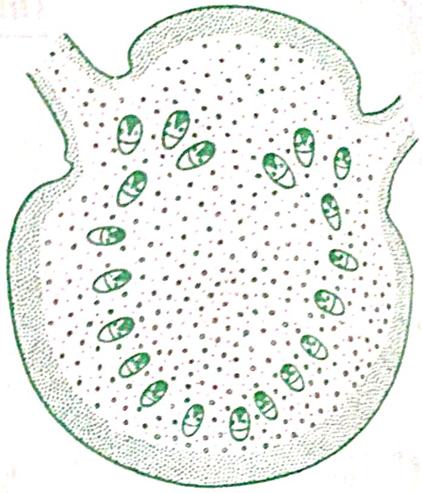
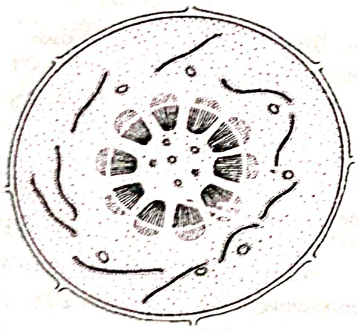
5

Cycadales: *Cycas*





The members of this order are commonly known as **cycads**. They originated from the seed ferns, i.e., Cycadofilicales, towards the end of the Carboniferous period and formed a dominant vegetation during the Triassic period of Mesozoic era. This period is also known as **'age of cycads'**. The order includes eleven living genera and about 100 species. They are usually woody trees except *Zamia pygmaea*. The stem is mostly unbranched and is covered by persistent leaf bases. The leaves are arranged in whorls at the apex of the stem; they are pinnately compound. The wood is manoxylic. The micro- and megasporophylls usually form male and female strobili (in *Cycas* the megasporophylls, however, do not form compact strobili). The male gametes are motile. Of the eleven genera, five, namely *Dioon, Ceratozamia, Zamia, Chigua* and *Microcycas* belong to the Western hemisphere, and the remaining six genera, viz. *Cycas, Macrozamia, Lepidozamia, Encephalartos, Stangeria* and *Bowenia* occur in the Eastern hemisphere.

The order Cycadales is divided into two families- Nilssoniaceae and Cycadaceae (Sporne, 1965). The former includes only fossil forms, whereas the latter has one fossil genus (*Palaeocycas*) and rest eleven living genera. In this chapter, the life-history of *Cycas* is described as the representative of the order Cycadales.

CYCAS

Systematic Position

Division	—	Cycadophyta
Class	—	Cycadopsida
Order	—	Cycadales
Family	—	Cycadaceae

Cycas is the most widely distributed genus of the order Cycadales. There are about 20 species which occur in wild state in China, Japan, Australia, Africa, Nepal, Bangladesh, Burma and India. Four species of *Cycas* — *C. circinalis, C. pectinata, C. rumphii* and *C. beddomei* — occur in natural state in India, chiefly in Assam, Orissa, Meghalaya, Andaman and Nicobar Islands, Karnataka and Tamil Nadu. *C. revoluta* and *C. siamensis* are widely grown in gardens.

Distribution and external morphology of the Indian species of *Cycas* is briefly described below.

[I] *Cycas pectinata*
It is mainly distributed in Nepal, Sikkim, Someshwar hills in Bihar and plains of Assam, Manipur, East Bengal and Chittagong. The plant is 2-3.5 m in height with a crown of leaves at the top of the unbranched stem. The leaves are 1.5-2 m long with flat and linear leaflets. The male cones are cylindric-ovoid and about 40 cm long. Each megasporophyll has 4-6 ovules.

[II] *Cycas revoluta*
It is a native of China and Southern Japan and is widely cultivated as an ornamental plant in India. It can be easily propagated by means of bulbils. The plant is 1.5-2m in height and has revolute leaflets (margins curved inwards). The male cones are cylindrical or ovoid-oblong. The tomentose megasporophyll bears 2-4 ovules.

[III] *Cycas beddomei*
It occurs in wild state in the hills of Cuddapah district of Tamil Nadu and eastern Andhra Pradesh. It has a dwarf trunk, only up to 40 cm high, and strongly revolute leaflets. The rachis is without spines, but the basal part of the rachis is covered with tufted hairs. The male cones are oblong-ovoid, and the megasporophylls are ovate-lanceolate with linear teeth.

[IV] *Cycas circinalis*
It is common in the western parts of Peninsular India, Western Ghats and Orissa hills. It is 1.5-3 m in height. The leaf has more than 160 pairs of flat and acuminate leaflets. The male cones are cylindric-ovoid and the tomentose megasporophyll bears up to 12 ovules.

[V] *Cycas rumphii*
This species occurs in Andaman and Nicobar islands. The plant is 1.5-4 m high with 1-2 m long leaves, each with 50-100 pairs of leaflets. The male cones are ellipsoidal and stalked, and the megasporophyll is linear-ovate and 6-10 ovulate.

[VI] *Cycas siamensis*
It is widely distributed in Burma, China, Thailand and Yunnan. In India, it is grown as an ornamental plant. The plant is about 3 m tall with nearly a meter long leaves. The male cones are ovoid-oblong, and the megasporophyll has two ovules.

Economic Importance

Species of *Cycas* are of considerable economic importance. Stems and seeds of several species are used for extracting starch (sago). Young succulent leaves are often used as vegetable in some parts of India, Malaya, Phillipines and Indonesia. Many species of *Cycas* are widely used in indigenous systems of medicine for the treatment of various ailments. The juice of young leaves of *C. circinalis* is used as a remedy for disorders of stomach, flatulence, blood vomiting and skin diseases. A hair wash prepared from the pounded and crushed stems of *C. pectinata* is used in Assam for the treatment of diseased hair roots. Decoction of young seeds of *C. circinalis* is purgative and emetic. A tincture prepared from the seeds of *C. revoluta* is used to relieve headache, giddiness and sore throat. Pollen grains of some species of *Cycas* are strongly narcotic, and microsporophylls of *C. rumphii* and *C. circinalis* are used as anodynes. A gum obtained from *C. rumphii* is effective in healing malignant abscesses. Leaves of *C. revoluta* are rich in nitrogen and they are used as green manure for rice, sweet potato and sugarcane.

Karyotype

Cycas circinalis, C. media, C revoluta and *C. siamensis* have similar karyotypes of 2n=22. There are 2 median-centromeric, 4 long submedian-centromeric, 4 short submedian centromeric and 12 terminal-centromeric chromosomes. Similarities of the karyotypes observed in the species of *Cycas,* suggest that speciation of the genus may have occurred without any major karyotypic change. *Cycas* thus appears to be a monophyletic group in morphological, anatomical and cytological characters (Stevenson, 1990; Kokubugata and Kondo, 1996).

SPOROPHYTE

External Morphology

Cycas is an evergreen slow-growing palm-like small tree with an average height of 1.5-3 m (Fig. 1A). It is commonly found in xerophytic habitats, such as exposed slopes of hills and other sunny places where water is scarce. It also grows well under cultivation in gardens. The sporophytic plant body is differentiated into roots, stem and leaves.

[A] Root

There are two types of roots in *Cycas*: (i) **normal tap roots,** and (ii) **apogeotropic coralloid roots**.

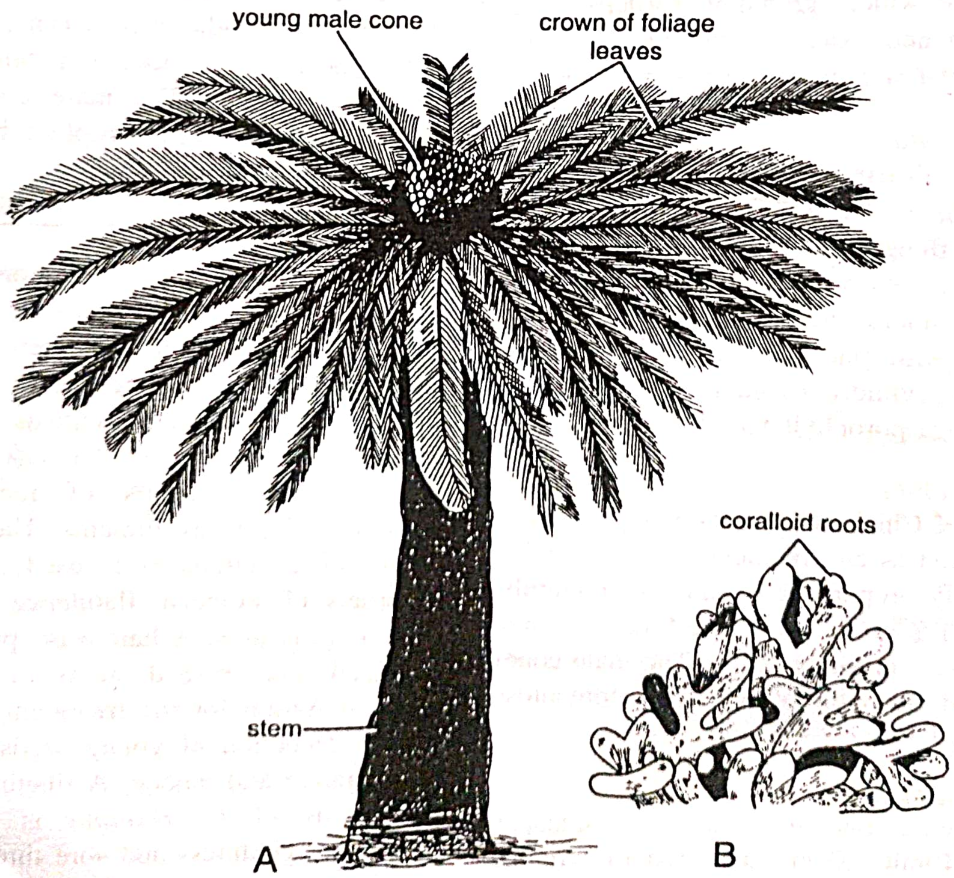


Fig. 1 A-B. *Cycas* **: A.** External morphology, **B.** Coralloid roots.

[I] Normal tap roots
Long-lived primary root forms tap root. The main tap root is usually thick and short but its lateral branches are thin and long. These roots are positively geotropic and their main function is anchorage and absorption of water and mineral nutrients.

[II] Coralloid roots
These are specialised apogeotropic roots which grow on the surface of the soil. They are repeatedly dichotomously branched and appear as coralline masses (Fig. 1B). They are more frequent on young plants. A specific algal zone with colonies of *Anabaena* and *Nostoc* or other blue-green algae is present in the cortex of these roots. The exact function of endophytic algae in coralloid roots is not known but these algae are perhaps helpful in nitrogen-fixation. The coralloid roots possess lenticels which help in respiration.

[B] Stem

The young stem is tuberous and subterranean and its apical part remains covered with brown scale leaves. In older plants, the stem becomes thick, columnar and woody. It is covered with persistent and woody leaf bases (Fig. 2). The stem is usually unbranched, but sometimes due to injury shoot apical meristem is divided into two parts and the stem appears as dichotomously branched.

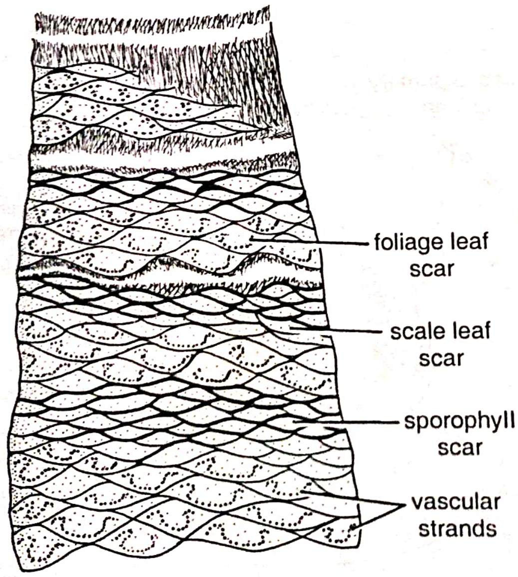


Fig. 2. *Cycas* : A part of mature stem surrounded by armour of leaf bases.

