

18MBO22C-U4

Paper – V – Anatomy and Embryology
Unit - 4

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Megasporophyll

(Carpel)

The gynoecium (pistil) is made up of one or more megasporophylls which may be either free (apocarpous) or fused (syncarpous) giving rise to one or more gynoecium. The megasporophylls are homologous with the leaves either arranged spirally or in whorl. In apocarpous gynoecium there is one style but in syncarpous gynoecium (made up of several fused megasporophylls) the styles may be used variously. When there is complete fusion of the megasporophylls, the style is one but when the fusion is only at the base or extends a little distance above, the number of styles is more than one depending upon the number of megasporophylls. The megasporophyll or carpel is differentiated into a proximal fertile ovule-bearing part; the ovary: a distal capitate, lobed, bifid or much branched pollen receptive part, the stigma; and a middle sterile short or long stalk, the style. The style is usually terminal on the ovary but appears lateral or basal in some advanced families of angiosperms. With the growth of ovules and seeds the terminal style gets displaced later acquiring the lateral or basal positions.

MEGASPORANGIUM (Ovule)

The megasporangium or ovule, located within the gynoecium, is developed from the placenta (cushioned part in the ovary) and is attached by a stalk to the placenta, i.e., funiculus. Its central tissue nucellus is more or less completely surrounded by one or two integuments assigning the names unitegmic or bitegmic to it, respectively. Rarely more than two integuments have been also reported in some of the taxa. Sometimes the ovules are devoid of the integuments as in *Loranthus* and *Santalum*. Most of the sympetalae have one integument. Members of Archichlamydeae and monocotyledons have two integuments but there are exceptions. The vegetative cells enclose the sporogenous cells in the nucellus. The basal part of the ovule, where the nucellus, integuments and funiculus merge, is termed chalaza. The ovule may possess a short, thick and straight or long, slender and curved funiculus at the base. If there is absence of funiculus the ovule becomes sessile. When the funiculus is long, it is used with the body of ovule, forming raphe. At the other end of the ovule, where the integuments do not completely overarch the nucellus, an opening called micropyle is present. It may be narrow or broad depending to the extent the nucleus is enclosed. Sometimes the integuments may show a vigorous growth beyond the nucellus forming a long and slender integumentary canal. A third integument has also been reported in some families. It is considered as an outgrowth of one of the two integuments. This integument is usually fleshy and is termed aril, e.g. *Asphodelus* and *Trilanthema* (Fig. 4-1 A). This term is also used for the fleshy outgrowths found on the other parts of the ovule and, therefore, is a much confusing term. Eames (1961) considers it unfortunate to call aril as third integument when it develops as an outgrowth on the integument. He is of the view that small fleshy outgrowths arising from the

integument may be called caruncle (Fig. 4-1 B, C, D) as found in Euphorbiaceae and if it is of large size should be termed aril. The caruncle is supposed to develop as a proliferation of the cells. The integumentary cells, situated at the micropylar end, get proliferated to give rise to the caruncle in the plants of Euphorbiaceae. At times, due to a vigorous growth, a bending is marked in this growth backward which nearly reaches up to the base of ovule. In *Opuntia* the funiculus grows to such an extent as to completely encircling the ovule, apparently looking like a third integument (Archibald, 1939) (Fig. 4-2).

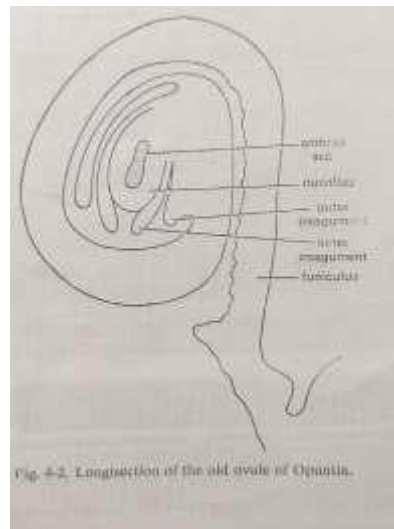
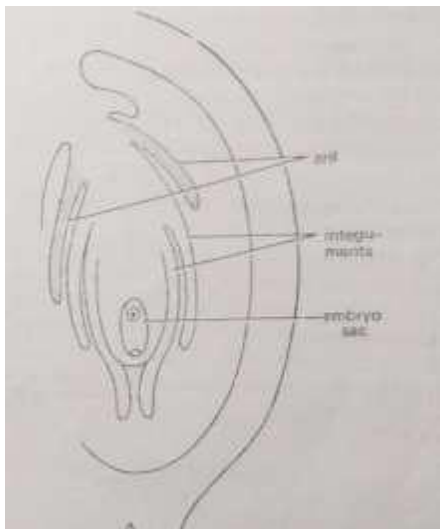


Fig. 4-2. Longitudinal section of the old ovule of *Opuntia*.

Development of ovule

The ovule takes its origin within the ovary as a small placental outgrowth and its primordium arises with the periclinal division of the hypodermal cells situated beneath the uppermost cell layer of the placenta. The primordium, conical in shape and with rounded tip represents the beginning of nucellar growth. The first sporogenous (archesporial) cell becomes visible in this primordial nucellus. It is differentiated from the rest in having a large nucleus and dense cytoplasm.

Integument

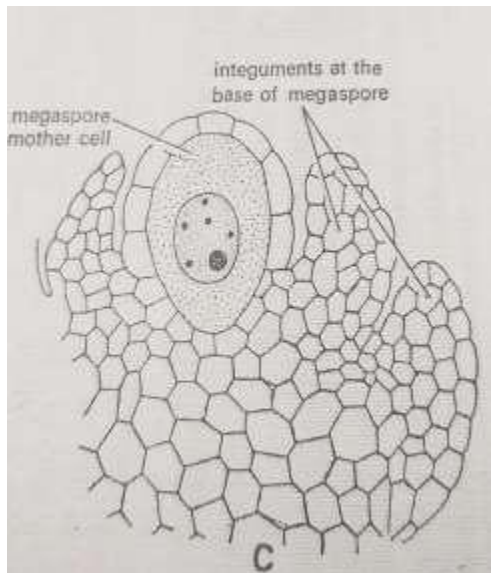
The growth of the integument and nucellus go together. The inner integument arises as a rim-like outgrowth from the surface cells of the nucellus, situated at a little distance back from the nucellar tip, undergoing periclinal divisions. Later, the rim-like outgrowth grows towards the nucellar tip surrounding it completely and leaving narrow opening, the micropyle, at the apex. In those plants where a second integument is found, the growth of this outer integument is initiated in the nucellus at a lower level in relation to the inner integument.

Micropyle

In most of the plants it is the inner integument which forms micropyle. The outer integument generally does not take part in the formation of micropyle as it never reaches up to the nucellar sper. Cases have also been reported where both the outer and inner integuments help to form the micropyle. Such a micropyle, developed from both the integuments, is in the form of a narrow canal and is termed as a micropylar canal.

Nucellus

The nucellus represents the bulk part of the ovule, The ovules are classified as crassinucellate and tenuinucellate depending upon the degree of nucellar development (Fig. 4-3). The former is differentiated from the latter in having well-developed parietal cells and with the presence of one to many layers of cells separating the megaspore mother cell from the epidermal cell of the nucellus. In the tenuinucellate type no parietal cells are present and the layer of cells are also not found between the nucellar epidermis and megaspore mother cell (Fig. 4-3 C).



The nucellus is large in crassinucellate ovule. It enlarges and more parietal cells are added or more cells are formed as a matter of periclinal divisions of the nucellar epidermis (Fig. 4-3 A). A nucellar beak may develop in some plants penetrating into the micropyle as in Caryophyllaceae (Fig. 4-3B). Sometimes the nucellar beak may project beyond the micropyle as in Euphorbiaceae.

The tenuinucellate ovule may either have a small nucellus and the primordia of integuments take their origin from its apex or have an elongated nucleus with the primordium of integument arising from its base (Fig. 4-3 C). With the growth of the embryo sac, the nucellar tissue gets gradually consumed by it and finally disappears altogether when the embryo sac is mature. In tenuinucellar type the nucellus gets used up much earlier. In some cases the nucleus is not completely used up and is present in the seed, called perisperm. Cases have also been reported where the cells of a prematurely developed nucellus degenerate and a large cavity appears around the embryo sac, called pseudo-embryo sac. The pseudo-embryo sac is either formed at the megaspore stage or after the fertilization. In Podostemaceae such embryo sac, with its cytoplasm and several free nuclei, provides nourishment to the developing embryo in the absence of endosperm.

Endothecium or integumentary tapetum

In tenuinucellate ovules, degeneration of the nucellus has been observed during the early stage of ovule development much before the embryo sac has developed. As a result of this, when the embryo sac develops, it comes in contact with the adjacent integument. In such cases the epidermal cells of the innermost layer get modified and form a nutritive layer, called endothecium or integumentary tapetum (Fig. 4-4). The cells of this specialised layer are generally radially elongated and sometimes are binucleate. Normally the endothecium is one-layered but in some plants of Compositae it may be several-layered. It is chiefly a nutritive layer surrounding the archesporium and later the embryo sac. It occupies the place of disorganizing nucellar tissue. Through endothecium the nutrients from the integuments are supplied to the embryo sac. The wall-ingrowths may, however, occur on the wall of embryo sac which indicate the nutrient-transfer activity (Newcomb and Steeves, 1971). The endothelial cells become cutinized and thick-walled forming a part of protective layers of the seed when the embryo is nearly approaching maturity. It is thus clear that from nutritive it takes up the protective function.

Hypostase and epistase

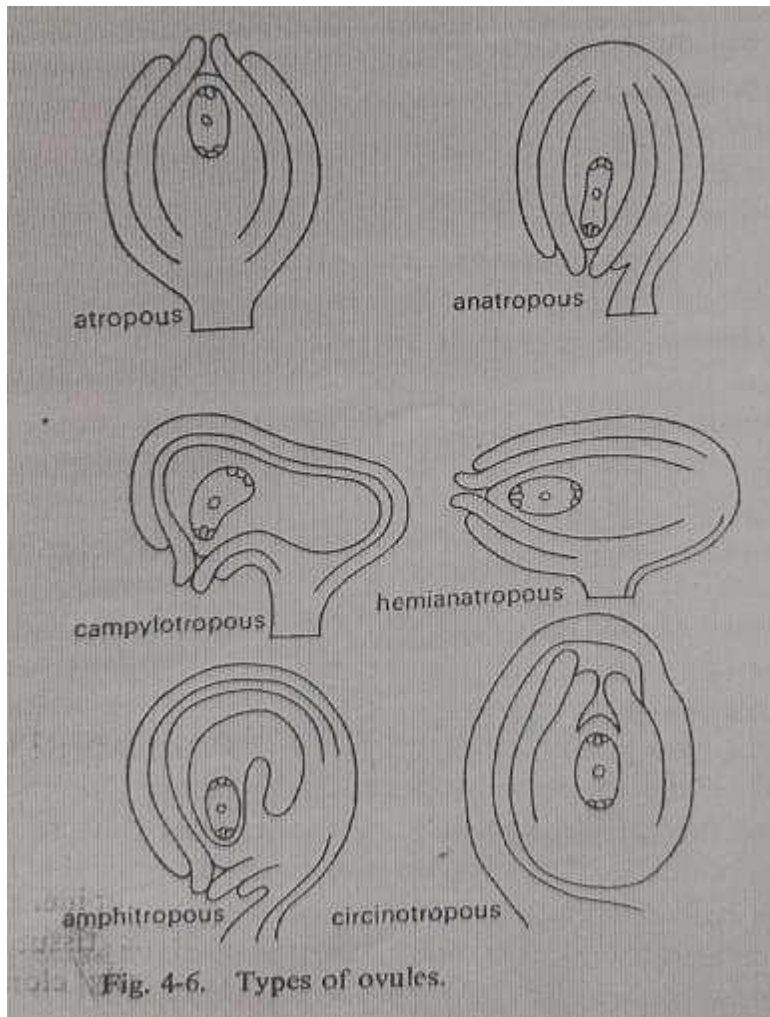
Van Tieghem (1901) observed a plate-like or cup-shaped group of specialized nucellar cells situated below the base of embryo sac, which he termed hypostase (Fig. 4-5). Being generally sclerenchymatous, these cells may also be collechymatous in some taxa. He was of the view that hypostase forms a sort of barrier or boundary for the growing embryo sac and prevents it from pushing into the base of ovule. It was considered to be supportive or protective in nature. Venkata Rao (1953) considers hypostase as a tissue which connects the vascular tissue of the funiculus with the embryo sac, thus helping nutrients transport. Exact functional significance of the hypostase is still to be found out.

Another well marked and cup-like tissue was also observed in the micropylar part of the ovule in some tax (Van Tieghem, 1901). It originates from the nucellar epidermis forming a cup-like structure over the embryo sac. This tissue is termed as epistase, the cells of which are usually radially elongated and thick-walled.

