EMBRYOLOGICAL STUDIES IN MALVACEAE—II

Fertilization and Seed Development

by C. Venkata Rao, *Department of Botany, Andhra University, Waltair*

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Introduction

In a previous article the writer (1954*a*) described the development of the anther, ovule and the gametophytes in fifteen species belonging to Malvaceae. In this paper fertilization, development of endosperm, embryo and seed are described in the following eight species: *Sida cordifolia* L., *S. veronicaefolia* L. (= *S. humilis* Willd.), *Abutilon indicum* G. Don., *Pavonia zeylanica* L., *Malachra capitata* L., *Hibiscus solandra* L. Herit., *H. hirtus* L. and *H. micranthus* L.

Material and Methods

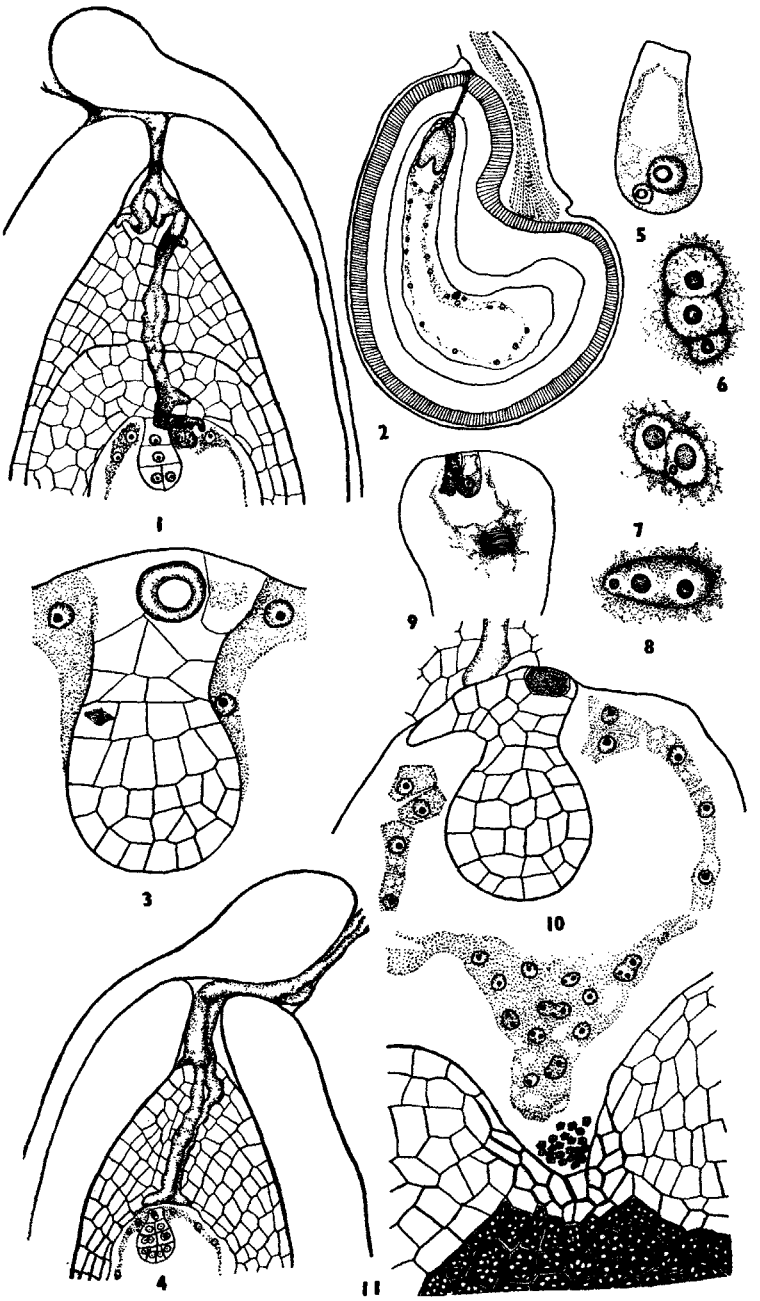
The material of *Malachra capitata* was obtained from Kakinada and the rest were collected locally. Sections were cut according to usual methods of microtechnique and stained with Delafield's and Heidenhain's haematoxylin.

Fertilization and early stages of embryogeny have been found to proceed at a rapid rate in all investigated Malvaceae. Therefore for a close study of these aspects, open flowers of *Hibiscus solandra* were labelled and the developing fruits were fixed at hourly intervals.

In all species studied, the stylar branches terminate in globose stigmas with either short (*Sida*) or elongated and tapering (*Hibiscus*) one-celled hairs. The styles which are solid (except in *Abutilon*) are provided with strands of transmitting tissue consisting of elongated, thin walled, richly protoplasmic cells full of starch grains. Stomata are found in the epidermis of the style and druses in the inner cells.

The ovules in *Pavonia zeylanica* and *Malachra capitata* are basal and erect, with the micropyle pressing against or standing very close to the base of the loculus or placenta, and the pollen tube enters the micropyle directly from the tissue of the placenta along which it traverses. In *Abutilon indicum*, however, several multicellular richly protoplasmic hairs arise from the base of the style and project into the cup-shaped cavity of the ovary below and function as an obturator. In *Hibiscus solandra*, similarly, a number of hairs arise from the placenta and bridge the gap between the placenta and micropyle, thus facilitating the entry of the pollen tubes into the ovules. Stenar (1925) also recorded the occurrence of such hairs in *Modiola caroliniana* which become especially prominent in fertilizable ovaries, though he did not ascribe any function to them. Such a hairy obturator is also seen in other Malvales like *Buettneria herbacea* of Sterculiaceae (C. V. Rao, 1954*b*) and *Triumfetta rhomboidea* of Tiliaceae (C. V. Rao and K. V. S. Rao, 1952).

The pollen grains are large and their cytoplasm is packed with reserve food in the shape of fat, aleurone grains and starch. As the pollen grains germinate these food materials pass into the pollen tubes, giving them a richly granular appearance and obscuring the gametic nuclei. The pollen grains are lodged in



FIGS. 1–11. Fertilization and endosperm development in Malvaceae.

FIG. 1. Micropylar part of the ovule of *Hibiscus micranthus* showing branching pollen tube. ×175.

