4. GNETUM

4·1 SYSTEMATIC POSITION

Division	-	Gymnospermae
Class	-	Gnetopsida
Order	-	Gnetales
Family	-	Gnetaceae
Genus	-	*Gnetum*

Fig. 4·1 : *Gnetum gnemon* - Sporophytic plant body

4·2 DISTRIBUTION

The genus includes 40 species, which are confined to the tropical rain forests of Amazon basin, West Africa, India, South China and Malaysia. Most of the species are endemic within the areas of their distribution. *Gnetum* species are not available in North America, Europe and Australia.

Gnetum is represented in India by 5 species. Of these *G. ula* is most commonly found in Western Ghats, *G. contractum* in Southern India, and *G. gnemon* in Assam.

(1) *Gnetum gnemon* : The plants are small trees or shrubs. The branches are drooping and bear elliptical leaves. They turn yellow grey on drying. The plants grow on Khasi, Assam, Manipur and Jayanthi Hills.

(2) *G. contractum* : It is a scandent shrub. The male infloresence is once branched. The plants are found in Nilgiri hills of Tamilnadu and Travancoor hills of Kerala.

(3) *G. ula* : It is a woody climber. The stem bears swollen nodes. Flowers are unisexual and simple. The plants are found in moist places of Nilgiri hills, Palni hills, Western Ghats, Orissa, Godavari and Visakhapatnam districts of Andhra Pradesh.

(4) *G. montanum* : It is a robust, woody climber with dark grey coloured stems. Leaves turn black on drying. The male and female infloresence are once branched. It grows in Assam, Sikkim, Burma, Manipur and Nalgonda region of Andhra Pradesh.

(5) *G. latifolium* : The plants are woody climbers with dark green leaves. Leaves turn black and brown on drying . Male infloresence is once branched. It occurs in Nicobar and Anadman Islands.

4-3 EXTERNAL CHARACTERS

The plant body of *Gnetum* resembles very much in its general appearance to that of angiosperms, particularly dicotyledons. The sporophyte is differentiated into root, stem and leaves.

Majority of the species of *Gnetum* are trailing or woody climbers (*G. ula*, *G. latifolium*, *G. montana*), but *G. contractum* is a scandent shrub and *G. gnemon* is a small tree. *G. trinerve* lives as a parasite on cinchona trees.

1. Root : It is profusely branched tap root which does not grow very deep. This is soon replaced by adventitious roots.

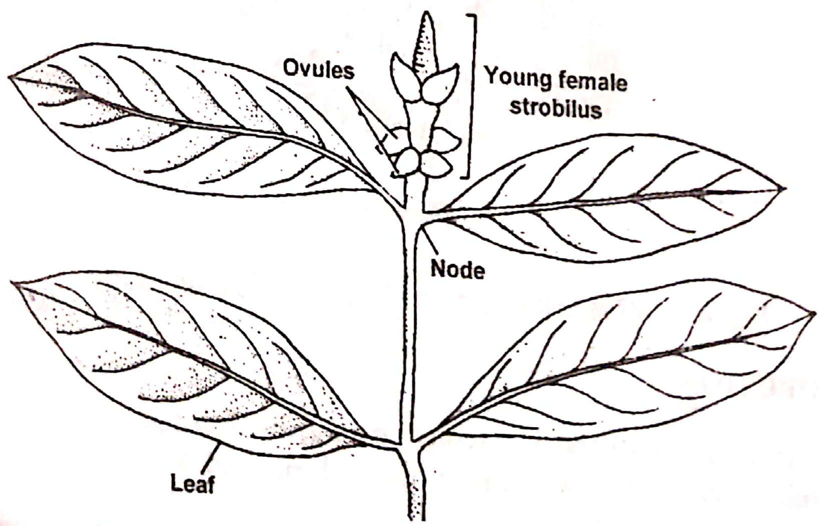

Fig. 4·2 : A portion of a twig with female strobilus

2. Stem : With the exception of *G. gnemon*, the main stem bears two kinds of branches - **dwarf shoots** of limited growth, and **long shoots** of unlimited growth. The stem is articulated and has prominent joints. The joint consists of two portions, one above the node and the other below the node, and the two are demarcated by an annular groove. Internodes break at these joints and fall to the ground and appear like bones. Such a phenomenon is very prominent in *G. gnemonoides*. In *G. gnemon*, all branches are of the same type.

3. Leaves : Leaves are also of two kinds. The **scale leaves** that occur only on the long shoots; and the **foliage leaves** that are borne in an opposite and decussate manner on the dwarf shoots. The foliage leaves bear axillary buds. They resemble dicotyledonous leaves in having a broad lamina and reticulate venation. They are stipulate, shortly petiolate with simple, entire and coriaceous lamina.

4·4 INTERNAL STRUCTURE

(A) Root : The root **resembles a dicot root** in its primary structure. The young root is almost circular in outline in a transection and is differentiated into epidermis, cortex and stele. The epidermis is single layered and some of the cells give out root hairs. The cortex is multi layered and parenchymatous. The cells are filled with starch grains. Groups of sclerenchymatous cells occur among the cortical cells. A single layered endodermis followed by a multilayered pericycle, separates the central vascular cylinder. The vascular cylinder is **di - or triarch, radial and exarch**. The primary xylem consists of tracheids and a few vessels. It becomes indistinct after secondary growth. Phloem consists of sievetubes and parenchyma. Mudullary rays are broad and parenchymatous.

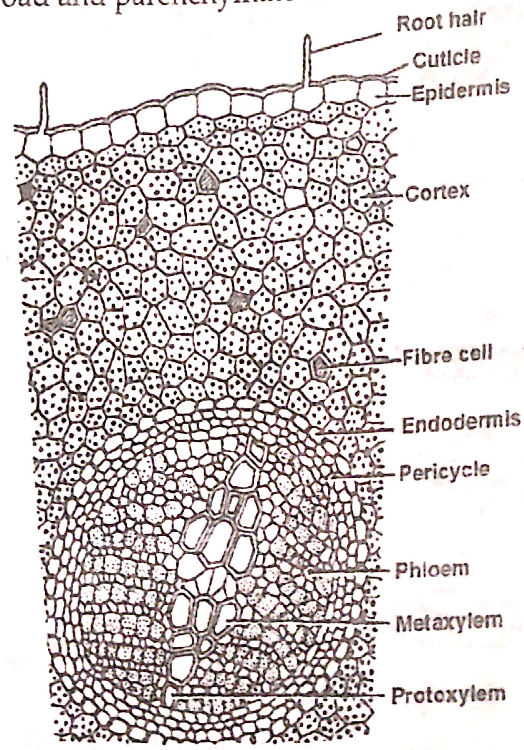

Fig. 4·3 : *Gnetum* - T.s. of young root

Secondary growth in root : The secondary growth is of normal type. Arcs of cambium are formed internal to the phloem groups and external to the xylem groups. These arcs join to form a complete ring of cambium. The secondary xylem is composed of tracheids, vessels and xylem parenchyma. The tracheids are elongated cells with tapering ends and possess circular bordered pits on their tangential and radial walls. The pits are arranged in uniseriate manner. But in the vessels, the pits are multiseriate with smaller diameters. Medullary rays traverse the secondary xylem. The ray cells are full of starch grains. The phloem consists of sieve cells and phloem parenchyma cells. Unlike angiosperms, the phloem originates from different cells of the cambium. Cork cambium originates from the outer most cortical layer. It produces phellem (cork) towards the outer side and phelloderm (secondary cortex) towards the inner side.

