1. Relationships of Gnetum:

Gnetum and Other Gymnosperms: Gnetum shows several resemblances with gymnosperms and has, therefore, been finally included under this group. Some of the characteristics common in both Gnetum and other gymnosperms are under mentioned: 1. Wood having tracheids with bordered pits. 2. No sieve tubes and companion cells are present. 3. Presence of naked ovules. 4. Absence of fruit formation because of the absence of ovary. 5. Anemophilous type of pollination. 6. Development of prothallial cell. 7. Cleavage polyembryony. 8. Resemblance of the vascular supply of the peduncle of the cone of Cycadeoidea wielandii with that of a single flower of Gnetum. 9. Resemblance of the structure of basal part of the ovule in Gnetum and Bennettites.

Gnetum and Angiosperms: A key position to Gnetum has been assigned by scientists while discussing the origin of angiosperms. Both Gnetales and angiosperms originated from a common stalk called “Hemi-angiosperm”. Thompson (1916) opined that the ancestors of both Gnetum and angiosperms were close relatives. Some other workers have gone up to the extent in stating that Gnetum actually belongs to angiosperms. Hagerup (1934) has shown a close relationship between Gnetales and Piperaceae.

In a beautiful monograph on Gnetum, Maheshwari and Vasil (1961) have stated that “Gnetum remains largely a phylogenetic puzzle. It is gymnospermous, but possesses some strong angiospermic features”.

Some of the resemblances between Gnetum and angiosperms are under mentioned:

1. The general habit of the sporophyte of many species of Gnetum resembles with angiosperms. 2. Reticulate venation in the leaves of Gnetum is an angiospermic character. 3. Presence of vessels in xylem is again an angiospermic character. 4. Clear tunica and corpus configuration of shoot apices is a character of both Gnetum and angiosperms. 5. Strobili of Gnetum resemble much more with angiosperms than any of the gymnosperms 6. Micropylar tube of Gnetales can be compared with the style of the angiosperms because both perform more or less similar functions. 7. Tetrasporic development of the female gametophyte is again a character which brings Gnetum close to angiosperms. 8. Absence of archegonia again brings Gnetum and angiosperms much closer. 9. Dicotyledonous nature of the embryo of Gnetum brings it quite close to the dicotyledons. 10. Wood of both shows Maule’s reaction. ***Because of Such characters Gnetum is called “Intermediate” between Gymnosperms & Angiosperms***.

2. Distribution of Gnetum: *[N.B.: Ignore figure numbers]*

Gnetum, represented by about 40 species is confined to the tropical and humid regions of the world. Nearly all species, except G. microcarpum, occur below an altitude of 1500 metres. Five species (Gnetum contractum, G. gnemon, G. montanum, G. ula and G. latifolium) have been reported from India (Fig. 13.1). Gnetum ula is the most commonly occurring species of India.

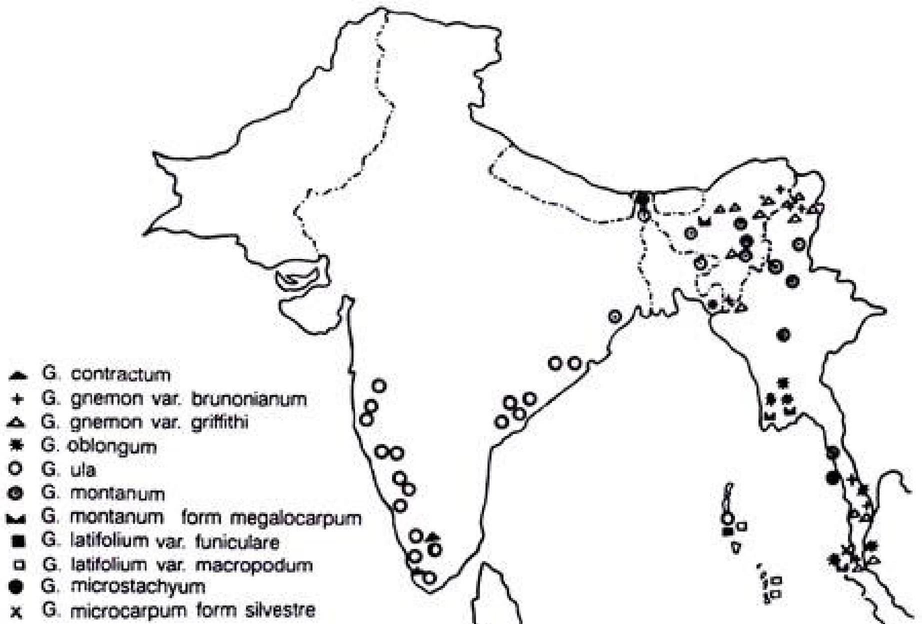


Fig. 13.1. The map showing distribution of different species of *Gnetum* in India, Bangladesh and Myanmar (modified after Bhardwaja, 1957).

