$84.00 January, 1959 £15 47 Strangeways Laboratory Cambridge, England after November

PROJECTION: about 30 mins. at 16 frames/sec.
FILM: 16 mm, silent.

MITOSIS IN ENDOSPERM. II. 1957.

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INTRODUCTION

The purpose of this introduction is to draw attention to certain aspects of chromosome movements during mitosis, especially those illustrated by the film.

MATERIAL AND METHODS

Endosperm of IRIS XIPHIOIDES, LEUCOJUM AESTIVUM and HAEMANTHUS KATHARINAE was used. Endosperm at a suitable stage of development is pressed out on a large cover slip on which a vaseline ring has been made, and which has been smeared with a thin layer of agar and glucose (0.4 - 0.5% agar and 3% glucose for LEUCOJUM, 3.5% for IRIS and HAEMANTHUS). The excess amount of liquid is removed and consequently the cells flatten more or less under influence of surface tention. In very flattened cells all chromosomes are arranged in one layer, which however does not disturb the course of mitosis (sequence No. 17). The cover slip containing the endosperm is covered with a second one also smeared with agar, and the edges are sealed with vaseline. The second cover slip does not touch the cells and they are observed in a very thin and flat hanging drop. The cover slip is mounted on a special holder, which fits the microscope stage. For observations longer than 12 hrs. sterile conditions are necessary, otherwise bacteria destroy the cells. Detailed data on the method have been given previously (Bajer 1955, 1957, Bajer and Molè-Bajer 1954).

Zeiss (Jena) phase contrast equipment was used (90x oil immersion lens and 4x eyepiece; on the film approximately 100x). Heat rays were eliminated and cells were illuminated only during photographic exposure.

THE COURSE OF MITOSIS.

A short description only will be given here; a more detailed one is to be found in original papers with the list of references (Bajer 1954, 1957, 1958, and Bajer and Molè-Bajer 1956).

Endosperm of young embryo sacs is often, but not always, found in the form of multinucleate masses and from older ones in separate cells. The division of the nuclei in the lobes, i.e. in the cytoplasmic mass is often precisely synchronised (sequences Nos. 18 - 19 and also 8). Separate cells have no cellulose cell walls and form protrusions, especially in prophase and telophase.

RESTING NUCLEI. Nuclei are usually spherical or ellipsoidal, their chromonematic structure being either distinctly visible (HAEMANTHUS sequences Nos. 1 - 2, LEUCOJUM No. 3), or almost invisible (IRIS sequence No. 4). The nucleoli vary in number and usually contain some small granules which have a higher refractive index (i.e. sequences Nos. 1 - 3). The nucleoli before disappearance are in a semi-liquid state (sequence No. 7).

PROPHASE. Early stages of prophase may be observed in LEUCOJUM and HAEMANTHUS (sequences Nos. 8 and 10). In early prophase the outlines of the chromosomes appear at first as denser areas or bands. This very short stage is followed by a very quick process of spiralisation of the chromosomes and then the chromosomes shorten and thicken slowly. The process of shortening may be a lengthly one and in HAEMANTHUS it may last till the nuclear membrane breaks (up to 5 - 10 hrs; in IRIS 1 - 2 hrs.).

SPINDLE FORMATION AND CONTRACTION STAGE. The process of formation of the spindle is similar in all species. The first sign of its formation is the appearance around the nuclei of the clear zone (e.g. sequences Nos. 11 - 12), which appears in mid-prophase. The clear zone (Bajer 1957) is the cytoplasmic constituent of the mitotic spindle, and grows slowly at first and then more rapidly. In elongated cells it tends to become wider towards the poles and looks like polar caps (sequence No. 11). There is some evidence

that the growing of the clear zone is initiated by substances migrating from the nucleus (Bajer 1957). When the clear zone reaches its maximal dimensions the nuclear membrane breaks, after which the area occupied by the chromosomes increases slightly, as the arms at the periphery of the prophase mucleus straighten. This stage lasting a few minutes is followed by a mitotic contraction stage (Bajer 1954, 1958, Bajer and Molè-Bajer 1956). The latter is the stage preceding prometaphase and lasting for a few minutes, during which the scattered chromosomes which had in late prophase formed a loose ball, aggregate abruptly into a tighter central mass. During the contraction stage the nuclear and cytoplasmic components of the mitotic spindle (nuclear sap and clear zone respectively) mix together and the spindle gelates. This is indicated by the particles executing Brownian movements. They oscillate in all directions during prophase, stop their vigorous movements immediately after the contraction stage, and during the prometaphase move parallel to the long axis of the spindle towards the poles. After the contraction stage prometaphase begins, the kinetochores guide the chromosomes in their movements and the moment at which the co-operation between the spindle and the kinetochores begins is seen in some cells (kinetochore stretching - Bajer 1958, sequence No. 17).

