (1956) studies suggest that the regions involved are the most proximal portions of the chromosome arms rather than the centromere itself. In *Agapanthus umbellatus*, *Fritillaria meleagris*, *Rhoeo discolor*, and *Mecostethus grossus* he found that the centromeres are divided and well separated from each other at pro-metaphase II. He observed such division as early as AI in *Tradescantia virginiana*, *T. bracteata*, and *Secale cereale*. The small size of tomato chromosomes at stages subsequent to PI makes verification of his results difficult in this material.

In some mutants centromere precocity exhibited during the first meiotic division does not seem to continue into the second division. Daughter univalents thus fail to congress to the MII plates, as in asynaptic *Oenothera decipiens* (CATCHESIDE 1939). If the precocity does continue, the daughter univalents can go to the plates but not divide. This happens in asynaptics of *Lycopersicon esculentum* (SOOST 1951) and is typical of the *pc* mutant.

Daughter univalents also can divide following metaphase plate congression. This is unlikely to occur, however, since it involves two equational divisions in meiosis instead of the customary one. EKSTRAND (1932) has reported that such behavior is customary in daughter univalents of partially asynaptic barley, although the division follows AII separation of the unaffected chromosomes. One

other instance of regular double division of univalents at meiosis has been found (FEDERLEY 1931).

If the precocity of *pc* is expressed before AI, it appears to have no observable effect on chromosome pairing and chiasma formation. During AI the precocity occurs initially as a bipolarization of some chromosomes, following separation of homologues. These chromosomes lag and frequently divide in the first meiotic division. Otherwise most of the precocious division seems to take place during interkinesis. This conclusion follows from the observation that centromeres are often undivided at TI, while by PII the great majority of them are split.

Although the aberrant centromere behavior in *pc* has been interpreted as precocity, the possibility also exists that the centromere division time cycle is normal while that of the chromosomes is delayed. Precocity is the preferred explanation because there are no obvious differences in corolla length of buds from *pc* and normal plants containing microsporocytes in the same stages of meiosis. Studies of normal material in connection with an asynaptic mutant (CLAYBERG 1958b) having delayed meiosis showed that such measurements provide a fairly reliable means of ascertaining the meiotic stages in the respective buds.

The two-by-two chromosome associations seen at PII and MII are difficult to understand. One might be tempted to compare them with bivalents at MI in normal material, except for the presence of chiasmata in the latter. The close synapsis of homologues in bivalents where no chiasmata are observed (HUGHES-SCHRADER 1943) suggests that the forces holding bivalents together may be stronger than those acting on the second division *pc* chromosome associations.

The similarity between meiosis of *pc* plants and that of the tomato mutant reported by LAMM (1944) and described earlier in this paper is remarkable. Quite possibly the same locus may be involved in both. This unfortunately cannot be verified experimentally, since LAMM's cultures are no longer available.

The most marked resemblances between the two mutants are the precocious centromere division and orientation of the precociously divided chromosomes on the MII plates. LAMM's mutant differs from the present case in that his showed no lagging and dividing chromosomes at AI, formed plates at TI after which the centromeres divided, and usually gave rise to four spore "quartets."

The two varieties in which the aberrant types appeared seem to be completely unrelated, indicating that they represent independent mutations. Earlypak is a large-fruited, determinant tomato introduced about 1950 by the Ferry-Morse Seed Company. LAMM's mutant occurred in Danish Export, a long established variety with small fruits and indeterminate habit, supposedly developed in Denmark during the nineteenth century.

## SUMMARY

The almost complete sterility of a mutant in the tomato variety Earlypak results from an abnormality of meiosis controlled by a single recessive gene *pc*. The aberrant behavior is characterized by the regular occurrence of precocious meiotic centromere division. The precocity first appears at anaphase I in some daughter

bivalents which often lag and divide. The centromeres of those chromosomes not lagging in the first division divide in most instances by prophase II. This division probably takes place during interkinesis. All chromosomes *regularly* become oriented on the metaphase II plates. The precociously divided chromosomes migrate to the poles at random without further division. The considerable amount of chromosome lagging in the second division frequently results in the formation of restitution nuclei. Some of the diploid spores so produced are functional and give rise to polyploid offspring. Irregular chromosome segregation also results in gametes of unbalanced chromosome number as reflected in the appearance of trisomic progeny.

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