CHAPTER IV
FABACEAE

INTRODUCTION

The subfamily Faboideae (non-alter: Papilionoideae) of the family Fabaceae (non-alter: Leguminosae) comprises 375 genera and is characterised by gamosepalous calyx and the papilionaceous corolla. Although embryological studies in this subfamily are quite extensive, many genera remained uninvestigated. Maheshwari (1963) in this connection says "future descriptive work in plant embryology should either be on such families and genera which have so far escaped attention". Hacroptelium is one such genus where embryological information is not available. Hence the present investigation has been undertaken and the present report deals with the embryology of Hacroptelium atrocurpureum (DC.) Urb.

REVIEW OF PREVIOUS LITERATURE

Embryology of the subfamily Faboideae has earlier been reviewed by Schnarf (1931) and Davis (1966). Joshi (1938) gave a brief account on the development and structure
of ovule and embryo sac in *Papaverae acrylifolia*. Rau (1950a, b; 1951a, c; 1954) studied the development of embryo in some members of the Faboideae. He also studied the endosperm development in this subfamily (Rau, 1951b, 1953, 1955).

Rambert (1966, 1967, 1969, 1971, 1977) traced the megasporogenesis in some Faboideae and attributed phylogenetic significance to the megasporangium patterns. Based on his observations and information available earlier, Rambert (1971) recognised 12 different patterns in the subfamily and derived one type from the other.

The campylotropous form of ovule has been recorded in *Histeria sinensis* (Rambert, 1966), *Mucuna prurita* (Ugenjge and Padhye, 1986). However, ovules are reported to be anatropous in *Crotalaria intermedia* (Paul and Dutta, 1950), *Abrus precatorius* (Venkateswarlu and Seshavatharam, 1977), *Tephrosia* sp., *Sesbania* sp., *Gossia opininensis* (Seshavatharam, 1981, 1982b, c) or amphitropous in *Trifolium* sp. (Kolev and Sedmakova-Luchanska, 1972). Bharathi and Murthy (1984) reported hemianatropous ovules in *Arachis hypogaea*, *A. checcoana*, *A. glabrata* and *A. hagebeckii*. Seshavatharam (1982) reported that ovule in *Alviscarpus monilifer* is anacampylotropous. The ovules in all the members studied so far are bitemgic and crassinucellate. All the members investigated
so far exhibit Polygonum type of embryo sac except *Mastacia sinensis* (Rembert, 1967) where a bisporic *Allium* type of embryo sac development has been reported. A modified bisporic type of embryo sac has been met with occasionally in *Laburnum anagyroides* (Rembert, 1966).

Endosperm development in the subfamily Faboideae follows nuclear type. Endosperm may become cellular, completely or partially, or continue to remain free nuclear. There are enormous variations in different taxa in respect of (i) the number of free endosperm nuclei during initial development of embryo (ii) initiation of wall formation (iii) organisation of cellular endosperm and (iv) presence or absence of haustorium, its size, shape and structure (Rau, 1951b, 1953; Joshi and Garg, 1959).

embyronic group under period I, Megarchetype VI and series A according to Souèges system (Souèges, 1948). According to Johansen's (1950) system the embryogeny conforms to the Gaugrad type. But Deshpande and Untawale (1977) reported that embryo development in *Indigofera aneglyphila* (=I. *linneas*) falls under the Megarchetype V of Souèges. Embryo development in *Lotus* according to Souèges (1929) falls under the IVth Megarchetype. The works of Souèges (1951), Rau (1951a, 1955), Crété (1963), Goursat (1961, 1969), Cramen (1975) Deshpande (1977) and Kapuskar (1964) have indicated presence of variations of profound magnitude in respect of embryo development in the subfamily. The differences are not confined to the tribal, subtribal or generic level, but extend to the species level too. This is not all, even the same species may exhibit different patterns of embryonal development.

Apomixis is of rare occurrence in the subfamily. Hindmarsh (1964) reported somatic apospory in *Trifolium*

*H. A. 1982.*
The anthers are tetrasporangiate (Fig. 4A). The archesporium is hypodermal and consists of single row of cells. The archesporial cells undergo periclinal division forming a primary parietal layer just below the epidermis and primary sporogenous layer inside. The primary parietal layer divides periclinaly forming two layers of which the inner forms the tapetum. The outer layer divides once again to form an endothecium and single middle layer (Fig. 4B). Thus the anther wall development corresponds to the Dicotyledonous type (Davis, 1966).