PROMETAPHASE. There are two characteristic features of prometaphase:

1. The movements of kinetochores towards the equator of the spindle; they tend to arrange themselves in one plane (in non-flattened cells) or line (in flattened cells).

2. The straightening of chromosome arms; they tend to arrange themselves parallel to the long axis of the spindle.

These two processes are very complicated. The kinetochores do not always move towards the plate by the simplest and shortest path; they move along or across the spindle, or towards the pole and then return to the plate (sequences Nos. 11, 22) and while at the plate may execute slight oscillations or may be motionless. (Kinetochore movements cease during colchicine mitosis). The gradual straightening of the arms towards the poles begins

immediately after the contraction stage, the process being performed in one or several steps. The arms may also execute very peculiar abrupt bending movements (e.g. sequence No. 14), during which the arms are always bent first towards the equator of the spindle, and then straighten (Bajer 1958 b). These movements are caused probably by the changes in the structure of the spindle since they cease completely during c-mitosis. In c-mitosis the chromosomes show also a strong tendency to straighten during prometaphase (they usually appear as "straight-rods" - Molè Bajer 1958).

In prometaphase of normal and irradiated mitosis there is a strong tendency for unattached bodies to move from the spindle: persisting nucleoli or acentric fragments move towards the poles and pass into the cytoplasm (sequences Nos. 28 - 29). Chromosome arms uncoil mainly in prometaphase (sequence No. 13), sometimes with a speed as great as 0.7 revolution per minute.

METAPHASE. The metaphase plate is usually regular and metaphase lasts 30 mins. to 2 hrs. (HAEMANTHUS). Before the start of anaphase typical c-pairs are often formed in normal mitosis (sequence No. 17). They are much more visible in short chromosomes than in long ones. Their formation is much better seen during c-mitosis (especially sequence No. 36 but also 33 - 38) where they also last much longer.

ANAPHASE. During anaphase the guiding role of the kinetochores in chromosome movement is easily discernible. In flattened cells, however, some chromosomes may move with their arms directed towards the spindle poles (sequences Nos. 16, 17, 22) and not towards the spindle equator. This is caused by the mechanical conditions in flattened cells in which the chromosomes may not be able to turn freely. The action of the pushing body begins usually in mid-anaphase and the moment when it begins to act is marked by an increase in speed of the chromosomes (e.g. sequences Nos. 5, 6). The pushing apart of half-spindles is more marked in unflattened cells than in flattened ones.

TELOPHASE. The formation of the phragmoplast begins in late anaphase or at the beginning of telophase. Small particles (sequences Nos. 5 - 6), laggards, or acentric fragments (Nos. 30 and also 28) move from the phragmoplast towards the poles. In cells containing a large number of fragments one has the impression of a second anaphase going on during telophase (sequence No. 30).

The cell plate begins to form in the middle of the phragmoplast, but usually from the edges (e.g. sequence No.11, but also 12 - 15). In flattened cells the cell plate very often appears simultaneously, in the whole phragmoplast (sequence No. 17).

The shortening of the chromosomes in telophase lasts several minutes in HAEMANTHUS and later changes of the chromosome structure, leading to the formation of resting nuclei, usually last about 2 hrs. Nucleoli appear during the second or third hour after the beginning of the formation of the cell plate. In IRIS nucleoli appear much earlier, usually about 30 mins. to 1 hr. after the formation of cell plate. The symmetrical arrangement of nucleoli in daughter nuclei is observed more often in plants with smaller chromosomes (IRIS) than in plants with larger ones.

DESCRIPTION OF THE FILM.

The duration of all processes shown in the film: 7 days, 17 hrs. 42 mins. (185 hrs. 42 mins.).

PROJECTION: about 30 mins. at 16 frames/sec.; this speed is assumed for the accelerations given below.

PART I - NORMAL COURSE OF MITOSIS

1. HAEMANTHUS KATHARINAE. Resting nucleus - chromonematic structure easily discernible. No cellulose cell walls: formation of protrusions. A small vacuole inside the nucleus; inside the vacuole particles in Brownian motion. Recorded: 66 mins., speeded up: 300x; original frequency 3.2 frames/min.

2. HAEMANTHUS KATHARINAE. Resting nuclei. Nucleus in the middle revolves. 3 nucleoli. Inside the nucleoli, especially in two upper nuclei, small strongly refractile bodies, cf. also sequences Nos. 2 - 3. Recorded: 140 mins.; speeded up: 960x; original frequency 1 frame/min.