In some plants a thickened cup like tip of the integuments is observed around the micropylar opening, called operculum, According to Eames (1961) the three terms hypostase, epistase and operculum have no apparent morphological significance.

Vascular supply of ovule

Normally the vascular bundle, entering the ovule, does not go beyond the chalazal tissue but in some plants it produces some branches, out of which some of them extend upward and enter into one or both the integuments. The entry of vascular bundle in the integument of gymnosperms is considered as a common and primitive feature. Rarely these bundles may be also present in the nucellar tissue. In Casuarina (Swamy 1948) the vascular strand extends upto the base of sporogenous tissue.



Types of ovules

There are two chief types of ovules, i.e. orthotropous or atropous and anatropous but several intermediate stages have been recognized between them which appear as the axis of the ovule bends variously. The following types have been distinguished :

1. Orthotropous or atropous type of ovule is straight in which the micropyle, chalaza and funiculus lie in one straight line. It is primitive type found in Piperaceae, Polygonaceae and Urticaceae.
2. Anatropous type of ovule has an inverted body. The body of ovule becomes completely inverted so as to bring the micropyle very close to the hilum. The micropyle and chalaza lie along one line and the funiculus lies parallel to it. This type is most common in angiosperms and occurs in sympetalae and several families of dicotyledons and monocotyledons.
3. Hemianatropous or hemitropous is a rare type in which the body of ovule is bent at 90° to the funiculus. The micropyle and chalaza, lying in one straight line, are at right angles to the funiculus. The embryo sac is straight as in orthotropous and anatropous. Such ovule is found in Ranunculus.

4. Campylotropous type of ovule has a curved body but its curvature is less than that of the anatropous. In such ovule, the micropyle and chalazoid are never in straight line. This form occurs in Leguminosae

5. Amphitropous ovule has a pronounced curved body. The curvature even affects the embryo sac which becomes horseshoe shaped. Such ovule is found in *Alic e* and *Butomacan*

6. Circinotropous type of ovule is considered to be distinctive one found in *Opuntia*, *Plumbago*, etc. In such ovule, the nucellus and the axis of ovule first lie in the same straight line but due to continuous growth on one side, the ovule becomes anatropous. The curving does not stop and continues further till the ovule turns over completely, again becoming straight, bringing the micropylar end facing upward. Such ovule has a very much long funiculus which only encircles the body of the ovule (Fig. 4-2)

Archegonium and megasporogenesis

During the early development of the ovule, at the stage of appearance of integumentary primordia, either one or many hypodermal cells, situated at the apex of the ovule primordium, are differentiated from the neighbouring cells by their increased size, bigger nuclei and denser cytoplasm. Such differentiated cells are called primary archegonial cells. Generally only one archegonial cell is differentiated in most of the plants and lies at the apex of a series of nucellar cells.

In the plants with crassinucellate ovules, the archegonial cell divides periclinally into an outer smaller primary parietal cell and an inner bigger primary sporogenous cell (Fig. 4-7). In the plants having tenuinucellate ovules, the archegonial cell, without undergoing any division, directly functions as a sporogenous cell and finally matures as megaspore mother cell. It ultimately gives rise to a tetrad of megaspores. In the ovules where the nucellus is either little or absent, the archegonial cell directly forms the spore mother cell without undergoing any division.

The primary parietal cell thus formed may remain undivided or may divide several times by periclinal or both by periclinal and anticlinal divisions and a parietal tissue is formed which may be of few to many cells. The presence of a massive parietal tissue is considered as primitive whereas its absence as an advanced feature. The parietal tissue is responsible for the formation of a varied number of wall layers or a massive nucellar cap.

The primary sporogenous cell, in most of the cases without undergoing any further division, functions as megaspore mother cell. Due to the formation of a massive parietal tissue, the megaspore mother cells in many taxa get deeply buried into the nucellus. In some taxa epidermal cells of the nucellus may divide periclinally and add a little bulk to the wall layers.

The megaspore mother cells may easily be differentiated with the surrounding cell by their large size, thin walls, conspicuous nuclei and denser cytoplasm. Only one megaspore mother cell is found in most of the monocotyledons but some genera may even have more than one. The number of megaspore mother cells varies much in the dicotyledons. They may be more than one to several in number

Megasporogenesis

The megaspore mother cell divides meiotically to form a tetrad of four megaspores. In most of the taxa the plane of first and second wall formation is transverse and the four megaspores produced lie in a linear tetrad. The two cells formed after the first meiosis are called dyad cells. Divisions in other planes have been also reported to take place giving the megaspore-clusters of variable shapes. Sometimes T-shaped and shaped tetrads also occur and in rare case may be also arranged in isobilateral or tetrahedral tetrads.

Some of the following variations have been observed in the wall formation after the two meiotic divisions :

(1) Both the meiotic divisions are followed by the wall formations. As a result, four megaspores are formed which lie in a row. Generally, three megaspores at the micropylar end degenerate and the remaining one megaspore of the chalazal end remains functional. It later gives rise to the embryo sac.

(2) In Balanophora also four megaspores are formed and lie in a linear tetrad. Here one megaspore of the micropylar end is functional while the remaining three degenerate.

(3) In some plants first meiotic division is followed by a wall formation and dyad cells are formed. The second meiotic division is not accompanied by the wall formation. One of the dyad cells, with two haploid megaspore nuclei, becomes functional and develops the embryo sac whereas the remaining dyad cell degenerates

(4) Sometimes both the meiotic divisions are not accompanied by wall formations. Even if the walls are formed, they soon degenerate. Thus, all the four haploid megaspore nuclei, lying in a row, take part in the formation of the embryo sac. Functional megaspore

Normally, the surviving megaspore is the chalazal one which enlarges to produce the embryo sac and the remaining three disappear, but there are exceptions to this in Balanophora and some other genera it is the micropylar megaspore which is found to be functional, Both micropylar and chalazal megaspore are functional in Composite and some other taxa. Sometimes the second megaspore from the micropylar end in Rosa and third megaspore in

Aristotelia have been reported to be functional In Canarina (Swamy, 1948). Gloriosa, etc. any one of the four megaspores or all of them enlarge, divide and form the embryo sac

Megaspore haustorium

Several workers have reported megaspore Haustoria in some plants Each megaspore produces a tube-like structure from its lateral side which takes a turn upwards sometimes even penetrating the tissue of the integument as in Galton. Such megaspore tubes are historical in their nature. Subramanium (1967) reported the formation of such megaspore tubes in Sedum which travel upto the apical part of the nucleus towards the micropyle and form a tangle of haustoria. In state of competition only one megaspore tube breaks through the epidermal layer of the nucellus. The megaspore having the longest tube forms the embryo sac, perhaps getting better food supply.

Megagametophyte

(Female Gametophyte)

The male gametophyte or female gametophyte represents the embryo sac which is normally a seven-celled structure, having three distinct groups of cells—egg apparatus, central cell and antipodals. In the egg apparatus there are two synergids and one egg cell which are situated towards the micropylar end of the embryo sac. The central cell, nearly situated in the central region of the embryo sac, consists of two fused polar nuclei, one coming from the micropylar end and the other from the chalazal end of the embryo sac. There are three antipodals towards the chalazal end. All the nuclei of the embryo sac are haploid except the nucleus of the central cell which is diploid because it develops as a result of fusion of two polar nuclei.

As already described in the previous chapter, the megaspore mother cell, within the megasporangium, (ovule) undergoes two divisions to give rise to a linear tetrad of megaspores. Normally one of the megaspores out of these, situated towards the chalazal end, becomes functional and the rest disorganize. The functional megaspore elongates along the micropylar-chalazal axis before any nuclear division takes place. Several vacuoles appear in the cytoplasm which later fuse together to give rise to a large vacuole. It is followed by three successive nuclear divisions and eight-nuclear stage of the germinating megaspore is reached. After the first nuclear division, two resultant nuclei move to the two poles where they divide twice and eight-nucleate stage results. Thus a total of five nuclear divisions take place within the megaspore. Out of these five nuclear divisions the first division is reduction and the rest are ordinary divisions. By the end of five nuclear divisions, the embryo sac has considerably elongated.

The successive nuclear division stated above are followed by the cell wall formation. The nuclei of each micropylar and chalazal ends get organized into the cells leaving one free nucleus at each end. In most of the cases the free nucleus of the chalazal end approaches the free micropylar nucleus lying in the cytoplasm, fuses with it and gives rise to the secondary nucleus. This type of embryo sac development is met within most of the families of angiosperms.

With extensive researches, carried out during the last several years in the field of embryology, enough information has been accumulated. On the basis of these it has been held that deviations from the typical manner of the embryo sac development exist in many genera. Maheshwari (1950) has classified the embryo sac of the angiosperms into three main types—monosporic, bisporic and tetrasporic depending upon the number of the megaspore nuclei involved in its development. He has further sub-divided the three main

types taking into account the total number of nuclear divisions taking place between the stages of megaspore formation and differentiation of the egg cell. The total number of the nuclei present in the embryo sac during differentiation of various cells and their arrangement was also considered.

Types of embryo sac development

All the types and sub-types of the embryo sac developments have been discussed and diagrammatically represented in Fig. 5-1

TYPE		MEGASPOROGENESIS			MEGAGAMETOGENESIS			
		meg-mother cell	div. I	div. II	div. III	div. IV	div. V	mature embryo sac
monosporic 8-nucleate	Polygonum							
monosporic 4-nucleate	Oenothera						X	
bisporic 8-nucleate	Allium						X	
tetrasporic 16-nucleate	Peperomia						X	
tetrasporic 16-nucleate	Penaea						X	
tetrasporic 16-nucleate	Drusa						X	
tetrasporic 8-nucleate	Fritillaria						X	
tetrasporic 4-nucleate	Plumbagella					X	X	
tetrasporic 8-nucleate	Plumbago					X	X	
tetrasporic 8-nucleate	Adoxa					X	X	

Fig. 5-1. Important types of embryo sac development met within the angiosperms (Modified after Maheshwari.)

Monosporic type

In this type only one of the four megaspores, which may be either situated towards the micropylar or chalazal end, takes part in the development of the embryo sac. Examples of monosporic embryo sac are polygonum type and oenothera type.

1. Polygonum type. The Polygonum type of the embryo sac development is found in about 81 percent families of angiosperms (Davis, 1966) and is designated by this name as it was first discovered by Strasburger in *Polygonum divaricarum*. This type of development is also known as normal type.

The chalazal megaspore is functional. Its nucleus divides mitotically into two nuclei, out of which one moves to the micropylar and other to the chalazal end. These are also called primary micropylar and primary chalazal nuclei, respectively. Later, as a result of two successive nuclear divisions four nuclei are produced at each end. Now the organization of the cells occur. Three-cellulodes apparatus and the antipodal cella get organized at the micropylar and chalazal end, respectively. Two free polar nuclei fuse together nearly in the central region to give rise to a secondary nucleus.

The Polygonum type of embryo sac and 8-nucleate and the functional megaspore undergoes three nuclear divisions to give rise to the embryo sac.

2. Oenothera type. This type of embryo sac development was thoroughly studied by Geerts (1908) in *Oenothera lamarckiana* of Onagraceae.

Unlike Polygonum type in Oenothera type the functional megaspore the micropylar one. The megaspore nucleus undergoes only two free nuclear division to give rise to four nuclei all of which remain in the micropylar part. three nuclei out of four get organized in the egg apparatus and one nucleus is left as unorganized polar nucleus which later presents the uninucleate central nucleus. Due to the absence on third nuclear division and aggregation of the nucleus in the micropylar part, the animal cells and chalazal polar nucleus are absent. Oenothera type of the embryo sac is 4-nucleate and the functional megaspore undergoes two nuclear divisions to give rise to the embryo sac.

Bisporic type

In the development of bisporic type of embryo sac the megaspore mother cell nucleus divides into two nuclei. This nuclear division is followed by a wall formation during first meiosis and two dyad cells are formed. The upper dyad cell, facing the micropylar end is smaller in size than the lower and soon degenerates. The lower dyad cell (facing the chalazal end) is functional. Example of bisporic embryo sac is *Allium* type.

Allium type. Strasburger (1879) described the development of bisporic type of embryo sac in *Allium fistulosum*. All the species of *Allium* show this type of embryo sac. It is the chalazal dyad cell which is functional. This undergoes second meiotic division to give rise to two haploid nuclei. No cell wall formation takes place after the second. Both the megaspore nuclei take part in the embryo sac development. One of the nucleus migrates to the micropylar and other to the chalazal end of the megaspore. Two mitotic divisions follow in

each nucleus with the result that four nuclei are formed at each end. Later the eight nuclei get organized as in Polygonum type.

The embryo sac organization in Allium type is normal, i.e., the egg apparatus consists of two synergids and one egg cell towards the micropylar end and three antipodals to the chalazal end. The two free polar nuclei fuse together giving rise to a secondary nucleus.