The anther wall at the pollen mother cell stage consists of epidermis, endothecium, two middle layers and tapetum (Fig. 4C). The additional middle layer has arisen by periclinal division of the middle layer. The tapetum is uniseriate with uninucleate cells in the initial stages, but becomes binucleate during the later stages (Fig. 4C). The tapetal cell walls remain intact till its degeneration. Thus the tapetum is of secretary type, otherwise known as glandular type.
The middle layers are ephemeral and degenerate during meiosis of pollen mother cells. The sub-epidermal layer endothecium develops fibrous thickenings forming fibrous endothecium (Fig. 4D). The epidermal layer persists even up to maturity (Fig. 4D). At the time of the dehiscence of the anther the anther wall comprises of two layers viz., the epidermis and endothecium (Fig. 4D).

The primary sporogenous cells divide forming two to three rows of pollen mother cells. These pollen mother cells undergo meiosis followed by simultaneous cytokinesis resulting in microspore tetrads (Fig. 4F-M). The microspore tetrads are tetrahedral and decussate (Fig. 4I, M), but the tetrahedral arrangement is more frequent. The microspores are enclosed in a mucilaginous sheath and later on get liberated from it. The microspores are spherical and uni-nucleate. These microspores with a centrally situated nucleus increase in size. Later a vacuole appears in the centre (Fig. 4N) and the nucleus migrates to the peripheral layer of cytoplasm. These microspores develop an outer exine which is smooth and inner intine (Fig. 4N). The microspores are trirporate and the exine is discontinuous at the region of germ pores (Fig. 4N). The nucleus of the microspore
divides to form a small ellipsoidal generative cell towards the periphery and a large vegetative cell. The generative cell gets pinched off into the vegetative cell (Fig. 40) where it divides to form two male gametes. The pollen grains are triporate and 3-celled at the time of shedding (Fig. 4P).

Ovule:

The ovule arises as a papillate outgrowth from the marginal placenta. The ovule of Macroptelium atropurpureum is at first anatropous bitegmic and crassimucellate (Fig. 4Q, S). The ovule at maturity becomes campylotropous (Fig. 4R). The outer integument is massive and the inner unitegument is 2 layers thick (Fig. 4S). Micropyle is formed by both the integuments and the path is zig-zag (Fig. 4S).

Megasporogenesis and female gametophyte:

A single hypodermal female archesporial cell differentiates at the early stage of ovule development. Occurrence of more than one archesporial cell is also observed (Fig. 5B). The archesporial cell undergoes periclinal division giving rise to an outer parietal cell and inner megaspore
mother cell (5A). The perietal cell undergoes anticlinal and periclinal divisions resulting in the formation of a parietal tissue of 2-4 layers of cells (Fig. 5A-E). Due to the formation of parietal tissue the megaspore mother cell becomes deep seated (Fig. 5D). Thus the ovule becomes grass-innucellate. The megaspore mother cell elongates (Fig. 5D) and divides meiotically followed by cytokinesis to produce a linear tetrad of 4 megaspores (Fig. 5F). The chalazal megaspore functions, while the micropylar three megaspores degenerate (Fig. 5G).

The functional megaspore enlarges and elongates and undergoes mitotic division resulting in two nuclei. These two nuclei move to the opposite poles and they are separated by a vacuole (Fig. 5H, I). The two nuclei undergo another mitotic division resulting a 4-nucleate embryo sac (Fig. 5J). These four nuclei divide once again mitotically to produce eight nuclei, 4 at each pole. Of these 3 micropylar nuclei organise into egg apparatus (with an egg and two synergids), 3 chalazal nuclei organise into 3 antipodal cells while the remaining two nuclei fuse at the centre of the embryo sac forming a diploid secondary nucleus (Fig. 5K). Thus the development of the embryo sac follows the monosporic Polygonum type. The egg apparatus shows a pear-shaped egg.
and two synergids on either side. The antipodals are ephemeral. Synergids degenerate soon after fertilization.

Fertilization:

Fertilization is porogamous. Syngamy and triple fusion occur more or less simultaneously.

Endosperm:

The development of the endosperm is of the nuclear type. The ovule and the embryo sac enlarge before the division of the primary endosperm nucleus. The primary endosperm nucleus undergoes few divisions without wall formation (Fig. 6A). The free nuclei in the cytoplasm are distributed in the embryo sac, but it is dense around the embryo (Fig. 6A-C). During the early divisions of the endosperm nuclei the embryo sac encroaches the surrounding nucleus, ultimately abutting on the inner epidermis of the inner integument. The cells of the later become radially elongated and have dense cytoplasm forming an integumentary tapetum like layer. The endosperm remains free nuclear even up to the globular stage of the embryo. Wall formation in the endosperm sets in when the embryo is globular (Fig. 6B-D) from the micropylar end and gradually extends up to the micropylar half of the embryo sac.
The chalazal region of the free nuclear part assumes a haustorial role (Fig. 6C). The haustorium is vesicular and remains free nuclear. It is active and functional even after cotyledons are well developed.