According to Bhardwaj (1957) various species of Gnetum occur in India in the following regions:

Gnetum ula: It is a woody climber having branches with swollen nodes. It is found in Western Ghats near Khandala, forests of Kerala, Nilgiris, Godawari district of Andhra Pradesh and Orissa.
Gnetum contractum: A scandent shrub growing in Kerala, Nilgiri Hills and Coonoor in Tamil Nadu.
Gnetum gnemon: A shrubby plant found in Assam (Naga-Hills, Golaghat and Sibsagar).
Gnetum montanum: A climber with smooth, slender branches, swollen at the nodes. It is found in Assam, Sikkim and parts of Orissa.
Gnetum latifolium: A climber found in Andaman and Nicobar Islands.

[N.B**.: Reproduction of Gnetum**:Gnetum is dioecious. The reproductive organs are organised into well-developed cones or strobili. These cones are organised into inflorescences, generally of panicle type. Sometimes the cones are terminal in position. A cone consists of a cone axis, at the base of which are present two opposite and connate bracts. Nodes and internodes are present in the cone axis. Whorls of circular bracts are present on the nodes. These are arranged one above the other to form cupulas or collars (Fig. 13.10). Flowers are present in these collars. Upper few collars may be reduced and are sterile in nature in G. gnemon.]

3. Male Strobilus & Male Flower: [N.B.: Ignore figure numbers]

The male flowers are arranged in definite rings above each collar on the nodes of the axis of male cone. The number of rings varies between 3-6. The male flowers in the rings are arranged alternately. There is a ring of abortive ovules or imperfect female flowers above the rings of male flowers. Each male flower contains two coherent bracts which form the perianth (Fig. 13.11). Two unilocular anthers remain attached on a short stalk enclosed within the perianth. At maturity, when the anthers are ready for dehiscence, the stalk elongates and the anthers come out of the perianth sheath. In Gnetum gnemon a few (2-3) flowers are sometimes seen fusing each other (Fig. 13.12).

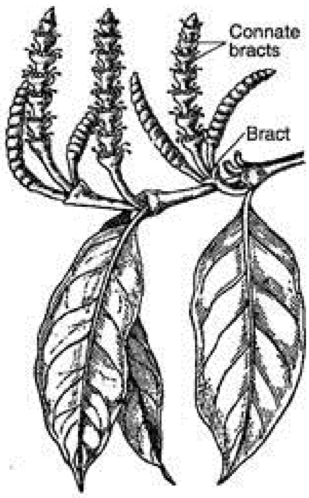


Fig. 1.73 : *Gnetum gnemon* : A twing bearing male inflorescences

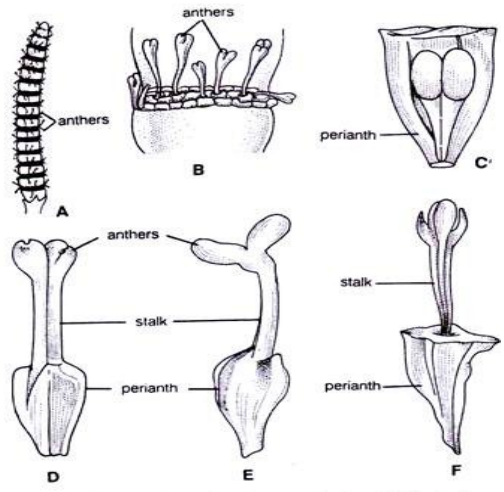


Fig. 13.11. *Gnetum ula.* A, A male cone; B, A part of 'A' showing male flowers; C, L.S. male flower; D-E, Male flowers with anthers emerged out of a perianth; F, A dehisced male flower.

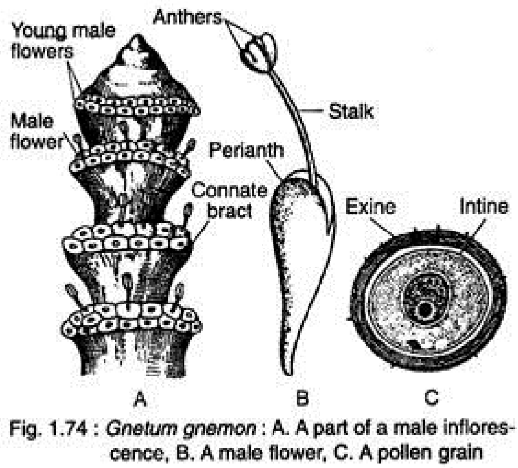


Fig. 1.74 : *Gnetum gnemon* : A. A part of a male inflorescence, B. A male flower, C. A pollen grain

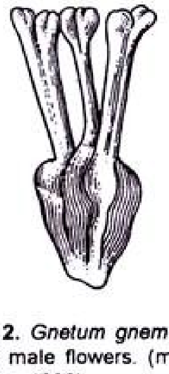


Fig. 13.12. *Gnetum gnemon.* Showing fusion of male flowers. (modified after Madhulata, 1960).

