GNETALES

Gnetum

Gnetales

- **Distributed in the tropical and humid regions of the world**
- **Includes trees and lianas**
- **Leaves: large, dorsiventral, unicostate reticulate venation**
- **Female gametophyte; tetrasporic**
- **Archegonia- absent**
- **No free nuclear phase in the embryogenesis**

The order includes single family- Gnetaceae. The family is monogeneric. *Gnetum* is the only genus representing Gnetaceae.

Gnetum

- ***Systematic position:***
- **Class- Gnetopsida**
- **Order- Gnetales**
- **Family- Gnetacceae**
- **Genus- *Gnetum***

- **Distribution and habit**
- **It consists of thirty species, widely distributed in the tropical and sub-tropical zones of the world.**
- **Most of the species are lianas.**
- **Common Indian species: *G. ula,***
  - ***G. gnemon,***
  - ***G. latifolium,***
  - ***G. montanum,***
  - ***G. contractum***

Reproduction

- -*Gnetum* reproduces sexually.
- *-Gnetum* is dioecious and both the male and female strobili (inflorescence) are compound.
- -The inflorescence is either axillary or terminal in position. The inflorescence may be single or in groups.
- -The inflorescence is composed of a stout long axis with two opposite decussate, connate bracts at the base and a series of cup-like bracts called cupules or collars that are superposed one above the other.
- There are many rings of flowers in the axil of collars. The collars are developed in acropetal succession and the flowers are initiated as mounds of meristematic cells from the lower surface of a collar.
- Male strobilus
- The male strobilus has a long slender axis. The male strobilus is branched and branching may be of several kinds. The axis bears 10-25 whorl of bracts (collars).
- -About 12-25 male flowers are arranged in
- three to six rings above each collar.

- In each collar, there are three to six rings of 12-15 or more male flowers and a single ring of 7-15 imperfect female flowers or abortive ovules is present above male flowers.
- A young strobilus is compact due to much reduced axis with very short internodes and the collars appears to be continuous.
- **Male flower:**
- A male flower has two unilocular anthers enclosed in a small sheathing perianth. Its stalk is called antherophore which elongates at maturity. Consequently, the anther emerges beyond the collar through a slit in the perianth. The number of anthers in a male flower may also vary.
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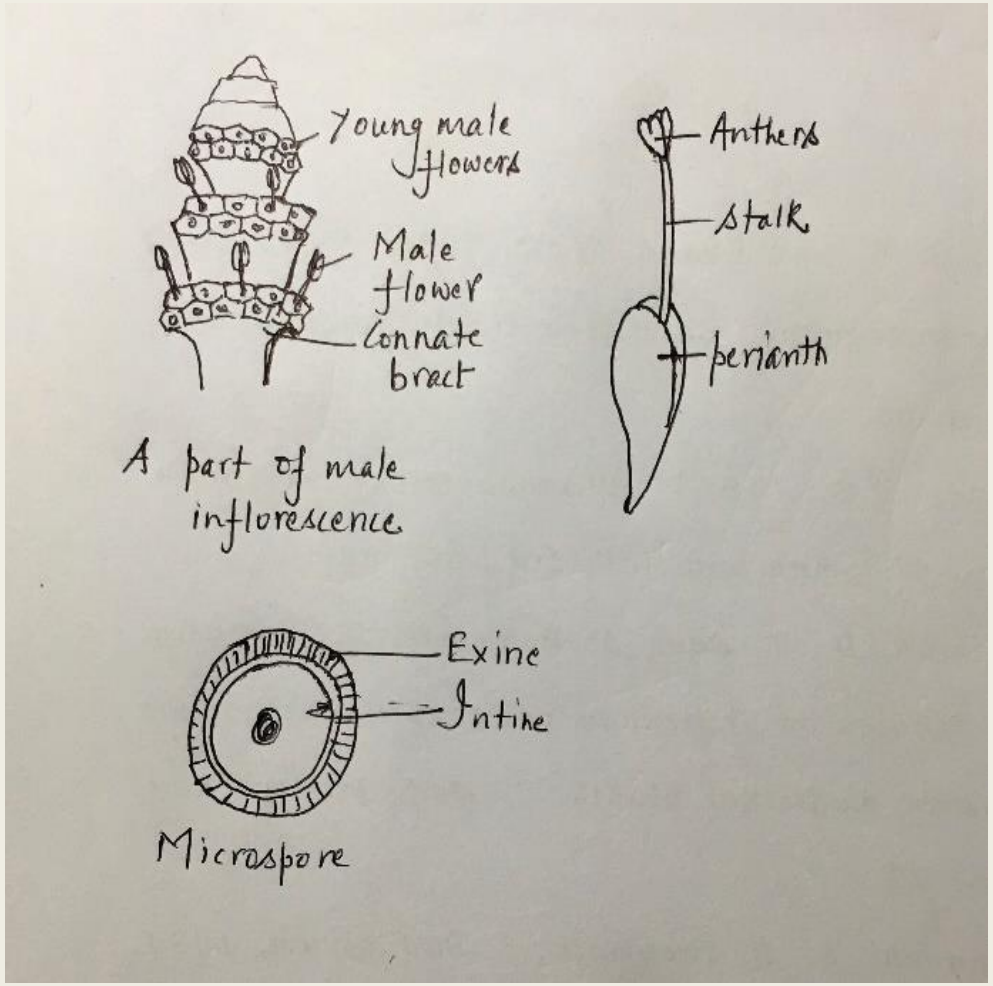


