THE DEVELOPMENT OF THE STAMENS AND CARPELS OF TYPHA LATIFOLIA.[1]

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(WITH PLATES IV–VI)

SINCE the Typhaceæ are perhaps to be considered among the lowest of the monocotyledons, and show some rather peculiar characters in connection with their inflorescence, it seemed desirable to study the history of the development of the stamens and carpels from the very earliest appearance of these organs to their mature condition. Such a study should give some hints as to whether the peculiar floral structures are to be regarded as primitive or reduced.

The material used was killed in chrom-acetic acid and in Flemming's fluid, and preserved in 70 per cent. alcohol. The paraffin method of imbedding was employed, and the sections were stained on the slide. The stains used were anilin-safranin and gentian-violet, iron-alum-haematoxylin, and Delafield's haematoxylin. Because of the extremely small size of the cells, Typha is not a favorable type for cytological study, and a high power is needed to make out even the ordinary cell structures. Some difficulty was experienced in imbedding the older stages, which was overcome, however, by imbedding rather large pieces of the spikes and afterwards cutting away the hard woody stems, when sections could be obtained containing a large number of stamens or carpels.

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The Typhaceæ, as might be expected from their aquatic habit, have preserved many of the characteristics which may be regarded as primitive. The indefinite number of the flowers

[1] Contributions from the Hull Botanical Laboratory, VI.

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with spiral arrangement, with no definite perianth and often entirely naked, combined with the anemophilous habit, certainly indicate a condition somewhere near the beginning of flowering plants. The prominent leaf sheaths, which furnish protection and take the place of a perianth, are little modified from ordinary leaves, and the sporophores are without doubt cauline structures.

DEVELOPMENT OF THE STAMENS.

In the very young spike the beginnings of the stamen clusters appear as irregularly projecting outgrowths from the sides of the axis (*figs. 1, 2*). These are of various shapes and sizes, depending upon the number of branches the future stamen cluster is to contain. Soon the branching begins to make its appearance by smaller wartlike processes developing on the primary projections from the axis. The separate stamens or branches attain quite a size before any difference can be detected in their cells to indicate the primary sporogenous cells (*figs. 3, 4*). Indeed, although one may feel sure that certain cells represent the primary sporogenous layer by their position, it would be quite arbitrary to draw any line and call some cells sporogenous and others not. After the stamen has increased somewhat in size, the sporogenous cells may be distinguished more readily by their position and size, although there is no apparent difference in their structure (*fig. 5*). At this stage several layers of cells are already differentiated in this way, and it appears that division may be going on both on the inner and outer parts of the sporogenous tissue (*fig. 5*). It was not possible for me, with the stages at hand, to determine the origin of the tapetum, and the layers of cells between the tapetum and the epidermis. When the stamen is in the early pollen mother cell stage the tapetum is already cut off, and between it and the endothecium is a single layer of cells (*figs. 6, 7*). As the stamens with the sporangia enlarge, the tapetum begins to increase in size also, although it does not take on its glandular appearance until the pollen mother cells have separated (*figs. 8,*

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9). While the pollen mother cells are growing and forming the tetrads, the tapetal cells increase greatly in size, and the nucleus of each cell usually divides into two. Toward the end of this process the layer between the tapetum and the endothecium breaks down, and the enlarged endothecial cells are multinucleate (*fig.* 10).

The multinucleate condition is also quite normal in the peculiar stellate cells of the leaves (*fig.* 11). From such appearances it might be inferred that the multinucleate condition stands in some relation to the increase in the volume of the cell.

After the tetrads are formed, the tapetal cells disintegrate, and at the same time the endothecial cells begin to acquire their characteristic thickenings (*figs.* 12–14). At the points where dehiscence is to take place no thickenings are developed (*fig.* 13). As appears from the mode of development, the stamen clusters do not represent a coalescence of filaments, but are cauline in origin. Sometimes as many as five or more stamens branch thus from a common axis. The hairs of the staminate spike are not situated on the stamen clusters, but directly on the axis (*fig.* 15). They are multicellular, and in a cross section usually from fifteen to twenty cells can be counted (*figs.* 16, 17).

DEVELOPMENT OF THE MALE GAMETOPHYTE.

