EMBRYOLOGICAL STUDIES IN MALVACEAE.

I. DEVELOPMENT OF GAMETOPHYES

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INTRODUCTION

The family Malvaceae comprising 50 genera and about 1,000 species (Rendle, 1938), is better known embryologically than the remaining families of Malvales or Cumniferae. The observations of the previous investigators like Warming (1873), Jonsson (1878), Strasburger (1884), Hegelmaier (1885), Hofmeister (1849), Guignard (1890, 1906, 1904), Byxbee (1900), Lantis (1912), Woycicki (1911, etc.), Yamada (1926), Youngman (1927) and others, have been summarized by Schnarf (1931). Stenar's (1925) work is the most extensive and covers about 25 species distributed over a dozen genera. On account of its economic importance, the genus *Gossypium* has received the special attention of morphologists, cytologists as well as embryologists like Cannon (1903), Balls (1906), Denham (1924a, 1924b), Kearney and Harrison (1924), Beal (1928), Banerji (1928), Singh (1931), Barit (1932), Gore (1932), Harland (1932), Ayyar and Ayyangar (1933), Longley (1933), Skovsted (1933), Gulati (1934), Jacob (1942), etc. The cytology of several other members of the family was studied by Youngman (1931), Burkett (1932), Kesseler (1932), Latter (1932), Davie (1933) and L. N. Rao (1941). The pollen grains are especially large and suitable for intensive study; Lang (1937) investigated their morphology and cell inclusions and Iyengar (1938) studied the pollen tubes of *Gossypium*. Reeves (1936) made a special study of the seed anatomy of several members of the family.

In all species investigated, the cells of the anther tapetum which are sometimes multinucleate, form a periplasmidium. In some members like *Malva* species, *Lavatera trimestris*, *Anoda cristata*, *Sidalcea candida* and *Gossypium herbaceum*, the pollen mother cells stand in a uniseriate manner in the anther loculus while in others like *Malvastrum capense*, *Sida napacea*, *Abutilon Theophrasti*, they undergo a secondary increase and stand in a multiseriate manner. In the usual named species, Lantis (1912) described that every primary sporogenous cell gives rise to four microsporangenous cells. Cytokinesis takes place by furrowing. Though usually the pollen grains are shed at the 2-nucleate stage, Woycicki (1911) found that in *Malva silvestris*, *M. rotundifolia* and *Althaea officinalis* 10-20% of the grains become 3-nucleate. Guignard (1904) noticed the division of generative nucleus in the pollen tube in *Althaea*, *Hibiscus* and *Lavatera*.

The ovules are bitemgic, crassinucellate and slightly or markedly campylotropous. In *Gossypium* species (e.g. *G. peruvianum*, *G. barbadense* and *G. hirsutum*, Gore, 1932), and *Thebesia* (Reeves, 1936), the ovules are anatropous. Stenar (1925) as well as the previous investigators that the archesporium of the ovule consists of a single sub-epidermal cell. The primary parietal cell cut off to the outside gives rise to several layers of parietal cells, while the epidermis itself forms a massive nucellar cap. Stenar (1925) drew attention to one interesting feature which occurs in several Malvaceae namely one or more parietal cells

VOL. XX.—No. 2.
secondarily assume the characters of sporogenous cells. These are distinguished as 'accessory sporogenous cells' from those which function from the beginning which are termed 'definitive cells'. These cells function till the tetrad stage or early embryo sacs. The occurrence of these cells, however, is variable even within a genus like Malva. Both linear and T-shaped tetrads occur and the chalazal megaspore develops into the embryo sac according to the Normal-type. The report of Balls (1906) that in cotton the micropylar megaspore functions, was contradicted by Gore (1932) who found that in all the three species of Gossypium investigated by him only the chalazal megaspore functioned. Since there was only one megaspore mother cell to start with, Gore (1932) attributed the occasional occurrence of two embryo sacs in one ovule of cotton, to the functioning of two megaspores of the same tetrad. The synergids are reported to show a filiform apparatus only in cotton (Gore, 1932). Usually the polar nuclei fuse only at the time of fertilization, though in Lavatera thuringiaca (Stenar, 1925), they were found to fuse earlier. Super-numerary and binucleate antipodals were recorded in Lavatera thuringiaca, Anoda hastata and A. crispa. Starch grains are absent from the embryo sac (Stenar, 1925) but present in the cells of placenta, chalaza and integument of cotton (Gore, 1932).

The emergence of pollen tubes is polysiphonous. Stenar (1925) counted up to 14 pollen tubes in pollen grains of Malva neglecta germinating on the stigma, while Lang (1937) counted 20–30 tubes from a single grain of Anoda hastata and Lavatera species germinating in artificial medium. The tubes traverse endotropically through the transmitting tissue of the style which is richly supplied with starch grains. The distal part of the tube is closed off with callose plugs and usually the vegetative nucleus disintegrates in situ (Iyengar, 1938). More than one pollen tube was seen to enter an ovule, though polyspermy was not noticed. Guignard (1904) as well as Stenar (1925) observed that the pollen tube branches in the region of the nucellus.

Endosperm is nuclear and cell wall formation commences after a large number of nuclei are formed.

A perusal of the previous literature shows that while the development of the gametophytes and fertilization were studied in some detail, comparatively little attention was paid to the study of the embryogeny. The only complete account of this phase is that of Souèges (1922) in Malva rotundifolia. The embryo in this species develops according to the Asterad Type and resembles closely that in Urtica pilulifera (Souèges, 1921); Johansen (1950) classed it in the Urtica variation of the Asterad Type.

This paper deals with the development and structure of the anther, pollen, ovule and embryo sac in the following 15 species of Malvaceae distributed in 11 genera.


URENACEAE: Urena lobata L., Malaviscus arboreus Cav., Pavonia zeylanica L., Malachra capitata L.


