SUB UNIT 4B GNETOPSIDA: *GNETUM*

Structure

4B.1 INTRODUCTION

In the previous sub unit you have studied *Ephedra,* and in this sub unit you will study ***Gnetum*** because it is the only genus representing Gnetaceae. ***Gnetum*** has many important feature which have resemblence with angiosperms.

Objectives

You have by now become familiar with the main categories of gymnosperms. In this unit you will be able to:

- state the distribution of ***Gnetum*** in world as well as in India,
- describe morphology of both vegetative and reproductive structures,
- distinguish between the anatomy of root, stem and leaf,
- describe the structure of micro-and megagametophytes,
- give an account of pollination, fertilization and seed development and
- compare relationship of ***Gnetum*** to other gymnosperms and with angiosperms.

4B.2 DISTRIBUTION, HABITAT AND GENERAL FEATURES

Most species inhabit the tropical rain forest below 1500 m altitude.

The genus ***Gnefum*** consists of thirty species, widely distributed in the tropical and sub-tropical humid zones of the world. Of these 7 occur in tropical America, 2 in western Africa and the remainder in tropical Asia, 5 species are found in India.

Gnetum resembles more an angiosperm than a gymnosperm. Most of the species are climbers with twinning stem.

G. ula, a woody climber, is most common and abundant, ahd occurs in the coastal regions of peninsular India. *G. contractum* and *G. montanum* both are also lianas, the former occurs in Kerala and Tamil Nadu, whereas the latter grows in Assam and Sikkim. Another climber, *G. latifolium* is found in Andamans. *G. gnemon* a tree is restricted to the north-eastern parts of India G. trinerve is reported as a parasite.

4B.3 VEGETATIVE STRUCTURE

4B.3.1 Root

The plant has a tap root system with well developed lateral roots. The outermost layer or epidermis is followed by many layered parenchymatous,starch-filledcortex.Thick walled fibre cells are common in the cortex. The endodennis encloses a multilayered pericycle. The primary xylem is diarch. The tracheids have uniseriate bordered pits. Phloem is composed of uniform cells. Secondary growth occurs in the normal manner.

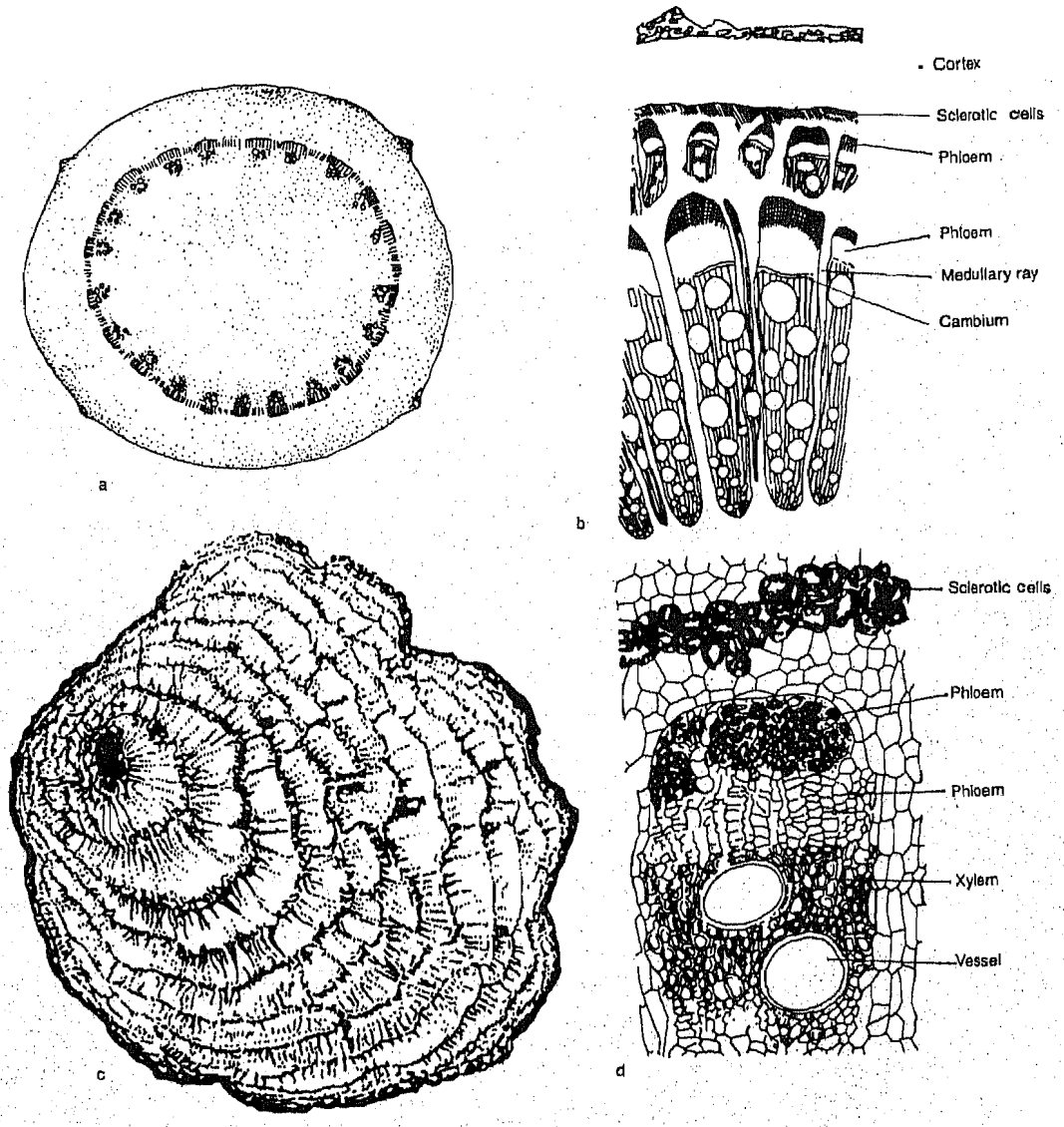

Fig. 4B.1 : *Gnetum* sp.a) T.S. of young stem (diagrammatic). b) T.S. stem showing accessory rings of vascular bundles. c) Same, a part enlarged to show two vascular rings. d) One vascular bundle from accessary ring enlarged. Note the presence of phloem fibres towards the periphery of the bundle forming a patch and a thick layer of sclerotic cells immediately above it. Two prominent vessels are seen in the xylem tissue (after Maheshwari & Vasil, 1961a).

4B.3.2 Stem

It exhibits two types of branches, viz, branches of limited growth and branches of unlii growth. This distinction is not there in the shrub by or tree species of Gnetum, such a: *gnemon*. Some species have articulate stems; the joints have two parts, one just abovr the other below the node, and are separated by an annular groove.

A young stem shows a single layered epidermis of rectangular cells with a thick coatin cuticle and sunken stomata. The cortex consists of 12-16 layers of parenchymatous cel some cells in the inner zone become fibrous with narrow lumen. In older stems, a ring o parenchymatous cells becomes sclerenchymatous in the inner cortex, and it is referred the ring of spicular cells. Endodermis and pericycle are not distinct. The vascular bund (20-24) are collateral and endarch, and are arranged in a ring. The xylem consists of trac and few vessels. Medullary rays between vascular bundles are high and broad. The pit parenchymatous. Laticiferous elements are seen in both pith and cortex (Fig. 4B. la).

In tree species of *Gnetum*, such as G. *gnemon*, the secondary growth is normal. In the

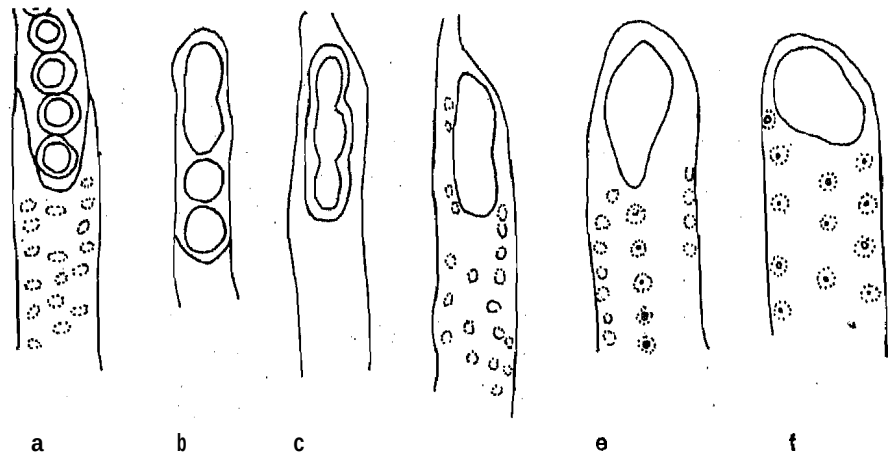

Fig. 48.2 : Perforations in the end walls of the vessels of G. *africanum* (After Duthie, 191

climbing species, like G. *ula* and *G. africanum*, the secondary growth is normal to begin with but, later, due to the formation of new cambium, several rings of xylem and phloem, separated into wedge-shaped bundles because of medullary rays, are produced. You can see in Figure (4B.1b) that some of these accessory rings may be incomplete with the result that either the pith or the arrangement of vascular bundles is eccentric. The detailed structure of each vascular bundle is shown in Figure (4B.1c,d.).