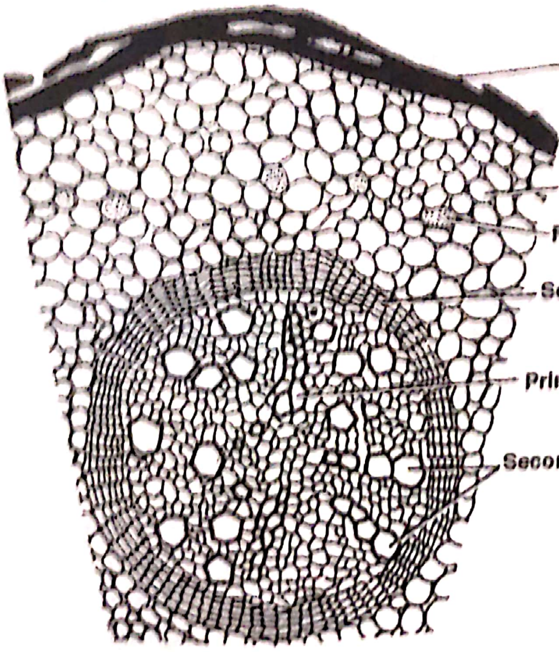

Fig. 4·4 : *Gnetum* - T.s. of old root

(B) Stem : The primary structure of *Gnetum* stem is similar to that of a dicotyledonous stem. A transection of the young stem is more or less circular in outline and shows the following structure.

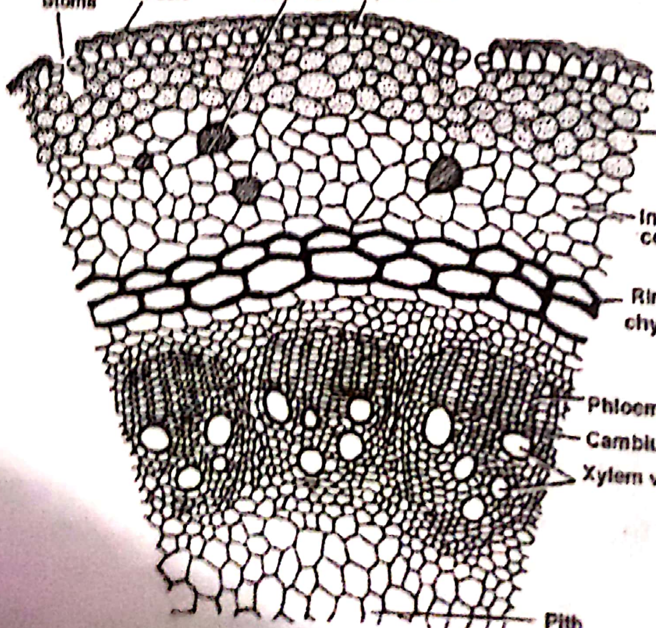

Fig. 4·5 : *Gnetum* - T.s. of young stem

(i) Epidermis : It consists of a single layer of rectangular cells which bear papillate outgrowths. The cuticle is thick. The continuity of the epidermis is interrupted by the presence of sunken stomata.

(ii) Cortex : The cortex is usually differentiated into three distinct regions. The outer cortex is made up of 5-7 layers of polygonal cells which contain many chloroplasts. The middle cortex is composed of a few layers of thin walled compactly arranged parenchyma cells. Many fibrous cells are also present in this region. The inner zone consists of 2-5 layers of thick walled cells. These cells have branched or un-branched pit canals in their walls. This region is often referred to as ring of *spicular cells.*

(iii) Endodermis and pericycle : These two layers are not clearly defined in young stems.

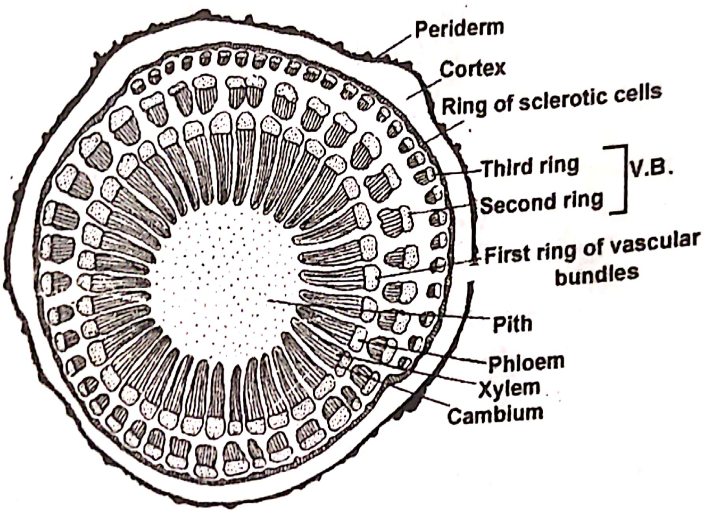

Fig. 4·6 : T.s. of old stem *Gnetum ula*

(iv) Vascular tissues : The vascular cylinder consists of 20 - 24 primary vascular bundles arranged in a ring. The bundles are conjoint, collateral, endarch and open. They are separated from one another by broad parenchymatous medullary rays. The xylem consists of both tracheids and vessels. Xylem fibres are absent and xylem parenchyma is scanty. Primary phloem consists of sieve cells and phloem parenchyma. The xylem and phloem are separated by cambium.

(v) Pith : A parenchymatous pith is present in the centre of the stem. The cells are polygonal in out line. Laticiferous elements are seen in pith as well in cortex.

Secondary growth in the stem : Secondary growth is of normal type in trees and shrubs (e.g. *G. gnemon*). **Cambium ring** is formed in the usual manner which cuts off secondary phloem towards the outerside and secondary xylem towards the innerside. The amount of xylem formed is much more than the phloem. The primary phloem is crushed due to the pressure of the secondary vascular tissues. They appear as arc like areas over the secondary vascular tissues.

A **phellogen** or **cork cambium** arises in the hypodermal region during the third or fourth year of the growth of the stem. It produces periderm on the outside.

In *G. ula* and *G. africanum*, due to unequal meristematic activity of the phellogen, islands of sclerenchymatous cells and thin walled cells become embedded in the cork cells.

Secondary xylem consists of three types of elements viz, **tracheids, xylem parenchyma** and **vessels**. Tracheids have circular borderded pits which are uniseriate in arrangement on the tangential as well as radial walls. Xylem parenchyma consists of living thin walled cells. Vessels are elongated cells with tapering ends. They show one or two rows of small round perforations on their end walls. Such a condition simulates the vessels in angiosperms. In *Gnetum* the vessels develop from tracheids whose end walls have a number of bordered pits. The closed bordered pits increased in size, followed by disappearance of middle lamella and torus, thus forming a single large perforation. However in angiosperms, the vessels with a single perforation are formed by the disappearance of bars from perforations of scalariforn type of pitting. There is thus, a difference in the mode of development of vessels in angiosperms and *Gnetum*. Secondary phloem consists of sieve tubes and phloem parenchyma. The companion cells are altogether absent. The secondary medullary rays are multiseriate, broad and of considerable height. The cells are radially elongated and some of them contain crystals of calcium oxalate.

