that the *Fucus* egg cell contains growth substance in a much higher concentration than the vegetative cells of the plant. With the use of a special technique of applying growth substances to a small portion of a single egg cell, it was shown that the polarity of the egg cell can be regulated by growth substances. In this technique egg cells were placed over the bore of vertical micro-capillaries filled with growth substance. The rhizoid of the egg cell originated toward the capillary, whereas the origination of rhizoids in egg cells on control capillaries was at random. It appears that the growth substance not only is present in the egg cell of *Fucus* but that it plays an important role in its polarity, in the so-called "group effect" as well as in other responses.

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# FURTHER EVIDENCE FOR THE UPWARD TRANSPORT OF MINERALS THROUGH THE PHLOEM OF STEMS [1]

Felix G. Gustafson and Marjorie Darken

NUMEROUS INVESTIGATIONS have had as their objective the determination of the path of transfer of the mineral elements in plants. Of necessity these experiments have for the most part been concerned with chemical analyses. As everyone familiar with analysis of plant tissue knows, there are considerable variations between different lots of the same plant material. The interpretation of the results is also very difficult. Therefore the results and conclusions drawn from such investigations have been confusing and conflicting. In this paper it is not our purpose to review and analyze previous work, as that has recently been done (Curtis, 1935; Mason and Phillis, 1937), but merely to present data obtained by an entirely new method. A preliminary report has already been published (Gustafson and Darken, 1937).

EXPERIMENTAL METHODS.—The University of Michigan recently installed a cyclotron equipment, made famous by Lawrence of California, whereby radioactive material was made available to us. After considerable thought, phosphorus was chosen as the element to be irradiated. Phosphorus is an important element found naturally in all plants so that there is not the introduction of an element not normally found in the plant. It also has a long half life (fifteen days)—i.e., the period during which half of the radioactivity is lost. This fact enables one to run fairly long experiments, if desirable, or several experiments can be conducted with the same material, saving the time consumed in the preparation of the solution. Red phosphorus was activated and oxidized to phosphoric acid with $HNO_3$ and neutralized with $K_2CO_3$ to $KH_2PO_4$, which was used as a 0.5 per cent aqueous solution at a pH of 5 to 6.

Rooted cuttings of willow, geranium, *Sedum praealtum*, and *Bryophyllum calycinum* were use as plant material. These plants were chosen because they were available during the winter, they root readily, and the bark is easily separated from the wood. No experiments were conducted with cuttings that had not formed a callus and roots because we were interested in having the material and conditions as near natural as possible.

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We take this opportunity of expressing our thanks to Professor J. M. Cork, of the Physics Department, for supplying us with the irradiated phosphorus.

The cuttings were placed in sand to start rooting, and as soon as the first roots made their appearance they were transferred to tap water in test tubes 1 × 8 inches. These test tubes were covered with black paper to protect the roots from light. In order not to disturb and injure the roots, the plants usually were not taken out of these tubes until after the experiments were completed. When the plants were to be experimented with, the water was poured out of the tube and the radioactive phosphorus solution poured into the tube in its place. During the period of rooting and absorption of phosphorus the plants were kept in the greenhouse. Many more plants were rooted than were needed, which enabled us to use only those plants that had good root systems. All of these precautions insured that the phosphorus entered the plants in the usual way, through uninjured roots.

noninjurious to plants. In these experiments a piece of wax paper was inserted between the bark and wood to keep them separated. The results of one of these experiments is given in table 1.

This experiment shows that there was nearly as much radioactive phosphorus in the separated bark, level for level, as there was in the xylem underneath, though not as much as in the bark connected to the xylem on the opposite side of the stem. The fact that the section of bark above the separation and the bark on the opposite side of the stem had a greater activity than either the separated bark or the xylem is evidence that there was a diffusion of the active phosphorus from the xylem into the phloem, or that the injury attendant on separating the bark interfered with transport through it. The gradient of activity in the separated phloem decreased with distance from the solution until in the section that was

TABLE 1. *Time required to discharge the electroscope. Bryophyllum bark 1 cm. wide, separated from the wood for a distance of 8 cm. The plant was in the solution 48 hours.*

| Distance in cm. above solution | Time in minutes | | |
|---|---|---|---|
| | Bark (detached) | Xylem under detached bark | Bark (attached) on opposite side |
| 5 (below separation) ..... | 19.50 | 19.00 | 20.00 |
| 7 (opposite separation) ..... | 20.25 | 20.00 | 21.50 |
| 9 (opposite separation) ..... | 24.00 | 19.50 | 20.75 |
| 11 (opposite separation) ..... | 29.00 | 24.00 | 19.25 |
| 13 (opposite separation) ..... | 32.00 | 27.25 | 21.75 |
| 15 (above separation) ..... | 20.00 | 28.00 | 22.00 |

The plants were kept in the radioactive solution from a few to seventy-two hours, depending upon the activity of the solution. The radioactivity of the plant tissue was determined by means of a Lauritsen electroscope in which a fine quartz hair indicated on a graduated scale the rate of discharge.