MATERIALS AND METHODS

Malaviscus arboreus and Hibiscus hirtus are grown commonly as garden plants in S. India and Thespesia populnea as an avenue tree. The material of Kydia
calycina was collected from Anantagiri hills, Visakhapatnam district, where the plants grow wild. The materials of Urena lobata and Malachra capitata were collected from Kakinada and the rest locally. Formalin-acetic-alcohol was used as the fixative. After following the customary methods of dehydration and infiltration, the material was embedded in paraffin wax. Delafield’s and Heidenhain’s haematoxylin were used as stains, of which the former gave more satisfactory results. Addition of a pinch of safranin powder to material in 1:1 alcohol xylool mixture proved useful in locating the tannin bearing and starch containing cells and also in bringing out more prominently the pollen tubes.

**Flowers**

The flowers present typical malvaceous features. The flowers of Kydia calycina are polygamous. The staminodes of the female flowers show abortive pollen grains. The ovules of pistillode degenerate after the embryo sac is fully formed. Unlike in the bisexual and female flowers, the style in the male flowers remains included in the staminal tube (Figs. 65, 66). In Kydia, there are 3 carpels; in the different species of Sida studied they range from 5-10; in Abutilon and Althaea they are numerous and in the rest five. Multicellular hairs are present on sepals, bases of petals, staminal tube and ovary wall.

**Organogeny**

The sequence in the development of floral organs is: epicalyx (where present), calyx, corolla plus androecium and lastly gynoecium. In Malvaviscus arboreus (Figs. 8-10) which has epicalyx, the bracteoles arise on the convex floral primordium and reach a considerable size before the appearance of the sepals. To the inside of the latter arises an annular zone which represents the common primordium of the corolla and androecium. In Sida cordifolia (Figs. 1-7) which has no epicalyx, the sepals attain a considerable size before the primordia of petals and stamens arise. In Malvaviscus arboreus when the common corolla androecium primordium has attained the height of sepals, the primordia of the five petals appear on its outer surface (Fig. 9), while the inner zone continues to grow up and gives rise to the stamen primordia later (Fig. 10). As in Sterculiaceae, the petals grow in a tardy manner initially; they do not cover up the essential organs, protection being given by calyx and epicalyx (Figs. 4, 11, 12). After the sporogenous cells are organised in the anthers, the apex of the floral axis which is still convex, becomes cup-shaped and develops into the ovary. It becomes lobed and the infolded carpellary margins later develop into septa, while the rim of the cup closes and grows up to form the style. The style is hollow to start with in all species; in Abutilon and Althaea, it remains hollow even in the open flower while in others it becomes solid.

There are two kinds of styles in Malvaceae which show interesting features of development; terminal as in Hibiscus and gynobasic as in Sida, Althaea and Abutilon. In Hibiscus, the rim of the cup-shaped ovary primordium grows upwards without bending and cleaves at the top into the stigmatic branches. The ovules arise on the inner margins of carpellary wall (Fig. 14). In Sida cordifolia (Figs. 5-7) and Althaea rosea (Fig. 13), the central part of the ovarian cup grows to form a lobed column simultaneously as the rim of the cup grows to form the style. From the apex of the central column the ovule primordia arise and bend into the loculus so that the ovules are pendulous. The basal part of the stylar region bends inwards so as to touch the placental column (Figs. 5, 13). The line of contact between the two can be clearly seen even in the mature ovary of Sida (Fig. 7). In this genus, the top of each carpel grows to form two spinescent processes making the style in the open flowers relatively more deep seated. So the gynobasic style is also terminal in origin but establishes contact with the base of the ovary by bending inwards at
Figs. 1–7. Organogeny of flower and development of ovary and ovule of *Sida cordifolia*. Figs. 1–3, × 45; Figs. 4–7, × 30.

Figs. 8–10. Organogeny of flower of *Malvaviscus arboreus*. × 30.

Fig. 11. L.s. of flower of *Pavonia zeylanica*. × 30.

Figs. 12 and 13. L.s. of flower and ovary of *Althaea rosea*. × 10 and × 45 respectively.

Fig. 14. L.s. of ovary of *Hibiscus hirtus*. × 35.
Figs. 15–32. Microsporogenesis and male gametophyte in Malvaceae.  
Fig. 15. T.s. of young anther of *Sida cordifolia*. ×400.  
Fig. 16. L.s. of anther of *Sida carpinifolia*. ×400.  
Fig. 17. T.s. of older anther lobe of *S. cordifolia*. ×400.  
Fig. 18. A bilateral tetrad of (Continued at foot of next page.)
base. In *Malachra capitate*, the style is terminal as in *Hibiscus* to start with, but becomes slightly gynobasic in the open flower not by bending of the base of style but due to the growth of the apex of each carpel (Figs. 109, 110). The gynoecium in *Abutilon indicum* is interesting since in each loculus occur ovules which are pendulous (as in *Sida* and *Althaea*) as well as horizontal and descending (as in *Hibiscus*). The reason for this becomes evident by a study of the development of the ovary. As in *Sida* and *Althaea* the style is gynobasic. The axial part of the ovary grows slightly not in the form of a solid column as in the above genera but as a cup, and bears one tier of ovules which are pendulous. In addition to these, the margins of each carpel bear two ovules which are variously inclined. The rim of the ovarian primordium bends inwards and again grows up to form the open style. In the early stages, there is a large space between the placental column and base of the style, which becomes smaller in the open flower. Several multicellular hairs arise from the base of the style and project into this cavity and function as obturator (Figs. 88, 89).

