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DEHISCENCE OF THE FRUIT OF
PAPAVER ORIENTALE L.

by
Lloyd C. Ayres

Submitted to the graduate committee of South Dakota State
College, Brookings, South Dakota, as a partial requirement for the
degree Master of Science.

June, 1953

DEHISCENCE OF THE FRUIT OF PAPAVER ORIENTALE L.

By

Lloyd C. Ayres

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This thesis is approved as a creditable independent investigation by a candidate for the degree, Master of Science, and acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

I wish to take this opportunity to express my appreciation to Dr. Ward L. Miller, and to thank him for his suggestion of the problem and guidance throughout the investigation.

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DEHISCENCE OF THE FRUIT OF PAPAVER ORIENTALE

INTRODUCTION

Dehiscence is the process of opening in anthers, spore cases and dry fruits. The dry fruit described here is a capsule. When one speaks of capsule dehiscence, four types are considered: (1) poricidal dehiscence - by pores at the apices of carpels; (2) loculicidal dehiscence - lengthwise along the middle of each carpel; (3) septicial dehiscence - lengthwise along the line of union of adjoining carpels; and (4) circumscissile dehiscence - along a circular line perpendicular to the main axis. It is the first type of dehiscence with which this study is concerned.

In many plants there seems to be no elaborate histological structure associated with dehiscence; the opening takes place along sutures, which are planes of structural weakness where adjacent carpels have fused to one another. It is evident in the capsule of *Papaver orientale* that the pores do not develop lengthwise along the middle of the carpels; they do not develop along the lines of fusion (sutures), and although the pores are in a circular line, they are separated by areas of tissue; therefore, it is a challenging problem to discover just how poricidal dehiscence occurs and how it differs from other plants in their manner of dehiscence.

Fruit dehiscence in *Papaveraceae* has been mentioned by Saunders (10). In her discussion on carpel polymorphism, she says, "due to the arrangement of alternating valve and solid carpels in *Papaveraceae*, we find a clue to the characteristic mode of dehiscence of the fruit by pores, a result due simply to the separation of the valve carpel

and its apex from the solid carpel". However, this contribution has been made from observations in connection with her theory of carpel polymorphism and has very little histological support.

Arber (1), in her studies in flower structure, has made a morphological interpretation of the gynaecea of four species of Papaver. She is not in agreement with the theory of carpel polymorphism in Papaveraceae. In the summary of Miss Arber's study, she says, "it is not until a relatively late stage that the apices of the median regions of the carpels break away from the base of the stigmatic crown, thus forming the dehiscence pores". Since she makes no statement as to the method of "breaking away" in her observations, it is assumed that she bases this conclusion on external rather than internal observations.

This amounts to all the research done by workers on the problem of dehiscence in Papaveraceae. Observations of gross aspects are useful only as mere hints to the true method of dehiscence. Therefore this study, using histological methods, was undertaken to solve the method of dehiscence in the fruit of *P. orientale*.

REVIEW OF LITERATURE

There has been a number of investigations dealing with dehiscence, though many of these have been in the area of anther dehiscence, Matthews and Maclachlan (6). Early investigations in fruit dehiscence were made by foreign workers, but these were no more than gross observations.

Contributions on the subject of dehiscence in other fruits have been made. Guppy (4) found, in his observations of loculicidal dehiscence of *Viola tricolor* and *Iris foetidissima*, that the detached capsules will dehisce in wet moss, but fail altogether to open when allowed to dry. He says, "drying, therefore, though it develops strains, the relief of which ends in the dehiscence of fruits, is not a necessity for their opening". Yen (12), in investigation of septicidal dehiscence in *Firmiana simplex*, concludes that it is due to mechanical breaking or rupturing of the tissue, approximately along the old line of the former suture. Retheke (9), found that circumscissile dehiscence is due to a disorganization of parenchyma tissue, and an alinement of cells which provides a zone of weakness where splitting can easily occur. Holden (5), in investigating the pod fruit of *Astragalus canadensis*, concludes that dehiscence is the result of vertical and horizontal strains set up by differential drying of the parenchyma tissue which surrounds the sclerenchyma tissue. Brenekamp (2), in studying the opening mechanism of the Acanthaceous fruit, found that the valves spring apart when a drop of water dissolves the already partially hydrolyzed middle lamella in the sclerenchymatous tissue.

However poricidal dehiscence in the capsule may occur, it is evident from the above contributions that other factors than those concerned with drying may go to determine the process of dehiscence.

MATERIALS AND METHODS

Papaver orientale L. is the most commonly grown perennial poppy in the United States. It is known to flower gardeners as the Oriental poppy. It is a herb with a milky colored juice, and has regular flowers. The ovules are numerous on the placentae. Generally the stigmas are in a 12-18 rayed disc resting on the summit of the ovary. The capsule is short and turgid, with hardened tissue in the ovary wall and the stigmatic disc.

Developmental stages of the fruit were collected from a local flower garden during the summer of 1952. These were fixed and killed in formalin-acetic-alcohol. Later the material was embedded in paraffin by the butyl-alcohol method. Fruits were then sectioned at six to twelve microns with a rotary microtome, and sections mounted on slides in series. The fruits were sectioned transversely, tangentially, and radially. Safranin and fast green were the principal stains used; however, some series were stained with iron-alum-haematoxylin and orange G, and also a triple stain of safranin, fast green, and Orange G was used.

Photomicrographs were made of selected representative sections. Diagrams and detailed drawings of portions of sections were made, and photographed. All diagrams and drawings were made with the aid of a camera lucida.

INVESTIGATION

The capsule fruit consists of two parts, the ovary and the stigmatic disc. The habits of the capsule prior to dehiscence and after dehiscence are shown in figures 1 and 3, respectively. In an immature fruit, the stigmatic disc is folded down over the upper portion of the ovary (Fig. 1). When the fruit is mature and dehiscence has occurred, pores are found at the top of the ovary beneath the margin of the stigmatic disc (Fig. 3).

Surface views of the stigmatic disc, prior to dehiscence and after dehiscence are shown in figures 2 and 4. The capsule shown in figure 2 is of the same age as the immature capsule in figure 1.

The fifteen stigmatic rays extending radially from the center are double in nature, as they are formed by the stigmatic surfaces of adjoining carpels. The double stigmatic rays fold down at the periphery, as they lie on the lobes of the stigmatic disc (Fig. 1). A portion of the stigmatic disc in figure 4 is removed to show that the pores under the stigmatic disc alternate with the lobes and double stigmatic rays.

Early in the investigation it was discovered that, to satisfy the manner of dehiscence, it would be necessary to learn the relationship existing between the ovary and stigmatic disc. The initial phase of this investigation was directed toward that end.

A transverse section (slightly oblique) of a capsule before dehiscence is shown in figure 5. The section was cut at the level where the extremities of the stigmatic lobes lap over the ovary. It is this level of the capsule which concerns the greater part of the investigation. Because of the obliquity of the section, different levels of the capsule are represented. From it, the terminology of parts and their relationships can be closely correlated.



Fig. 1. *Papaver orientale*; habit of immature capsule, (x2). Lobes of the stigmatic disc are shown lapping down over the top of the ovary.



Fig. 2. Same capsule as in figure 1, (x2); but showing a top surface view of the stigmatic disc with its doubled rays.