When prepared for testing the plants were cut up into pieces 2 cm. long and the bark separated from the wood. When comparisons were to be made, pieces of approximately the same thickness were used to insure having the same volume of material. The sections were placed on an aluminum window on the electroscope on thin pieces of paper, and the time required to discharge the electroscope the proper amount was noted. The natural leak of the electroscope was three scale divisions per hour. In all of these measurements the time recorded was that required to discharge the instrument to the extent of two divisions on the scale. The same spaces on the scale were always used. If no radioactive material was present, the electroscope was discharged the standard amount in forty minutes.

EXPERIMENTAL DATA AND DISCUSSION.—In several early experiments a strip of bark was separated from the xylem for a distance of 5 to 10 cm.; both ends of the bark remained attached to the wood. Both the bark and wood, where the separation had been made, were coated with lanolin. This was done in all experiments, as lanolin prevented the tissue from drying up. Lanolin has previously been found to be attached to the xylem where there was a large increase. This fact would seem to indicate that there was not a downward diffusion of phosphorus. The experiments, however, were considered somewhat unsatisfactory, and therefore not many of this type were conducted.

In another set of experiments, short sections of xylem and pith were removed, leaving the leaves connected to the roots only through the bark. In one of these experiments a well-rooted *Bryophyllum* plant had a section of xylem 1.3 cm. long removed. The inside of the phloem was covered with lanolin in the usual way. The plant was supported by wooden splinters tied around the stem. Table 2 gives the result of this experiment. Tables 3 and 4 give the results for *Sedum* and willow plants similarly treated.

TABLE 2. *Time required to discharge the electroscope. A Bryophyllum plant with xylem removed for a distance of 1.3 cm. The plant remained in the solution for 45 hours.*

| Distance in cm. above solution | Time in minutes | |
|---|---|---|
| | Bark | Xylem underneath bark |
| 0.5 ..... | 2.25 | 14.25 |
| 2.5 (xylem removed) .. | 7.75 | |
| 5.8 ..... | 10.75 | 22.00 |
| 9.8 ..... | 26.75 | 28.75 |
| 16.1 ..... | 28.50 | 33.75 |

TABLE 3. *Time required to discharge the electroscope. A plant of Sedum praealtum with a 1.5 cm. section of xylem removed was left in an active phosphorus solution for 40 hours.*

| Distance in cm. above solution | Time in minutes | |
|---|---|---|
| | Bark | Xylem |
| 2.0 | 14.00 | 25.75 |
| 7.0 (xylem removed) | 16.00 | |
| 9.0 | 17.75 | 28.75 |
| 14.0 | 27.00 | 33.00 |
| 16.0 | 32.50 | 36.50 |
| 18.0 | 35.75 | |
| 20.0 | 36.75 | |

TABLE 4. *Time required to discharge the electroscope. A willow plant with a 1.5 cm. section of wood removed 15 cm. above the solution was left in the active phosphorus solution for 6.75 hours.*

| Distance in cm. above solution | Time required to discharge the electroscope, with bark |
|---|---|
| 3.0 | 17.00 |
| 7.0 | 23.00 |
| 13.0 | 28.00 |
| 15.0 (xylem removed) | 32.00 |
| 17.0 | 35.50 |
| 19.0 | 38.75 |

All of these experiments show that when a section of xylem is removed, phosphorus is conducted upward in the bark. To discover how the amount present compared with that in plants which had the xylem intact, plants were paired and one used as control while the other had a section of xylem removed. These plants were as similar as could be obtained; they were placed in the same phosphorus solution and kept there the same length of time; the activity was determined section for section, alternately, to insure that there was no inequality in the treatment. Tables 5, 6, and 7 give the results of three of these experiments.

