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CONTRIBUTION TO THE EMBRYOLOGY OF *CASSIA MIMOSOIDES* L.[1]

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ABSTRACT

Anther wall development conforms to the Dicotyledonous type. Anthers dehisce by apical pores. Thickened epidermal cells impegranated with tannin persist. Tapetum is of amoeboid type. Microspore tetrads are both tetrahedral and cross shaped. Tricolpate pollen grains are 2-celled at anthesis. Bitegamic crassinucellate ovule is anatropous. Parietal tissue is dual in origin. Megaspore tetrads may be linear or T-shaped. Embryo sac development follows Polygonum type. Synergids persist after fertilisation. Antipodals are ephemeral. Fertilization is porogamous. Endosperm *ab initio* is free nuclear. A tube like coenocytic endosperm haustorium is present. Endosperm cells radially elongated and situated below the micropyle are coenocytic and haustorial in nature. Embryo follows Asterad type of development.

INTRODUCTION

The embryological literature on the sub-family Caesalpinoideae has been meagre. The main contributions to our knowledge have been by Guignard (1881), Saxton (1907), Ghosh and Alagh (1933). Datta (1934), Pantulu (1945), Rau (1951), Pellegrini (1954) and Venkatesh (1956a, 1956b, 1957). In recent years additional information is made available by Goursat (1963), Rembert (1969), Venkateswarlu and Seshavatharam (1971), Bhasin (1972) and Gomkale (1977) who studied a few more members belonging to this sub-family.

MATERIAL AND METHODS

Cassia mimosoides L., belonging to the tribe Cassieae of the Caesalpinoideae, is a herb, with compoud leaves. The flowers are axillary and stamens ten in number are alternately longer and shorter.

The material at different stages of development, collected from the University campus, Nagpur, was fixed in 70% FAA. The customary methods of dehydration and embedding were followed. The sections cut at 10-14 μm in thickness were stained in Delafield's haematoxylin.

OBSERVATIONS

Microsporogenesis and microgaemtophyte : The tetra-sporangiate anther (Fig. 1) prior to dehiscence presents a bilocular appearance. The anther primordium consists of a homogenous mass of parenchymatous cells. The younest stage in development of anther, observed consists of mass of sporogenous cells surrounded by tapetum followed by 1/2 middle layers and a hypodermal layer (Figs. 1-3). The further periclinal divisions in hypodermal and the middle layers add to the thickness of anther wall (figs. 2-4).

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However, the mature anther wall consists of six layers of cells including the epidermis (Fig. 5). The tapetum is derived from inner secondary parietal layer (Figs. 2, 3). The anther wall development conforms to Dicotyledonous type of Davis (1966).

The cells of outermost wall layer i.e., epidermis become thick walled and get filled with tannin like substance during the formation of microspore tetrads (Fig. 9). These tannin filled epidermal cells persist at the dehiscence of anther (Fig. 20). A few cells of epidermis along the would be longitudinal line of dehiscence, elongate to produce unicellular hairs (Figs. 18-20) which remain entangled with each other not allowing the anther to dehisce by longitudinal slit. On the other hand, the cells of anther epidermis situated at the extreme apex show pronounced radial elongation, become thick walled with outer tangential walls showing achinulate appearance (Figs. 16, 17). These cells separate from each other along the longitudinal line of dehiscence to produce a pore through which pollen grains get disseminated (Fig. 16).

The hypodermis, as well defined layer and devoid of fibrous thickenings, persists at dehiscence of anther (Fig. 16). Of the three middle layers, one next to the tapetum is first to collapse. It degenerates prior to onset of reduction division in pollen mother cells (Fig. 5). The layer next to it degenerates soon after meiosis II (Fig. 9). The outer middle layers, however, persists for a considerable time (Figs. 12, 16, 17).

The uninucleate tapetal cells (Fig. 2) soon after meiosis II lose their radial and inner tangential walls. This is followed by inflow of cell contents into the anther locule around the developing pollen grains (Fig. 9, 12). The tapetum, thus, conforms to the amoeboid type. It is completely absorbed by developing grains (Fig. 17). Consequent to the disappearance of tapetum, globular markings appear on inner tangential walls of the persisting middle layer. The globules resemble exine in staining capacity (Figs. 16, 17) and very much simulate 'Ubisch' granules.