Fig. 3. *P. orientale*; habit of mature capsule after dehiscence, (x2). Stigmatic disc is shown with its lobes elevated. Dehiscence pores are separated from one another by the ventral bundles of the fused carpels.



Fig. 4. Same capsule as in figure 3, (x2), but showing a top surface view of the stigmatic disc. Part of the disc has been cut away to reveal the dehiscence pores under it. Pores are seen to have developed, not merely under the disc, but also alternate with its lobes and rays.

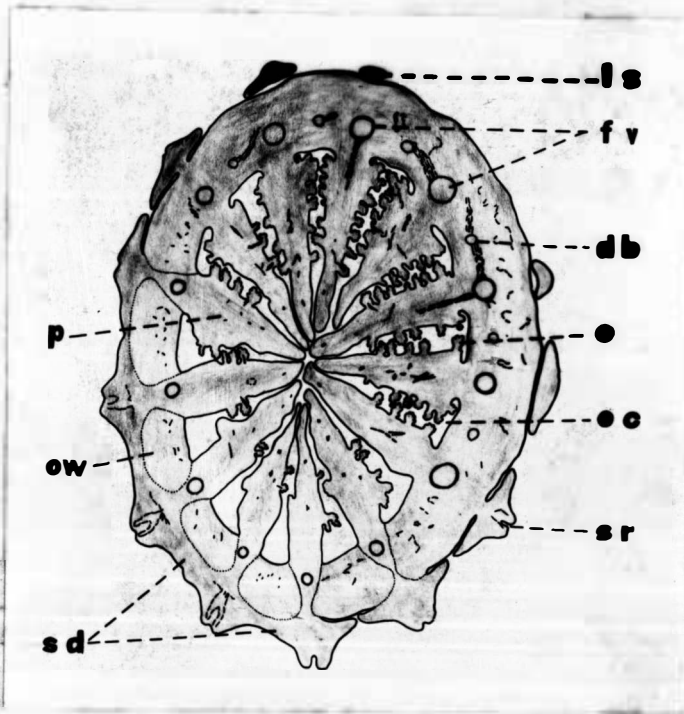


Fig. 5. Transverse section (slightly oblique) of a young capsule, (xl2). Section taken at a level corresponding to the extremities of the disc lobes in figure 1. Ovules have two integuments developed. db, dorsal bundle; fv, fused ventral bundles; ls, lobes of stigmatic disc; o, ovule; oc, ovary cavity; ow, ovary wall; p, placenta; sd, rim of stigmatic disc; sr, stigmatic ray.

Organization of the ovary.

The ovary is compound, being formed from a single whorl of carpels. The carpels are fused together along their ventral margins. The placentae are double as they arise as inward growths from the united inrolled margins of adjacent carpels. Numerous ovules are borne on the surfaces of the parietal placentae (Figs. 5 through 7). At the base of the ovary and at the apex of the floral axis, the inner edges of the placentae are pressed together, giving the ovary the appearance of being multilocular. However, at higher levels in the ovary, the placentae project freely and the ovary is definitely unilocular (Figs. 5 and 6).

As the level of the stigmatic disc is reached, the placentae are again in such close approximation to each other that it is suggestive of a multilocular ovary (Figs. 7 through 9). At a slightly higher level, the placentae do not bear ovules and become pressed close together along their entire surface (Fig. 9).

The dorsal bundles (median bundles) occur on radii which alternate with those passing through the fused ventral bundles (Fig. 5). The dorsal bundles do not become lignified until some time after ovules have developed their integuments. In sections of the ovary some distance below the stigmatic disc, there is a great amount of anastomosing of vascular tissue between the fused ventral bundles and dorsal bundles (Figs. 6 and 7), the latter branch often forming a highly developed network, which supplies the ovary wall with many traces (Fig. 6).

As the level just below the stigmatic disc is reached, the anastomosing of vascular tissue is no longer evident (Figs. 5 and 8). Also the upper limit of the dorsal bundle is reached and that bundle is not found to exist at higher levels (Figs. 5 and 9).

The ventral bundles (marginal bundles) of adjacent carpels are fused and are located on the same radii with the placentae (Fig. 5). The fused ventral bundles supply the ovules; and traces can be seen leaving these bundles and extending into the placentae (Figs. 5 and 7). The fused ventral bundles become lignified, while the capsule is still immature (Fig. 6).

The fused ventral bundles play an active role in supplying the stigmatic disc. In the central portion of the right side of figure 10, two strands of vascular tissue may be seen to separate from the same ventral bundle and to enter different members of the stigmatic disc. These members are parts of adjacent carpels. The vascular tissue is clearly evident in transverse sections of the stigmatic portion of the carpels (Figs. 11 and 12).

Organization of the stigmatic disc.

In a series of transverse sections from the ovary to the apex of the capsule, the first parts of the stigmatic disc to be seen are the individual lobes (Figs. 5 and 7). In transverse sections higher in the capsule, it is seen that the lobes are not individual, but are actually extensions of the stigmatic rim (Figs. 5 and 9). The lower edge of the rim of the stigmatic disc is not fused to the outer part of the ovary wall, but merely laps over it. A space can be seen between the rim and the ovary wall, indicating the lack of fusion (Fig. 9).

A section of the capsule at the level of the rim, shows that the double stigmatic rays are on the same radii as the lobes, fused ventral bundles, and placentae (Figs. 5, 8 and 9). This is significant. It has been shown previously that the fused ventral bundles supply the placentae and also the stigmatic disc. Since all these parts exist on

the same radii, although portions are at different levels, it is seen how perfectly it is set up for the fused ventral bundles to supply the placentae and also the stigmatic rays.

The vascular tissue separates from the fused ventral bundles and enters separate portions of the stigmatic disc (Fig. 10). These separate portions of the disc are adjacent carpels. Their margins are the paired stigmatic rays as seen in previous sections.

Near the apex of the capsule, the stigmatic portions of the carpels are distinctly separated (Fig. 11). The close approximation of the double stigmatic rays is due to the receptive papillae lining the margins of the carpels at this level. There is no tissue in the center of the stigmatic disc (Figs. 11 and 13). This open center results from the incomplete fusion of the carpels at their apices. Such an opening in the immature fruit has no detrimental effect upon the young tissue, for it is still enclosed and protected by the petals and is not exposed to the air. When the placentae increase in size as the fruit grows, the sterile portions of the placentae are pressed together, closing the opening (Fig. 9).

At the apex of the capsule, the stigmatic portions of the carpels are completely separated from one another (Fig. 12). The vascular tissue is evident in each. The separation of the stigmatic portion of the carpels at this level, clearly shows that the double stigmatic rays belong to adjoining carpels.

Figs. 6 - 12 are photomicrographs of transverse sections from a series through the capsule of an immature fruit such as that shown in figure 1.