**Microsporogenesis and Male Gametophyte**

As the anthers are monoecious, the archesporium differentiates only at two places in the anther primordium. At each place there are one or two rows of cells (Figs. 15, 25). The number of cells in a row varies with the size of the anther; in *Sida cordifolia* (Fig. 16) there are about five cells; in *Abutilon indicum* (Fig. 22) about 10 cells and in *Pavonia zeylanica* (Fig. 26), about 15 cells in a row. The cells divide periclinally and give rise to the primary parietal cells to the outside and the primary sporogenous cells to the inside (Fig. 15). Divisions in the primary parietal cells and their derivatives result usually in the formation of three layers of wall cells below the epidermis (Figs. 16, 17, 24–27). The epidermal cells become tangentially stretched and accumulate some deep-staining contents probably tannin (Fig. 23). The hypodermal layer develops into the fibrous endothecium and the innermost wall layer forms the tapetum while the middle layers ultimately get crushed. Some of the cells of the tapetum divide periclinally and make it two-layered at places (Fig. 27).

In all species investigated, the tapetum is of the plasmodal type, a feature reported in all the previously investigated members (Schnarff, 1931). The tapetal cells enlarge considerably and take deeper stain at all stages of development, than the sporocytes. Their nuclei undergo the first mitotic division when the microsporocytes are in prophase I and most of the cells remain binucleate. In a few cells, however, mitotic divisions continue (Fig. 29), as a result of which they become 3–20 nucleate. Such cells are more frequently met with in *Hibiscus solandra* (Fig. 30) and *Malaviscus arboreus* (Fig. 32). In some cells, the nuclei again fuse to form large multinucleate polyploid nuclei (Fig. 31). As the meiotic divisions proceed in the sporocytes, the tapetal cells separate out as a layer from the wall cells (Figs. 17, 27). After the pollen grains grow to some extent and produce the exine with its spineous outgrowths, the walls of the tapetal cells break down and the protoplasts which remain intact, wander into the loculus and closely surround the pollen grains.

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*S. cordifolia*. ×400. Fig. 19. One nucleate pollen grain of *S. cordifolia* surrounded by periplasmadium. ×335. Fig. 20. Two-nucleate pollen grain of *S. carpiniifolia* with remnants of periplasmadium. ×220. Fig. 21. Mature pollen grain of *S. veronicaefolia*. ×220. Figs. 22 and 23. L.s. and t.s. of anther lobe of *Abutilon indicum*. Fig. 22, ×400; Fig. 23, ×335. Fig. 24. Older anther of *Abutilon indicum* showing 1-nucleate pollen grains and periplasmadium. ×220. Figs. 25 and 26. T.s. and l.s. of anther lobe of *Pavonia zeylanica*. Fig. 25, ×335; Fig. 26, ×106. Fig. 27. T.s. of young anther of *Althaea rosea*. ×335. Fig. 28. Pollen grains of *Althaea rosea* surrounded by periplasmadium. ×335. Figs. 29 and 30. Tapetal cells of *Hibiscus hirtus*. ×400. Figs. 31 and 32. Tapetal cells of *Malaviscus arboreus*, ×400.
Figs. 33–48. Microsporogenesis and male gametophyte in Malvaceae. Figs. 33–36. Bilateral and tetrahedral tetrads in *Hibiscus hirtus.* ×425. Fig. 37. A linear tetrad of *Hibiscus hirtus.* ×355. Fig. 38. Two nucleate pollen grain of *Hibiscus micranthus,* note generative cytoplasm. ×425. Fig. 39. Two nucleate pollen grain of *H. hirtus.* ×285. Fig. 40. Microspores of *Urena lobata* being liberated from special wall. ×425. Figs. 41 and 42. Young and mature pollen grains of *Malachra capitata.* ×285. Fig. 43. Two nucleate pollen grain of *Pavonia zeplanica.* ×285. Figs. 44–47. Pollen grains of *Hydia calycina.* ×285. Fig. 48. Abortive pollen grain of *Hibiscus solandra.* ×285.

(Figs. 24, 28). It is evident from this that the tapetum does not initiate the sculpturing of the exine. The exine and the rudiments of the spines and pores are already apparent on the microspores even before the latter are liberated from the special wall (Figs. 40, 41). It is possible, however, that the periplasmodium may hasten the further growth of the exine because both the exine and pollen grains are seen to show sudden and considerable growth after this stage (Figs. 19, 28). This
Fig. 49. Ovule primordium of *Sida carpinifolia*. × 390.

Figs. 50–52. Various stages in the development of megaspore mother cell and parietal tissue in the ovule of *S. cordifolia*. Figs. 50 and 51, × 390; Fig. 52, × 260.

Fig. 53. Nucellus of *S. cordifolia* showing megaspore mother cell and accessory sporogenous cell. × 390.

Fig. 54. Nucellus with young embryo sac of *S. cordifolia*. × 125.

Fig. 55. Mature ovule of *S. carpinifolia*. × 70.

Figs. 56 and 57. Micropylar and antipodal parts of embryo sac of *S. cordifolia*; note filiform apparatus in fig. 56; one antipodal cell has divided in fig. 57. × 390.
becomes clear on comparing the pollen grains of the two loculi of the same anther. As the microspores enlarge, the protoplasts of the tapetal cells which still retain their individuality, become smaller and smaller and ultimately they get absorbed (Figs. 19–21). They may disappear even before the microspore nucleus has divided as in Urena lobata, or their remnants may persist till the pollen grains have become 2-nucleate and nearly mature as in Sida carpinifolia (Fig. 20) and Pavonia zeylanica (Fig. 43).