After the pollen mother cells have separated, the tetrads are formed by three usually successive divisions (*figs.* 18–20). The microspores, as is well known, do not separate, but begin immediately to develop very thick cell walls (*fig.* 21). The tetrad pollen grains are often irregular in shape, and do not form a typical tetrad (*fig.* 22). Such forms are no doubt produced by a partial separation of the spores. When the spores germinate the two nuclei are about the same size (*fig.* 22), but later the vegetative nucleus increases in size and the generative nucleus sinks to one end of the pollen grain and organizes a definite cell, being cut off from the rest of the grain by a very

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definite cell wall (*figs. 23, 25, 26*). Each grain of the pollen tetrad has a bare, circular, germinating pore for the exit of the pollen tube (*fig. 24*). Although it is generally stated that the tetrads in *Typha latifolia* do not separate until after shedding, I often found them in large numbers entirely separated for some time before the anther was ready to dehisce (*figs. 25, 26*). This cannot be given, therefore, as a character to separate it from *T. angustifolia*, as is frequently done.

DEVELOPMENT OF THE CARPEL.

The carpels originate in a manner quite similar to the stamens, appearing first as small irregular papilla-like protuberances on the axis (*figs. 27, 28*). As the young branch, which is destined to become the carpel, increases in size, irregular outgrowths appear on its sides, which represent the beginnings of the carpellary hairs. These are entirely epidermal in origin, and are produced in acropetal succession, being irregularly arranged on the axis (*figs. 29, 32, 44*). It is not at all probable that such irregular epidermal appendages represent reduced perianth structures, and I am inclined to regard these hairs as having merely a physiological significance, developed for the protection and dissemination of the seed. After the carpellary branch has attained some size, there arises on its summit an annular zone, leaving a deep depression, on the inner face of which the nucellus is developed, while the part of the ring opposite the nucellus develops into the spatulate stigma (*figs. 32, 34*).

The nucellus is lateral in position and soon becomes pendulous because of its downward growth and the increase in depth of the cavity below (*figs. 33–38*). The ring above the nucellus is soon constricted, leaving little if any opening to the exterior (*figs. 33, 37*). After the integuments begin to appear the ovule gradually takes on its anatropous condition until the nucellus is turned outward and points in exactly the opposite direction from its original position (*figs. 38–48*). The integuments are two in number, although the outer one is not developed on the side

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toward the funiculus. The ovule receives a fibrovascular bundle which, as it leaves the funiculus, passes down through the wall of the carpel (*fig. 48*) and unites below with the bundle which passes up on the other side into the leaf-like stigma. From this it appears that the ovule is an axillary structure developing at the end of a fibrovascular bundle which represents a branch of the main bundle of the carpel.

DEVELOPMENT OF THE MACROSPORE AND FEMALE GAMETOPHYTE.

In the young nucellus there can be distinguished, at a very early stage, a hypodermal cell which is somewhat larger than the surrounding nucellar cells (*fig. 33*). This, as its subsequent history shows, is the archesporial cell. This cell divides and cuts off one primary tapetal cell (*fig. 35*), and subsequently the primary tapetal cell divides by a vertical wall, forming a tapetum of two cells (*figs. 37–41*). In the rear of the primary sporogenous cell, or the macrospore mother cell, a long axial row of cells is developed (*figs. 38–41*). Often, if the section is not quite longitudinal, so that only three or four of the cells of the axial row are left back of the macrospore mother cell, there is an appearance as though there were a row of four or five macrospores. It is evident that extreme care must be taken not to mistake the large cells of the axial row for potential macrospores. It is possible that misinterpretations may sometimes have been made in this way. In Typha I was only able to determine conclusively the real fate of the macrospore mother cell by tracing out its development step by step, so closely did the cells of the axial row agree in size, structure, and staining reaction with the macrospore mother cell. The macrospore mother cell develops directly into the fertile macrospore without any division, and soon after the integuments have made their appearance it begins to encroach upon the tapetal cells which are destroyed in a short time (*figs. 41–43*).

It is surprising that Typha, which represents such a primitive condition in the organography of its flowers, should represent what must be regarded as a highly modified archesporial region

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One would be prepared to expect at least several archesporial cells and some division of the macrospore mother cell. The only thing which reminds one at all of a primitive condition is the division of the primary tapetal cell by a vertical wall. Were one to compare Typha, in this respect, with Salix and Ranunculus, it would appear as a more modern form than either of them. And were one to take the Typhaceæ as primitive representatives of monocotyledons and the Ranunculaceæ and Salicaceæ as ancient representatives of dicotyledons, an inference might be drawn favorable to the derivation of the monocotyledons from the dicotyledons. But such deductions, based on single characters, are treacherous and cannot be taken seriously.