In some genera it is the micropylar dyad cell, instead of chalazal dyad cell, which is functional. The degeneration of chalazal dyad cell is also delayed till the four-nucleate stage of the embryo sac. Allium type of the embryo sac development, as reported by Maheshwari, is also met in several families of dicotyledons and monocotyledons but showing minor variations

Totrasporic type

In the plants exhibiting tetrasporic type of the embryo sac development, the first as well as the second meiotic divisions are not followed by the cell wall formation. Thus, after the second meiotic division four free nuclei are present in the cytoplasm of the megaspore. All these four nuclei take part in the embryo sac development. Many variations have been found occurring in the tetrasporic type of embryo sacs ; some selected ones are :
Peperomia, Penaca, Drusa, Fritillaria, Plumbagella, Plumbago and Adoxa types.

1. Peperomia type. This type of the embryo sac development was reported by Campbell (1899 a.b. ; 1901) and Johnson (1900) in Peperomia pellucida. All the four nuclei of the megaspore, after second meiosis, take part in the embryo sac development. The four megaspore nuclei divide mitotically twice resulting in 16 nuclei which get uniformly arranged near the periphery in the thick cytoplasm of the developing embryo sac. The two nuclei lying in the micropylar part get organised into an egg and a synergid. Eight nuclei come to fuse in the central region resulting into a secondary nucleus and the rest six nuclei form antipodal cells near the periphery of the chalazal end of the embryo sac. Several variations, regarding the arrangement of the sixteen nuclei and organization of the embryo sac after second mitotic division, have been also reported by many workers.

2. Penaca type. All the four megaspore nuclei divide mitotically twice to give rise to sixteen nuclei which get arranged in four groups of four nuclei each in the cytoplasm of the germinating megaspore. The four groups of nuclei are situated at the four ends of the developing embryo sac. One nucleus from each group of the four nuclei moves to the centre where all the four polar nuclei fuse together to form a secondary nucleus. The three nuclei

situated at the micropylar end organize into two synergids and an egg. The remaining twelve nuclei also get organised into the cells.

The development of the Penaea type of embryo sac has been reported in Euphorbiaceae, Malpighiaceae and in some genera of other families. However, Maheshwari and Johri (1941) pointed out that *Acalypha indica* (Euphorbiaceae) presents much variation in the organization of the embryo sac, The most common variation is being described here. The development of the embryo sac upto 16-nucleate stage is the same as in Penaea but after that 2 nuclei from each of the four groups migrate to the centre and fuse to form the secondary nucleus. The remaining two nuclei of each group are organized into the cells, The egg apparatus in the mature embryo sac consists of only one synergid and an egg.

3. Drusa type. The embryo sac development of the Drusa type was first reported by Hokansson (1923) in genus *Drusa* of Umbelliferae and later by many workers in several other plants. As a result of first and second meiotic divisions, four megaspore nuclei are formed out of which 3 remain in the chalazal part and 1 in the micropylar part of the embryo sac. Now two mitotic divisions follow and 16 nuclei are formed, i.e. 4 nuclei in the micropylar part and 12 in the chalazal part. The 3 nuclei of the micropylar part get organized into the egg apparatus and 11 nuclei of the chalazal part into the antipodal cells. One free nucleus from each pole fuses in the central region giving rise to a secondary nucleus. Thus, a 16- nucleate embryo sac is developed in which the organization of the cells differs from that of 16- nucleate embryo sac of *Peperomia* and *Penaea* types.

4. Fritillaria type. Treub and Mellink (1880) and several other workers reported an interesting case of the embryo sac development in various species of *Lilium* and observed that after the second meiotic division, one nucleus of the micropylar part moves to the chalazal part and fuses with the two nuclei of that part forming a triploid nucleus. Now the megaspore containing one haploid nucleus of the micropylar part and one triploid nucleus of the chalazal part undergoes two mitotic divisions. Thus, 4 haploid nuclei at the micropylar end and 4 triploid nuclei at the chalazal end are formed. The organized embryo sacs in *Fritillaria* and *Lilium* have haploid egg apparatus, i.e. with 2 haploid synergids and one haploid egg. Three antipodal cells at the chalazal end are all triploid. One haploid nucleus from the micropylar end and one triploid nucleus from the chalazal end fuse in the central region giving rise to a tetraploid secondary nucleus.

5. Plumbagella type. This type of embryo sac development was first described by Fagerlind (1938 b) in *Plumbagella micrantha*. Like *Fritillaria* type, however, in this type also four haploid megaspore nuclei are formed at the end of two meiotic divisions. One of the nuclei from the micropylar end moves to the chalazal end and fuses with two nuclei already present there to develop a triploid nucleus. Now the nuclei of the both the ends divide mitotically to form two haploid nuclei in the micropylar end and two triploid nuclei in the chalazal end. However, unlike *Fritillaria* type, in *Plumbagella* type second mitotic division does not occur. In the mature embryo sac the egg apparatus consists of only one egg cell, the synergids being absent. There is one triploid antipodal cell. One haploid nucleus from

the micropylar end and another triploid nucleus from the chalazal end fuse, producing a secondary nucleus.

6. Plumbago type. Haupt (1934) described this type of the embryo sac development in *Plumbago capensis* of Plumbaginaceae. This type seems to be confined to this family only (Maheshwari, 1950). After the second meiotic division, 4 haploid megaspore nuclei are formed. These get arranged towards the periphery in the cytoplasm of the megaspore in a cross-like manner. The mitotic division follows and 8 haploid nuclei are formed which are in four pairs. One nucleus of the micropylar pair gets organized into an egg cell. One haploid nucleus from each pair which function as polar nuclei, slightly increases in their size, migrate to the central region of the developing embryo sac and fuse giving rise to a tetraploid secondary nucleus. The remaining three haploid nuclei of the three pairs generally degenerate at their places. Sometimes these one, two or three haploid nuclei escape degeneration and are cut off to form peripheral egg-like cells at their original places.

7. Adoxa type. The Adoxa type was described by Jonsson (1879-1880) in *Adoxa moschatellina*. As a result of first and second meiotic divisions the megaspore mother cell nucleus divides into 4 haploid nuclei of the megaspore. Two of these nuclei occupy the micropylar end and the remaining two chalazal end. This arrangement differs with that of *Plumbago* where the four nuclei of the megaspore occupy four sides in a cross-like manner. All the four haploid nuclei of the megaspore take part in the development of the embryo sac, Only one post-meiotic mitotic division takes place and 8 nuclei are formed. Each end of the developing embryo sac possesses four nuclei. The egg apparatus is organized in the micropylar part with two synergids and an egg cell. Three antipodal cells are cut off at the chalazal end. One polar nucleus from each pole approaches in the central region and fuse with the other to give rise to a secondary nucleus. Though the organization of the embryo sac differs with that of *Plumbago* but in both the cases it is 8-nucleate.

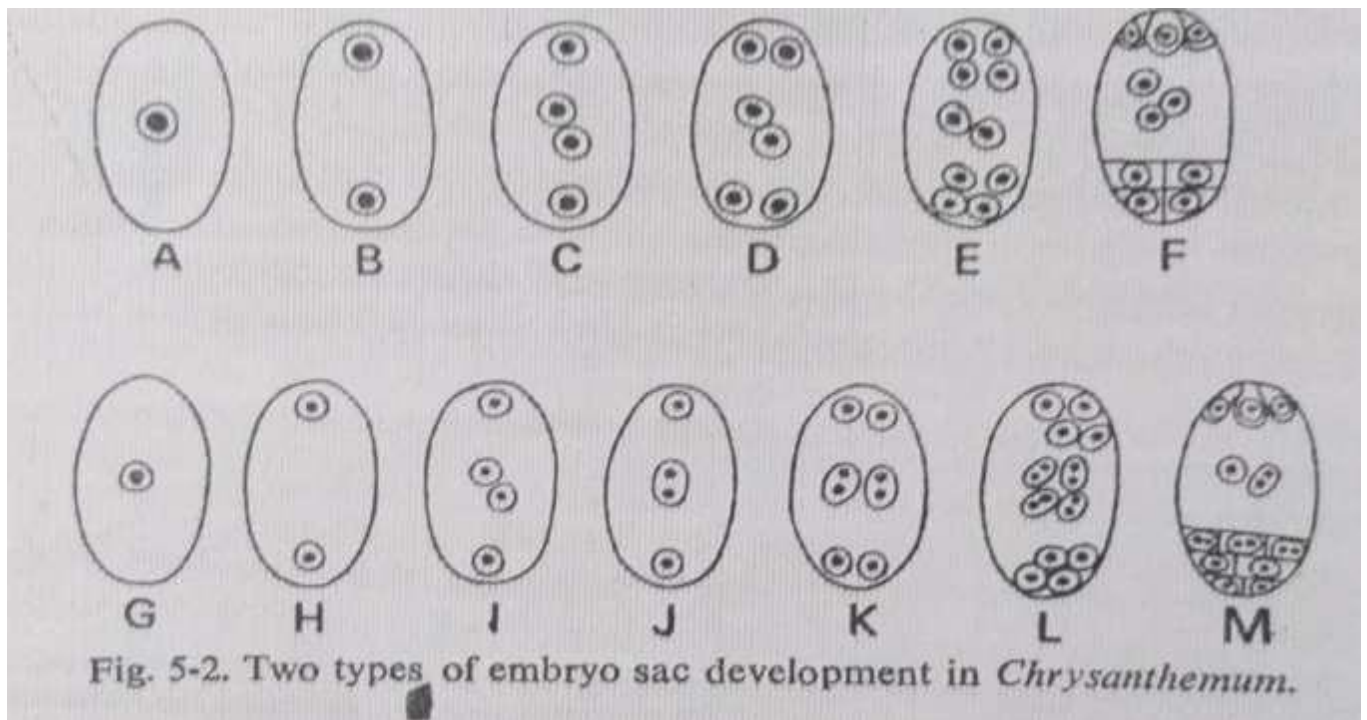
Special types of embryo sac (tetrasporic)

Martinoli (1939) has described a special type of the tetrasporic embryo sac in *Chrysanthemum cinerariactollum*. The megaspore mother cell, after meiotic division, gives rise to a 4-nucleate megaspore in which the four nuclei get arranged in 1+2+1 manner, i.e. one nucleus at each micropylar and chalazal end and two nuclei in the central region. Two types of variations are observed during megagametogenesis. The two central nuclei of the megaspore remain in close association. Either these two nuclei fuse together giving rise to a diploid nucleus or may not fuse at all and remain free in the centre prior to megagametogenesis.

In the former case (where 2 central nuclei fuse) two mitotic divisions follow and three groups of four nuclei are formed, i.e.. four haploid nuclei in the micropylar end, four diploid nuclei in the central region and four haploid nuclei in the chalazal end. During cellularisation of the embryo sac, three haploid nuclei of the micropylar quartet give rise the egg apparatus

and the remaining one nucleus moves to the central region as a polar nucleus. The three diploid nuclei of the central quartet and four haploid nuclei of the chalazal end form antipodal cells, i.e. seven antipodal cells are produced out of which three diploid ones are called additional antipodals. One diploid nucleus of the central quartet and one haploid nucleus coming to the central region as a polar nucleus from the micropylar end from the central nuclei (Fig. 5-2 G-M).

In the later case (where 2 central nuclei do not fuse) one nucleus of the micropylar end and one of the chalazal end divide by two mitotic divisions but the two central nuclei remain undivided. As a result, a micropylar quartet and a chalazal quartet are formed. The developing embryo sac is 10-nucleate where all the nuclei are haploid. During cellularisation of the embryo sac, three nuclei of the micropylar end get organized into the egg apparatus and the remaining one nucleus moves to the central region of the embryo sac as a polar nucleus. No polar nucleus is spared from the chalazal end and all the four nuclei of the chalazal quartet form antipodal cells (Fig. 5-2 A-F). The mature embryo sac, however, sometimes may be less than 10-nucleate depending upon the number of mitotic divisions or its total failure.



Mature embryo sac

The polygonum type of mature embryo sac is supposed to occur in most of the families of angiosperms and is termed as normal type. It is 7-nucleate at the time of fertilization, i.e. have one egg, two synergids, one central nucleus (of two fused polar nuclei) and three antipodals. The central cell has a diploid nucleus and the remaining cells have haploid nuclei. The Adoxa, Allium and Fritillaria types of embryo sacs also have the same organization but differ in their mode of development. The egg is of universal occurrence in all the types of embryo sacs and in majority of the cases is associated with two synergids. In Phumbagella and Plumbago types the synergids are absent whereas in Peperomia type only one synergid is associated with the egg. The number of antipodal cells may vary from one to many and are either haploid or triploid. In Ocnothera type no antipodal are found. A typical (monosporic, bisporic or tetrasporic) embryo sac, at the time of fertilization, has an egg apparatus, the polar nuclei forming the nucleus and antipodals.

Egg apparatus

The egg apparatus is situated in the micropylar part of the embryo sac and consists of three closely associated haploid cells, i.e., one egg and two synergids.