The primary sporogenous cells divide mitotically to increase the number of microspore mother cells (Figs. 2-5). Each microspore mother cell undergoes normal meiosis. The resulting two nuclei remain embedded in common cytoplasm (Figs. 6-8). The cytokinesis of simultaneous

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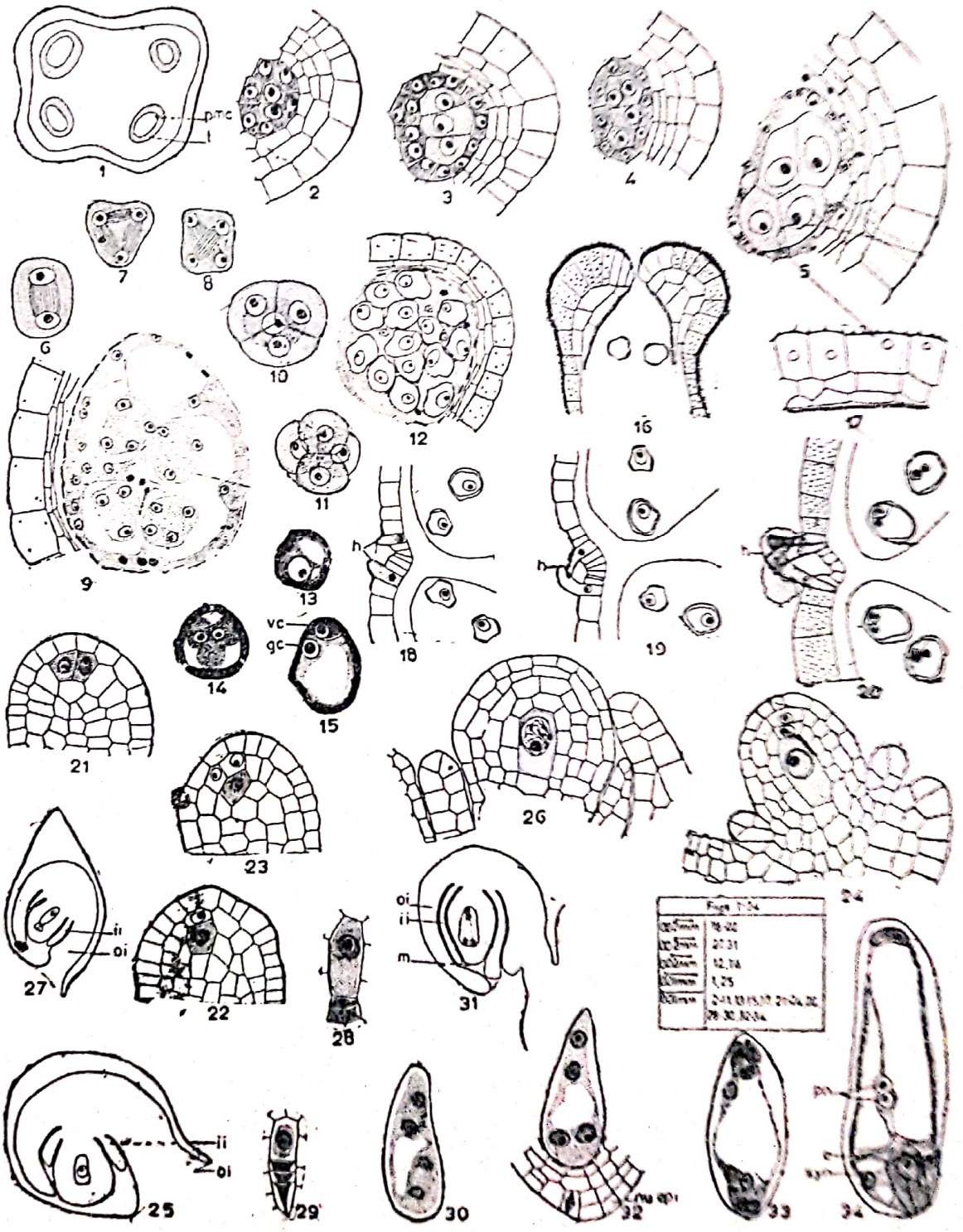
Text Figs. 1-34 : Micro and megasporogenesis and gametophytes.