[C] Leaves

Cycas has dimorphic leaves: (i) **foliage** or **assimilatory leaves**, and (ii) **scale leaves**.

[I] Foliage or assimilatory leaves
Large, pinnately compound foliage leaves (Fig. 3A) form a crown at the top of the stem. Each leaf has 80-100 pairs of leaflets which are arranged on both sides of the rachis in opposite or alternate manner. The leaflets are sessile, elongated and ovate or lanceolate with flat (*C. rumphii*, Fig. 3B) or revolute (*C. revoluta*, Fig. 3C) margins.

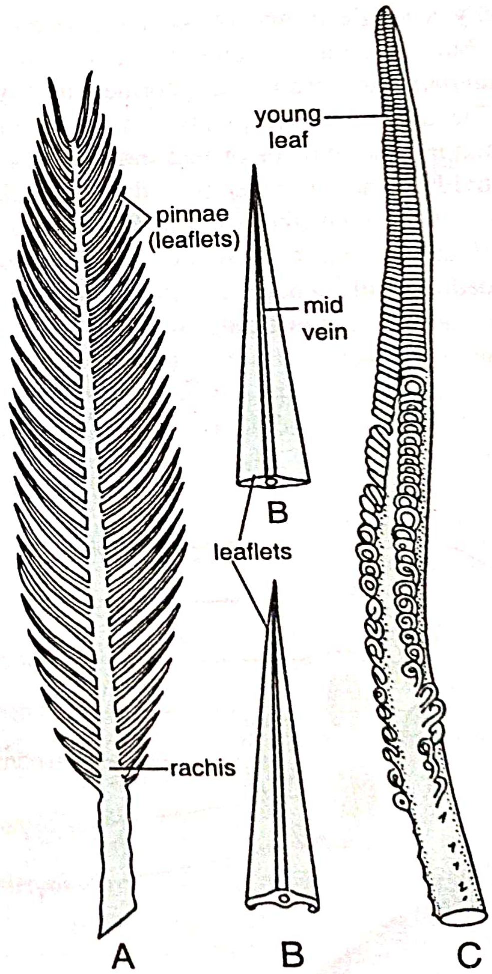


Fig. 3 A-D. *Cycas* : A. A foliage leaf, **B.** A part of leaflet of *C. rumphii*, **C.** A part of leaflet of *C. revoluta*, **D.** A young foliage leaf showing circinate vernation of leaflets.

The apex is acute or spiny. The leaflet has a single midvein; lateral veins are absent.

The rachis of a very young leaf is circinate with circinately coiled leaflets like those of ferns (Fig. 3D). The young leaves are covered with ramenta.

[II] Scale leaves

The scale leaves (cataphylls) are small, rough, dry and triangular. They are thickly covered with ramenta. They are incapable of carbon assimilation and their main function is to protect apical meristem and other aerial parts. The scale leaves also have persistent leaf bases which form part of the armour of the old stem.

The foliage and scale leaves are arranged in close alternate whorls at the apex of the stem. Usually a single crown of leaves is formed in a year but in some species (e.g., *C. circinalis*, *C. rumphii*) two crowns are formed in a year.

The age of *Cycas* plants can be determined by counting the number of leaf bases on the trunk and dividing their number by half the number of leaves in the crown (the two season's growth being present at any time). Two crowns of leaves are produced annually, one of the spring and the other during monsoon, coinciding with the favourable seasons of growth.

Internal Structure

[A] Root

[I] Normal root

Internal tissues of root are differentiated into **epiblema**, **cortex** and central **vascular tissue** (Fig. 4).

Epiblema is composed of a single layer of thin walled cells. Some cells of epiblema give rise to hairs.

Cortex is a multilayered zone of thin-walled parenchymatous cells which are filled with starch. Some tannin cells and mucilage cells are also present in this region. The innermost layer of the cortex forms **endodermis**. The endodermal cells are characterized by the presence of casparian bands.

Pericycle is multilayered and consists of parenchymatous cells.

Vascular tissue forms a central **diarch** stele. The xylem is exarch and tracheids of the protoxylem have spiral thickenings and those of the metaxylem scalariform thickenings. The **pith** is reduced or completely absent.

The mature normal root shows secondary growth which starts by the formation of cambium strips inner to the primary phloem strands. These

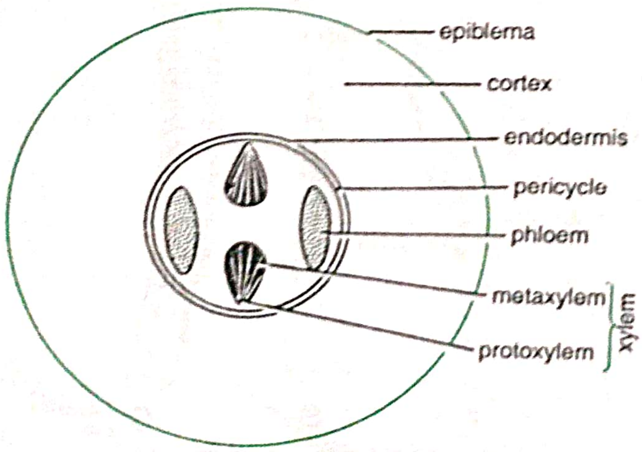


Fig. 4. ***Cycas*** **:** Diagrammatic representation of transverse section of normal young root.

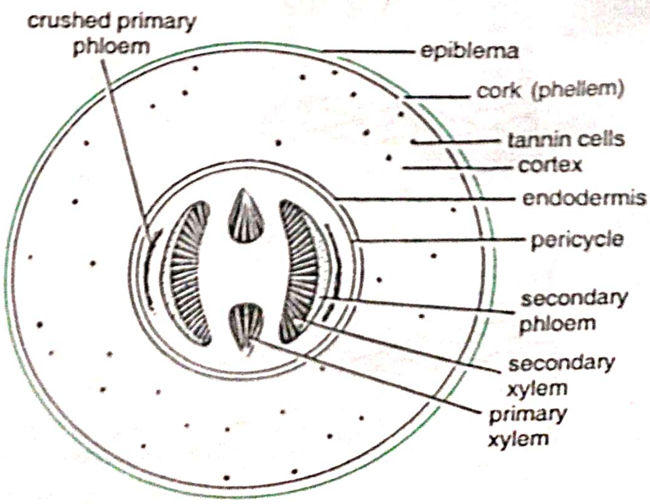


Fig. 5. ***Cycas*** **:** Diagrammatic representation of transverse section of normal old root.

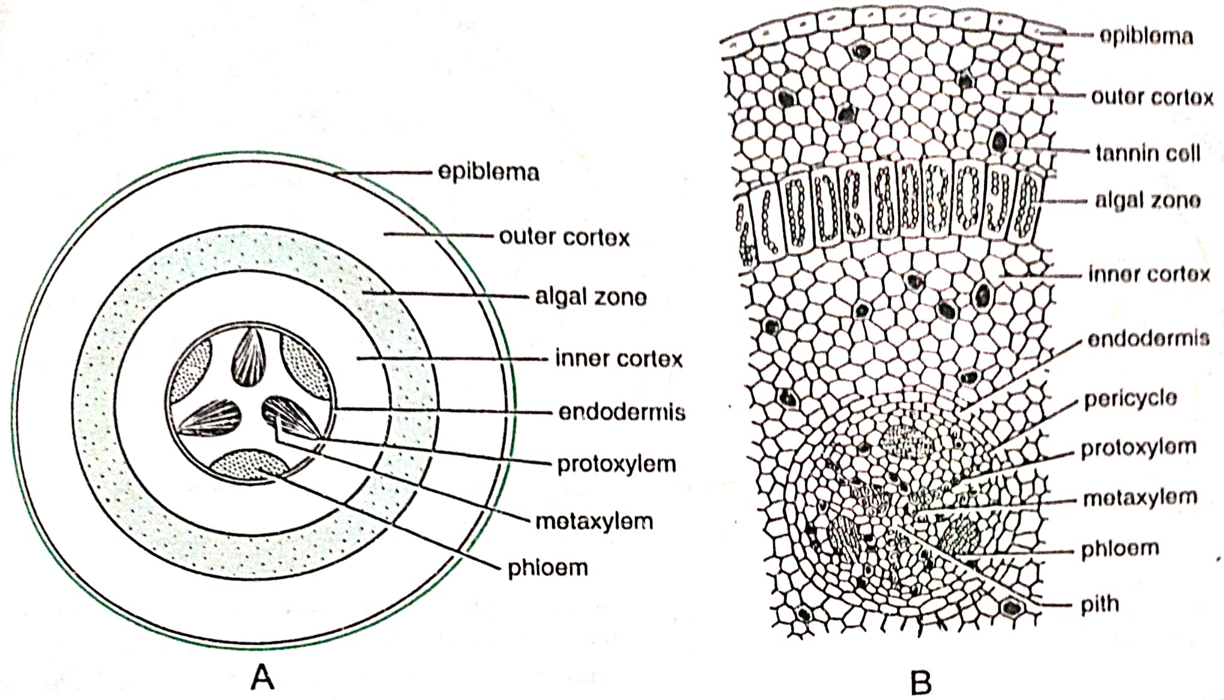


Fig. 6 A-B. *Cycas* : Coralloid root; A. Diagrammatic representation of transverse section, **B.** A part showing cellular details.

cambium strips cut off secondary phloem towards the outer side and secondary xylem towards the inner side. The secondary xylem is manoxylic with abundant multiseriate rays. The tracheids show scalariform and pitted (bordered pits) thickenings. Due to the pressure of secondary tissues, the primary phloem is crushed but the primary xylem can be seen in the centre of the stele (Fig. 5). A distinct layer of phellogen or cork cambium arises in the outer region of the cortex which gives rise to cork (phellem) on its outer side and phelloderm or secondary cortex on its inner side. Phellem, phellogen and phelloderm are collectively known as periderm. Due to the development of periderm, epiblema is ruptured.

[II] Coralloid root

The internal structure of coralloid roots is similar to that of normal roots. But in coralloid roots cortex is differentiated into three distinct regions: (i) **outer cortex**, composed of compact polygonal cells, (ii) **inner cortex** of thin walled parenchymatous cells, and (iii) **middle cortex** which forms algal zone. The algal zone consists of a single layer of loosely connected thin walled and radially elongated cells. In the algal zone blue-green algae, such as *Anabaena cycadae, Nostoc punctiforme* and *Oscillatoria* spp. occur which live symbiotically. Besides, some fungi and bacteria (e.g., *Pseudomonas, Azotobacter*) are also found in this zone. Development of the algal zone in the coralloid roots takes place after the entrance of endophytic algae. According to some investigators, presence of algal zone is not a universal character of coralloid roots. Coralloid roots show little or no secondary growth (Fig. 6A, B).

In some species of *Cycas*, viz. *C. circinalis, C. revoluta* and *C. rumphii*, non-coralloid aerial roots are found. These roots are positively geotropic, adventitious and grow out from the lower sides of the bulbils or leaf bases. These roots are di- to polyarch, and show a wide cortex and a mixed parenchymatous pith with scattered xylem elements. The older roots exhibit fair amount of secondary growth, showing unusually branched xylem elements. The characteristic algal zone of coralloid roots is, however, absent in these roots.

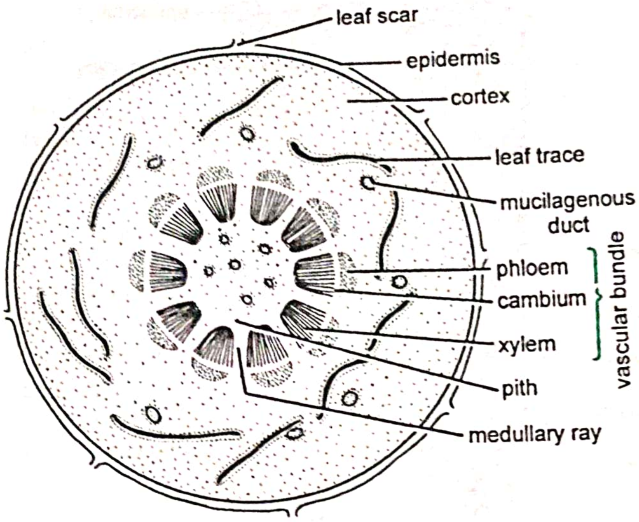


Fig. 7. ***Cycas*** **:** Diagrammatic representation of transverse section of young stem.