These experiments show, as do those in tables 2, 3, and 4, that when the xylem is removed, phosphorus travels in the bark. They also show that the rate of movement in the bark alone of the plants having the xylem removed is not much different from what it is through the whole stem in the control plants, where both xylem and bark are present. In the geranium the time required to discharge the electroscope was a little less with the control plant than with the experimental plant, but with the *Sedum* and willow the reverse was true. We do not maintain from this that normally all of the phosphorus is conducted in the bark, because it is difficult to get exactly the same volume of material, but there certainly is strong evidence that the bark is perfectly capable of conducting the phosphorus.

In still another group of experiments, three similar plants were chosen. One plant had a section of xylem removed, a second plant had a ring of phloem removed, and the third plant was left as control. The plants were of course treated simultaneously for the same length of time in the same solution. The activity was determined section for section, alternately in the three plants. Tables 8, 9, and 10 give the results of some of these experiments.

According to these experiments phosphorus can ascend the stem through either the xylem or the phloem. There is some evidence that when both are present there is more of the active element present in the plant than when either bark or xylem alone is present, which may be interpreted to mean that minerals are conducted up the stem in both the xylem and the phloem.

In five experiments with *Bryophyllum*, strips of bark to which were attached leaves were completely separated from the wood except at the base of the strip. In three experiments the wood was left intact, and the bark on the stem opposite the loosened bark was left in place. In two experiments the stem was cut off a half centimeter above the solution, except for the strip of bark with the leaves, which was left at the top of the plant (fig. 1). In all of these experiments that part of the plant which was in the solution was composed of roots, bark, and wood.

Sections of opposite leaves attached to the bark 4 cm. above separation were also tested for activity, sections along the midrib 2.5 × 1.25 cm. being used. The section from the leaf attached to the bark which

TABLE 5. *Time required to discharge the electroscope. Sedum. A 0.5 cm. section of xylem was removed 7.0 cm. above the solution from one plant; the other was left intact. The plants were placed side by side in the same solution and kept there for 40 hours.*

| Distance in cm. above solution | Time in minutes | | | |
|---|---|---|---|---|
| | Bark | | Pith and xylem | |
| | Control | Exp. | Control | Exp. |
| 3.0 | 19.00 | 15.50 | 26.00 | 19.00 |
| 7.0 (xylem removed) | 21.00 | 17.25 | | |
| 11.0 | 26.75 | 20.25 | 32.00 | 24.25 |
| 15.0 | 30.00 | 26.50 | 35.50 | 29.00 |
| 19.0 | 38.00 | 32.50 | 39.00 | 37.75 |

TABLE 6. *Time required to discharge the electroscope. Geranium. A 2.0 cm. section of xylem was removed 10 cm. above the solution from one plant; the other plant was left intact. The plants were kept side by side in the same solution for 48 hours.*

| | Time in minutes | | | |
|---|---|---|---|---|
| | Bark | | Pith and xylem | |
| Distance in cm. above solution | Control | Exp. | Control | Exp. |
| 5.0 | 6.00 | 7.25 | 8.25 | 12.00 |
| 10.0 (xylem removed) | 9.00 | 10.75 | | |
| 15.0 | 15.75 | 17.50 | 20.50 | 24.00 |
| 20.0 | 17.00 | 18.25 | 22.75 | 29.00 |
| 25.0 | 33.75 | 36.00 | 37.75 | 39.00 |

TABLE 7. *Time required to discharge the electroscope. Willow. In this experiment a section of xylem 1 cm. long was removed 9 cm. above the solution from plants 1 and 2, while plant 3 served as a control. The plants were in the solution 7.5 hours.*

| | Time in minutes required to discharge the electroscope with bark | | |
|---|---|---|---|
| Distance in cm. above solution | 1 | 2 | 3 (control) |
| 9.0 (xylem removed) | | | |
| 9.5 | 4.75 | 4.00 | 5.25 |
| 11.5 | 8.25 | 7.25 | 9.00 |
| 13.5 | 12.75 | 11.00 | 13.25 |
| 15.5 | 20.00 | 18.00 | 21.75 |
| 17.5 | 26.25 | 22.50 | 27.50 |
| 19.5 | 34.50 | 28.00 | 34.75 |
| 21.5 | 38.00 | 32.00 | 39.00 |