Fig. 1 : T.S. anther locule (diagrammatic). Figs. 2-4 : T.S. part of anther showing stages in the development of wall layers. Fig. 5 : Same as above showing 6 layered anther wall. Figs. 6-8 : Pollen mother cells showing stages in meiosis I and II. Fig. 9 : T.S. part of anther ; note two degenerating middle layers, amoeboid tapetum and tannin filled epidermal cells. Figs. 10-11 : Tetrahedral and cross shaped tetrads, Fig. 12 : T.S. anther (Part) ; note periplasmodial nature of tapetum. Fig. 13 : Uninucleate microspore. Figs. 14-15 : 2-celled Pollen grains. Fig. 16 : L.S. Part of anther at anthesis; note persisting epidermis with hairs, endothecium without fibrous thickening and ubisch granules. Fig. 17 : L.S. part of anther wall; note Ubisch granules. Figs. 18-20 : T.S. part of anther (diagrammatic) showing hairs at stomial region. Figs. 21-23 : L.S. young ovule showing unicellular archesporial cell having divided periclinally in Figs. 21-22 : twin archesporial cells in Fig. 23. Figs. 24, 26 : L.S. young ovule ; note, megaspore mother cell and developing integuments. Fig. 25 : L.S. ovary (diagrammatic) at M. M. C. stage. Fig. 27 : same as above at tetrad stage. Figs. 28, 29 : T-shaped and linear megaspore tetrads. Figs. 30, 32, 33 : 4 and 8 nucleate embryo sacs ; note periclinal division in nucellar epidermis in Fig. 32. Figs. 31 : L.S. ovule (diagrammatic) at 4 nucleate stage of embryo sac. Fig. 34 : L.S. mature embryo sac.

(*e*—egg ; *gc*—generative cell ; *h*—hairs ; *ii*—inner integument ; *m*—micropyle ; *nuepi*—nucellar epidermis ; *oi*—outer integument ; *pmc*—pollen mother cells ; *pn*—polar nuclei ; *syn*—synergid ; *t*—tapetum, *vc*—vegetative cell).

type, occurs by furrowing. The tetrads produced are tetrahedral or cross shaped (Figs. 10-11). The microspores soon separate from each other (Fig. 12) and each secretes its own wall which differentiates into outer thick exine and inner thin intine (Fig. 13).

The uninucleate microspore with centrally situated nucleus (Fig.12) undergoes increase in size. Now a vacuole



appears in the centre and the nucleus migrates to the peripheral layer of cytoplasm forming a large vegetative cell and a small densely cytoplasmic generative cell (Figs. 14, 15). The pollen grains are tricolpate and bicelled at anthesis. However, the dark staining substance within the cytoplasm impares the structure of mature pollen grain.

Megasporogenesis and megagametophyte : The monocarpellary gynoecium consists of 6-8 ovules produced from the marginal placentae. The mature ovule is bitegmic, crassinucellate and anatropous (Figs. 30, 35, 37).

The integument initials differentiate from nucellar epidermis. Initials of both the integuments arise almost simultaneously (Figs. 21, 22). The inner rather slow in growth (Figs. 25-27), fails to grow over the nucellar apex (Fig. 30), a stage at which it appears as if the outer integument alone contributes in the formation of a micropyle. Late during development the inner integument grows further and gets involved in the construction of a micropyle (Figs. 35, 37, 38).

The ovule primordium straight, to begin with (Fig. 21, 22) due to unilateral growth undergoes a curvature (Figs. 25, 27). The mature ovule is anatropous (Fig. 31).

The hypodermal archesporium consists of a single cell (Figs. 21, 22). Occasionally two cells are observed (Fig. 23).

The archesporial cell characterized by dense cytoplasm and a conspicuous nucleus, divides periclinally producing a primary parietal cell on the outer and a primary sporogenous cell on the inner side (Fig. 21). The periclinal and anticlinal divisions in the former (Figs. 22, 24) produces a three layered parietal tissue at megaspore mother cell stage (Fig. 26). Further periclinal divisions in cells of both praietal layers and nucellar epidermis (Fig. 31) produce massive parietal tissue (Fig. 38).