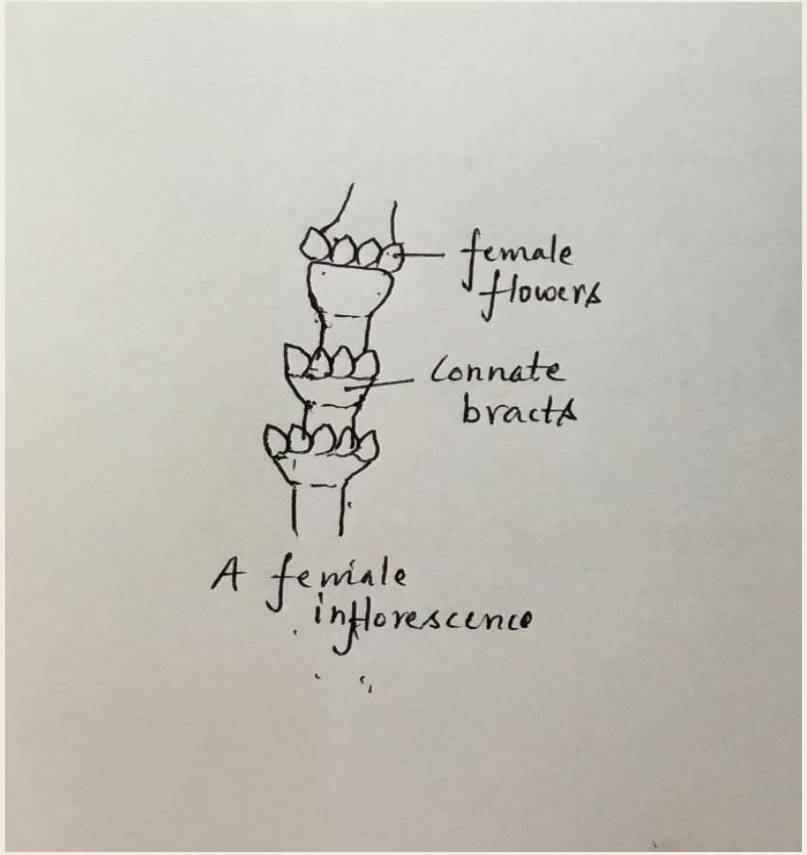
Microsporangium and microsporogenesis:

- Two groups of hypodermal archesporial cells form multicellular archesporium by repeated divisions.
- The outermost layer of the archesporial cells divides to form the primary parietal and the sporogenous cells.
- The parietal layer, by periclinal division, gives rise to a wall layer towards outside and tapetum towards inside.
- The tapetal cells become densely cytoplasmic and are normally binucleate (rarely multinucleate). The nuclei may fuse and become polyploidy. The tapetal cells start degenerating after meiosis.
- The sporogenous cells divide and increase in number, the last cell generation of which differentiates into microspore mother cells(2n).
- Broad cytoplasmic channels interconnect microspore mother cells or meiocytes forming a syncytium.

