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Early Floral Development in Gaura coccinea

Edward Olson

EARLY FLORAL DEVELOPMENT IN GAURA COCCINEA

By

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A thesis submitted to the Committee on Advanced Degrees, South Dakota State College of Agriculture and Mechanic Arts, in partial fulfillment of the requirements for the degree of Master of Science.

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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.

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INTRODUCTION

Most flowers are hypogynous; the ovary is superior, being inserted on the tip of the torus. But there are nevertheless many flowers which are epigynous, the ovary being inferior, due to a deepening of the cup-shaped torus which may be continuous with the ovary.

The inner part of the ovary wall of epigynous flowers is generally considered to be carpellary, except in forms like the Compositae where ovules are cauline and only the roof of the ovary is carpellary.

The controversy then centers around the nature of the outer region of the ovary wall. Some investigators interpret this region as appendicular in nature, being formed by fusion of the bases of sepals, petals, and stamens with the ovary wall. Other investigators interpret the region as receptacular in nature, formed by the continuity of the receptacle and the ovary wall to form a receptacle cup.

Gaura coccinea, a member of the evening primrose family, is suitable for a study of epigyny in that the flower has a long hypanthium with the sepals, petals, and stamens diverging far above the ovary. The flower is polypetalous, the stamens are discrete, and the sepals are fused to each other along their margins, but not to other floral parts. Furthermore Gaura coccinea ranges from Manitoba to Texas and west to Alberta and California, and has not attracted the attention of floral morphologists. The purpose of this research is two-fold: first to discover the plan of organogeny, and second to discover the nature of the inferior ovary and therefore epigyny in this species.

LITERATURE

A review of the literature revealed a number of investigators who have made some contribution to the subject of floral development.

According to Eames (3) the flower is a determinate axis, appendages of which are like leaves. McCoy (9), Satina and Blakeslee (11), and Eames and MacDaniels (4) brought forward substantial information on the initiation of the floral organs by periclinal splitting of the cells in the inner tunica layer, and the further development of the floral primordia. McCoy (9) investigated Frasera caroliniensis, in which he found that the vegetative shoot and the floral apex consist of two histogens, a corpus and a two-layered tunica. All floral organs were initiated laterally by a periclinal splitting of the cells in the inner tunica. Satina and Blakeslee (11) worked on Datura stramonium which has three germ layers. The first layer forms the epidermis, and the second forms the primordia.

The nature of the inferior ovary has been one of the most debated subjects in floral morphology for over a century. Tillson (14) working on Kalanchoideae, Jackson (6) in a study of Rosa and certain related genera, Douglas (2) in a review of the literature, and Eames and MacDaniels (4), regard this region as appendicular in nature, being formed by fusion of the bases of sepals, petals, and stamens with the ovary wall. On the other hand; Langdon (8) in a study of the flower and fruit of the Fagaceae and Juglandaceae, Satina and Blakeslee (11) in their investigation of Datura, Wilson and Just (15) in their review of the morphology of the flower, and Henslow (5) in his book on the origin of floral structures, regard this area as receptacular, formed by the continuity of the receptacle with the ovary wall to form a receptacular cup. An investigation of Gaura should contribute to one or the other of these opposed interpretations.

INVESTIGATION

Inflorescences of Gaura coccinea were collected at Lake Campbell near Brookings, South Dakota, June 8, 1952. The inflorescences were dissected, flowers being taken from the tips of the axis of healthy plants. The flowers were killed and fixed in formalin-acetic-alcohol. Inflorescences and individual flowers are very pubescent, and the margins and top of the sepals in unopened buds fuse to each other forming an inverted cup over the floral meristem enclosing numerous air pockets. A centrifugal pump was used to remove the entrapped air in the case of inflorescences and also individual flowers. Treatment was according to the paraffin method, the dehydrating medium being butyl alcohol. Sections were cut from five to eight microns in thickness and stained in safranin and fast green, hematoxylin and orange G, and crystal violet, safranin and orange G. All drawings were made from permanently mounted sections by the use of a Spencer camera lucida.

The mature flowers of Gaura coccinea are in a simple spike and are light rose in color. The flower has its receptacular tube extended to nearly one half the length of the flower beyond the summit of the ovary. The receptacle is pubescent, being covered by long unicellular, non-glandular hairs. There are four sepals, which are long and slender and also covered with unicellular hairs. The petals are four in number, alternating with the sepals. The petals differ from the sepals in that the top half is expanded, and the distal end is rounded. At the base petals narrow down nearly to a filament. The petals are sparsely covered with unicellular hairs. The stamens are eight in number and are opposite the sepals and petals. The filament is long and narrows somewhat where it attaches just below the center of the anther. The ovary is continuous with the receptacle and is not seen externally. The style is formed by the fusion of the upper parts of the four carpels. It extends as high as the stamens, and is topped by four stigmas.

The first evidence of floral development is seen in the adult apex of the flowering shoot. This apex has a two-layered tunica, but its cells frequently show periclinal divisions; during the development of the floral primordium, divisions in the inner layer of the tunica are not always anticlinal. The greatest variability in cell divisions occurs during very early development, and in somewhat older floral primordia the layers of the tunica divide quite regularly (compare figs. 2 and 3).

After its initiation, the floral primordium is hemispherical in shape (fig. 2). Subsequently its apex widens, and just before sepal initiation its summit is flattened. Sepals are initiated at the periphery of the flattened top as is shown in fig. 2. At the time of sepal initiation, the floral apex still appears much like that of an ordinary vegetative shoot. It has a two-layered tunica, and the corpus as well as the tunica layers is meristematically active. The sequence of initiation of the floral appendages is: sepals, petals, stamens, and carpels. The primordium of the flower grows rapidly and soon becomes the largest part of the apical meristem.

Sepals are initiated at the margins of the floral primordium, when the latter is about seventy microns in diameter. The process follows a pattern now well established for development of floral organs of many of the dicotyledonous angiosperms. This process is as follows.

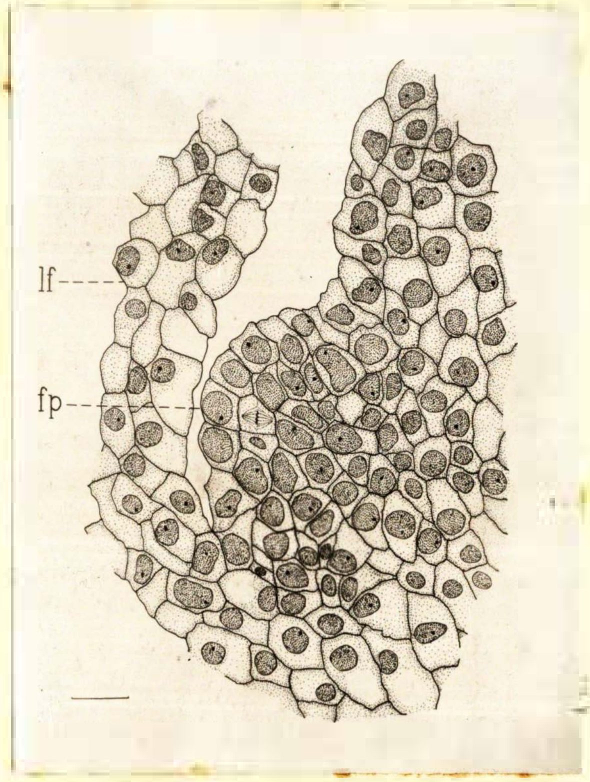

Fig. 1. Longitudinal section of a young floral primordium showing periclinal divisions in the inner tunica layer. X777. lf, leaf; fp, floral primordium.