[B] Stem

[I] Young stem

The stem is irregular in outline due to the presence of numerous persistent leaf bases. Its internal structure is similar to that of a dicotyledonous stem. It is differentiated into epidermis, cortex and vascular cylinder (Fig. 7).

Epidermis is the outermost layer, covered with a thick cuticle. It is usually discontinuous due to the presence of persistent leaf bases.

Cortex forms the major part of the stem and it is composed of parenchymatous cells, rich in starch grains. The cortex is also traversed by several mucilagenous canals and many leaf traces. The inner wall of the mucilagenous canals is made up of radially elongated secretory cells.

The innermost layer of the cortex is **endodermis** and it is followed by **pericycle**. However, both endodermis and pericycle are indistinct.

In the young stems, the **vascular cylinder** is very small in comparison to the cortex. There are several vascular bundles arranged in a ring, forming an **ectophloic siphonostele.** The vascular bundles are conjoint, collateral, endarch and open. The individual bundles are separated by parenchymatous medullary rays. The **xylem** is composed of tracheids and xylem parenchyma only; vessels are, however, absent. The tracheids of protoxylem have spiral thickenings, whereas those of metaxylem, scalariform thickenings. The phloem is composed of sieve cells and phloem parenchyma; companion cells are absent.

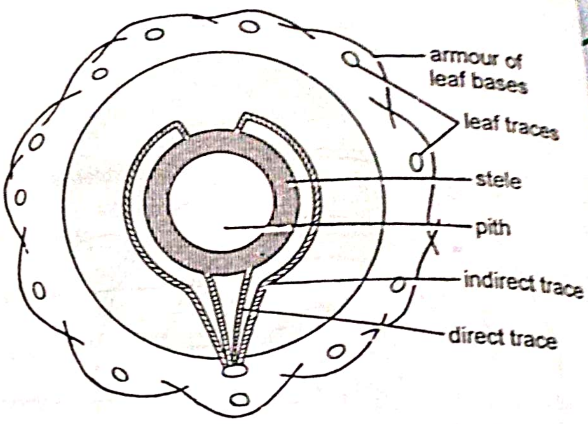


Fig. 8. ***Cycas*** **:** Transection of stem showing the course of leaf traces.

In a transection of stem, numerous leaf traces can be seen in the cortical region. They are vascular strands which supply the leaves. Each leaf receives four leaf traces (Fig. 8). Of these, two arise on the same side as the leaf and they enter directly into the leaf. These traces are known as **direct (or radial) traces**. These traces choose a straight course through the cortex. At times traces of other leaves, which are passing through the cortex join. The other two arise opposite the leaf and enter the leaf after turning around the vascular cylinder. These traces as such form a girdle around the vascular cylinder, hence they are called **girdle traces**. The two girdle traces, after joining with radial traces and branches of other girdle traces enter the leaf as its two main bundles. All these bundles exhibit endarch protoxylem and the metaxylem elements are centrifugally placed.

Mucilage canals are common throughout the plant body. They are lined with epithelial cells. The mucilage is first formed in the cells of the epithelial layer and is subsequently secreted into the canal.

There is a parenchymatous **pith** in the centre of the stem. The pith cells are rich in starch, and several pith cells also contain tannins and mucilagenous substances.

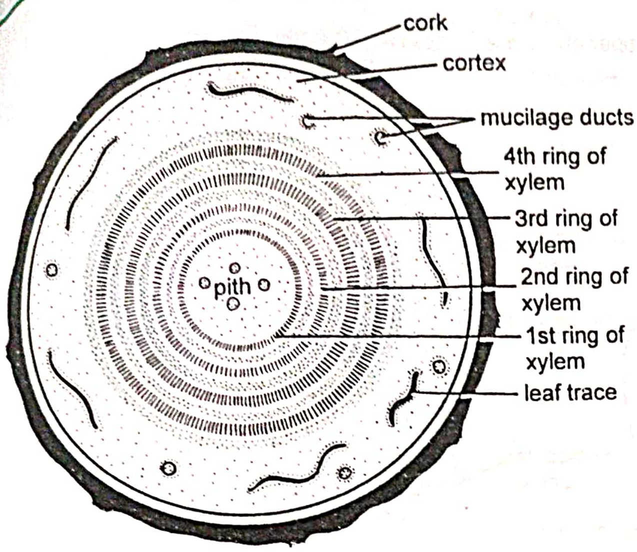


Fig. 9. ***Cycas*** **:** Diagrammatic representation of transverse section of mature stem.

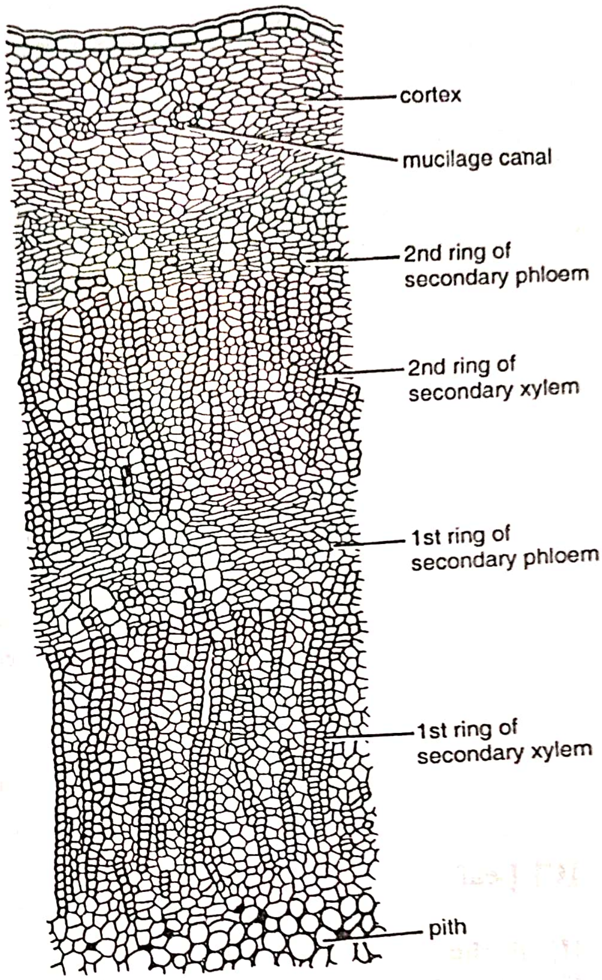


Fig. 10. ***Cycas*** **:** A part of transverse section of mature stem.

[II] Secondary growth

The stem of *Cycas* shows normal secondary growth in early stages, similar to that of a dicotyledonous stem. Interfascicular cambium strips developed between the two vascular bundles join with intrafascicular cambium strips and as such a complete ring of cambium is formed. This cambial ring cuts off secondary xylem on the inner side and secondary phloem on the outer side. Multiseriate bordered pits are present on the walls of the secondary xylem.

In a longitudinal section, the individual sieve elements show numerous sieve areas on their radial walls. The sieve areas, arranged in a scalariform or reticulate manner, constitute the compound sieve plate characteristic of the gymnosperms. There are no companion cells, instead certain phloem parenchyma cells, termed as albuminous cells, are found closely associated with the sieve cells.

In addition to secondary vascular tissue, the cambium also forms well developed parenchymatous medullary rays.

The ray cells and cortex are full of starch. Calcium oxalate crystals also occur frequently.

The cambial ring remains functional only for a short time and thereafter its activity ceases. It is succeeded by another cambium, formed independently in the pericycle or the inner layers of the cortex. The new cambium like old cambium forms secondary xylem towards the inner side and secondary phloem towards the outer side. This cambium also becomes inactive after sometime, and is superseded by another cambial ring formed in a similar fashion. In *C. pectinata*, as many as 20 rings of cambium may be formed. Thus the young stem of *Cycas* which is monoxylic becomes polyxylic later on (Figs. 9, 10). Extrastelar secondary growth takes place by the formation of phellogen (cork cambium), which forms phelloderm (secondary cortex) on the inner side and phellem (cork) on the outer side.

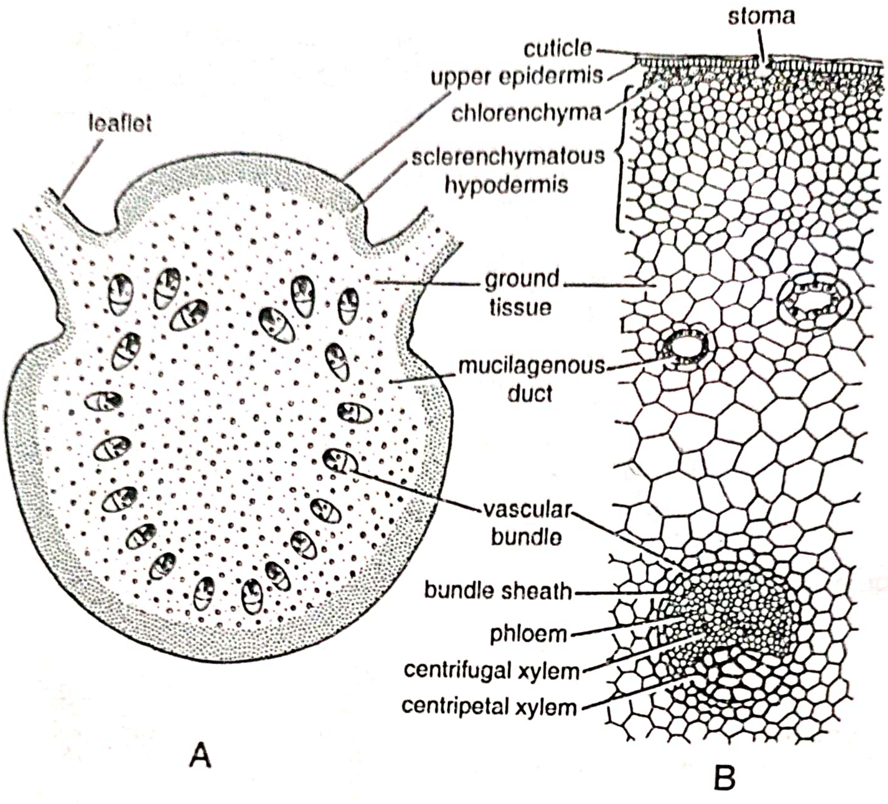


Fig. 11 A-B. ***Cycas*** **: Rachis; A.** Diagrammatic representation of transverse section, **B.** A part showing cellular details.

[C] Leaf

[I] Rachis

In a transverse section rachis is circular in outline. It has two rows of leaflets inserted on the adaxial side. The rachis is differentiated into epidermis, hypodermis, ground tissue and vascular tissue (Fig. 11 A, B).

The outermost layer forms **epidermis**; it is covered with a thick cuticle. The epidermis is interrupted by sunken stomata; each stoma consists of two guard cells and two subsidiary cells. The epidermis is followed by **hypodermis** which is composed of two types of cells. The outer 2-3 layers are composed of thin-walled chlorenchymatous cells and the next 4-5 of sclerenchymatous cells. There are only 2-3 layers of sclerenchymatous cells on the adaxial side of the rachis.

Next to hypodermis is parenchymatous **ground tissue** with many mucilage canals.

The vascular bundles show an interesting behaviour. The two bundles which enter the leaf base from stem are endarch. These bundles then split into many branches soon after their entry. Thus, there are several vascular bundles in the ground tissue and they are arranged in a typical **inverted omega-like arc**. The vascular bundles are conjoint, collateral and open, and each is surrounded by a single layered bundle sheath, composed of thick-walled cells. They are **diploxylic**, i.e., they have both centrifugal and centripetal xylem (Fig. 12 A, B).