Anomalous secondary growth : Climbing species (*G. africanum, G.ula*) show anomalous secondary growth. The fascicular cambium caeses to function after the first vascular ring is formed. Several rings of cambia develop from successively deeper layers in the cortex. These **cambial rings are eccentric**. They cut off secondary phloem and xylem outward and inward respectively. Due to the formation of medullary rays in the secondary tissue, distinct wedge - shaped vascular bundles appear. When the first ring of cambium becomes non - functional, a second ring appears outside it and produces secondary tissues in similar manner. In this way several rings of secondary vascular tissues are formed.

Some times the rings may remain incomplete, thus causing eccentric condition of the growth rings. The growth rings should not be mistaken for annual rings of angiosperms.

(C) Leaf : The leaves of *Gnetum* resemble closely with those of dicotyledons not only in their general appearance, texture and venation but also in the internal structure. The leaves are dorsiventral with reticulate venation. A transverse section of the leaf shows epidermis, mesophyll and vascular region.

The upper and lower surfaces of the leaf are covered by a single layered epidermis. The epidermal cells are undulating. The upper epidermis is covered by a thick layer of cuticle. Stomata are confined to the lower epidermis. Stomata may be syndetochelic (*G. gnemon*) or haplochelic type (*G. ula*).

The mesophyll consists of distinct palisade and spongy parenchyma. The palisade consists of a single layer of elongated cells, rich in chloroplasts. The spongy parenchyma consists of loosely arranged and lobed cells. In the mid -

region the parenchyma cells are polygonal and compactly arranged. Stellately branched sclereids with lignified walls occur in the spongy tissue on the abaxial side of the leaf. Latex tubes and fibres are also present in the mesophyll.

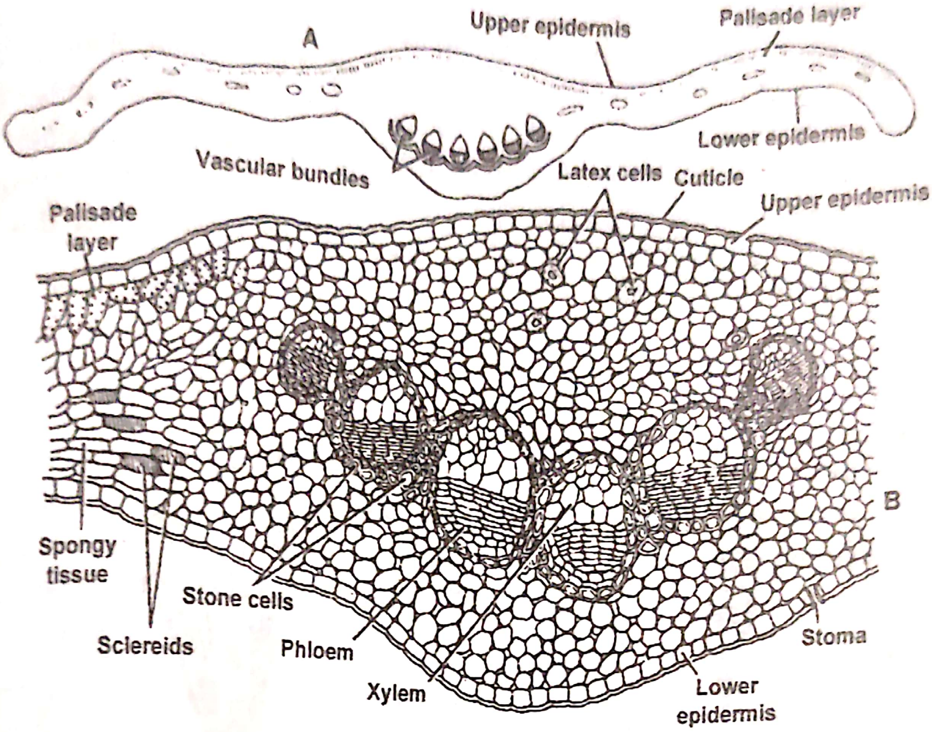

Fig. 4·7 : *Gnetum* - T.s. of leaf

The mid -rib consists of a number of vascular bundles, arranged in the form an arc. Vascular bundles are **conjoint, collateral** and **endarch**. The xylem faces upwards (adaxial) and phloem downward (abaxial). Each vascular bundle is surrounded by a sheath of thick walled cells. Xylem consists of tracheids, vessels and xylem parenchyma. The phloem is composed of sieve cells and phloem parenchyma arranged in distinct files. Thick walled pitted cells form a patch outside the phloem (*G. ula*). Transfusion tissue is present in the petiole intermixed with the vascular bundles.

4-5 REPRODUCTION

All the species of *Gnetum* are dioecious. The reproductive organs of *Gnetum*, often referred to as flowers, are organised into cones or strobili. These strobili are organised into well - defined compound strobili or inflorescences, which are usually *panicles*. Inflorescences are usually axillay in position, but terminal inflorescences are also not uncommon. The inflorescene consists of a stout long axis, bearing several flowers. The flowers arise in the axils of decussate pairs of bracts. The bracts are connate throughout their length and forming a **cup-like collar** which surrounds the axis.

There are 10 - 25 collars in each strobilus. They lie very close to each other because of the suppression of inter nodes. As the leaves fall off before the strobili develop, the branches bearing strobili are leaf less.

A Male strobilus :

The male strobilus has a short stout axis arising in the axil of connate bracts. The axis is divided into nodes and internodes. At each node a pair of decussate bracts are borne. These bracts are fused along their margins and form a cup - shaped structure around the axis. This cup like structure is called the **cupule** or the **collar**. Each cone possess 10-25 collars. In the axil of each collar, there are several male flowers arranged in 3 - 6 whorls. In each whorl, there will be a number of male flowers (25-30). In some cases, just above the male flowers, there is a single ring of abortive female or ovulate flowers. The strobilus is very compact when young, but at maturity it becomes loose as collars separate from each other due to the elongation of internodes.

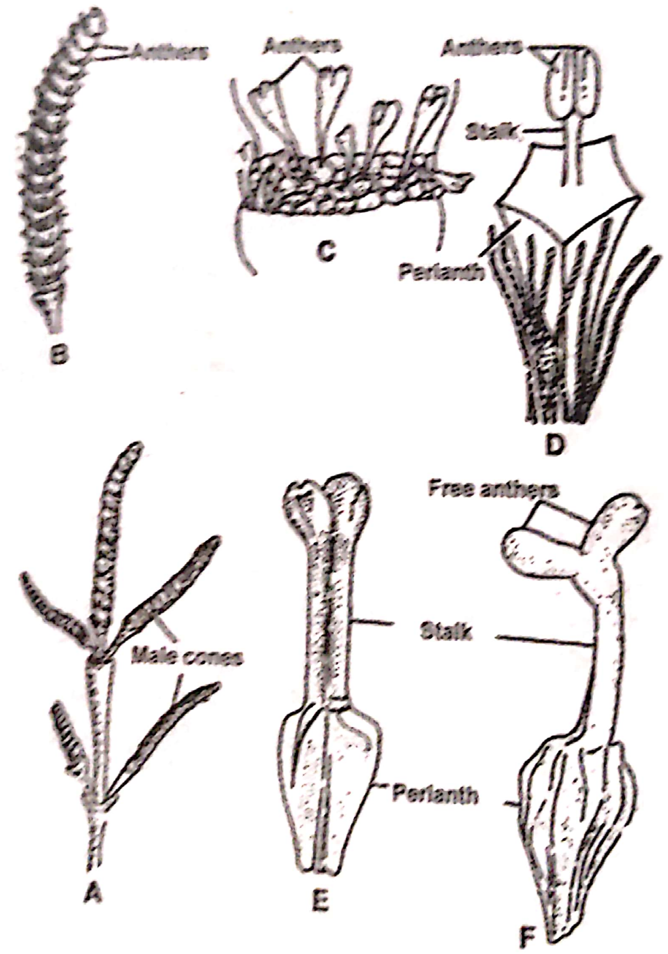

Fig. 4·8 : *Gnetum* - Structure of male strobilus
(A) Panicle, (B) Male inflorescence(C) A part of a male strobilus showing whorls of male flowers at the node, (D, F.)Single male flowers with anthers emerged out of the perianth