Egg. The egg represents the female gamete. The lower part of the egg, pointing towards the chalazal end, possesses most of its cytoplasm and the nucleus. A large vacuole, facing the micropylar end, is present in the upper part of the egg. Rarely the nucleus is more or less centrally situated surrounded by several small vacuoles present near the periphery of the cell wall as in Zea. Neither the hook nor tentations are present in the egg cell. However, in those embryo sacs where the synergids are absent, the egg cell develops prominent projections near its micropylar end directed towards the micropyle. These projections resemble with the filiform outgrowths generally found in the synergids. In the absence of the synergids, the egg cell itself has the nutrients with the help of these projections.

Synergids

The synergids are also known as helping cells as they seem to direct the growth of the pollen tube towards the egg by secreting some substance. A space is formed after they are degenerated in which the male cells of the pollen tube are delivered. The synergids are situated near the micropyle and are generally pear shaped cells associated with each other and also in contact with the egg cell. Each synergid is provided with a prominent hook towards its micropylar end. The hooked part is separated from the lower part of the synergid by a prominent notch. The upper part of the synergid is also provided with a filiform apparatus which consists of finger-like projections arising from its cell wall and penetrating into the cytoplasm (Fig. 5-3). Previously these were simply considered as striations, converging towards the micropylar part of the synergid, helping the transfer of materials. The electron microscopy of the filiform apparatus has revealed that each finger-

like projection represents well packed microfibrils containing polysaccharides within a sheath which is not fibrillar in nature. Though several workers believe that this apparatus helps the synergid in its nutritive role but others are doubtful. The nucleus along with large amount of the cytoplasm is found just below the hook region. A large vacuole is present in the lower part of the synergid.

The synergids are regarded as ephemeral structures which generally degenerate entirely either soon after the fertilization or even prior to it. Several cases have been reported where:

- (1) One synergid may degenerate before the pollen tube has entered into the embryo sac and the other degenerates after the pollen tube has discharged the male gametes.
- (2) One of the two synergids may even persist after the fertilization has taken place.
- (3) One or both the synergids may persist for a considerable period and remain active.
- (4) One of the synergids start degenerating after the development of the embryo sac in *Allium*.

Synergids as haustoria. In most of the plants the synergids are simply confined within the limits of the embryo sac but in some, the tips of the synergids elongate considerably and act as haustoria, absorbing the food material from the neighbouring or distant tissues. Well developed synergid haustoria have been reported by Johri and Agarwal (1965) in *Quinchamalium chilense* of Santalaceae where their tips considerably increase in length, reaching less than half the distance of style. There are many cases where synergid haustoria are met within the other species.

Antipodals. The antipodals are short lived. Generally, three antipodals are found in the chalazal end of the embryo sac. Large number of antipodal cells have been reported in *Gentiana* and *Graminaceae*. Their large number is due to their repeated mitotic divisions. A maximum number of 300 antipodals has been reported in *Sasa paniculata* of *Bambusaceae*.

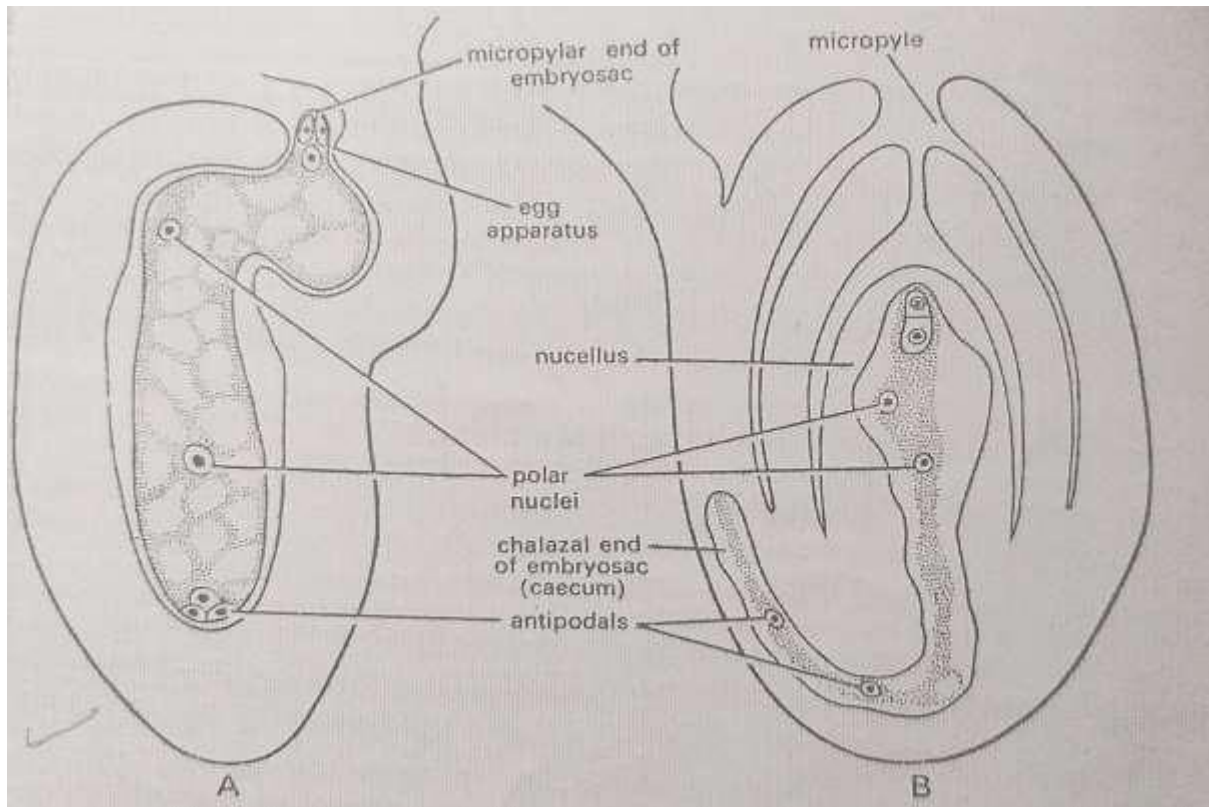
The antipodals exhibit much diversity in their number of nuclei. The multinucleate condition of the antipodals is brought about by the additional nuclear divisions and incomplete cell wall formation. *Phyllis*, *Tagetes*, *Zea*, etc., possess multinucleate antipodals. In *Zea mays* and some other grasses the antipodals proliferate into an ephemeral tissue. The cells of this tissue bordering the nucellus are provided with wall ingrowths which could be compared with the filiform apparatus found on the walls of synergids. These are rich in the organelles indicating increased respiration and synthesis. However, the antipodals are functionally not very important and usually disorganise either before or soon after the fertilization. Contrary to this some workers have found persistent antipodals playing a nutritive role. The presence of the outgrowths on the antipodal cell walls in maize leads us to believe that they have perhaps a nutritive role to play and help in the food transfer to the embryo sac. The antipodals are considered as representing the vegetative tissue of the female gametophyte.

Antipodal haustoria. Though in most of the cases antipodals degenerate either before or just after the fertilization but in some genera they persist for some time and exhibit haustorial behaviour. In *Galium* and *Putoria* of Rubiaceae only the lower antipodal cell, out of the three antipodals, becomes much elongated and functions as haustorium. In *Argemone* the antipodals persist even after the fertilization. These increase too much in their size and absorb the food material from the chalazal tissue situated in their vicinity.

Secondary nucleus. Except in some plants, where either the polar nucleus coming from the micropylar or chalazal end is bigger than the other, they are much identical and it is not possible to differentiate between them just before their fusion in the central region of the embryo sac. The two polar nuclei, one coming from the micropylar end and the other from the chalazal end fuse together in the central region of the embryo sac to give rise to a secondary nucleus. Thus the central nucleus is diploid. The fusion of the polar nuclei may either occur before or during, or when the pollen tube has entered within the embryo sac. The secondary nucleus may be situated either close to the egg apparatus, or in the central region of the embryo sac, or near the antipodal cells. When the two male nuclei are set free within the embryo sac during fertilization, one of the nuclei fuses with the egg to produce the zygote and the other with the secondary nucleus to give rise to a nourishing tissue called endosperm.

Embryo sac haustoria

The entire general surface of the embryo sac which is surrounded by the tissue of nucellus and integument has been reported to be absorptive in nature. These surrounding tissues become obliterated and absorbed by the general surface of the embryo sac. In some plants the micropylar and chalazal ends of the embryo sac exhibit pronounced growth, become haustorial in function and absorb the nutrients from the nucellar tissue. In those cases where the nucellar tissue gets entirely absorbed, the inner integumentary layer also gets affected and absorbed. In some genera the nucellar tissue is completely absorbed and in such case the embryo sac may also establish contact with the placenta, absorbing food material from it. Some genera of Loranthaceae show marked elongation of the embryo sac at both its ends. In comparison to the chalazal end, the micropylar end shows more vigorous growth reaching either upto the base of style or upto a certain distance in the stilar tissue. Under such situation the fertilization may occur either in the basal region or at a certain distance above in the stilar region. Some cases have been also reported where the micropylar haustorial end of the embryo sac elongates so much as to reach upto the stilar tip. However, after the egg has been fertilized the developing embryo is pushed towards the chalazal end with the help of developing suspensor. In some other genera the embryo sac shows down ward growth and its chalazal end digests its way through the nucellar tissue. The haustoria, developing from the synergids and antipodals, have already been described (Fig. 5-4).



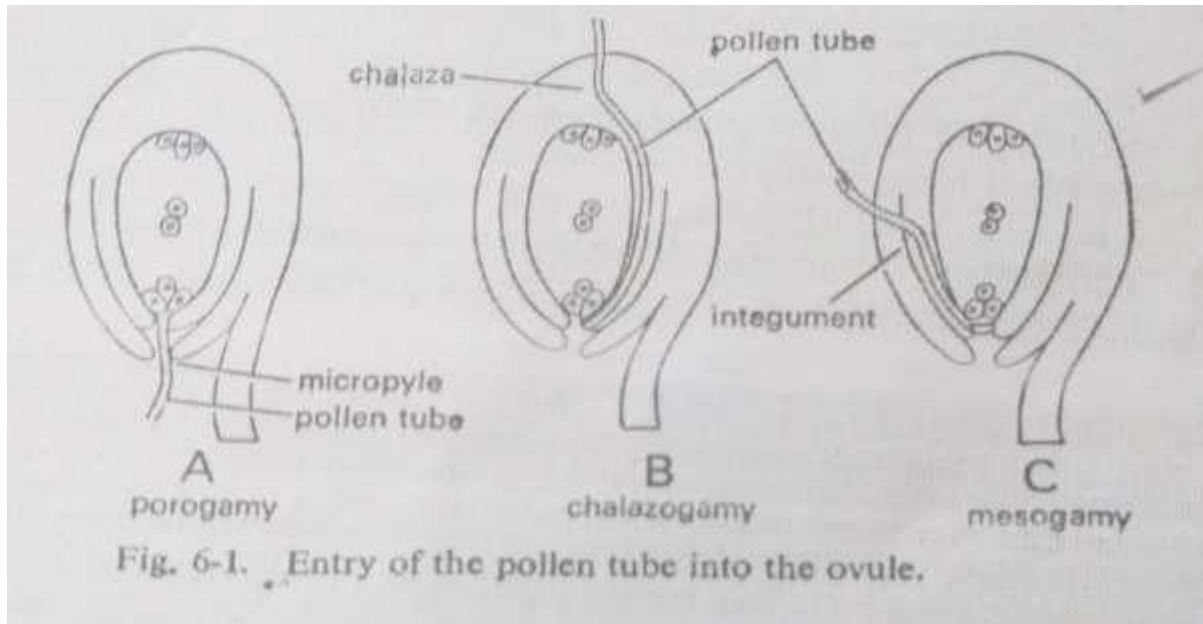
Fertilization

As described earlier, the pollen grain germinates on the stigmatic surface and produces a pollen tube. Its germination may either be immediate or after some period of its transfer to the stigma. Generally, one unbranched pollen tube develops from a pollen grain but the pollen grains of Campanulaceae, Cucurbitaceae and Malvaceae are polysiphonous, i.e. several pollen tubes emerge from one pollen grain. In some species a pollen tube may be branched appearing like a fungal mycelium. However, only one pollen tube finally matures containing two male gametes or sperms. The shortest time taken by the pollen tube to reach the embryo sac has been reported to be fifteen minutes and the longest time as a few days to a few months. In Orchidaceae it has been found to be six to seven months as the development of the ovule is much delayed. Pollen tubes have the shortest period of germination in the annuals which is considered as an advanced character.

Generally, the pollen grain germinates rapidly and the emerging pollen tube travels in between the stigmatic papillae, making its way downward into the style. There is much variation in regard with the length of the style in different species. It may be long, short or sometimes absent. The style may be also hollow or solid. When it is hollow, the pollen tube grows on the surface of the transmitting tissue or epidermal cells which form the inner lining of the styliar canal. In those cases where the style is solid, the pollen tube pushes its

way downward through the intercellular spaces and between the cells of the solid column of the stilar tissue. In very rare cases the pollen tube may push its way through the cells of the style. As the pollen tube grows through the intercellular space in the stilar region, some enzymes are secreted from its tip bringing about the dissolution of middle lamellae and widening the spaces between the cells.