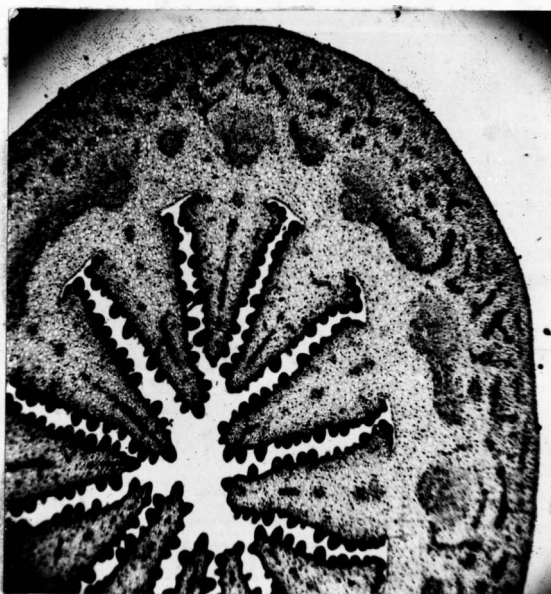


Fig. 6. Portion of a transverse section through the ovary, just below the lobes of the stigmatic disc, (x30). The integuments of the young ovules are not yet developed. Fused ventral bundles of the ovary wall lie on the same radii with the placentae, while the dorsal bundles alternate with them. Branches frequently connect the two. Ovary wall contains many vascular traces. Ovary cavity is unilocular.

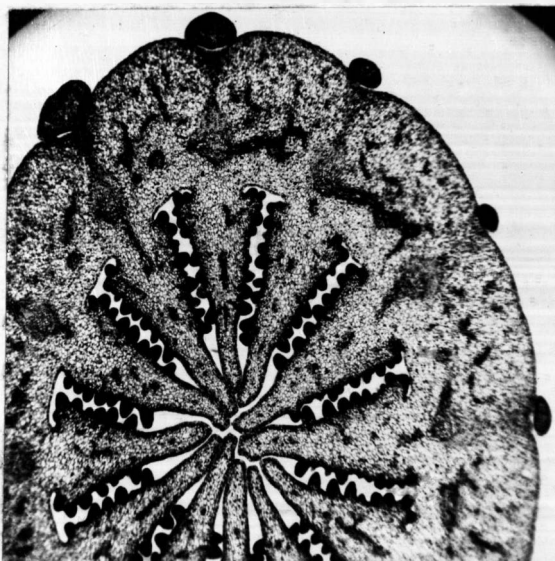


Fig. 7. Similar to figure 6, but at a higher level, (x30). Around the periphery of the ovary, are seen five of the over-lapping lobes of the stigmatic disc. Note their positions opposite the placentae and in direct line with the fused ventral bundles. Innermost margins of the placentae are pressed together, giving a false multilocular appearance.

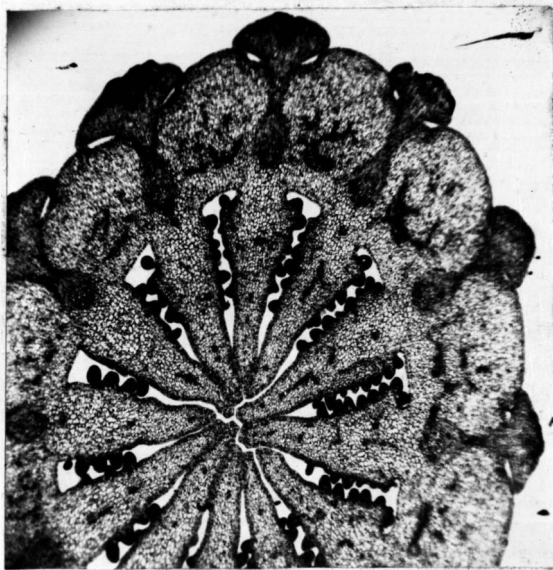


Fig. 8. Similar to figure 7, but at a slightly higher level (x30). Tissue connections between fused ventral bundles and stigmatic lobes are more evident. Dorsal bundles are represented only by traces. Ovary walls contain less vascular tissue (see Fig. 6). Note again, false multilocular appearance of ovary.



Fig. 9. Similar to figure 8 at a still higher level, through the rim of the stigmatic disc, (x30). This is above the lobed margin of the stigmatic disc, except at the lower right hand corner of the figure. The double nature of stigmatic rays is pronounced here. The dorsal bundles do not reach this level.

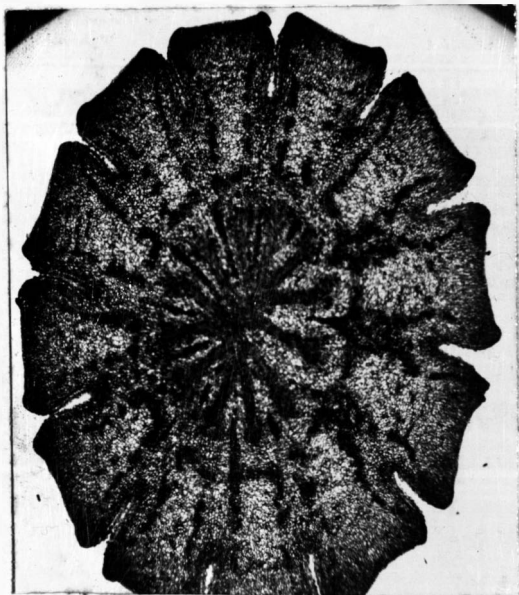


Fig. 10. Similar to figure 9, at a higher level above the lobes, (x30), where vascular connection between the fused ventral bundles and stigmatic rays is evident.

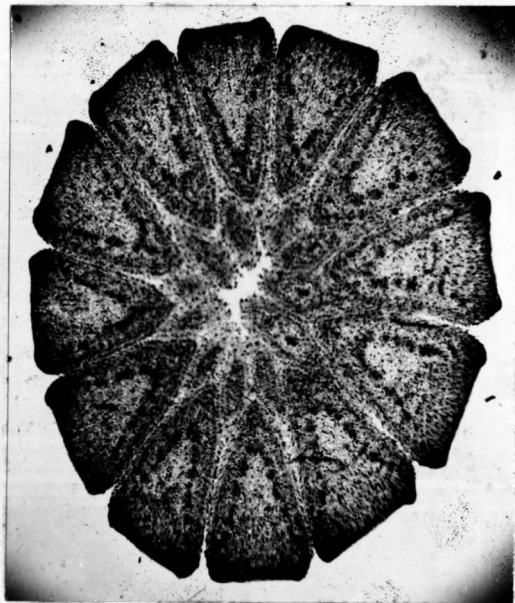


Fig. 11. Transverse section at a higher level than figure 9. (x30). Upper limits of the placental tissue are present. Stigmatic portions of the carpels are separated by papillae.

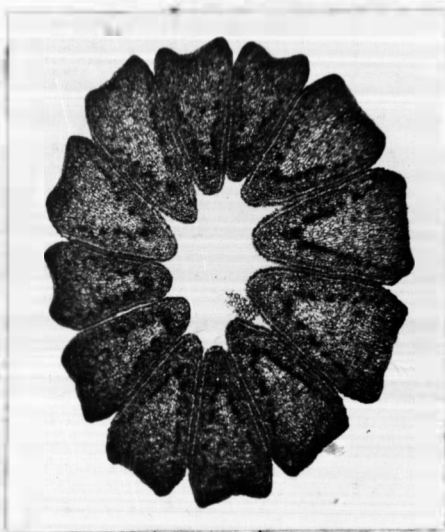


Fig. 12. Transverse section of the stigmatic disc, (x30). The stigmatic portions of the carpels are completely separated at this level. The center of the disc is open. Vascular tissue to the stigmatic rays is evident.

Dehiscence.