The arrangement of xylem and phloem differs in vascular bundles in the basal, middle and upper regions of the rachis (Fig. 13A). The vascular bundles in the basal region have only centrifugal xylem (Fig. 13B). The protoxylem in these bundles lies towards the centre of the rachis, i.e., they are endarch in nature. A little higher up centrifugal xylem is reduced; only a few protoxylem elements remain endarch and the rest begin to move in lateral directions (Fig. 13C). In the middle of the

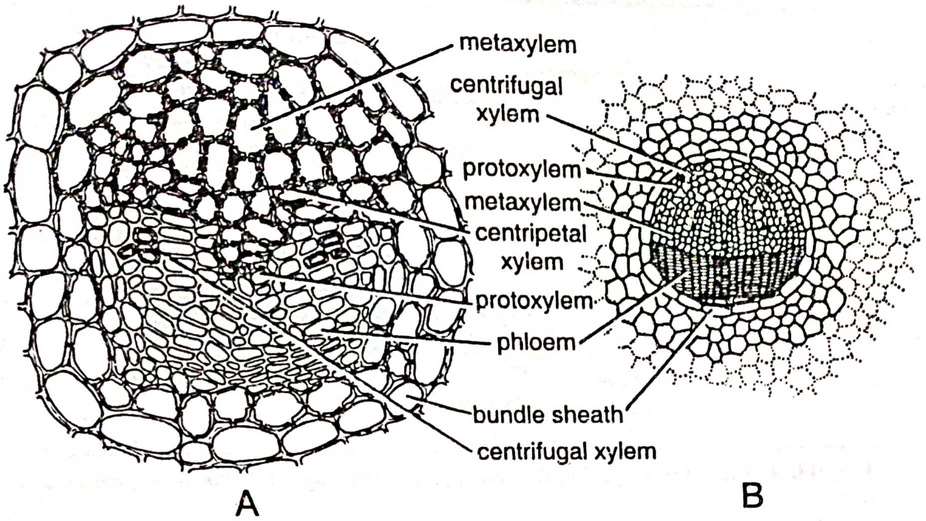


Fig. 12 A-B. *Cycas* : Vascular bundles; **A.** Vascular bundle with both centrifugal and centripetal xylem, **B.** Vascular bundle with only centrifugal xylem.

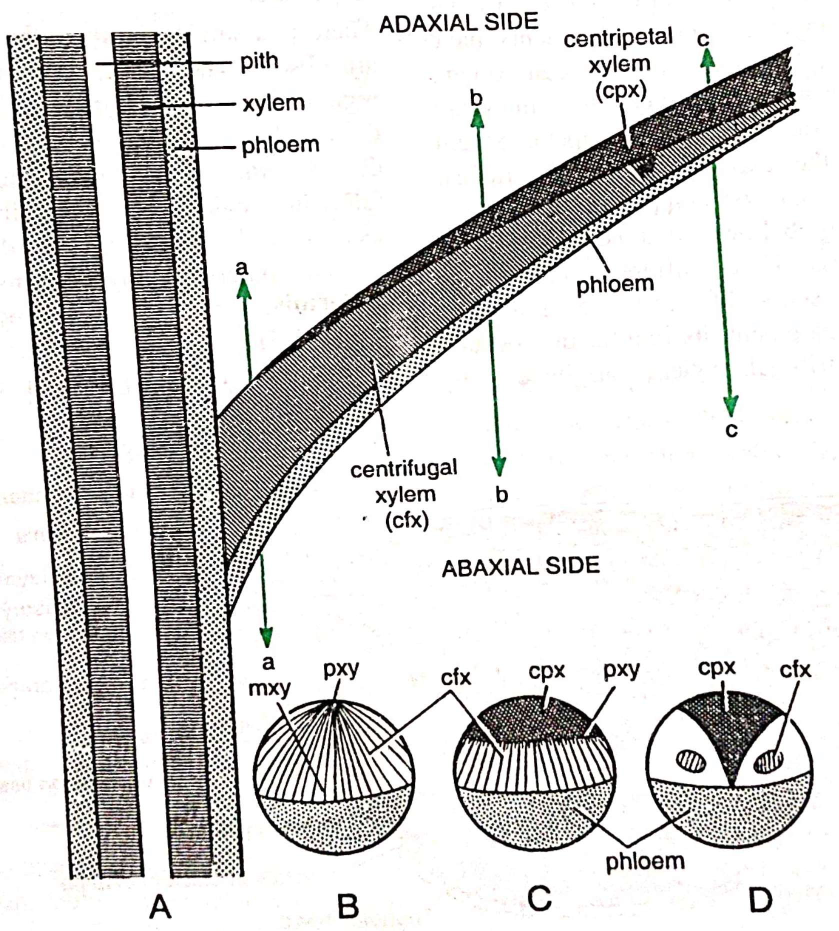


Fig. 13 A-D. *Cycas* : Anatomy of rachis; A. Longitudinal section of stem and rachis, **B-D.** Vascular bundles at different heights in the rachis (a-a, b-b, c-c, cfx-centrifugal xylem, cpx-centripetal xylem, mxy-metaxylem, pxy-protoxylem).

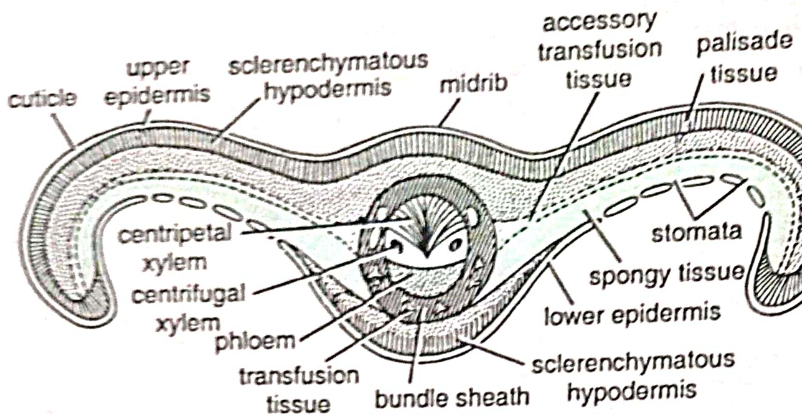


Fig. 14. *Cycas revoluta* **:** Diagrammatic representation of vertical section of a leaflet.

rachis, groups of thick walled cells develop just behind the protoxylem elements and these finally differentiate into centripetal xylem. The vascular bundles in the upper region of the rachis have more centripetal xylem than the centrifugal xylem. At this stage, centrifugal xylem lies in small groups on both sides of the centripetal xylem (Fig. 13D). At the extreme tip of the rachis, centrifugal xylem may be completely absent.

It is generally believed that centrifugal and centripetal xylems have different origin — centripetal xylem starts differentiating at a very early stage of development, its lignification occurs slowly, but centrifugal xylem originates by secondary growth.

[II] Leaflet

There is a single midrib in the leaflet; lateral veins are absent. The leaflet is swollen in the mid-rib region. The margins of the wings are revolute in *C. revoluta* and *C. beddomei* and straight in *C. circinalis, C. pectinata* and *C. rumphii.* The following regions are discernible in a transverse section of the leaflet (Figs. 14,15).

The outermost layer forms one-celled thick **epidermis**, which is covered by a thick layer of cuticle. The upper epidermis is continuous, whereas the lower epidermis is interrupted by

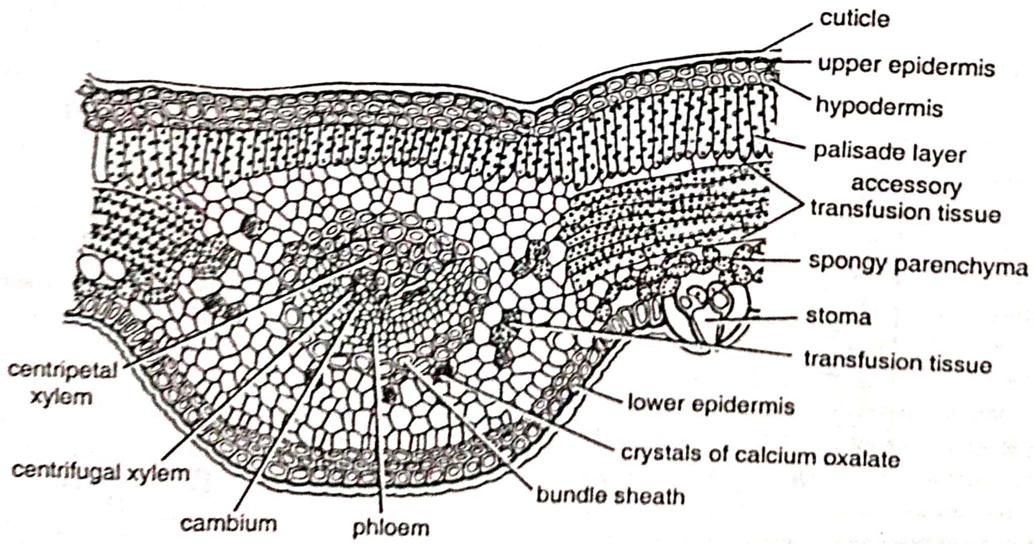


Fig. 15. ***Cycas*** **:** Vertical section of leaflet.

sunken haplocheilic stomata, which are confined to the wings. The stomata possess a crater-like appearance. The two guard cells lie at the bottom of the crater and between them is the slit-like pore. The guard cells are bordered by 8-10 subsidiary cells arranged in a ring-like manner. In later stages these are not easily distinguishable from the rest of the epidermal cells.

The epidermis is followed by a layer of sclerenchymatous **hypodermis**. The hypodermis forms a continuous layer on the dorsal surface but on the ventral surface it is confined only to the mid-rib region. In *C. revoluta,* however, hypodermis is also present in the wings. The hypodermis serves as a screen and protects the plant from over-heating and excessive transpiration.

Next to hypodermis, there is a well developed **mesophyll** which is differentiated into palisade and spongy parenchyma. The **palisade** is a single continuous layer of columnar cells. The **spongy parenchyma** consists of several layers of loosely arranged oval or irregular cells that are confined to the wings. The cells of both the palisade and spongy parenchyma are rich in chloroplasts.

There are groups of tracheid-like cells on the lateral sides of the vascular xylem in the mid-rib region. These cells are small and broad and have reticulate thickenings or bordered pits on their walls. They represent **transfusion tissue.** In the wing region long colourless and transversely elongated parenchyma cells are present in between palisade and spongy parenchyma. They represent **secondary** or **accessory transfusion tissue.** The secondary transfusion tissue is connected with centripetal xylem, abutting on the bundle sheath. Since lateral veins are lacking in *Cycas,* accessory transfusion tissue helps in lateral conduction of water and nutrients.

A single **vascular bundle** is present in the midrib region. It is surrounded by a parenchymatous bundle sheath. The vascular bundle is conjoint, collateral, open and diploxylic. It has a large and triangular centripetal xylem and two small groups of centrifugal xylem, one on either side of the centripetal protoxylem. Phloem is present on the adaxial side of the xylem. It is composed of parenchyma and sieve tubes. A thin layer of cambium is present between the xylem and phloem.

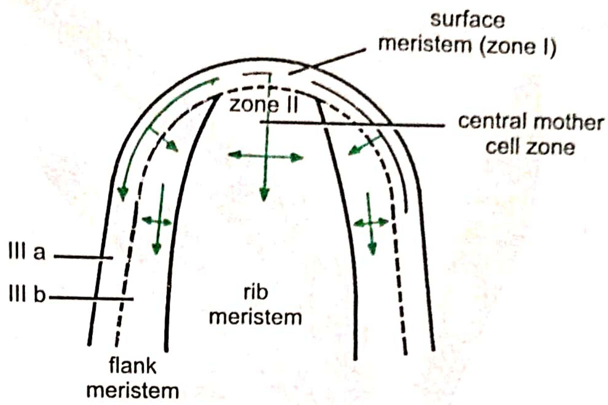


Fig. 16. ***Cycas*** **:** Shoot apex organization.