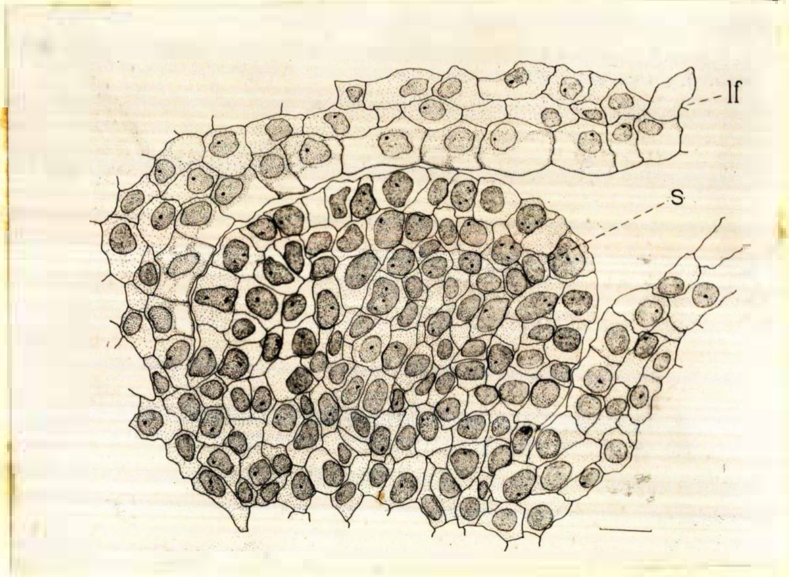

Fig. 2. Longitudinal section of an older floral primordium showing periclinal divisions in the initiation of a sepal. X700. s, first initiation of a sepal; lf, leaf.

The outer layer of the tunica divides only anticlinally, while periclinal divisions occur in the first and second layers immediately beneath it. Fig. 2 shows a flower just before the appearance of sepal primordia, with periclinal divisions appearing in the second layer of the tunica. Differentiation of the median procambial strand in the sepal primordium appears to be acropetal.

The four sepal primordia are initiated at about the same time, as is indicated by their nearly equal size in the early stages of development. (See fig. 4 which is nearly median for the sepal primordia.) Shortly after initiation the sepal primordia resemble young leaves in appearance (fig. 3). After a short period of growth the submarginal initials cease their meristematic activity, and the young sepal elongates by rapid growth in the apical region. Further development is intercalary, the internal cells acting as a meristem in which anticlinal divisions, vacuolation, and cell enlargement occur throughout.

The sepal primordia grow apically and curve sharply over the floral apex. Fig. 4 illustrates a sepal primordium which is still growing apically. Cell vacuolation begins on the abaxial side of the young growing sepal. Fig. 5 represents a transverse section of sepals which are in about the same stage of development as those shown in fig. 4. Further curvature of the sepals brings their apices together, and the epidermal cells of contiguous sepals dovetail so that the four become united throughout. Physical contact of the apposed sepals is brought about by marginal growth and the extension of the meristem to the whole circumference of the receptacle, and is followed by an interlocking of the epidermal cells accompanied by random mitotic divisions to form an inverted cup over the rest of the floral parts

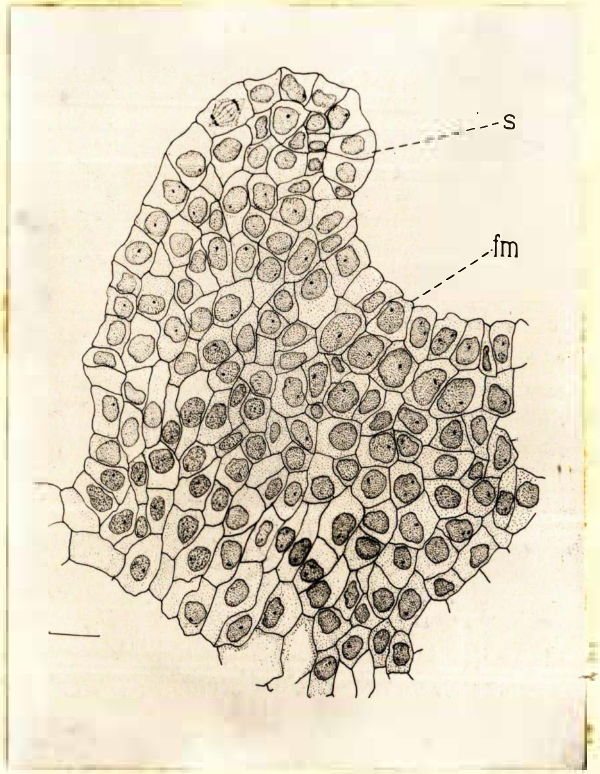

Fig. 3. A young sepal primordium shown in longitudinal section, the appearance is much like that of a young leaf. X700. s, sepal; fm, floral meristem.

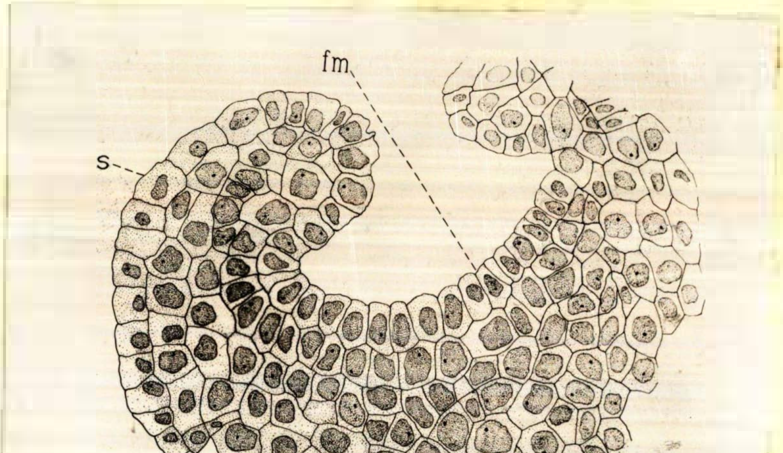

Fig. 4. Longitudinal section of somewhat older sepal primordia showing the sepals curving over the floral meristem. X700. s, sepal; fm, floral meristem.