The secondary phloem is composed of sieve cells and parenchyma. Both elements show great regularity in their arrangement – sieve cells in uniform rows and parenchymatous cells in angles between them. In their location, size and contents the parenchymatous cells resemble companion cells, although their origin is very different.

The wood of *Gnetum* is remarkable in showing vessels with a single pore on their end walls (Fig. 4B.2.a). Besides vessels, tracheids and xylem parenchyma are also present. The tracheids are long and show uniseriate bordered pits on both radial and tangential walls. The xylem parenchyma cells possess simple pits (Fig.4B.2b,c).

Stem apex: The shoot apex of *Gnetum* has assumed an mgiospermous character. It exhibits atypical tunic.-corpus organisation. The tunica is the outennost single layer of cells extending from the first pair of leaf primordia over the shoot apex. The corpus consists of subapical initials, central mother cell zone, flanking layers and pith rib meristem. You will read more about this in Unit-8.

4B.3.3 Leaf .

The *Gnetum* plant resembles dicotyledons in the leaf shape and venation. The leaves are large, oval-shaped with reticulate venation and entire margin (Fig. 4B.3a). The short shoots are usually unbranched, and bear 9 or 10 decussately arranged leaves on each branch.

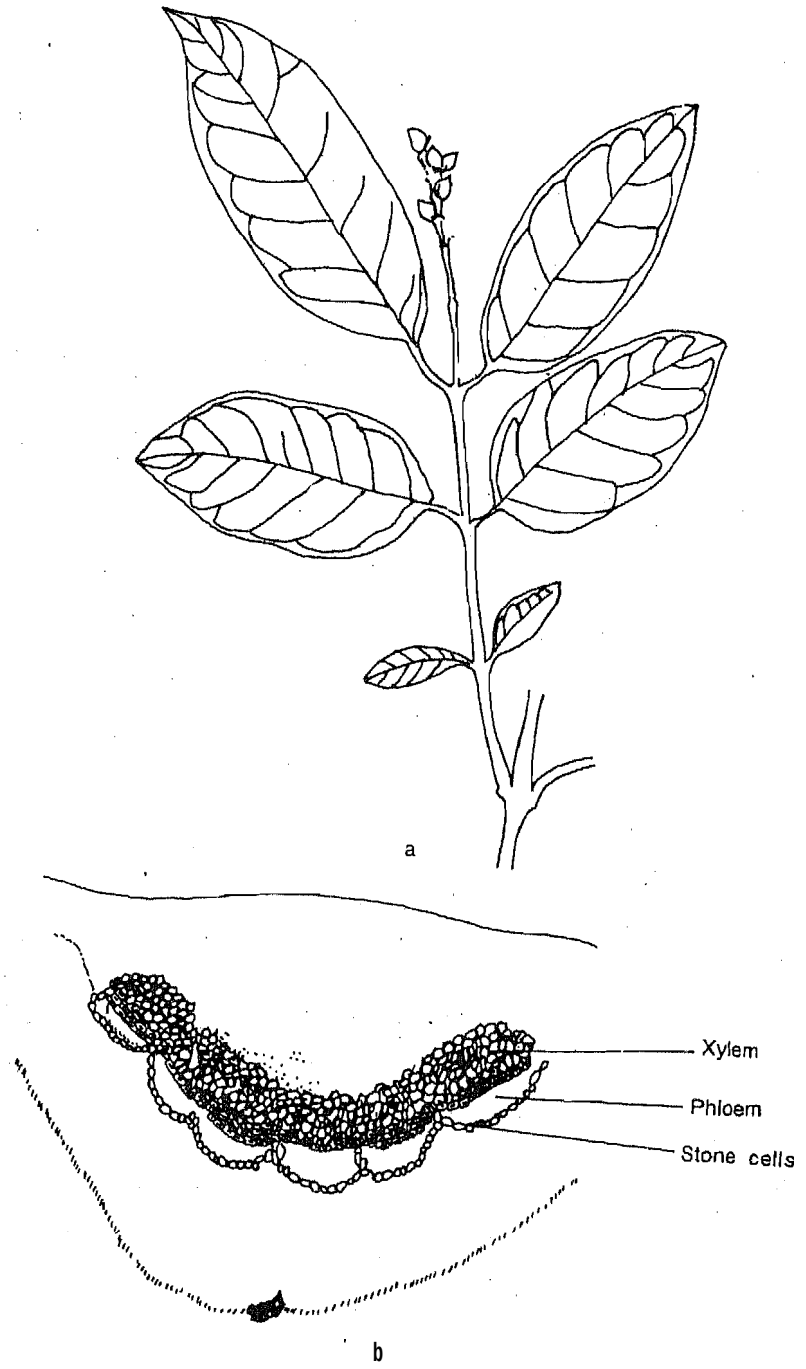

Fig. 48.3: *Gnetum* sp. a) *Gnetum indicum:* Leaves with reticulate venation b) V.S. older leaf in the region of midrib, Note distinct patches of stone cells outside the phloem tissue (after Mnheshwari &Vasil, 1961a).

In leaves the epidermis has undulating walls with a thick cuticle. The mesophyll is distinguishable into palisade and spongy parenchyma. The palisade consists of a single layer of compact cells which show the presence of stellately branched sclereids near the lower epidermis. Fibres and latex tubes are abundant, especially in the midrib region. Stomata occur only on the lower surface and are irregularly oriented. The pattern of stomatal development is haplocheilic. Vascular bundles are arranged in a curve (Fig. 4B.3b). Xylem consists of vessefs, tracheids and parenchyma. The phloem is arranged in regular rows just beneath the xylem. Thick walled pitted cells form a patch outside the phloem.

SAQ 1

Fill in the blanks using the correct alternative.

1 *Gnetum* plants are found in ..... (Kashmir/Kerala).

2. *Gnetum* is a plant of ..... (arid/moist) tropical zones.

3. The leaves of *Gnetum* show .....(reticulate/parallel) venation.

4. *Gnetum* shows presence of ..... (vessels/sclereids) and hence resembles angiosperms.

5. The presence of..... .(laticifers/resin ducts) is seen in the stem of ***Gnetum.***

SAQ 2

1. Comment on the statement that "***Gnetum*** shows an angiospermous shoot apex?"

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2. Anamolous secondary growth occurs in some species of *Gnetum.* How does *it* differ from the normal growth?

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3. What is characteristic of the wood of *Gnetum*?

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4B.4 REPRODUCTIVE STRUCTURES

4B.4.1 Male Strobilus and Gametophyte

Male and female strobili ("cones") develop on separate plants i.e *Gnetum* is dioecious. Figure 4B.4 shows the morphology of the male and female branches.

Male Strobilus : The "inflorescence" is a solitary or fascicled panicle. It is axillary on a short shoot and is unbranched. Apart from microsporangia it shows a whorl of sterile ovules. The strobilus consists of an axis with two sterile, connate opposite bracts at the base and a series of circular bracts (cupules or collars) which are superposed one above the other (Fig. 4B.5a). A young strobilus appears compact because of a reduced axis with very short internodes and the collars appear to be continuous. As the axis elongates the collars get separated. The upper two or three collars in G. *gnemon* are much reduced and sterile.