In some species like Althaea rosea, Pavonia zeylanica and Sida cordifolia, the primary sporogenous cells function directly as microspore mother cells, while in others like Abutilon indicum they undergo a few mitotic divisions to increase the number of sporogenous cells. In the latter case, the sporogenous cells are arranged in several rows (Fig. 23). In any case, the number of sporogenous cells per loculus is much smaller than in other families of the order and their size larger. Their nucleoli show densely chromatic peripheral and a vacuole like central region inside which there may be a crystalline body as also reported by L. N. Rao (1941) in Hibiscus trionum. Usually the microspores are arranged in a tetrahedral manner (Figs. 35, 36), bilateral tetrads being noticed occasionally (Figs. 18, 33, 34). One case of linear tetrad was found in Hibiscus solandra (Fig. 37). The wall of the microsporocyte lasts till telophase II and before this has broken down, the protoplast gets invested by a special wall of callose (Fig. 33). The secondary spindle fibres which connect the tetrad of nuclei play no part in cytokinesis; even before they disappear, furrows develop in the periphery of the cytoplasm and wedges of special wall follow them till they meet at the centre and encircle the microspores completely (Figs. 35, 36). L. N. Rao (1941) believes that the special wall plays some part in the formation of the spore coat since its transparency increases as the exine and the sculpturing become more and more prominent.

The nucleus of the microspore undergoes division while the cytoplasm is still vacuolated. Within a short time of its formation, the partition between the two cells gives way and the generative cell migrates into the vegetative cytoplasm. In the early stages, the generative cytoplasm can be seen as a relatively hyaline sheath around the nucleus (Figs. 38, 44), which is brought out more clearly in preparations stained in DelafIELD's haematoxylin. In course of time, it becomes obscure due to the accumulation of numerous starch grains and protein granules in the vegetative cytoplasm.

Various kinds of cell inclusions are noticed in the cytoplasm of the pollen grain, namely fat, proteins and starch grains of which the last are most abundant. They vary in their size and shape, being irregular, dumb-bell shaped, circular and lenticular. Sometimes an oily matter is secreted by the protoplast which accumulates on the exine in the shape of droplets and makes the pollen grains stick together.

Usually the pollen grains are shed at the 2-nucleate stage (Figs. 39, 42). In the mature pollen grains of Sida veronicaefolia (Fig. 21) and Kydia calycina (Fig. 45), the generative nucleus becomes ellipsoidal and attains the prometaphase stage. It is surrounded at the sides by the hyaline generative cytoplasm; at the two ends are seen conical caps of relatively deep staining cytoplasm (Fig. 45), thus presenting a structure closely similar to what was observed in Triumfetta rhomboidea (C. V. Rao and K. V. S. Rao, 1952). In a few pollen grains of Kydia calycina, the generative nucleus divided and formed 2 spherical male nuclei (Figs. 46, 47). The pollen grains are relatively large and range from 60 μ as in Abutilon indicum to 120 μ as in Hibiscus solandra. In several species, some degenerating pollen grains which are probably formed as a result of irregular meiotic divisions, are found associated with normal ones (Fig. 48).

The pollen grains are spinecent and multiporate. The spines may be long, tapering and sparse as in Hibiscus, or short, somewhat blunt, broad based and closely set as in Sida. The exine is thick, ranging from 5 μ as in Sida to 10–12 μ as in Malachra capitata. In general, it shows two layers: an inner thicker, homogeneous,
Figs. 58–64. *Sida veronicaefolia*. Fig. 58. Young ovule with definitive and accessory megaspore mother cells; note development of obturator. ×105. Fig. 59. Nucellus showing T-shaped tetrad (of which one megaspore is out of focus) and an accessory sporogenous cell. ×400. Figs. 60 and 61. Linear tetrads and accessory sporogenous cells. ×400. Fig. 62. Mature ovule with obturator. ×65. Fig. 63. Antipodals. ×665. Fig. 64. Micropylar part of the ovule magnified to show the obturator and micropyle. ×265.

Figs. 65–71. *Kydia calycina*. Figs. 65 and 66. L.s. of bisexual and male flowers. ×10. Fig. 67. Two collaterally placed tetrads from one ovule, of which the lowest megaspores have formed 1- and 2-nucleate embryo sacs. ×400. Fig. 68. Nucellus with 2 embryo sacs. ×265. Fig. 69. Two 2-nucleate embryo sacs from one ovule. ×400. Fig. 70. Two superposed 8-nucleate embryo sacs from one ovule. ×265. Fig. 71. Two collaterally placed mature embryo sacs from one ovule. ×400.
Figs. 72-87. *Althaea rosea*.  
Fig. 72. L.s. loculus of ovary showing ovule primordium. ×140.  
Fig. 73. Ovule primordium showing multicellular archesporium. ×425.  
Figs. 74 and 75. Nucelli showing definitive megaspore mother cell and development of accessory sporogenous cells. ×425.  
Figs. 76-79. Formation of dyads and tetrads by the definitive megaspore mother cells. ×425.  
Figs. 80-82. Development of embryo sacs. ×285.  
Fig. 83. Nucellus with 1- and 2-nucleate embryo sacs and degenerating cells. ×285.  
Fig. 84. L.s. of ovule with embryo sac. ×30.  
Fig. 85. Micropylar part of embryo sac. ×165.  
Figs. 86 and 87. Antipodals. ×715.
non-stainable zone and an outer thinner stainable one in which bar-like striations are clearly seen. These project to the outside and present a granular or reticulate pattern to the surface view. Like the spines, the germ pores are distributed uniformly on the exine. Applying the theory put forward by Wodehouse (1935) in case of Chenopodiaceae and Polygonaceae, Lang (1937) concluded that the pores in Malvaceae are morphologically equivalent to furrows which have become so shortened as to coincide in extent with their enclosed germ pores. Evidence for this was found in pollen grains of *Hibiscus vitacefolius* in which the pore was surrounded by a circular depression. From an intensive study of pollen grain characters, Lang (1937) believes that the length of spines and their shape, their distance apart, number, size and distribution of the germ pores, the relation they bear to the spines and the nature of starch grains stored within, are useful characters for distinguishing genera and even species.

