A MORPHOLOGICAL STUDY OF THE FLOWER AND EMBRYO OF SPIRAEA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXVI.

JONATHAN E. WEBB.

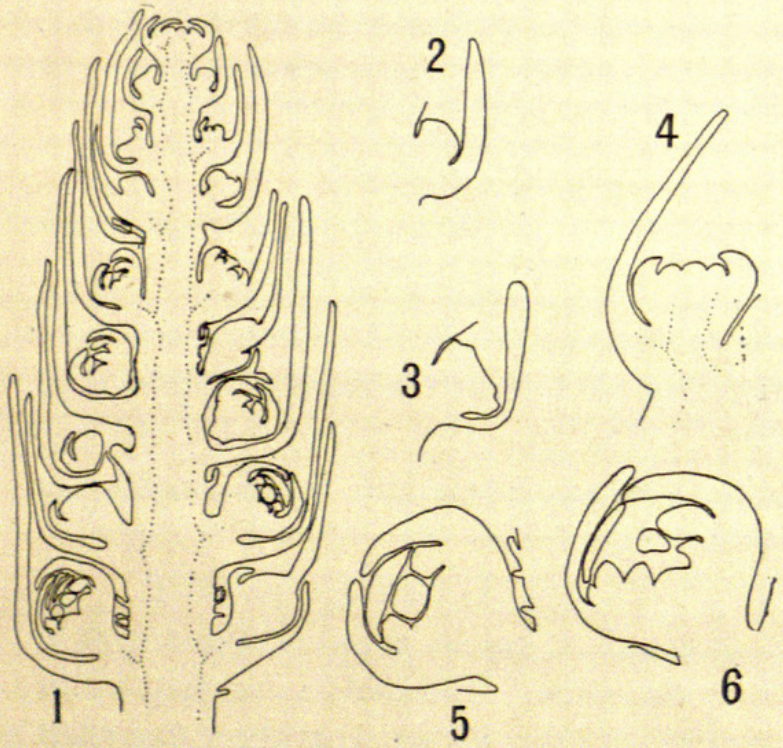
(WITH TWENTY-EIGHT FIGURES)

THE material used in preparing this paper was obtained largely from the Washington Park greenhouse, Chicago. Specimens of *Spiraea salicifolia* in various stages of development were secured from Grand crossing and East Chicago, Illinois, and from Marquette, Michigan. The species chosen for study was *Spiraea Japonica*, and this was supplemented by *S. astilboides planiflora* and *S. salicifolia*. Specimens were killed in chrom-acetic acid, Carnoy's mixture, and Flemming's mixture. All material was imbedded in paraffin, cut in serial sections with a microtome, and stained on the slide. Delafield's haematoxylin alone or in combination with erythrosin or iron alum was used chiefly, but cyanin and erythrosin, or the safranin, gentian-violet, orange G combination were used in certain cases. The Carnoy mixture was perhaps the most useful in every respect as a killing agent, and gave very satisfactory results.

ORGANOGENY OF THE FLOWER.

Spiraea affords an excellent opportunity for the study of the development of floral organs, as a longitudinal section of a spike gives many stages (*fig. 1*). At an early stage the rudiment of the flower appears as a protuberance in the axil of a bract (*fig. 2*). Five rather narrow ridges arise on the margin of this protuberance, and these ridges are the beginnings of the sepals, two of which are shown in section in *fig. 3*. Next there appears within this circle of ridges a whorl of papillae, the beginning of the inner five stamens, each opposite a sepal, and that this whorl does follow next is shown by the greater development of stamens

in that position (*fig. 10*). Immediately the third whorl of papillae appears, the individual members alternating with the second, and forming the second cycle of stamens, smaller and shorter than the first, and at a greater distance from the floral center (*fig. 9*). Contemporaneously with the second whorl of papillae, and while the first three whorls have as yet merely roughened the surface of the floral protuberance, two ridges, each strongly curved and with concave parts facing each other, arise at the center of the receptacle (*fig. 7*). These ridges fail to develop on the inner face except at their extremities, and the result is two carpels with cavities facing each other and nearly filled by the large development of the ridge-ends, which form the placentae. The transverse sections in *figs. 8* and *9* show this cavity, and how it is filled by the placentae before the development of the ovules. Although there are five carpels in *Spiraea salicifolia* and two in *S. Japonica*, leaving opportunity for variation from two to five, no evidence was found of the rudi-



Spiraea Japonica.