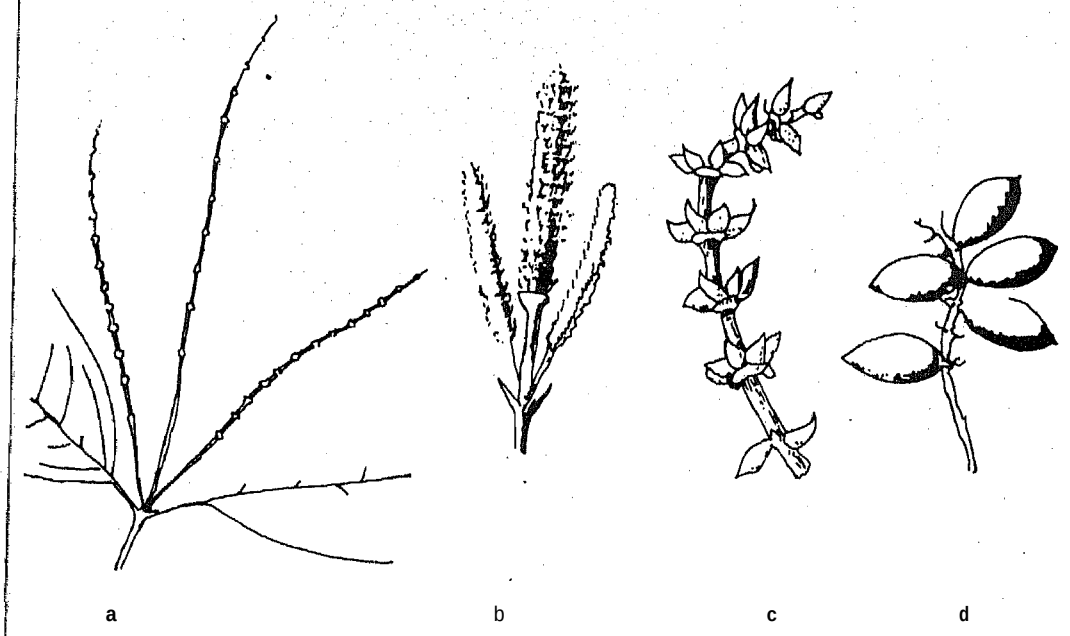

Fig. 4B.4: *Gnetum sp.*a) Reproductive branch. b) male strobilus. c) female strobilus. d) seed bearing branch (after Kubitzki, 1990).

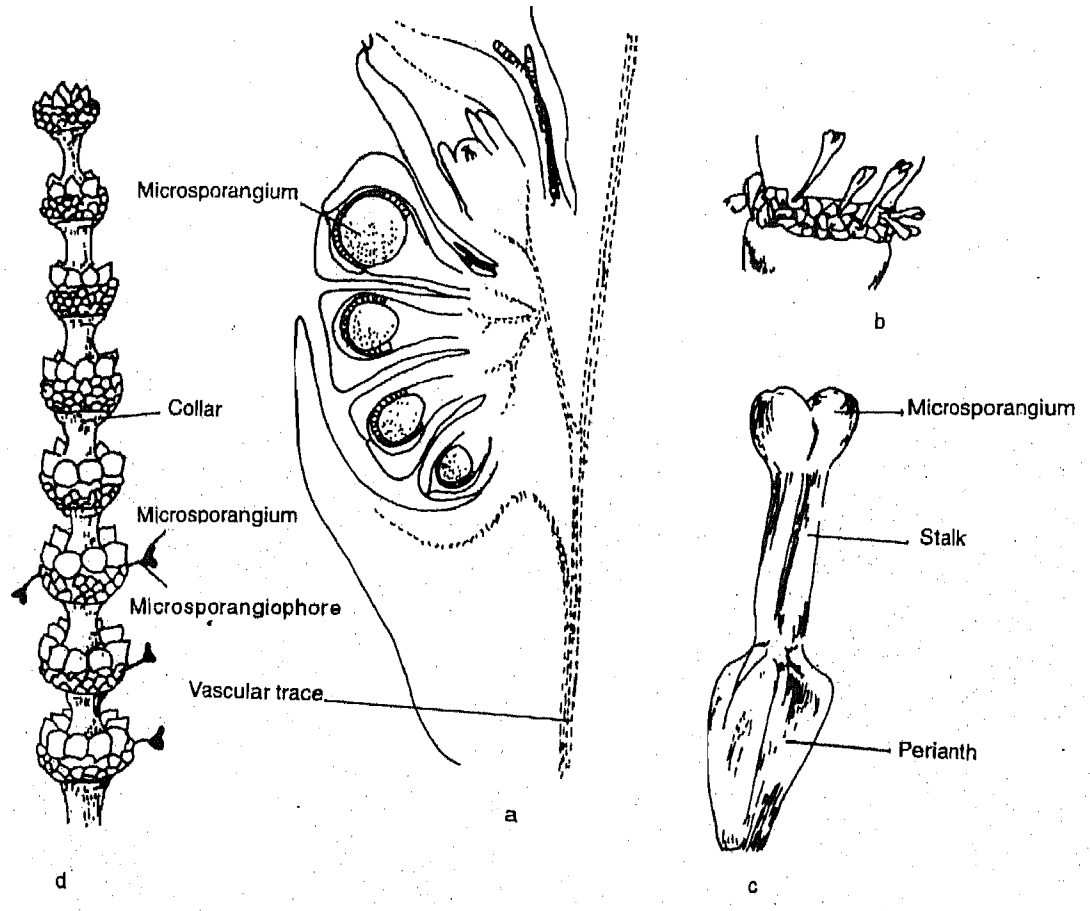

Fig. 4B.5 : a-c) *Gnetum* sp. : a) Branch bearing a panicle of male cones at dehiscense. At each collar, just above male flowers, there is a ring of imperfect female flowers or abortive ovules. b) Portion from an enlarged; male flowers are dehiscing. c) Elongation of stalk and emergence of anthers from perianth. d) L.S. part of male cone to show the position of sporangia and ovule and vasculature to collar, male flowers and ovule. (a-c, after Vasil, 1959 ; d-g, after Sanwal, 1962).

Each collar bears three to six rings of 12–15 male flowers and above them a single ring of 7–12 imperfect female flowers or abortive ovules (Fig. 4B.5a, b). Each male flower has two unilocular anthers on a stalk (antherophore) enclosed in a sheath of bracts or perianth (Fig. 4B.5d). The stalk elongates at maturity and the anthers come out of the perianth cover through a slit. (Fig. 4B.5c). During the development of the male strobilus, the collars are formed in an acropetal succession.

The shape of collars their number and internode length are of taxonomic importance.

A ring of meristematic cells differentiates at the base (axil) of each collar. The microsporangium is formed by a hump of tissue which becomes notched to form 2 anthers with a stalk. Two groups of hypodermal archesporial cells, by repeated divisions, give rise to multicellular archesporium (Fig. 4B.6a). The outermost layer of the archesporial cells divides to form the primary parietal layer and the sporogenous cells (Fig. 4B.6b). The primary parietal layer, by periclinal division, gives rise to a wall layer towards outside and tapetum towards inside. The wall layer is the first to degenerate. The tapetal cells become densely cytoplasmic and are normally binucleate; the nuclei may fuse and become polyploid. The tapetal cells start degenerating after meiosis and their remnants are discernible at uninucleate stage of microspores (Fig. 4B.6c). Übisch granules or orbicules are seen on the wall of the tapetal cells. The epidermis is the only layer which persists in the mature sporangium which dehisces by a median longtitudinal slit. The sporogenous cells divide and increase in number, the last cell generation of which differentiates into microspore mother cells. Broad cytoplasmic channels interconnect microspore mother cells or meiocytes forming a syncytium. A space is formed between the plasmalemma and the mother cell wall. The latter is gradually dissolved away followed by the rounding off of the protoplasm. As the mother cell enters meiosis, it is surrounded by a thick layer of callose. The meiosis results in the formation of decussate, tetrahedral or isobilateral tetrads still embedded in the callose cover. This covering is soon absorbed releasing individual haploid microspores. (See Fig. 4B.6c).