The sygote divides transversely resulting in a terminal cell $a$ and a basal cell $b$ (Fig. 6F). The terminal cell divides vertically and the basal cell transversely resulting in a 4-celled T-shaped proembryo (Fig. 6G). The derivatives of $b$ are designated as $p$ and $q$. As clear stages were not available we could not assign the embryo development to any type.

**DISCUSSION**

In the development of the anther, particularly in having tetrasporangiate nature, Dicotyledenous type of anther wall development and secretary tapetum, *Macropelium atropurpureum* (present study) resembles other investigated members. Both uninucleate and binucleate tapetal cells are observed in *Macropelium atropurpureum*. Uninucleate tapetal cells throughout anther development were reported in *Alysicarpus monilifer* (Seshavatharam, 1982a), *Tephrosia maxima* (Seshavatharam, 1982b). Pollen grains are triplicate and are shed at 3-celled stage in *Macropelium atropurpureum* (present study) as in *Tephrosia maxima*, *T. purpurea*, *T. pusilla* and *T. villosa* (Seshavatharam, 1982b). But shedding of pollen
grains at two-celled stage was reported in *Alvaicarpus monilifer* (Seshavatham, 1962a), *Glycine max* (Prakash and Chan, 1976) etc.

The female archesporium in the ovule is hypodermal in all the species investigated so far including the present investigation of *Macroptelium strompurpureum*. But Renbert (1969) reported a sub-hypodermal archesporium in *Desmojium puniceum*. The archesporium in the ovule is single -celled in *Tephrosia maxima*, *T. purpurea*, *T. villosa*, *T. purpurea* (Seshavatham, 1962a) while it is represented by a plate of 3 or 2 cells in *Sebania grandiflora* and *S. aculeata* (Seshavatham, 1962c). In *Macroptelium strompurpureum* female archesporium is 1-celled but rarely 2-3-celled archesporium is met with. Monosporic Polygonum type of embryo sac development was observed in *Macroptelium strompurpureum* (present study). The same was reported in *Lathyrus sativus*, *Vicia villosa*, *V. sepium* (Renbert, 1969), *Vicia sativa*, *Cicer arietinum* (Seshavatham, 1969), *Alvaicarpus monilifer* (Seshavatham, 1962a), *Sebania grandiflora*, *S. aculeata*, *S. procumbens* (Seshavatham, 1962c), *Glycine max* (Prakash and Chan, 1976), *Trifolium repens* (Renbert, 1977), *Tephrosia purpurea*, *T. villosa*, *T. purpurea* (Seshavatham, 1962a), *Abrus precatorius* (Venkateswarlu and Seshavatham, 1971).
Histeria sinensis (Ramberg, 1967), Coriaria diphylla (Deshpande and Bhasin, 1976), Indigofera annephrilla (Untawal and Deshpande, 1968), Peorosae aclylifolia (Joshi, 1939), Robinia pseudogracilis (Ramberg, 1969) and Mucuna prurita (Ugemuge and Pedhye, 1986).

Allium type of embryo sac development was reported occasionally in Laburnum anagyroides (Ramberg, 1966) and in Pongania minneta (Seshavatharam, 1969).

Variation in the embryo sac development with the occurrence of both Polygonum and Allium types were reported in Eugenia coxinsensis (Seshavatharam, 1981), Psoraria lobata (Ramberg, 1969) and Histeria sinensis (Ramberg, 1967).

In Macropteliun acrophorum (present study) the endosperm is nuclear and wall formation is initiated from the micropylar end and the chalazal part functions as haustorium. A similar feature has earlier been reported by Rau (1953) in Potamium tristwim, D. tortulorum, D. pulchellum and in Aeschynomena indica by Kapuskar (1964), Alveicarpus sonilier (Seshavatharam, 1982a) and in many other members of the sub-family.
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Fig. 4 A - S: *Heterosporinae* strobilus

**Fig. 4 A**
- T.s. of Tetrasporangiate anther

**B**
- L.s. part of anther lobe showing wall layers and sporogenous cells

**C**
- L.s. part of anther lobe showing wall layers and pollen mother cells

**D**
- Fibrous endothecium and epidermis

**E**
- Anther tapetal cell

**F - K**
- Pollen mother cells in meiosis

**L, M**
- Tetrahedral and decussate microspore tetrads respectively

**N**
- One-nucleate pollen grain

**O**
- Two-celled pollen grain

**P**
- Three-celled pollen grain

**Q - S**
- Stages in the development of ovule
**Fig. 5 A - K**

**Fig. 5 A - K**: *Macropelium stromanpurum*

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Fig. 6 A - H: *Macropeltis atrorubens*

**Fig. 6 A:** 4-celled embryo and nuclear endosperm

**B, C:** Micropylar and chalazal parts respectively of the endosperm

**D:** Heart-shaped embryo and endosperm

**E:** Dicotyledonous embryo and endosperm

**F - H:** Stages in the development of embryo