- **As the mother cells enter meiosis, it is surrounded by a thick layer of callose.**
- **Meiosis results in the formation of decussate, tetrahedral or isobilateral tetrads of microspores(n) still embedded in the callose cover.**
- **The callose covering is soon absorbed releasing individual haploid microspores.**
- **The microspore/pollen wall has an outer thick exine with minute spines and an inner thin intine.**

Female strobilus:

- It is similar to the male strobilus in the young stages.
- In a female strobilus, a ring of four to ten female flowers (ovules) is present above each collar.
- There is a total absence of any male flowers. Initially all the ovules look alike, but layer only a few grow to maturity. The upper few collars lack ovules.



***Megasporangium/ovule*:**

The integumented megasporangium is called ovule.

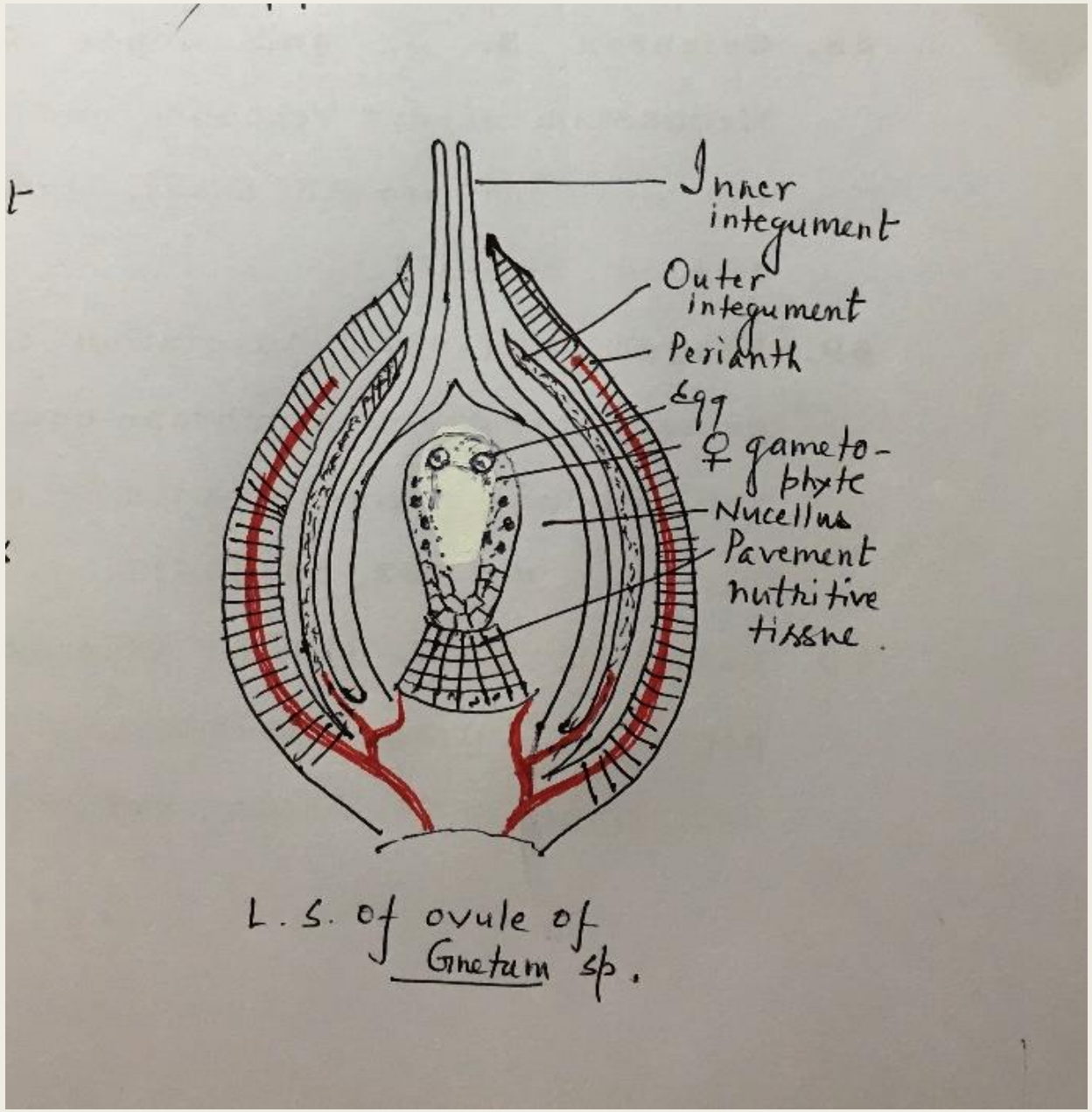
The ovule is stalked in *G. ula*, but may be subsessile or even sessile.