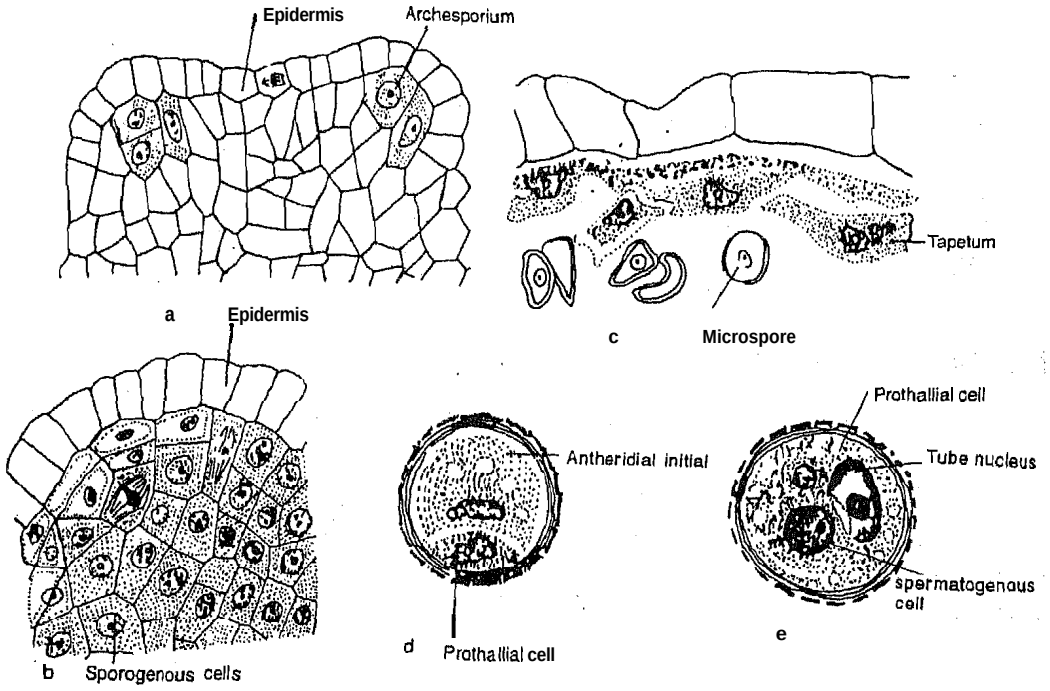

Fig. 4B.6 : *Gnetum* sp. **Microsporogenesis** and male gametophyte. a) L.S. very young male flower to show few hypodermal archesporial cells. b) Same, at a later stage; primary parietal layer has been cut off above sporogenous tissue. c) Part of sporangium showing degenerating tapetal cells and a few microspores. d) Two-nucleate pollen grain; prothallial cell has been cut off, e) Mature, three-celled (prothallial cell, tube cell and spermatogenous cell) pollen grain at shedding stage (after Sanwal, 1962).

The microspore nucleus divides to form a small lens-shaped prothallial cell and a large antheridial initial (Fig. 4B.6d). The prothallial cell rounds up and does not undergo any further division and degenerates as such. 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 the spennatogenous cell, Pollen grains are shed at the 3-celled stage (Fig. 4B.6e). Double pollen grains have occasionally been observed in several species. They probably arise due to the non-separation of two or more cells of a tetrad. The pollen is sticky in nature.

4B.4.2 Female Strobilus and Gametophyte

Female Strobilus: The female strobilus resembles the male strobilus when young. However, as the strobilus grows, the distinction becomes clear. In a female strobilus, a ring of four to ten female flowers (ovules) is present above each collar. There are no male flowers. All the ovules look alike initially but, later, only a few grow to maturity. The upper few collars usually lack ovules and are thus sterile.

Nearly four to ten ovular primordia differentiate from an annular meristem or rim below each collar of the female cone. The ovular primordium lies on a cushion. The three envelopes (outer, inner and integument) arise in a centripetal manner. The ovule is stalked or subsessile. Of the three envelopes, the, outer one differentiates first. Often called perianth, this envelope gets thickened and somewhat succulent at maturity (Fig. 4B.7a). The outer epidermis shows stomata.

The inner envelope is next to arise, and is sometimes called as the outer integument. The female flowers in the male cone lack this envelope. The apical part forms a tapering ring-shaped rim. Stomata differentiate in the outer epidermis. Laticifers are also formed at the time of pollination. The major part of the stony layer of the seed coat is formed by the fibrous elements and sclereids in this envelope.

The third envelope or the integument is last to be formed, and is fused with the nucellus in the lower part. It elongates considerably into a micropylar tube or the so-called "style" projecting beyond the apical cleft of the outer envelope, The exposed part is nearly one-third the length of the mature ovule. This part starts degenerating before or at the time of pollination. The apical lobes of this envelope become prominent and their number varies from 7 to I I. The lobes are large and irregularly twisted. Unlike the other two envelopes (Fig. 4B.7a), neither stomata nor sclereids develop in the integument.

Nucellus : The nucellus is well developed and quite massive. Its epidermis divides forming a nucellar cap.

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", and its cells are densely stained when the female gametophyte is free nuclear. As the female gametophyte grows in the chalazal region, the pavement tissue gets absorbed. This tissue is thought to be nutritive in function.

Mcgasporogenesis and Female Gametophyte : Generally two to four hypodermal archesporial cells differentiate in the young nucellus (Fig. 4B.7b). They cut off primary parietal cells towards outside and primary sporogenous cells towards inside. As stated earlier, the parietal cells together with nucellar epidermis produce a massive nucellus. The primary sporogenaus cells divide forming 8–16 sporogenous cells, that are linearly arranged and function as megaspore tnother cells.

Since no walls are laid down after meiosis I and II (Fig. 4B.7d), a tetranucleate coenomegaspore is produced. To begin with, the four nuclei lie in the centre of coenomegaspore but later they move to the periphery. The development of the female gametophyte is, thus, tetrasporic.

Although several coenornegaspores develop in the same nucellus generally only 2 or 3 grow beyond 16-nucleate stage.

As the female gametophyte develops, a large vacuole appears in the centre and the nuclei in the peripheral cytoplasm undergo repeated divisions (Fig. 4B.7c). Later, as divisions

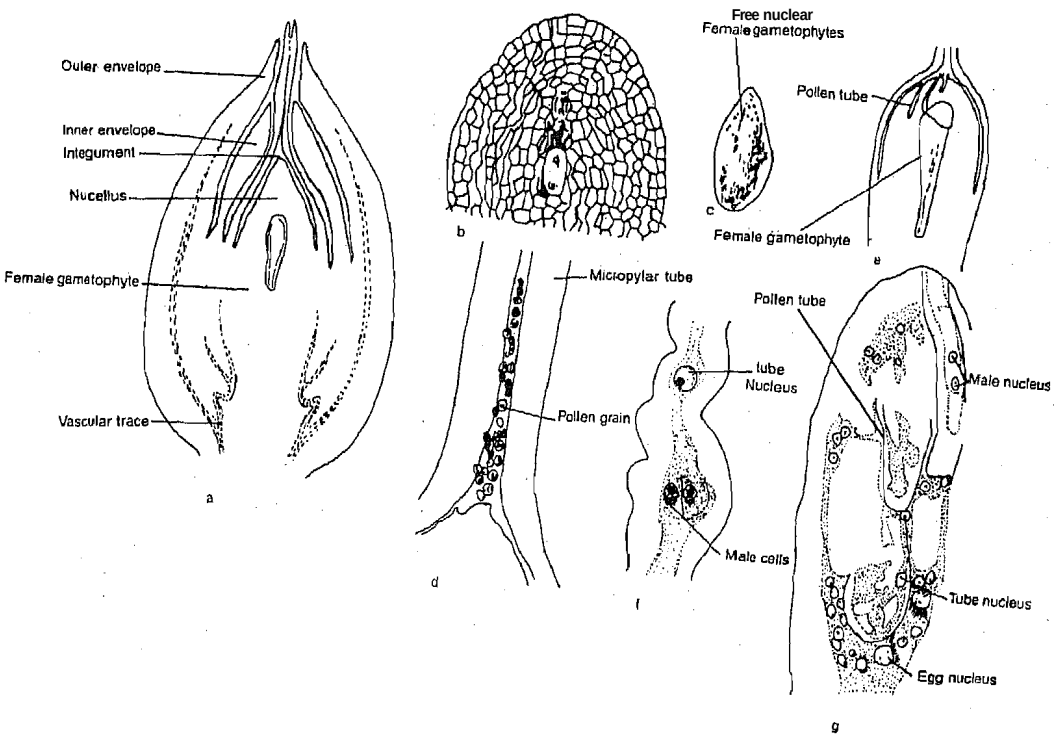

Fig. 46.7: *Gnetum* **sp.** a) **LS.** ovule to show outer and inner envelopes, integument and well developed nucellus; the integument forms the micropylar tube. The female gametophyte is at the **free** nuclear stage. Dotted lines represent the vascular supply to various parts. b) A two nucleate megaspore mother cell. c) Free nuclear female gametophytes, d) L.S. part **of** micropyle showing entrapped pollen grains, e) **L.S.** ovule to show three pollen tubes in **nucellar** tissue. One of the pollen tubes is about to enter the lower female gametophyte. f) Portion of **pollen** tube showing tube nucleus and two equal male cells. g) L.S. upper part of female gametophyte with several pollen tubes. Two **large** nuclei with radiatlng cytoplasm near the lower pollen tube will function as egg nuclei, (c-e after **Vasil,** 1959; a-b after **Madhulata,** 1960; f-g after **Sanwal,** 1962).