The primary sporogenous cell functions as megaspore mother cell (Fig. 24, 26). It increases in size and divides meiotically to produce a linear or T-shaped tetrad of megaspores (Figs. 28, 29). The chalazal megaspore functions (Figs. 28, 29) to give rise to Polygonum type of embryo sac (Maheshwari, 1950).

The first mitosis in functional megaspore is followed by polar disposition of daughter nuclei. Each daughter nucleus again divides twice producing a 4- and finally 8-nucleate embryo sac (Figs. 30-33).

In an organized embryo sac the egg hangs below the synergids (Fig. 24). The hooked synergids have filiform apparatus and show normal structure (Fig. 41). The polars fuse to form a secondary nucleus prior to fertilization (Fig. 34). The antipodals are ephemeral and disintegrate during the mature organization of embryo sac (Figs. 33, 34).

Fertilization : The fertilization is porogamous (Fig. 35). The pollen tube during entry, may penetrate one of the synergids and destroys it (Figs. 39, 42). However, at times both the synergids continue to remain intact during formation of endosperm (Fig. 41). the triple fusion preceedes syngamy (Fig. 36).

Endosperm : The primary endosperm nucleus undergoes synchronous nuclear divisions (Figs. 39-42). The first division in zygote occurs only after formation of 16 or more endosperm nuclei (Figs. 42-44). Later divisions are non-synchronous (Fig. 46). The nuclei produced lie embedded in the peripheral layer of cytoplasm (Fig. 45). The cytoplasm around the proembryo, as the latter attains 8-celled stage, undergoes clevage to pro-

duce uninucleate units (Fig. 46). Soon, this is followed by wall formation (Fig. 47). The endosperm around the embryo is first to become cellular (Fig. 47). Though, the wall formation gradually extends downwards (Fig. 50) the entire endosperm does not become cellular and the nuclei at the narrow chalazal end continue to lie embedded in common cytoplasm. The coenocytic structure, thus, formed functions as haustorium (Figs. 48, 49).

The endosperm cells in the micropylar region particularly those above the suspensor of embryo elongate considerably and become multinucleate due to mitotic activity so that each cell contains within it 4-8 nuclei (Figs. 48, 51). Such coenocytic cells constitute a micropylar haustorium, completely a new structure for the Caesalpinoideae.

Embryo : The first transverse division in fertilized egg (Figs. 52, 53) produces a bicelled proembryo consisting of two superposed cells, viz., a terminal cell *ca* and a basal cell *cb*. The next division in the terminal cell *ca* is vertical (Figs. 54, 55, 58) while it is transverse in the basal cell *cb* (Figs. 54, 55). The proembryo, thus, produced at the end of second cell generation consists of 4-cells disposed in 3 tiers, viz., *ca*, *m* and *ci* (Fit. 54). The resulting proembryo tetrad belongs to category A_2 of Souèges system of classification (1951).

The plane of segmentation in tier *ca*, at times, is obliquely vertical (Fig. 60). Under this situation the next division in one of the derivatives of terminal tier *ca* is by a wall oriented at right angle to the first oblique wall producing a superior pyramid shaped cell designated as epiphysis initial (*e*) (Figs. 61, 62). The differentiation of epiphysis initial in *Cassia mimosoides*, thus, depends upon the plane of orientation of first wall in the terminal cell *ca* of a two celled proembryo.