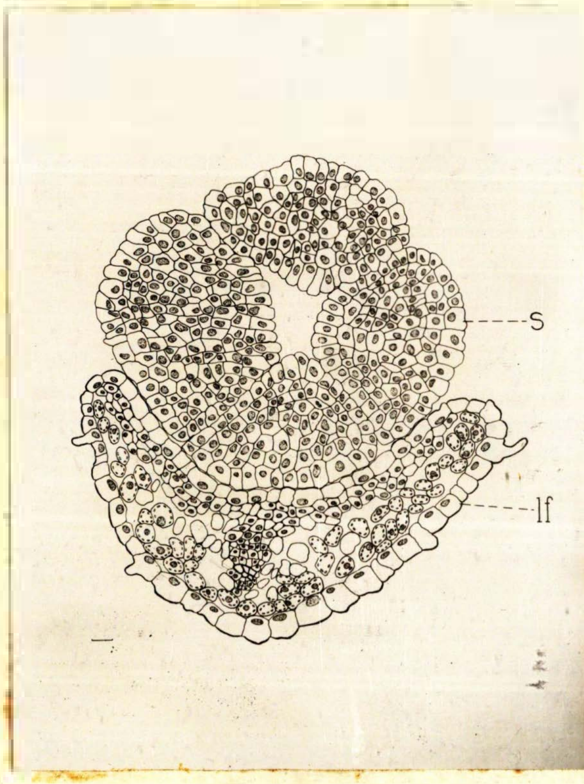

Fig. 5. Transverse section of young sepals and the subtending leaf, at about the same stage as fig. 4. X300. s, sepal; lf, leaf.

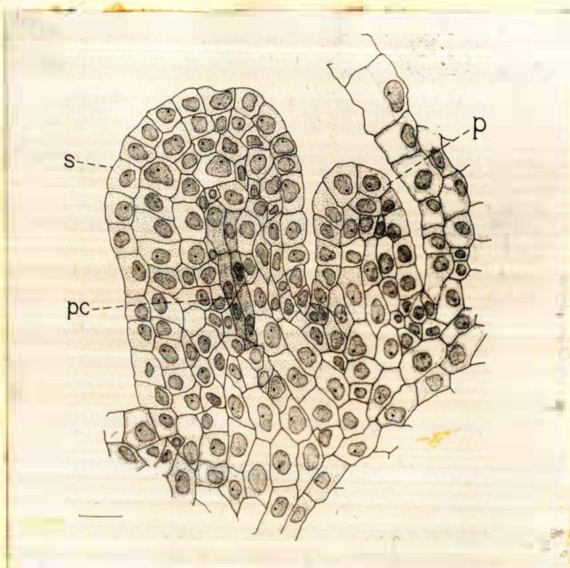

Fig. 6. Longitudinal section of young petal and stamen primordia. The stamen primordium shows the beginning of the procambial strand. X550. s, stamen; p, petal; pc, procambial strand.

(figs. 8, 9, and 18).

When mature, the epidermal cells along the margins and top of the sepals rupture, freeing the individual lobes. The mature sepal has a median vascular bundle with four laterals on either side, which are progressivly smaller towards the margins (fig. 31).

Petals are the next to arise and are initiated at the periphery of the floral meristem, just within the cycle of sepals. They are adaxial to, and alternate with the sepals. The size of the sepals when petals are initiated (fig. 4) indicates that there has been a time lapse between the two. Petal initiation is indistinguishable from sepal initiation in method. Initiation occurs when the receptacle is somewhat concave, and at about the same time as stamen initiation. The petals show several differences from the sepals in the later stage of development however; they do not have as long a period of localized growth as do the sepals, and do not curve over the floral meristem, nor fuse along their margins.

As in the case of the sepals, the earliest sign of petal initiation in a median longitudinal section of the floral axis is evidenced by periclinal cell divisions in the inner tunica layer (fig. 4). The general appearance of petals in the very early stages of their development is quite similar to that of the sepals. The mature petals have a median vascular bundle and two laterals, as shown in fig. 31.

Before the initiation of petals and stamens, which arise at about the same time, the floral meristem is approximately 110 microns in

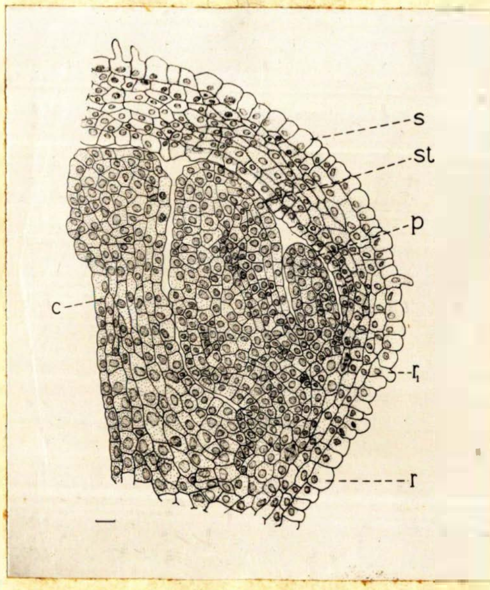

Fig. 7. Longitudinal section of the right half of a young flower showing sepal, petal, stamen, and carpel primordia. The receptacular tube is being started. Note the definite hypogynous character of the flower. X250. s, sepal; p, petal; c, carpel; r_1, upper receptacular tube; r, lower receptacular tube.

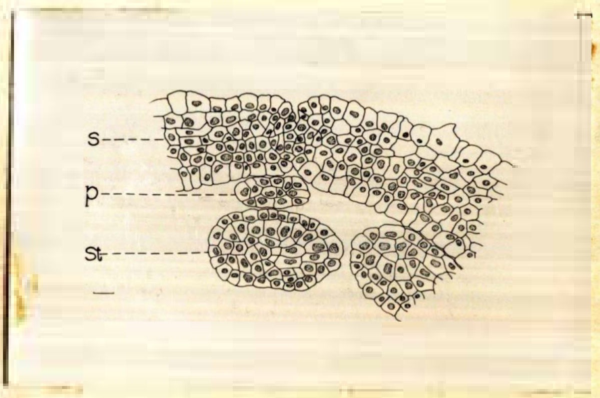

Fig. 8. Transverse section of sepal, petal, and stamen, at about the same stage as shown in fig. 7. The line of fusion between sepals is shown. X250. s, sepal; p, petal; st, stamen.

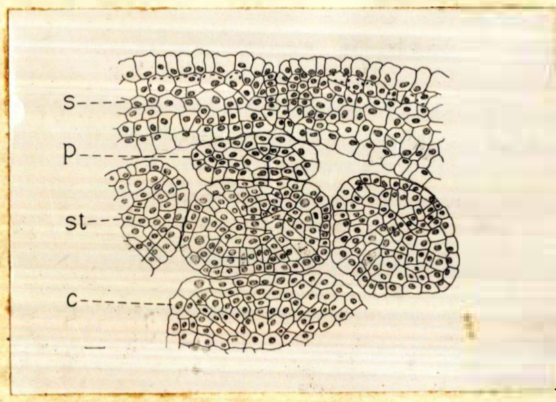

Fig. 9. Transverse section of a somewhat older sepal, petal, and stamen, showing a stage in the development of the stamen, and the line of fusion between the sepals. X250. s, sepal; p, petal; st, stamen; c, carpel.

diameter and the summit is concave. During petal and stamen initiation, it is still concave and shows a distinctly two-layered tunica (fig. 4). This concave feature of the floral meristem is brought about by early growth at the periphery of the receptacle, and is the area from which the hypanthium later develops.