Shoot Apex Organization

The shoot apex shows variation in shape from a low mound to an almost flat plateau. Three major zones of tissue (Zones I, II and III) can be recognised in the shoot apex (Fig. 16). Zone I (surface meristem) appears as a shallow cap of thin-walled small cells at the summit of the apex. It does not show any recognizable apical initials and all its surface cells are morphologically similar. The cells of this zone divide anticlinally, periclinally and diagonally. They give rise to epidermis and other apical meristematic zones. Zone II (central mother cell zone) consists of large, highly vacuolated cells and has its origin from the innermost cells of zone I. Zone III (flanking zone) is divisible into an outer peripheral region (zone IIIa) and an inner region (zone IIIb). The peripheral region shows several irregular layers of very small deeply stained cells, which are derived from the peripheral edges of the surface meristem (zone I). The cells of this zone divide both periclinally and anticlinally. The cortex, procambium and leaf primordia develop from this zone. The inner region (zone IIIb) consists of larger cells derived by anticlinal or oblique divisions in the peripheral cells of zone II. In the upper region of this zone vertical rows of cells are obvious. These differentiate basipetally into pith cells.

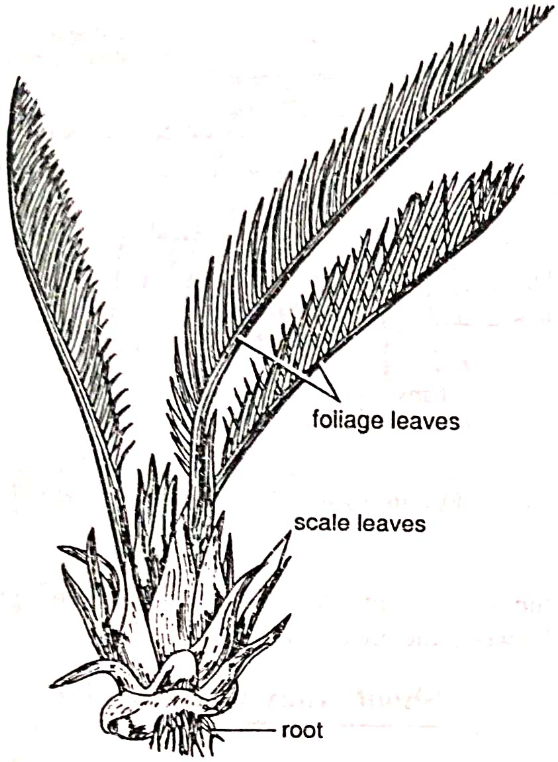


Fig. 17. ***Cycas*** **:** A bulbil.

Reproduction

Cycas reproduces by **vegetative** and **sexual** means.

[A] Vegetative Reproduction

Vegetative propagation takes place by **adventitious buds** or **bulbils.** They develop in the basal part of the stem from parenchymatous cells of the cortex, in the crevices between persistent leaf bases. The decurrent base of the bulbil is covered with scale leaves and a few foliage leaves develop from its centre (Fig. 17). It is a common method of propagation in *C. revoluta,* as male plants of this species usually donot occur in Northern India and in their absence sexual reproduction is not possible. Bulbils formed on male plants give rise to male plants and those developed on female plants form female plants.

In *C. circinalis,* vegetative propagation takes place by suckers which develop from the roots. They grow horizontally in the ground for some distance and then form new plants.

[B] Sexual Reproduction

Cycas is a heterothallic plant; the male and female gametophytic phases develop from two different kinds of spores. The male gametophyte develops from microspore and the female from megaspore. The micro- and megaspores are formed in microsporangia and megasporangia respectively.

Species of *Cycas* are strictly **dioecious** and either male cones or megasporophylls are formed on a plant. In India, most of the plants of *C. circinalis* are male and those of *C. revoluta* are female.

[I] Male strobilus

The male strobilus (cone) develops at the apex of the stem in between the crown of foliage leaves

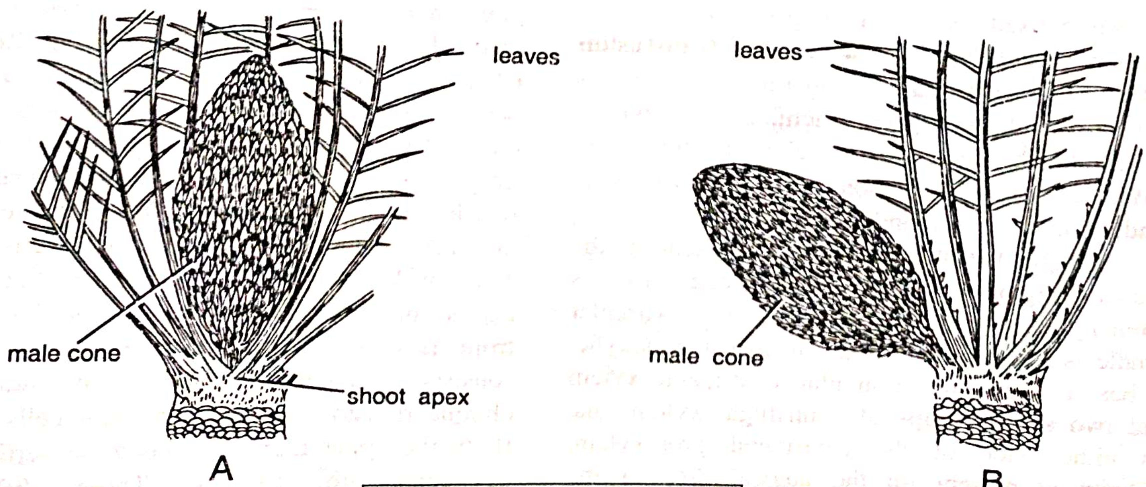


Fig. 18 A-B. ***Cycas*** **:** Male cones.

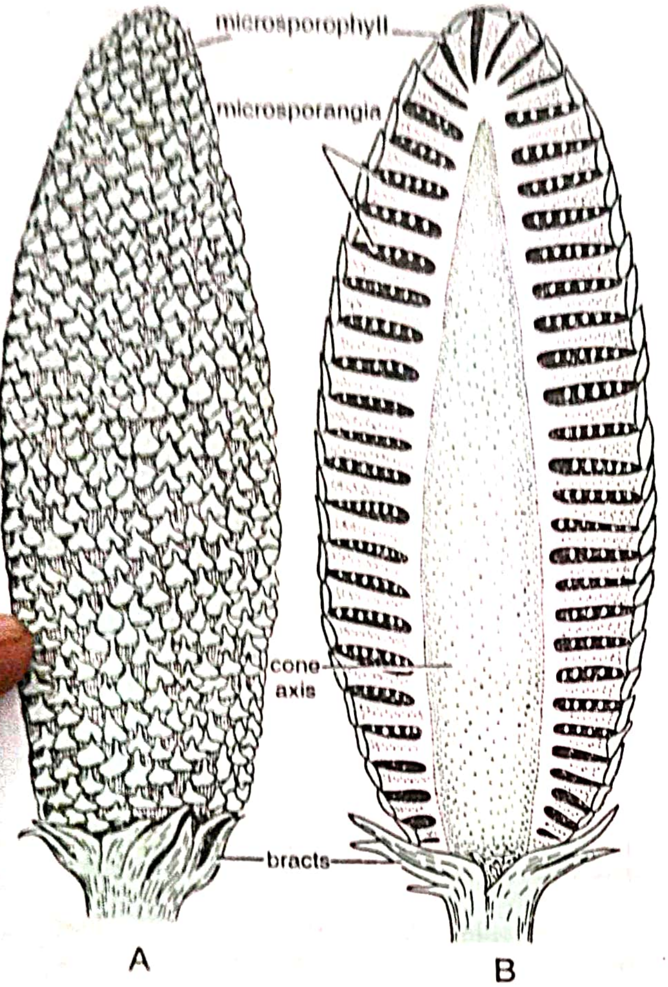


Fig. 19 A-B. *Cycas* : Male cone; A. Entire, B. Longitudinal section.

(Fig. 18A). In its development apical meristem of the stem is utilised and as a result the future stem becomes sympodial (Fig. 18B).

The male cone is a shortly stalked, compact, oval or conical woody structure (Fig. 19A). It is 40-80 cm in length, perhaps the largest amongst the plant kingdom.

The male cone consists of several microsporophylls which are arranged spirally around a central cone axis (Fig. 19B). The microsporophyll is a woody, more or less horizontally flattened and nearly triangular structure. Each microsporophyll is parenchymatous, has a hairy epidermis, stomata are present mainly on the lower surface, and numerous vascular bundles and mucilage ducts traverse through it. A mature microsporophyll is differentiated into a proximal wedge-shaped fertile part which expands distally from a narrow point of attachment and a distal sterile part, tapering into an upcurved apophysis (Fig. 20 A,B). The upper (abaxial) surface of the fertile part of the microsporophyll is sterile, while on the lower (adaxial) surface there are 700-1,000 microsporangia, arranged in definite groups, known as **sori**. There are 3-6 microsporangia in a sorus, arising from a central **indusial papilla** (Fig. 20C). Many delicate hairs are also present on the surface of the

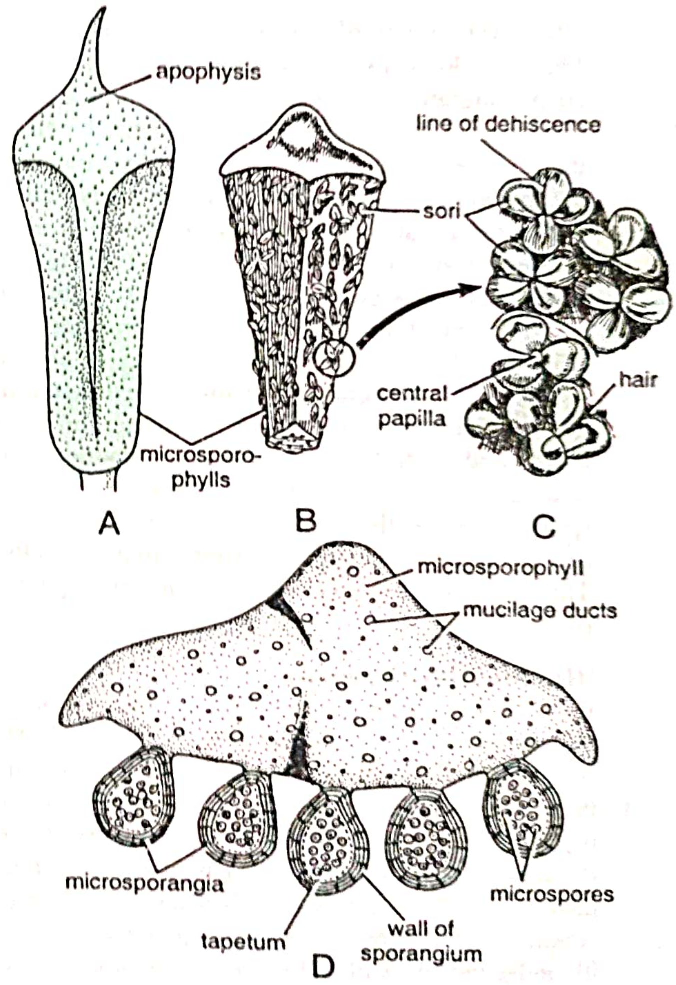


Fig. 20 A-D. *Cycas* : Microsporophyll; A. Adaxial surface, B. Abaxial surface, C. Sori, D. Transverse section of microsporophyll.

microsporophyll amongst sporangia. They protect young sporangia and perhaps also help in dissemination of microspores.

The microsporangia are sessile or are attached to the lower surface of the microsporophyll by a very short stalk (Fig. 20D). The wall of the microsporangium is differentiated into three regions- an outer **exothecium**, consists of thick-walled and cutinized cells; a middle **endothecium**, made up of 3 or 4 layers of thin walled cells; and an inner nutritive **tapetum**, which mostly consists of small cells with large nuclei and thick granular cytoplasm. There are a very large number of microspores in a sporangium.