Entry of pollen tube into ovule



As a large number of the pollen grains germinate on the stigmatic surface, several pollen tubes are produced forward in the direction of ovary, passing through the stilar region. After reaching the ovary, the pollen tube tries to penetrate into the ovule. A pollen tube may penetrate into an ovule either through the micropyle, chalaza or funi ulus (Fig. 6-1). Usually in large number of plants it penetrates into the ovule through the micropyle. This condition is known as porogamy and the fertilization through this method is called porogamic fertilization. Some Cases have been reported where a distinct micropyle is not found because either the integuments do not reach upto the tip of the nucellus or the integuments are completely absent. In such cases the embryo sac elongates to such an extent as to meet the pollen tube at certain height in the style. The chalazogamy is the condition when the pollen tube penetrates into the ovule piercing through the chalazal tissue. It is less common condition and the fertilization through this process is called chalazal fertilization as in *Casuarina* (Swamy, 1948) and *Pistacia*. In mesogamy the pollen tube penetrates into the ovule either passing through the funiculus or integuments as in *Cucurbita*. The fertilization through this situation is termed as mesogamons fertilization.

No phylogenetic importance should be attached to the above three types of courses adopted by the pollen tubes in penetrating the ovules because sometimes it has been observed that in the ovules of the same plant, c.g. *Brassica oleracea* the pollen tubes may adopt both the courses, i.c. porogamy and chalazogamy.

A special organ called the obturator, develops from the placenta in the form of a swelling which facilitates the penetration of the pollen tube into the ovule. The obturator grows towards the micropyle and forms a bridge for the pollen tube to approach the ovule. It may be noticed before the fertilization fitting like a hood over the nucleus but disappears when the fertilization has taken place (Fig. 6-2).

Recent studies have made it quite clear that whatever method of penetration of the pollen tube into the ovule may be, the pollen tube grows through the nucellar tissue and after passing over the surface of the embryo sac makes contact with its micropylar end. It penetrates into the embryo sac only through the micropylar end where the egg apparatus is situated. It does not pass through the cells but grows in between them. In many cases the cells of the obturator appear as glands or are much elongated in their shape. Sometimes the basal cells of the stilar canal develop into long hairs and make contact with the nucellar tissue. Even the cells of the inner integument have been found increasing in length and reaching into the stilar canal, Such outgrowths also serve the purpose of the obturator.

Penetration of pollen tube into embryo sac

After the pollen tube has entered the ovule, it penetrates into the embryo sac through the micropylar end. Usually, it may either pass between the wall of the embryo sac and a synergid or between a synergid and the egg cell) Jensen (1973) reported that in many species the pollen tube enters into one of the synergids through a filiform apparatus and its contents are discharged within the cells. Usually, one synergid is destroyed due to the entry of pollen tube whereas the other synergid remains for sometime and later gets degenerated. In *Triticum vulgare* both the synergids degenerate together. Rarely both the synergids remain intact and do not disintegrate at the time of entry of the pollen tube. The fact that the synergids have been found degenerating in some cases much before the entry of the pollen tube into the embryo sac and are totally lacking in others, leads us to believe that they have no important role in fertilization.

Discharge of pollen tube contents

Much variation has been reported in the manner of discharge of the pollen tube. Usually the pollen tube apex swells and in some plants even bifurcates into two short branches before it bursts. Rarely the entire pollen tube tip does not rupture, as sub terminal openings are formed, through which the male gametes or sperms get liberated, close to their mates. The two sperms are set free either along with the vegetative cell or its remains and enter into the cytoplasm of the embryo sac

Fusion of gametes

It was previously accepted that the two sperms, discharged from a pollen tube, differ in their size and behaviour, i.e. the bigger one fuses with the secondary nucleus or the polar nuclei and the smaller one with the egg cell or oosphere but there exists no sufficient evidence to make it a general acceptance.

After the release of two sperms from this pollen tube, one approaches the egg and makes its contact with the membrane delimiting the cytoplasm next to the cell wall of the egg (plasma-lemma) and finally the nucleus of the sperm fuses with that of the egg. It is the real fertilization called syngamy giving rise to a diploid zygote. The other sperm approaches the central nucleus or polar nucleolus and fuses to produce a primary endosperm nucleus.

Double fertilization

It is a unique feature of angiosperms which was first demonstrated by S. G. Nawaschin (1898). Both the sperms, discharged from a pollen tube, are responsible for the fertilization. One of the sperms fuses with the egg and the other with two polar nuclei, or, if they have fused earlier before the fertilization, with the secondary nucleus (two fused polar nuclei). This type of fertilization, i.e. of the egg into a diploid zygote and the secondary nucleus into usually a triploid (Sometimes it may be polyploid when several polar nuclei fuse together in the central region of the embryo sac as in *Peperomia*, *Penaea*, *Fritillaria*, *Plumbagella*, *Plumbago*, etc. In *Oenothera* it is diploid due to only one polar nucleus fusing with the sperm) primary endosperm nucleus is termed double fertilization. The development of endosperm (a nutritive tissue) is initiated by the primary endosperm nucleus which is commonly triploid, as stated above, because a total of three nuclei take part in the combination, i.e. one sperm nucleus and two polar nuclei.

Double fertilization is responsible for the development of viable seeds. After the second fertilization, two fused or unfused polar nuclei get stimulated and vegetative tissue, i.e. endosperm is developed. It serves as a store house of the food materials for the future seedling. Triple fusion

In most of the plants, as already stated above; one polar nucleus from the micropylar end and other from the chalazal end move to the central region of the embryo sac and fuse together to give rise to a secondary nucleus. During second fertilization, the nucleus of one sperm combines with two fused polar nuclei resulting into a triploid primary endosperm nucleus. It is not true fertilization. Such fusion of three nuclei is termed triple fusion. There are several exceptions as stated under 'double fertilization'. When either one or more than two polar nuclei participate during the second fertilization, the expression triple fusion has no meaning.

Polyspermy

The polyspermy is an unusual situation when more than two sperms are discharged within an embryo sac. Usually only one pollen tube penetrates into an embryo sac but occasionally more pollen tubes may penetrate an embryo sac and release the sperms in double the number of the pollen tubes. In such cases the egg is fertilized with more than one sperm nucleus and a polyploid zygote develops. Sometimes extra sperms, delivered in the embryo sac, fertilize the synergids or antipodals. With this situation, multiple embryos develop and the phenomenon is known as polyembryony. The cases have been also reported that a pollen tube penetrating the embryo sac may contain more than two sperms. It is believed that additional divisions of the two sperms are responsible for their greater number. Another abnormality also occurs when more than one pollen tube penetrates an embryo sac discharging several sperms. One of the sperms of one pollen tube fuses with the egg and another sperm from the other pollen tube fuses with the secondary nucleus. This abnormality has been termed heterofertilization. Besides some unusual situations described above several other abnormalities have been worked out by many workers from time to time.

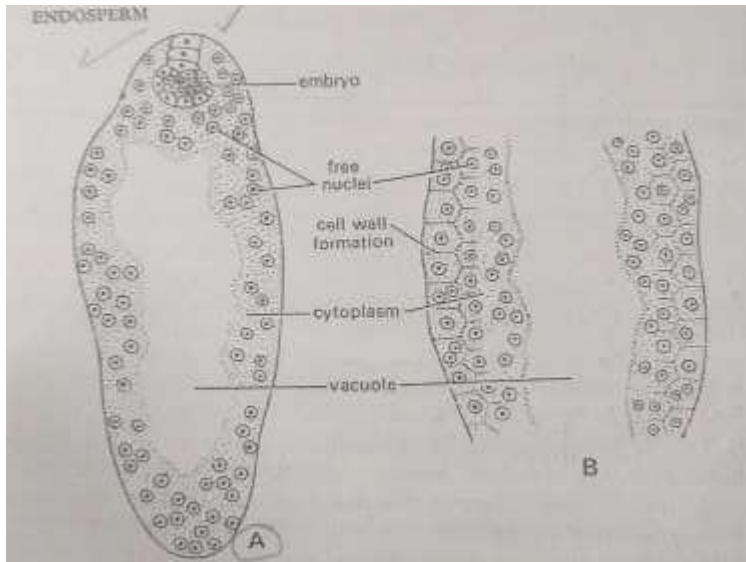
Haustorial pollen tube

In most of the cases the pollen tube, after discharging its contents in the embryo sac, degenerates and ultimately disappears after the fertilization but rarely it may persist for a long time till some stage of the embryo development and sometimes even upto the seed development, acting as a haustorial organ to nourish the embryo sac or the embryo. In some members of Cucurbitaceae and Onagraceae, when the pollen tube approaches the embryo sac, its apical part produces several branches. One of the branch, carrying the sperms penetrates the embryo sac and helps the fertilization, while the remaining ones ramify into the other tissues of the ovule and absorb the food materials for the embryo

Endosperm

The endosperm is altogether a new storage tissue found in monocotyledons and dicotyledons. It usually develops from the primary endosperm nucleus ($3n$) and provides food materials to the growing embryo as well as the seedling. It is comparable with the female gametophyte of gymnosperms and morphologically is analogous to it. Although in gymnosperms it is a part of the female gametophyte and is haploid but in angiosperms it is not a part of it and is mostly triploid. The endosperm in angiosperms is generally a product of triple fused nuclei, i.e, one male nucleus and two polar nuclei. In many plants of Papilionaceae, it is entirely digested by the developing embryo. The seeds of such plants are termed exalbuminous, the cotyledons of which become thickened due to the food storage. In other category of plants, e.g. Ricinus, Triticum, Zea, etc, the seeds are called albuminous

and the endosperm is present in them during their germination. In a few families like Orchidaceae, Podostemaceae and Trapaceae, its development is either suppressed or lasts only for a very short time, The endosperm may be diploid, triploid or polyploid, depending upon the number of nuclei taking part in the fusion to give rise to the primary endosperm nucleus. A few cases of Casuarina, Balanophora, Limnocharis, etc. have been reported where the endosperm may develop from one or both the polar nuclei, without their fusion. Its development has been also found to be independent of fertilization.



Three main types of endosperm formation have been recognized, i.e. 1. Nuclear Endosperm, 2. Cellular Endosperm and 3. Helobial Endosperm. In all these types, the primary endosperm nucleus undergoes mitotic divisions which start before any division is initiated in the zygote. The above three types are being discussed below:

NUCLEAR ENDOSPERM

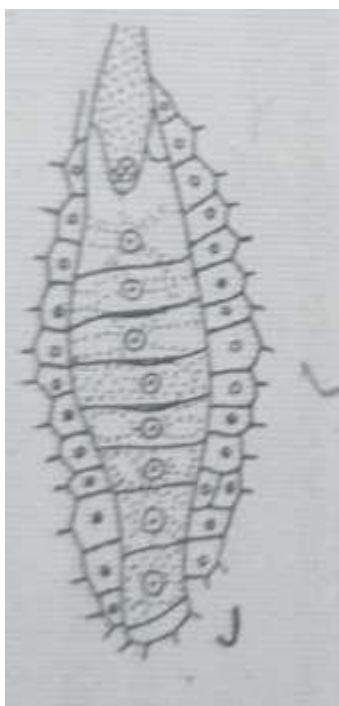
In the nuclear type of development the primary endosperm nucleus divides freely in a large number of nuclei without any immediate cell wall formation. First few divisions of the nuclei are synchronous but in later stages the nuclei are observed in their different stages of divisions and they are no more in multiples of two. A few thousand nuclei, thus produced, are pushed more and more towards the periphery of the embryo sac. The central part of the embryo sac, the gets occupied by a large vacuole (Fig 7-1). A large number of nuclei are accumulated at the micropylar and chalazal ends and the remaining few, lying in the cytoplasm, form a thin layer along the periphery of the embryo sac. Sometimes the free endosperm nuclei of the chalazal part are larger than those of the micropylar part. It has been observed that in some plants, after the formation of a few or more free nuclei, further development of the endosperm ceases and no wall formation takes place ICOCOM

Generally, as in *Capsella*, after the free nuclear division, cell wall formation starts. In most of the cases either the cell walls are laid down starting from the periphery of the embryo sac

advancing towards the centre or from the apex progressing towards the base. Rarely it may start from the chalazal par proceeding towards the micropylar part or operating at the same time in all the places of the embryo sac. Either one or more free nuclei become enclosed within a cell. When more than one nuclei are captured within a cell, nuclear fusion may occur and the resultant nucleus may be diploid, triploid or polyploid depending upon their number. Ultimately, in most of the plants the central vacuole of the embryo sac disappears due to the formation of the endosperm. In some cases the endosperm tissue is limited to only one or two peripheral layers of the cells or to only a patch of micropylar tissue and the rest of the parts of the embryo sac possess free nuclear endosperm.