4.Female Strobilus & Female Flower: ***[N.B.: Ignore figure numbers]***

The female strobilus is very much similar to that of the male strobilus in the young stage. Like male strobilus, the female strobilus consists of an axis bearing several whorl of collars arranged one above the other (Fig. 1.75A). A ring of 4-10 ovules (female flowers) is present above each collar (Fig. 1.75B). The male flowers are not found in the female strobilus. The upper few collars are devoid of ovules and are thus sterile (Fig. 1.75B). The female cones resemble with the male cones except in some definite aspects. A single ring of 4-10 female flowers or ovules is present just above each collar (Fig. 13.15). Only a few of the ovules develop into mature seeds (Fig. 13.15B). In the young condition, there is hardly any external difference between female and male cones. All the ovules are of the same size when young but later on a few of them enlarge and develop into mature seeds. All the ovules never mature into seeds.

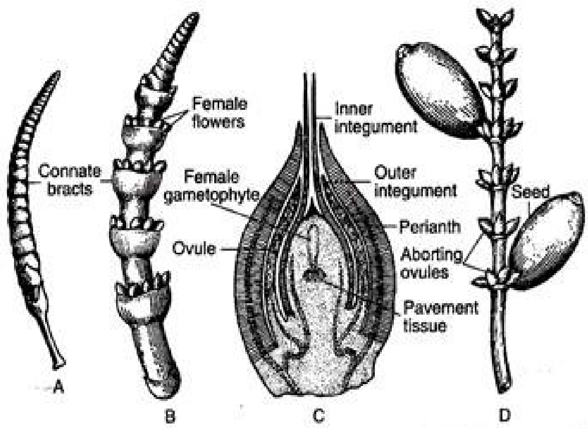


Fig. 1.75 : *Gnetum ula* : A. An young female inflorescence, B. A mature female inflorescence, C. Median L.S. of a female flower, D. A female inflorescence bearing two mature seeds

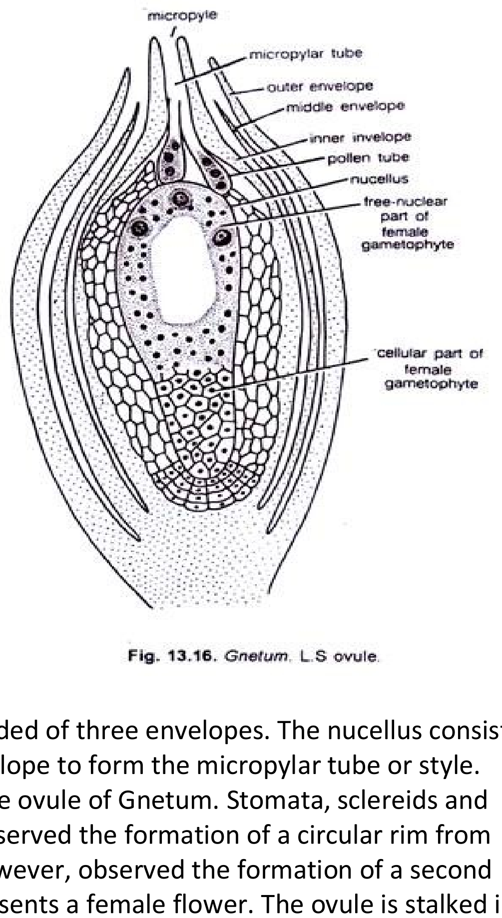


Fig. 13.16. *Gnetum*. L.S ovule.

Ovule or Female Flower: Each ovule (Fig. 13 16) consists of a nucellus surrounded of three envelopes. The nucellus consists of central mass of cells. The inner envelope elongates beyond the middle envelope to form the micropylar tube or style. The nucellus contains the female gametophyte. There is no nucellar beak in the ovule of Gnetum. Stomata, sclereids and laticiferous cells are present in the two outer envelopes. Madhulata (1960) observed the formation of a circular rim from the outer epidermis of the inner integument in G. gnemon. Thoday (1921), however, observed the formation of a second such rim at a higher level. The ovules in G. ula are stalked. A single ovule represents a female flower. The ovule is stalked in G. ula, but may be sub- sessile or even sessile. The ovules are orthotropous, crassinucellate (with massive nucellar tissue) and are protected by three envelopes (Fig. 1.75C). The outer envelop which becomes thickened and succulent at maturity is considered to be the perianth corresponding to the perianth of male flower. The middle and the inner envelopes are actually the integuments. Numerous laticiferous ducts and sclerides are present in the perianth with some epidermal stomata. The middle envelop is called the outer integument which is anatomically similar to the outer envelop. The inner envelop, i.e., the inner integument, elongates far beyond the apical cleft of the perianth and forms a long micropylar tube (Fig. 1.75C). Anatomically, the inner integument is different from the other two envelopes, because neither sclerides nor stomata develop in the inner integument. The inner integument is free from the nucellus except at the chalazal end. Two sets of vascular bundles are formed (Fig. 1.75C), of which the outer set passes to the perianth and the inner set again divides and one of its branches passes to the outer integument and the other to the inner integument. All the three envelopes of ovules develop in acropetal manner. A shallow pollen chamber is present at the tip of the nucellus.
[N.B.:Gametophyte of Gnetum: The spore is the first phase of gametophyte generation. The microspore or pollen grain represents the male gametophyte, while the tetranucleate coenomegaspore represents the first phase of female gametophyte which develops into a female gametophyte.]