,, 2. L.S. of developing seed of *Abutilon indicum* showing embryo with cotyledon primordia, endosperm which has become cellular around the embryo and persistent pollen tube. ×30.

large numbers on the stigma and germinate within a few minutes of pollination. Self-pollination occurs in *Hibiscus solandra*. Pollen tubes were already formed in flowers plucked just after opening. Flower buds enclosed in cellophane paper bags

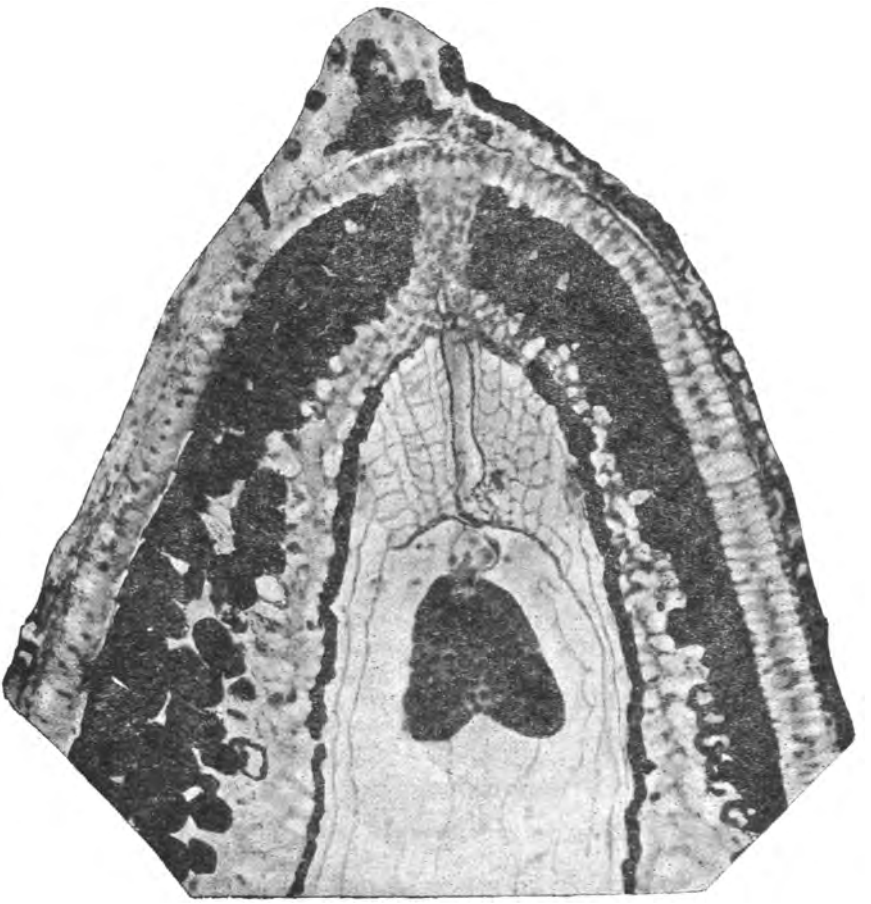


FIG. 12.

FIG. 12. Microphotograph of L.S. of upper part of the seed of *Hibiscus solandra* showing embryo, persistent pollen tube and tannin and starch bearing cells of the integuments. ×165.

FIG. 3. Micropylar part of the embryo sac of *Hibiscus hirtus* showing globular embryo and the cut end of pollen tube which looks like a tracheid. ×370.

„ 4. Micropylar part of the ovule of *Hibiscus hirtus* showing penetration of two pollen tubes. ×175.

„ 5. Fertilization of egg in *Abutilon indicum*. ×370.

FIGS. 6–8. Formation of the primary endosperm nucleus in *Pavonia zeylanica*. ×780.

FIG. 9. Upper part of the embryo sac of *Hibiscus micranthus* showing fertilized egg and first division of the primary endosperm nucleus. ×175.

„ 10. Micropylar part of the embryo sac of *Hibiscus micranthus* showing embryo with boot. shaped suspensor, endosperm which has become cellular, persistent pollen tube and remnant of a synergid. ×250.

„ 11. Antipodal end of embryo sac of *H. micranthus* showing super-numerary persistent antipodals, endosperm (note nuclear fusions), and food bearing cells of the chalaza. ×250.

fruited in due course. As Stenar (1925) and Lang (1937) have already noticed, the emergence of pollen tubes is polysiphonous. Stenar (1925) suggested that the accessory pollen tubes might be serviceable in keeping the large pollen grains anchored to the stigma by getting entangled with the stigmatic hairs.

The pollen tubes in *Hibiscus solandra* reach the base of the style in about four hours of pollination. After reaching the tip of the nucellus, they give off a few short branches which end blindly, while the main tube carrying the gametic nuclei progresses towards the embryo sac (Fig. 1). The pollen tubes in Malvaceae are especially interesting. They are 15–20 μ wide and persist till a very late stage in the development of the seed (Figs. 2, 12). They do not collapse after discharging their contents but remain intact. They are lined with protoplasm-like material and their wall is pretty thick; its avidity for safranin might indicate that it is lignified. In one section (Fig. 3), its tip had been cut transversely by chance and it appeared very much like a tracheid. The structure and behaviour of the pollen tube suggest that it may serve a nutritive function by acting as a channel for the transport of food materials from the starch bearing cells of the integuments to the growing embryo. Longo (1903) in *Cucurbita* and Foster (1943) in *Carica papaya* also have credited the pollen tube with a similar function. In several cases, two pollen tubes were seen to enter an ovule (Fig. 4) as Iyengar (1938) also found in *Gossypium*, though polyspermy was not noticed.

The male gametic nuclei figured by Stenar (1925) in *Malva rotundifolia* and *Lavatera thuringiaca* (his text-figs. 52–55) do not show nucleoli; but in the present studies these nuclei were found to show distinct nucleoli at the time of fertilization. Like the nucleolus of the egg (and pollen mother cells), these nucleoli also show densely chromatic peripheral and a vacuole-like central region (Fig. 5).