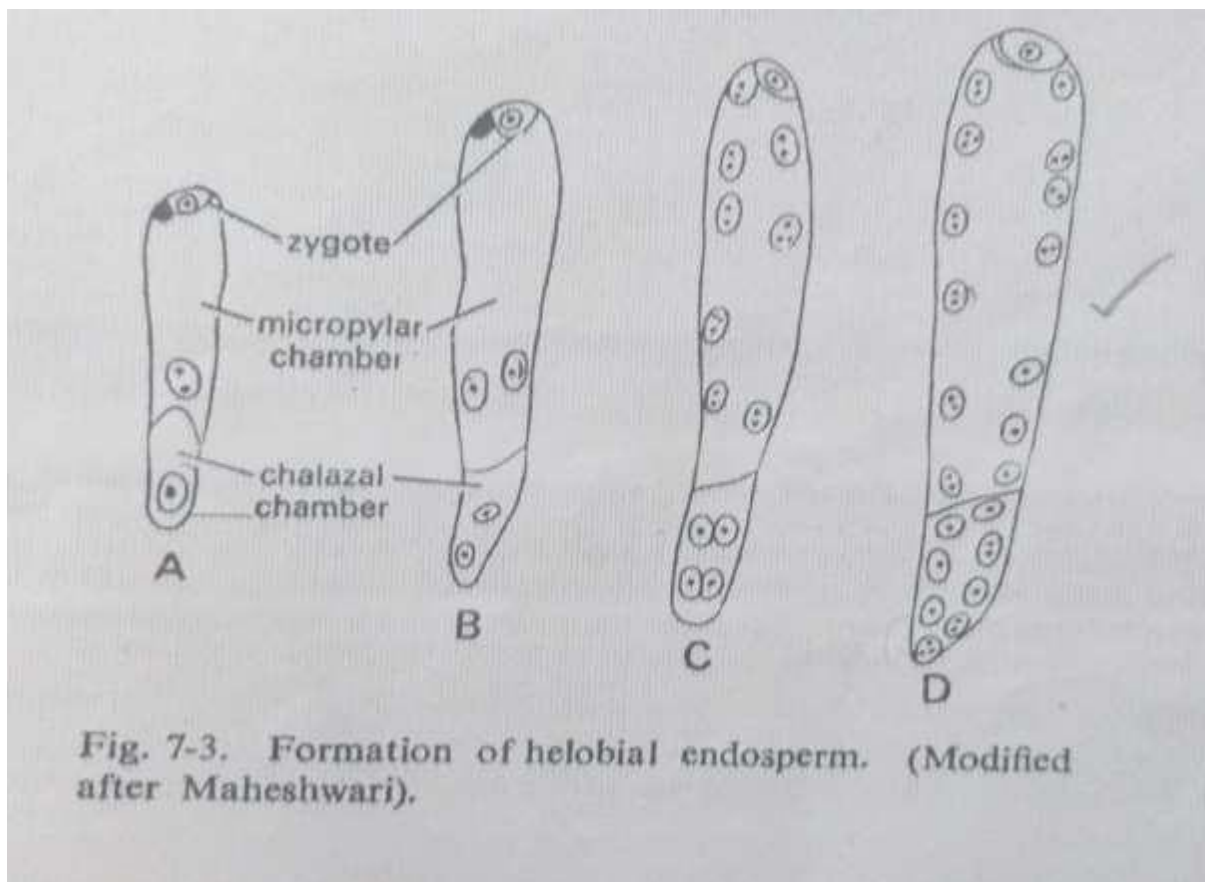
CELLULAR ENDOSPERM

The cellular type of endosperm differs chiefly with the nuclear type in the fact that in the form, the division of primary endosperm nucleus is immediately followed by the wall formation. The free nuclear stage of the embryo sac does not exist. The first wall may be either transverse, vertical or even oblique, generally dividing the embryo sac into two equal chambers, i.e. micropylar chamber and chalazal chamber. The size of the two chambers may also depend upon the position of the primary endosperm nucleus. The subsequent nuclear divisions, followed by regular cell wall formations first coinciding with the plane of the first cell wall and later in all the planes give rise to the endosperm the cells of which are irregular in their arrangement (Fig. 7-2). Such endosperm formation occurs chiefly in dicotyledons, saphrophytes and parasites, *Cuscuta* being the exception



HELOBIAL ENDOSPERM

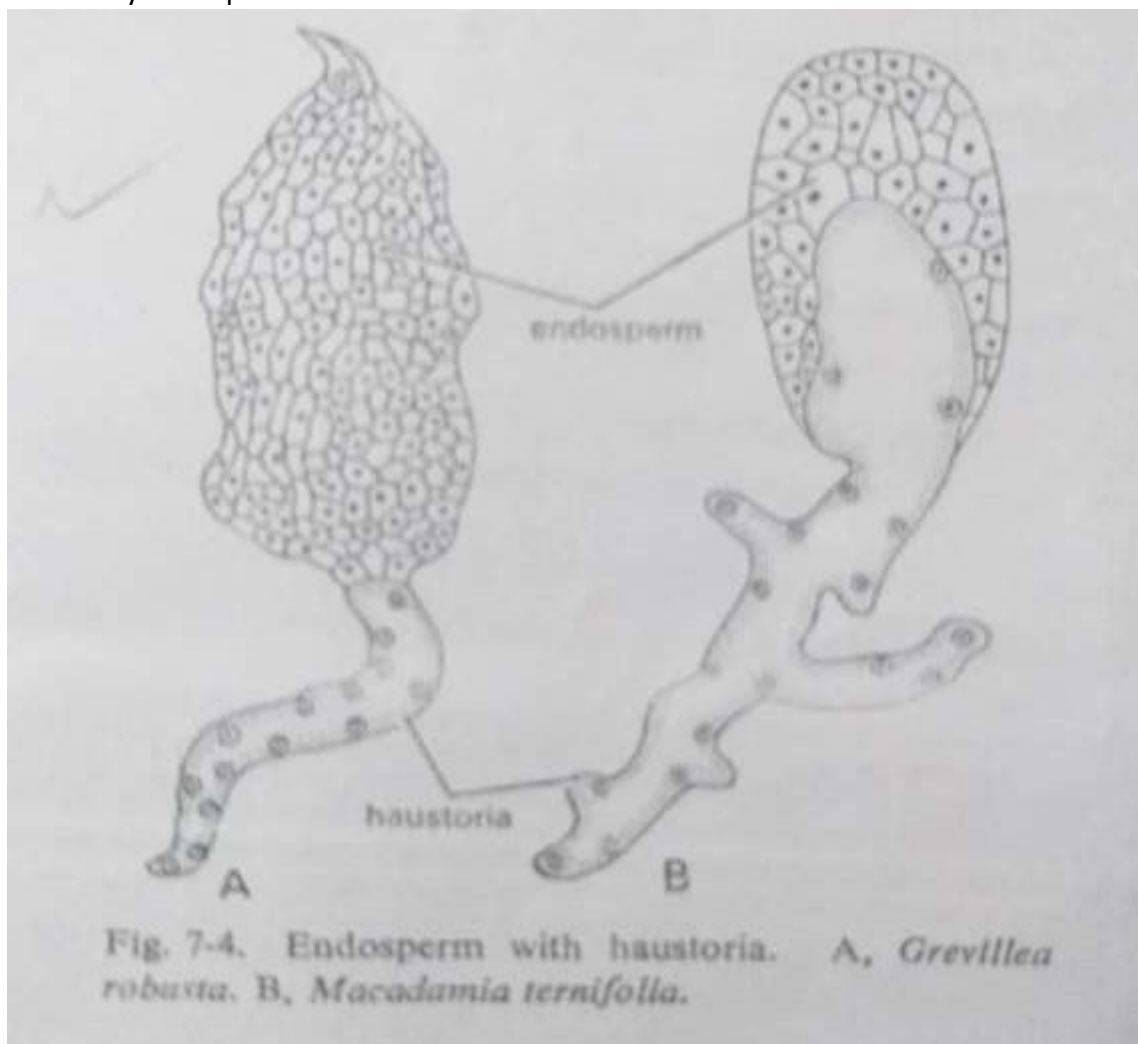
The development of helobial type of endosperm is somewhat of intermediate type between the nuclear and cellular endosperms and combines the chief features of both. It is commonly found in Helobieae, an order of monocotyledonae. The primary endosperm nucleus first divides by a transverse wall and the embryo sac gets divided into a large micropylar chamber and a small chalazal chamber (Fig. 7-3). It is due to the fact that, prior to the first division, the primary endosperm nucleus, from the central region of the embryo sac moves towards its chalazal end. Now the free nuclear divisions occur in both the chambers. These nuclear divisions are comparatively more rapid in the micropylar chamber than the chalazal chamber. Thus, the number of free nuclei in the micropylar chamber are more in number than the nuclei of the chalazal chamber. Sometimes, the nucleus of the chalazal chamber may not divide at all. Normally, the cell wall formation occurs in the micropylar chamber and the chalazal chamber, containing undivided or a few nuclei, finally degenerates. Thus, the cellular tissue, developed with the nuclei of the micropylar chamber, represents the endosperm. It has been also observed in some plants that as a result of free nuclear divisions followed by the wall formation, a small mass of cells is formed in the chalazal chamber also which does not last long.



Endosperm haustoria

Some of the groups of plants develop haustorial structures from their endosperm which invade various nutritive tissues of the ovules and absorb the food materials by penetrating into them. It is considered as an extra device to collect the food material. The absorbed food materials are transported to the endosperm tissue to be utilized by the embryo during its growth. Such haustoria develop in all the three types of endosperm, Some of the selected types of such haustoria are being considered here. *Grevillea robusta* (Kaushik, 1942). It belongs to Proteaceae

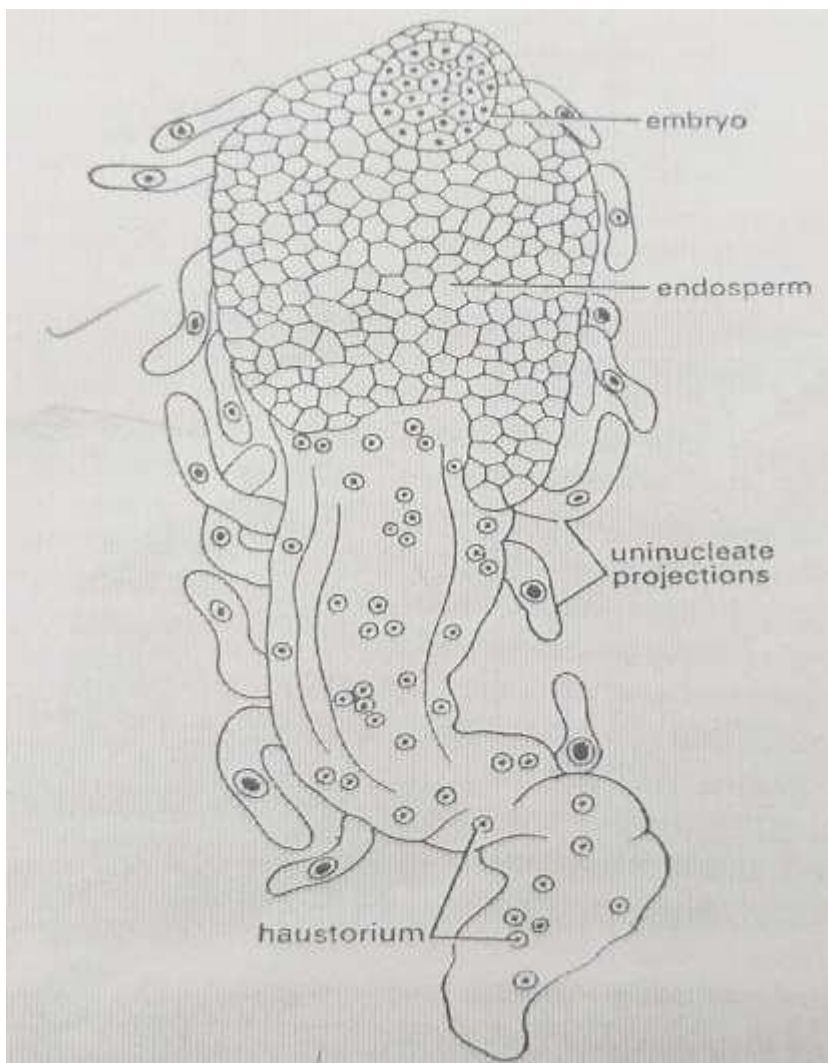
and exhibits nuclear type of endosperm development. In this plant the upper part of the endosperm is cellular but its lower part develops into a more or less worm-like, tubular and coiled structure called vermiform appendage which remains non-cellular and multinucleate (Fig. 7-4 A). The vermiform appendage, acting as haustorium, invades the chalazal tissue till this tissue is completely obliterated and absorbed. The vermiform appendage, in the later stage, however, becomes divided into several multinucleate partitions giving rise to a secondary endosperm.