In G. *gnemon*, the pollen tube **traverses** laterally along the **gametophyte** and nuclei in the vicinity of the pollen tube enlarge **several** times and acquire dense cytoplasm around them. These are the egg nuclei.

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 garnetophyte becomes elongated and acquires the shape of an inverted flask **(Fig. 4B.7e)**.

An interesting feature of the female gametophyte is the absence of archegonia, a feature ***Gnetum*** shares with *Welwitschia*. When the pollen tube makes contact with the female garnetophyte, one or more nuclei in the equatorial region of the dilated part, can be easily demarcated from the other nuclei by their large size and dense staining. These are the egg nuclei whose usual number is two **but,** rarely, one or three nuclei may also develop into eggs. The differentiation of the egg is stimulated by the presence of the **pollen** tube in the vicinity of the female gametophyte (Fig. **4B.7g).** The most interesting part of the egg development is that all the eggs do not **mature** simultaneously nor all the pollen tubes reach the gametophyte at the same time. **Differentiation** of additional eggs continues even after fertilization **of the** first one. The garnetophyte 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.

4B.5 POLLINATION AND FERTILIZATION

The pollination takes place when the female gametophyte shows 250 nuclei in *G. ula* and 32 or 64 nuclei in *G. gnemon*. Pollination may be carried out by wind or insects. The tip of the micropylar tube becomes flared and lacerated. The pollination drop, which is rich in sugar, is exuded at the tip and collects pollen. As the fluid dries, the pollen grains are sucked into the micropylar canal and lodged in the pollen chamber (Fig. 4B.7d). Ants are known to visit the pollination drop which is formed by the degenerated cells of the nucellar tip.

The pollination biology of a dioecious (shrub) species, *G. gnemon* has been studied. During evening both male and female strobili emit a strong, putrid odour; pollination droplets are also secreted from the ovules. Evaporation of the exposed pollen droplet is very slow at night in the tropical rain forest. This nocturnal entomophily is attained by replacing showy petals with a strong odour.

At the time of pollen germination, the exine is cast off. The pollen grains are devoid of germ pores. The pollen grain puts out a tube which grows and traverses the nucellus through intercellular spaces. When the pollen tube has travelled almost half the length of the nucellus, the spermatogenous cell moves into the tube whereas the prothallial cell degenerates in situ. On division, the spermatogenous cell forms two male cells (Fig. 4B.7f). The male gametes move ahead of the tube nucleus and come to lie near the tip of the pollen tube (Pig. 4B.7g).

A pollen chamber develops at the apical portion of the nucellus. When niegasporogenesis is complete, the cells in the upper region start degenerating. The degeneration of the cytoplasm is followed by the breakdown of nuclei and cell walls. Eventually, a shallow pollen chamber is formed into which pollen grains will be lodged. The cells between tlie pollen chamber and female gametophyte are gorged with starch grains. The growing endosperm (female gametophyte) nearly consumes the nucellus and, in a mature seed, the cells in the apical portion become cutinized and persist.

During post-pollination stages, a ring shaped swelling appears just above the insertion of inner envelope. Another swelling or proliferation develops in the apical part below tlie pollen chamber.

At the time of pollination, a circular rim or an umbrella-shaped structure, called "flange" develops from the integument. Its function is not clear.

Micropylar Closing **Tissue** : Another tissue (closing tissue) is formed by the proliferation of inner epidermis of integument at the level of the flange. This results in the closure of the micropylar canal. The closure is due to the elongation and interlocking of the inner epidermal cells. The micropylar closing tissue may grow downward filling the pollen chamber. The plugging tissue has been called "obturator" as it fits in the pollen chamber.

SAQ 3

1 If archegonia are absent in *Gnetum*, where is the egg nucleus present.

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2. Explain the process by which pollen is transferred from male strobilus to the ovule.

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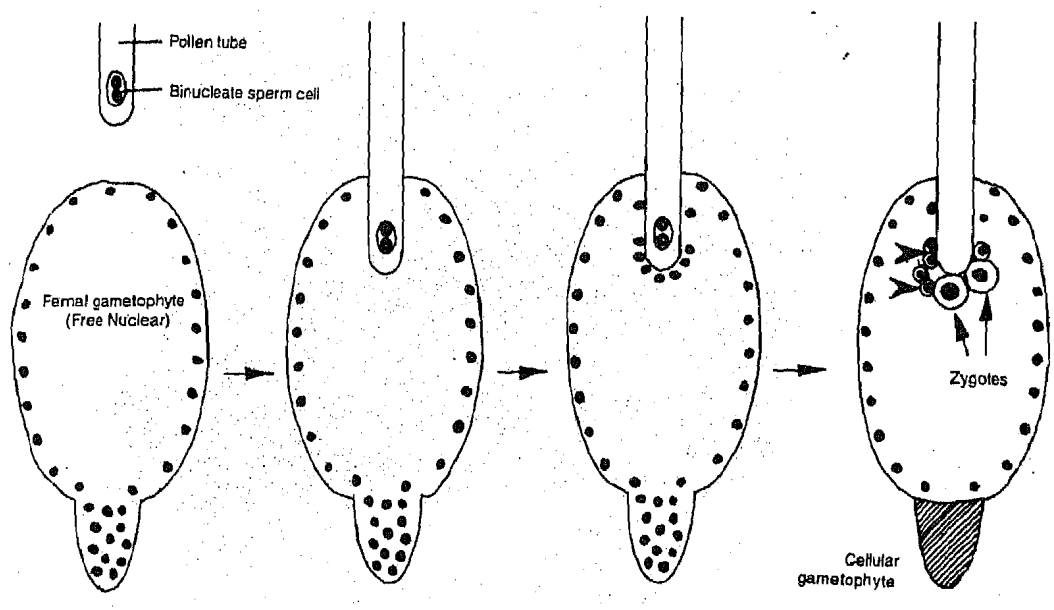

Fig. 4B.8: **Diagram** illustrating double fertilization in *Gnetum gnemon*. **Binucleate** sperm cells are produced within pollen tubes that enter a coenocytic female gametophyte. Shortly after pollen tubes enter, **free nuclei** within the female garnetophyte **migrate** around the tips of pollen tubes, None **of** the female **nuclei** differentiate as eggs and all represent potential gametes. Pollen tubes discharge both sperm nuclei into surrounding **female** cytoplasm and each **sperm** nucleus fuses with a **separate** female nucleus. Double **fertilization** results In the **formation** of two viable zygotes. Although unfertilized **female** nuclei may become cellular **(arrowheads),** they ore clearly distinguishable from diploid **zygotes.** Concurrent with fertilization, the **chalazal** region of the female gametophyte becomes **cellular, will** eventually enlarge and serve to nourish developing embryos. As many **as** six pollen tubes may fertilize a single female gametophyte, (after **Friedman** 1996).

SAQ 4

State whether the following statement is true or false. Write T for true and F for false in the given bracket.

1. In Gnetum the pollen grain is shed at three nucleate stage, [ ]
2. In *G. ula* the pollination take place when female garnetophyte shows 250 nuclei. [ ]
3. The pollination drop is rich in protein and vitamins. [ ]
4. In the stern of some species of ***Gnetum*** several accessory rings of **vasculature** of which **some may** be incomplete are formed due to secondary growth. [ ]
5. The **development of the female gemetophyte** in *Gnetum* **is** tetrasporic. [ ]

There **are** reports of double fertilization in the genus ***Gnetum.*** It occurs regularly in **G.** ***gnemon,*** and is possible because two **sperms** per pollen tube have access to at least two **fecundable** female nuclei in the garnetophyte, **In** Gnetum ***gnemon*** a binucleate **sperm** cell is formed in the pollen tube. In the **free** nuclear female garnetophyte, undifferentiatedfemale **nuclei function as eggs.** The two **sperm** nuclei are released in the **surrounding** female **cytoplasm and** each **fuses** with a separate female nucleus thus causing *double fertilization,* resulting in two diploid **zygotes. After** fertilization each zygote **nucleus** develops into an embryo, but **usually** only one attains maturity in **the** seed. You must study Fig, 4B.8 for the details.