A complete series of stages was not at hand to trace out in detail the development of the embryo sac. The macrospore continues to enlarge until the ovule has become almost completely anatropous before any division takes place. The nucellus beyond the macrospore consists of a single layer of epidermal cells, there being no periclinal divisions (*figs. 45–47*). In the fully developed embryo sac just before fertilization the synergids are well formed, with the oosphere lying immediately behind them (*figs. 49, 51*). The three antipodals are already left in a cæcum-like pocket at the lower part of the sac, while no definite cell walls can yet be distinguished (*figs. 50, 52*). The behavior of the antipodals in Typha, therefore, seems to be the same as has been found for *Sagittaria variabilis*, *Lilium Philadelphicum*, and some other monocotyledons, where the same kind of a pocket is developed for the antipodals.

The two polar nuclei come in contact somewhere near the middle of the embryo sac and fuse there before the pollen tube enters the sac (*figs. 49–53*). In this case, therefore, the definitive nucleus is formed without any stimulus from the entrance of the pollen tube, and it may be questioned whether such stimulus is ever necessary for the complete fusion of the polar nuclei.

It is not necessary, in this connection, to discuss the literature pertaining to the Typhaceæ, although most of the views

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here presented have been published before. Those who desire to know the history of the various views will find the appended bibliography helpful.

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EXPLANATION OF PLATES IV–VI.

The plates are reduced two-thirds. The magnifications given refer to the original magnifications of the drawings before reduction. The combinations used were for the most part a $\frac{1}{12}$ Leitz immersion objective, and nos. 2, 4, and 12 Reichert oculars.

Plate IV.

FIG. 1. Longitudinal section of stem, showing the origin of the young stamen branches. × 135.

FIG. 2. Longitudinal section of young stamen branch. × 780.

FIG. 3. The same a little older. × 780.

FIG. 4. Cross section of young stamen at the same age as *fig. 3*. × 780.

FIG. 5. Longitudinal section of young stamen, showing sporogenous cells. × 1200.

FIG. 6. Young stamens with pollen mother cells in the sporangia. × 135.

FIG. 7. Longitudinal section of stamen, showing pollen mother cells, tapetum, endothecium, epidermis, and one layer of cells between the tapetum and the endothecium. × 1200.

FIG. 8. Cross section of microsporangium, showing the pollen mother cells and tapetum. × 1200.

FIG. 9. Cross section of microsporangium, showing the pollen mother cells somewhat separated. × 1200.

FIG. 10. Cross section of microsporangium, showing the disintegration of the immediate cells. × 1200.

FIG. 11. Section of a young leaf showing multinuclear stellate cells. × 650.

FIG. 12. Cross section of microsporangium, showing disorganization of the tapetal cells. × 1200.

FIG. 13. Cross section of an anther just before dehiscence. × 650.

FIG. 14. Longitudinal section of the wall of the microsporangium. × 1200.

FIG. 15. A young branched stamen, showing the position of the hairs. × 40.

FIG. 16. Cross section of one of the interstaminate hairs. × 1200.

FIG. 17. The same. × 1200.

Plate V.

FIG. 18. First division of the pollen mother cell. × 1200.

FIG. 19. Second division of the pollen mother cell. × 1200.

FIG. 20. Tetrad. × 1200.

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FIG 21. Tetrad with one-celled microspores with very thick walls. × 1200.

FIG. 22. Irregular pollen tetrad. × 1200.

FIG. 23. Nearly mature pollen tetrad. × 1200.

FIG. 24. Two pollen grains showing circular germinating pores. × 1200.

FIG. 25. Pollen grain before shedding, showing the generative cell and tube nucleus. × 1200.

FIG. 26. The same. × 1200.

FIG. 27. Outline of cross section of stem showing the origin of the carpels. × 135.

FIG. 28. Longitudinal section of young carpel. × 650.

FIG. 29. Longitudinal section of young carpel, showing epidermal origin of the hairs which are produced in acropetal succession. × 1200.

FIG. 30. Section of carpel a little older. × 1200.

FIG. 31. Section of carpel showing the annular zone which gives rise to the ovary cavity. × 1200.

FIG. 32. Section of carpel just before the appearance of the nucellus × 780.

FIG. 33. Section of carpel showing the origin of the nucellus with one archesporial cell. × 1200.

FIG. 34. Section of carpel a little older. × 420.

FIG. 35. Nucellus with primary tapetal cell and macrospore mother cell × 2250.