The young capsules show no evidence of dehiscence and give no indication of cell differentiation where dehiscence is seen to occur in mature capsules (Fig. 14). The cells are thin-walled, non-vacuolate with dense cytoplasm, which indicates vigorous growth. As the integuments of the young ovules begin to develop, there appears an oblique alignment of cells in the stigmatic disc (Fig. 15). The cells are still growing vigorously. This oblique alignment of the cells is the result of faster growth of the sterile portions of the placentae in the center of the capsule. Such growth of the placentae pushes the stigmatic disc up in the center and also closes the opening in the center of the capsule.

In an older capsule, after fertilization, the obliquely aligned cells of the stigmatic disc have thickened their walls. The cells in the ovary wall remain thin-walled, but are becoming vacuolate, except for a definite boundary of cells appearing between the stigmatic disc and the ovary wall. This boundary is the separation mechanism, which is made up of two layers of small isodiametric cells (Figs. 17 and 18). The cells are non-vacuolate and possess dense protoplasm. The double separation layer is formed by cell division of one layer of cells at the upper portion of the ovary wall immediately beneath the stigmatic disc. The double separation layer is formed all around the entire capsule. Over the region of the relatively short dorsal bundle the separation layers extend from the outer edge of the ovary wall to the ovary cavity (Fig. 16). Through the region of the fused ventral bundles, however, the separation layers extend only from the outer edge of the ovary wall to the bundles themselves (Fig. 19). The separation layers

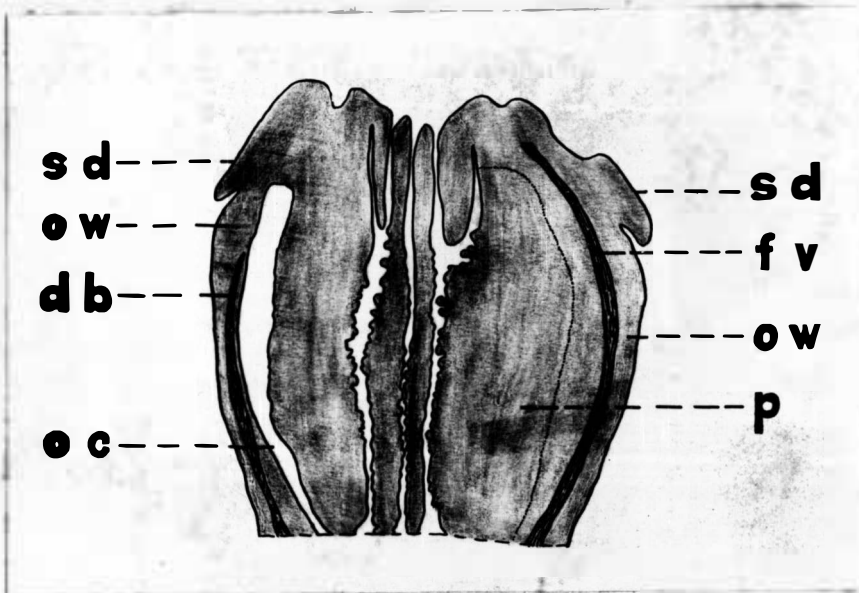


Fig. 13. Longitudinal section of a young capsule, (x20). Note open center in region of stigmatic disc (see Fig. 12). The placentae are on same radii as the fused ventral bundles. Dorsal bundle does not extend to the stigmatic disc. Fused ventral bundle supplies stigmatic disc. db, dorsal bundle; fv, fused ventral bundles; oc, ovary cavity; ow, ovary wall; p, placenta; sd, stigmatic disc.

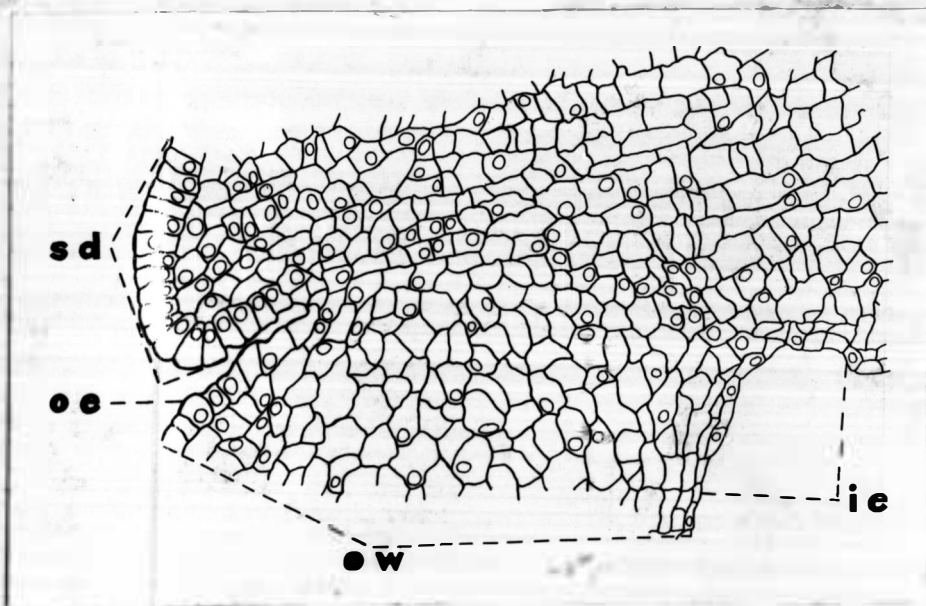


Fig. 14. Longitudinal section of the area limited by sd and ow on the left side of capsule in figure 13, (x280). This is the area where the separation layer will form. All cells are in the same condition, thin-walled, non-vacuolate. No indication of separation layer. ie, inner epidermis; oc, outer epidermis; ow, ovary wall; sd, stigmatic disc.

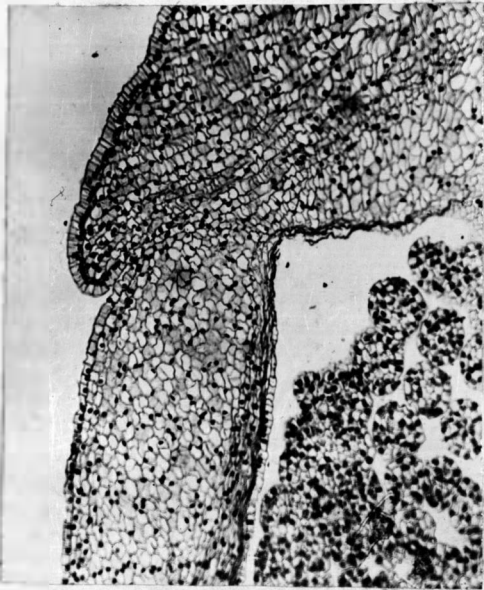


Fig. 15. Longitudinal section of a portion similar to figure 14, (x94). A slightly older capsule at the time when integuments are appearing on young ovules. Note oblique alinement of cells in the stigmatic disc.