Male flower : Each male flower consists of a sheath like perianth enclosing a single stamen. The sheath is formed due to union of two bracts. The stamen consists of a stalk (antherophore) which at its apex bears two unilocular anthers or microsporangia. When the anthers mature, their stalk elongates and grows out of the perianth through a slit.

The number of anthers and the relative sizes of the anther lobes is variable. In *G. gnemonoides* the stalk bears only one anther lobe. In *G. ula*, *G. gnemon* and *G. africanum* the number of anthers on one stalk varies from two to four.

Development of microsporangium : The development of microspo- rangium is of *eusporangiate* type. In a young anther two groups of hypodermal *archesporial cells* distinguish below the epidermis. They divide and redivide to give rise to multicellular **archesporium**. The outermost layer of the archesporial cells divide to form an outer layer of *primary parietal cells* and an inner layer of *sporogenous cells*. The parietal layer, by periclinal divisions, gives rise to a wall layer towards outside (beneath the epidermis of the another lobe) and *tapetum* layer towards inside. The wall layer may become two layered at certain places. The sporogenous cells undergo a few divisions to form the *microspore mother cells*. They contain dense cytoplasmic contents and distinct nuclei. At this time the tapetal cells becomes conspicuous with dense cytoplasmic contents. They become bi-nucleate (rarely multinucleate). The nuclei may fuse and become polyploid. The wall layers become compressed due to the pressure of the enlarging spore mother cells. Now the spore mother cells undergo meiosis and form isobilateral, decussate or tetrahedral tetrads of haploid *microspores*. The microspores enlarge and become free after breaking the original mother cell wall. The microspores are uni-nucleate.

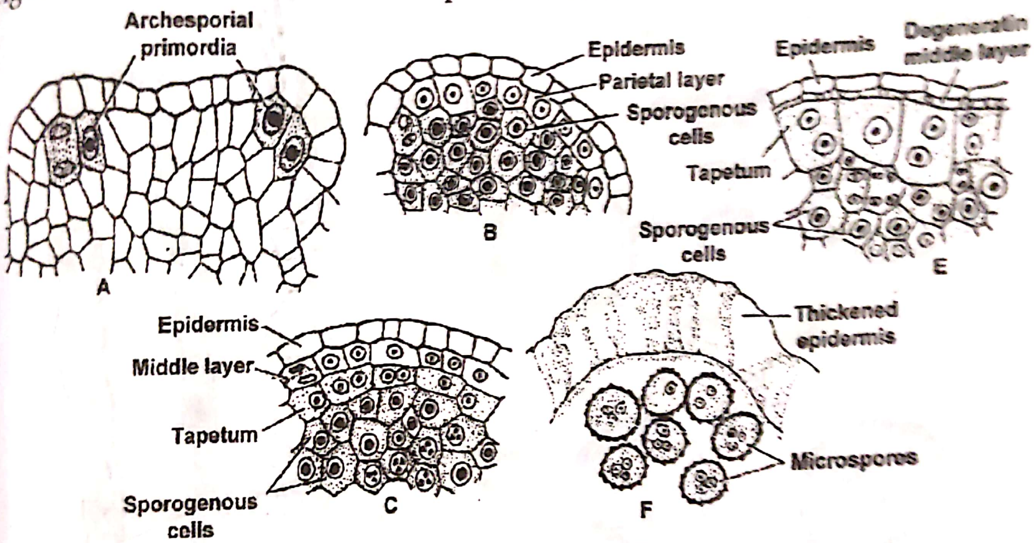

Fig. 4·9 : *Gnetum* - Stages in the development of microsporangium

As the mother cells are undergoing meiosis, the wall cells and tapetal cells start degenerating. The anthers dehisce by longi- tudinal slits to release pollen grains.

Male gametophyte : The microspore (pollen grain) represents the earliest stage of the male gametophyte. It is roughly spherical, uninucleate and is enveloped by a thick and spiny *exine* and a thin and smooth *intine*. Microspores are shed at the three celled stage. There is difference of opinion as to the nature of these three nuclei.

(i) *Pearson* (1914) studied the development of male gametophyte in *G. gnemon* and *G. africanum*. The microspore nucleus first divides into two daughter nuclei; one of these nuclei devides again so that three nuclei are formed, which lie free in the cytoplasm. These nuclei are called ***prothallial nucleus, generative nucleus*** and ***tube nucleus***. At this stage pollen grains are released and further development takes place in the pollen chamber. The exine ruptures and intine grows into a pollen tube. The tube nucleus migrates first into the pollen tube. The generative nucleus now gets surrounded by a distinct cell membrane and form the **generative cell**. It also migrates in to the pollen tube and later divides into two unequal ***male gametes***. The prothalial nucleus remains within the pollen grain.

(ii) However, some workers like Thompson (1916) believe that there is no **prothallial cell** in the male gametophyte. The first division of the microspore nucleus gives rise to a ***tube nucleus*** and a ***generative nucleus***. The generative nucleus later divides to form a ***stalk cell*** and ***a body cell***. The body cell migrates into the pollen tube, where it divides to form two male cells.

(iii) Negi and Madhulatha (1957) observed that in both *G. ula* and *G. gnemon*, the first division of the microspore nucleus resulted in the formation of a small lenticular **prothallial cell** and a large **antheridial cell**. The antheridial cell divides to form a **generative cell** and a **tube nucleus**. The generative cell together with the tube nucleus migrates in to the pollen tube. In the pollen tube, the generative cell produces two **male gametes**. The stalk cell and body cell are not formed.

Further growth of male gametophyte takes place after pollination.

