J. Indian bot. Soc., 61 : 39—46, 1982.

EMBRYOLOGICAL STUDIES IN *PROSOPIS JULIFLORA* (SW.) DC.[1]

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ABSTRACT

The paper deals with the embryological features of *Prosopis juliflora*. Male archesporium is hypodermal and consists of two longitudinal rows of cells. Anther wall follows Monocotyledonous type of development. The tapetum is of secretory type. Microscopores are 3-celled at anthesis. The anatropous ovule is bitegmic and crassinucellate. The embryo sac development is of Polygonum type. Endosperm is nuclear and forms haustorial structures at chalazal end. Embryo development conforms to Onagrad type or follows Grand period I, series A_2 or A_1 and Megarchetype IV.

INTRODUCTION

During the last two decades much work has not been done on embryology of the subfamily Mimosoideae except seed morphology (Vassal, 1971) and pollen structure (Caccavari, 1971 ; Robbertse, 1973). The embryology of *Porsopis juliflora* which grows wild around Nagpur is described.

MATERIAL AND METHOD

The material was fixed in FAA Dehydration and embedding was done as per routine methods. Sections were cut between 8 14 μ and stained with Heidenhains iron-alum haematoxylin with counter stain of erythrosin.

OBSERVATIONS

Microsporogenesis and male gametophyte :

In each lobe of an anther primordium, in hypodermal region, differentiates a plate of two cells, which constitute the archesporium. They divide periclinally (Fig. 1) to produce a primary parietal layer on the outer and a primary sporogenous layer on the inner side (Fig. 1). The former divides both anticlinally and periclinally. Of the two layers, thus produced the outer differentiates into endothecium while the inner by a periclinal division gives rise to two layers (Fig. 2). The inner differentiates into tapetum (Fig. 3) whereas the other by one more periclinal division (Fig. 3) produces two middle layers. The anther, thus, consists of five wall layers (Fig. 3) and development conforms to Monocotyledonous type (Davis, 1966).

The epidermal cells during development strech tangentially and become vacuolate (Fig. 5). They in the region of stomium are papillose and persist till anthesis (Fig. 5). The hypodermal layer, at two celled stage of pollen grains, develops fibrous thickenings and differentiates as endothecium (Figs. 5, 6). Of the two middle layers the inner is first to degenerate (Fig. 4). The remains of the outer middle layer persist for some time.

1. Accepted for publication on February 26, 1981.

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The tapetal cells continue to remain uninucleate but enlarge and become vacuolate during meiosis in the microspore mother cells (Fjg. 4). As the microspore tetrads are being organized walls of tapetal cells disintegrate and the protoplasmic contents besiege the developing tetrads but never protrude into the anther locule. The microspore tetrads are temporarily enclosed within a thick callose sheath but later the microspores lie scattered in the anther locule.

The uninucleate microspore increases in size. Its nucleus which migrates to the peripheral cytoplasm due to appearance of vacuole in the centre, divides to form a large vegetative cell and a small generative cell (Fig. 5). Prior to dehiscence, the generative cell divides to produce two spindle shaped male gametes (Fig. 6).

The spherical microspore characterized by the alveolar cytoplasm is provided with thick smooth exine and thin intine (Fig. 6.).

Megasporogenesis and female gametophyte :

The primordia of both entiguments differentiate simultaneously from nucellar epidermis (Fig. 8). The outer grows faster (Fig. 12) along the dorsal suture of the carpel and forms a flap over the inner integument. At mature embryo sac stage both the integuments do not completely cover the nucellus to form the microphyle (Fig. 13).

The unicellular hypodermal archesporium (Fig. 7) divides periclinally producing an outer primary parietal and inner primary sporogenous cell. The tissue produced from primary parietal cell consists of three to four layers (Fig. 9). Cells of nucellar epidermis also divided periclinally, add to the parietal tissue and form a conspicuous nucellar cap.

The primary sporogenous cell functions as megaspore mother cell. It divides meiotically to produce a linear tetrad of megaspores (Figs. 9, 10). The synchronization during meiosis II may be lacking (Fig. 10). The embryo sac is derived from chalazal megaspore (Fig. 11).