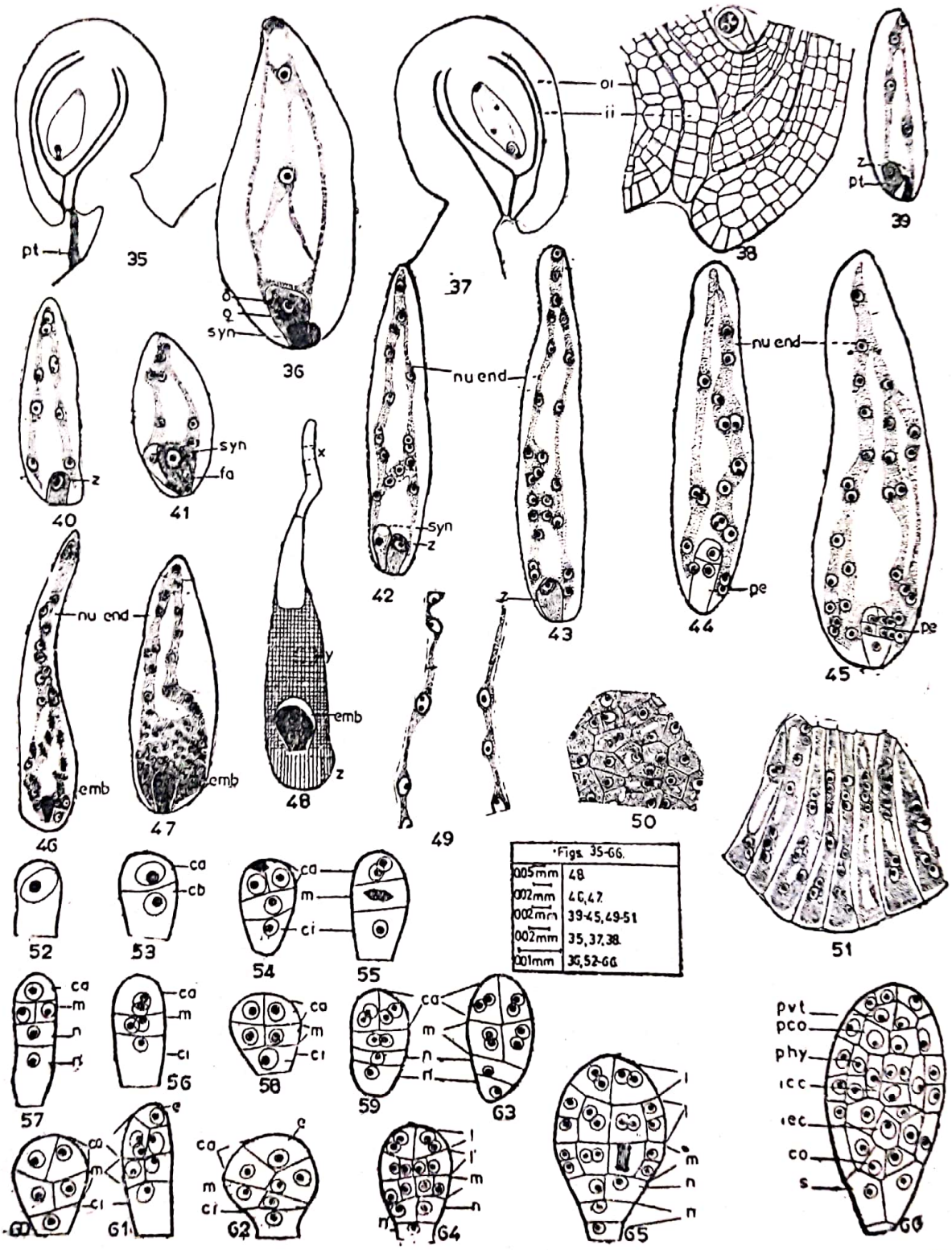
Normally, the first vertical division in tier *ca* is followed by another vertical division, but at right angle to the first resulting in a quadrant (*q*) (Figs. 59, 63). Each cell of the quadrant (*q*), now segments transversely and two superposed quadrants, thus, produced are designated as *l* and *l'* (Figs. 64, 65).

The first vertical divison in tier *m* (Figs. 55-59) followed by another vertical division but at right angle to the first results in four circumaxial cells (Fig. 63). The divisions in tiers *ca* and *m* occur almost simultaneously (Figs. 55, 56, 58) though at times those in *m* may precede divisions in *ca* (Fig. 57).

The dermatogen gets delimited first in tiers *l'* and *m* and later proceeds to tier *l*. Further divisions in tiers *l*, *l'* and *m* occur in different planes to produce a globular embryo (Fig. 66). The derivatives of entire tier *l* or epiphysis initial (*e*), when present, engender stem tip (*prt*). The elements produced from tier *l'* and *m* give rise to cotyledons (*pco*), hypocotyledonary region (*phy*) and a central cylinder of root (*icc*).

The transverse division in cell *ci* of a 4-celled proembryo produces two superposed cells, viz., *n* and *n'* (Figs. 57, 59, 63). The tire *n* undergoes a longitudinal division (Figs. 64, 65) while tier *n'* divides transversely. The derivatives of tier *n'*, viz., *o* and *p* produce a short suspensor. The tier *n* by transverse segmentation produces two superposed tiers of which the derivatives of superior tier are responsible for origin of root cortex (*ice*) while those of inferior tier produce root cap (*co*) (Fig. 66).