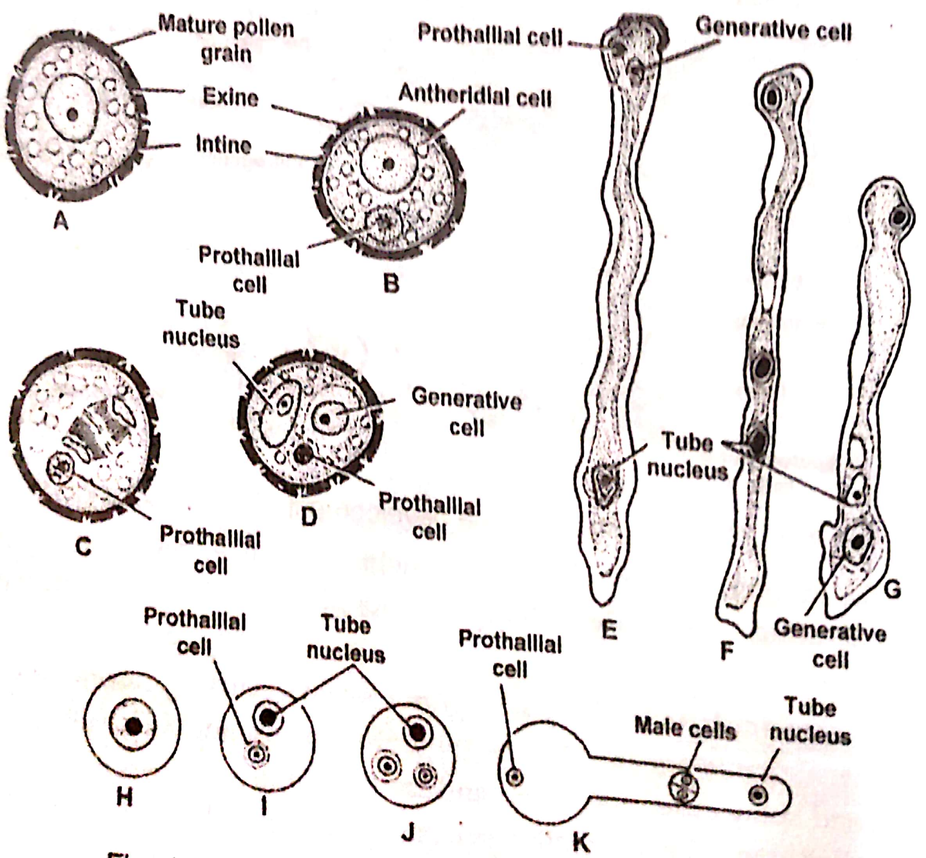

Fig. 4·10 : *Gnetum* - Development of male gametophyte
(A-D) Stages in the development of male gametophyte,
(E-G) Formation of pollen tube, H-K. Thompson's (1916) view regarding the development of male gametophyte

8. Female strobilus :

The female strobilus is also called the ovulate cone. The organisation of the female strobilus is quite similar to that of the male strobilus. It arises in the axil of a leaf or terminally. It has a stout axis with several collars arranged one above the other at short intervals. A whorl of [illegible] 10 ovules or female flowers is present above each collar. All the ovules develop at the same rate initially, but subsequently, the growth of most of the ovules is arrested and only a few are able to mature into seeds. The ovules may not develop in the uppermost collars. Several uniseriate hairs are interspersed among the ovules.

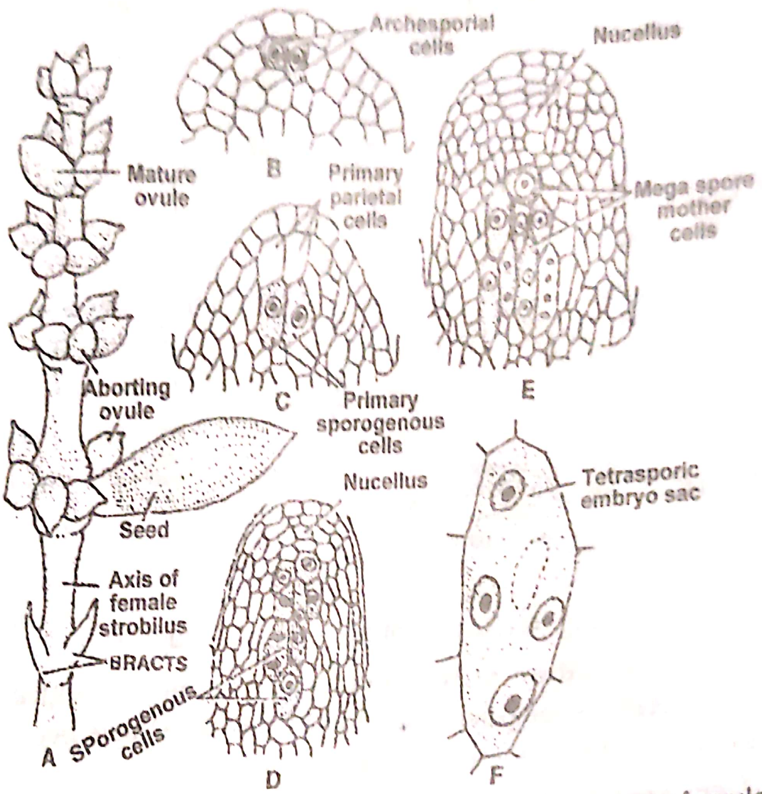

Fig. 4·11 : *Gnetum* - Female strobilus and development of ovule (A) Female strobilus, (B-E) Stages in the development of ovule and embryo sac, (F) Tetrasporic embryo sac

Female flower : Each female flower is represented by a single ovule. The ovule consists of a central mass of cells called the **nucellus**. The nucellus is surrounded by **three envelopes**. The inner envelope grows beyond the middle one and forms a narrow and cylindrical tube called the **micropylar canal or the style.** The outermost envelope is called the **perianth**, the middle is designated as the **outer integument,** whereas the innermost is called the **inner integument**. The inner integument is fused with the nucleus in its lower part and is free above. Stomata are formed in the epidermal layer of outer two envelopes only. The outer envelope or the perianth becomes thick and fleshy in the seed. The middle envelope forms the stony layer. A rudimentary pollen chamber is present at the apex of the nucellar apex. Nucellar beak is absent. The nucellus encloses the female gametophyte. **Archegonia are absent**. One or more nuclei become larger at the micropylar end of the female gametophyte and act as *egg nuclei*.

The cells of the nucleus lying below the female gametophyte divide to form a fan-shaped tissue made up of several rows of cells. This tissue was named as **pavement tissue** by Coulter (1908). This tissue is later absorbed.

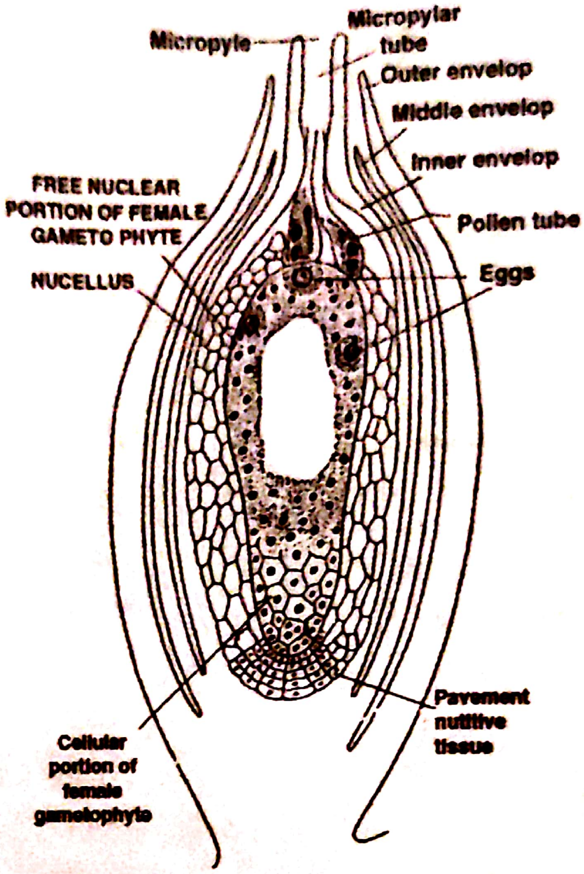

Fig 4.12 : L.S. of ovule of a Gnetum sp

Morphological nature of the envelope : The morphological nature of the envelope of the ovule is long debated and several views have been put forwarded from time to time. Some of these views are as follows.