Fertilization occurs after the formation of the primary endosperm nucleus or after its division. At first, the egg as well as the male gamete contain nuclei which are in the resting condition but just before syngamy a 'spireme' can be made out in both the nuclei. The nucleus of the fertilized egg shows dense chromatin and usually two but occasionally three nucleoli. Stages in syngamy are met with in material of *Hibiscus solandra* fixed 10–12 hours after pollination.

Endosperm

The polar nuclei in all investigated species stand pressed together but do not fuse before fertilization. The male nucleus fuses first with one polar nucleus and then fusion occurs with the second polar to form the triploid 3-nucleolate primary endosperm nucleus (Figs. 6–8), as was also noticed in members of Sterculiaceae (C. V. Rao, 1954*b*) and Tiliaceae (C. V. Rao and K. V. S. Rao, 1952; Banerji, 1933). The primary endosperm nucleus divides within 12–15 hours of its formation in *Hibiscus solandra* and 4–8 endosperm nuclei are already formed when the fertilized egg undergoes the first division. The spindle during the first division of the primary endosperm nucleus in *Hibiscus micranthus* is oriented transverse to the embryo sac (Fig. 9).

The developing endosperm shows accumulations around the embryo and at the antipodal end of the sac, while it is relatively thin at the sides. Cell wall formation commences in the endosperm from the micropylar end when the embryo has reached the size of a fairly large globular mass or is already showing the cotyledonary primordia, and proceeds towards the antipodal end (Fig. 10). The nucellus about this time is almost crushed out at the sides of the embryo sac. In the micropylar region, however, it persists for a longer time, with the pollen tube intact, though the cells are devoid of cytoplasm. The endosperm in the antipodal part extends into the socket of thick walled cells described in the previous paper and seems to draw directly upon the reserve food contained in the cells of the chalaza (Fig. 11). In *Hibiscus hirtus* and *H. micranthus*, the antipodals do not degenerate after

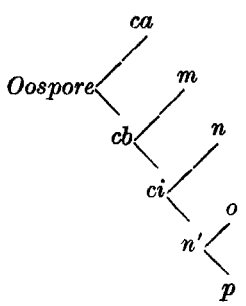
fertilization. On the other hand, they divide to form about 25–50 cells (Fig. 11). These antipodal cells are much smaller than the surrounding nucellar cells and stain deeper. As they stand between the endosperm and the food bearing cells of the chalaza, they seem to help in the transport of food into the sac, just as the pollen tube facilitates food transport at the micropylar end. Such antipodals are seen in highly evolved families like Rubiaceae, Compositeae and Gramineae. In the antipodal part of the endosperm nuclear fusions sometimes occur which result in large sized polyploid nuclei (Fig. 11), as are also seen in some members of Sterculiaceae like *Abroma augusta* and *Pentapetes phoenicea* (C. V. Rao, 1954*b*).

The endosperm during cell formation first gets cut up into uninucleate protoplasts by a process of furrowing or indentation (Fig. 10) as Gore (1932) described in cotton. Later the cell walls are secreted. The embryo sac at this time is very large and the cytoplasm relatively scanty. It continues to enlarge rapidly even afterwards so that the nucellus of the ovule is completely eaten up. No perisperm is found in the seed. In the mature seeds of *Hibiscus micranthus* (Fig. 125) almost the whole of the endosperm is consumed; in *Sida cordifolia* (Fig. 28), *S. veronicaefolia* (Fig. 46), *Pavonia zeylanica* (Fig. 61) and *Abutilon indicum* (Fig. 71), however, a little of it could be seen in the fully formed seed.

Embryogeny

The development of the embryo occurs in a uniform manner in all species studied, except for slight variations. It will be described in *Sida* species and any minor variations will be pointed out in the remaining species. The development keys out to the *Urtica* variation of the Asterad Type.

Sida cordifolia L. and *S. veronicaefolia* L.—The fertilized egg (Fig. 13) divides transversely (Fig. 14) and gives rise to the terminal cell *ca* and the basal cell *cb* (Figs. 15, 29). The two cells next undergo division simultaneously, *ca* dividing longitudinally and *cb* transversely so that a 4-celled T-shaped embryo is formed (Figs. 16, 30). The two cells formed by *cb* are designated *m* and *ci*. The two cells of the terminal tier now divide in a vertical manner in a plane perpendicular to that of the first division forming quadrants termed *q* (Figs. 17, 31). *M* divides vertically and *ci* transversely forming two cells designated *n* and *n'* (Figs. 17, 31). The quadrants of the tier *q* divide in an oblique manner giving rise to four centrally placed cells termed *a* and four peripherally placed ones called *b* (Figs. 18, 32). The walls of these cells may touch the horizontal (Fig. 18) or vertical wall of this tier (Fig. 20). Vertical divisions occur in the cells of *m* which result in formation of circumaxially arranged quadrants. *N* also divides vertically into two cells (Figs. 18, 33) and *n'* by a transverse division gives rise to two cells *o* and *p* (Fig. 18). The embryo at this stage is 16-celled and 5-tiered as in Sterculiaceae and the destination of the tiers is also similar as shown in the following schematic representation:



.. .. stem tip and cotyledons

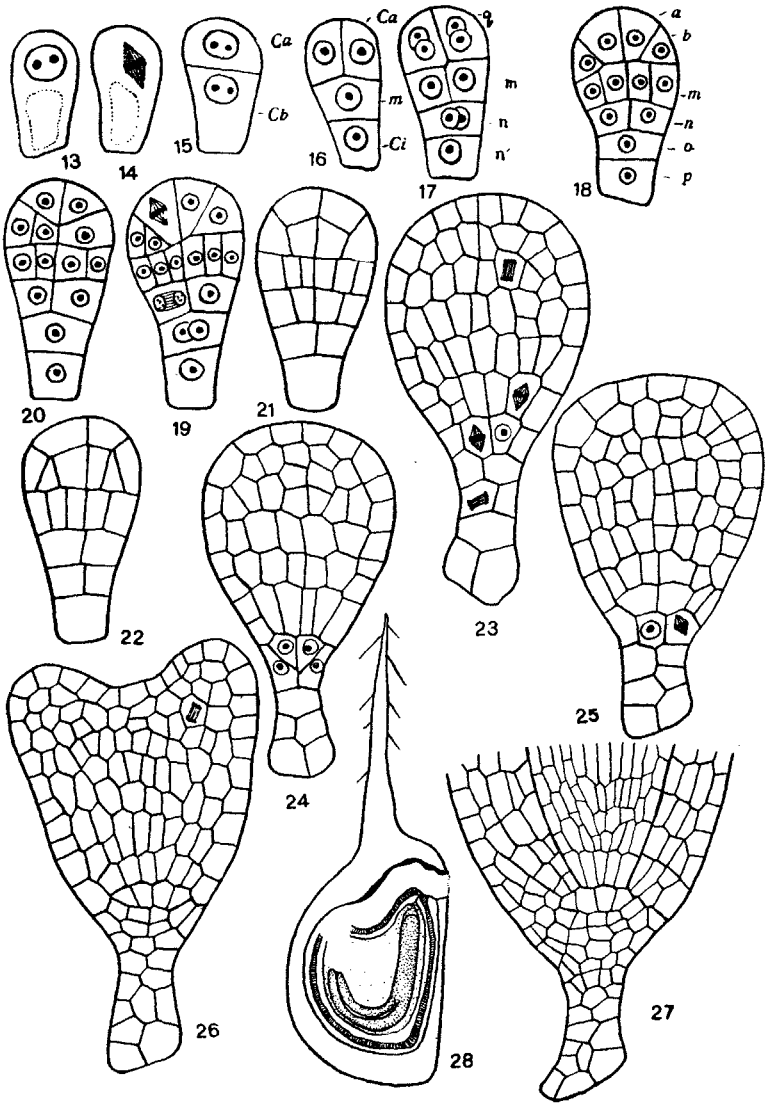
.. .. hypocotyl

.. .. root tip

.. .. dermatogen of root tip and root cap

.. .. suspensor

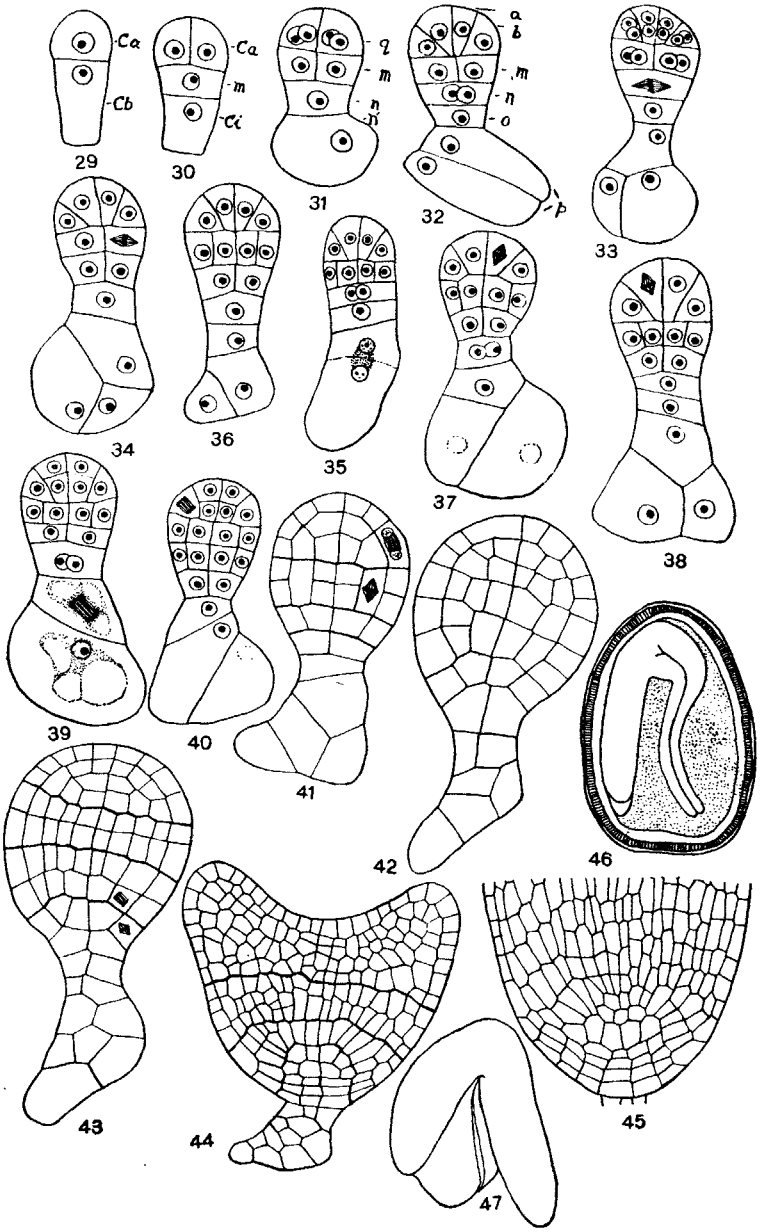
After this stage, the quadrants of *m* undergo periclinal divisions to demarcate the dermatogen initials to the outside and the common periblem-plerome initials



FIGS. 13–28. *Sida cordifolia.*

FIGS. 13–26. Various stages in the development of the embryo. ×330.
FIG. 27. Lower part of the embryo showing suspensor, root tip and root cap. ×215.
„ 28. L.S. of fruitlet. ×10.

to the inside (Figs. 18, 19, 34, 35). The demarcation of dermatogen in the terminal tier occurs first in the cells of *a* and then in the group of cells *b* (Figs. 19, 37–40), though sometimes the reverse happens (Fig. 20). Divisions in *n* occur in the same manner as in *m* and result in the demarcation of the three histogenic layers (Figs. 20, 21, 39, 40). *O* functions as the hypophysial cell; at first it undergoes two vertical divisions which result in the formation of a plate of four cells (Figs. 21, 22, 40). These cells next undergo oblique divisions (as occur in the terminal tier), forming a group of four cells to the inside, and four to the outside which function



FIGS. 29–47. *Sida veronicaefolia.*

FIGS. 29–43. Various stages in embryo development. ×355.
FIG. 44. Embryo with cotyledon primordia. ×240.
,, 45. Part of the root tip of mature embryo. ×240.
,, 46. L.S. mature seed. ×10.
,, 47. Entire embryo. ×10.

as the root cap initials (Figs. 23, 24). In *Sida cordifolia*, the group of cells formed to the inside undergo another division giving rise to a second layer of root cap initials to the outside and the dermatogen initials of the root tip to the inside. The two layers of root cap initials undergo periclinal and anticlinal divisions so that the root cap of the mature embryo becomes several layered (Figs. 25–27, 44, 45).