5.Development of Male Gametophyte: ***[N.B.: Ignore figure numbers]***

Microsporogenesis: Two archesporial cells are distinguished below the epidermal layer (Fig. 13.19A). Archesporial cells divide and re-divide to form many-celled archesporium (Fig. 13.19B). The outermost layer of the archesporium divide periclinally to form an outer layer of parietal cells and inner layers of sporogenous cells (Fig. 13 .19C). The parietal cells form the wall layers and tapetal layer by periclinal divisions (Fig. 13.19D). The sporogenous cells develop into microspore mother cells by some irregular divisions. Tapetal cells later on become bi-nucleate (Fig. 13.19D, E). Microspore mother cells divide reductionally to form haploid microspores.

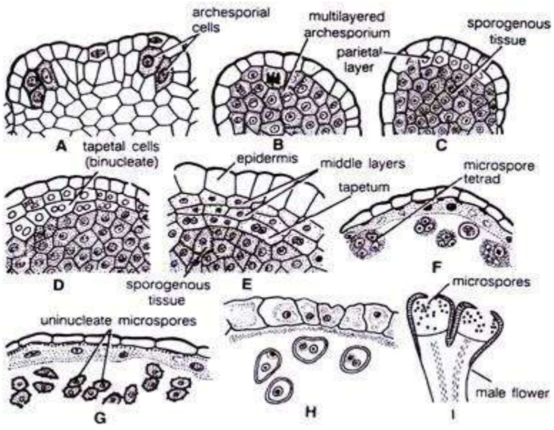
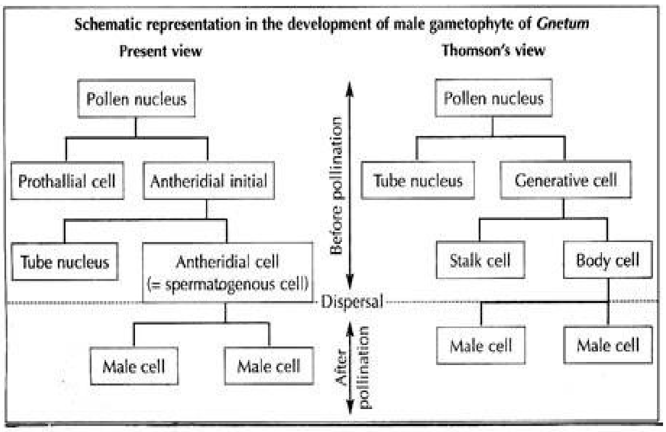


Fig. 13.19. Development of microsporangium in *Gnetum*.



Microgametogenesis: Before Pollination: The pollen grain is inapeturate and spherical, bounded by the two concentric wall layers: the outer thick, spiny exine and the inner thin intine (Fig. 1.74C). The pollen nucleus divides mitotically to produce a small lens-shaped prothallial cell and a large antheridiai initial (Fig. 1.76B). The prothallial cell does not divide further and eventually degenerates. The antheridiai initial divides to form an antheridiai cell and a tube nucleus (Fig. 1.76C). The antheridiai cell directly functions as spermatogenous cell. The pollen grains are released from the microsporangium at this 3- celled stage (one prothallial cell, an antheridiai or spermatogenous cell and a tube nucleus).

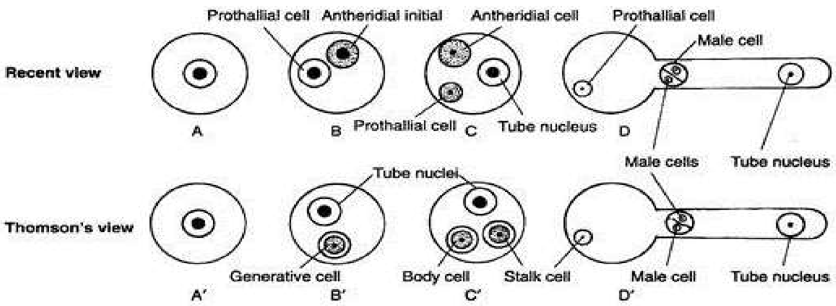


Fig 1.76 : Genetum: The development of male gametophyte : A-D. Recent view, A'-D'. Thomson's View

According to Thomson (1961), the prothallial cell is not formed in Gnetum. He proposed that the pollen nucleus cuts off a tube nucleus and a generative cell (Fig. 1.76B'). The generative cell again divides forming a stalk cell and a body cell (Fig. 1.76C'). Thus, the pollen grains are released at this 3-celled stage (tube nucleus, stalk cell and body cell).