[II] Development of microsporangium

The development of microsporangium is of **eusporangiate** type, i.e., it develops from a group of initials (Fig. 21A). Each hypodermal cell of the lower fertile surface of the sporophyll functions as **sporangial initial**. It divides by a periclinal wall into an outer **primary wall cell** and an inner **archesporial cell** (Fig. 21 B). The former undergoes repeated periclinal and anticlinal divisions and forms a 5-6-layered sporangial wall (Fig. 21 C, D). The outermost layer of the sporangial wall forms **epidermis** or **exothecium**. The cells of this layer have thickenings on their inner and radial walls. The archesporial cell undergoes several irregular divisions to form **sporogenous cells**. These cells increase in size and eventually function as **spore mother cells**. They are the ultimate cells of the sporophytic phase.

[III] Microsporogenesis

Each spore mother cell forms four haploid **microspores** by a reduction division (Fig. 21 E). After meiosis I, a ring-like thickening appears on the callose wall of the mother cell in the equatorial plate. Usually, the wall laid down after meiosis I is thicker than the one which develops after meiosis II. The cytoplasm of each microspore contracts and secretes a membrane which forms its independent wall. Thus, each member of a tetrad is contained within its own chamber. The original wall of the mother cell is, however, collapses and no trace is left after a week of division.

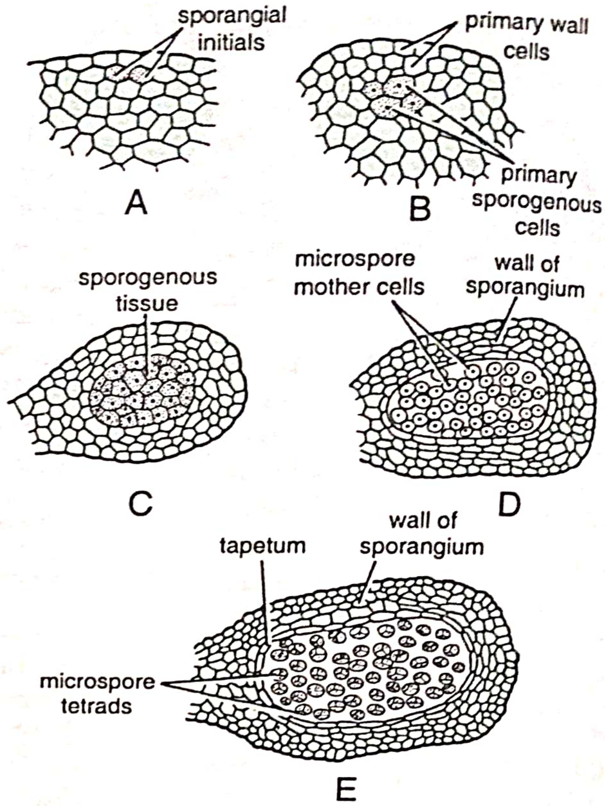


Fig. 21 A-E. ***Cycas*** **:** Stages in the development of microsporangium.

As the sporangium matures, the innermost layer of the sporangial wall or the outermost layer of the sporogenous tissue differentiates into **tapetum**. The tapetum provides nourishment to the developing microspores.

[IV] Dehiscence of microsporangia

With the maturation of microspores the axis of the male strobilus elongates. This results in separation of microsporophylls and the groups of sporangia present on their dorsal surface are thus exposed. The walls of the exposed sporangia dry up and break at the line of dehiscence thus releasing the microspores. The lines of dehiscence of sporangia are radial to the indusial papilla. The cells of the axis of mature strobilus lose turgidity and as such conduction of water is hampered. The microsporophylls thus become hard and shedding of microspores starts from the top most sporophylls and proceeds towards the base.

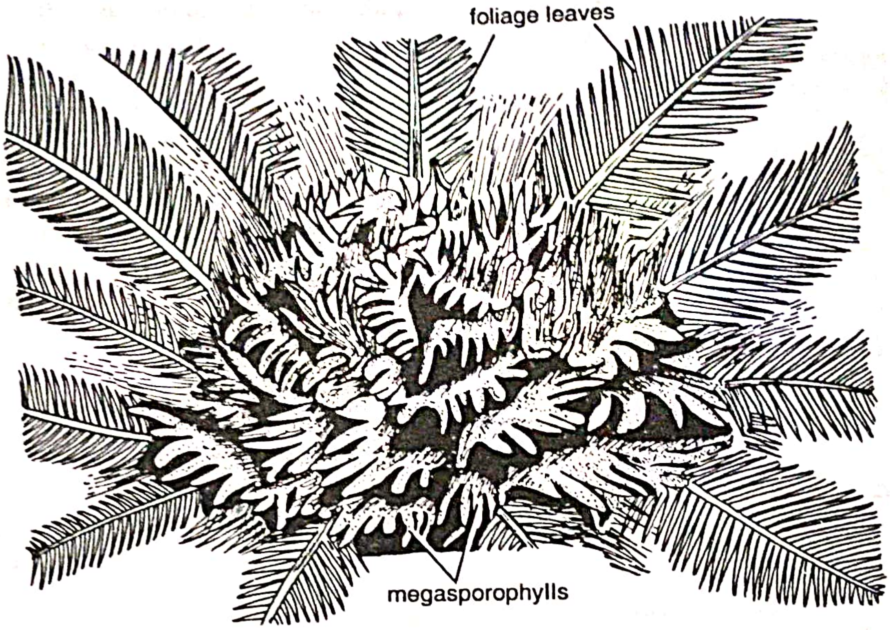


Fig. 22. ***Cycas*** **:** Apex of the stem with a group of megasporophylls.

[V] Microspores (Pollen grains)

The **microspores** (pollen grains) are globular, uninucleate and haploid structures and show an oval germinal furrow on its distal face. The spore wall is differentiated into an outer **exine** and an inner **intine**. The exine is uniformly thickened, whereas the intine is thickened only at the two opposite poles.

According to Gullvag (1996), in *C. revoluta*, the exine is made up of two layers. The outer one comprises orbicules and/or a sculptured granular layer, while the inner layer is lamellated.

[VI] Female reproductive structures

The megasporophylls of *Cycas* are not organized into cones and instead they occur in close spirals in acropetal succession around the stem apex of the female plant (Fig. 22). New megasporophylls are produced every year like the foliage leaves. They are produced in larger numbers than the foliage leaves. The megasporophylls of a year occupy position between the successive whorls of foliage leaves. The growth of the apical meristem of the female plants is monopodial; the axis continues to grow as if produces foliage leaves and megasporophylls.

The megasporophylls are considered to be modified leaves. They are flat and dorsiventral structures, measuring 15-30 cm in length. A **megasporophyll** is differentiated into a **basal stalk** and an **upper pinnate lamina.** Ovules are formed on the lateral sides of the stalk. The number of ovules varies from 2-10, depending on the species. There is a great variation in the structure of megasporophylls in various species. The species of *Cycas* can be identified on the basis of number of ovules and the structure of megasporophylls.

In various species there is a gradual reduction in the expanded part of the sporophylls. The megasporophyll of *C. revoluta* is 10-25 cm in length. The lamina of the sporophyll is very much dissected and tapers into a point. There are 2-4 ovules arranged in two lateral rows on the stalk. The megasporophyll is covered by a felt of brown hairs (Fig. 23A). In *C. circinalis,* the megasporophylls are ovate to lanceolate with dentate margins and acuminate apices. They are

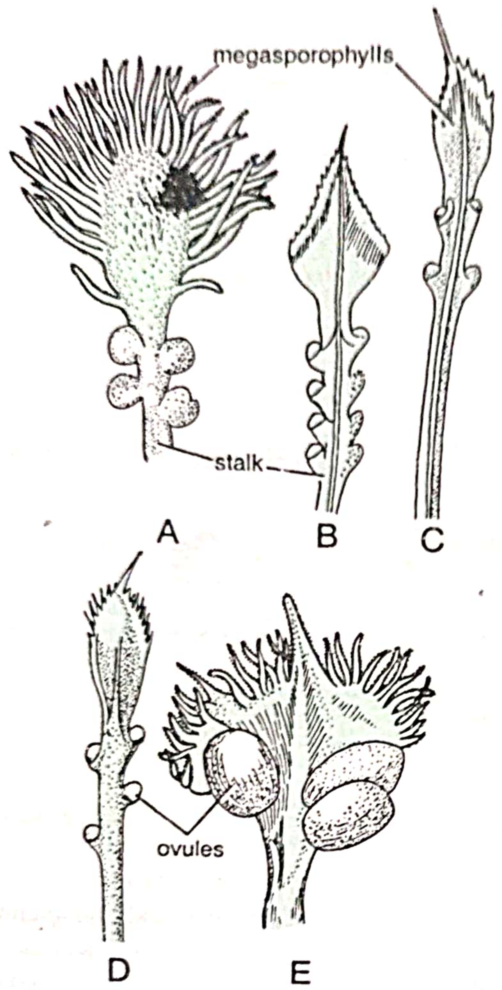


Fig. 23 A-E. *Cycas* : Megasporophylls; A. *C. revoluta*, **B.** *C. circinalis*, **C.** *C. rumphii*, **D.** *C. beddomei*, **E.** *C. pectinata*.

15-20 cm long. The number of ovules is up to 12 per megasporophyll (Fig. 23B). The megasporophylls of *C. rumphii* are ovate-lanceolate with acuminate apices. They are thickly covered by hairs. They measure 20-25 cm in length and have 6-10 ovules (Fig. 23 C). The megasporophylls of *C. beddomei* resemble very much with those of *C. rumphii.* They are 15-21cm in length and the upper pinnate part is about 8 cm long and 3 cm wide. The margins are dentate and the apex is acuminate and pointed. Each megasporophyll has 6-10 ovules (Fig. 23 D). In *C. pectinata*, the megasporophylls are about 15 cm long. The pinnate lamina is orbiculate with subulate-pectinate margins. The stalk is as long as the lamina. Each megasporophyll has 4-6 ovules (Fig. 23 E). In *C. normanbyana*, the sporophyll is highly reduced and bears only two ovules.

[VII] Ovule

The ovule of *Cycas* is **orthotropous** and **unitegmic**. It is sessile or shortly stalked and perhaps largest in the plant kingdom; about 6 cm in length and 4 cm in diameter. The ovule consists of a large nucellus surrounded by a single integument (Fig. 24). The integument remains fused with the body of the ovule except at the apex of the nucellus, where it forms a nucellar beak and micropyle.

The **integument** is very thick and is differentiated into three distinct layers — the outer and inner layers are fleshy, whereas the middle layer is hard and stony. The inner fleshy layer remains fused with the nucellus and it is short-lived. In mature ovule, it is in the form of a papery layer. Mucilage canals and tannin cells are frequently present in the integument. In some species of *Cycas*, stomata are found on the outer surface of the integument. Some cells of the nucellar beak dissolve to form a pollen chamber that lies in the central region of the beak. The

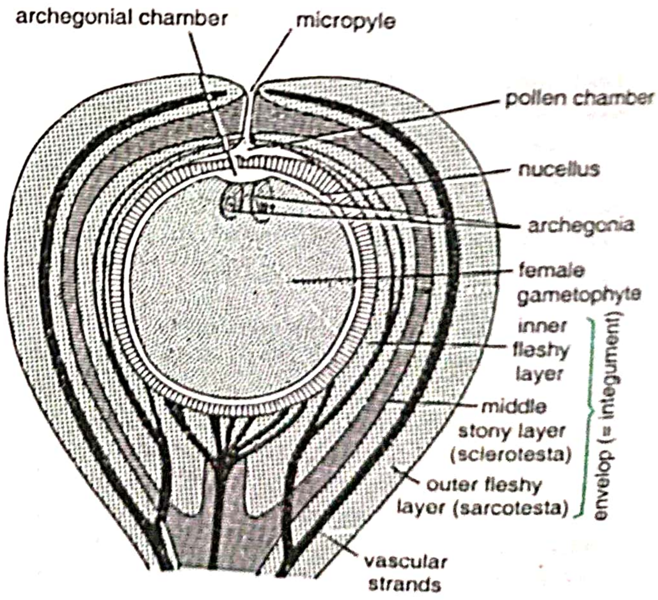


Fig. 24. *Cycas* : Longitudinal section of ovule.