FIG. 36. Section of carpel. × 200.

FIG. 37. Nucellus, showing the primary tapetal cell divided into two × 2250.

FIG. 38. Section of nucellus, showing a long axial row back of the macrospore mother cell. × 1200.

Plate VI.

FIG. 39. Section of nucellus, showing origin of the integuments. × 2250.

FIG. 40. Section of nucellus a little older than *fig. 38*. × 1200.

FIG. 41. Section of nucellus, showing the macrospore mother cell developing directly into the fertile macrospore. × 2250.

FIG. 42. Section of nucellus showing disorganization of the two tapetal cells. × 2250.

FIG. 43. Section of nucellus, showing further disorganization of the tapetal cells. × 2250.

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FIG. 44. Section of a carpel, showing position of the hairs and the ovule. × 80.

FIG. 45. Section showing the ovule becoming anatropous. × 1200.

FIG. 46. Section showing further development of the ovule. × 1200.

FIG. 47. Section of ovule somewhat diagonal, which accounts for the cells appearing between the macrospore and epidermis at the micropylar end. × 1200.

FIG. 48. Section of a carpel, showing position of the ovule at the time of the mature embryo sac. × 420.

FIG. 49. Section of embryo sac, showing egg apparatus and the two polar nuclei in contact. × 1200.

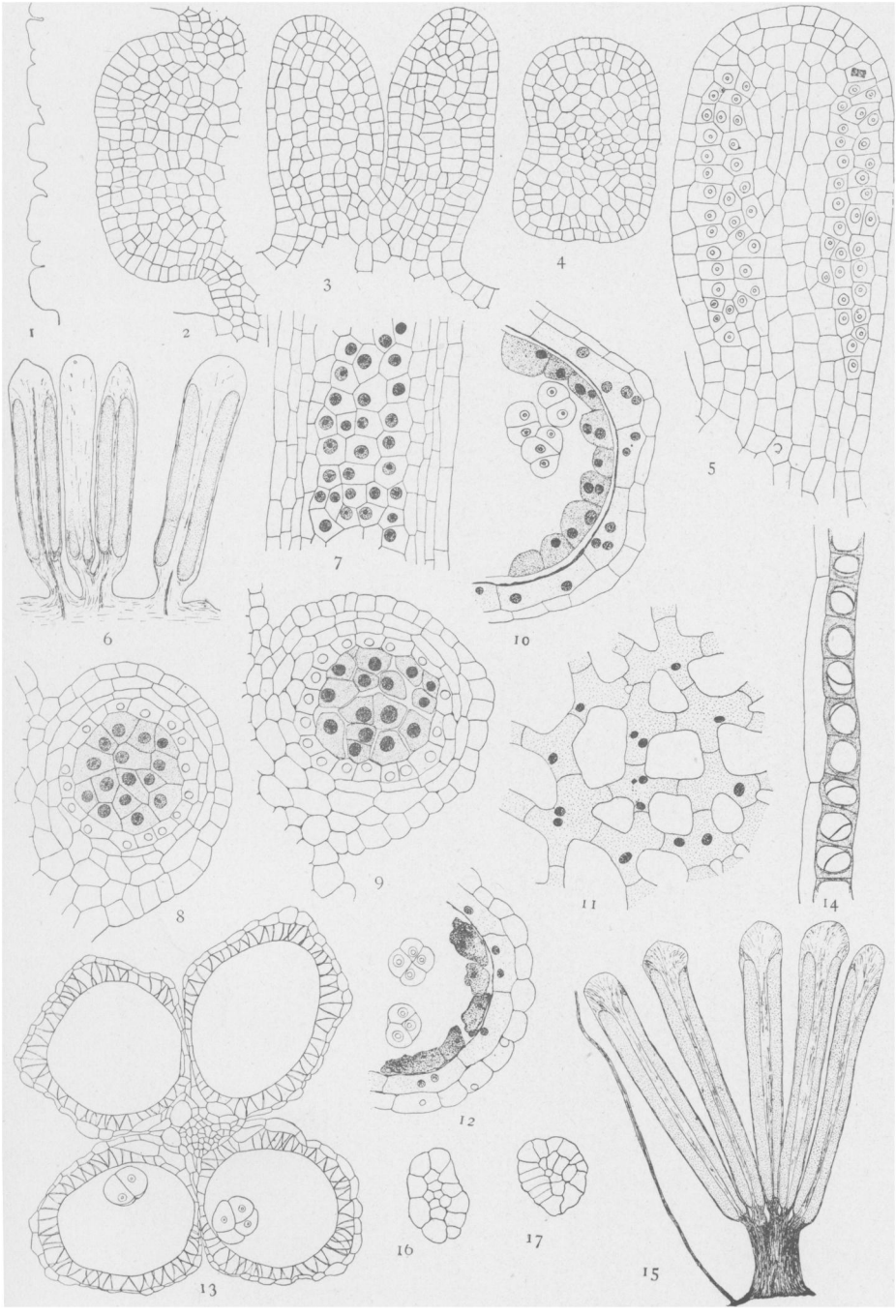
FIG. 50. Section of embryo sac, showing the antipodal nuclei and conjugating polar nuclei. × 1200.