Microgametogenesis: After Pollination: The exine is cast off during pollen germination. The tube cell of the pollen comes out in the form of a pollen tube which traverses the nucellar tissue through intercellular spaces. The prothalial cell remains within the pollen grain and eventually disorganises. The spermatogenous cell moves into the pollen tube and subsequently it divides to form two equal (e.g., G. ula, G. gnemon) or unequal (e.g., C. africanum) male cells just prior to fertilisation (Fig. 1.76D). The male cells are actually the male gametes which are non-motile. However, according to Thomson (1961) the stalk cell remains within the microspore and eventually degenerates. The body cell moves into the tube where it divides to form two male cells (Fig. 1.76D').

6.Development of Female Gametophyte: ***[N.B.: Ignore figure numbers]***

Megasporogenesis: In the young conditions, an outer epidermal layer is distinguishable in the nucellus. Two to four archesporial cells develop below the epidermis at a later stage. The archesporial cells divide periclinally to form outer primary' parietal cells and inner sporogenous cells. The primary parietal cells and the epidermal layer divide periclinally and anticlinally several times resulting into a massive nucellus. The sporogenous cells divide and re-divide to form megaspore mother cells which remain arranged in linear rows. All the megaspore mother cells may divide reductionally and form tetrasporic embryo-sacs but ultimately all, except one, degenerate.

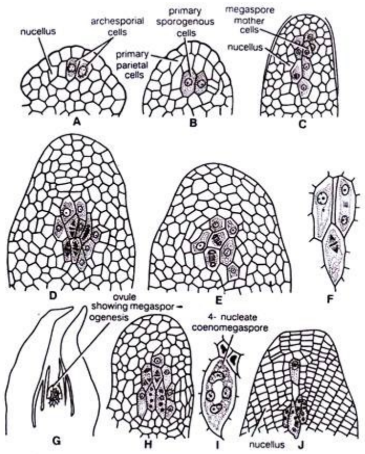


Fig. 13.17. *Gnetum*. Showing stages of megasporogenesis in different species. (A, C, D & E, in *Gnetum ula*; B, F to J in *G.gnemon*).

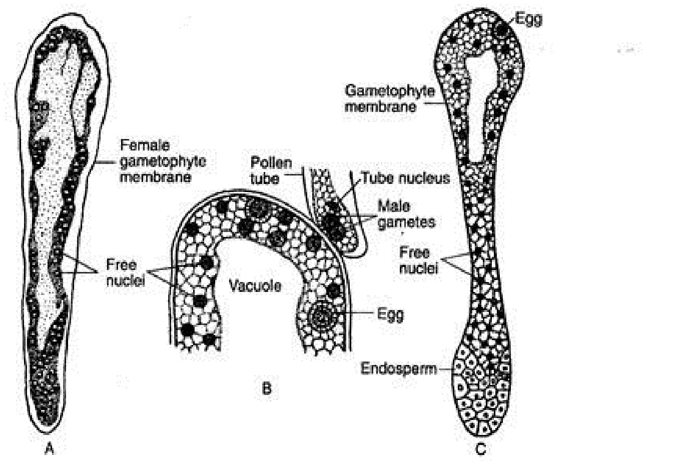


Fig. 1.77 : *Gnetum ula* : A. A female gametophyte in free nuclear stage, B. Top of the female gametophyte showing eggs, C. Female gametophyte showing first part of endosperm at base

At the initial stage, before the gametophyte formation, the nucellar cells immediately below the megaspore mother cell divide to form a tissue. The cells of this tissue are arranged in radiating rows. This tissue is termed as 'pavement tissue' which eventually gets absorbed and seems to be nutritive in function.

Megagametogenesis: There is a free nuclear division in the coenomegaspore, as a result a large number of free nuclei are formed (Fig. 1.77A). The number of nuclei thus formed varies in different species, viz. 256 in G. gnemon, 512 in G. africanum and 1500 in G. ula. At this stage, a large central vacuole appears and the free nuclei lie in a thin film of cytoplasm around the vacuole towards the periphery (Fig. 1.77B). Later, the nuclei in the peripheral cytoplasm divide repeatedly. At this stage, the upper part of the gametophyte surrounding a vacuole widens, while the lower part of the gametophyte shows accumulation of cytoplasm. Thus, the gametophyte becomes an inverted flask-shaped structure (Fig. 1.77C). The wall formation starts very slowly from the chalazal end towards the micropylar end. Thus, the nuclei remain free at the microphylar end even at the time of fertilisation. The important characteristic in the female gametophyte of Gnetum is the absence of archegonia. One to three nuclei of the gametophyte in the micropylar end enlarge several times and accumulate dense cytoplasm around them. These large and densely cytoplasmic cells are the eggs (Fig. 1.77B). It is important to note that all the eggs do not mature simultaneously.