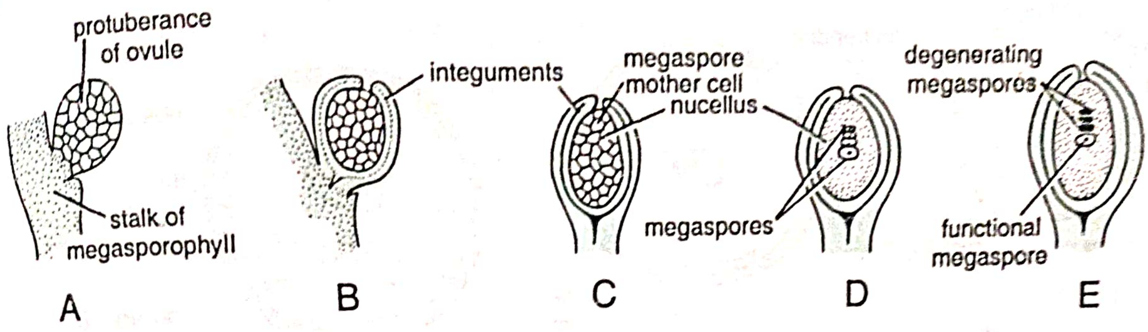


Fig. 25 A-E. ***Cycas*** **:** Stages in the development of ovule.

young ovule is green and is covered by minute multicellular hairs. At maturity it becomes red or orange in colour and hairs disappear.

The ovule is supplied by three vascular strands from megasporophyll. The median vascular strand enters the inner fleshy layer after piercing the outer fleshy and the middle stony layers. It extends up to the chalazal end of the nucellus where it divides abruptly into a number of small traces. The two lateral vascular strands divide into two each, one branch supplies the outer fleshy layer and the other the inner fleshy layer.

[VIII] Development of ovule

The ovule develops from the superficial cells of the basal fertile part of the megasporophyll. A small outgrowth is formed by repeated divisions of the ovule initial (Fig. 25 A, B). This outgrowth forms the **nucellus** by further divisions. Divisions in the basal cells of the nucellus give rise to an integument which surrounds the nucellus. Initially the nucellus and integument are free from each other but afterwards the integument in the chalazal part fuses with the nucellus due to intercalary growth. The upper free region of the integument forms a small aperture, known as **micropyle**.

A deeply situated cell of the nucellus differentiates into **megaspore mother cell** (Fig. 25 C). It can be distinguished by its large size, dense cytoplasm and prominent nucleus. It undergoes a reduction division and forms linear tetrad of four haploid **megaspores** (Fig. 25 D). However, in *C. rumphii*, the upper dyad fails to divide, so that a row of three cells is formed. The lowermost megaspore is functional and the upper three degenerate to provide nourishment to the functional megaspore (Fig. 25 E).

GAMETOPHYTE

Cycas is **heterosporous**; it produces two types of spores — **microspores** and **megaspores**. The microspore develops into male gametophyte and the megaspore into female gametophyte. The spores represent the last phase of the sporophytic generation.

Male Gametophyte

The microspores germinate within the sporangium before dissemination. Thus the male gametophyte develops partially inside the sporangium before pollination and partially within the pollen chamber of the ovule after pollination.

[A] Development of Male Gametophyte Before Pollination

The development of the male gametophyte before pollination takes place inside the microsporangium. The microspore divides by a transverse wall into two unequal cells, a small lenticular **prothallial cell** and a large **antheridial cell** (Fig. 26 A, B). The prothallial cell persists and remains attached to the lower region (proximal) of the pollen grain wall. The antheridial cell divides to form a small **generative cell** (adjacent to the prothallial cell) and a large **tube cell** (Fig. 26 C). Thus the microspore becomes 3-celled. The dispersal of microspores takes place at the 3-celled stage.

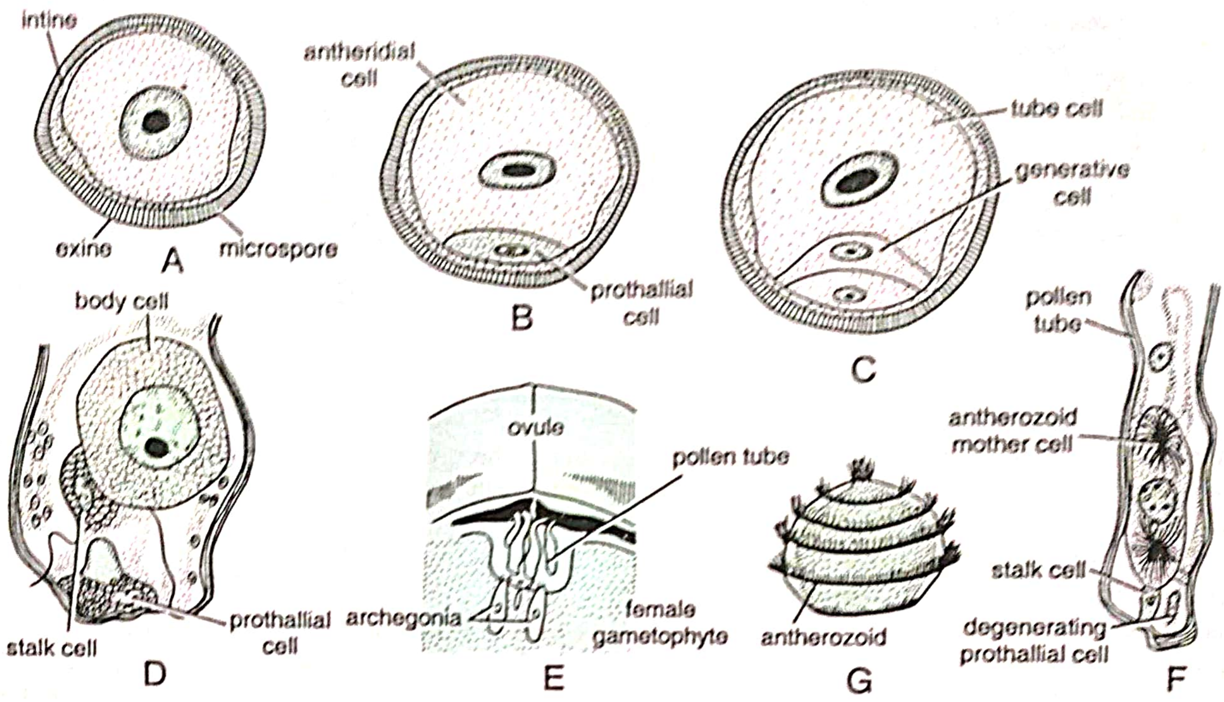


Fig. 26 A-G. *Cycas* : Development of male gametophyte; A-C. Stages before pollination, **D-F.** Stages after pollination, **G.** An antherozoid.

Further development occurs in the pollen chamber of the ovule after pollination.

[B] Pollination

The male cones mature when the young megasporophylls have emerged on the female plant, and the ovules are at the free- nuclear gametophytic stage and ready for pollination.

The 3-celled microspores are shed in the air after the dehiscence of the sporangium. They are very light in weight and are carried by air currents.

[C] Dehiscence of Microsporangium

The microsporangia dehisce by longitudinal slits. The lines of dehiscence of various sporangia radiate out from the centre of the sorus towards the tip of the sporangia. After the sporangia open, the cone axis elongates and the tightly packed sporophylls separate from each other; this helps in the release of pollen.

In synchronization with the time of dispersal of the microspores, some cells of the nucellar beak disorganise to form a viscous fluid. This fluid oozes out from the micropyle in the form of a **pollination drop.** Some of the microspores, carried by air current, are entangled in the pollination drop. As the pollination drop dries up, the microspores are sucked into the pollen chamber through the micropylar canal. As the result of drying of the viscous fluid, the micropylar canal of the pollinated ovules is plugged. After pollination, the ovule increases in size. But unpollinated ovules dry up and wither away. The reproductive organs of some species of *Cycas* emit a very penetrating odour at maturity.

[D] Development of Male Gametophyte After Pollination

Further development of the 3-celled male gametophyte takes place within a week of pollination in the pollen chamber of the ovule. The generative cell divides to form a **stalk cell** and a **body cell** (Fig. 26 D). About the same time, the exine ruptures and the intine protrudes out in the form of a pollen tube. The pollen tube penetrates the nucellar tissue and grows towards the female gametophyte (Fig. 26 E). In *Cycas*, the pollen tube is not only a sperm carrier but it is also haustorial in nature.

The stalk cell does not divide, whereas the body cell divides to form two male gametes (antherozoids) just before fertilization (Fig. 26 F). The antherozoids swim freely in the cytoplasm of the pollen tube. There is an interval of about four months between the pollination and fertilization.

The male gametes are naked, top-shaped structures, measuring 180-210 μm. The blepharoplast of the antherozoids elongates into a large spirally arranged structure with many cilia (Fig. 26 G).

Female Gametophyte

The female gametophyte develops from the functional megaspore which is deeply situated in the ovule. The nucleus of the megaspore divides by free nuclear divisions to form a large number

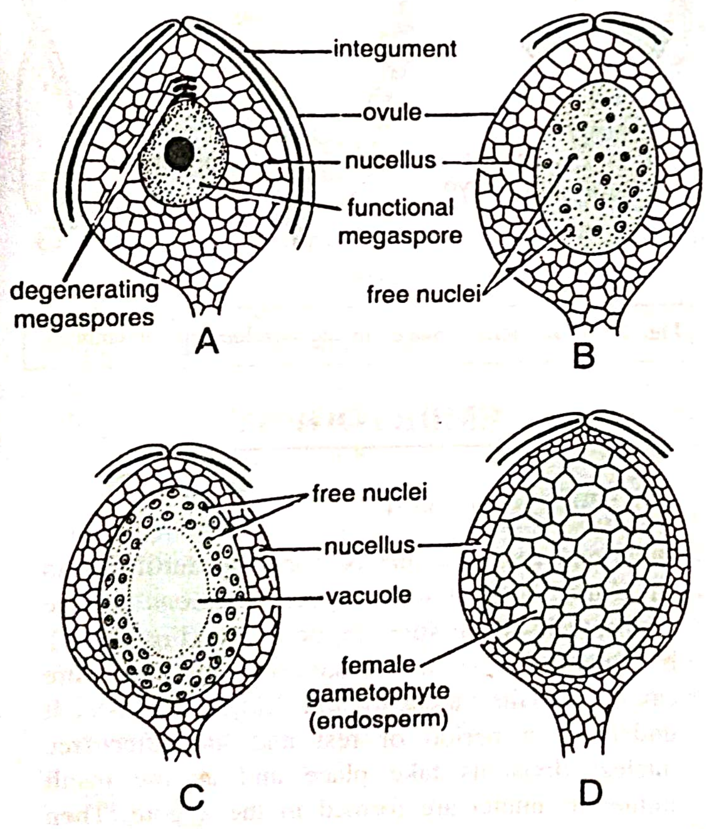


Fig. 27 A-D. ***Cycas*** **:** Stages in the development of female gametophyte.

of nuclei (Fig. 27 A, B). Simultaneously, the megaspore also increases in size. A vacuole develops in the centre of the megaspore which forces the cytoplasm towards the periphery (Fig. 27 C). The vacuole contains a whitish fluid formed by disintegration of the cells in the vacuole region.

Formation of cell walls starts from the periphery and extends towards the centre. The wall formation is a very rapid process and the entire gametophyte becomes cellular shortly (Fig. 27 D). The tissue thus formed is called **female prothallus** or **endosperm**. The cells of the endosperm are haploid. The nucellus is used up as the gametophyte develops and it is represented by a very thin layer in the mature gametophyte.

Development of archegonia. Some superficial cells (usually 2-6) of the female gametophyte at the micropylar end enlarge in size and function as archegonial initials (Fig. 28 A). An archegonial initial divides by a periclinal wall to form an outer **primary neck cell** and an inner **central cell** (Fig. 28 B). The primary neck cell divides by a vertical wall and gives rise to two **neck cells**. The neck cells divide once again, just before fertilization, to form four neck cells. These cells form the archegonial neck (Fig. 28 C). By the time the nucleus of the central cell is ready to divide, the neck cells become large and turgid and project into the archegonial chamber. The central cell enlarges considerably in size and its nucleus divides to form a small **venter canal nucleus** and a large **egg nucleus** (Fig. 28 D). The egg of *Cycas* is the largest amongst the living plants. It is approximately 0.5 mm in diameter in *C. circinalis*..