FIG. 1.—Longitudinal section of a young spike, showing floral development. × 23.

FIG. 2.—Floral papilla in the axil of a bract. × 54.

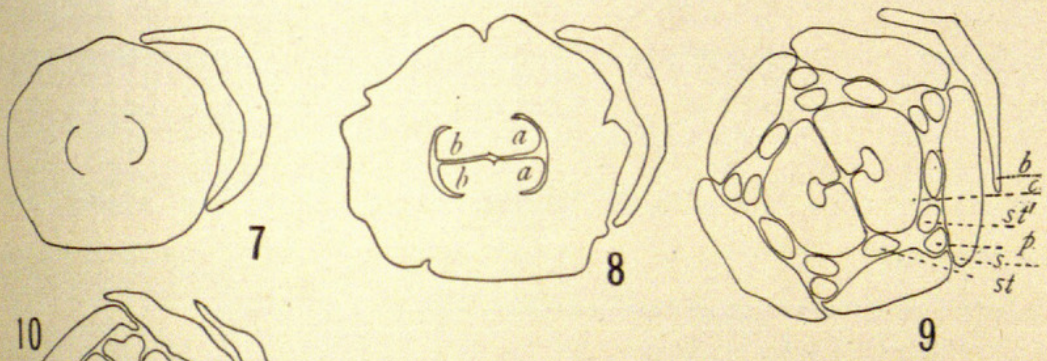
FIG. 3.—A later stage showing first appearance of sepals. × 54.

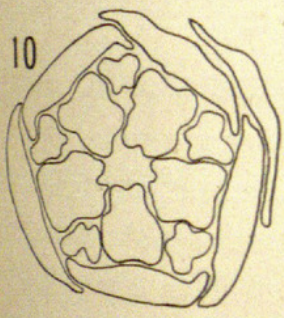
FIG. 4.—A stage showing sepals and stamens. × 54.

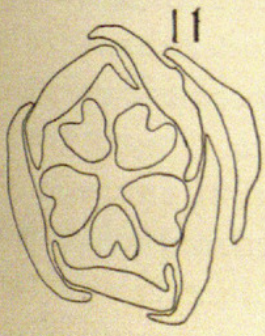
FIG. 5.—Longitudinal section passing through one side of the center of a flower, showing three stamens. × 54.

FIG. 6.—A longitudinal section of the same flower exactly through the center, showing that the capillary cavity is not yet closed above, and showing first appearance of petals. × 54.

ments of more than two carpels in the latter species. Once the form of the carpel is established, a rather uniform enlargement of all parts gives the necessary room for the many ovules. At the stage indicated in *fig. 9* the last cycle of floral parts, that of the corolla, has appeared, the petals alternating with the sepals, and lying just within their edges.







Spiraea Japonica.

FIG. 7.—Transverse section of flower at the base of the carpellary layer. × 54.

FIG. 8.—Section of same flower at point of maximum development of placenta; *aa*, *bb*, the ends of the two ridges enlarged, thickened, and curved. × 54.

FIG. 9.—Transverse section immediately above the plane of insertion of stamens and petals upon the receptacle; *b*, bract; *s*, sepals; *st*, stamen of the inner whorl; *c*, carpel; *st*, stamen of the outer whorl; *p*, petal. × 54.