Pollination: Gnetum is wind-pollinated. The pollen grains are dispersed from the anther and remain suspended in the air for some time. At the free nuclear stage of the female gametophyte, the nucellar beak in the ovule disorganises forming a viscous sugary liquid which comes out through the microphyle in the form of a pollination drop. The pollen grains are caught in the pollination drop. Due to the drying off of the fluid, the pollen grains are sucked into the micropylar canal and are finally collected in the pollen chamber. The mouth of the micropyle is then sealed from the outer environment due to the development of flage (a circular rim or an umbrella-shaped structure develops from the inner integument) and micropylar closing tissue (a tissue develops by the proliferation of the inner epidermis of integument at the level of flage).

Fertilisation: The pollen tube enters the female gametophyte and the male gametes move ahead of tube nucleus (Fig. 1.77B). The pollen tube ruptures to discharge the male gametes into the egg cell.

The cell sheath of male cell is left outside the egg cell. Usually one of the male nuclei fuses with the egg nucleus and thus a zygote is formed. Sometimes, two male gametes may fuse two different eggs if those eggs are in the vicinity of the pollen tube.

Endosperm: In gymnosperms, endosperms are cellular and haploid and are formed before fertilisation. However, in Gnetum the development of endosperms starts before fertilisation very slowly from lower part of the gametophyte which eventually proceeds upward. After fertilisation, the wall formation starts in such a way that the cytoplasm divides into many multinucleate compartments (Fig. 1.78A). Later, the nuclei in each cell fuse to form a single polyploid nucleus (Fig. 1.78B). In this stage, the lower part of the gametophyte becomes cellular, while the upper part remains free nuclear even after fertilisation (Fig. 1.77C). Thus, the development of endosperm takes place even after fertilisation. There is a great variation in the development of endosperm in Gnetum. In some cases, the wall formation starts either from the upper part or from the middle part of the gametophyte instead of the lower part and the whole gametophyte may become cellular. Though some portions of the endosperms are formed after fertilisation, the characteristic triploid endosperm through double fertilisation is, however, absent in Gnetum.

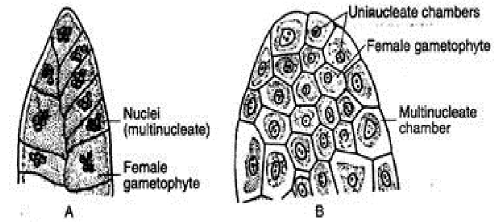


Fig. 1.78 : *Gnetum ula.* Development of endosperm : A. A portion of female gametophyte showing multinucleate endosperm, B. Uninucleate and multinucleate chambers

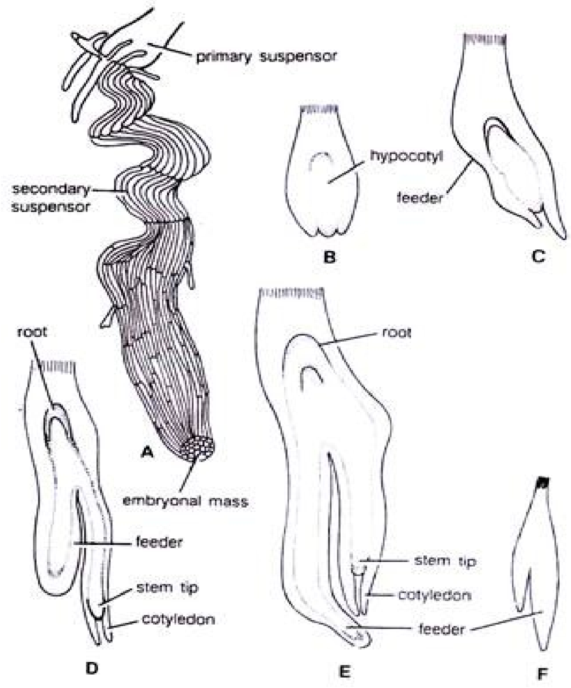


Fig. 13.25. *Gnetum ula.* Development of embryo.