TABLE 8. *Time required to discharge the electroscope. Sedum. Plant 1 had a ring of bark 1 cm. wide (long) removed 6 cm. above the solution. Plant 2 had a 2.0 cm. long section of wood removed 5 cm. above the solution, while plant 3 served as control. The plants were in the active phosphorus solution 48 hours.*

| | Time in minutes | | | | |
|---|---|---|---|---|---|
| | Bark | | | Xylem | |
| Distance in cm. above solution | Bark removed | Xylem removed | Control | Bark removed | Control |
| 8.0 | 21.50 | 20.75 | 18.75 | 15.00 | 14.00 |
| 12.0 | 27.00 | 29.00 | 21.75 | 20.00 | 20.75 |
| 16.0 | 32.75 | 33.75 | 24.00 | 24.75 | 25.00 |

TABLE 9. *Time required to discharge the electroscope. Bryophyllum. A 1.5 cm. section of xylem was removed from one plant; a ring of bark of the same width was removed from a second plant, both operations being made 4.0 cm. above the solution. The third plant served as control. All plants were in the solution 47.75 hours.*

| | Time in minutes | | | | | |
|---|---|---|---|---|---|---|
| | Bark | | | Xylem | | |
| Distance in cm. above solution | Bark removed | Xylem removed | Control | Bark removed | Xylem removed | Control |
| 6.0 | 16.25 | 22.00 | 20.50 | 21.50 | 14.50 | 16.00 |
| 12.0 | 20.75 | 33.00 | 23.25 | 24.75 | 23.00 | 25.00 |
| 18.0 | 28.50 | 38.50 | 27.75 | 39.75 | 35.00 | 34.00 |

TABLE 10. *Time required to discharge the electroscope. Geranium. A 1.0 cm. long section of xylem was removed from one plant; a ring of bark of the same width was removed from a second plant, both operations being made 6.0 cm. above the solution. The third plant served as control. All plants remained in the solution 48 hours.*

| | Time in minutes | | | | | |
|---|---|---|---|---|---|---|
| | Bark | | | Xylem | | |
| Distance in cm. above solution | Bark removed | Xylem removed | Control | Bark removed | Xylem removed | Control |
| 8.0 | 15.50 | 12.00 | 16.25 | 14.50 | 22.50 | 16.50 |
| 16.0 | 26.75 | 15.75 | 17.50 | 25.50 | 27.00 | 22.25 |
| 22.0 | 33.50 | 20.50 | 18.75 | 37.75 | 28.50 | 26.00 |

TABLE 11. *Time required to discharge the electroscope. Bryophyllum. A whole plant which had a strip of bark 11 cm. long, 1 cm. wide, with 3 leaves, separated from the xylem except at the base, remained in an active phosphorus solution for 40 hours.*

| | Time required to discharge the electroscope with | | |
|---|---|---|---|
| | Bark | | Xylem |
| Distance in cm. above separation | Separated | Attached to wood on opposite side of stem | Under separated bark |
| 4.0 | 5.5 | 4.5 | 9.5 |
| 6.0 | 27.0 | 16.5 | 12.75 |
| 8.0 | 29.0 | 26.0 | 24.0 |

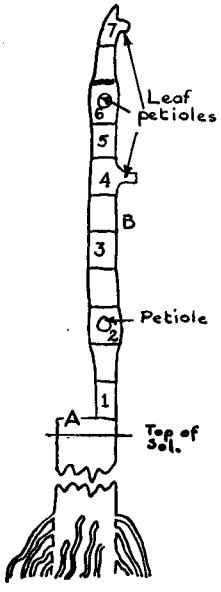


Fig. 1. This figure represents a *Bryophyllum* plant as used in one type of experiment. A strip of bark 23 cm. long with four leaves (represented by the petioles) was separated from the xylem, which was cut off at *A* about half a centimeter above the solution. The top of the plant then consisted of a strip of bark to which were attached four leaves without any xylem. The data for the experiment represented by this figure were given in the preliminary report under table 1 (Gustafson and Darken, 1937).

was separated from the wood required 28.75 minutes to discharge the electroscope; the leaf on the opposite side of the stem, where the bark was attached to the xylem, required 29.5 minutes. The difference in the rate of charge of the sections from the two leaves is not significant, and these experiments supply further evidence that phosphorus and no doubt other elements, too, are conducted upwards through the bark of the plant.

In still further experiments attempts were made to introduce the active phosphorus into the plant through the roots that were attached only to the bark. To accomplish this, a strip of the bark was separated from the wood at the lower end of the plant. This section of bark with roots was placed in active phosphorus solution, while the remaining roots were in tap water. To accomplish this, a narrow test tube with active phosphorus solution in it was placed in a larger tube containing tap water. The solution levels were so adjusted that only the roots of the detatched bark dipped into the active phosphorus solution, and the bark did not come in contact with the solution. In this way we were certain that whatever phosphorus was found in the plant must have entered through the roots and been conducted upward through the bark. These experiments were conducted with *Bryophyllum* and willow plants.