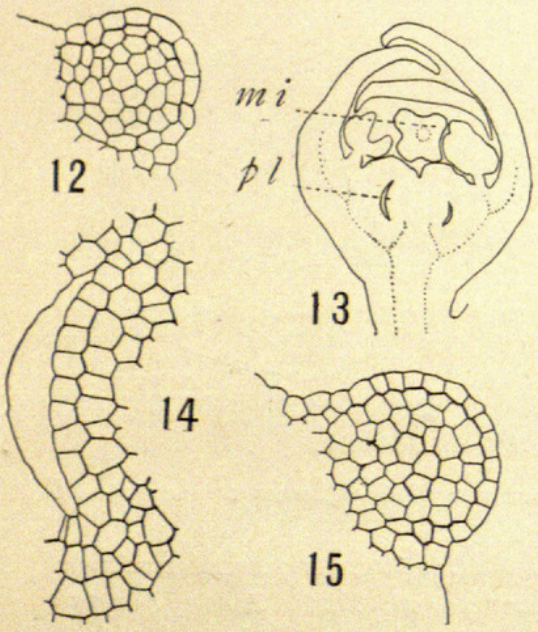
FIG 10.—Transverse section immediately above the top of the carpels, with ten stamens in section. × 54.

FIG. 11.—Transverse section near top of the largest stamens. × 54.

This development of floral parts in Spiraea shows that the order is as follows: sepals, inner stamens, carpels and outer stamens, petals (*figs. 9, 10*).

The development of microsporangia and megasporangia is rapid, and maturity is reached in a week or two; the megasporangia, however, attain their full development later than the microsporangia. At an early stage the anthers have, to some extent, become rounded and enlarged, while the carpellary cavity even has not yet been closed over above (*fig. 6*). Again, when the four microsporangia of an anther are well marked, the

placentae are still wholly undifferentiated (*figs. 14* and *15*). The ovules are yet without integuments at a time when the microsporangia have a well marked tapetum and the sporogenous tissue has neared the spore mother cell stage (*figs. 17* and *18*). The initiation of the integuments on the ovules occurs at the time of the tetrad stage of the microsporangia, or while the pollen grains are separating and becoming round, and before the dominant megaspore has been determined. At this stage the microsporangium is inactive until the pollen is shed.



Spiraea Japonica.

FIG. 12.—Transverse section of a young stamen, showing homogeneous character of the archesporial mass. × 54.

FIG. 13.—Section through center of flower after carpellary cavity is complete, showing placenta; *mi*, microsporangium; *pl*, placenta. × 54.

FIG. 14.—Longitudinal section through placenta of same flower. × 350.

FIG. 15.—Microsporangium of same flower. × 350.

THE MICROSPORANGIUM.

In the development of the flower the second whorl of papillae to arise on the receptacle is that of the stamens. These papillae early become stalked below, enlarged and rounded above. In Typha[1] this enlargement does not occur until much later. While the placenta is still composed of large, undifferentiated cells, and before the appearance of the ovules, the microsporangia have attained their characteristic quadrilocular form, and the epidermal layer is separated from the hypodermal by heavier walls (*figs. 12* and *15*). This is the first differentiation of any kind in the cells of the microsporangium, characterized by size of cells, thickness of cell walls, or depth of stain; and no archesporial cell or plate of archesporial cells appears at any stage in a close

[1] SHAFFNER, BOT. GAZ. **24**: 94–95. 1897.

series of preparations. Shortly thereafter the peripheral layer of the hypodermal mass may be distinguished by its lighter color and incipient periclinal division, which results in two narrow layers of cells derived from the archesporial tissue, as shown in *fig. 18*, the latter showing this division of the hypodermal layer partially completed, and with no precise differentiation of the cells of the included sporogenous mass. For although the separation of tapetum from sporogenous tissue has already been made, there is nothing which shows this conclusively but the peripheral position of a layer of cells, and the number of cells in a cross section equal, as it is, to the number in later stages. On the other hand, the cells of the tapetal cylinder clearly show by their shape and intimate association with those of the central sporogenous mass that the origin of tapetal and sporogenous cells is one. The chance of position alone keeps the former from being sporogenous cells. Their position, however, compels them to act as purveyors of nutrition to the other sporogenous cells, a task for which they are eminently fitted by their kinship. Yet by the very accomplishment of this task they are so changed as to be incapable of acting, like their sisters, as spore mother-cells.