4B.6 EMBRYOGENY AND SEED DEVELOPMENT

The **zygote may** give rise to a small protuberance into which the nucleus moves (Fig. 4B.9a). It **may** even divide into two cells and both or one of the cells may give out a tube (Fig. 4B.9b).

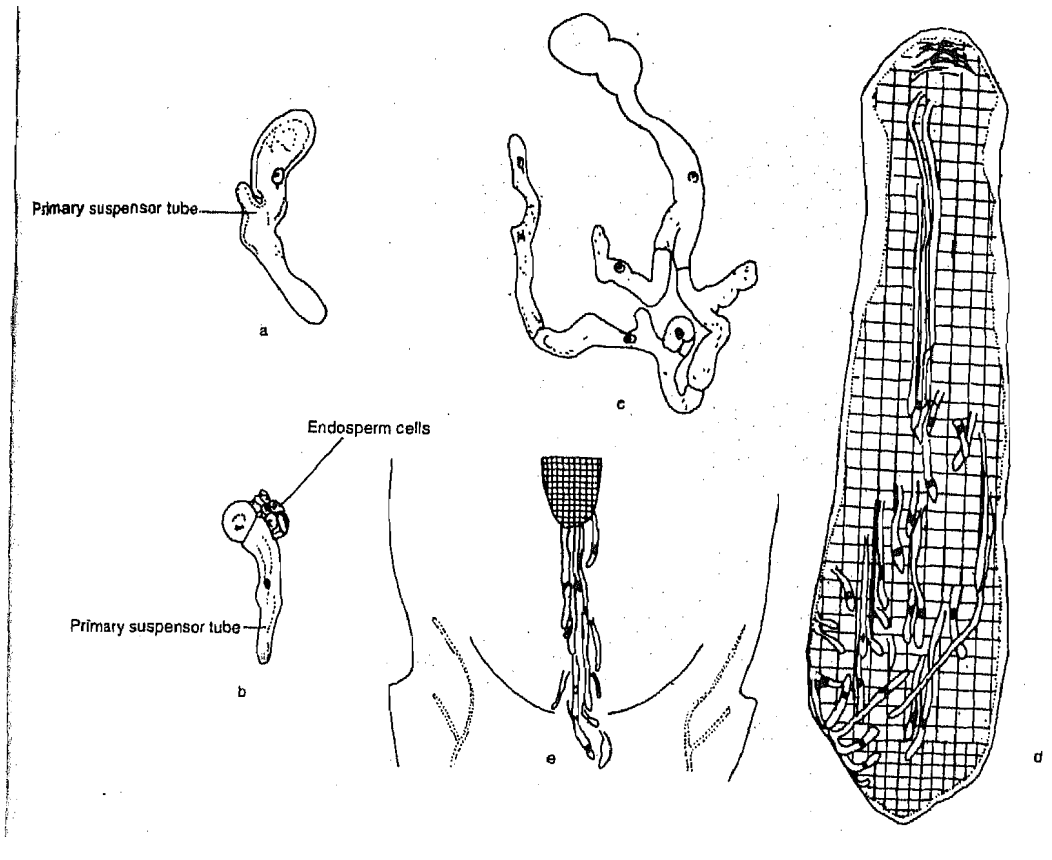

Fig. 4B.9a-e: Stages in development of embryo of *Gnetum gnemon*. a) Zygote giving out primary suspensor tube, b) Two-celled zygote; some endosperm cells are also seen. c) Branched primary suspensor tube. d) L.S. ovule showing numerous primary suspensor tubes penetrating the female gametophyte. e) Lower portion of ovule showing the primary suspensor tubes growing beyond endosperm in the nucellar tissues.

The tubes have variously been designated as primary suspensor tubes to differentiate them from the secondary suspensor which will be described later. The tubes become septate and much elongated and coiled, and penetrate the female gametophyte or endosperm (Fig. 4B.9c). These primaty suspensor tubes always move downwards i.e., towards chalazal end (Fig.4B.9 d, e).

Embryo development starts at the tips of some of these primary suspensor tubes. The nucleus of the primary suspensor tube migrates towards the tip and divides into two unequal nuclei (Fig. 4B.10a, b). The smaller one becomes rounded and divides twice producing four cells. Subsequent divisions are irregular forming a mass of cells, upper cells of which give rise to the secondary suspensor (embryonal tubes) (Fig. 4B.10c, d). Cells at the tip of the secondary suspensor are compact and form the embryo proper (Fig. 4B.10e). The secondary suspensor becomes quite massive appearing like a folded plate of cells. Some cells elongate producing long tubes growing on the sides of the primary suspensor tube which ceases to function (Fig. 4B.10f).

Embryo Development : Of the many primary suspensor tubes, only few continue to develop and the remaining embryos along with their primary suspensor system degenerate. The growing embryo exhibits a conical mass of cells with the shoot apex at the tip of the cone. On the sides of the embryonal mass tip, the cells divide actively to form two cotyledons covering the central zone of the shoot apex. The root tip is differentiated at the opposite end. The root cap cells are confluent with the massive secondary suspensor. After the formation of the shoot and the root apices, a small protrusion appears in the region between the two

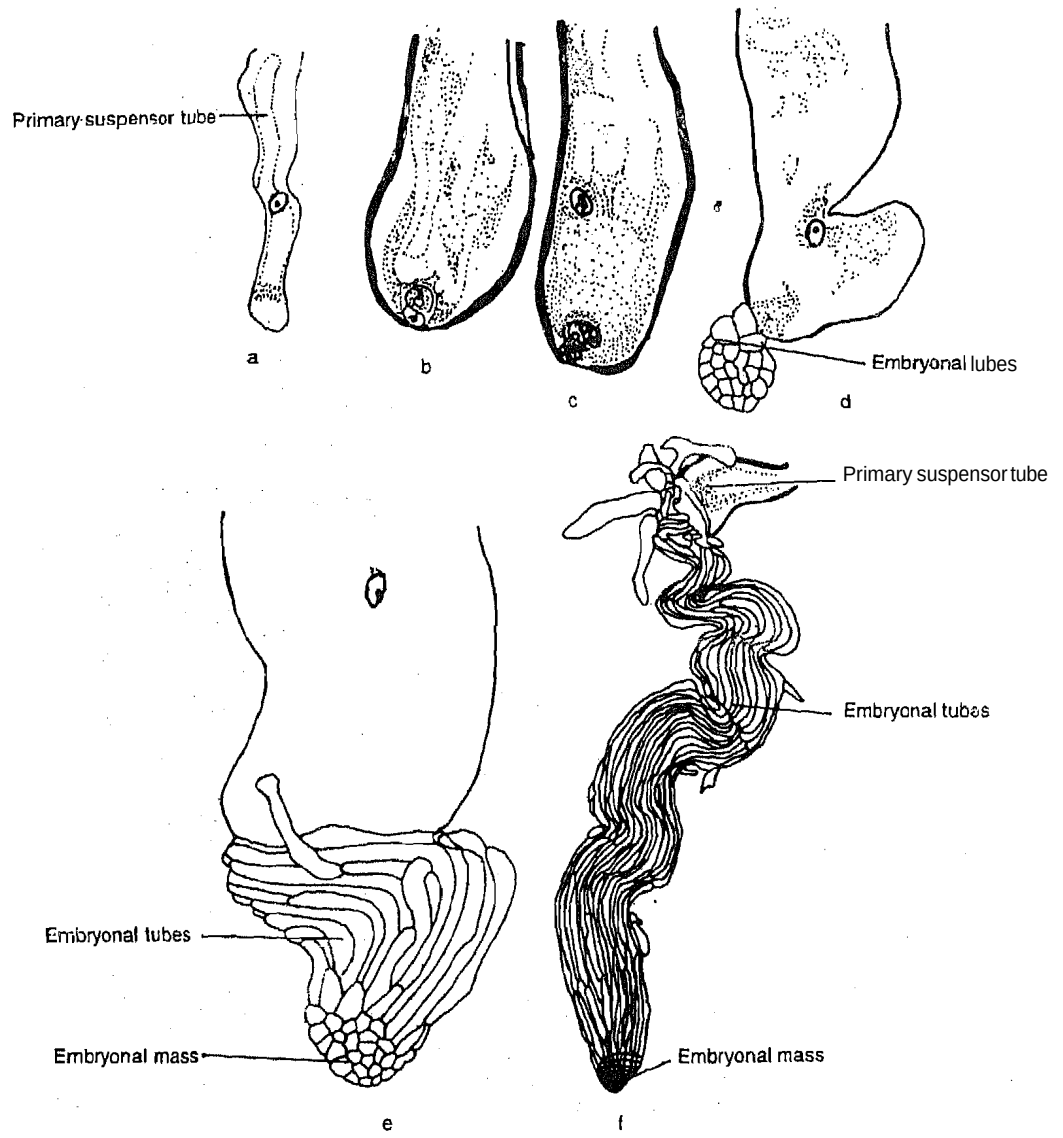

Fig. 4B.10: *Gnetum* sp. (et, embryonal tubes). a) **Tip** portion of primary suspensor tube. b, c) **Same** showing 2 **and** 8 celled stage; nucleus of primary suspensor tube Is **persistent.** d, e) Upper cells of the cellular **mass** have enlarged and undergone division to **give rise** to secondary suspensor (embryonal tubes) f) Young embryo **showing** primary **suspensor** tube with long, coiled **multicellular** secondary suspensor. A few cells of secondary suspensor have elongated to produce long tubes growing on the sides of primary suspensor tube (after Vasil 1959).