P builds up the suspensor. In *Sida veronicaefolia*, it is vesicular and richly protoplasmic. It also undergoes the first division earlier than in other species, even before *o* divides (Fig. 32). The first formed cells are large and glandular and equal in volume the whole of the embryonal mass (Figs. 39, 40). By successive divisions they become smaller and smaller (Figs. 41–43). They are not vesicular in *Sida cordifolia* and resemble those in other members of the family like *Abutilon indicum* and *Pavonia zeylanica*. In all cases, the suspensor is large and somewhat boot-shaped (Figs. 27, 42–44) in the fully formed embryo. It differs in this respect from that of the remaining families of Malvales. It seems to be a specialized organ exposing a large area for absorption of food materials which the rapidly growing embryo needs. Schnarf's (1931) remark that 'in general Malvaceae seem to possess a strikingly short suspensor' seems to be based on inadequate data and is no longer quite correct.

The mature seed shows a large embryo with foliaceous folded cotyledons (Figs. 28, 46, 47). The cells of the embryo are packed with reserve food materials in the form of starch and protein.

Pavonia zeylanica L.—The segmentation of the oospore and the derivation of the embryonic organs follow the same course as in *Sida*. The hypophysial cell divides relatively late in development of the embryo. The suspensor in this species remains 1-celled for a relatively longer time. It undergoes the first division after *n* has formed the quadrants. The suspensor cells remain small from the beginning.

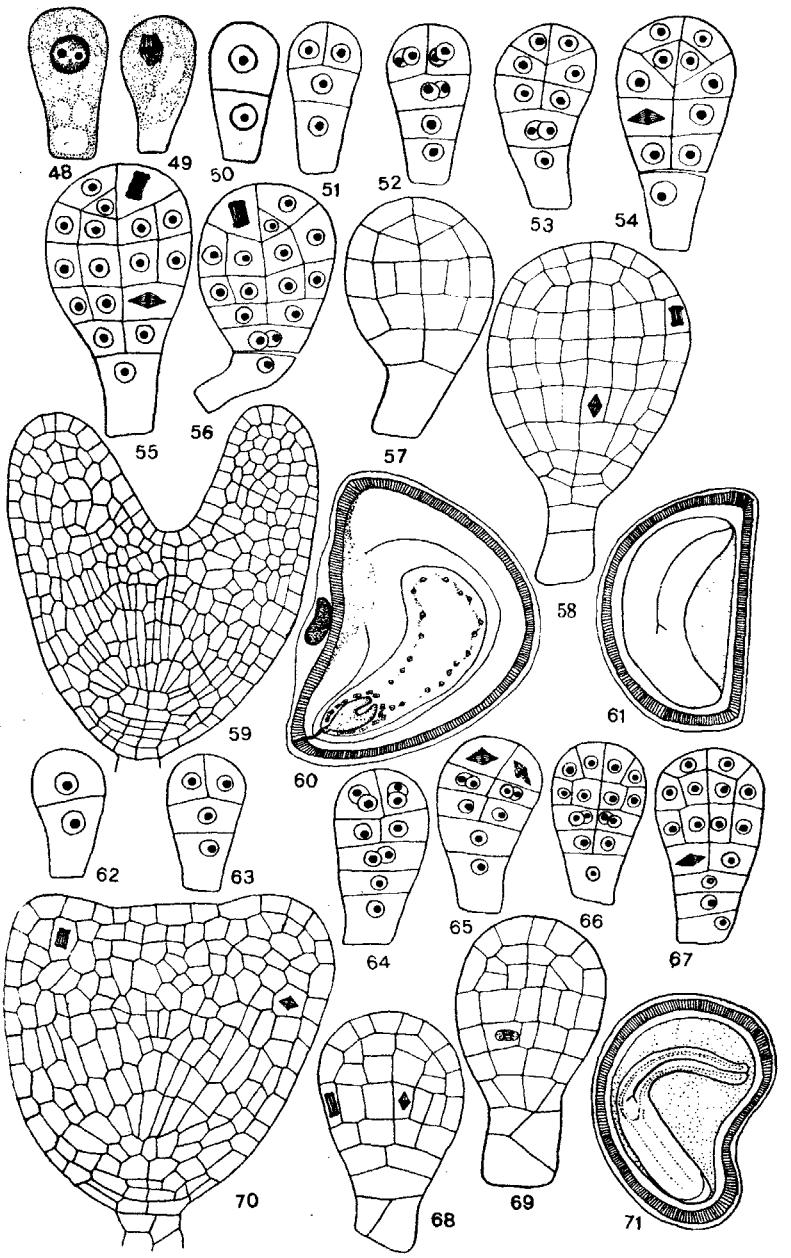
Abutilon indicum G. Don.—Development of the embryo follows closely that in *Sida* and *Pavonia*. The suspensor cells are not vesicular. The root cap initiating layers are variable being one or two as Souèges (1922) also found in *Malva rotundifolia*.

Malachra capitata L.—This species resembles *Pavonia zeylanica* in the organization of the suspensor. The rest of the embryo development is the same as in the other species studied.

Hibiscus solandra L. Herit., *H. hirtus* L., and *H. micranthus* L.—The young embryos in *H. solandra* appear more elongated than those of the other two species of *Hibiscus*. In *H. hirtus* and *H. micranthus* the suspensor cell of the young embryo is somewhat vesicular (Figs. 101, 113). In *H. solandra* occasionally a slight variation is seen in the segmentation of the cells *a* of the tier *q*. Ordinarily these cells divide transversely cutting off the dermatogen initials to the outside but sometimes one of these cells divides in an inclined manner so as to form a cell that looks like an epiphyseal cell (Fig. 89). In subsequent divisions, however, the derivatives of this cell become indistinguishable from the rest. Such deviations have been noticed by Souèges (1922) also in *Malva rotundifolia*.