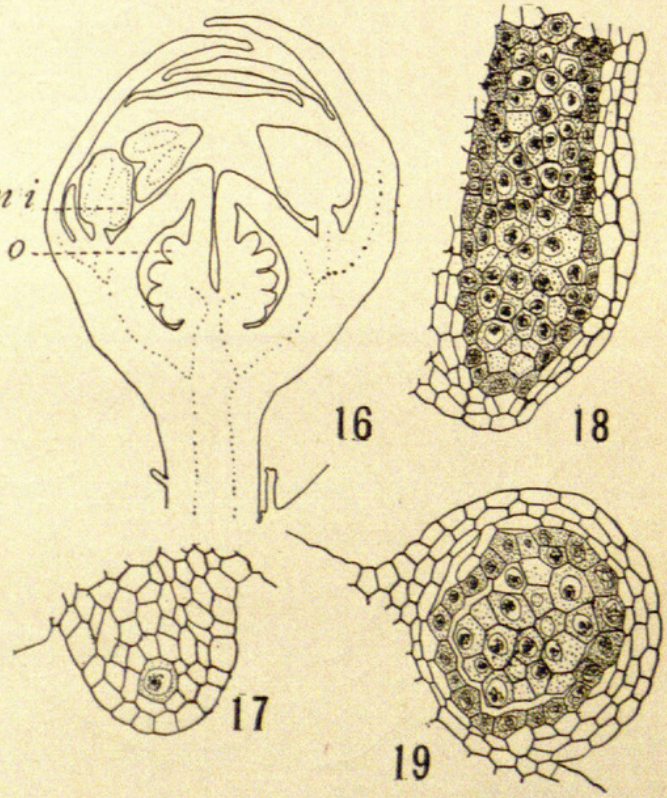


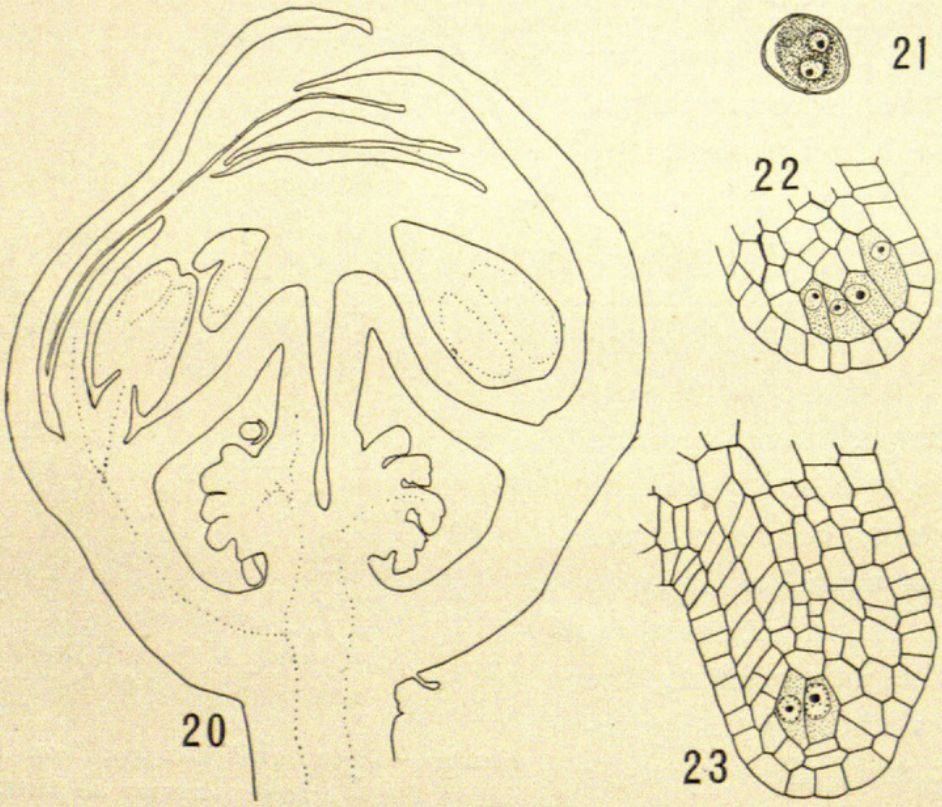
FIG. 16.—*Spiraea astilboides planiflora.* Longitudinal section of a flower, showing all parts, including petals and ovules; *mi*, microsporangium; *o*, ovule. × 54.