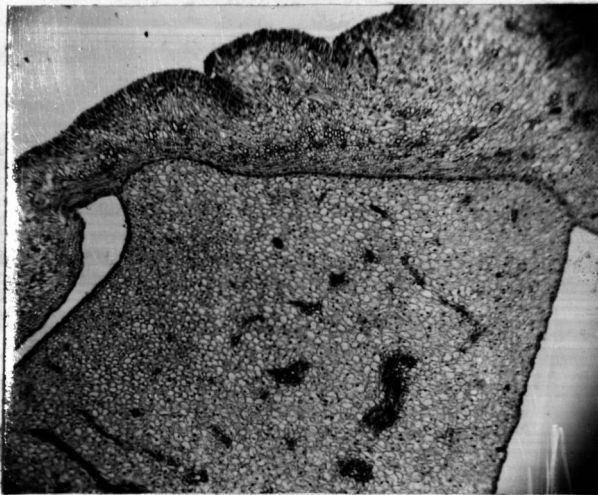


Fig. 16. Longitudinal section of a portion of the capsule, similar to figure 15, (x27). An intermediate capsule, after fertilization. Obliquely oriented cells in the stigmatic disc have thickened their walls. The separation layers have formed a definite boundary between the stigmatic disc and ovary wall. The separation layers extend from the outer edge of the capsule to the ovary cavity.

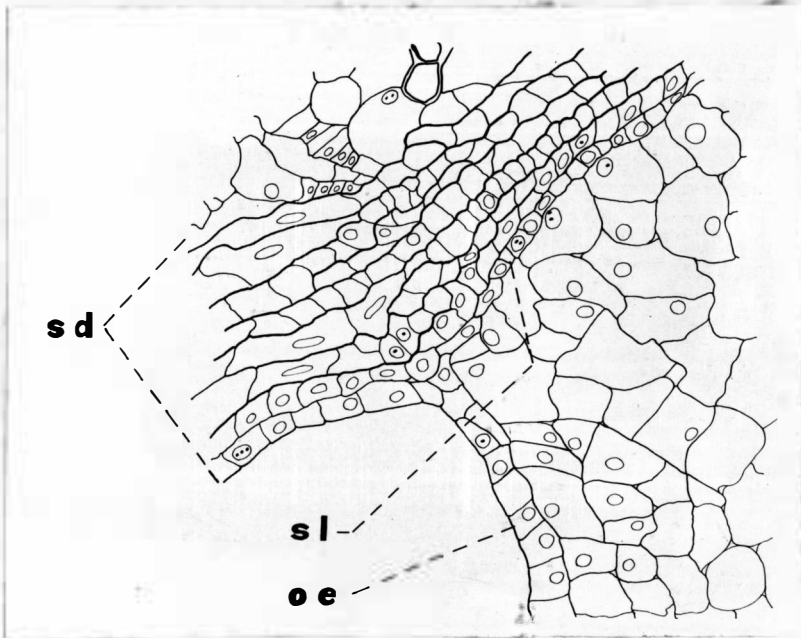


Fig. 17. Longitudinal section of a portion of figure 16, at outer edge, (x370). Relationship of separation layers to stigmatic disc and ovary wall. Parenchyma cells of the ovary wall remain thin-walled. Cells of the stigmatic disc have thickened their walls. oe, outer epidermis; sd, stigmatic disc; sl, separation layer.

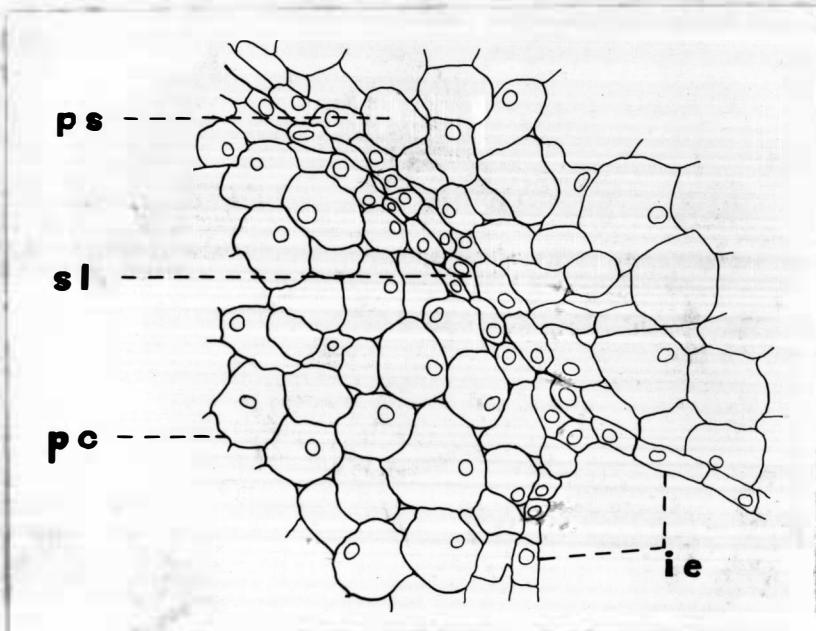


Fig. 18. Longitudinal section of a portion of figure 16 at the ovary cavity, (x370). Separation layers bordered by parenchyma cells of the ovary wall and stigmatic disc. Small intercellular spaces occur between some cells of the separation layers. ie, inner epidermis; pc, parenchyma cells of ovary wall; ps, parenchyma cells of stigmatic disc; sl, separation layers.

therefor do not extend through the fused ventral bundles. They turn down and extend a short distance on the outer side of the bundle. Because the separation layers do not pass through the fused ventral bundles, these bundles come finally to separate the openings or pores from one another (Fig. 3). It is also the ventral bundles that hold the stigmatic disc to the ovary after dehiscence is complete.

An almost mature capsule, before dehiscence, reveals the prominent separation layers. Thick, lignified sclerenchyma tissue of the disc and the thin-walled, highly vacuolate parenchyma cells of the ovary wall lie on opposite sides of the separation layers (Fig. 20). The two layers of cells forming the separation mechanism differ from the other cells in size, in form, and in the appearance of their protoplasm. Their dense and homogeneous cytoplasm is non-vacuolated in contrast to the bordering cells whose cytoplasm is characteristically vacuolated. Such a homogeneous cytoplasm, common to all the cells in the separation layers, indicates a specialized kind of activity. This activity might well be the resorption of the middle lamella. Intercellular spaces occurring between the cells, indicate that the middle lamella is undergoing a change and is becoming functionless. It is no longer retained as a cementing substance between the cells, and they are allowed to separate. The lignified cells of the stigmatic disc are associated with thin-walled, fully distended cells, which prevent any shifting of the sclerenchyma tissue.

Dehiscence begins at the outer surface of the capsule (Fig. 21). There has been little if any change in cell contents of the ovary wall, and the stigmatic disc still consists of parenchyma, sclerenchyma, lignified vascular tissue, and lactiferous glands. It is clearly shown

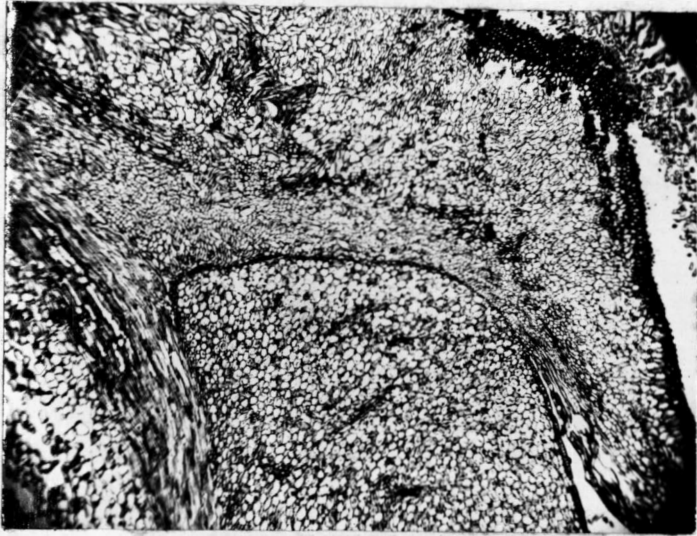


Fig. 19. Longitudinal section of the separation layers in the vicinity of one fused ventral bundle on the left (x22). The double separation layer turns down and extends a short distance on the outer side of this fused ventral bundle. After dehiscence, the fused ventral bundle separates the pores, and functions as a fulcrum between stigmatic disc and ovary wall.