The nucleus of functional megaspore divides mitotically to produce an eight nucleate embryo sac. The three, uninucleate antipodal cells are placed either in two superposed tiers with upper having two cells or are arranged in a linear row (Figs. 13, 14).

The egg apparatus consists of two synergids and an egg (Fig. 13). The hooked synergids are provided with a distinct filiform apparatus (Fig. 14). The

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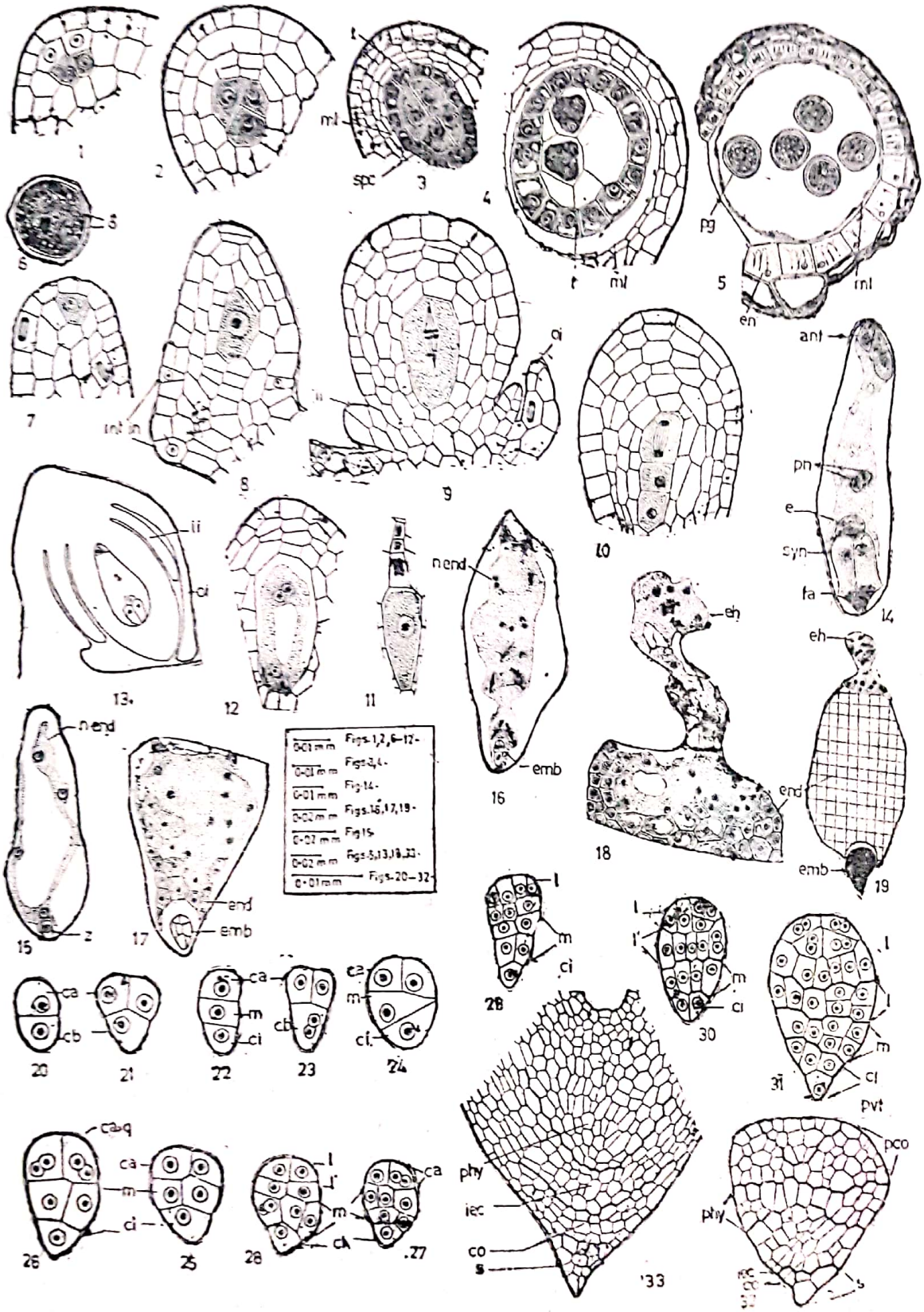
Figs. 1 to 33. Development of gametophytes, endosperm and embryo in *Prosopis juliflora* (Sw.) DC. Figs. 1—5. Portion of anther lobes in t.s. showing stages of development. Fig. 6. A three-celled pollen grain. Figs. 7—10. L. S. ovule showing different stages of development; note—archesporium in Fig. 7, integument initials in Fig. 8, non-synchronous division in the cells of dyad in Fig. 10. Fig. 11. Megaspore tetrad with chalazal functional megaspore. Fig. 12. Four nucleate embry sac with part of nucellus. Fig. 13. Anatropous ovule at the mature embryo sac stage. Fig. 14. Mature embryo sac. Figs. 15-18. Embryo sacs in L.S., showing stages in development of endosperm.; note non-synchronous nuclear division in Fig. 16. endosperm houstoria in Fig. 18. Fig. 19. Dissected embryo sac showing chalazal haustorium. Fig. 20—33. Stages in the development of embryo; note the part of cordate embryo in Fig. 33.