The ovules are orthotropous, crassinucellate and are protected by three envelopes.

The outer envelope is thick and succulent at maturity. It is considered to be the perianth.

The middle and the inner envelopes are actually the integuments. The middle envelop is called the outer integument which is anatomically similar to the outer envelope.

The inner envelope, i.e., the inner integument, elongates for beyond the apical cleft of the perianth and forms a long micropylar tube or the so-called 'style'. The inner integument is free from the nucellus except at the chalazal end. Two sets of vascular bundles are formed which the outer integument and the other to the inner integument.



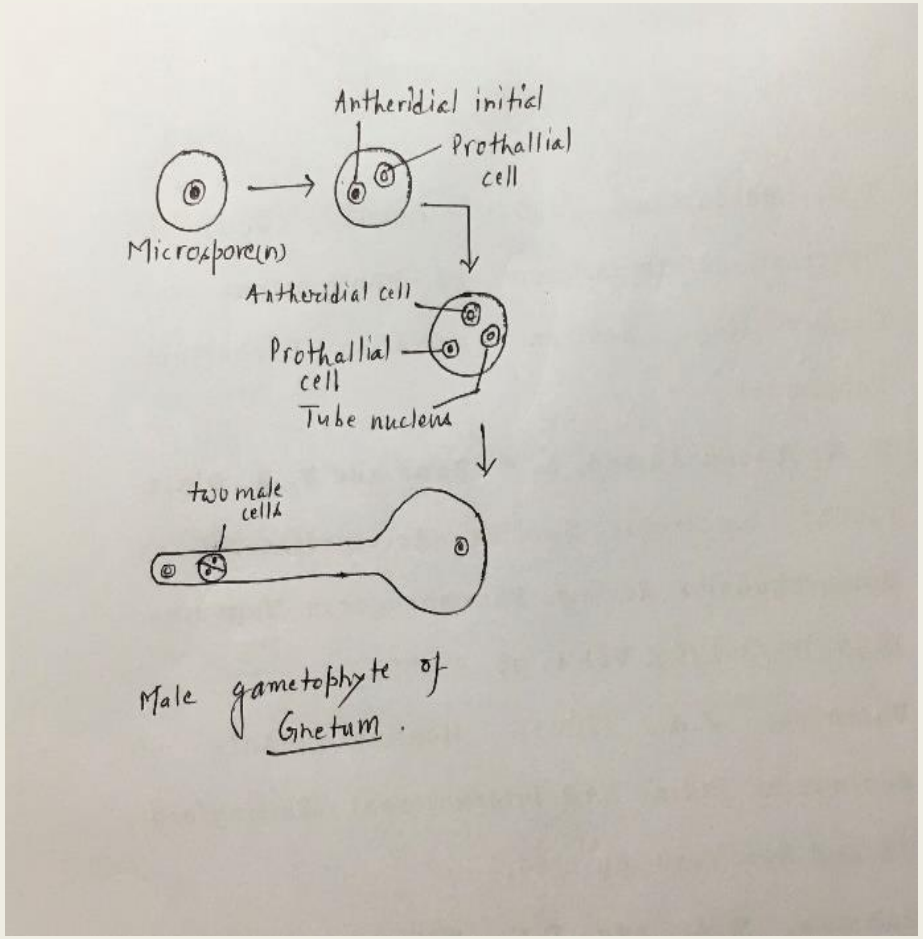
L.S. of ovule of Gnetum sp.

The nucellus is well developed and quite massive. Its epidermis divides, forming a nucellar cap. There is a clear demarcation between the nucellar cap and the parietal tissue.

Prior to meiosis in the **megaspore mother cells,** some nucellar cells below them divide to form a tissue wherein cells are arranged in radiating rows. This is termed as the **pavement tissue.** This tissue is nutritive in function. With growth of the female gametophyte the pavement tissue gets absorbed and obliterated.