apices.This is the beginning of the so-called "feeder". It shows epidermis, cortex, vascular bundles and pith. In the mature embryo the feeder is very prominent and is generally longer **than** the hypocotyl (Fig. **4B.**11a).

Polyembryony is very common in Gnetum (Fig. 4B.1 lb). Both simple and cleavage polyembryony are recorded. The cleavage polyembryony may occur from the embryonal mass of the primary or the secondary suspensor tubes. Sometimes cells of the secondary suspensor may become meristematic and produce many **embryos at** the tip.

Endosperm : Unlike other gymnosperms where a cellular endosperm (female **gametophyte)** 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 polyploid nucleus,

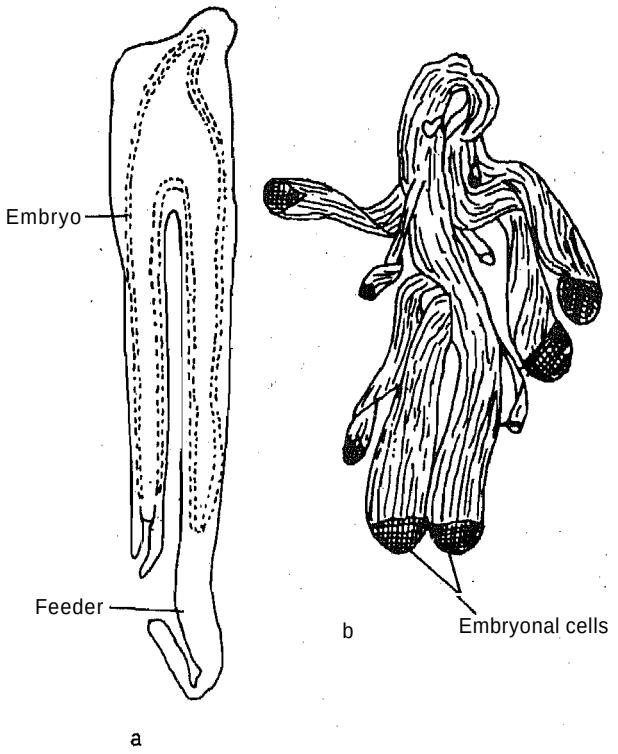

Fig. 4B.11 : *Gnetum gnemon* a) L.S. mature embryo **showing** a well developed feedrr which is much longer than the embryonal axis. The dotted lines represent **vasculature.** b) Polyembryony; note the **development** of additional embryos from **primary suspensor** tube (after **Sanwal, 1962).**

As the endosperm grows, its shape changes with the lower part becoming broader than the upper. It even overgrows **chalaza**l part. These cells undergo transverse divisions producing a distinct area called axial tissue. The upper part is gradually consumed **by** downgrowing suspensors, and later becomes compressed and crushed. The endosperm is rich in starch **and oil** droplets, and provides nutrition to the undifferentiated embryo **which** continues to grow even after the seed has fallen to the ground.

Seed : The seed in most species of *Gnetum* is oval. its colour ranging from green to red. The

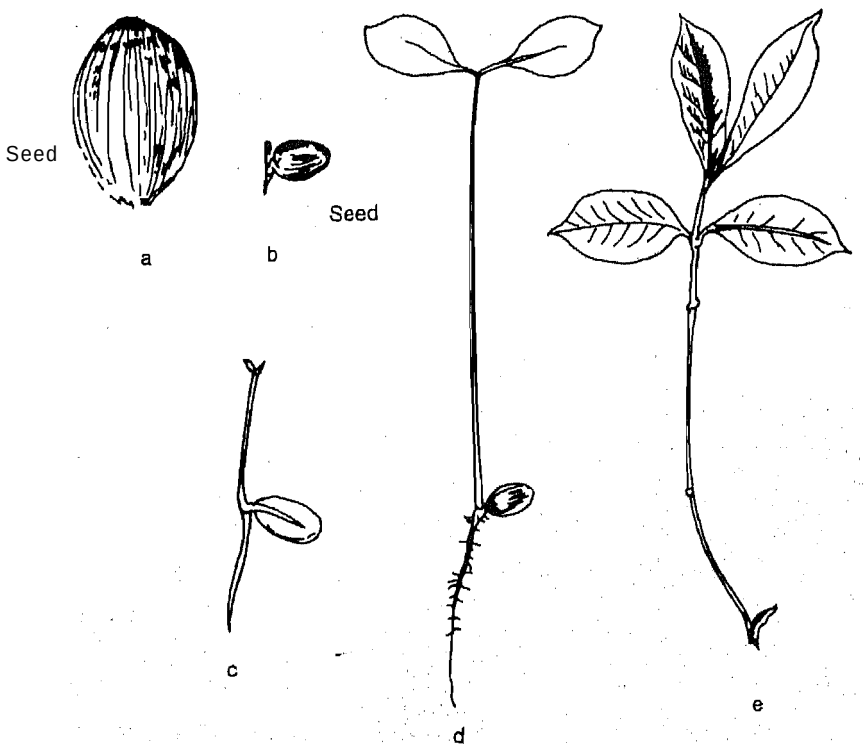

Fig. **4B.12:** a-e) Cerminrtion of seed and seedling formation in *Gnetum* **(after Maheshwari & Vasil,** 1961).

The **life** cycle of *Gentum ula* growing wild in the Western Ghats takes nearly 18 months from the time of initiation of strobilus to **seed germination.** Seeds take about **1** year to germinate after being shed. In N.E. **India** (Assam) seeds of *G gnemon* arc **shed** in June/ **July** and they **germinate** in September next year.

seeds are shed at a stage when the embryo is not fully formed. The nucellus represents a thin strip at the apex; the endosperm is massive, surrounded by a three-layered seed coat.

There is always a time lag between seed shedding and seed germination. In *G. gnemon* seeds are shed in April and germinate in September, whereas in G. *ula* they take one year to germinate. The germination is epigeal (Fig. 4B.12).

SAQ 5

State whether the following statements are true or false. Write T for true and F for false in the given bracket.

1. In *Gnetum* a coiled secondary suspensor is formed which pushes the developing embryo deep into the endosperm. [ ]
2. In *Gnetum* 'feeder' is very prominent in mature embryo and is generally longer than the hypocotyl. [ ]
3. Polyembryony is not very frequent in *Gnetum*. [ ]
4. In *Gnetum* the seed consists of a three-layered seed coat. [ ]
5. In all the species of *Gnetum*, the seed germinates after one year of shedding. [ ]

SAQ 6,

1. What is unique about fertilization in *Gnetum?*

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2. What types of polyembryony are recorded in Gnetum?

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3. Is the embryo fully mature when the seed is shed? Comment.

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4. How is the endosperm of gymnosperms different from that in angiosperms?,

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Economic Importance

Gnetum gnemon is cultivated in Malaysia and Indonesia and some other southeast Asian Islands for its edible seeds. Young leaves and inflorescence are also eaten as vegetable. The bark yields a fibre from which ropes are made. Kernels of *G. ula* yield an oil which is used in Kerala for massage in rheumatism. G. *montanum* is reported to posses piscicidal properties.