(*ant*—antipodals ; *e*—egg cell ; *eh*—endosperm haustoria ; *emb*—embryo ; *end*—endosperm ; *fa*—filiform apparatus, *ii*—inner integument ; *int in*—integument initials ; *ml*—middle layers ; *n end*—nuclear endosperm ; *oi*—outer integument ; *pg*—pollen grains ; *pn*—polar nuclei ; *spc*—sporogenous cells ; *syn*—synergids ; *t*—tapetum ; *z*—zygote ; ♂ —male gametes.)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polars meet in the centre and fuse prior to fertilization.

Endosperm :

The primary endosperm nucleus, divides earlier than the zygote (Fig. 15). The free nuclear divisions are synchronous and nuclei lie scattered in peripheral layer of cytoplasm. The synchronization, however, is absent (Fig. 16) during later stages of development. The wall formation commences at the micropylar end at about 8 to 16 celled proembryo stage (Fig. 17) and gradually extends down-, wards. From the extreme chalazal end which continues to remain free nuclear (Figs. 18, 19) arises a few tubular processes. These are haustorial in nature and persist even after the differentiation of cotyledons in the embryo (Fig. 19).

Embryo :

The division in the zygote is transverse and results in a terminal cell *ca* and a basal cell *cb* (Fig. 20). The basal cell invariably divides transversely (Fig. 22), though occasionally by an obliquely vertical wall (Figs. 23, 24). The division in the terminal cell is invariably vertical (Figs. 21, 23-25). The proembryo produced at the end of second cell generation consists of a pair of juxtaposed cells derived from *ca* and two superposed cells, viz., *m* and *ci* produced from *cb*. The proembryo tetrad conforms to category At_2, but tendency toward category A_1 is occasionally met with (Figs. 23, 24).

Next vertical division in the terminal tier is vertical but at right angles to the first (Fig. 26), resulting in a quadrant *q*. The horizontal segmentation in cells of *q* gives rise to superposed tiers, *l* and *l'* (Figs. 28, 29). The elements of tier *l* by further divisions differentiates into (*a*) group of axial cells and (*b*) peripheral cells. The stem tip (*pvt*) owes its origin to the former while the cotyledons (*pco*) are produced from the latter. The dermatogen differentiates first in the derivatives of tier *l* (Fig. 31).

Segmentations in tier *l'* is slow and occur both in transverse and longitudinal planes (Figs. 29, 30). The hypocotyledonary region (*phy*) and central cylinder of root (*icc*) are products of tier *l'* (Figs. 32, 33).