Stamen primordia appear so soon after petal initiation that it is difficult to find sections which show petal primordia without stamen primordia. This indicates that the interval between the appearance of petals and stamens is much shorter than that between the appearance of sepals and petals. There are few observable differences, other than position, between sepal, petal, or stamen initiation, as may be seen in figs. 3, 4, and 6.

A procambial strand does not appear in the stamen primordium until the latter is quite well developed, and it is not traceable until the primordium is about 55 microns high (fig. 6). Even then the cells are not yet well differentiated. The procambial strand appears as a dark-staining row of cells surrounded by cells with lighter cytoplasm.

Fig. 7 shows that it is not difficult to differentiate stamen and petal primordia when they are seen in a near median longitudinal section of the young flower. A stamen primordium is thicker in proportion to its height than a petal primordium. Following initiation, the stamen primordium grows in length by means of apical and sub-apical initials. Soon after this the development of the sporogenous tissue begins and further growth is intercalary.

The epidermal layer of the stamen is derived exclusively from the outer layer of the floral apex. The hypodermal layer, which is a derivative of the inner tunica layer undergoes periclinal and anticlinal divisions and produces the sporangium wall under the epidermis of the stamen, part of the tapetum, and all of the sporogenous tissue.

Cell patterns in figs. 10 through 14 suggest the following sequence in divisions. In cross sections of a potential microsporangium, at the proper stage of development, there are two to four hypodermal cells, each of which divides periclinally (fig. 10). The inner derivative is a primary sporogenous cell. Primary sporogenous cells divide sparingly or not at all, and then differentiate into microspore mother cells. The outer derivative in forming the microspore mother cell divides either anticlinally or periclinally (fig. 11). When the first periclinal division occurs, it cuts off a primary tapetal cell and a primary parietal cell. The outer derivative of the hypodermal cell may give rise to one to four primary parietal cells. The primary parietal cell divides periclinally once or twice and each of its derivatives may divide anticlinally. The blocks of cells formed are shown in fig. 12. The microsporangium wall then is formed under the epidermal layer and from the derivatives of the primary parietal cells. The primary tapetal cells divide mostly in an anticlinal plane, thus forming a one layered tapetum when mature (fig. 13). As the microsporangium grows, the inner wall cells tend to collapse so that only two cell layers are conspicuous at the time the pollen grains are maturing (fig. 15).

While petals and stamens appear in quick succession, the size of the stamen primordia when carpels are initiated indicates that there is a time lapse between these two. The floral apex is flat to saucer shaped following stamen initiation and when carpels are initiated.

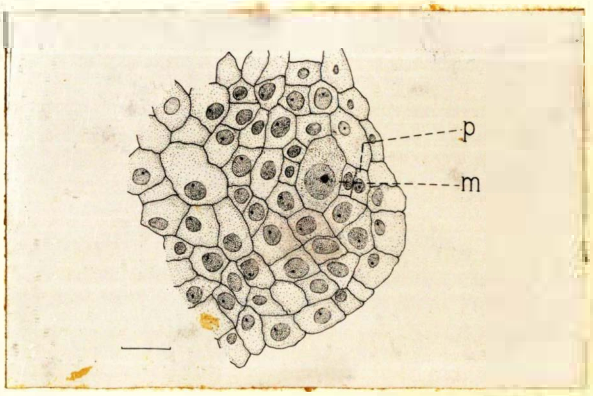

Fig. 10. Transverse section of a lobe of a young anther showing periclinal division of the parietal cells and a microspore mother cell. X605. p, primary sporangium wall cell; m, microspore mother cell.

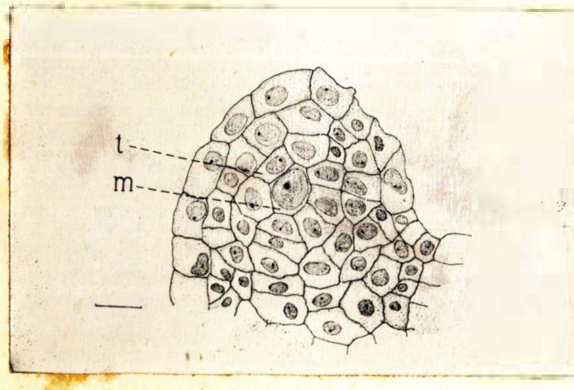

Fig. 11. Transverse section of a lobe of an older anther showing tapetal cells and a microspore mother cell. X605. t, tapetal cell; m, microspore mother cell.

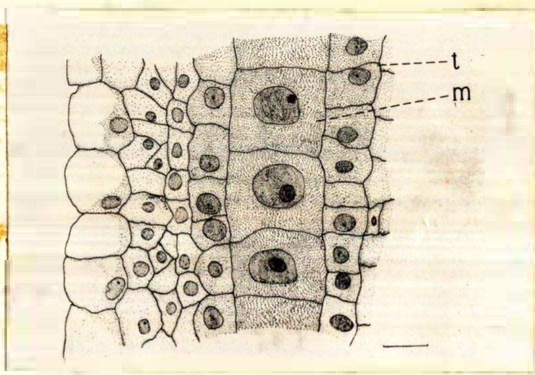

Fig. 12. Longitudinal section of a lobe of an anther showing epidermal, parietal, tapetal and microspore mother cells. X605. t, tapetal cell; m, microspore mother cell.

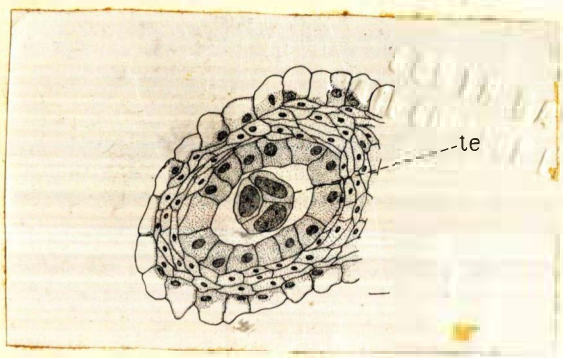

Fig. 13. Transverse section of an anther lobe showing a spore tetrad. X250. te, spore tetrad.

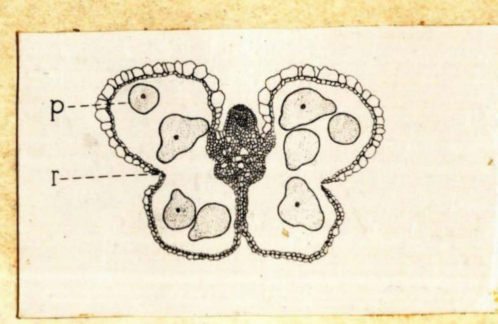

Fig. 14. Transverse section of a mature anther showing pollen grains. X20. p, pollen grain; r, point of rupture of the pollen sac.