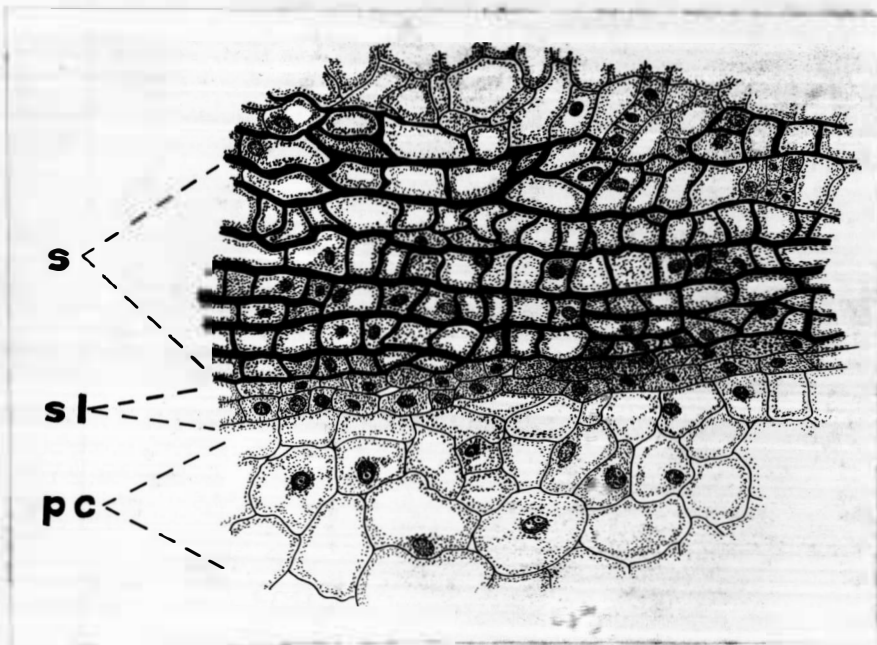


Fig. 20. Longitudinal section of the double separation layer shortly before dehiscence, bordered by sclerenchyma tissue above and parenchyma tissue below, (x320). The cells of the separation layers have a dense, homogeneous cytoplasm in contrast to the neighboring cells whose cytoplasm is characteristically vacuolated. Note intercellular spaces between the separation layers. pc, parenchyma cells of the ovary wall; s, sclerenchyma tissue; sl, separation layers.

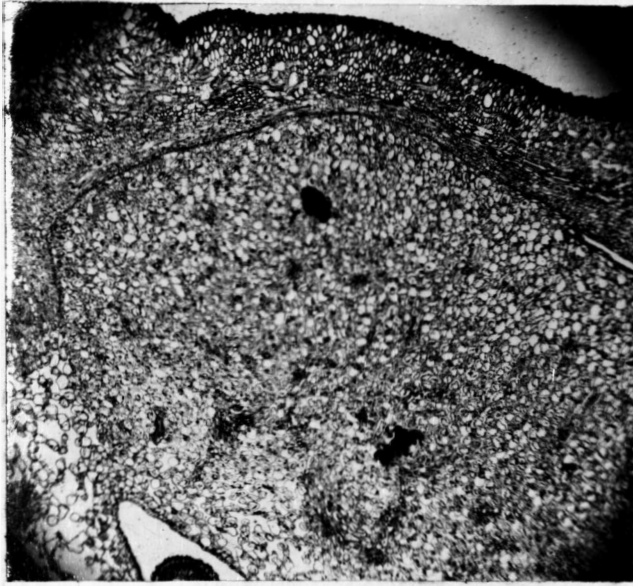


Fig. 21. Longitudinal section of a portion of a maturing capsule showing the separation layers dehiscing at the right, (x24). The separation layers extend to the ovary cavity at the lower left of the figure. Part of a young seed can be seen in the ovary cavity. There has been no dehydration of cells in either the stigmatic disc or ovary wall. Note disorganization of placental cells at the far left.

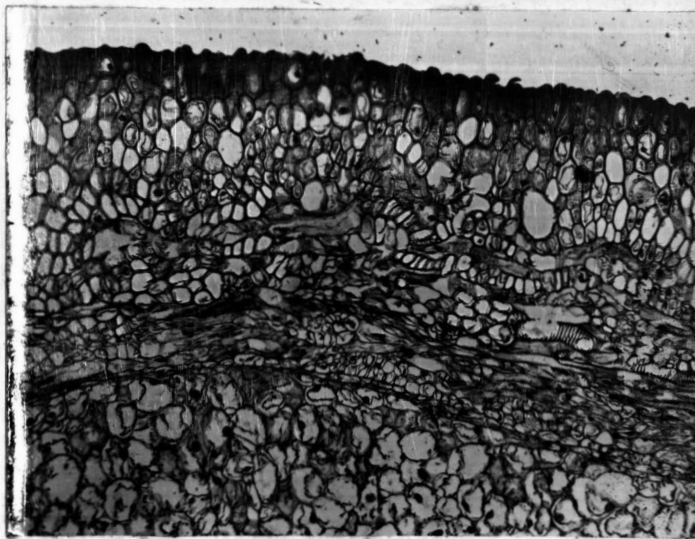


Fig. 22. Longitudinal section of a portion of capsule shown in figure 21, (x120). The upper three-fourths of the figure is the stigmatic disc. The lower fourth shows the parenchyma cells of the ovary wall. Between the two can be seen the double separation layers. Cells of the stigmatic disc are variously oriented and represent parenchyma, sclerenchyma, lignified vascular tissue, and lactiferous glands.

that, at the time dehiscence begins, there is no indication of dehydration of cells in either stigmatic disc or ovary wall (Fig. 22). Dehiscence occurs between the cells of the double separation layer, and it is due to the parting of the cells along their common walls. There is no rupture of cells in the separation layers, as one would expect if the separation were due to drying and shrinking, but rather a parting of layers of whole cells (Figs. 23 and 24).

As dehiscence proceeds, the stigmatic disc begins to lift upward and away from the ovary wall. The stigmatic disc lifts up along the outer edge of the capsule because the cells of the placentae have disorganized (Fig. 21). The breakdown of the placentae removes the supporting structures at the center of the capsule. This causes the stigmatic disc to sink at the center and, since it is rigid, this swings the periphery of the stigmatic disc up and away from the ovary wall. The fused ventral bundles function as fulcrums in this process. When the stigmatic disc lifts up, the thin-walled cells of the ovary wall are exposed to the drying air, and not until then do they dehydrate and rupture. This tends to speed up the process of dehiscence. The thin-walled cells of the stigmatic disc are ruptured and only a framework of lignified cells remains (Fig. 26). The rupture of these parenchyma cells allows the stigmatic disc to bend, lifting its margins higher from the ovary wall. The separating of cells, followed by the dehydration and rupture of other cells, soon completes the process of dehiscence, and the ovary cavity is exposed. As soon as the ovary cavity is exposed to the air, the remaining cells of the placentae dehydrate and die leaving the seeds free in the ovary cavity.