Macadamia ternifolia. It is another member of Proteaceae where the endosperm is nuclear type. Like *Grevillea robusta*, in *Macademia* too, the cell wall formation takes place only in the upper part, as most of the nuclei are aggregated in this portion and the endosperm tissue develops in the upper part of the embryo sac. The lower part of the embryo sac, with less number of nuclei, remains coenocytic and develops much lobed and aggressive haustorial structure (Fig. 7-4 B). This invades the nutritive issue, situated in the basal part of the ovule. Such haustorial lobes are only active till the food materials are present in the host tissue and later become functionless.

Lomatia. In this plant also the endosperm tissue develops only in the upper parts of the embryo sac whereas the lower part remains coenocytic and haustorial absorbing food materials from the chalazal and other tissues of the ovule. Several unicellular out growths develop on the surface of the chief haustorium and endo- sperm tissue for the additional absorption of the food (Fig. 7-5). materials

Besides the above three interesting types of endosperm haustoria reported in the nuclear type of the development of endosperm, several plants belonging to Cucurbitaceae, Papilionaceae, etc., also possess haustorial endosperm of notable sizes.



Impatiens roylei. Here the development of the endosperm is cellular type. The division of the primary endosperm nucleus is followed by laying down of the first transverse wall giving rise to a small micropylar and a large chalazal chamber. The micropylar chamber (upper chamber) then divides transversely into three cells. A very much branched prominent haustorium develops from the uppermost cell, the branches of which penetrate even upto the funiculus to absorb the food materials (Fig. 7-6). It is considered as an example of aggressive micropylar haustorium.

Nemophila. The primary endosperm nucleus divides into two nuclei and a transverse wall is laid down between them. Thus, two equal cells are produced. Generally, the lower cell as such, functions as a chalazal haustorium. Sometimes it may produce a long lateral branch which penetrates into the funiculus and may reach even upto the placenta to absorb the food materials. *Nemophila aurita* develops large micropylar and chalazal haustoria

Ruellia. In *Ruellia* and several other genera of *Acanthaceae*, the endosperm develops both micropylar and chalazal haustoria. After the first nuclear division of the primary endosperm nucleus and a cell wall formation, the two cells, i.e.. micropylar cell and chalazal cell are formed. The chalazal cell develops a small chalazal haustorium which remains conocytic. With a transverse division, the micropylar cell produces two cells out of which the upper cell develops the micropylar haustorium. The endosperm is partially cellular and without nucleus.

Monochoria. This genus belongs to *Pontederaceae* in which the development of endosperm is helobial type. The chalazal chamber, with less number of nuclei, remains smaller than the micropylar chamber with more nuclei. It is due to comparatively more active divisions of the nuclei in the micropylar chamber. Later, two tubular outgrowth develop from the two sides of the micropylar chamber, embracing the chalazal chamber on its each side (Fig. 7-8). These outgrowths or lateral haustoria grow in the direction of chalazal tissue, penetrate into it and function as aggressive absorptive organs. Thus, the endosperm haustoria developed in several species of *Monochoria* are always lateral instead of micropylar or chalazal.

Some plants like *Globularia vulgaris* have been observed developing micropylar, chalazal and secondary haustoria together (Maheshwari, 1950) but such examples are few in number. Secondary haustoria in such cases develop as tubular finger-like outgrowths from the cells of endosperm lying in association with the chalazal haustorium.

Mature endosperm

Physiologically the endosperm represents a non-living tissue of a fully developed seed or a grain. The mature and permanent endosperm is a food storage tissue, typically made up of homo Bencats cells without any intercellular spaces. Generally it is a simple non-chlorophyllous tissue, the cells of which are non-pitted and thin walled. The starch, along with other food substances like oils and protein, are accumulated in the protoplasts. Thick walled cells form horney endosperm as in the members of Palmae and Umbelliferae. The thickness of the cell walls is due to the deposit of hemicelluloses on them. In coconut, the horney endosperm develops as a result of settling of free nuclei present in the coconut milk, near the peripheral region of the embryo sac. The horney endosperm may remain hollow as in coconut or solid as in Areca catechu.

In Gramineae, the outer layers of endosperm are meristematic which contribute thin-walled cells towards inside. The newly cut cells later get filled with the starch. During the maturation of seed, the cells of the outermost peripheral layer, lose their meristematic activity, become bigger in size and get packed with the aleurone grains. This outermost layer of thick walled cells is formed which is supposed to secrete certain enzymes which change the stored food materials to make it fit for the use of embryo at the time of seed germination:

In some plants of Amaryllidaceae, the endosperm continues to grow even after it has filled the embryo sac. With such growth the seed coat or even the ovary wall ruptures and the endosperm gets exposed to light. Under such situation the cells develop chlorophyll, remain succulent and form intercellular spaces. Sometimes the dissolution of the seed coat and even the pericarp may take place during the seed formation which also brings about the above change in the endosperm. In these cases where the integuments are absent and there stands no possibility of the seed coat formation, the cells of the outermost layer of the endosperm get suberized to form a protective layer.

The endosperm in Piperaceae is not a storage tissue. It digests and passes the food materials to the embryo from the abortive perisperm, which is a real food-storage tissue. In most of the cases with the growth and maturation of the embryo sac, the nucellus gets used up and finally disappears. In Piperaceae and Scitamineae, the nucellus is not completely used up and persists in the form of a thin layer in the seed enclosing the embryo and the endosperm. This is termed as perisperm. It may also represent the nutritive tissue of the integuments. Sometimes the perisperm and endosperm may occur together generally when the endosperm is present, the other is absent. The perisperm is of two types--nucellar perisperm and integumentary perisperm. The nucellar perisperm is uncommon, because with the maturation of the embryo it gets completely used up :

exceptions are Piperazine and Scitamineae) as already stated above: The integumentary perisperm is more common and is found in most of the taxa. The integumentary tissues, which store the food material, form the integumentary perisperm. The perisperm is considered as an accessory nutritive tissue supplying the food material to the embryo.

Ruminate endosperm

In Annonaceae, Myristicaceae, Rubiaceae and Palmaceae, the endosperm is mostly ridged and furrowed. The ridges and furrows are often very sharp and irregular. There are two chief reasons for the formation of the ruminated endosperm.

(1) The development of the ruminated endosperm may be due to the irregular development of the inner surface of the seed coat forming irregular foldings in it. When the growing endosperm expands into the furrows of the inner surface of the seed coat (or integument) it develops ruminations,

(2) The outer tissues of the nucellus and integuments may invaginate into the endosperm forming a ring about the inner condition of the endosperm

Mosaic endosperm

The mosaic endosperm is not a type of endosperm formation but is a condition where patches of two shades of colours appear in the endosperm tissue, apparently providing a mosaic design. In Zea mays, red and white patches are sometimes observed irregularly mixed together like a mosaic pattern

Embryo

Mostly the zygote, after its formation, shows a minor or sometimes major shrinkage in its size. In cotton, its size gets practically reduced to half the size of the egg (Jensen, 1968). Now the zygote undergoes a period of rest, which is also known as the period of dormancy. It greatly varies from plant to plant. During this period, large vacuoles, present in the upper part of the newly fertilized egg cell, disappear and the cytoplasm becomes more or less homogeneous. In angiosperms, first nuclear division of the zygote is immediately followed by a wall formation like that in the lower vascular plants. The embryogeny in angiosperms differs in this respect from that of gymnosperms where a period of free nuclear divisions is followed by the cell wall formation. The division of the zygote and primary endosperm nucleus may go together; but generally this does not happen and the zygote starts dividing when the primary endosperm nucleus has already divided. In rare cases the zygote begins to divide earlier than that of the primary endosperm nucleus.

Though there is much resemblance in the early stages of embryo development in monocotyledons and dicotyledons, but marked differences are noted in later developments and mature structure of their embryos. Apart from a few exceptions, the plane of first division of the zygote is always transverse.

Development of dicotyledonous embryo

The nucleus of the zygote first divides into two nuclei followed by a transverse wall. Now the zygote becomes two celled (two celled proembryo). One of the cell, situated towards the micropyle, is termed basal cell (upper cell) and the other terminal cell (lower cell). Usually the basal cell undergoes several transverse divisions to develop long suspensor and the terminal cell with subsequent transverse or longitudinal divisions develops the embryo. In some of the genera, the basal cell remains undivided and develops large sac-like structure as reported by Wardlaw (1955). Sauton, the famous French embryologist is of the view that the mode of origin of four celled proembryo and the contribution made by each of these cells to the adult embryo serve as most important means in classifying the embryonal types. Later Schnarf (1929), Johansen (1945) and Maheshwari (1950) have recognized five chief types of embryos among the dicotyledons which can be easily distinguished from one another as indicated below:

1. Terminal cell of the two-celled proembryo divides longitudinally

2. Basal cell either does not participate in the development of embryo or plays a minor role in its formation. Crucifer or Onagrad type. develop

2, Both basal and terminal cells contribute to the development of embryo Asterad type,

1. Terminal cell of the two-celled proembryo divides transversely

3. Basal cell either does not participate or participates only partially in the development of embryo

4. Basal cell usually forms two or more-celled suspensor Soland type

4. Basal cell does not divide at all and if a suspensor is present it is derived from the terminal cell Caryophyllad type.

3. Both basal and terminal cells participate in the development of embryoChenopodiad type.

Crucifer type

(*Capsella bursa-pastoris*)

The crucifer type of embryo development is found in *Capsella bursa-pastoris* of Cruciferae which represents a typical dicotyledonous type of the embryo development. A detailed study of such development was made by Hanstein (1870) and Sodeges (1914, 1919) in *Capsella bursa-pastoris*. The zygote first divides by a transverse wall into a basal cell (cb) and a terminal cell (ca) (Fig. 8-1). The basal cell then divides by a transverse wall and the terminal cell by a longitudinal wall and a four-celled proembryo is formed. Another longitudinal wall, perpendicular to the first longitudinal wall, appears in the two terminal cells, already developed. This, a quadrant stage is reached. The four cells of the quadrant stage now divide transversely to form an octant stage of eight cells which are arranged in two tiers of four cells each. The lower tier is responsible for giving rise to the stem tip and cotyledons while the upper one is meant for the formation of hypocotyl. Now a periclinal division occurs in each of the octant cells to give rise to eight outer cells and eight inner cells. The outer eight cells form the dermatogen. The cells of dermatogen further divide anticlinally and develop the epidermis. With the longitudinal and transverse division of the inner eight cells, the periblem and plerome regions get differentiated just below the dermatogen and centrally, respectively. The cortex develops from the periblem and the stele from the plerome. While the above development is taking place, two cells, developed from the basal cell of the four-celled proembryo, divide several times to form a long suspensor or six to ten cells. The upper-most cells of the suspensor, situated towards the micropyle, becomes enlarged and vesicular and acts as haustorium. Generally, it remains unbranched but in some plants, a e. g. *Sedum acre* it develops a branched haustorium. The lower most cell of the suspensor, nearest to the developing embryo, is known as hypophysis, which later forms a part of the embryo. The hypophysis, resembling the other cells of suspensor, becomes rounded at its lower end. It divides by a transverse wall to produce two cells. These cells further divide by two longitudinal walls at right angles to each other. Thus, two four-celled tiers are formed. Out of these two tiers, four cells of the tier nearest to the suspensor cells function as root cap and root epidermis initials. Remaining four cells of the other tier become initials of root cortex. With further division of these eight cells, the root cap, epidermis and cortex of the radicle are contributed.

By further divisions in the embryo proper, especially at these two places where the cotyledons are to be developed, the embryo appears to be heart-shaped in a longitudinal section. Both hypocotyl and cotyledons soon begin to elongate, helped by mostly transverse divisions of the cells. A continued enlargement of the hypocotyl and cotyledons brings about a marked curvature in the cotyledons which get placed within the ovule more or less parallel to the axis of embryo. The embryo, at this stage, appears as a horse-shoe-shaped structure. It all happens as there is short of space within the ovule for an embryo of this type with big cotyledons. In the mature embryo, the stem tip is terminal and the two cotyledons occupy a

lateral position. The crucifer type is also called Onagrad type because such type of the development of the embryo is also characteristic to Onagraceae in addition to Cruciferae.