The first vertical division in cell *m* produces two juxtaposed cells (Fig. 25). Next division in them is longitudinal (Figs. 28, 30) followed by a transverse one resulting in two superposed tiers (Fig. 29). Derivatives situated next to tier *l'*, function as hypophysis (*h*) to give rise to root cortex (*iec*) and root cap (*co*) (Figs. 32, 33).

The cell *ci* divides irregularly and its derivatives along with the derivatives of *m* form a short suspensor, which persists even after the differentiation of cotyledons.

The embryo development in *Prosopis Juliflora*, thus, conforms to the Onagrad type (Johansen, 1950) or follows Grand period 1, Series A_2 or A_r and Megarchetype IV of Souèges (1951).

Seed Coat :

Soon after fertilization the funiculus elongates considerably and integuments grow over the nucellus to organise a micropyle (Figs. 34, 34A). The funicular vascular supply extends up to the tip of the outer integument in the mature seed (Figs. 34, 35).

The inner integument disintegrates and the mature seed coat is derived from the outer one. The hypodermal and subhypodermal cells of the outer integument divide periclinally to make it six to nine layered thick. The outermost layer i.e. the epidermis constitutes the palisade

layer. The cells of the hilar region in continuation with the outer integument, too, differentiate into palisade cells. The thickenings in the palisade cells initiate along the outer tangential walls and gradually extends to the radial walls ; the outer walls become gelatinous to form a mucilagenous stratum covered by a thin and smooth layer of cuticle (Fig. 36). A groove in palisade layer referred to as pleurogram by Corner (1951) is seen in transverse sections. A layer situated immediately below the palisade differentiates into hour glass cells which are thick walled with wide air spaces between them (Fig. 36). The reduced lumen of cells is filled with tannin. The cells of the inner epidermis, too, become thickened (Fig. 36).

The middle layers of the outer integument, also thick-walled, show presence of wide intercellular spaces and constitute mesophyll. A few cells of it function as procambium and are responsible for post chalazal extension of vascular strand.

Pericarp :

The unicellular hairs having tapering distal ends are derived from a few cells of the outer epidermis of ovary wall (Fig. 37). Its hypodermal and sub-hypodermal layers divide periclinally during embryo development. The pericarp now differentiates into three zones. The outer constitutes the epicarp and consists of epidermis below which are 3-4 layers of collenchymatous cells in valve region (Figs. 38A, 40).

The next is the zone of mesocarp which forms the bulk of the fruit (Figs. 38A, 40). Its cells initially polygonal and isodiametric (Fig. 38A) later become greatly enlarged (Fig. 40) but continue to remain parenchymatous. In peripheral region of mesocarp are present numerous vascular bundles each provided with a sclerenchymatous cap (Figs. 38, 38A, 40). The cap cells are longitudinally oriented to the long axis of fruit.

In the region of suture mesocarp consists of continuous zone of sclerenchyma and the cap from vascular bundles is absent (Fig. 39).

The endocarp, innermost zone, differentiates into the sclerenchymatous stratum next to the mesocarp (Figs. 38A, 40) followed by a parenchymatous tissue (Fig. 40). The orientation of fibres next to mesocarp is parallel whereas those away transverse to the long axis of the fruit (Fig. 40). The sclerenchymatous stratum is followed by loosely arranged parenchymatous cells (Fig. 40).