**Ovule**

In all species studied, the ovules are bitegmic and crassinucellate. In *Kydia calycina* (Fig. 65) and *Thespesia populnea* (Figs. 133, 136), they are anatropous and in the rest slightly or markedly campylotropous. The initials for both the integuments arise when the archesporium differentiates in the ovule (Figs. 49, 50, 73, 111), or a little later (Fig. 144). The outer integument grows faster than the inner and covers up the nucellus by the time the megaspore mother cell is full grown (Figs. 52, 58, 109, 113, 137). In *Urena lobata* (Fig. 100), and *Thespesia populnea* (Fig. 131), the inner also closes by this time. In most genera the outer integument is 2-3 layered while the inner is 4-8 cells thick. In *Thespesia populnea*, on the other hand, the outer integument is 5-6 cells thick and the inner 10-12 layered (Fig. 131). This genus and also *Gossypium* and *Ingenhousia* (Reeves, 1936), differ from the rest of the family in showing integumentary vascular bundles (Figs. 133, 135, 136). The vascular bundle of the funicle gives off from its chalazal end, 6-9 branches which traverse the outer integument nearly to the micropyle, branching on the way. The outer integument of *Thespesia*, when cleared in chloral hydrate shows a number of druses, the significance of which is doubtful. The cells of the epidermis of the ovule lose their cytoplasmic contents and accumulate tannin. The inner epidermis of the inner integument also accumulates tannin, except in a cap-like region around the micropyle (Figs. 64, 148), as in some members of Sterculiaceae like *Melochnia corchorifolia* (C. V. Rao, 1951). Tannin and starch grains are stored also in the median layers of the inner region of the micropyle (Fig. 64). An air space develops between the integuments on the side opposite to the funicle (Figs. 84, 90) or allround (Fig. 135). In *Sida cordifolia* (Fig. 6), *S. veronicaeifolia* (Fig. 58), *S. carpiniifolia*, *Urena lobata* and *Malachra capitata* (Fig. 109), the outer integument gets separated from the inner very early and becomes attached to the inside of the ovary wall in which condition it remains even in the fertilisable ovary (Figs. 7, 55, 62, 102, 110). The micropyle which is formed by both the integuments, has the usual zigzag form (Fig. 64). In *Sida veronicaeifolia*, a knob-like outgrowth of radially elongated richly protoplasmic cells develops at the base of the funicle even before the megaspore mother cell has divided (Fig. 58). In the fertilisable ovule it presses against the integuments and functions as the obturator (Figs. 62, 64). Other species of *Sida* studied, namely *S. cordifolia* and *S. carpiniifolia* do not show such a structure. The position of the micropyle varies in different species according to placentation. In *Pavonia zeylanica, Malachra capitata, Urena lobata, Malvaviscus arboreus* and *Althaea rosea*, it faces the base of the ovary, the raphe being ventral. In *Sida* species, it is directed towards the top of the loculus, the raphe being dorsal. In *Abelmoschus esculentus*, the ovules are slightly inclined and the micropyles point towards the ovarian axis. In *Abutilon indicum, Hibiscus micranthus*, and *H. hirtus*, the ovules are variously inclined and the micropyles point towards the axis of the ovary, top or base of the loculus (Fig. 143).
Figs. 88–98. *Abutilon indicum*. Figs. 88 and 89. L.s. of young and mature ovaries showing placentation, gynobasic style and development of obturator. Fig. 88, ×25; Fig. 89, ×10. Fig. 90. A mature ovule. ×75. Figs. 91–93. Ovule primordia with archesporium and megaspore mother cells. ×425. Fig. 94. Nucellus showing definitive and accessory sporogenous cells. ×425. Figs. 95 and 96. Formation of tetrads by definitive sporogenous cells. ×425. Fig. 97. Nucellus with 1- and 2-nucleate embryo sacs. ×285. Fig. 98. Antipodals. ×715.
Figs. 99-110.—Explanation at foot of next page.
The nucellus may be straight as in *Kydia calycina* (Fig. 65) and *Thespesia populnea* (Fig. 133) or slightly bent as in *Urena lobata* (Fig. 102), *Malachra capitata* (Fig. 110) and *Pavonia zeylanica* or markedly curved as in *Sida* species (Figs. 7, 55, 62), *Abutilon indicum* (Fig. 90) and *Hibiscus solandra* (Fig. 148). Accordingly the embryo sac also may be straight or curved to a varying degree. The micropylar part of the nucellus consists of partly the several layered epidermal cap and partly the tissue derived from one or more primary parietal cells cut off by the hypodermally situated archesporial cells. Periclinal divisions of the cells of the nucellar epidermis occur at a very early stage (Figs. 99, 125). In *Urena lobata* (Fig. 100) and *Thespesia populnea* (Fig. 132) in which the parietal tissue is more extensive than in the rest, the cells stand out prominently by their richer deep-staining protoplasm and form a sort of ‘epistase’. The whole of the parietal tissue gets crushed by the enlarging embryo sac and only the epidermal cap or a part of it persists in the fertilisable ovule. Laterally the embryo sac is surrounded by several layers of cells which are more on the side of the funicule in campylotropous ovules. In *Urena lobata* (Fig. 100), *Malavavicus arboreus* (Figs. 113, 115), *Sida* species (Figs. 6, 52, 58, 59), *Abutilon indicum* (Fig. 93), *Pavonia zeylanica* (Fig. 137), *Hibiscus hirtus* (Fig. 145), *H. solandra* (Fig. 147) and *H. micranthus* (Fig. 149), the megaspore mother cells have their lower ends extending to the chalaza. In these species the antipodal end of the embryo sac reaches the tannin and starch bearing cells of the chalaza (Figs. 7, 54, 62, 102, 119, 148). Two or three layers of cells surrounding the extreme end of the sac become thick-walled (Fig. 57). In other species like *Althaea rosea* (Fig. 83) and *Thespesia populnea* (Fig. 132) there are several layers of nucellar cells below the group of megaspore mother cells. These cells later become elongated and thick-walled and form a hypostase (Figs. 133, 134). As the cells stand more or less in regular rows and connect the embryo sac and the vascular bundle in the chalaza, they seem to facilitate the conduction of food materials into the sac. In this feature, these species resemble some members of Sterculiaceae and Tiliaceae.