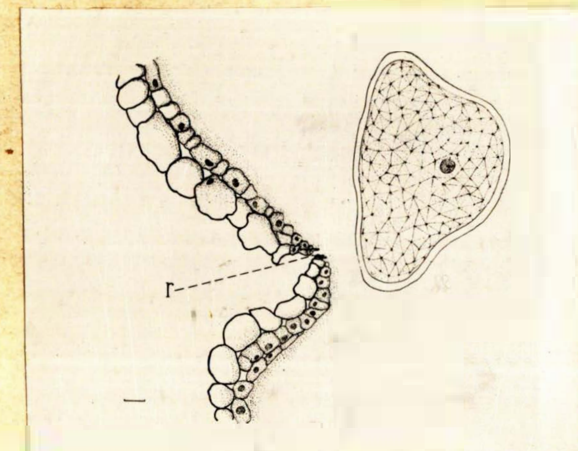

Fig. 15. Transverse section of a portion of fig. 14, showing a pollen grain, the point of rupture, and the nature of the mature anther wall. X250. r, point of rupture of the pollen sac.

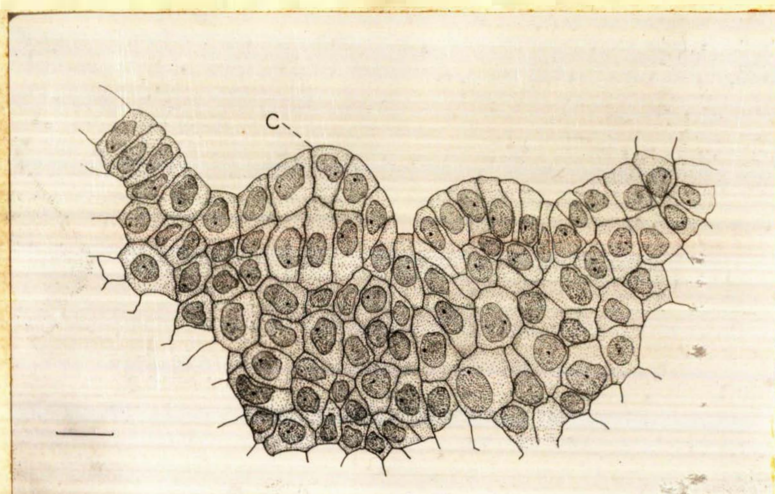

Fig. 16. Longitudinal section of young carpel primordia. X777. c, carpel primordium.

Early carpel development is similar to that of the other floral appendages, and a description would be repetitious. Following initiation in the inner tunica layer there is a short period in which growth is conspicuous (fig. 16). The carpel primordia grow toward each other until their tips touch (fig. 17), at which time the apical growth slows down. Marginal growth occurs at the lower portions of each of the four primordia so that the margins curve ventrally. The carpel bases are at first C-shaped in cross sections. They soon become closed by further marginal growth, and each is fused to its two neighboring carpels by the in-rolled dorsal surfaces. The carpels appear to be sunken into the floral receptacle; this is brought about by meristematic activity in the periphery of the receptacle. The carpels become united by an ontogenetic fusion which is so complete that the carpel limits are obscured (fig. 21). Continued marginal growth brings the four fused margins together in the center to form a central placenta. This results in an ovary with four locules (figs. 28 and 30).

Growth takes place at the upper extremities of the carpels (fig. 19), the result being the upward development, in the center of the perianth, of four styles which are fused along the surface of contact, except for the immediate center where there is a pollen canal (fig. 31). The stigma of each carpel is developed separately, so that the stigmas are not united as are the style and ovarian portions of the carpels.

Activity in the receptacle does not cease with the production of the floral primordia but elongates noticeably, carrying the sepals, petals, and stamens up and over the young ovary.

When first initiated, the receptacle is dome-shaped (fig. 1).

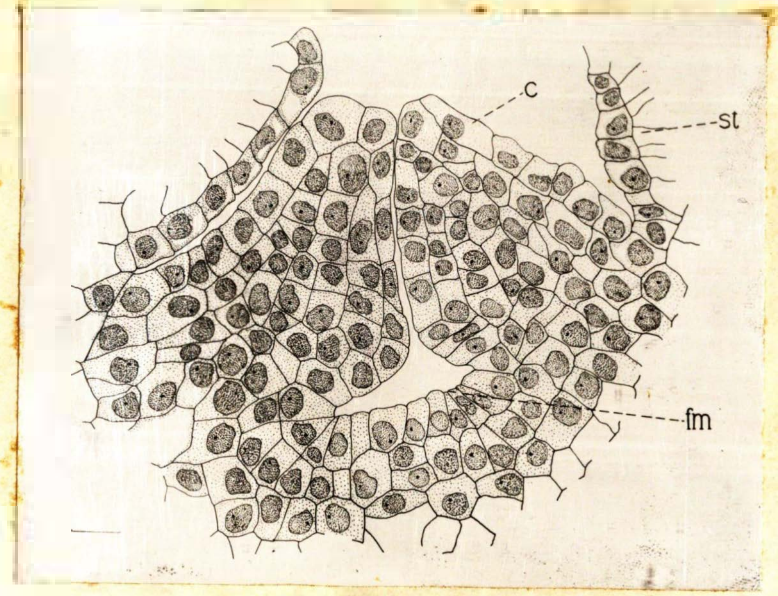

Fig. 17. Longitudinal section of older carpels, showing growth of the apicies toward each other. X700. c, carpel; fm, floral meristem; st, stamen.

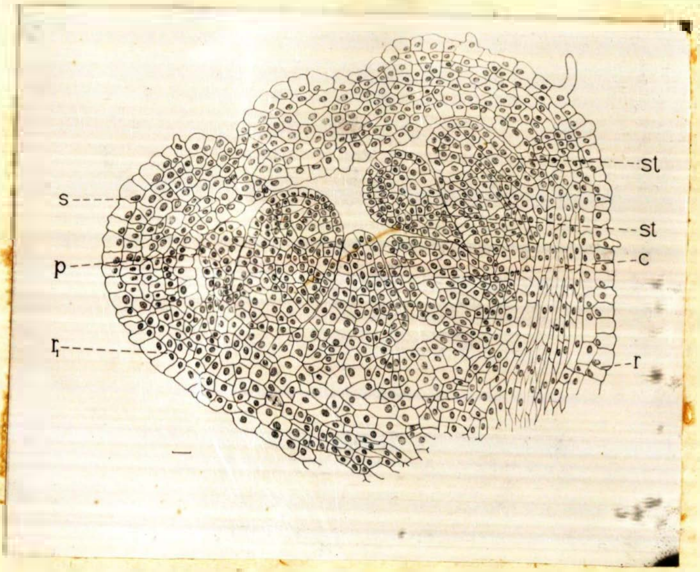

Fig. 18. Longitudinal section of a young flower, showing the upward elongation of the receptacle. X250. st, stamen; p, petal; s, sepal; c, carpel; r_1, upper receptacle tube; r, lower receptacle tube.

Subsequently the apex widens, and just before sepal initiation its summit becomes flattened (fig. 2). Before the initiation of the petals and stamens the receptacle is somewhat concave. This is brought about by early growth of the periphery of the receptacle, and is the area from which the hypanthium later develops.