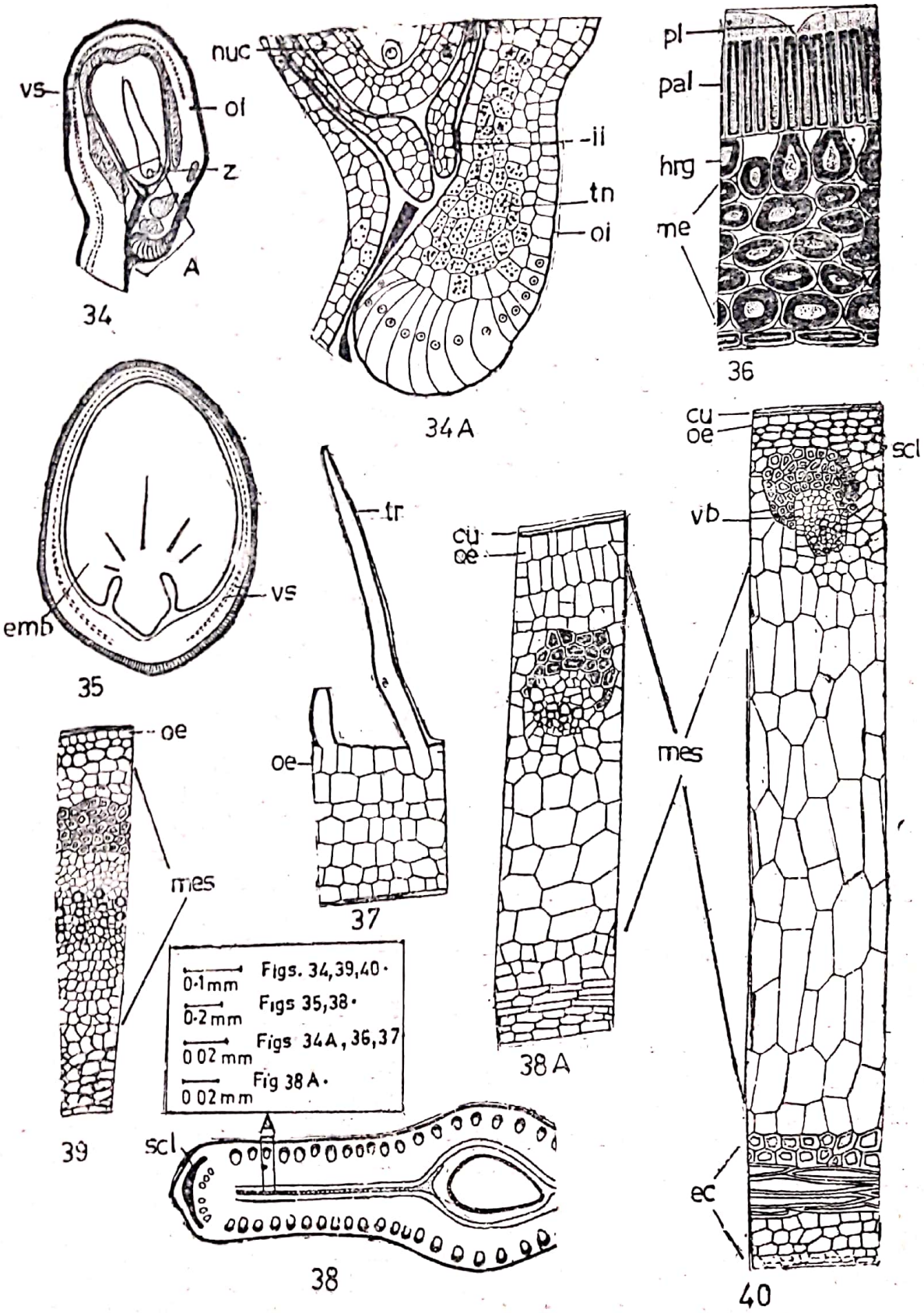
DISCUSSION

The genus *Prosopis* has been assigned to the tribe Adenantherieae by Gamble (1935). The anthers, in this genus are gland crested, contrary to earlier record (Dnyansagar, 1954a).

The wall layers in anther vary in number in members belonging to the sub-family Mimosoideae. Dnyansagar (1957) in *Prosopis* reported 3 or 4 wall layers. However, in *P. julifolora*, they are five. Further, in *Prosopis juliflora* the anther wall development conforms to the Monocotyledonous type (Davis, 1966).

As the walls of tapetal cells break protoplasmic contents form a continuum around the developing microspores. The tapetum in *Adenanthera pavonina* is described as of intermediate type (Dnyansagar, 1958). In the Leguminosae the tapetum, however, appears to be *sensu stricto* of the secretory type.