FIG. 51. Section of embryo sac, showing one synergid, the oosphere, and the conjugating polar nuclei. × 1200.

FIG. 52. Section of embryo sac, showing the synergids and antipodal nuclei. × 1200.

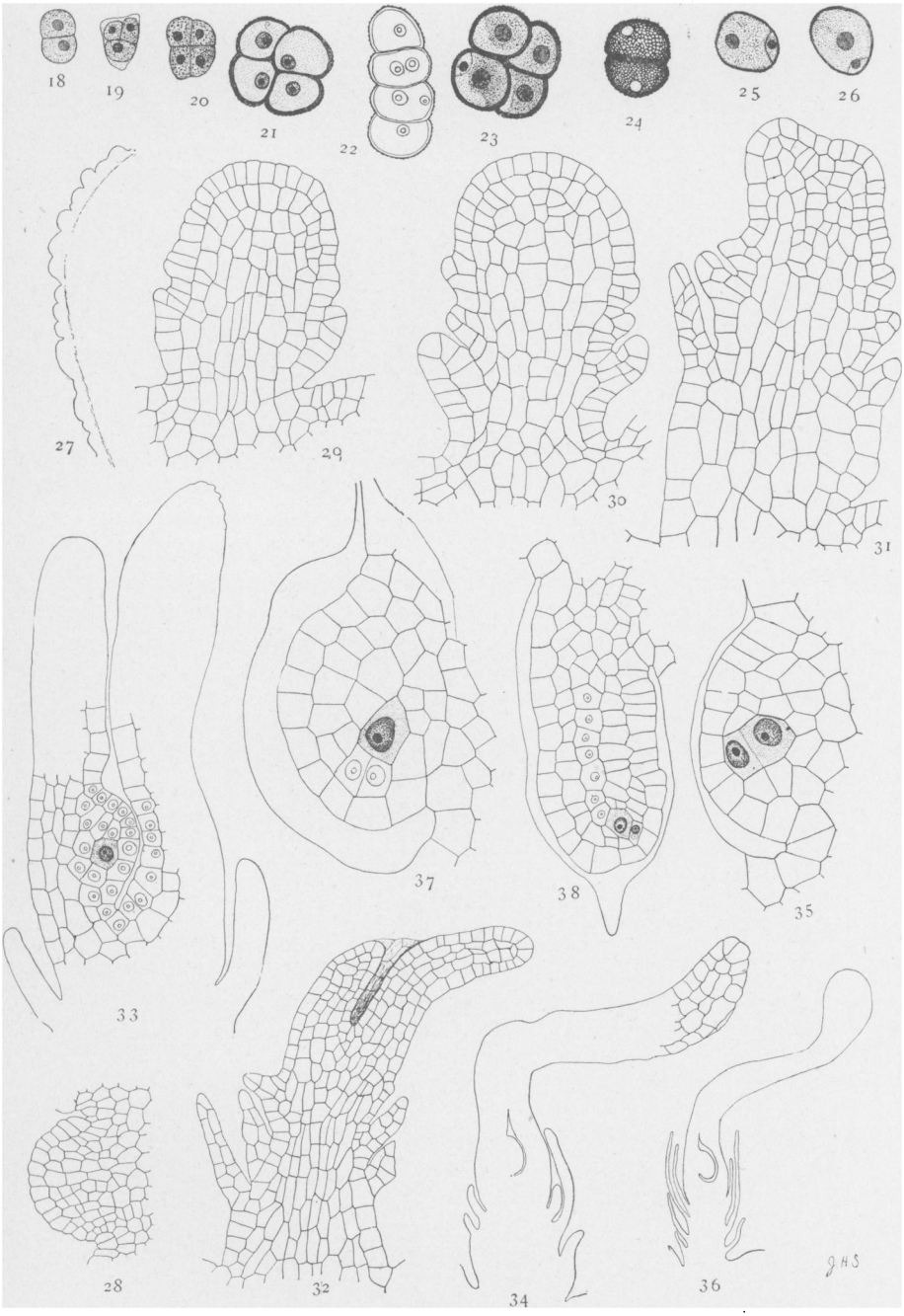
FIG. 53. Section of embryo sac, showing the synergids and the definitive nucleus. × 1200.