**Megasporogenesis**

The archesporium of the ovule may consist of a single hypodermal cell as in *Sida carpinifolia* (Fig. 49), *S. cordifolia* (Figs. 50, 51), *Abutilon indicum* (Figs. 91, 92), *Hibiscus hirtus* (Fig. 144) and *Hibiscus solandra* (Fig. 146) or a group of hypodermal and sub-hypodermal cells as in *Althaea rosea* (Figs. 72, 73), *Urena lobata* (Fig. 99), *Malavavicus arboreus* (Fig. 111) and *Thespesia populnea* (Figs. 123, 129). In the latter case, there are two types: in some like *Althaea rosea, Malachra capitata* (Figs. 103, 105, 109), *Malavavicus arboreus* (Fig. 112) *Pavonia zeylanica* (Figs. 137, 138), only one hypodermally placed cell continues to function while the rest merge into the nucellus. Only occasionally two cells may function till megaspore mother cell stage (Fig. 104) or more rarely till embryo sacs are formed (Figs. 67, 69, 71). In others like *Urena lobata* (Figs. 100, 101) and *Thespesia populnea* (Figs. 124–128) several cells continue to function and form tetrads or embryo sacs. None of the

Explanation of Figs. 99–110 (p. 14).

Figs. 99–102. *Urena lobata*. Fig. 99. Young ovule with several megaspore mother cells; note periclinal divisions in nucellar epidermis. ×285. Fig. 100. Nucellus with fully grown megaspore mother cells and accessory sporogenous cell; note epistase like structure. ×230. Fig. 101. A group of sporogenous cells in meiosis; note degeneration of one of the sporogenous cells. ×425. Fig. 102. Ovule showing entry of pollen tube. ×45.

Figs. 103–110. *Malachra capitata*. Figs. 103 and 104. Ovules with 1- and 2-functional megaspore mother cells. ×285 and 425 respectively. Fig. 105. Nucellus with megaspore mother cell showing formation of nucellar cap. ×425. Fig. 106. Nucellus with linear tetrad of which the lowest megaspore is enlarging. ×425. Fig. 107. Mature embryo sac. ×285. Fig. 108. Antipodals; note two-nucleate condition in two of them. ×425. Figs. 109 and 110. Loculi of young and old ovaries; note development of ‘gynobasic’ style. ×135 and 45 respectively.
Figs. 111–122. *Malva moschata* var. *arboretum*. Fig. 111. Ovule primordium with multicellular archesporium. \( \times 420 \). Fig. 112. Ovule showing divisions in primary parietal cell. \( \times 420 \). Fig. 113. Ovule with definitive and accessory sporogenous cells. \( \times 115 \). Fig. 114. Nucellus showing megaspore mother cell and development of accessory sporogenous cell and parietal layers. \( \times 420 \). Fig. 115. Ovule with megaspore mother cell in meiosis I. \( \times 115 \). Fig. 116. Sporogenous cells from the above magnified. \( \times 445 \). Fig. 117. Formation of tetrads by definitive and accessory sporogenous cells. \( \times 445 \). Fig. 118. Three 2-nucleate embryo sacs derived from different tetrads. \( \times 420 \). Fig. 119. Ovule with two mature embryo sacs. \( \times 65 \). Fig. 120. Ovule showing degeneration of embryo sacs. \( \times 45 \). Fig. 121. Micropylar part of embryo sac. \( \times 255 \). Fig. 122. Antipodals. \( \times 445 \).
Figs. 123–130. *Thespesia populnea.* Fig. 123. Ovule primordium with multicellular archesporium. ×425. Fig. 124. Young ovule showing development and structure of integuments and parietal tissue. ×135. Fig. 125. Nucellus showing sporogenous cells and development of parietal layers and nucellar cap. ×255. Figs. 126–128. Group of sporogenous cells in meiosis. ×425. Fig. 129. T.s. through a group of sporogenous cells. ×425. Fig. 130. Micropylar part of an embryo sac; note hooked synergids and starch grains in egg cytoplasm. ×285.
Figs. 131-142.—Explanation at foot of next page.
previous investigators reported such typically multicellular archesporium with several functional cells in Malvaceae. The archesporium in these species resembles that in *Pterospermum* species, e.g. *P. suberifolium* (C. V. Rao, 1952) and *Triumfetta rhomboidea* (C. V. Rao and K. V. S. Rao, 1952). In several species with a single functional cell, accessory sporogenous cells develop from one or more cells of parietal tissue, a feature to which Stenar (1925) has already drawn attention, e.g., *Sida cordifolia* (Fig. 53), *S. veronicaefolia* (Figs. 58–61), *Althaea rosea* (Figs. 74–79), *Abutilon indicum* (94–96), *Urena lobata* (Figs. 100, 101) and *Malvaviscus arboreus* (Figs. 113–117). The accessory sporogenous cells become demarcated at the time of meiosis of the definitive cells. In this connection Stenar (1925) makes a significant remark: 'in order to make sure whether accessory sporogenous cells are present or not, it is not enough to observe the early stages of ovules in which only a few cover cells are present, but such ovules in which the definitive sporogenous cells are undergoing divisions'.