The endosperm in *P. juliflora* is nuclear as described by Narsimhachar (1948) and Dnyansagar (1955). There is considerable variation with regard to onset



of cellular phase. The entire endosperm, however, does not become cellular. Its lower free nuclear portion gives rise to tubular process, and functions as haustorium. The latter persists at the advanced stage of embryo. The haustorial function of endosperm has earlier been reported in *Leucaena glauca*, *Calliandra haematocephala* (Dnyansagar, 1949, 1958). The tubular process in *Leucaena glauca*, *Mimosa hamata* and *Dichrostachys* (Dnyansagar, 1949, 1951 a, 1954 c) are provided with a vesicular tip while in *Calliandra hematocephola* & *C. grandiflora* (Dnyansagar, 1958) it is coiled.

The perusal through the literature on the embryo development reveals that the suspensor in the Mimosoideae does not differentiate from the embryo proper (except in *Leucaena glauca*– Dnyansagar, 1954 b) and mode of segmentations is difficult to determine as the partitions occur in varying directions (Newman, 1933 ; Narsimhachar, 1948, 1951 ; Dnyansagar, 1951 b, 1957, 1958, 1967)· The mode of development of embryo is described as following Trifolium variation of the Onagrad type of Johansen (1950) of a Period I, Series A and Megarchetype VI of Souèges (1951).

The proembryo tetrad in *P. juliflora* invariably conforms to category A_2. Occasionally the transverse wall in basal cell *cb* is obliquely oriented. Thus, partition of a basal cell by a wall transverse or obliquely so suggests participation of its derivatives in the formation of embryo proper as according to "Law of Parsimony" 'Enti a non sunt multiplicandi practer necessitatem'. Thus, each and every cell produced has a reason for existence. In *P. juliflora* the superior derivatives of tier *m* function as hypophysis initial (*h*). Guignard (1881) working on *Mimosa delehartri* also suggested the possibility of formation of root cap from the derivatives of basal cell *cb*. The particpation of a basal cell *cb* in the development of embryo, thus, is not ruled out.

Further, in *P. juliflora* epiphysis initial (*e*) does not differentiate. The central (axial) cells of the tier *l* which engender stem tip very much simulate the epiphysis initial. The suspensor, though short, is distinct from the embryo proper.

Present study on *P. juliflora* indicates that embryogenesis in this taxon does not follow Trifolium variation of the Onagrad type but comes nearer to Myosurus variation and belongs to megarchetype IV.

The seed coat presents the features described by Corner (1951) for the Leguminosae. However, the stellate ends of hour glass cell in the species are not conspicuously distinguishable. The endocarp in the Leguminosae according to Fahn & Zohary (1955) is made up of

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Figs. 34—40 : Stages in development of seed coat and fruit wall in *Prosopis juliflora* (Se.) DC. Fig. 34. L. S. ovule at zygote stage showing vascular strand; note zones of tannin filled cells in the integuments. Fig. 34A. Portion marked A in Fig. 41 magnified to show extent of integuments and palisade cells of outer integument near micropyle. Fig. 35. V. S. mature seed. Fig. 36. T. S. mature seed coat. note pleurogram & hour glass cells in the seed coat. Figs. 37—40. Stages in the development of pericarp. note trichome in Fig. 37 and orientation of fibres in endocarp of valve region in Fig. 40. Fig. 38. T. S. developing fruit in part. Fig. 38A. Portion marked as A in fig. 38 magnified. Fig. 39. T. S. Pericarp in suture region.

(*cu*—cuticle ; *ec*—endocarp ; *emb*—embryo ; *end*—endosperm ; *f*—funiculus ; hr g—hour glass cells ; *ie*—inner epidermis ; *ii*—inner integument ; *me*—mesophyll ; *mes*—mesocarp ; *nuc*—nucellus ; *oe*—outer epidermis ; *oi*—outer integument ; *pal*—palisade layer ; *pl*—pleurogram ; *scl*—sclerenchyma ; *tn*—tannin ; *tr*—trichome ; *vb*—vascular bundle ; *vs*—vascular strand ; *z*—zygote).

sclerenchyma. However, in *P. juliflora* it gets differentiated into outer sclerenchymatous and inner parenchymatous stratum.

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