The mature archegonium consists of 2-4 **neck cells** and an **egg**. The **venter** is surrounded by a nutritive jacket of cells formed by the gametophyte cells. This jacket is called **archegonial jacket**. The number of archegonia in an ovule varies in different species of *Cycas;* for example, 3-6 in *C. rumphii,* 3-8 in *C. circinalis* and 2-8 in *C. revoluta.*

The nucellar tissue above the archegonial initials disintegrates to form an **archegonial chamber**.

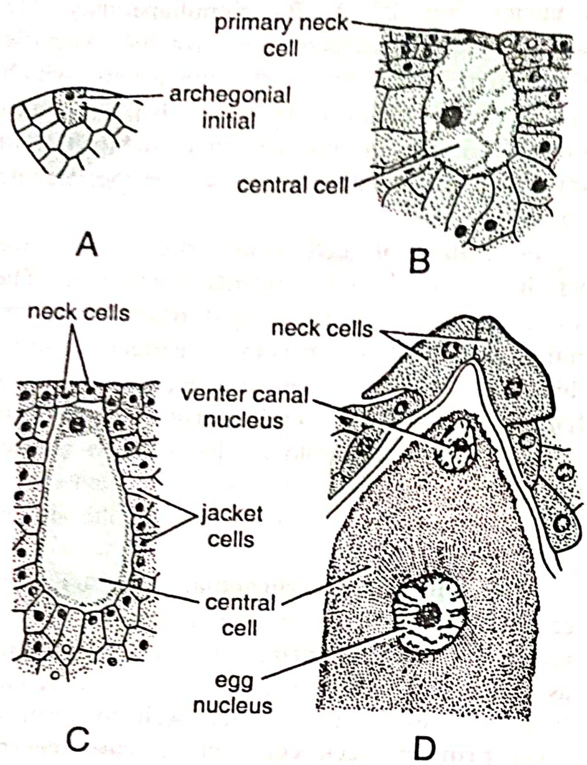


Fig. 28 A-D. ***Cycas*** **:** Stages in the development of archegonium.

Fertilization

The pollen tube reaches the archegonial chamber by breaking the nucellar passage. As it is filled with the fluid of high osmotic pressure, it bursts and releases its contents, including the male gametes, into the archegonial chamber. After releasing the contents, the pollen tubes become flaccid. As soon as the male gamete comes in contact with the neck cells of the archegonium, it is sucked in violently. Normally, only one male gamete enters the archegonium. The nucleus of the male gamete fuses with the egg and thus a zygote is formed. If per chance more than one male gametes enter in an archegonium, all except one, disorganise. The phenomenon of entrance of more than one male gametes in an archegonium is known as **polyspermy**.

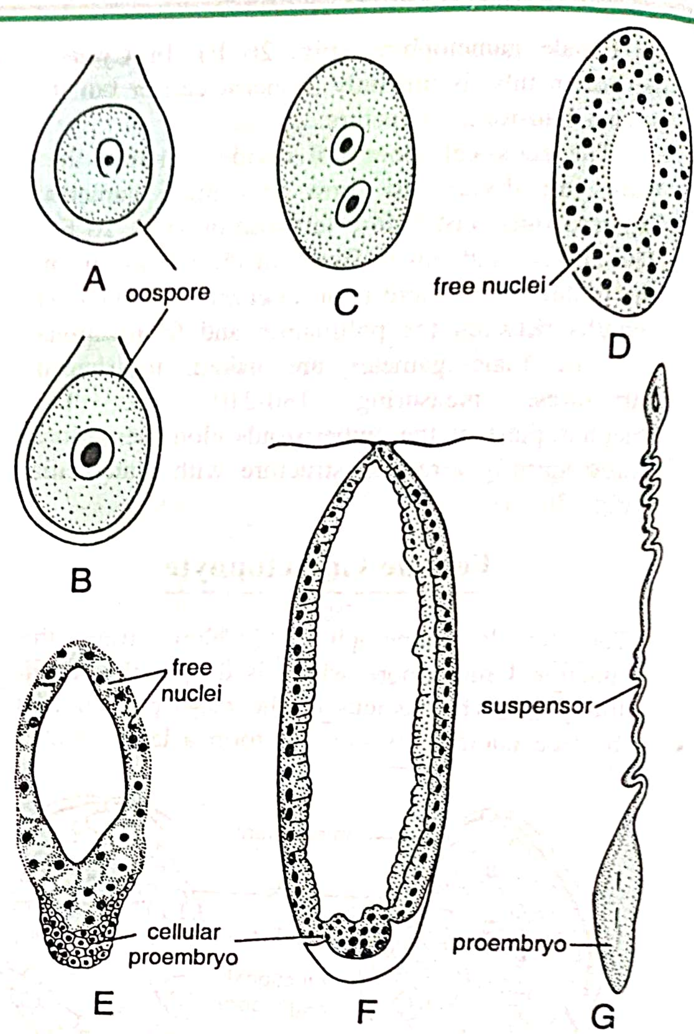


Fig. 29 A-G. ***Cycas*** **:** Stages in the development of embryo.

EMBRYOGENY

[A] Embryo Development

Only one archegonium is normally fertilized in an ovule. The diploid zygote functions as the mother cell of the sporophytic phase (Fig. 29 A). It increases in size and occupies almost the entire cavity of the archegonium (Fig. 29 B). It undergoes a period of rest and thereafter free nuclear divisions take place and as the result numerous nuclei are formed in the zygote. Then a central vacuole appears and the nuclei are pushed to the periphery (Fig. 29 C, D). The nuclei in the basal region are more compactly arranged than in the upper region. The cell wall formation starts in the basal region and extends to the upper region. The cellular structure thus formed is known as **proembryo** (Fig. 29 E, F). The cells in the upper part of the proembryo have indistinct cell walls, whereas in the basal part the cells are well organised. The proembryo eventually differentiates into three regions (Fig. 29 G): (i) the uppermost **haustorial region** at the micropylar end, (ii) the middle **suspensor region**, and (iii) the basal **embryonal region**.

The cells of the **haustorial region** absorb nutrients from the micropylar end and provide them to the developing embryo.

The cells of the **suspensor** region are elongated and much coiled. They push the embryo deep into the female gametophyte (endosperm).

The **embryonal region** forms the main part of the embryo. The embryo takes about one year for its complete development. The embryonal cells are a mass of parenchymatous cells which divide rapidly. After some time the growth is checked in the centre but continues at the margins. Thus two cotyledons are differentiated. Sometimes, as in *C. circinalis,* three cotyledons differentiate. The plumule is formed in the central depression between the cotyledons. The radicle is differentiated quite late in embryogeny from the upper side of the stem apex. The region between the radicle and the stem apex is known as **hypocotyl**. The radicle is enclosed in a pad-like hard covering, known as **coleorrhiza**. The coleorrhiza provides protection to the radicle. Usually, more than one archegonium in an ovule is fertilized, and the development of multiple zygotes leads to simple polyembryony. At first, all the zygotes in an ovule appear to develop with equal vigour, but ultimately only one embryo develops while the rest abort at various stages of development.

[B] Seed

The ovule is transformed into seed after fertilization. The maturation of embryo in seed takes over a year after fertilization. The seed is shed at any stage during this period, and the development of the embryo is completed on the ground. The inner fleshy layer of the ovule wall and the major part of the nucellus are consumed in providing nourishment to the developing embryo. Thus both these parts persist in the seed in the form of a thin layer.

The **mature seed** is red, orange or dark brown in colour. It is surrounded by a fleshy seed coat formed by the three layers of the integument of the ovule. The outer fleshy layer of the integument forms **sarcotesta** and the middle stony layer **sclerotesta**, while the inner layer remains thin and papery. The seed coat has a sweet taste and pleasant odour. These provide attraction to birds and animals which help in dispersal of seeds. There is a straight embryo and the number of cotyledons varies from one to three, closely adpressed to one another and appear as a single structure.

The seed of *Cycas* represents three generations. The seed coat, formed by the integument of the ovule, represents the first sporophytic stage, the endosperm the gametophytic stage and the embryo the next (new) sporophytic stage.

[C] Germination of Seed

The seed germinates without undergoing any rest period. It remains viable only for few months. The germination is **hypogeal** and cotyledons do not come out of the seed and the soil.

During germination, the seed absorbs water through the micropyle. The seed coat ruptures and the radicle emerges out through the micropyle by piercing the coleorrhiza (Fig. 30 A, B). The radicle forms the primary root. The cotyledons are haustorial in function and they derive nourishment from the endosperm for the developing seedling. The cotyledons shrivel when their function is over. The plumule develops into a leaf bearing shoot (Fig. 30 C,D). The young leaves show circinate vernation. The first crown of foliage leaves is formed after several years of plant growth.

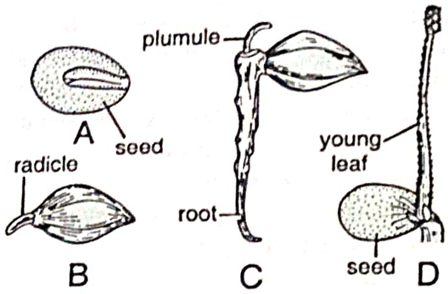


Fig. 30 A-D. *Cycas* : Stages in seed germination.

AFFINITIES OF CYCADS

Members of Cycadales are derived from the Filicales either directly or through the Cycadofilicales. They show affinities with ferns, pteridosperms, Bennettitales, Cordaitales, Ginkgoales and angiosperms.

[A] Affinities with Ferns

The cycads have several traits in common with the ferns. In both the groups, the leaves possess circinate vernation and the antherozoids are motile by means of countless cilia.

[B] Affinities with Pteridosperms

The cycads are readily distinguished from the pteridosperms by their well-organised strobili. The female reproductive organ of *Cycas* indicates that the cycadaceous ovulate strobilus is a derivative of the seed-bearing frond of the pteridosperm type.

The seeds of cycads closely resemble those of the pteridosperms in having two systems of vascular bundle. Both the groups also show affinity in the manoxylic wood, large pith, pollen morphology, seed anatomy and extensive persistent cortex.

[C] Affinities with Bennettitales

The habit of the sporophyte is similar in both the groups, having a barrel-shaped trunk. The stem anatomy of cycads is similar to that of the Bennettitales with a very thick cortex, relatively thin vasculature and large pith. The embryo, in both the groups, is dicotyledonous.

On the other hand, differences are more pronounced in the two orders. While the cycads are characterised by terminal strobilus, the members of Bennettitales have axillary strobilus. Furthermore, the strobili are monosporangiate in cycads and bisporangiate in the Bennettitales. The stomata are haplocheilic in the Cycadales and syndetocheilic in the Bennettitales. The leaf trace in the Cycadales half encircles the stem before entering the leaf; the leaf-trace in the Bennettitales passes straight out through the cortex.

[D] Affinities with Cordaitales

The cycads resemble with the members of Cordaitales in the presence of abundant sclerenchyma in the leaf, large pith, comparatively simple and fairly large seeds and motile sperms.

[E] Affinities with Ginkgoales

The cycads resemble with Ginkgoales in the production of large female gametophytes (bearing archegonia with large eggs), extensive free-nuclear divisions during the early stage of embryogeny and ripe seed consisting of an endosporic embryo with two cotyledons. However, they differ with Ginkgoales in respect of the habit, organography and general anatomy of the sporophyte.

[F] Affinities with Angiosperms

Though the cycads are not assumed to be in the direct line of angiosperm evolution, they probably represent an offshoot from it. The girdling bundle is a peculiarity of the Cycadales. On the basis of such leaf traces, a parallel similarity appears between *Liriodendron* (Magnoliaceae) and living cycads. But the origin of leaf traces is different in the two groups and is independent of each other.