The remains of the ruptured parenchyma tissue in the ovary wall show no indication of that tissue's former relationship to the

separation layers (Fig. 25). The dehydration and rupture of the cells in the ovary wall result in small pores extending into the ovary cavity (Fig. 26). The inner epidermis of the ovary has become lignified during the process of dehiscence and still persists, bending toward the outer surface of the capsule (Figs. 25 and 26). The bending of the inner epidermis in this manner makes for a smooth surface over which the seeds can slide out from the ovary cavity, when the capsule is shaken by the wind.

The pores produced are separated by the fused ventral bundles. Were it not for this fact, and if dehiscence had developed through these bundles, then the opening process would be much like that found in circumscissile dehiscence, Rethke (8). However, in circumscissile dehiscence the parting of cells does not occur along a definite line, but follows the path of least resistance; while in poricidal dehiscence, as found here, the parting of cells occurs along a definite line formed by a double separation layer.

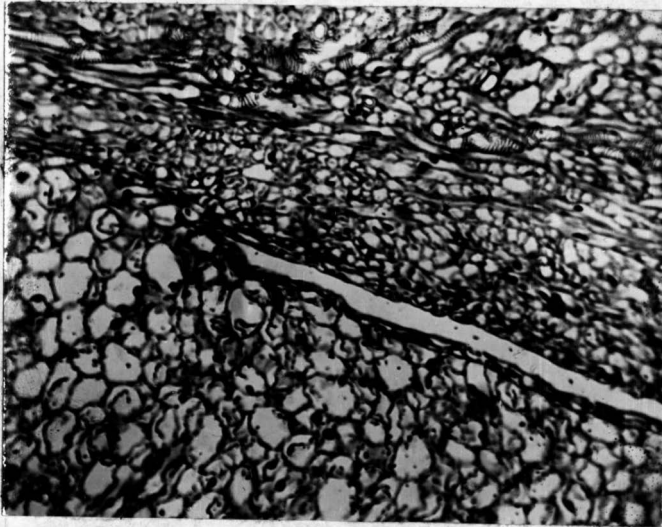


Fig. 23. Longitudinal section of the dehiscence, showing the smooth surfaces of the parting cells, (x120). There is no dehydration nor rupture of cells when dehiscence begins. Dehiscence begins because of the break-down of the middle lamella common to the separation layers.

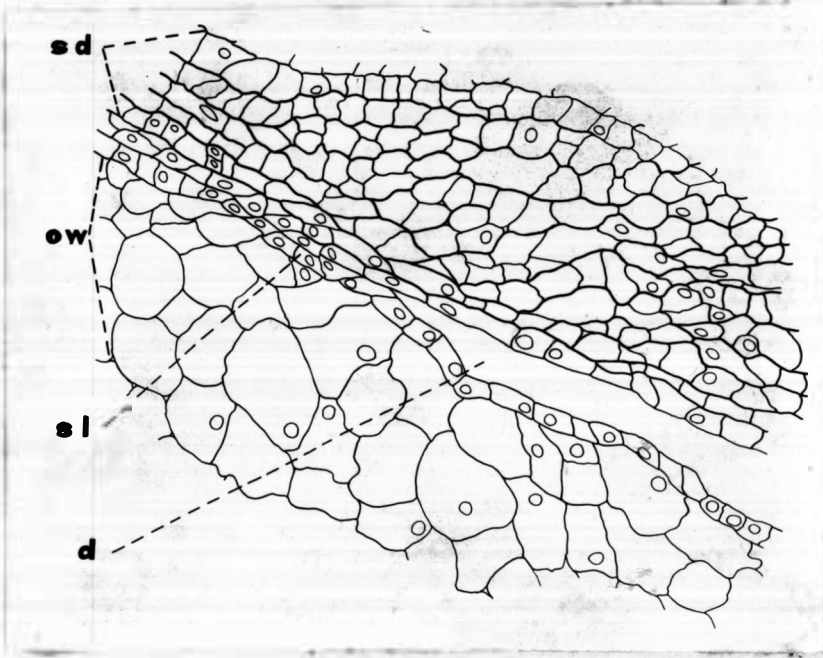


Fig. 24. Longitudinal section of a portion of the dehiscence as shown in figure 23, (x320). Parting of the separation layers is due to the breakdown of the middle lamella. d, dehiscence; ow, ovary wall; sd, stigmatic disc; sl, separation layers.

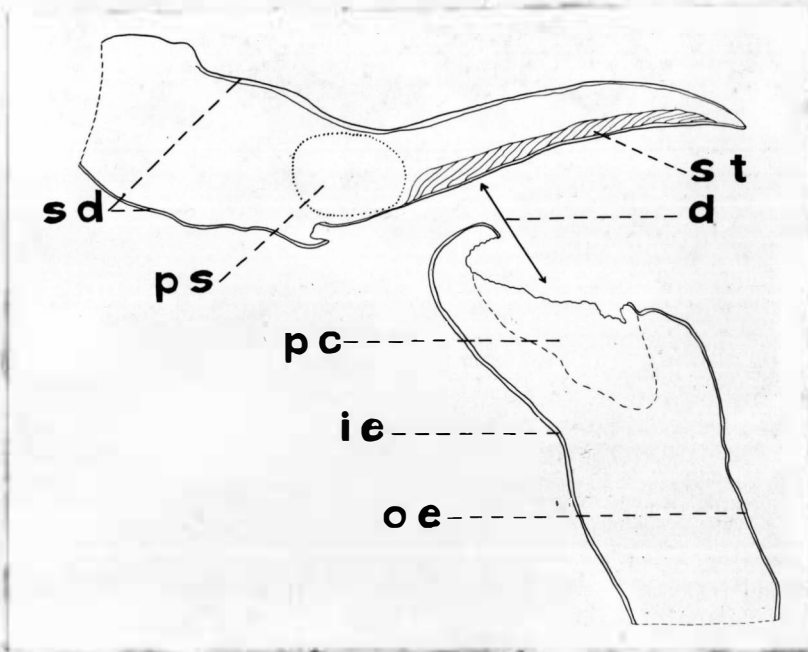


Fig. 25. Longitudinal section of a portion of the right side of a dehiscent capsule, (x10). d, dehiscence; ie, inner epidermis; pc, parenchyma cells; ps, parenchyma of stigmatic disc; sd, stigmatic disc; st, sclerenchyma tissue.