The embryo in *Cassia mimosoides*, thus, is derived from tier *ca* and *cb* of a two celled proembryo and development corre-



sponds to Asterad type of Johansen (1950) or follows Grand Period I Series A, Megarchetype II of Souèges (1951) system of classification.

DISCUSSION

The Leguminosae are characterised by considerable variations in the pattern of development, in their different organs. The hypodermal male archesporium is described as uni-and multi-cellular (Datta, 1934 ; Mukherjee and Thakur, 1959 and Bhasin, 1972). The variations in the number of wall layers is commonly met in the Caesalpinioideae, e.g. in *Cassia mimosoides* (present study), there are present 6 wall layers, while Bhasin (1972) reported their number to be 6-7 in *Cassia absus* and as many as 10-11 in *Cassia auriculata*. In *Cassia* sub genus *Fistula* and *Senna* there are present 10 wall layers (Venkatesh, 1956a, 1957). The anther wall development conforms to Dicotyledonous type of Davis (1966).

The hypodermal layer does not show fibrous thickenings in the present study. Further the unicellular hairs prohibit the anther wall from splitting longitudinally. The members where dehiscence does not occur by a longitudinal slit the thickenings fail to develop e.g. genus *Cassia* sub-genus *Fistula*, *C. absus* (Venkatesh, 1956a, b) and *C. auriculata* (Bhasin, 1972). On the other hand in *C. absus* (Venkatesh, 1956b) the hypodermal layer starts degenerating early during development. However, in *C. auriculata* not only the cells of hypodermis but also those of the middle layers next to the hypodermis become thick walled and persist at dehiscence (Bhasin, 1972). In *Cassia mimosoides*, too, hypodermal and a middle layer persist for a considerable time.

The amoeboid type of tapetum, has been reported in *Cassia mimosoides* (Venkatesh, 1956b). The present investigation supports this finding. However, in members belonging to the Caesalpinoideae investigated by Gomkale (1977) the tapetal cells even though lose their walls the protoplasmic contents remain *in situ* forming a sort of sheath around the developing microspores i.e., contents never migrate within the locule between the developing microspores. Thus, according to him, true periplasmodium is absent. In *Cassia absus*, periplasmodium has been reported by Venkatesh (1956b) but Bhasin (1972), working on the same species failed to observe the protrusion of protoplasmic contents within the anther

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Text Figs. 35—66 : Stages in the development of endosperm and embryo.

Fig. 35 : L.S. ovule (diagrammatic) at zygote stage ; note pollen tube. Fig. 36 : L.S. embryo-sac; note male gamete in egg cytoplasm, degenerating synergids and antipodals. Fig. 37 : L.S. ovule (diagrammatic) showing zygote and free endosperm nuclei. Fig. 38 : L.S. micropylar part magnified. Figs. 39-45 : L.S. embryo-sac, showing stages in the development of nuclear endosperm; note persisting synergids and filiform apparatus in Fig. 41. Fig. 46 : L.S. embryo-sac showing cytoplasmic cleavage in endosperm at micropylar region and non synchronous nuclear division. Fi. 47; L.S. embryo- sac ; note endosperm cellular at micropylar and free nuclear at chalazal end. Fig. 48 : L.S. embryo-sac (diagrammatic) showing nature of endosperm. Fig. 49 : Part marked 'X' in Fig. 48 magnified to show free nuclear chalazal endosperm haustorium. Fig. 50 : Part marked 'Y' in Fig. 48 magnified ; note mitotic activity in cellular endosperm. Fig. 61 : Part marked 'Z' in Fig. 48, magnified ; note multinucleate enlarged cells of endosperm. Figs. 52-56 : Stages in development of embryo (for details see text).

(*emb*—embryo, *end*—endosperm, *end*—endosperm haustorium, *fa*—filiform apparatus ; *ii*—inner integument ; *nu end*—nuclear endosperm, *oi*—outer integument, *pemb*—proembryo, *pt*—pollen tube, *syn*—synergid, *z*—zygote, ♂ —male gamete, ♀—female gamete).

locule. She observed their degeneration *in situ*. thus, contradicting the earlier statement.