3. LEUCOJUM AESTIVUM. Resting nucleus. The marked acceleration shows up changes in the shape of the nucleus and nucleoli. Recorded: 463 mins.: speeded up: 960x; original frequency 1 frame/min.

4. IRIS XIPHIOIDES. Resting nucleus. 7 nucleoli. The nucleus seems to be optically empty - no chromonematic structure visible. Recorded: 18 mins: speeded up: 200x; original frequency 4.8 frames/min.

5. IRIS XIPHIOIDES. Prophase - telophase. During formation of metaphase plate the length of the spindle decreases and width increases, i.e. metaphase plate becomes broader. The action ofthe pushing body ("Stemmkörper" of Belar 1928) is marked: the length of the spindle increases and the distance of chromosome separation is greater than the length of the spindle in metaphase. In telophase small particles inside the phragmoplast move towards the poles (cf. No. 30 where acentric chromosomes execute the same type of movements). Chondriosomes inside the phragmoplast are stretched during telophase (cf. also Nos. 12, 17). Formation of the nucleoli in the daughter nuclei. Recorded: 216 mins: speeded up: 141x; original frequency 5.1 frames/min.

6. IRIS XIPHIOIDES. Prophase - telophase. Marked contraction stage. Spindle formation and chromosome behaviour like No. 5. Recorded: 149 mins.; speeded up: 200x; original frequency 4.8 frames/min.

7. LEUCOJUM AESTIVUM. Prophase - telophase. Nucleolus before disappearance is in a semi-liquid state and changes considerably its position. Numerous starch grains in the cytoplasm. Recorded: 191 mins.; speeded up: 253x; original frequency 3.8 frames/min.

8. LEUCOJUM AESTIVUM. Prophase - telophase. Differentiation of the chromosomes from very early prophase. Comparison of duration of different stages of mitosis. Interruption of the film in telophase 3 hrs. 30 mins. Strong contraction stage.

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Regular metaphase plate. Notice micronucleus (towards lower left corner) with 3 chromosomes. One of them is eliminated towards the left of the microspindle. Simultaneous division of the micronucleus and normal nucleus (cf. also Nos. 18 - 19 - divisions in the cytoplasmic mass). Micronuclei in normal endosperms are rare. They are found occasionally in LEUCOJUM but never observed in IRIS and HAEMANTHUS. Recorded: 574 + 210 mins.; speeded up: 685x; original frequency 1.4 frames/min.

9. LEUCOJUM AESTIVUM. Prophase - telophase. Numerous starch grains in the cytoplasm. Elimination of small particles from the phragmoplast towards the poles in telophase. Cf. cells Nos. 5 - 6. Recorded: 263 mins.; speeded up: 253x; original frequency 3.8 frames/min.

10. HAEMANTHUS KATHARINAE. Differentiation of chromosomes from very early prophase. Prophase long compared with stages without nuclear membrane. Bacteria appear at telophase (non-sterile preparation; cf. methods) especially in the lower part of the frame. Recorded: 649 mins.; speeded up: 685x; original frequency 1.4 frames/min.

11. HAEMANTHUS KATHARINAE. Prophase - telophase; unflattened call. Clear zone formation; particles move from the area around the nucleus. Clear zone is wider at the poles. Nucleus becomes rounded before the nuclear membrane breaks. Marked contraction stage. During prometaphase some (i.e. their kinetochores) move to the poles and then return to the plate (long chromosomes with subterminal kinetochores - lower and middle part of the right half-spindle). Straightening of the arms during prometaphase (arms arrange themselves parallel to the long axis of the spindle). Recorded: 274 mins.; speeded up: 240x; original frequency 4 frames/min.

12. HAEMANTHUS KATHARINAE. Prophase - telophase. Cell half flattened. The exact moment when the nuclear membrane disappears is readily perceived, cf. also No. 11. Contraction stage not as marked as in cell No. 11. Regular metaphase plate. Chondriosomes are stretched in the phragmoplast during anaphase. Vacuoles in the cytoplasm disappear, fuse, or are formed de novo. Recorded: 320 mins.; speeded up: 240x; original frequency 4. frames/min.

13. HAEMANTHUS KATHARINAE. Prometaphase - telophase. Cell half flattened. Uncoiling of the chromatids in prometaphase; long arms in the middle of the left half-spindle. Recorded: 227 mins.; speeded up: 300x; original frequency 3.2 frames/min.