FIG. 17.—Ovule of same section, with tapetum cut off. × 350.

FIG. 18.—Microsporangium of same section, with division to form the endothecium. × 350.

FIG. 19.—*Spiraea salicifolia.* Transverse section through microsporangium with well developed tapetum. × 350.

Although such an explanation of the tapetal layer is impossible for many microsporangia, as in Cnicus,[2] yet its possibility has been suggested by Coulter in Ranunculus.[3] By gradual changes the tapetal layer is clearly differentiated from the spore mother-cells until it stains more deeply, has a more homogeneous appearance, and acquires a tendency to separate from the spore



Spiraea Japonica.

FIG. 20.—Longitudinal section through flower with all parts represented and showing beginning of the integuments. × 54.

FIG. 21.—Pollen grain with two nuclei at time of shedding. × 550.

FIG. 22.—Longitudinal section of young ovule with four archesporial cells. × 550.

FIG. 23.—Longitudinal section with the first layer of tapetal cells and two potential megaspore mother-cells. × 550.

mother-cells, although several cells in the layer might from their appearance be either tapetal or sporogenous (*fig. 19*). This stage is followed by the thickening of the tapetum, until it becomes a layer rich in food material, homogeneous throughout,

[2] COULTER, Contributions to the life history of Ranunculus. BOT. GAZ. **25**: 73–88. *pls. 4-7.* 1898.

[3] COULTER, *ibid.*

surrounding the spore mother-cells in a late synapsis stage, and itself surrounded by two layers of narrow, lightly staining wall cells. This condition persists for some time as regards the tapetum, until one of the wall layers is absorbed and the other has become very much thickened at the stage of the division of the spore mother-cells into tetrads; then the microspores round up, and at the time of shedding they have disorganized the tapetal cells and have absorbed their contents. Of the two layers between tapetum and epidermis, mentioned above, the inner has now disappeared, having been absorbed by the tapetum for the benefit of the sporogenous tissue. The outer or endothecium has become a thick layer by reason of the enlargement of its cells in which the nuclei are not conspicuous, but the walls have characteristic thickenings. At this stage there are two nuclei in the pollen grain (*fig. 21*).

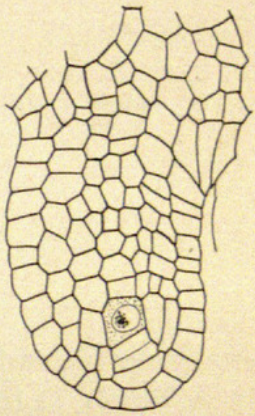


FIG. 24.—*Spiraea Japonica.*—Longitudinal section through an ovule showing a row of three tapetal cells and one large megaspore mother-cell. × 550.

THE MEGASPORANGIUM.

The comparative rate of development of stamens and ovules has already been stated. Long-before the appearance of the integuments, and while the ovules are but slightly developed on the placenta, several hypodermal cells at the tip of the ovule become enlarged, and their nuclei differ in size and arrangement of contents from those of neighboring cells (*fig. 22*). This mass of archesporial cells in the ovule of Spiraea is comparable to that found in *Rosa livida* by Strasburger.[4] Ensuing periclinal division results in forming two masses, the hypodermal being the tapetal mass, and the other the sporogenous mass. Successive divisions of the cells of the tapetal layer by periclinal walls result in adding much to the length of the ovule and the distance from the sporogenous tissue to the epidermis. Periclinal divisions in the epidermis itself also add to the length of the ovule

[4] STRASBURGER, Angiospermen und Gymnospermen. 1879.