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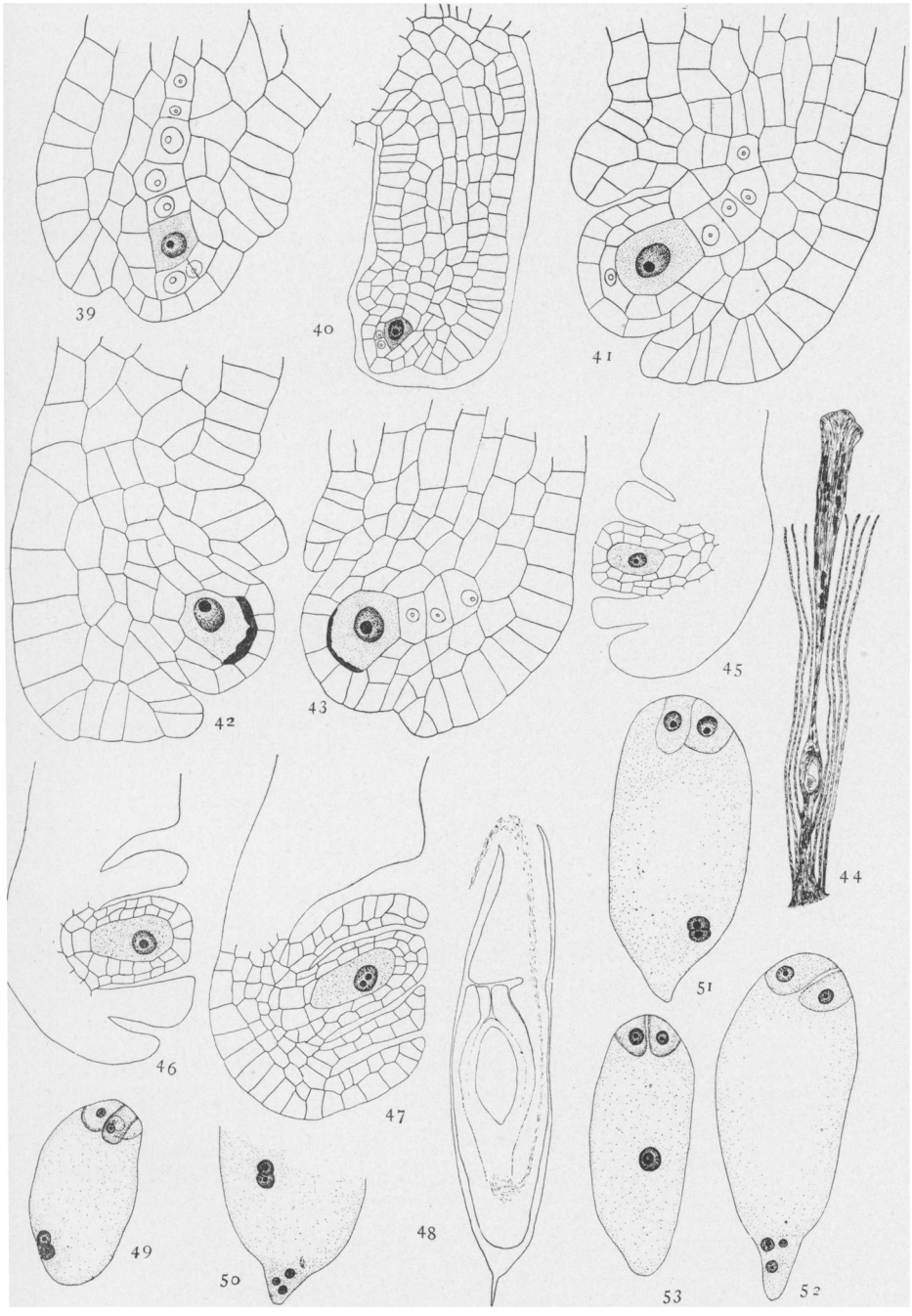


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