Male gametophyte

- **Development of male gametophyte before pollination**
- **The microspore nucleus divides to form a small lens shaped prothallial cell and a large antheridial initial**
- **The prothallial cells rounds up and does not undergo any further division.**
- **The antheridial initial divides forming an antheridial cell and a tube cell. Since a stalk cell is not formed in *Gnetum*, the antheridial cell directly functions as a spermatogenous cell.**
- **At the three celled stage the pollens are shed. (one prothallial cell, an antheridial or spermatogenous cell and a tube nucleus).**



Megasporogenesis and female gametophyte

- Two to four hypodermal cells in the nucellar tissue at the micropylar end is differentiated into **primary parietal cells** towards outside and the **primary sporogenous cells.**
- Towards inside, the primary parietal cells together with nucellar epidermal cells divide repeatedly to produce a massive nucellus.
- The primary sporogenous cells divide to form 8-20 **sporogenous cells** which are linearly arranged.
- The sporogenous cells function as megaspore mother cells which undergo **meiotic division.**
- Since no walls are laid down after meiotic division of megaspore mother cells, all the four megaspore nuclei remain within the mother cell to form a **tetranucleate coenomegaspore.** Thus, the female gametophyte of ***Gnetum*** is **tetrasporic.**
- A **pollen chamber** develops at the apical portion of the nucellus after megasporogenesis is complete.

- ***Flange***: **At the time of pollination, a circular rim or an umbrella shaped structure, called 'flange' develops from the integument just above the level of inner integument.**
- ***Micropylar closing tissue***: **Another tissue is formed by the proliferation of the inner epidermis of integument at the level of the flange. This results in the closure of the micropylar canal. The plugging tissue has been called 'obturator.**
- **Only 2 or 3 coenomegaspores grow, although several develop in the same nucellus.**
- **There is a free nuclear division in the coenomegaspore, as a result a large number of free nuclei are formed. The number of nuclei may be 256 in *G. gnemon*, 512 in *G. africanum* and 1500 in *G. ula*.**
- **Later, as divisions continue, the gametophyte in the upper part widens and contains a vacuole, whereas in its lower part the gametophyte shows accumulation of cytoplasm. With further growth, the gametophyte becomes elongated and acquires the shape of an inverted flask.**

- **The gametophyte which, for most of its part, is free nuclear, starts becoming cellular in its upper portion soon after one of the eggs is fertilized.**
- **Eventually the upper part of the gametophyte becomes almost cellular.**
- **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.**

Pollination

- **Development of male gametophyte before pollination**
- **The pollen grains are shed at the three-nucleate stage.**
- **The pollination drop, which is rich in sugar, is exuded at the top and collects pollen.**
- **As the fluid dries, the pollen grains are sucked into the micropylar canal and lodge in the pollen chamber.**
- **Ants are known to visit the pollination drop which is formed by the degenerated cells of the nucellar tip.**
- **Development of male gametophyte after pollination**
- **The exine is casts off during pollen germination.**
- **The tube cell of the pollen comes out in the form of a pollen tube which traverses the nucellus through intercellular spaces.**
- **The prothallial cell remains within the pollen grain and eventually disorganizes.**
- **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., *G. africanum*) male cells just prior to fertilization. The male gametes move ahead of the tube nucleus and come to lie near the tip of the pollen tube.**
- **The male cells are actually the male gametes which are non-motile.**

***Fertilization*:**

- **Both the male nuclei are discharged into the egg cell. Of these one enlarges slightly and moves towards the egg nucleus.**
- **The other male nucleus, which is non-functional, remains in the periphery of cytoplasm and degenerates. Only the nucleus of the male gamete enters the egg; the sheath is left outside.**

***Endosperm*:**

- **Unlike almost all gymnosperms where a cellular endosperm is formed before fertilization, in *Gnetum* although the cellularization begins before fertilization, a part of the gametophyte remains free nuclear.**
- **Wall formation results in multinucleate compartments. The nuclei in each cell eventually fuse forming a single polyploidy nucleus. In *G. ula* the wall formation starts at the base of gametophyte and extends upwards. The upper part remains free nuclear of upper part of the female gametophyte also becomes cellular. The cellular basal portion exhibits dense and compact cells. The endosperm, later on, enlarges by consuming the surrounding nucellar cells. The endosperm is rich in starch and oil droplets and provides nutrition to the undifferentiated embryo which continues to grow after the seed has fallen to the ground.**