(*fig. 25*). This method of division causes a radial appearance in a longitudinal section from the region of the embryo sac to the micropyle, which has been figured for *Rosa livida* by Strasburger,[5] and occurs in other members of the rose family, such as *Pirus Malus*. There are variations in the number of megaspore mother-cells which enlarge for division. This number is usually one, but often two or three begin to divide, and then

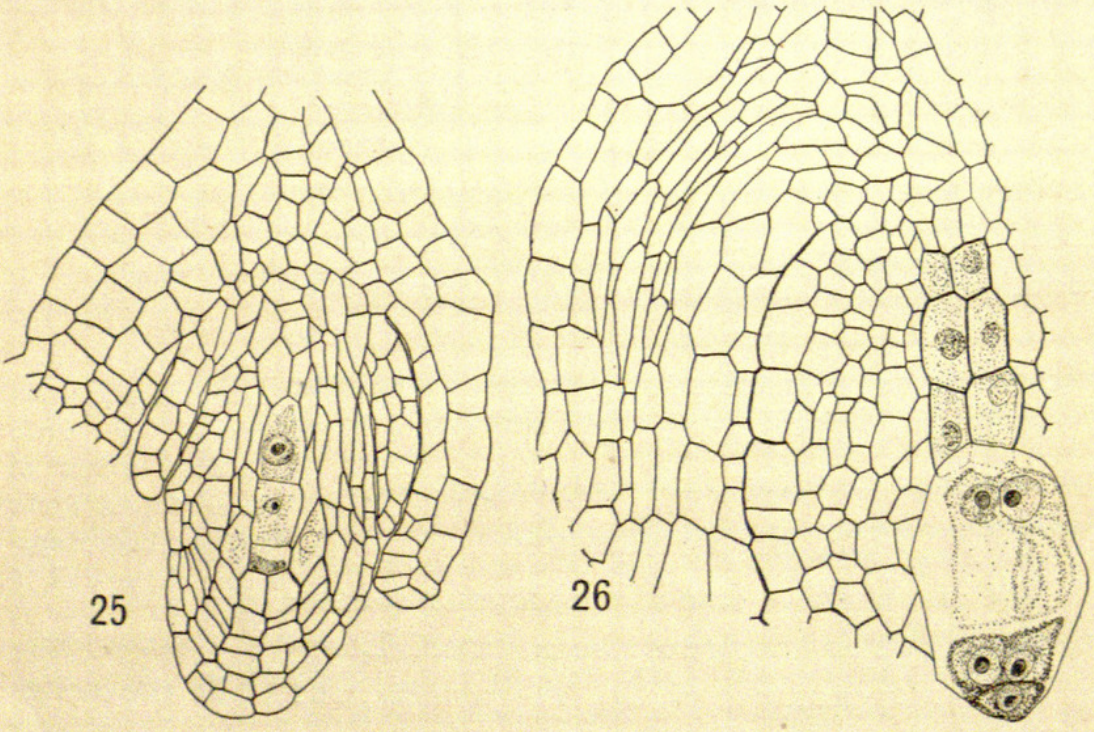


FIG. 25.—*Spiraea Japonica*. Longitudinal section of an ovule with integuments, large tapetal development, three large potential megaspores, and several megaspores breaking down. × 550.

FIG. 26.—*Spiraea Japonica*. Longitudinal section of mature embryo sac normally developed, showing thick nutritive cells in the chalazal region. × 550.

all but one break down. The successful megaspore is the one nearest the chalazal end of the sac, and it may be one of two, three, or four (*fig. 25*). It is very seldom that a megaspore nearer the micropyle shows any signs of reaching the fertilization period, although this doubtless happens in some cases, as is indicated by *fig. 27*, in which the megaspore nearer the micropyle has begun to develop, and is evidently the one which will reach maturity.

[5] STRASBURGER, *ibid.*

The embryo sac follows the normal order of development, and at an early stage there occurs a thickening of cells in the chalazal region adjacent to the megaspore (*fig. 26*), and this spreads until it includes the whole of the layer of integument adjacent to the nucellus (*fig. 27*). At this stage the contents of the embryo sac are rich in food material, especially starch.