One abnormal embryo was found in *Hibiscus solandra* (Fig. 88). The cells of the tier *q* in this case, appear normal but those of the remaining tiers instead of showing dense cytoplasm characteristic of embryonal cells, showed vacuolated cytoplasm and hypertrophied nuclei with large nucleoli. The cells of the subapical tier were much elongated; while one cell had divided longitudinally and demarcated the dermatogen initial, another (in sectional view) had divided in a transverse manner. A similar transverse division had also occurred in one of the cells derived from *n*.

The suspensor in *H. hirtus* (Fig. 106) and *H. micranthus* (Fig. 118) becomes large and boot-shaped earlier than in *H. solandra*. In *H. hirtus o* divides relatively later than in other species of the genus in which respect it resembles *Pavonia zeylanica*. The number of root cap initiating layers is variable but more commonly



FIGS. 48–71.

FIGS. 48–61. *Pavonia zeylanica*. Figs. 48–58. Stages in embryo development, ×320. Fig. 59. Embryo with cotyledon primordia, ×215. Fig. 60. L.S. of a developing seed showing embryo with cotyledon primordia, endosperm aggregation around the embryo which has become cellular and a persistent pollen tube, ×30. Fig. 61. L.S. of mature seed, ×6.

„ 62–71. *Abutilon indicum*. Figs. 62–69. Stages in embryogeny, ×320. Fig. 70. Embryo with cotyledon primordia, ×215. Fig. 71. L.S. mature seed, ×6.

it is two. The embryo in the fully formed seed is large and nearly fills the seed cavity, the little endosperm left, being confined to the folds of the cotyledons.

Seed Coats

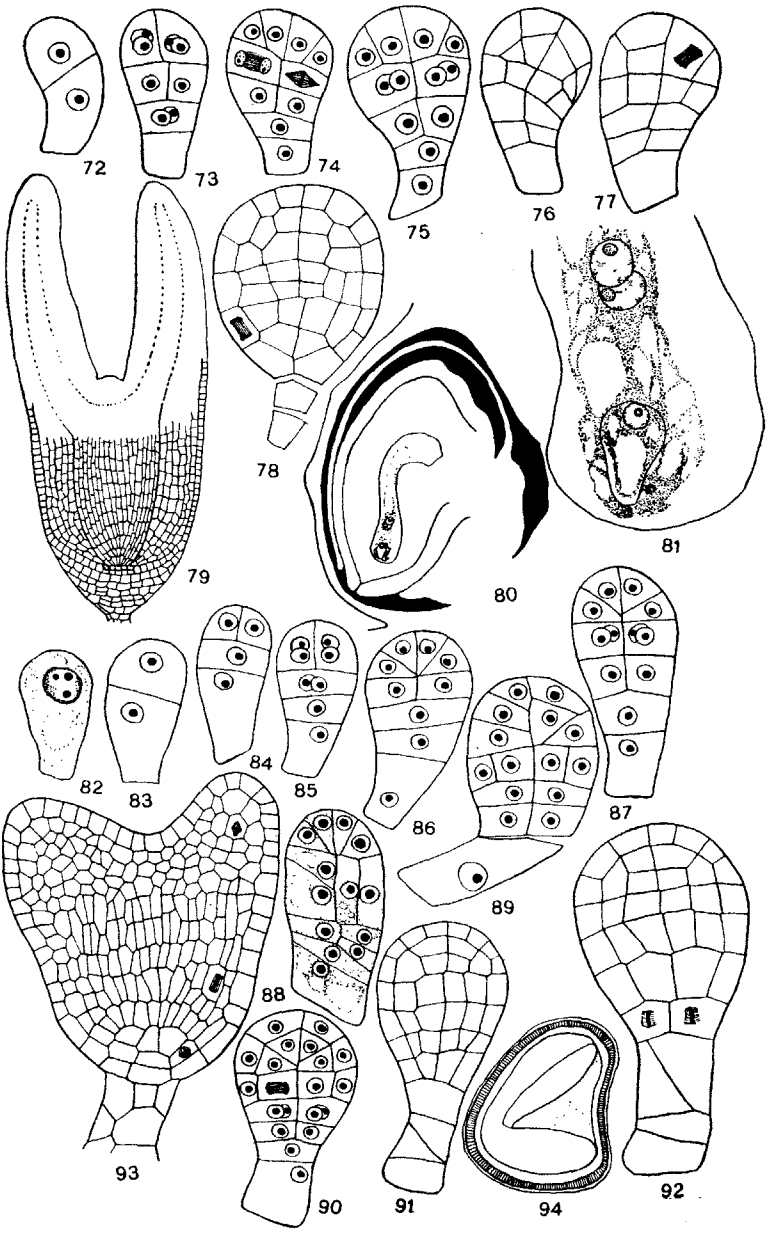
The writer's observations on the development and structure of the seed coats in *Sida cordifolia, Pavonia zeylanica, Malachra capitata, Abutilon indicum* and *Hibiscus* species are in close agreement with those of Reeves (1936).

The outer and inner integuments of the fertilizable ovule are usually 2-3 and 5-6 cells thick respectively, with an air space in between. After fertilization, the inner integument becomes 8–10 layered while the outer remains of the same thickness and forms a membraneous testa, and the air space disappears. In some members of the family, like *Hibiscus micranthus* and *H. hirtus*, the testa develops hairs while in others including *H. solandra*, it remains smooth. In all species at first the outer epidermis of the outer integument in the fertilizable ovule consists of uniform isodiametric cells. In species which develop epidermal hairs, when the embryo has become 8–16 celled, some of the epidermal cells become conspicuous by their larger size, denser cytoplasm and more prominent nuclei. These cells occur in pairs; each cell then divides asymmetrically and forms a larger and a smaller cell. So the cells lie in linear rows of four before the development of hairs (Fig. 119). The nucleus of the elongating cell may divide once mitotically (Fig. 120). The lumen of the mature hair gets filled with deep staining matter (Fig. 121). In the remaining species with smooth testa, the cells of the epidermis of the outer integument are more tangentially flattened and devoid of cytoplasm and filled with tannin. In *Hibiscus solandra* and *Pavonia zeylanica*, the cells do not develop into hairs but become papillate. In the latter species, the tannin filled, deep staining cells are so arranged among the colourless cells as to give a pattern of rectangles to the surface view of the testa.