4B.7 RELATIONSHIPS

4B.7.1 Relationships with *Ephedra* and *Welwitschia*

For a long time, the order Gnetales used to include, besides ***Gnetum, Ephedra*** and *Welwitschia* also. Some of the characters which these three genera share are a) the presence of tracheids and vessels in the wood, b) the male and the female reproductive parts borne on fertile shoots resembling flowers, arranged in compound strobili, c) better protection of the ovules as compared to other gymnosperms, and d) formation of a micropylar tube by the prolongation of the integument.

The group Gnetopsida was considered to be the most evolved amongst gymnosperms approaching towards angiospermous stock. However, two basic characters, which the three genera share with other gymnosperms are a) naked ovules borne in strobili and b) absence of style and stigma, and c) pollination being totally an ovular activity.

The present day botanists, agree to split the order into three separate orders viz. Ephedrales, Gnetales and Welwitschiales, each having a monotypic family namely Ephedraceae, Gnetaceae and Welwitschiaceae. The differences between ***Gnetum*** and ***Ephedra are*** well marked. Since the genus *Welwitschia* is not fully studied, it offers only few points. Some of the major differences between *Gnetum* and ***Ephedra*** are:

Gnetum is restricted to humid tropics or subtropics, whereas ***Ephedra*** grows in ***dry*** regions and even at high altitudes. The plants of ***Ephedra*** are bushy with minute leaves showing parallel venation, whereas those of *Gnetum* are trees or lianas possessing broad "angiospermous" leaves having reticulate venation. The stem of ***Ephedra*** shows typical xerophytic characters and is assimilatory in nature, It is green due to the presence of palisade tissue in the cortical region. The stele is simple. The stem of some species of ***Gnetum,*** on the other hand, shows anomalous secondary growth.

Though both ***Ephedra*** and *Gnetum* possess vessels, there is a marked difference in the basic nature of vessels. The vessel in ***Gnetum*** has a single large perforation in the end wall, whereas in ***Ephedra,*** it has a large number of bordered pits in which middle lamella is lacking. The ovule in ***Ephedra*** originates as a terminal organ on a lateral appendage af a fertile shoot, whereas in *Gnetum* it is cauline (at the tip of the shoot ***axis)*** in nature. This morphological difference is very significant and indicates a great phyletic gap between Ephedraceae on one hand, and Gnetaceae and Welwitschiaceae on the other.

The division of cells in the pollen grains of ***Ephedra*** follows the gymnospermous plan. The pollen grains are shed at five-celled stage consisting of two prothallial cells, stalk and spermatogenous cells and a tube nucleus. In *Gnetum* the pollen grains are shed at the three-celled stage, comprising a prothallial cell, a tube nucleus and the spermatogenous cell.

The development of the female gametophyte is monosporic in ***Ephedra,*** whereas it is tetrasporic in ***Gnetum.***

The female gametophyte in ***Ephedra*** becomes cellular before fertilization takes place, whereas it is partly free nuclear in ***Gneturn*** at that stage.

A "tent pole" is present in many species of ***Ephedra*** but is absent in ***Gnetum,*** except for ***a*** rudimentary structure in *G. africanum.*

Archegonia are formed in *Ephedra,* whereas they are absent in ***Gnetum.***

4B.7.2 Relationshipswith Angiosperms

Gnetum resembles angiosperms in many respects

i) ***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.

ii) 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.

iii) The tunica and corpus arrangement of shoot apex of *Gnetum* is angiospermous. However, the presence of central mother cells is atypical gymnospennous character.

iv) The integument of the ovule in *Gnetum* elongates to form a well developed micropylar tube. Germinating pollen grains have also been found at times in the tube. The situation strongly reminds of a style of an angiosperm carpel.

v) The megasporogenesis in ***Gnetum*** is tetrasporic which is not found in gymnosperms (except ***Welwitschia)*** and is common in many angiosperms. The formation of archegonium is completely suppressed in both groups. Some free nuclei of female gametophyte act as eggs in ***Gnetum.***

vi) The storage tissue or endosperm in angiosperms develops after fertilization and is triploid (result of triple fusion). In ***Gnetum,*** though the cellularization starts prior to fertilization, it is complete only after fertilization and is haploid.

vii) The zygote does not undergo any free nuclear division.

Based on the above apparent resemblances it is regarded that angiosperms passed through some stage during the evolution which is now presently shown by ***Gnetum.*** It is thought that ***Gnetum*** has closest phylogenetic affinities to angiosperms than any other group of plants.

SAQ 7

1 Give two resemblances between ***Ephedra*** and ***Gnetum.***

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2 Why is it said that ***Gnetum*** approaches angiosperms in some respects? Give two salient features.

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4B.8 SUMMARY

The genus ***Gnetum*** is widely distributed in the tropical and subtropical parts of the world. Five species occur in India chiefly in Western Ghats and Assam. ***Gnetum*** resembles more an angiosperm than a gymnosperm. ***Gnetum*** is dioecious and the inflorescence is either solitary or a fascicled panicle. Both male and female strobili look alike when young, but as the strobili grow the distinction becomes clear. The pollen grains are shed at the 3-celled stage (prothallial, tube and spermatogonous). During megasporogenesis tetranucleate coenomegaspores are produced. The female gametophyte is tetrasporic. Several gametophytes start growing but only 2 or 3 grow beyond 16-nucleate stage. An interesting feature is the absence of archegonia. Usually two free nuclei develop into eggs. In ***G. gnemon*** two sperm nuclei are releasedin the surrounding female cytoplasm, each fusing with a separate female nucleus thus causing double fertilization, resulting in two zygotes, After fertilization, only one of the zygotes develops into embryo. Only one or two embryos reach maturity, whereas the rest degenerate. Both simple and cleavage polyembryony are recorded. The seeds are shed at a stage when the embryo is not fully formed. ***Gnetum*** shares some characters with ***Ephedra*** and ***Welwitschia,*** and some characters with angiosperms.

4B.9 TERMINAL QUESTIONS.

I. On what basis is *Gnetum* classified as a gymnosperm and not an angiosperm.

2 Is the origin of *Gnetum* well understood or is it still a puzzle? Comment.

3. **Describe the megasporangium of *Gnetum* with diagrams.**

4. **Describe the female gametophyte of Gnetum.**

5. **How does pollination occur in *Gnetum*?**

4B.10 ANSWERS

Self **Assessment** Questions

I) 1. Kerala
2. moist
3. reticulate
4. vessels
5. laticifers.

2) 1. Please refer to section **4B.3** – Subsection – Shoot apex

2. Please refer to section **4B.3** – Subsection – Stem

3. The wood of ***Gnetum*** is characterised by the presence of vessels and a single pore on their walls.

3) 1. In *Gnetum* archegonia are absent but when pollen tube makes contact with the female gametophyte, one or more nuclei in the equatorial region of the dialated part become large in size and dense staining. These are the egg nuclei whose usual number is two but, rarely, one or three nuclei may also develop into eggs.

2. Please see section 4B.5 Pollination and fertilization.

4) 1. True
2. True
3. True
4. False

5) 1. True
2. True
3. False
4. True
5. False

6) 1. In *Gnetum* double fertilization occurs resulting in two diploid zygotes. After fertilization each zygote develops into an embryo, but usually only one attains maturity in the seed.

2. Refer to section **4B.6** – Embryogeny and seed development subsection Embryo development.

3. See Subection – Embryo development.

4. Refer to section **4B.6** – Embryogeny and seed development subsection endosperm.

7) 1. Both ***Gnetum*** and Ephedra have
   i) tracheids and vessels in the wood.
   ii) male and female reproductive parts borne on fertile shoots resembling flowers, arranged in compound strobili.

2. See subsection 4B.8.2 – relationships with angiosperm.

Terminal Questions

1. The ***Gnetum*** plant externally resembles a typical dicotyledonous plant but there are several differences.
   i) The vessel is present in both angiosperms and *Gnetum* but their origin is different.
   ii) The Tunica Corpus arrangement of shoot apex of ***Gnetum*** is angiospermous. However, the presence of central mothercel Is is a typical gymnospermous character.
   iii) Endosperm is also found in ***Gnetum*** but it is haploid in nature and not triploid as in angiosperms.
   On the above given characters ***Gnetum*** is classified as a gymnosperm and not as an angiosperm.

2 See section **48.1**1 – Relationships Points for reference.
   i) its affinities both with gymnosperms as well as with angiosperms make origin of ***Gnetum*** as puzzle.

3. See section **4B.4** – Reproductive structure and subsection 4B.4.2 Gametophyte.

4. See section **4B.4** – Reproductive structures and subsection 4B.4.2. Female strobilus and gametophyte.

5. See section 4B.5 – Pollination and Fertilization.