In this same experiment leaves 17 cm. above the solution were examined for active phosphorus. Two leaves from the control plant required 32.75 minutes, and two leaves from the experimental plant required

38.5 minutes to discharge the electroscope. The leaves from both plants were of the same size.

The phosphorus entered the roots, passed into the bark, and was conducted up the plant and reached the leaves 17 cm. above the solution. Not as much phosphorus was present in these leaves as in the leaves from the control plants, but the number of roots that were in the solution was probably not more than one-third as great as in the control plant, where the whole root system was immersed in the solution.

TABLE 12. *Time required to discharge the electroscope. A willow plant with roots attached only to a strip of bark, separated from the xylem except at the top, had these roots immersed in active phosphorus solution for 38 hours. A control plant (roots attached to bark which was connected with the xylem) was also placed for the same length of time in the same active solution.*

| Distance in cm. above solution | Time required to discharge electroscope with bark from | |
|---|---|---|
| | Experimental plant | Control plant |
| 0.5 | 16.75 | 7.25 |
| 2.5 | 28.75 | 22.00 |
| 4.5 | 38.50 | 34.75 |
| 6.5 | | 39.00 |

In all of these experiments we used the whole of the bark and do not therefore know whether the conduction took place in the inner or outer bark. In several experiments the bark was separated into inner, middle, and outer bark, and the activity determined in these parts.

One of these experiments, in which a strip of bark with a leaf was separated from the wood except at the base, is given in table 13. Bark attached to the wood at the same level, as well as that which was separated, was cut up into pieces of equal length and width and then divided into inner, middle, and outer parts. Attempts were made to have all of equal thickness. The pieces of bark were taken 4.1 to 5.3 cm. above the solution.

TABLE 13. *Time required to discharge the electroscope. Bryophyllum bark divided into outer, middle, and inner sections.*

| Time in minutes | | | | | |
|---|---|---|---|---|---|
| Bark separated from xylem | | | Bark not separated from xylem | | |
| O | M | I | O | M | I |
| 16.5 | 11.25 | 6.75 | 16.0 | 11.5 | 6.75 |

Other experiments show essentially the same difference between the inner and outer bark. It is of course impossible to make a definite statement, but it is very likely that the phosphorus found in the outer part diffused into it from the inner phloem and was not transported there at all. From the fact that the concentration was so much greater in the inner portion, one is justified in assuming that most of the conduction takes place in the more recently formed phloem.

The various experiments which we have performed, some of which are given in this paper, undoubtedly prove that at least one mineral is conducted upward in the phloem of a plant. At the same time they give undoubted evidence that minerals are also conducted upward in the xylem. Our experiments are not quantitative in the sense that we can definitely state how much is conducted in the xylem and how much in the phloem. Many of the experiments do give rough indications that both parts of the stem are about equal in their ability to conduct minerals. To make quantitative determinations one would have to ash the whole top of a plant and determine the activity of the ash as well as compare the cross sections of the bark of the plant having the xylem removed with that of the xylem of the plant having a section of phloem removed. The plants would of course have to be immersed in the same solution for the same length of time. The plants would also have to be as near alike as is possible to make selection. Comparisons between quantities conducted in phloem and xylem alone should also be compared with the conduction in plants having both xylem and phloem present. This is an important experiment; we have so far, however, made no attempt to carry it out.

## SUMMARY

All of the experiments described in this paper prove beyond a doubt that at least phosphorus is conducted upward in the inner bark of willow, geranium, *Sedum praealtum*, and *Bryophyllum calycinum*. If phos-

phorus is conducted in the phloem, there is no reason to suppose that other minerals are not likewise conducted in the phloem. Further, the experiments show that phosphorus and presumably other elements are also conducted in the xylem, and we are convinced that both the xylem and phloem function in upward transport of minerals.

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# CHROMOSOME BEHAVIOR IN TRIPLOID DATURA. II. THE FEMALE GAMETOPHYTE *

Sophia Satina and Albert F. Blakeslee

THE PRESENT is the second of a series of papers having to do with the behavior of chromosomes in 3*n* *Datura*. The first [3] presented the results of a study of the male gametophyte. Since a study of the female gametophyte requires sectioned material, it has not been possible, without undue labor, to count chromosomes in so large a number of dividing cells in the female as in the male gametophyte. The data in the present study, however, are adequate, we believe, to demonstrate the essential differences in chromosomal behavior in male and female gametophytes.