Embryogeny :

- ***Gnetum*** **represents an intermediate stage between gymnosperms and angiosperm as there are both free nuclear divisions and cell divisions.**
- **The early development of the zygote in different species of *Gnetum* shows variation. The zygote may divide into two cells and both or one may give out the tube. Alternatively, it gives rise to a branched tube. The tubes are designated as either proembryonal tubes, suspensor tubes, or primary suspensor tubes. The tubes become septate and much elongated and coiled, and penetrate the female gametophyte or endosperm.**
- **These primary suspensor tubes always move downwards i.e., towards chalazal end.**
- **Embryo development starts at the tips of some of these primary suspensor tubes where a small cell is cut off at the tip.**
- **The first division of the embryonal cell is always transverse. This is followed by longitudinal divisions in both the \cells to form the quartet. Further divisions in this quartet of cells result in a globular embryo.**

- **The upper four cells (proximal tier) divide longitudinally and elongate considerably to form the embryonal tubes or secondary suspensor.**
- **The secondary suspensor system is very prominent and it pushes the developing embryo deep into the endosperm. The primary suspensor system by now has ceased to function.**
- **The four cells of the lower tier (distal tier) divide transversely to give rise to two tiers of four cells each. The cells of the middle tier now divide vertically to form eight cells; four inner and four outer cells divide anticlinally to give rise to protoderm.**
- **There are several ways by which polyembryony occurs in *Gnetum*. Each of the primary suspensor tube may develop an embryo at its tip resulting in the formation of many embryos.**

The embryonal mass at the tip of the secondary suspensor may proliferate to give rise to additional embryos. Sometimes the cells of the secondary suspensor may become meristematic producing numerous embryos. In a primary suspensor tube, instead of one, two or more groups of cells may be produced forming many embryos at the top.

The nucellus represents a thin strap at the apex; the endosperm is massive, surrounded by a three-layered seed coat. The integument (endotesta) is fused with the nucellus for major part of its length. A ring of well developed bundles enters the base of the seed. Each bundle bifurcates, the outer series supplying the sarcotesta. The inner series again bifurcates; the outer supply the sclerotesta and the inner entering the endotesta.

The embryo is immature when the seed is shed.

Germination: The germination is epigeal.

Relationship with Angiosperms:

- ***Gnetum*** **plant in its external appearance resembles a typical dicotyledonous plant.**
- **The reticulate venation in the leaves of *Gnetum* is similar to that seen in a dicot.**
- **Both the groups exhibit vessels in their xylem. The origin of vessels is however, different in the two groups. In *Gnetum*, the vessels have evolved from tracheids having a number of bordered pits on the end wall, whereas the angiospermous vessels have evolved from tracheids with narrow scalariform perforations. It is interesting to note here that in the family Rosaceae of Angiosperms (even in the same species of Potentilla) both the types of vessels occur simultaneously.**
- **The formation of archegonium is completely suppressed in both groups.**
- **The tunica and corpus arrangement of shoot apex of Gnetum is angiospermous. However, the presence of central mother cells is a typical gymnospermous character.**
- **The integument of the ovule in G*netum* elongates to form a well developed micropylar tube.**
- **Germinating pollen grains have also been found at angiosperm carpel.**
- **The megasporogenesis in *Gnetum* is tetrasporic which is not found in gymnosperms and is common in many angiosperms.**

- **The storage tissue or endosperm in angiosperms develops after fertilization (result of triple fusion). In *Gnetum*, though the cellularization starts prior to fertilization, the mature endosperm develops only after fertilization. Double fertilization and synergids, too, are absent in Gnetum.**
- **Carmichael & Friedman have shown that double fertilization occurs regularly in *Gnetum gnemon*. Each of the two sperm nuclei fuses with a separate, undifferentiated female nucleus in free nuclear female gametophyte giving rise to two zygotes.**
  - **Based on the above apparent resemblances Maheshwari (1950) regarded angiosperms to have passed through some stage during the evolution which is now presently shown by *Gnetum*. Later, Maheswari & Vasil (1961a) concluded that *Gnetum* still remains a phylogenetic puzzle.**