14. HAEMANTHUS KATHARINAE. Prometaphase - telophase. Abrupt bending movements (Bajer 1958 b) during formation of metaphase plate; chromosomes bend towards the plate and then straighten again towards the pole, e.g. long arm in the middle of the left half-spindle. This type of movement ceases during c-mitosis, cf. Nos. 34 - 38. Recorded: 126 mins.; speeded up: 240x; original frequency 4 frames/min.

15. HAEMANTHUS KATHARINAE. Prophase - telophase. Half - flattened cell. Cell rounds off slightly during prophase and flattens again in later stages. During anaphase some chromosome arms move in front of kinetochores because the mechanical conditions do not permit the chromosomes to turn - cf. more flattened cell No. 17. Recorded: 344 mins.; speeded up: 300x; original frequency 3.2. frames/min.

16. HAEMANTHUS KATHARINAE. Prophase - telophase. Particles in Brownian motion inside the nucleus during prophase (especially upper left-hand part of the nucleus) stop their movements after the contraction stage. Notice also the turning of two small chromosomes in prometaphase (upper part of the right half-spindle). Clear zone formation. Uncoiling of chromatids during prometaphase. Recorded: 303 mins.; speeded up: 209x; original frequency 4.6 frames/min.

17. HAEMANTHUS KATHARINAE. Prophase - telophase. Very flattened cell. The movements of single chromosomes may be traced from prophase to telophase. Stretching of the kinetochores in prometaphase, especially in the small chromosome placed just above a long one (lower left part of the nucleus) where the right-hand part of a longer chromosome is turning through a full circle. The small chromosome is slightly bent and the kinetochore is stretched especially in the direction of the centre of the nucleus. This kinetochore is approximately 1/3 of length of the chromosome from

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the end of the left arm. This kinetochore and kinetochores of other chromosomes are seen as white spots (cf. also other cells of HAEMANTHUS). The cell plate turns over in telophase which permits the measurements of cell thickness (cf. also cells Nos. 5, 9, 10, 12, 15, 16, 29 in this respect). Small accessory phragmoplast above the upper part of the right nucleus. Details of cell plate formation. Recorded: 450 mins. speeded up: 240x; original frequency 4 frames/min.

18. HAEMANTHUS KATHARINAE. Metaphase - telophase. Formation of phragmoplasts in cytoplasmic mass between sister and non-sister nuclei. Preparation from young endosperm. Recorded: 287 mins.; speeded up: 344x; original frequency 2.8 frames/min.

19. HAEMANTHUS KATHARINAE. Anaphase - telophase. Like No. 18. Two chromosome groups fuse and form one hexaploidal nucleus (left side). Recorded: 147 mins.; speeded up; 300x; original frequency 3.2 frames/min.

PART II - DISTURBANCES IN MITOSIS.

A. SPONTANEOUS DISTURBANCES AND INFLUENCE OF METHANOL.

20. HAEMANTHUS KATHARINAE. Death of the cell under influence of strong concentration of methanol. Rapid coagulation and long post-morten changes. Cells die in different ways but this type of death is very often found. Cf. also No. 24. Recorded: 169 mins.; speeded up: 320x; original frequency 3 frames/min.

21. HAEMANTHUS KATHARINAE. Prophase - telophase. Formation of clear zone. Nuclear membrane and exact moment of its breaking very distinctly distinguishable. Breaking of a chromosome during anaphase (dicentric chromosome after sister reunion) - upper part of the left half-spindle, arm directed to the left. Recorded: 349 mins.; speeded up; 344x; original frequency 2.8 frames/min.

22. HAEMANTHUS KATHARINAE. Prophase - telophase. Very flattened cell; chromosomes cannot move very far apart because of the lack

of space and consequently a bridge is formed during anaphase. Notice also the movement of the chromosomes towards the pole and their return to the plate during prometaphase (two small chromosomes - upper part of the left half-spindle). Recorded: 426 mins.; speeded up: 344x; original frequency 2.8 frames/min.

23. LEUCOJUM AESTIVUM. Prophase - telophase. Tripolar anaphase probably caused by flattening the cell too much. Chromosome bridges in anaphase. One of the nucleoli (lower part of the nucleus) does not disappear in prometaphase and splits into smaller ones during anaphase. They persist throughout mitosis and are not included in the telophase nucleus. Recorded: 342 mins.; speeded up: 253x; original frequency 3.8 frames/min.

24. HAEMANTHUS KATHARINAE. Metaphase - telophase. Tripolar anaphase caused by the action of methanol (experiments with Dr. G. Ostergren, University of Lund, SWEDEN). Recorded: 294 mins.; speeded up; 320x; original frequency 3 frames/min.