1. Van Tieghem (1869) suggested that the outer envelope is equivalent to an ovary or a structure analogous to ovary; and the inner two envelops represent the two integuments of the ovule.
2. Strasburger (1872) thought that the three envelopes are formed by the splitting of a single integument.
3. Beccari (1877) regarded the inner two envelopes as the two integuments like those that occur in the angiosperm ovule and the outermost envelope represents the perianth. Coulter (1908) also supported this view and is even now regarded to be more reasonable.
4. Lignier and Tilson (1912) and Thompson (1916) put forward a different explanation. They regarded the inner envelope as an ovary and the outer two as perianth lobes.
5. Vasil's (1959) observation on *G. ula* also support the fourth view put forward by Lignier and Tilson. She observed that in some specimens of G. the innermost envelope is abortive or partially developed. In its place

middle envelope develops into micropylar tube (style). Sometimes the middle as well as the inner envelopes were observed to grow in to the styles. In some ovules fourth envelope is situated between the middle and inner envelopes and sometimes grew as long as the micropylar tube. Basing on these observations, she regarded the inner and middle envelopes as ovaries because of their capacity to form styles.

Development of megasporangium : Four to ten **ovular primordia** differentiate from an annular meristem or rim below each collar of the female strobilus. The ovular primordium lies on a cushion and divides to form a mass of cells around which the three envelopes develop one after the other in a centripetal manner. The outer envelope develops first and is followed by the second and third envelopes. Of the three envelopes, only the inner one is the integu- ment. The outer envelope, often called perianth, gets thickened and some what succulent at maturity. The third envelope is fused with the nucleus in the basal region, but is free in the upper region and grows into a long micropylar tube or style.

The nucellus is well developed and quite massive. The female gametophyte develops from the cells of the nucellus. At the time of formation of inner envelope, 2-4 **archesporial cells** are differen- tiated in hypodermal region of the nucellus. The archesporial cells divide periclinally to form **outer primary parietal cells and inner sporogenous cells.** The nucellar epidermis and the parietal cells divide repeatedly to form a massive nucellar tissue above the sporogenous cells. As a result, the sporogenous cells become deep seated in the nucleus.

The sporogenous cells divide to form 8 - 12 **megaspore mother cells.** Each megaspore mother cell undergo meiosis to form four nuclei which are not separated by walls. Since no walls are laid down, all the four megaspore nuclei remain within the mother cell and take part in the development of female gametophyte. The female gametophyte is thus **tetrasporic** as in some angiosperms. All the megaspore mother cells may undergo meiosis to form tetrasporic embyosacs, but ultimately one develops to maturity.

Female gametophyte : The functional megaspore (coenomega- spore) is more or less ovoid in shape and has the four free nuclei aggregated in the centre, like other gymnosperms. The development of female gametophyte begins with a series of free - nuclear divisions. The number of nuclei formed is 256 in *G. gnemon*, 512 in *G. africanum* and 1500 in *G. ula*. At this stage, the female gametophyte elongates towards the chalazal end and appears almost spathulate (spoon - shaped) in outline. It has a large central vacuole and the free nuclei are arranged in the peripheral layer of the cytoplasm. Wall formation takes place at the chalazal end but nuclei remain free at the micropyler end. **So the gametophyte is party cellular and party free nuclear.**

Archegonia are absent in *Gnetum*. Some of the free nuclei of the gametophyte at the micropylar end become larger, accumulate some cytoplasm and function as the *eggs*. In this respect, *Gnetum* resembles angiosperms. The differentiation of the egg is stimulated by the presence of pollen tube in the vicinity of the female gametophyte.

A **pavement tissue** consisting of several rows of cells develops at the base of the young embryo sac. The pavement tissue is in the form of radiating rows of cells. This tissue gets dissolved during later stages of embryosac development.

There is no nucellar beak in *Gnetum*, but the apical cells undergo degeneration to form a small pollen chamber.

4-6 POLLINATION

The pollen grains are carried by wind to the micropylar tube of the ovule. The micropylar tube secretes a drop of sweet fluid at its tip. The pollen grains are caught in this liquid which later evaporates and the pollen grains are with drawn into the tube and down to the pollen chamber.

The exine rupture and the intine grows into a pollen tube opposite to the point where the tube nucleus lies. The pollen tube traverses through the intercellular spaces between the nucellar spaces. The pollen tube secretes enzymes and absorbs its nutrition from the nucellar cells. The tube nucleus and the generative cell move into the pollen tube. The generative cell divides to form two unequal male gametes. Now the growth of the tube shows slackness and the male cells move to the tip of pollen tube. The tube nucleus lies behind them.

4-7 FERTILIZATION

The pollen tube pierces through the membrane of the female gametophyte at the micropylar end. The tip of the pollen tube bursts and releases the male cells one of which enters the egg cell. It leaves its sheath outside the egg cell. The male and female nuclei lie side by side and ultimately fuse together to form the zygote. Sometimes both the male gametes are functional and can fertilise two eggs present side by side. In such cases, two zygotes are formed (Car Michael and Friedman, 1996).

Endosperm : The development of endosperm begins even before fertilisation. It develops from the female gametophyte. Before fertilisation, only the lower part of the female gametophyte becomes cellular, but after fertilisation wall formation also occurs in the upper part and the whole gametophyte becomes cellular. Wall formation takes places by cleavage of cytoplasm. Since, cell formation is taking place after fertilisation, the tissue is called **endospoerm**. But the nature of endosperm is entirely different from angiosperm, where it develops from the endosperm nucleus after the process of triple fusion.

The endosperm formation in *Gnetum* is not regular. Some of the cells are uninucleate, while others are multinucleate. Sometimes nuclei fuse to form a polyploid nucleus. This is called graduate ploidy and the nuclei vary from haploid to 12 n in the same gametophyte.

Endosperm of *Gnetum* differs from the other gymnosperms in the following respects : (i) Delay in cell formation till the entry of Pollen tube ; (ii) Presence of uni - and multinucleate cells.

4·8 EMBRYOGENY

The development of embryo varies in different species of *Gnetum*. In *G. gnemon* the zygote produces a protuberance on one end, which grows down towards the endosperm tissue. Some times more than one protuberance may develop and then only one of the protuberances receives the nucleus and survives. The other tubes degenerate. The surviving tubular outgrowth elongates, becomes branched and grows in different directions within the intercellular spaces of the endosperm. These tubes are called *primary suspensors* or the *proembryonal tubes*. All primary suspensor tubes generally stay coiled around each other.