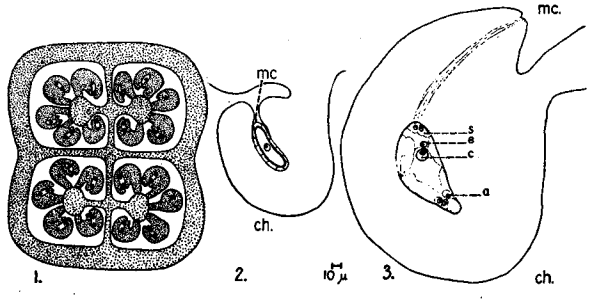


Fig. 1–3.—Fig. 1. Diagrammatic cross section of ovary showing four locules with ovules containing M. M. C. with 1 and 2 nuclei.—Fig 2. M. M. C. with resting nucleus within ovule. mc, micropylar end; ch, chalazal end.—Fig. 3. Ovule with embryo sac. e, egg nucleus; c, central nucleus; s, synergids; a, antipodal nuclei.

STAGES IN FEMALE GAMETOPHYTE.—A series of drawings will illustrate various stages in the development of the female gametophyte. Figure 1 is a somewhat diagrammatic representation of a cross section of an ovary showing the four locules with young ovules. Figure 2 shows an ovule at an early stage with the large megaspore mother cell in the middle. Figure 3 is an older ovule in which a series of five divisions has given rise to an embryo sac with eight nuclei, two of which have united to form the large fusion central nucleus in the center above which is seen the egg. Stages between figures 2 and 3 are shown in detail in figures 4 to 8. Figure 4 is a drawing of the megaspore mother cell at first metaphase with five of the twelve trivalents showing in the section. Figure 5 shows the result of the first meiotic division; 17 chromosomes had gone to the upper or micropylar end (mc) and 19 to the lower or chalazal end (ch). Figure 6 represents the second meiotic division. The nucleus at the chalazal end is in telophase while the nucleus at the micropylar end is in metaphase. In both figures 5 and 6 lagging chromosomes may be observed. Figures 7 and 8 show stages in the disintegration of the three cells toward the micropylar end and the enlargement of the cell at the chalazal end to form the embryo sac. Renner [2] found in *Oenothera* that the chalazal cell at times aborted and the embryo sac was developed from one of the other

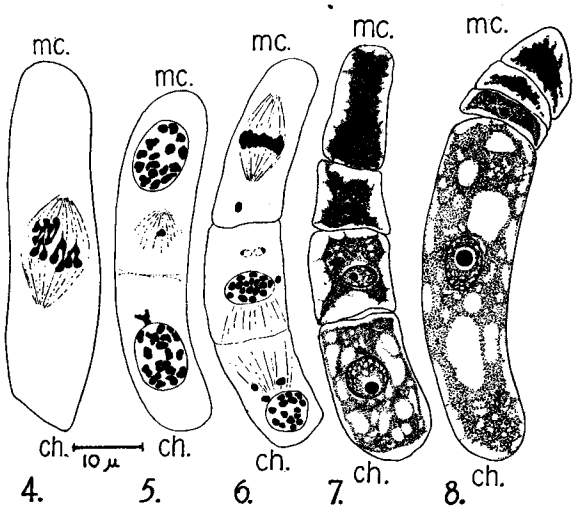


Fig. 4–8.—Fig. 4. Section of M. M. C. at I M; 5 of the 12 trivalents are shown on the spindle.—Fig. 5. Section of M. M. C. at I T, Cell at micropylar end contains nucleus with 16 chromosomes plus 1 lagger. Cell at chalazal end contains nucleus with 18 chromosomes plus 1 lagger.—Fig. 6. M. M. C. at II division. Nucleus at mc. end is in II M with chromosome outside the spindle which had been eliminated at I division. Cell at ch. end contains 15 chromosomes in nucleus plus 3 laggers. Sister cell contains 2 microcytes formed by division of a lagging chromosome eliminated at I division.—Fig. 7, 8. Stages in disintegration of 3 cells at mc. end and enlargement of megaspore at ch. end.

* Received for publication August 13, 1937.
Superscript numbers refer to literature citations.