INFLUENCE OF IRRADIATION (B particles)

Fruits irradiated with 10 μC sample of radioactive strontioum and caesium 8 hrs. (distance 0.3 - 1 cm). Preparations from irradiated fruits were made 36 - 48 hrs. after irradiation (except cell No. 32). More detailed data given elsewhere (Bajer 1958 c).

25. HAEMANTHUS KATHARINAE. Metaphase - telophase. 2 acentric fragments on the poles of the spindle. Chromatid breakage - left half-spindle. Recorded: 78 mins.; speeded up: 240x; original frequency 4 frames/min.

26. HAEMANTHUS KATHARINAE. Metaphase - telophase. Two chromatids form in triradial (three-armed) chromosome - left half-spindle. Bridges during anaphase; cell plate cuts the lower one but not the upper. Recorded: 125 mins.; speeded up: 240x; original frequency 4 frames/min.

27. HAEMANTHUS KATHARINAE. Metaphase - telophase. Triradial chromosome composed from 3 chromatids - right half-spindle. During anaphase two chromatids move to the right pole and one to the left.

One fragment caught in telophase by the cell plate. Recorded: 105 mins.; speeded up: 240x; original frequency 4 frames/min.

28. HAEMANTHUS KATHARINAE. Prophase - telophase. Elimination of some of the acentric fragments towards the poles during prometaphase. Only some of the chromosomes form the metaphase plate. Acceleration of chromosome movement towards the poles during phragmoplast formation (cf. cell No. 30). Recorded: 836 mins.; speeded up: 531x; original frequency 1.8 frames/min.

29. HAEMANTHUS KATHARINAE. Prophase - telophase. The same as cell No. 28. Recorded: 471 mins.; speeded up: 480x; original frequency 2 frames/min.

30A. Elimination of fragments during prometaphase - Haemanthus

30.B HAEMANTHUS KATHARINAE. Metaphase - telophase. Acceleration of the chromosome movement during phragmoplast formation after breaking of chromosome bridges. The movement of fragments during telophase suggests the appearance of an anaphase-like movement (cf. Bajer 1958 c). Notice ring chromosome with two kinetochores. Recorded: 308 mins.; speeded up: 320x; original frequency 3 frames/min.

31. HAEMANTHUS KATHARINAE. Metaphase - telophase. Persistent bridges in telophase and consequently one nucleus. Disturbances of cell plate formation. The material for the cell plate accumulates in the form of strongly refractile bodies between chromosome bridges. Recorded: 310 mins.; speeded up: 344x; original frequency 2.8 frames/min.

32. LEUCOJUM AESTIVUM. Micronuclei 4 days after irradiation. Recorded: 181 mins.; speeded up: 253x; original frequency 3.8 frames/min.

COLCHICINE MITOSIS - C-MITOSIS

Influence of 50 ppm of colchicine in agar. More detailed data given elsewhere (Molè-Bajer 1958).

33. HAEMANTHUS KATHARINAE. Anaphase - telophase. Anaphase is stopped and a restitution nucleus is formed. Colchicine has begun to act within 53 mins. Recorded: 107 mins.; speeded up: 480x; original frequency 2 frames/min.

34. HAEMANTHUS KATHARINAE. Prophase - telophase. Normal contraction stage. Notice the strong tendency of chromosomes to straighten and not to touch each other (cf. also Nos. 35 - 38 in this respect). The change in structure in the telophase nucleus begins in its outer part. Colchicine has begun to act within 3 hrs. Recorded: 349 mins.; speeded up: 320x; original frequency 3 frames/min.

35. HAEMANTHUS KATHARINAE. Metaphase - anaphase. Formation of c-pairs and repulsion of chromatids after division of kinetochores e.g. long chromosome on the right (the angle between chromatids increases). Colchicine has begun to act within 8 hrs. Recorded: 109 mins.; speeded up: 320x; original frequency 3 frames/min.

36. HAEMANTHUS KATHARINAE. Metaphase - anaphase. The formation of c-pairs especially in the lower part (small chromosomes). Colchicine has begun to act within 8 hrs. 45 mins. Recorded: 209 mins.; speeded up: 320x; original frequency 3 frames/min.

37. HAEMANTHUS KATHARINAE. Prometaphase - telophase. Chondriosomes are seen as long threads above the chromosomes. Colchicine has begun to act within 1 hr. Recorded: 329 mins.; speeded up: 480x; original frequency 2 frames/min.

38. HAEMANTHUS KATHARINAE. Prophase - telophase. Poorly marked contraction stage (upper left part of the nucleus) and delayed disappearance of the nucleolus. Typical course of c-mitosis. Colchicine has begun to act within 2 hrs. Recorded: 475 mins.; speeded up; 480x; original frequency 2 frames/min.

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