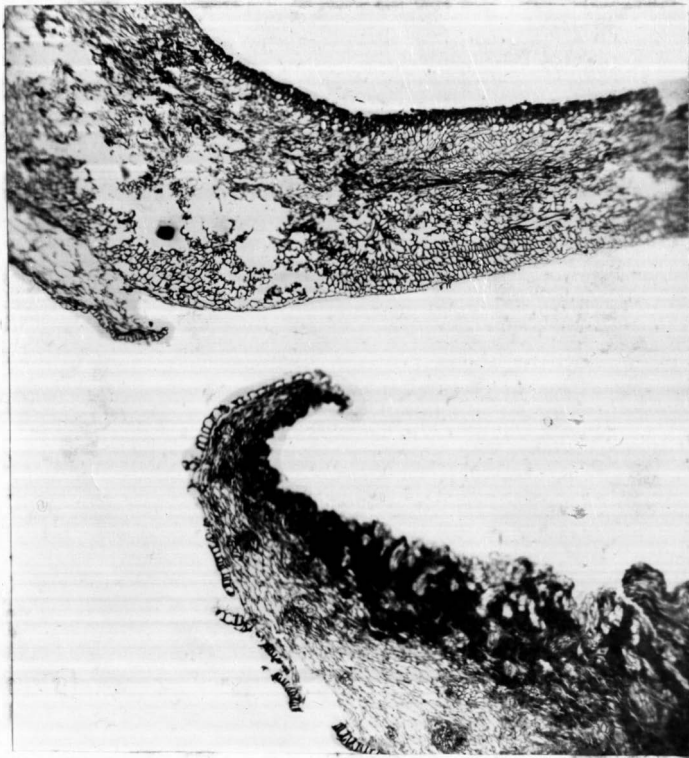


Fig. 26. Longitudinal section of a dehiscent capsule as shown in figure 25, (x24). The thin-walled parenchyma cells in the stigmatic disc are ruptured and only a framework of lignified cells remains. Dehydration and rupture of the parenchyma cells of the ovary wall have formed the pore into the ovary cavity.

DISCUSSION

The photomicrographs of transverse sections give evidence that the capsule is formed from a single whorl of carpels, all of the same type. The ovules are borne on placental outgrowths formed from the united, inrolled margins of adjacent carpels. This is the theory which, on the evidence of external features, has been adopted generally by systematists and has been opposed by Saunders (11). The dorsal bundles are reduced, not reaching as high as the stigmatic disc. The fused ventral bundles are highly developed in correlation with their function as the supply channels for the placentae and stigmatic disc. In figure 10, it can be seen that the fused ventral bundles separate into two parts at the base of the stigmatic disc. These parts pass into adjoining members of the disc, to which they belong. This is in agreement with Miss Arber's study of *Papaver Argemone* L.; *P. nudicaule* L.; *P. hybridum* L.; and *P. Rhoeas*.

There is complete continuity of cells between the ovary wall and the stigmatic disc, as shown in figures 9, 14, and 15. There is no separation of tissue due to valve carpels and solid carpels, as hinted by Saunders (11). The paired stigmatic rays are not continuous at the periphery of the stigmatic disc, since they belong to adjacent members. According to Saunders (10), "the ends of each pair of parallel stigmatic lines are continuous at the periphery of the stigmatic plate, so that they form a very narrow 'v', a shape we might expect if compression were accompanied by a shearing action forcing inwards, the tissues of the carpel lamina on either side of the midrib". This might be assumed from an external observation. However, by using histological methods, it is shown that the paired

stigmatic rays are not fused. Their surfaces are lined with papillae and they are only in close approximation to each other. This is clearly shown in figures 11 and 12.

The factor leading to dehiscence is the division of a layer of ovary wall cells immediately beneath the stigmatic disc. They divide and form a double separation layer totally unlike the procedures in other types of dehiscence. The dense, homogeneous cytoplasm common to all the cells of the double separation layer indicates a specialized kind of activity, certainly meristematic and probably digestive, at least so far as the middle lamella is concerned. Microchemical tests would give an interpretation of the chemical nature of the non-living constituents in the separation layers, and maybe of the protoplasm also.

Whether or not the formation of this separation mechanism should be considered a process of abscission in the sense usually understood may be questioned. When one mentions abscission, the implication is that some appendage is being cut off from the main body, because it has been so often associated with falling of leaves and fruits from trees. This concept is probably too narrow; it is due to the fact that observations of many other plant parts, which also form abscission layers, are often overlooked.

There are numerous investigations dealing with abscission of leaves, floral parts, fruits, and foliage branches. James and McDaniels (3), in relating abscission of floral parts to that found in leaves, say, "the abscission of floral parts is not markedly different from the abscission of leaves. A separation layer is formed, but not long in advance of the fall of the floral appendage, nor is there the

specialization and differentiation of layers associated with leaf abscission. However, the cells of the separation layer undergo changes similar to those found in leaf abscission".

Abscission is a process of cutting off of living cells in a special separation layer. This definition does not fit the mechanism found in the present investigation. There is a formation of two layers of cells into a special separation mechanism; however, there is no cutting off of any parts. The stigmatic disc remains attached to the ovary after dehiscence is completed.

This is the third investigation of dehiscence to come from this laboratory. The first was an investigation of *Portulaca grandiflora*, by Rethke (3). It opened a relatively new line of study in this country. He described circumscissile dehiscence as due to the formation of a zone of weakness provided by the disorganization of parenchyma tissue and the alignment of cells. Splitting does not occur along a definite line, but follows the path of least resistance. In circumscissile dehiscence of *Portulaca grandiflora*, there is a complete separation of two parts of the capsule. The splitting force separating the lid from the base, is provided by the development and expansion of many seeds in the ovary cavity.

Although numerous seeds are produced in the *Papaver orientale*, they are not a contributing factor in the process of dehiscence. Preserved material of capsules with separation layers developed, were allowed to dry and they gave complete dehiscence at the end of one hour. When preserved material of young capsules, before the formation of the separation layers, were allowed to dry, a shrunken capsule resulted with no sign of dehiscence. In the former case, the seeds

along with the tissues of the capsule had been fixed and killed, and yet upon drying, dehiscence occurred without any pressure being exerted from developing seeds.

The second investigation of dehiscence from this laboratory was by Holden (5). In this investigation of the pod fruit of *Astragalus canadensis*, it was found that two zones of dehiscence are formed. One zone is formed in the former ventral suture where a path of parenchyma is bordered on two sides by fibers. The other zone is formed in the tip of the dorsal bundle by a strand of cells remaining parenchymatous in the center of the fibers capping the dorsal bundle. The splitting of the pod is the result of vertical and horizontal strains set up by differential drying of the parenchyma tissue which surrounds the sclerenchyma areas. Such strains bring about the rupturing and tearing of cell walls.

The dehiscence of the *P. orientale* capsule is not a result of tensions, which are set up by differential drying and disruption of tissues along previous lines of fusion, nor is there any separation of carpels from one another. The pores occur wholly within the individual carpels.

Dehiscence is the result of the parting of a double separation layer around the top of the ovary, interrupted only by the ventral bundles, which are left separating the pores. The middle lamella common to the cells of the double separation layer become functionless, and the cells separate. Differential drying of tissues is secondary. It helps complete the process of dehiscence, but does not initiate it.

SUMMARY

1. The capsule consists of a single whorl of identical carpels, which are equal in number to the placentae, and the double stigmatic rays.

2. In the ovary, adjacent carpels are fused along the ventral surfaces of their inrolled margins, and the placentae represent extensions from these united edges; a placenta is thus duplex in origin.

3. The stigma portions of the carpels are not fused together, but lie in close approximation to each other by the papillae lining their edges.

4. A separation mechanism is formed in the capsule after fertilization, when cells at the apex of the ovary wall divide and form a double layer of isodiametric cells.

5. Dehiscence begins with the parting of the double separation layers due to the break down of the middle lamella.

6. Lignified sclerenchyma tissue developed in the stigmatic disc above the separation mechanism forms a rigid structure which lifts up and away from the ovary wall as the cells of the separation layers part.

7. Dehydration and rupture of the thin-walled parenchyma tissue beneath the separation layers occur and in so doing, form pores into the ovary cavity.

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