The thickness of the tegmen varies in different parts of the same seed. In the region of the micropyle it is thinner, while on the side of the funicle and chalaza it is thicker (Fig. 60). The cells of its outer epidermis are at first isodiametric and richly protoplasmic. After the embryo becomes globular, the cells begin to elongate radially and develop into the palisade layer (Figs. 122, 123). Ultimately they become very thick walled and show a prominent light line. The lignified inner half of the cell wall stains with phloroglucinol while the outer half which consists of cellulose does not. The lumen of the cell with degenerate remnants of the protoplast is confined to the outer half of the cell (Fig. 124). The cell wall is striated. One or two layers of large tannin and starch bearing cells immediately below the palisade layer constitute the 'pigment layer'. These cells are more numerous in the region of the micropyle and on the side of the funicle. The cells between the pigment layer and the inner epidermis of the inner integument are large, thin walled and parenchymatous (Fig. 12) and get crushed in the developing seed. The inner epidermis of the inner integument termed the 'fringe tissue' consists of tangentially flattened cells. Their cell walls stain deeply with safranin and appear to be lignosuberized, as Reeves (1936) also noted. Their lumens contain tannin which stains very deeply. The tegmen of the mature seed consists of the palisade layer, which accounts for more than half the thickness of the seed coats, the pigment layer and the fringe tissue with the remnants of the crushed cells in between. In general there is a close similarity in the development and structure of the seed coats in all the families of Malvales.

Sterility and Unfertilized Ovules

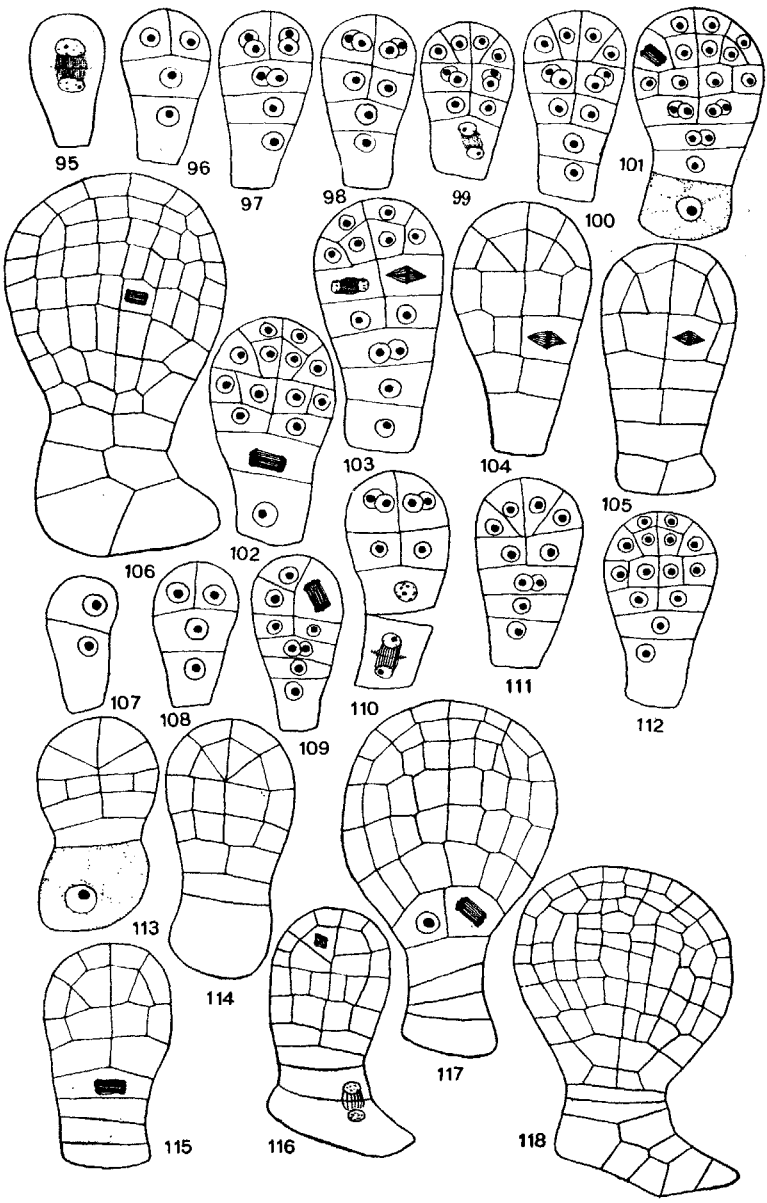
In *Malvaviscus arboreus* Cav. studied by the writer (1954*a*), the flowers are sterile and drop off without setting seed. The embryo sacs are normally formed,



FIGS. 72–94.