7. Embryogeny: ***[N.B.: Ignore figure numbers]***

In all angiosperms (except, Paeonia), the division of zygote is accompanied by wall- formation; while in all gymnosperms (except Sequoia, Welwitschia), there is a free nuclear phase in the zygote during the development of embryo. However, Gnetum occupies an intermediate stage between gymnosperms and angiosperms with regard to embryo development by having both the free-nuclear divisions as well as cell divisions. There is a great variation in the early development of the embryo in different species of Gnetum. In C. gnemon, the zygote develops 1-3 small tubular outgrowths. Only one of the pro-tuberances receives the nucleus and survives, while the remaining protuberances die out (Fig. 1.79A). The surviving tubular outgrowth becomes much elongated and branched and develops in various directions invading the intercellular spaces of the endosperm. These tubes are called primary suspensor tubes or proembryonal tubes (Fig. 1.79B). All the primary suspensor tubes remain coiled around each other. At the tip of the primary suspensor tube, a small cell is cut off which eventually divides by a transverse wall, followed by a longitudinal wall resulting into four cells. This is further fol-lowed by irregular divisions to form a group of cells. Now, further divisions take place in some of these cells which eventually elongate to form secondary suspensor. The rest of the cells at the tip form an embryonal mass (Fig. 1.79C, D).

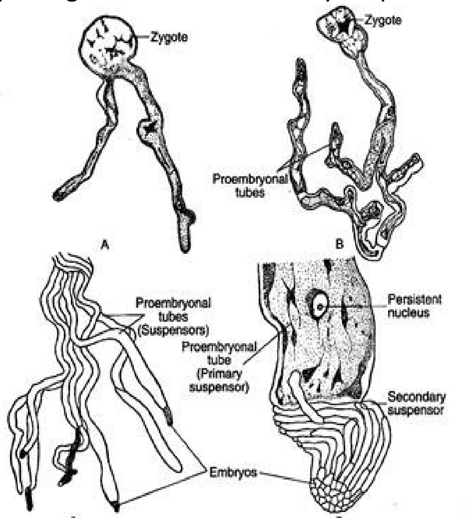


Fig. 1.79 : A. Germination of *Gnetum gnemon* zygote, B. Branching of *G. gnemon* suspensor tube to form several proembryonal tubes, C. Interwined primary suspensor or proembryonal tubes and embryo initials in young seed of *G. ula*, D. Tip of proembryonal tube with growing embryo in *G. ula*

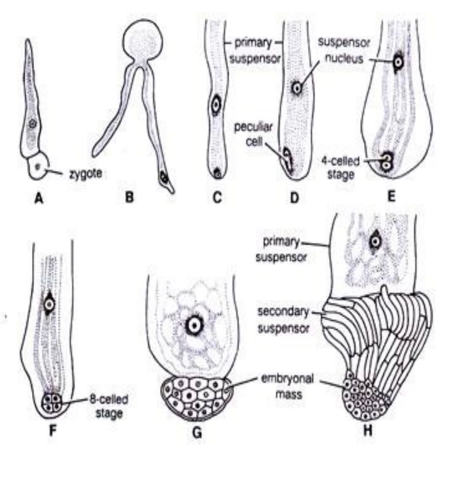


Fig. 13.24. *Gnetum ula.* Development of embryonal mass. A-B, Germination of zygote; C-D, Formation of peculiar cell; E-F, Formation of 8-celled stage of embryonal mass; G, Embryonal mass formed by peculiar cell; H, Formation of secondary suspensor.

In G. ula, the early development of the embryo up to the primary suspensor cells is almost similar to that of G. gnemon. The nucleus of the primary suspensor cell (Fig. 1.80A) divides to form two unequal nuclei, of which the smaller nucleus is cut-off by a thin wall. This cell is called peculiar cell which forms the embryo (Fig. 1.80B). The peculiar cell divides twice forming a four-celled stage (Fig. 1.80C, D) which further divides transversely resulting into a 8-celled embryo (Fig. 1.80E). The embryonal mass increases in size by the further irregular divisions (Fig. 1.80F). Some cells of the embryonal mass adjacent to the primary suspensor elongate to form the secondary suspensor.

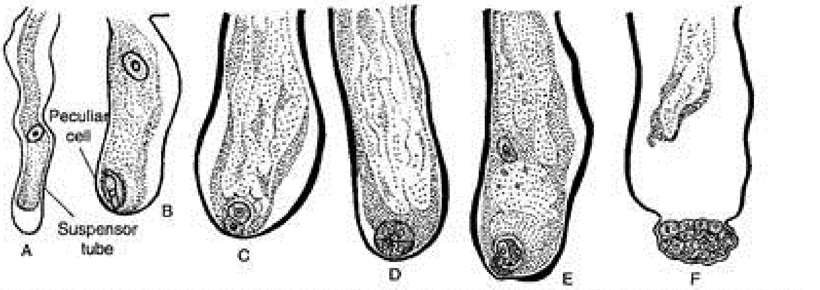


Fig. 1.80 : *Gnetum ula* : A. Tip of primary suspensor tube, B. Formation of peculiar cell, C–E. Peculiar cell dividing to form two (C), four (D) and eight (E) cells, F. Mass of cells formed by the peculiar cell