In the early stages of development the flower is definitely hypogynous, since the sepals, petals, and stamens are attached to the receptacle below the carpels. The lower extremities of the young sepals, petals, and stamens may be seen by tracing their epidermal layers in fig. 7. The primordia are seen to arise distinctly separate on the receptacle, and no fusion is taking place to form an appendicular tube.

In referring to the receptacle tube, it is convenient to make a distinction between its two parts. The section of the receptacle above and free from the ovary is referred to as the upper tube: the lower tube is the part of the receptacle that is continuous with the ovary wall. The latter is the first to be formed. Soon after initiation of the carpel primordia, there is a renewal of zonal mitotic activity in that area of the receptacle beneath the sepals, petals, and stamens, with a checking of growth in that area beneath the carpels. This elongation under the sepals, petals, and stamens proceeds at about the same rate as does that of the developing carpels and attached receptacle (fig. 18). This leaves the locules embedded in the receptacle cup. Figs. 7, 27, and 29 show the continued growth in this area.

Fig. 22 is an enlargement of the receptacle that is continuous with the ovary wall, and is at about the same stage in development as fig. 18, in which carpel elongation is taking place. Fig. 23 represents

Fig. 19. Longitudinal section of older carpels showing the formation of the style. X300. c, carpel; st, stamen; r, receptacle.

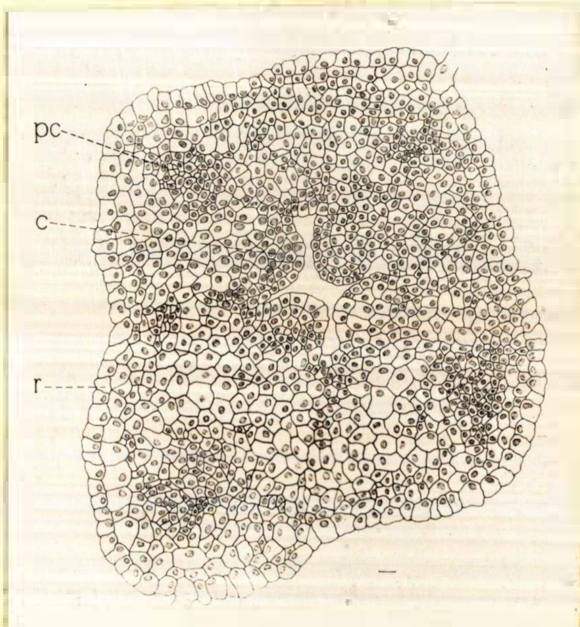

Fig. 20. Transverse section through the ovary showing the infolding of the carpel margins to form four locules. X197. pc, procambial strand; c, carpel; r, receptacle.

the lower receptacle tube, continuous with the ovary in a later stage of development, comparable to fig. 27, cell divisions are still taking place as well as cell elongation. Fig. 24 shows a section of the lower receptacle tube in an advanced stage, mitotic divisions are still taking place but have been restricted to the inner area of the receptacle. All further growth in this area is by cell elongation. The stage represented here is comparable to that in fig. 28. It is obvious then that sepals, petals, and stamens are being pushed upward by an elongation of the receptacle below them.

The upper receptacle tube is somewhat later in beginning its growth, as may be seen in fig. 18. This is the zone directly beneath the sepal, petal, and stamen insertion that is free from the ovary. The development of this upper tube is similar to that of the lower tube. Transverse cell divisions and elongation result in a lengthening of the receptacle in this area. The stage shown in fig. 25 and a later stage (fig. 26) show its rapid development. As the flower approaches the opening stage, meristematic activity becomes more and more restricted to the lower portion of the tube, and then all further lengthening is by cell elongation. Growth of this area does not cease until the flower approaches the opening stage.

DISCUSSION

The present investigation of the flower of Gaura coccinea discloses that the sepals appear first, then the petals develop within and alternate with the sepal lobes, followed by the appearance of the stamens. The carpels are last to appear and develop around the central portion of the receptacle.

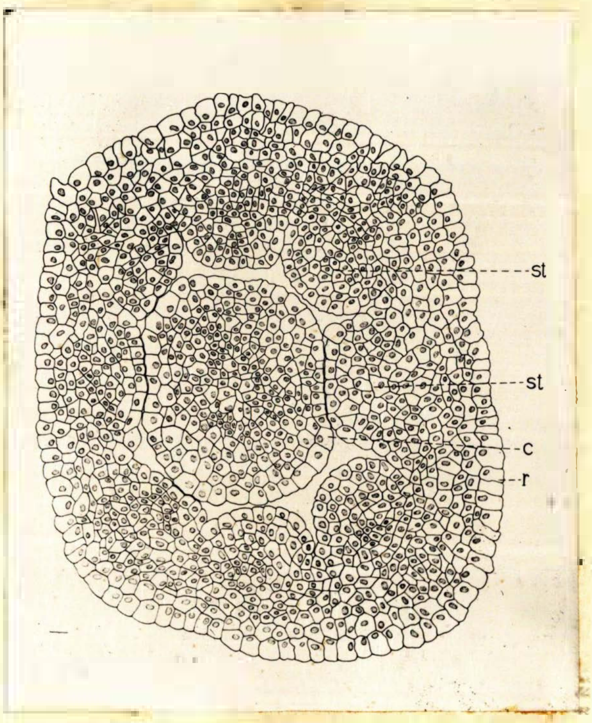

Fig. 21. Transverse section of a young flower at a level below stamen insertion on the receptacle, and showing the fused ends of the carpels forming the style. X197. st, area of stamen insertion; c, carpels; r, receptacle.

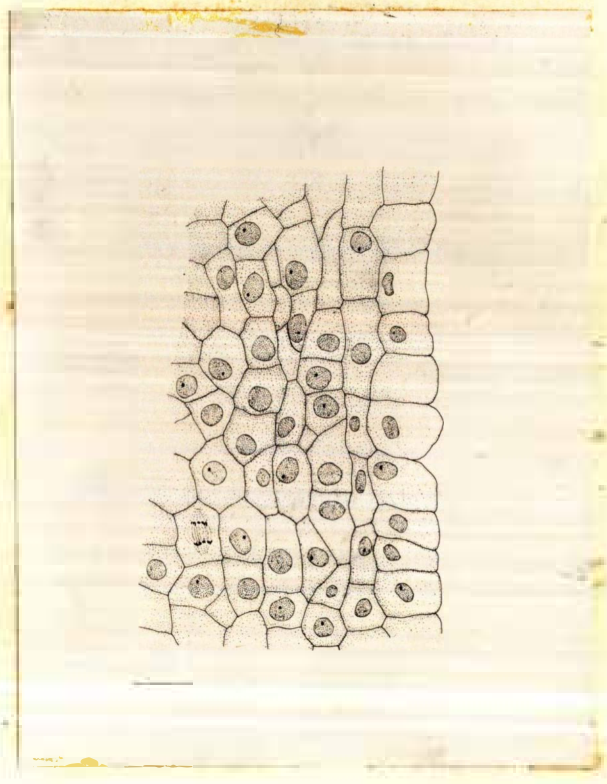

Fig. 22. Longitudinal section of a young receptacle at a level opposite the ovary. Note anticlinal divisions. X750.