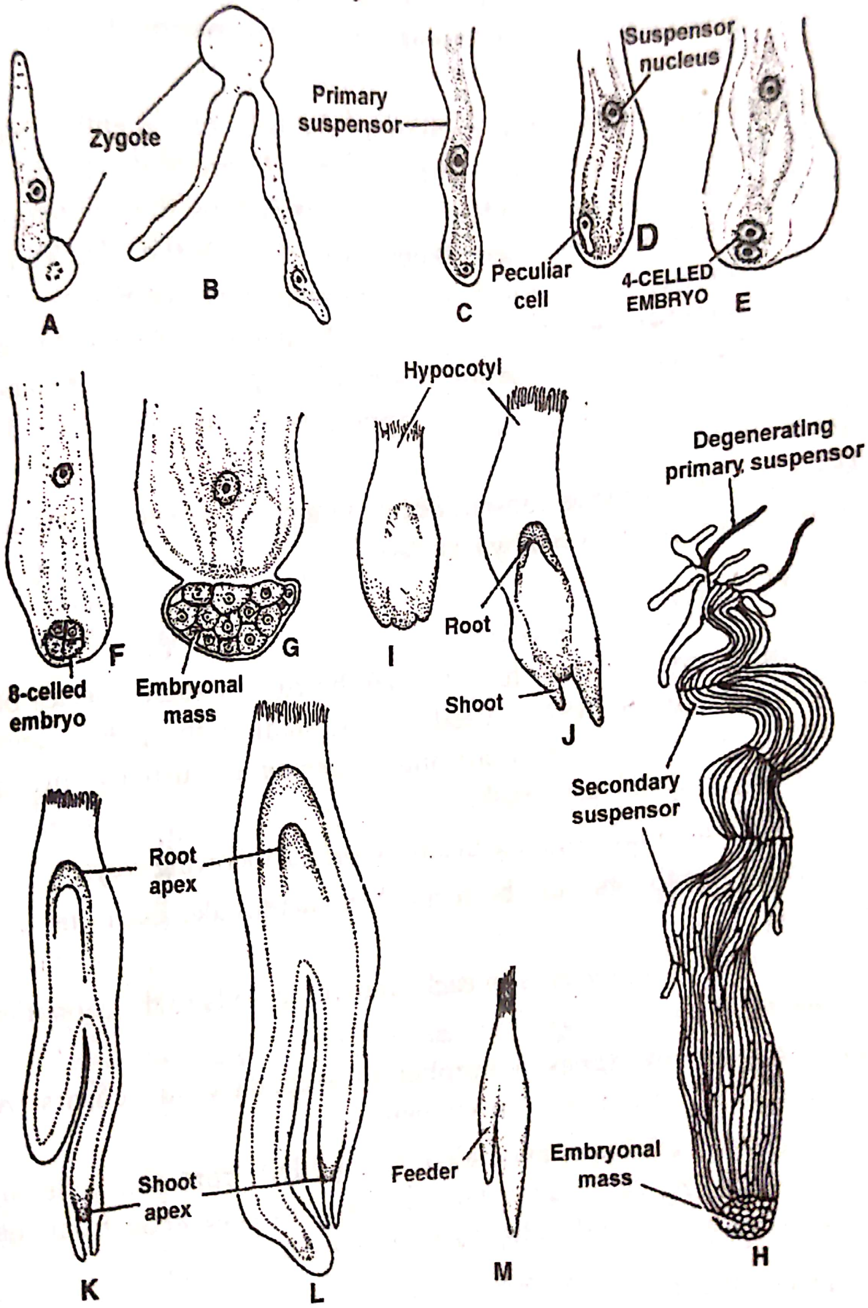

Fig. 4·13 : *Gnetum* - Stages in the development of embryo

At the tip of the primary suspensor tube, a small cell is cut off which soon divides first by a transverse wall and then by a longitudinal wall forming four cells.

This is followed by irregular divisions and thus a group of cells is formed some of these cells divide further and then elongate, forming *secondary suspensor*, the rest of the cells form an *embryonal mass*.

However in *G. ula* a small cell is cut off at the tip of the primary suspensor tube and this cell is known as *peculiar cell*. This peculiar cell is responsible for the formation of embryo. It divides to form two cells, both of these cells divide again to form a four - celled embryonal mass. The four - cells divide transversely to form an *octant*. Further divisions are irregular and form a mass of cells at the tip of the suspensor tube. As the embryonal mass increases in size, some cells lying towards the primary suspensor tubes elongate to form the *secondary suspensors*. The cells lying at the lower end of the secondary suspensor eventually form the embryo proper.

Whatever may be mode of formation, the cells of the embryonal mass are small, and densely cytoplasmic. The stem tip differentiates at the end of the embryonal mass. It is surrounded by two cotyledons that develop from cells surrounding it. The root tip differentiates lower down at the other end, so that the cells of the root cap are in touch with the secondary suspensor cells. A small protrusion appears between the two regions. It later enlarges and becomes distinct and is called the **feeder**. The feeder has its own epidermis, cortex and vascular tissue. The suspensors shrivel up and appear as fine threads attached to the root tip or the radical.

A mature embryo thus consists of two orange - pink cotyledons, a stem tip, a large feeder and a root covered by root cap.

4-9 POLYEMBRYONY

Polyembryony has been found to be the rule in some species of *Gnetum*. Bower (1882), Hanning (1920), Vasil (1959), Madhulatha (1960) have reported instances of polyembryony in ***G. ula*** and ***G.gnemon***. But usually only one embryo attains maturity and the rest perish.

Polyembryony may originate in any one of the following ways.

(1) Several embryosacs may be formed in each ovule. Each one produce one embryo.

(2) Fertilization of many eggs in each embryosac leads to the formation of many embryos.

(3) Each zygote produces a number of secondary suspensors. Additional embryo's may also develop from them.

(4) Additional embryo's may also be budded from the cells of primary suspensors. In *G. gnemon* lateral chains of cells arise from the primary suspensors and start developing into embryos.

4-10 SEED

The mature seed is oval or slightly elongated and green to red in colour. The seed consists of three envelopes. The outer envelope is green in colour and becomes succulent in the seed and is free from the other envelopes. It is made up of parencymatous cells with many sclerids and fibres. The middle layer is stony and is the main protective covering of the seed. Sclereids, fibres and latex tubes are present in this layer besides, a layer of palisade like cells is also present below the epidermis. The innermost envelope is made of parenchymatous cells and lignified cells.

This envelope is fused with the nucellus up to two third of its length. Its free end encircles the nucellar cap and projects beyond the nucellus. A massive endosperm lies within the envelope, which projects upwards in the form of a tent pole. It has thick and lignified walls and it supports the nucellar cap. The endosperm encloses the dicotyledonous embryo.