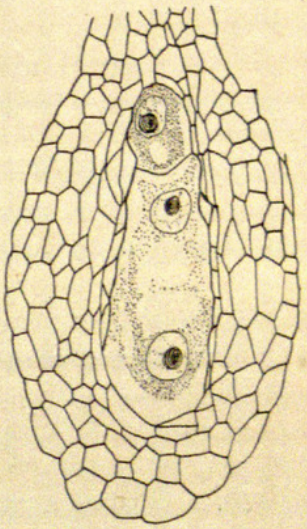


FIG. 27.—*Spiraea Japonica.* Megasporangium in which two megaspores of the same row, resulting from one division of the megaspore mother-cell, have begun to develop, with the micropylar spore ahead. × 550.

THE EMBRYO.

In reference to the embryo, it need only be said that the development is regular and normal, and that the suspensor, unlike that of the legumes, but in accordance with typical illustrations of suspensors, consists of but a single row of cells of no extraordinary size (*fig. 28*). Their purpose is evidently that of directing the food supply derived from the embryo sac, and supplied by the endosperm, which surrounds or clings to the embryo at this stage, to the embryonic root region.

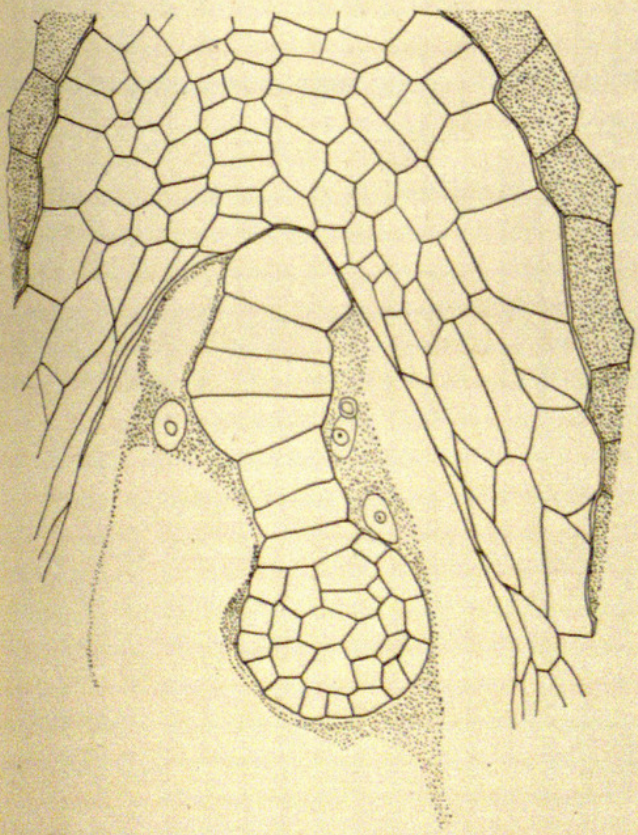


FIG. 28.—*Spiraea Japonica.* Longitudinal section through a young embryo with simple suspensor. × 550.

CONCLUSIONS.

1. The order of floral development is as follows: sepals, inner stamens, carpels, outer stamens, petals.

2. The microsporangia reach maturity before the megasporangia.

3. No archesporial cell or plate of archesporial cells is differentiated in the microsporangium.

4. The tapetum is cut off from the outside of the sporogenous mass.

5. Several archesporial cells are differentiated in the megasporangium. These cut off tapetal cells, by the divisions of which the megaspore mother-cells become deep-seated.

6. The megaspore mother-cell which is centrally located develops, and the megaspore near the chalazal end of the ovule is usually the successful one.

7. Enlargement of certain cells with thicker walls and denser staining contents takes place in the chalazal region of the nucellus as nutrition is supplied through these cells for the development of the embryo sac.

8. The development of the embryo is normal, and the suspensor is simple.

The work in preparation for this paper was done at the University of Chicago, under the direction of Professor John M. Coulter and Dr. Charles J. Chamberlain.

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