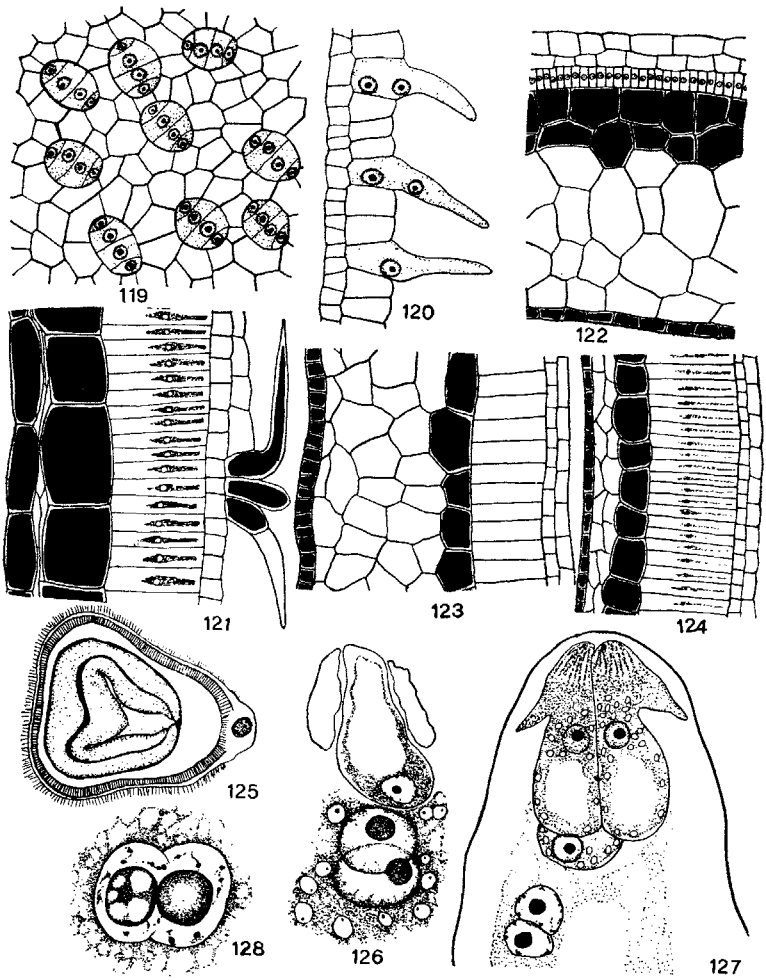
FIGS. 72–81. *Malachra capitata*. Figs. 72–78. Stages in development of the embryo, ×340. Fig. 79. Mature embryo, ×100. Fig. 80. Ovule with a giant unfertilized embryo sac, ×100. Fig. 81. Part of the embryo sac in the above magnified, ×205.

„ 82–94. *Hibiscus solandra*. Figs. 82–92. Stages in embryogeny, ×340. Fig. 93. Embryo with cotyledon primordia, ×230. Fig. 94. L.S. mature seed, ×10.



FIGS. 95–118.

FIGS. 95–106. Various stages in the embryo development of *Hibiscus hirtus*. ×320.
„ 107–118. Stages in the embryogeny of *Hibiscus micranthus*. ×320.



FIGS. 119–128.

FIGS. 119–125. Development and structure of seed coats in Malvaceae. Fig. 119. Surface view of the testa of *Hibiscus micranthus*, ×230. Fig. 120. Development of hairs from testa of *H. micranthus*, ×230. Fig. 121. Seed coats of *H. micranthus*, ×230. Fig. 122. Seed coats of *Hibiscus solandra*. ×160. Fig. 123. Seed coats from young seed of *Sida cordifolia*, ×160. Fig. 124. Seed coats of *S. veronicaefolia*, ×160. Fig. 125. T.S. seed of *Hibiscus micranthus*, ×10.

„ 126–128. Unfertilized embryo sacs. Fig. 126. Part of the unfertilized embryo sac of *Pavonia zeylanica*; note starch grains in cytoplasm, ×570. Fig. 127. Upper part of an unfertilized embryo sac of *Sida cordifolia*; note starch grains in cells of egg apparatus, ×340. Fig. 128. Hypertrophied polar nuclei from an unfertilized embryo sac of *Hibiscus hirtus*, ×570.

but after reaching the 8-nucleate stage, the sacs as well as the ovules degenerate. In *Kydia calycina* the embryo sacs and ovules of the male flowers degenerate. In *Thespesia populnea*, a large number of flowers drop off without setting seed. The few fruits that develop show only one or two seeds each, though the ovary contains about 20 ovules. In all species in which the seeds develop normally, sometimes one or more ovules in any ovary may remain unfertilized. These ovules appear normal and occur along side with seeds containing well developed embryos (Figs. 80, 81). The cells of their integuments and nucellus remain intact but are devoid of cytoplasm. The embryo sac on the other hand enlarges a good deal, but continues to show normal contents. In one embryo sac of *Pavonia zeylanica* the synergids showed signs of degeneration but the egg and polar nuclei were still intact. Starch grains, normally absent from the embryo sac of this species, were present in this case (Fig. 126). In the fertilizable embryo sac of *Sida cordifolia*, starch grains are absent; but these were seen in the cells of the egg apparatus of an unfertilized embryo sac (Fig. 127). In *Hibiscus hirtus*, the polar nuclei in one unfertilized embryo sac became very large and hypertrophied; they show scanty chromatin and their nucleoli were vacuolated (Fig. 128). These instances might indicate a case of parasitism of an aggressive type of the female gametophyte on the sporophytic tissues in its struggle for survival. Stenar (1925) also noticed such unfertilized ovules in several species he investigated.

Summary

Fertilization, development of the endosperm, embryo and seed have been studied in *Sida cordifolia* L., *S. veronicaefolia* L. (= *S. humilis* Willd.), *Pavonia zeylanica* L., *Abutilon indicum* G. Don., *Malachra capitata* L., *Hibiscus solandra* L. Herit., *H. hirtus* L. and *H. micranthus* L.

Pollen grains germinate quickly on the hairy stigma and produce pollen tubes in a polysiphonous manner. They penetrate through the well marked transmitting tissue of the style and enter the ovule in a porogamous manner. Their entry is facilitated by a hairy obturator in *Abutilon indicum* and *Hibiscus solandra* and a knob-like one in *Sida veronicaefolia*. The pollen tubes are 15–20 μ wide and persistent; their structure suggests that they might be useful in the transport of nutrients to the growing embryo.

The male gametes show distinct nucleoli. Formation of the primary endosperm nucleus occurs within 10–12 hours of pollination and its first division in about 24 hours in *Hibiscus solandra*. The endosperm which is nuclear becomes cellular at a comparatively late stage, by a process of indentation. Seeds are either non-endospermic or provided with a little endosperm. They lack perisperm.

Embryo development occurs according to the *Urtica* variation of the Asterad Type. The terminal cell of the two celled proembryo forms the cotyledons and stem tip; the basal cell gives rise to the hypocotyl, root tip, root cap and suspensor. The suspensor is large and boot-like.

The outer integument forms a membraneous testa. Epidermal hairs develop in *Hibiscus micranthus* and *H. hirtus* while in *H. solandra* and *Pavonia zeylanica*, the cells become only papillate. The outer epidermis of the inner integument forms the palisade layer which shows well marked light line. The next one or two layers of cells constitute the pigment layer and the innermost, the fringe tissue. The median parenchymatous layers get crushed in the mature seed.

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