The megaspore mother cells have an elongated and tapering form (Figs. 52, 93, 138, 147, 149). Due to the position of the nucleus nearer to the micropylar end of the cell at prophase I, the upper dyad cell is always smaller than the lower (Fig. 150). In the second division the cell wall may be laid in a horizontal (Figs. 60, 61, 106, 139, 152) or oblique (Figs. 95, 117) or in a vertical manner (Figs. 78, 79, 140, 151) so that megaspore tetrads are not always linear. T-shaped tetrads are commonly formed by the deep seated cells probably due to spatial relations. Normally the chalazal megaspore functions (Figs. 59, 61, 67, 80–83, 97, 106, 139, 140). In *Althaea rosea*, in one case (Fig. 80) the second megaspore from the micropylar side was seen to be enlarging. The case sketched in fig. 68 of *Kydzia calycina* appears to be due to the functioning of two megaspores of the same tetrad. The third megaspore from the micropylar side is more precocious and has formed a 4-nucleate embryo sac while the lowest is still in the uninucleate stage. In another case (Fig. 70), two superposed 8-nucleate embryo sacs are seen which also appear to be derived from two megaspores of the same tetrad. Similar development of two megaspores of a tetrad was reported by Gore (1932) in cotton.

Usually the accessory sporogenous cells degenerate before undergoing the meiotic divisions. The more favourably placed sporogenous cells complete the meiotic divisions earlier (Figs. 59, 61, 77–79, 95, 96, 117) and one or more megaspores derived from them enlarge and crush out the nonfunctional cells (Figs. 80–82). Only rarely the accessory sporogenous cells divide earlier (Figs. 97, 117) in which case the megaspores derived from them have greater chances of functioning. Also when the accessory or definitive cells are collaterally placed, the megaspores derived from them have equal chances of functioning since they have equal nutritive facilities and the enlargement of one sac does not result in immediate crushing of the other as happens when the two are superposed. The embryo sacs in such cases reach maturity (Figs. 71, 118–120). In embryo sacs which are superposed, usually the enlargement of one results in crushing out the other (Fig. 70).

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**Explanation of Figs. 131–142** (p. 144).

**Figs. 131–136.** *Thespesia populnea*. Fig. 131. Ovule with several megaspore mother cells. x125. Fig. 132. Nucellus with megaspore tetrads; note 'epistase' like group of parietal cells. x70. Fig. 133. L.s. mature ovule; note integumentary vascular bundles and hypostase. x70. Fig. 134. Hypostase magnified. x155. Fig. 135. T.s. ovule showing integumentary vascular bundles. x35. Fig. 136. Seed with its vascular supply. x3.

**Figs. 137–142.** *Pavonia zeylanica*. Fig. 137. Young ovule with megaspore mother cell. x110. Figs. 138 and 139. Nucelli with megaspore mother cell and linear tetrad respectively. x400. Fig. 140. A T-shaped tetrad. x400. Fig. 141. Four nucleate embryo sac which has begun to curve. x265. Fig. 142. Mature embryo sac. x310.
Figs. 143-145. *Hibiscus hirtus*. Fig. 143. L.s. loculus of ovary. ×45. Fig. 144. Ovule primordium with one archesporial cell. ×400. Fig. 145. Ovule showing formation of parietal layers. ×400.

Figs. 146-148. *Hibiscus salandra*. Fig. 146. Young ovule. ×185. Fig. 147. Nucellus with full grown megaspore mother cell. ×400. Fig. 148. Mature ovule. ×280.

Figs. 149-154. *Hibiscus micranthus*. Fig. 149. Nucellus with full grown megaspore mother cell. ×400. Figs. 150-152. Dyads, T-shaped and linear tetrads respectively. ×400. Figs. 153 and 154. Micropylar and antipodal parts of embryo sac; Fig. 153, ×400; Fig. 154, ×665.
Embryo Sac

By three successive free nuclear divisions of the megaspore nucleus, the 8-nucleate embryo sac is derived. In campylotropous ovules, the embryo sac begins to curve at the 2- or 4-nucleate stage (Fig. 141) and the curvature increases with the growth of the sac (Fig. 142). The nuclei of the synergidls are derived from one parent nucleus and those of the egg and upper polar nucleus from another (Fig. 82). In *Sida cordifolia* (Fig. 56), *S. carpinifolia*, *S. veronicaefolia*, and *Thespesia populnea* (Fig. 130) the synergidls show prominent hooks. In the rest they are pear-shaped without hooks (Fig. 153). The synergidls and egg show normal vacuolation. In *Sida carpinifolia* and *S. cordifolia* (Fig. 56), the synergidls show filiform apparatus. In *Thespesia populnea*, starch grains are seen not only in the embryo sac but also in the cytoplasm of the egg (Fig. 130); these are absent from the embryo sacs of other species. The polar nuclei meet at about the middle of the sac and travel together upwards and remain in proximity to the egg apparatus. Only in *Althaea rosea* (Fig. 85) and *Malvaviscus arboreus* (Fig. 121) they were seen to fuse before fertilization. The antipodaln show much variation. In *Sida veronicaefolia* (Fig. 63), *Kydia calycina* (Figs. 70, 71), *Malvaviscus arboreus* (Fig. 122) and *Hibiscus solandra* (Fig. 148), they are three in number and 1-nucleate. In *Sida carpinifolia* (Fig. 57) in one case, one of the cells divided and formed two cells. In *Althaea rosea* (Figs. 86, 87), *Abutilon indicum* (Fig. 98), *Malachra capitata* (Fig. 108), and *Hibiscus micranthus* (Fig. 154) either the antipodal nuclei divide in free nuclear manner or a cell wall is formed after the division so that binucleate and supernumerary antipodals are formed. In *Hibiscus micranthus* they increased still further in number after fertilization and persisted till the embryo became a large globular mass.

Discussion

A comparative study of the embryological features of the various species investigated shows that while the characters of the microsporangium and male gametophyte are fairly uniform, there is some variation in the development and structure of the archesporium, embryo sac and ovule.