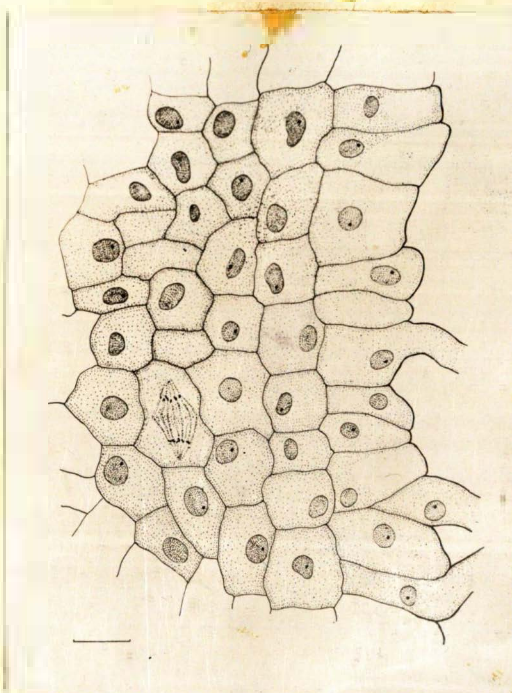

Fig. 23. Longitudinal section of an intermediate receptacle at a level opposite the ovary. Note anticlinal cell division and lengthening of the cells, vacuolation is beginning to take place in the outer cells. X750.

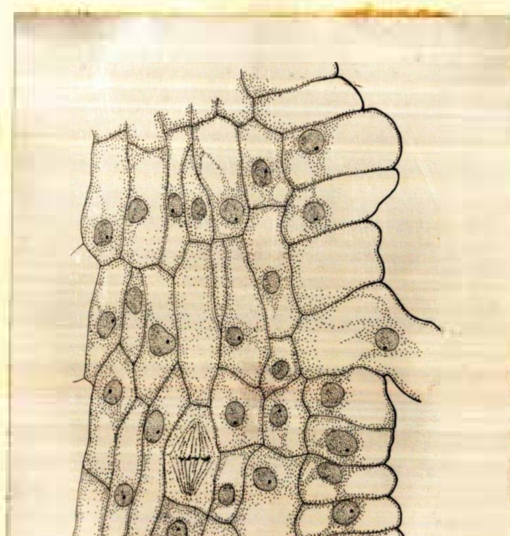

Fig. 24. Longitudinal section of an older receptacle at a level opposite the ovary. Note cell elongation and vacuolation. X750.

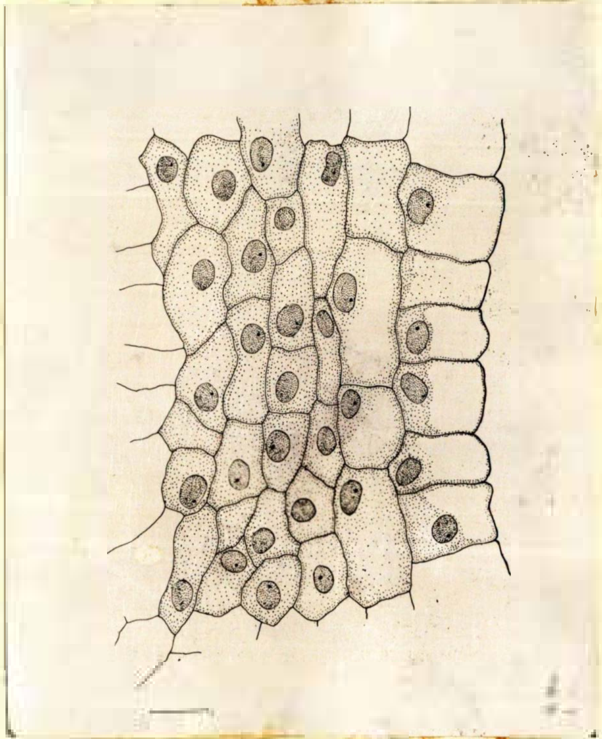

Fig. 25. Longitudinal section of the receptacle at a level above the ovary. Note cell elongation, and that vacuolation is beginning to take place in the outer cells. X750.

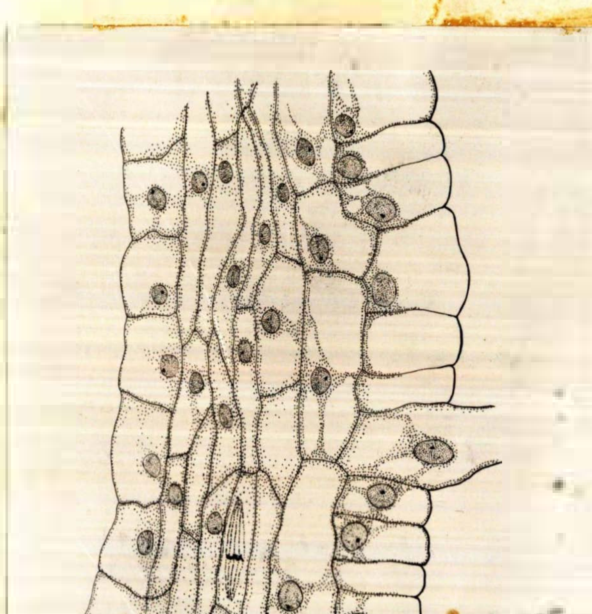

Fig. 26. Longitudinal section of an older receptacle at a level above the ovary. Note that cell division is still taking place. Vacuolation is now taking place in most of the cells. X750.

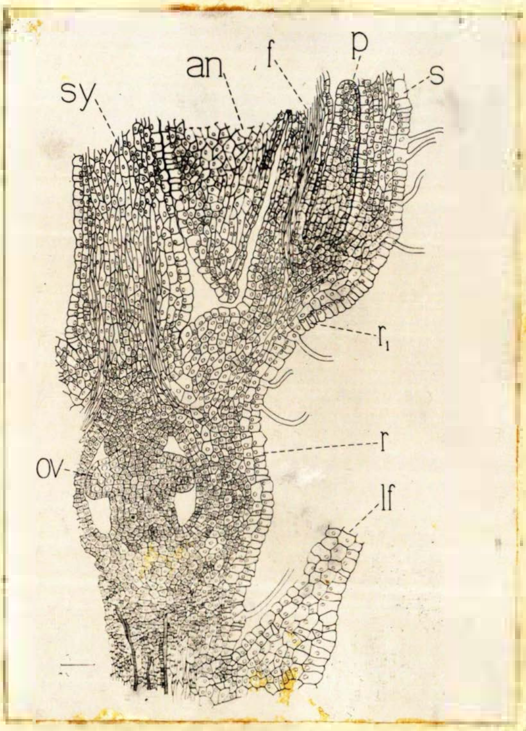

Fig. 27. Longitudinal section of an intermediate flower at about the same stage as figs. 25 and 25, showing the receptacle tube, locules, young ovules and other floral appendages. The line in the lower portion of the figure represents one-hundred microns. X44. sy, style; an, anther; f, filament; p, petal; s, sepal; ov, ovule; lf, leaf; r_1, upper receptacle tube; r, lower receptacle tube.