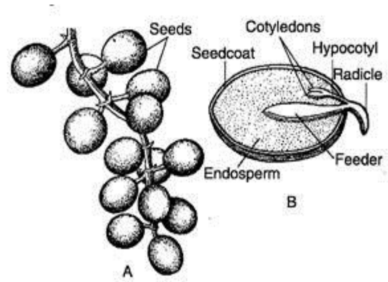


Fig. 1.81 : *Gnetum gnemon* : A. A twig containing seeds, B. Median L.S. of seed about to germinate

Irrespective of the pattern of formation of embryonal mass and secondary suspensor, the cell of the embryonal mass in Gnetum are small and compact with dense cytoplasm forming the embryo-proper. The cells of the secondary suspensor are thin-walled, uninucleate and highly vacuolated. Both the primary as well as secondary suspensors push the embryo deep inside the endosperm for the nourishment of the embryo. At the tip of the embryonal cells, a stem tip with two lateral cotyledons is differentiated (Fig. 1.81 B). A root tip with a root cap also develops at the opposite end of the stem tip. Simultaneously, a hump-like structure called feeder is developed in-between the stem and root tips (Fig. 1.81B). Thus, a mature embryo is composed of a stem tip, two cotyledons, a large feeder and a root tip covered with root cap.
In Gnetum, polyembryony takes place in various ways. Each of the primary suspensor tube may develop an embryo, thus a large number of embryos are formed from a single zygote (Fig. 1.79C). Sometimes additional embryos may develop due to the proliferation of the proembryonal mass present at the tip of the secondary suspensor. Sometimes, the primary suspensor tube branches giving rise to several primary suspensor tubes, each of which may develop an embryo at its tip.
Seeds: Gnetum seeds are oval in shape (Fig. 1.81 A) and green to brown-red in colour. The seeds remain covered with a three-layered envelop, of which outer is fleshy, middle is stony and inner is pepary. The nucellus is used up and the embryo is embedded within the endosperm. Gnetum shows one-year reproductive cycle where pollination, fertilisation and development of embryo take place in one year. The germination of seed is epigeal. The seeds of G. ula germinate after one year's of res-ting phase.

8. Life cycle of Gnetum.

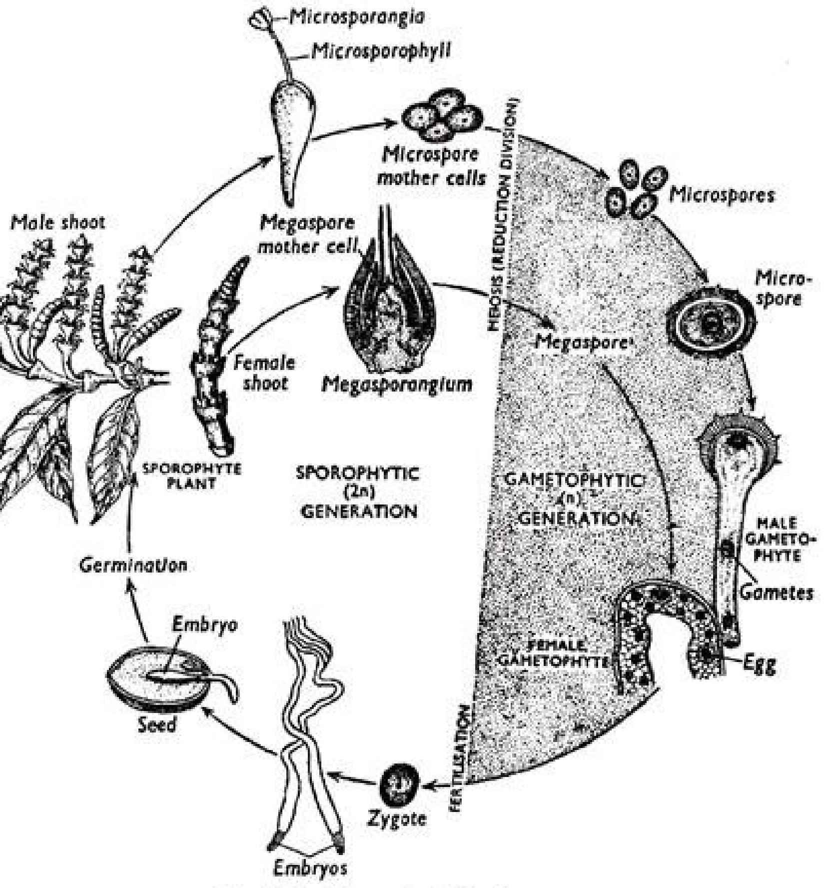


Fig. 1.82 : Life cycle of *Gnetum*