The patterns of microspore tetrads is determined by the orientation of spindles during meiosis II. The pollen grains at anthesis are two celled in *Cassia mimosoides*. This appears to be the characteristic feature of the entire Leguminosae (Tischler, 1925 ; Datta, 1934 ; Maheshwari, 1950 ; Venkateswarlu and Seshavatharam, 1971). However, according to Mukherjee and Thakur (1959) in *Caesalpinia cristata* pollen grains are 3-celled at anthesis but appear two celled because of early degeneration of vegetative cell. In *Bauhinia acuminata* (Gomkale, 1977) too, the grains are shed at 3 celled stage.

The initials for both the integuments differentiate rather early (Gomkale, 1977). A well organised zigzag micropyle, derived from both the integuments, as described by Rembert (1968), is true for the present species.

The female archesporium is hypodermal and may be uni- or bi-cellular. However, in *Cassia absus* (Bhasin, 1972) it is multicellular, a condition reported by Martin (1914), Maheshwari (1911), Mukherjee and Thakur (1959) and Rembert (1969). In *Cercis canadensis* according to Rembert (1969) the archesporium is subhypodermal and the same directly functions as megaspore mother cell. The deep seated archesporium, described by Rembert (1969) actually appears to be a megaspore mother cell produced after periclinal divisions in the archesporium and subsequent periclinal divisions in primary parietal cell. The megaspore tetrads within the family are both linear and T-shaped (Roy, 1933 ; Pantulu, 1945 ; Rembert, 1969 ; Bhasin, 1972) and same is true for species under investigation. The chalazal megaspore functions in the members belonging to the Leguminosae (Davis, 1966). However, in *Cassia tomentosa* (Saxton, 1907) and *Cassia purpurea* (Ghosh and Alagh, 1933) 3rd megaspore from micropylar end functions. In *C. auriculata* (Bhasin, 1972) both chalazal and sub-chalazal megaspores undergo increase in size but any one of these may function. In *C. abbreviata* var. *granitica* and *Gleiditisia triconthes* there is tendency on the part of sub-chalazal megaspore to persist for sometimes but mature embryo sac is always derived from the chalazal one.

The endosperm in the Leguminosae (Guignard, 1981 ; Rau, 1950 ; Pantulu, 1951 ; Bhasin, 1972 and present study) *sensu stricto* follows the nuclear type of development. Later, it becomes cellular. In *Cassia mimosoides*, however, the chalazal part continues to be free nuclear forming a highly elongated coenocytic haustorium In species of *Cassia*, viz., *C. occidenalis*, *C. auriculata* and *C. glauca*, the haustorial activity of the endosperm has been described by Pantulu (1951). The shape of haustorium in *Delonix* has been described as broad sac like while in *C. sophora* it is tubular with dialated tip (Johri and Garg, 1959).

A noteworthy feature in the present study, and hitherto not reported for the entire Leguminosae, is presence of haustorial activity of endosperm at the micropylar end.

Much is not known regarding the development of embryo in the Caesalpinoideae. The available information reveals that the pattern of dvelopment uniformally follows Asterad type (Pantulu, 1951 ; Pellegrini, 1954 ; Venkateswarlu and Seshavatharam, 1972 ; Bhasin, 1972 and present study). Guignard (1881) in *Caesalpinia mimosoides*, reported differentiation of epiphysis initial at 3rd cell

generation and non-delimitation of suspensor while in *Cassia corymbosa* suspensor is reported to be massive.

The only report of Onagrad type of embryo development in Caesalpinioideae is by Goursat (1963).

The embryo development in the Caesalpinoideae invariably correspnds to Megarchetype II. However, in *C. fistula*, *C. alata* and *Delonix alata* development, according to Venkateswarlu and Seshavatharam (1971), corresponds to Megarche type III.

In *Cassia mimosoides*, the embryo follows Asterad type of development. Occasionally epiphysis initial gets differentiated, depending upon the course of development during 2nd cell generation. The embryogeny in this species, corresponds to Polygonum variation in case epiphysis initial does not get differentiated or if differentiated comes nearer to Geum variation of Asterad type. This corroborates with the earlier findings of Bhasin (1972).

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