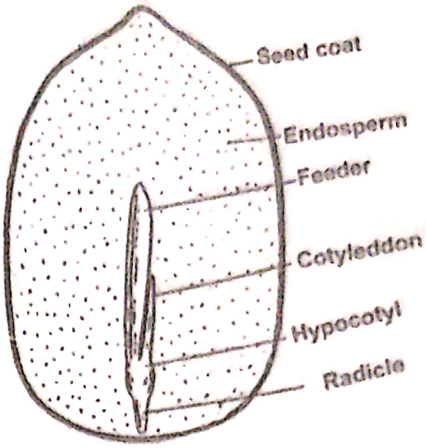

Fig. 4·14 : L.S. Seed of Gnetum

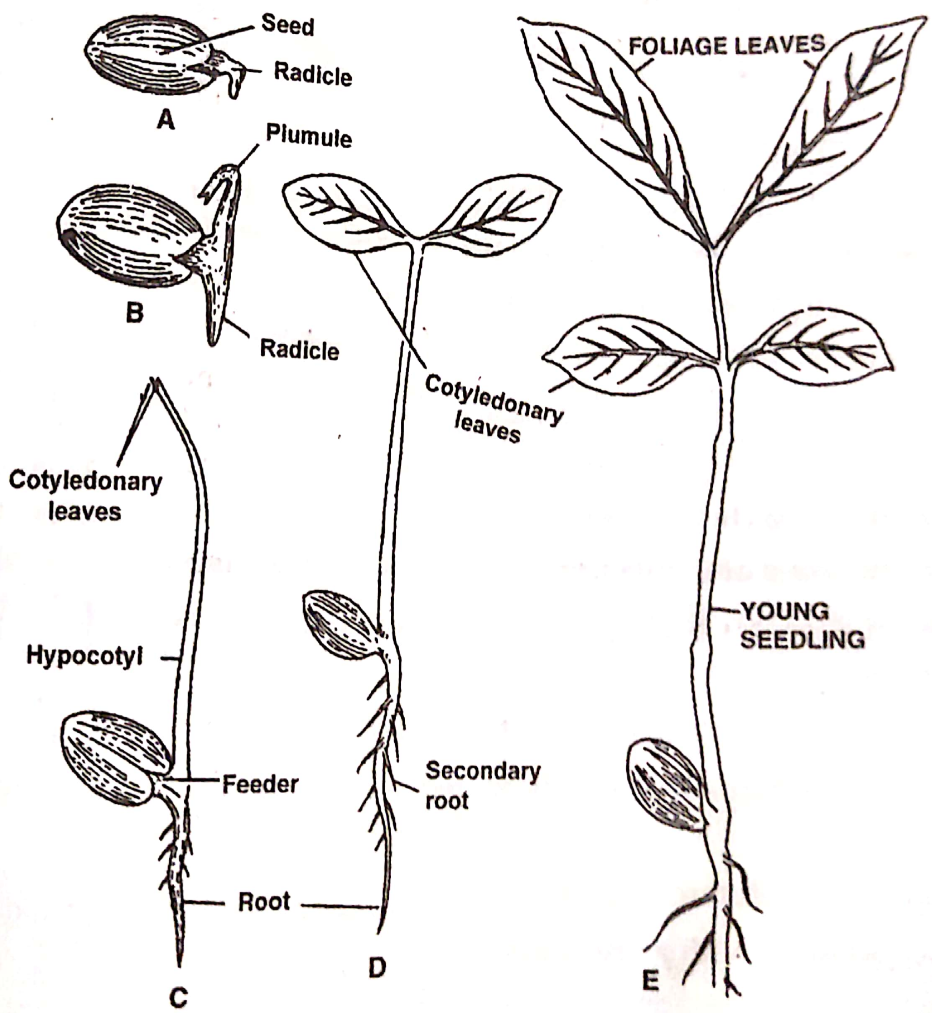

Fig. 4·15 : *Gnetum* - Stages in the germination of seed

Germination of Seed : Seeds are shed at a stage when the secondary suspensors are differentiating. Maturation of the seed takes place after 10-12 months of shedding from the mother plant. The germination of the seed is *epigeal*.

The root emerges first, it bends down, enters into the soil and forms the taproot system. As the hypocotyle elongates, cotyledons come out of the seed and above the soil. The cotyledons are the first green leaves. The plumule produces the first pair of foliage leaves that lie at right angles to the cotyledons. Cotyledons wither at a later stage. The feeder remains inside the seed and continues to absorb the nutrients from the endosperm, till the second or third pair of leaves have developed in the seedling.

4-11 ECONOMIC IMPORTANCE

Young leaves, inflorescence, fruits and seeds of *G. gnemon* are edible. The seeds of *G. gnemon, G. ula and G. latifolium* are roasted and eaten. The bark of *G. latifolium* yields a fibre of high tensile strength, suitable for paper pulp and fishing nets. Seed - kernels of *G. ula* yield an oil used for illumination and also as a massage oil in rheumatism. The oil obtained from *G. montanum* is reported to possess piscicidal properties (fish poison).

4-12 AFFINITIES OF GNETUM

Gnetum resembles with other Gymnosperms on the one hand and with Angiosperms on the other. At the same time *Gnetum* shows some fundamental differences with gymnosperms.

I. Resemblances with gymnosperms :

Gnetum shares the following characters with Gymnosperms.

1. Ovules are naked and style and stigma are absent.
2. A prothallial cell is present in the male gametophyte.
3. A small pollen chamber is present in the nucellus, and microspores are directly lodged on the nucellar surface.
4. Pollination is anemophilous.
5. Development of female gametophyte through free nuclear divisions.
6. The endosperm is a haploid or polyploid tissue and starts developing before fertilisation.
7. Presence of simple or cleavage type of polyembryony.
8. Xylem tracheids are with bordered pits and sieve cells are present in the phloem.
9. Seed coat with three layers.

II. Resemblances with angiosperms :

Gnetum resembles angiosperms in several respects such as habit, pressure of two cotyledons, reticulate venation of leaves, presence of vessels in the secondary wood, Catkin like inflorescence, the presence of two integuments in the ovule, and the reduction and loss of archegonium in the female gametophyte. Thus at one time *Gnetum* was considered as closely allied to angiosperms and their possible ancestor. (Arber and Parkin, 1907. Thompson, 1916, Hagerup, 1934).

Some important features which *Gnetum* shares with angio-sperms are as follows :

1. The general habit of sporophyte of Gnetum (climber or tree) resembles angiosperms.
2. The leaves are broad and green with reticulate venation and opposite decussate phyllotaxy.
3. The shoot apex organisation of *Gnetum* is similar to that of angiosperms.
4. Xylem with vessels in secondary wood.
5. The male and female reproductive organs of *Gnetum* are more close to angiosperms than gymnosperms.
6. The occurrence of free - nuclear divisions in the embryosac is on the angiospermic line.
7. Tetrasporic type of embyrosac as in angiosperms.
8. Complete elimination of archegonia in *Gnetum* as in angiosperms.
9. The embryo of *Gnetum* has two cotyledons like that of a dicotyledonous embryo.

However, it has been subsequently shown that many of these resemblances are superficial.

(i) The development of vessels in *Gnetum* and angiosperms is quite different.

(ii) In angiosperms, perforation of vessels arose through the dissolution of pit membranes in scalariform bordered pitting ; whereas in *Gnetum* they developed through modification of circular bordered pits.

(iii) The resemblances between the inflorescenses of *Gnetum* and amentiferous angiosperms are also superficial.

It is now generally believed that Amentifers have reduced flowers which are highly evolved. The primitive flowers of angiosperms are bisexual with a well developed perianth and numerous free stamens and carpels. It is difficult to derive such flowers from unisexual, scaly - bracteate, compound strobili of *Gnetum*. These similarities appear to be cases of parallel evolution and do not portray any close relationship. As Maheswari and Vasil (1961) stated "*The genus 'Gnetum remains largely a phylogenetic puzzle. It is gymnospermous, but possesses some strong angiospermic features* ".