The microspore mother cells in several species form a single row in the anther. The tapetum is of plasmoidal type. The pollen grains are multiporate and spinescent and distinctly differ from those of other families of the order in which they are predominantly smooth walled and triporate. Wodehouse (1936) is of the opinion that spinescent multiporate pollen is more evolved than the smooth walled and triporate pollen. On the basis of pollen grain characters, Malvaceae seems to be the most evolved family of the order. The campylotropous ovules which are common in Malvaceae are also not met with in other families of Malvales. In *Adansonia digitata* (Bombacaceae), the ovule is anatropous but the seed becomes campylotropous. The presence of epistase, hypostase, synergidls with filiform apparatus, well defined transmitting tissue in the style and obturator are again features of a specialised nature. In the presence of super-numerary, sometimes binucleate and persistent antipodals, Malvaceae differs from other families of the order and resembles highly evolved families like Rubiaceae, Compositae and Gramineae. Their persistence till a comparatively late stage in the development of the seed and their position between the endosperm and the food bearing cells of the chalaza suggest that they might assist in the transport of food materials into the embryo sac, a function which the persistent pollen tube seems to subserve in the micropylar part of the ovule (C. V. Rao, 1952a). From the above, it can be inferred that embryologically Malvaceae is the most advanced family among the Malvales.
Malvaceae is divided into four tribes (Schuman in Engler and Prantl, 1895), based on the disposition of carpels, nature of fruit, number of stylar branches, etc.

1. **Malopeae**: Carpels in vertical rows.
2. **Malveae**: Fruit schizocarp; stigmas as many as carpels. *Sida, Abutilon, Althaea, Kydia*.
3. **Ureneae**: Fruit schizocarp; stigmas twice as many as carpels. *Urena, Malaviscus, Pavonia* and *Malachra*.
4. **Hibisceae**: Fruit capsule; stigmas equal to the number of carpels. *Gossypium, Thepesia* and *Hibiscus*.

A comparison of the embryological features shows that there is much overlapping. Genera belonging to different tribes may show similar embryological features like the formation of accessory sporogenous cells in the ovules (*Sida, Malaviscus*) or typical multicellular archesporium with several functional cells (*Urena, Thepesia*). Similarly genera belonging to the same tribe may differ markedly in their embryological features. This point becomes clear on comparing the embryological features of the three genera of the tribe of Hibisceae, namely, *Gossypium, Thepesia* and *Hibiscus*. *Gossypium* and *Thepesia* resemble each other in their anatropous ovules, massive integuments, integumentary vascular bundles, and differ from *Hibiscus* which shows campylotropous ovules and no integumentary vascular supply. On the other hand, *Thepesia* differs from *Gossypium* in the presence of epistase and hypostase, multicellular archesporium with several functional cells in the ovule, hooked synergids without filiform apparatus and presence of starch grains in the embryo sac. Though Edlin (1935) considered on the basis of capsular fruits, that the tribe Hibisceae is the most primitive among Malvaceae and transitional between Bombacaceae and Malvaceae, it seems to be the most evolved on embryological grounds, a conclusion reached by Reeves (1936) also on study of seed anatomy. They show features of specialisation like organisation like epistase, hypostase, filiform apparatus in synergids, massive integuments and integumentary vascular bundles, epidermal hairs and resin glands in the testa and non-endospermic seeds with food reserve in the embryo.

**Summary**


Of the four layered anther-wall, the sub-epidermal layer develops into the fibrous endothecium and the innermost into the tapetum of the plasmodial type. The tapetum seems only to hasten the growth of the sculpturing of the exine but not initiate it. In some species like *Pavonia zeiylanica*, the primary sporogenous cells of the anther function as the microspore mother cells directly while in others like *Abutilon indicum*, they undergo a secondary increase. Microspore tetrads are usually tetrahedral bilateral and linear tetrads being noticed occasionally. Cytokinesis is by furrowing. The pollen grains are spinescent and multispore and are shed mostly in the 2-nucleate condition, though in *Kydia* a few 3-nucleate grains were met with. The generative cytoplasm forms a hyaline sheath around the nucleus in the initial stages and is later obscured by the starch grains, protein and fat that accumulate in the cytoplasm of the vegetative cell.

The ovules are bitegmic, crassinucellate, anatropous or more commonly campylotropous. The inner integument is more massive than the outer. Some cells of the integuments and chalaza accumulate tannin and starch grains. *Thepesia* shows integumentary vascular bundles. 'Epistase' occurs in the nucellus of *Urena* and *Thepesia* and also a hypostase in the latter.

The archesporium is typically one-celled in some members like *Hibiscus* species while it is multicellular with several functional cells in *Urena* and *Thepesia*. In several genera like *Sida, Malaviscus, Abutilon*, and *Althaea*, some of the parietal cells later assume characters of sporogenous cells and function as such till the formation of tetrads or embryo sacs. In *Kydia*, some-
times two megaspores of the same tetrad function and develop into 8-nucleate embryo sacs. Megaspore tetrads are linear as well as T-shaped, and embryo sac develops according to normal type. Synergids are hooked in *Sida* and *Thelesperma*; they show flliform apparatus in *Sida cordifolia* and *S. corprufolia*. Polar nuclei fuse only at the time of fertilization except in *Althaea rosea* and *Malvaviscus arboreus* in which they fuse earlier. In some like *Abutilon indicum*, *Hibiscus hirtus* and *H. microphyllum*, and *H. hirtus* they persist till a late stage in the development of the seed and seem to assist in transport of food materials from the starchy bearing cells of the chalaza into the embryo sac. Starch grains are seen in the cytoplasm of the embryo sac and egg of *Thelesperma populnea*.

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REFERENCES


Guignard, L. (1893). Recherches sur le developpement de la graine et en particulier du tegument seminal. *Jour. de bot.*, 7, 1-14, etc.


C. Venkata Rao: Embryological Studies in Malvaceae


——— (1931). Studies in the cytology of the Hibisceae—II. The behaviour of the nucleus during cell division in the root tip of Thespesia populnea and comparative observations of the phenomenon in some related plants. Ibid., 45, 49–72.

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