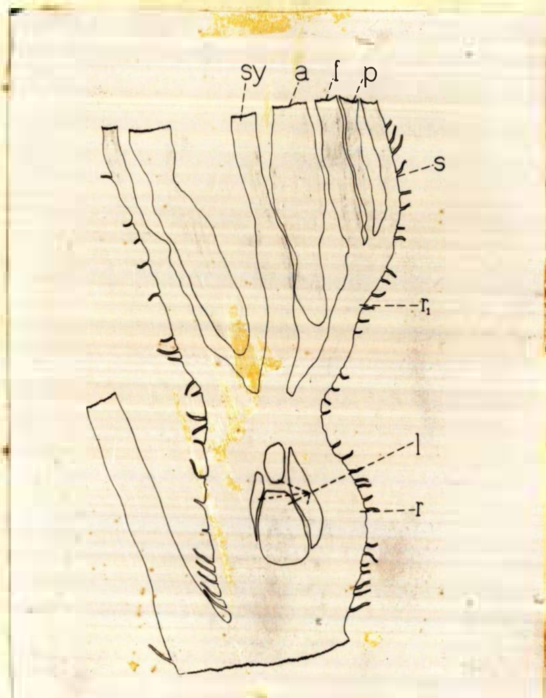

Fig. 28. Longitudinal section of an older flower showing the receptacle tube lengthened. This section shows all four locules. X20. sy, style; a, anther; f, filament; p, petal; s, sepal; l, locules; r_1, upper receptacle tube; r, lower receptacle tube.

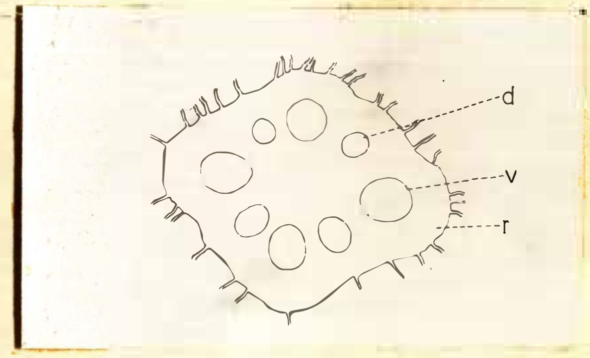

Fig. 29. Transverse section through the receptacle under the ovary showing the vascular bundles. X58. d, dorsal bundle; v, ventral bundle; r, receptacle.

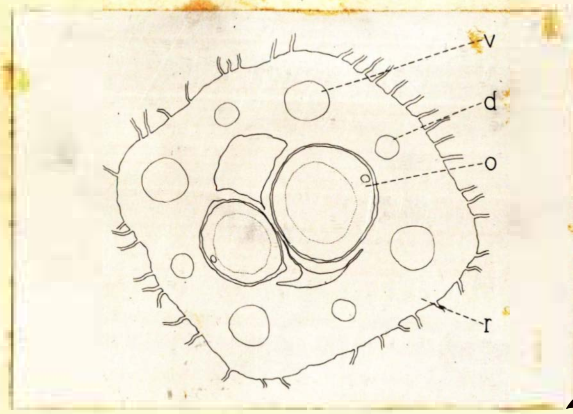

Fig. 30. Transverse section through the receptacle and ovary, showing the vascular bundles and the locules. X58. v, ventral bundle; d, dorsal bundle; o, ovule; r, receptacle.

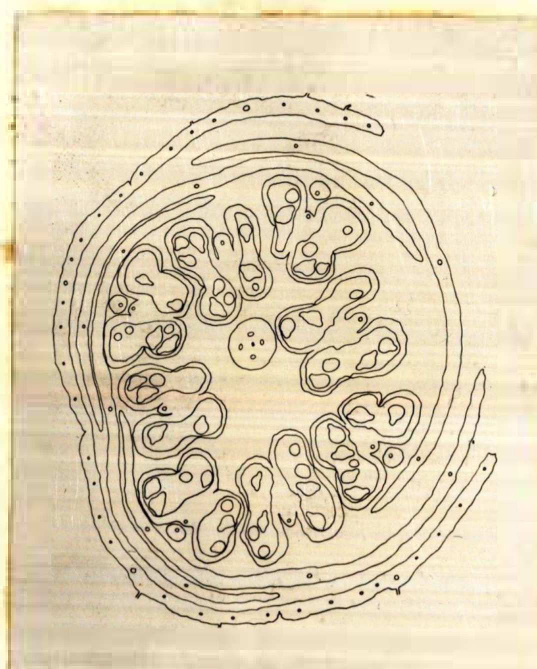

Fig. 31. Transverse section of a flower at the level of the anthers, showing the vascular system of the sepals, petals, and stamens. X29.

This agrees with the study by Goebel (Douglas 2) who found that in the apple floral parts appear: sepals, petals, stamens, and carpels. This he considered to be the order characteristic of flowers with inferior ovaries. The flower of Gaura is definitely epigynous. According to observations recorded here there is no ontogenetic fusion between carpels and stamens, between stamens and petals, between petals and sepals, nor between carpels and receptacle, unless continuity of tissue between the last two be interpreted as fusion in the phylogenetic sense. A study of both earlier and later stages shows that the tissues just below the sepals, petals, and stamens have not been separate at any time, and that the floral tube is a result of zonal development in the periphery of the receptacle. In any event the floral tube is not syngynous. This agrees with the findings of Judson (7) who worked on the pistillate flower of cucumber.

This conclusion conflicts with the appendicular theory held by Puri (10) in his review of floral anatomy in the solution of morphological problems, and by Eames and MacDaniels (4) in their book on plant anatomy. In this theory it is thought that the inferior ovary represents adnation in its extreme form, or that the floral tube is formed by the complete fusion of the bases of the sepals, petals, and stamens to the carpellary wall. In some other species the vascular anatomy of the hypanthium indeed suggests syngyny. It is not impossible that some species are epigynous while others are syngynous. There is no reason why all inferior ovaries have to arrive at their inferior positions by the same method.

A more complete interpretation of the origin of the tube of this flower must wait until other genera and species have been investigated. The ground work for such a study has now been laid. This study has been limited because the work has been confined to one species of Gaura. A morphogenetic study of this flower may also add to our information as to the true nature of the floral tube.

SUMMARY

1. All floral appendages of Gaura coccinea exhibit similar details in origin from the receptacle.
2. After their origin, development proceeds in different directions, resulting in diverse structures.
3. The sequence of initiation is: sepals, petals, stamens, and carpels.
4. The hypanthium of Gaura coccinea is receptacular except at the base where the receptacle and carpels are continuous.
5. The flower of Gaura coccinea illustrates true epigyny.

The writer wishes to take this opportunity of thanking Dr. W. L. Miller for his suggestions and help in bringing this investigation to a successful completion.

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