CYTOKINESIS OF THE POLLEN-MOTHER-CELLS OF CERTAIN DICOTYLEDONS. PP. 257-317

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BY

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(WITH PLATES 27–29)

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II. REVIEW OF THE LITERATURE

a. Division by cell-plate

Since the notable observations of Strasburger (**67*a***) in 1875 on the existence of the so-called cell-plate as a stage in the cytokinesis of higher plants, the assumption has become general that such a structure is universally present in angiosperms, gymnosperms, ferns, and bryophytes. Strasburger already in 1875 discussed the formation of the plate by fusion of thickenings on the central spindle-fibers, its splitting to form the boundaries of the daughter-cells, and the secretion of the cellulose wall or walls between the new daughter-cell boundaries. Strasburger's views have been critically confirmed and enlarged by Treub for the orchids, Mottier for the mother-cells of the lily, Hof for the root-tips of *Ephedra*, *Pteris*, and *Vicia*, Němec for *Allium*, and Timberlake for the root-tips of *Allium* and for the pollen mother-cells of the larch. In addition to this critical work there has appeared in the literature a vast number of more or less casual statements corroborating this interpretation with regard to the cells of various representatives of nearly all groups of the higher plants. Apparently in only one instance has a serious attempt been made to question the universal occurrence of cell-plate formation in the cytokinesis of higher plants, namely, the work of Baranetsky (**4**) in 1880 which has not been recognized as presenting such an exception to this rule, doubtless chiefly because it does not furnish the positive proof of how division may be accomplished without a cell-plate.

On the other hand, it has been just as carefully established that the animal cell divides without the formation of a cell-plate in the equator of the central spindle. Flemming's attempt to homologize the "zwischenkorper" of certain animal cells with the cell-plate of plants has not been generally accepted. The "zwischenkörper" has not been shown to play any part in the formation of the new plasma membranes, whereas this is recognized as a large part of the function and activity of the cell-plate.

Treub (**75***a*) in 1878 presented the first careful observations of cell-division in living material. His findings, in general, agree with those of Strasburger; but in *Epipactis*, he reports, the daughter nuclei travel from one side of the ce l to the other, while the cell-plate is being laid down progressively between them. He believed, however, that the cell-plate was of cytoplasmic origin.

In 1887 Went (**79**) for the first time presented the idea that the fibers in the center of the spindle disappear during the growth of the cell-plate. Mottier (**44***a*) in 1897 confirmed Strasburger's observations, using as material the mother-cells of *Lilium* fixed in Flemming's solutions and stained with the safranin, gentian-violet, and orange G combination. It must be remembered that Strasburger's initial work was done on alcoholic material. Mottier studied the process following the heterotypic nuclear division and found that there is "eine auffallende Verdickung der Fäden" in the equatorial region. The mother-cell-wall is shown in his figures to thicken meanwhile to about one twentieth of the diameter of the cell. Strasburger (**67***g*), from his study of *Lilium* and *Alstroemeria*, found that it is the fibers in the center of the spindle in which the equatorial swellings first occur. The elements composing the plate are pulled out and become extremely thin in the middle; and as soon as they break a middle layer appears between them. These equatorial swellings he had (**67***f*) previously designated by the name, "Dermatosomen"; but this term has not been extensively used since then. Hof (**30**) in 1898 stated that the cell-plate formation is accompanied by the shortening of the fibers of the central spindle, but showed no drawings to support this view. Wager (**78**) more recently has figured cell-plates in the root-tips of *Phaseolus*. Davis (**11**) concluded that the fibers involved in the formation of the cell-plates of the spore-mother-cells of *Anthoceros* are not those of the central spindle which remained from karyokinesis; but that they are newly organized in the cytoplasm after the disappearance of the latter. Mottier (**44***b*) in 1900 modified his former opinion as to the origin of the cell-plate in *Lilium*, and after a study of *Dictyota* makes the following statement: "That the cell-plate in the higher plants is formed by a lateral union or fusion of the thickened connecting fibers may be seriously questioned, for in some cases these fibers do not thicken very appreciably in the equatorial region, nor do they lie sufficiently close to one another to enable the slightly thickened middle parts to meet and fuse . . . the conclusion seems justifiable, that the cell-plate is formed by a homogeneous plasma which is conveyed to the cell-plate region and deposited there by the connecting fibers." He presents no new drawings of *Lilium* in support of this interpretation.