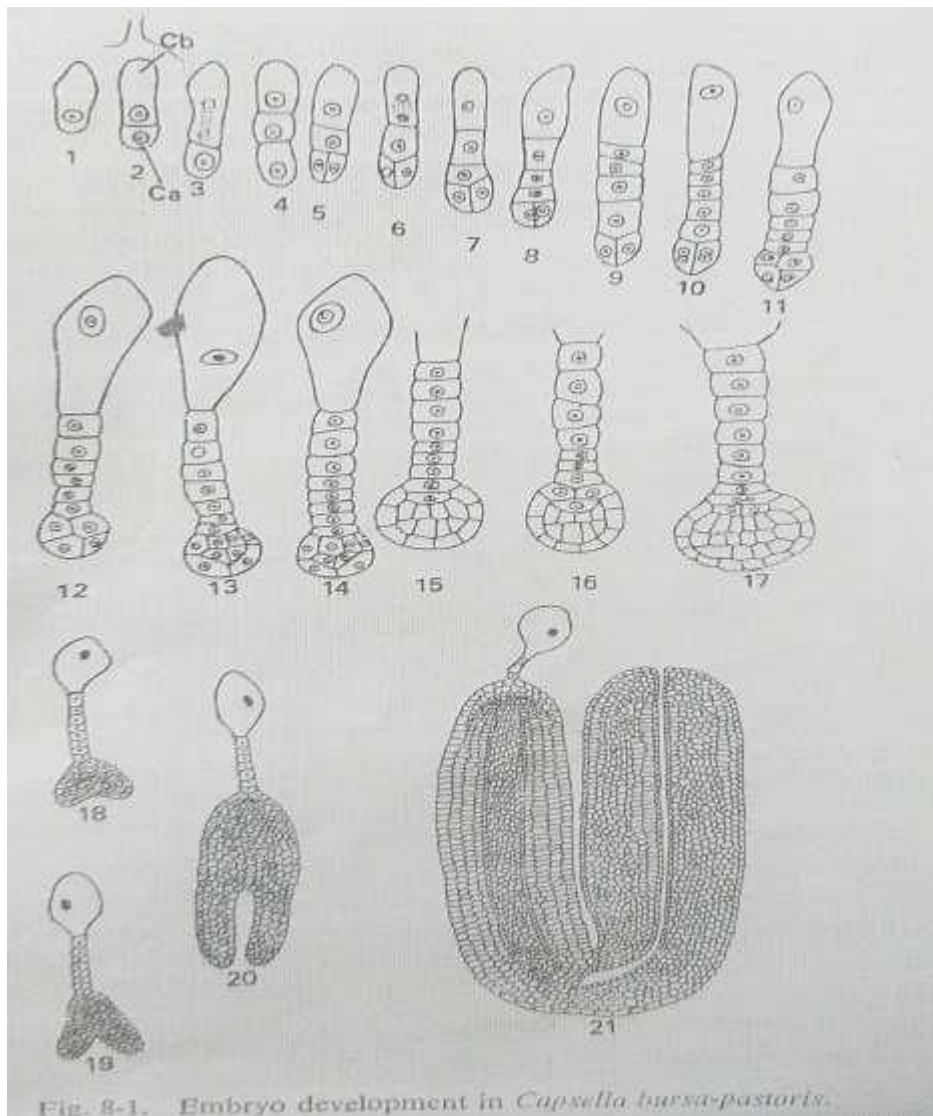


Fig. 8-1. Embryo development in *Capsella bursa-pastoris*.

Development of monocotyledonous embryo

The embryos of monocotyledons and dicotyledons do not exhibit any marked difference in their early divisions and developments, However, important differences are observed during their later developments and their mature embryos look quite different from each other. It has already been stated above that a mature embryo of dicotyledons has a terminal stem tip and two laterally placed cotyledons. A few plants of Umbelliferae and one of Ranunculaceae, i.s. *Ranunculus ficaria* are exceptions to this arrangement. Both these families belong to dicotyledons but only one cotyledon develops in the above two mentioned two plants.

In monocotyledons, a typical embryo has a lateral stem tip (shoot apex) and one terminally placed cotyledon. As it is not possible to consider the embryogeny of any one plant of monocotyledons as a typical type, the embryogeny of *Sagittaria sagittifolia* has been considered by several authors to represent the embryogeny of the primitive families of monocotyledons (Fig. 8-2).

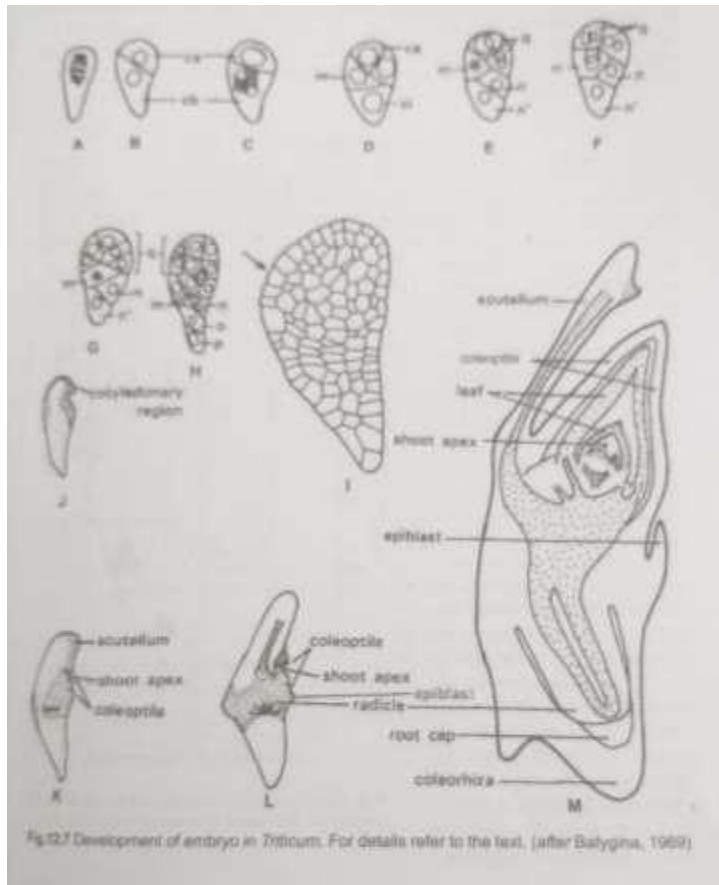
Grass embryo. The monocotyledonous embryo of grasses is strikingly different from that of other monocotyledons in its mature structure as well as development. A mature embryo of *Triticum* (Fig. 12.7 M), for example, has single cotyledon, called scutellum. In a median longitudinal section of the mature embryo it appears laterally attached to the embryonal axis. The portion of the embryonal axis below the level of scutellum is the radicle which bears an apical meristem and a root cap at the lower end. The radicle and its cap are enclosed in coleorhiza, which is the undifferentiated lower part of the proembryo. The portion of the embryonal axis above the level of scutellum is the epicotyl. It comprises a shoot apex with some leaf primordia, enclosed in a hollow foliar structure, the coleoptile. The latter has an apical pore. On one side the coleorhiza gives out a small outgrowth called epiblast.

Batygina (1969) has described in great detail the mode of embryo development in *Triticum*. All the four species of *Triticum* examined by her show a fixed pattern of embryogeny, which is so different from that in dicotyledons and other monocotyledons that she remarked: "the unique mode of embryogenesis in the Gramineae may allow the separation of a new type of embryogeny - Graminad Type. The early part of embryogeny

in *Triticum* is characterized by the regular occurrence of oblique divisions. The first nuclear division of the zygote (Fig. 127 A) is followed by laying down of an oblique wall, cutting a small apical cell (c) and a large basal cell (cb, Fig. 127 B). Cell cb again divides obliquely forming cells and m (Fig. 127 CD). The upper end of the wall formed during this division connects with the wall separating a and cb. The third division occurs in the cell ca, in a plane perpendicular to the first division of the zygote. Thus, a T-shaped proembryo (4-celled) is formed (Fig. 12.7 D). However, the orientation of the walls is very different from the T-shaped tetrads in either dicotyledons or other monocotyledons. This characterizes the wheat embryogeny

Cell ci divides by a wall at right angles to the wall between ci and m, resulting in the formation of cells n and n' (Fig. 12.7 E). Divisions of the daughter cells of ca are in the same plane as the first division in ca but at right angles to it, forming the typical quadrant q (Fig.

12.7 E,F). The cell m divides vertically into two cells (Fig 12.7 E-H). Further divisions occur in



The first organ to be initiated is the single cotyledon or scutellum. Its differentiation starts with growth in the apical-lateral region of the proembryo (Fig. 12.7A arrow marked), involving sectors, and n . With further development a constriction appears opposite the scutellum in the sector ca) demarcating it from the rest of the embryo (Fig. 12.7C). This is followed by the appearance of primordia of coleoptile and then the shoot apex close to the notch (Fig. 12.7KL.). The radicle differentiates endogenously in the central zone of the embryo (Fig. 12.7LM). As in *Najas*, in *Triticum* also the epicotyl is formed by the terminal tier (g). Its apparent lateral position in the mature embryo is a secondary feature. It arises due to active growth of the cotyledon leaving behind the epicotyl.

Suspensor

The occurrence of suspensor is a common feature of angiosperms during embryogeny. It develops as an ephemeral organ near the radicle, the chief function of which is to push the mature and globular embryo deep into the nutritive tissue of the endosperm so that there is no hindrance in the supply of food materials to the embryo at the time of germination. The suspensor is exceptionally too long in those plants where the embryo sacs have been

found growing upto a distance in the styler region. After the egg is fertilized some where in the style, a very long suspensor has to develop as to push the embryo much below into the endosperm. Such plans having long suspensors may be cited from Loranthaceae.

In some plants the suspensor may show a very prominent growth and develop large haustorium which penetrates between the cells of the endosperm and sometimes even encroaches upon the other ovular tissues surrounding the endosperm. The haustorial function of the suspensor has been observed by several workers since the beginning of the twentieth century. During the course of study of a comparative morphology of Rubiaceae, Lloyd (1902) state : "The function of the suspensor in these forms is, therefore, not alone to bring the embryo into favourable position with relation to the food supply in a mechanical sense, but to act as a temporary embryonic root". With the accumulation of the knowledge regarding the appearance of the suspensor during embryogeny of large number of angiosperms, its presence seems to be of wide occurrence. There is much variation in the structure and function of the suspensor found in different genera of angiosperms.

In *Capsella* the suspensor is long thread-like structure with enlarged and globular basal cell which survives for a long period (Fig. 8-3). Active metabolism occurs within the suspensor. It absorbs and translocates the nutrients to the developing embryo. In those plants where the endosperm is much reduced or absent, the suspensor haustoria show a vigorous growth. The suspensor may also be absent or is represented only by a group of oval cells in some

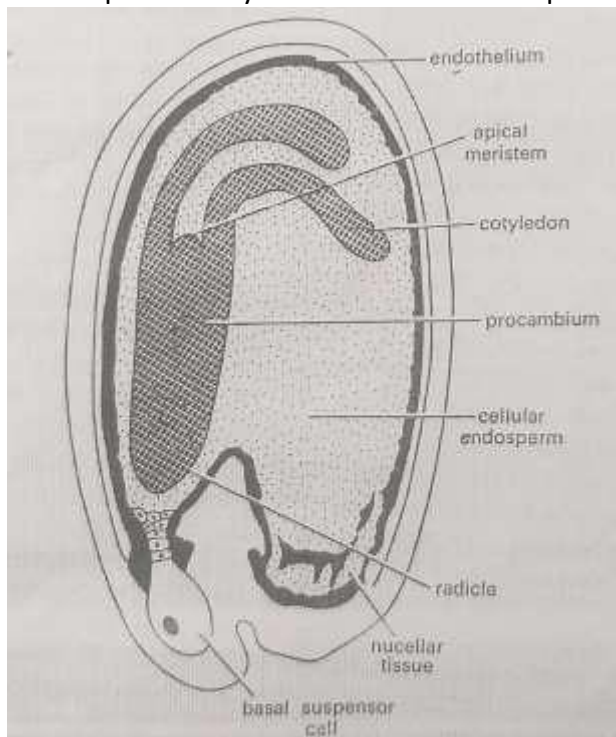


Fig 8-3. Embryo development in *Capsella bursa-pastoris* at bending stage of the cotyledons showing long suspensor and globular basal cell. (Modified after Esau).

plants of Mimosaceae. It may be either rudimentary as in *Trifolium*, filamentous as in *Ononis* and sometimes even represented by large and spherical mass of cells as in *Cytisus*.

In *Pisum* the suspensor is composed of two pairs of multinucleate cells. The cells of a pair situated near the micropyle are elongated and large in size whereas the cells of the other pair are spherical. In *Cicer*, two rows of uninucleate cells form the suspensor.

Lloyd (1902) and Soueges (1925) observed that in the members of Rubiaceae the suspensor originates like a multinucleate thread like structure. Later, lateral outgrowths develop from those cells of the suspensor which are close to the micropyle. Such lateral outgrowths with their swollen tips collect food by penetrating into the endosperm.

The development of aggressive haustorium in *Sedum* (Crassulaceae) is of much interest. Here the basal cell of two-celled proembryo does not divide, gets much elongated and branches profusely to give rise to a haustorium which penetrates into the testa of seed to obtain the nutrients (Fig. 8-4).

In *Dicraea* the haustorium develops from the enlarged basal cell containing two hypertrophied nuclei. Many haustorial branches are produced from this basal cell which get involved in the absorption of food materials from different ovular tissues.