The most extensive and satisfactory study of cell-plate formation in the higher plants in recent years is that of Timberlake (**73**) on the pollen-mother-cells of the larch and the root-tips of the onion. The author found that the two types of cells are very similar in their procedure in cell-plate formation; he notes, however, a number of differences which evidently seemed to him of minor importance, but in the light of the following discussion appear to be by no means insignificant. His drawings and photographs present the only adequate attempt since Strasburger's "Zellbildung und Zelltheilung" to arrange a sequence of stages in the formation of the cell-plate. The figures of cell-plates by others are mostly isolated and introduced merely incidentally.

In the onion root-tip Timberlake describes the process in less detail than in *Larix*. He believes that new connecting fibers are formed at the periphery of the spindle, both in the early stages of spindle enlargement and during cell-plate formation. Except for the violet-stained fibers the cytoplasm is homogeneous and without granules. The first indication of equatorial differentiation is in the appearance of an orange-staining zone in that region. With the triple stain this zone stains like the young cell-wall, but it does not take ruthenium red or iron-haematoxylin, so that it is probably of different constitution, though Timberlake believes it is of carbohydrate nature. He likens it to the orange zone in *Saprolegnia*, and the neutral zone in *Fucus*. The spindle fibers become apparently thinner in this orange zone, prior to the appearance of the cell-plate elements, which the writer describes as "thickenings of the spindle-fibers" or "swelling on the fiber." He is unable to find evidence of any movement of cytoplasmic granules toward the equator to form the cell-plate, as suggested by Treub. The cell-plate elements are found sometimes to appear before re-organization of the daughter nuclei.

In the larch the central spindle-fibers are found not to multiply by longitudinal division in the early stages of spindle enlargement, as Strasburger holds. But their apparent increase in number is due to their separation, after being aggregated in bundles by pressure of the chromosomes as they move to the poles. The equatorial thickenings on the fibers are much more pronounced than in the onion root-tip. In addition to them there are granules which are blue with Flemming's triple stain, and are variously distributed within the cell during the anaphases and telophases, sometimes "in rows and sometimes sticking to the connecting fibers." The central spindle-fibers at first thicken near the nuclei, giving the same appearance as the fibers of the onion, which are attenuated at the equator. The fibers of the larch then become of uniform diameter, and lastly thicken at the equator, giving rise to swellings. The process continues until the fibers begin to disappear near the nuclei, that is, shorten. "All of the fibers that form cell-plate elements are completely used up in the growth of the cell-plate." The swellings enlarge, come in contact, and fuse. They do not split before fusing. The central spindle grows peripherally, that is, centrifugally by the addition of fibers. The cell-plate splits in the center and the new wall is secreted (fig. 21). There are thus three processes going on: cell-plate formation, plasma membrane formation, and wall formation. In the larch they are all shown to take place centrifugally, and Strasburger (**67***a*) figured the same condition in *Anthericum* after the heterotypic division. Timberlake believes that the wall formation may occur by the secretion of an unstainable solution, perhaps a carbohydrate, between the two plasma membranes. The phenomenon of the separation of the two plasma membranes is discussed in some detail. Of the process he says: "It is hard to conceive of a layer of protoplasm becoming differentiated into two separate layers similar in all apparent respects to each other."

Studies in physical chemistry since the date of Timberlake's paper, especially in the behavior of colloids, should throw considerable light upon these processes of cell-division. The well-known fact of the crystalloid nature of cell-walls and starch grains made it seem likely that the cell-plate is not of this nature, but is more probably colloidal; and its being visible, both in living and fixed material, would indicate that it is probably a suspensoid. Though probably colloidal, it is not very different either physically or chemically from the rest of the cytoplasm, or a surface boundary would form between them, such as delimits the nucleus; in other words, the cell-plate differs from the plasma membranes to which it gives rise, in that it is apparently permeable to substances in the cytoplasm indiscriminately.

A number of interesting variations from the typical procedure are noted by Timberlake in larch. "Whether the mother-cell divides into four cells which form the pollen grains by successive or simultaneous division depends upon the number of spindle-fibers existing in connection with the first nuclear division. If