Reproduction and Life cycle of *Cycas sp*

Reproduction

Cycas reproduces both by vegetative and sexual methods.

Vegetative reproduction

Cycas reproduces vegetatively by means of **bulbils** or **adventitous buds**. These bulbils develop from the parenchymatous cells of the cortex in the base of the stem at the crevices between persistent leaf bases. Initially bulbils are covered only with scale leaves, but a few foliage leaves develop with further growth. Bulbil arising on male plant gives rise to male plant, if it forms on female plant it produces a female plant. This is a very common method of vegetative propagation in *C. revoluta*. The vegetative propagation in *C. circinalis* takes place by **suckers** that develop on roots. With further growth they start producing new plants.

Sexual reproduction

Cycas is strickly a **dioecious** plant, but the male and female plants are indistinguishable at the vegetative stage. The compact male cone develops at the apex of the stem in the male plant. However, *Cycas* is the only genus of Cycadaceae which does not produce any female cone. Instead, several megasporophylls arise spirally in acropetal succession around the stem apex of the female plant.

Male cone

The surface of male cone is covered with brown scales at young stage. At maturity, the male cone becomes very large (40-80 cm in length), oval or conical in shape (Fig. 1.17A) which emits odour that can be smelt from quite a moderate distance. The male cone of *Cycas* is the largest among the plant kingdom. The male cone has a central cone axis and numerous microsporophylls are arranged spirally and

Male cone of *Cycas circinalis*

acropetally around the axis. A single **microsporophyll** is a nearly triangular flattened woody structure. It is differentiated into a proximal wedge-shaped fertile part and a distal sterile part, tapering into an upcurved apex called **apophysis** (Fig. 1.17C). Numerous microsporangia (700 in *C. circinalis,* 1100 in *C. media*) are borne on the abaxial (lower) surface of the microsporophyll except at the apex and the base (Fig. 1.17B). Microsporangia are borne in groups of 3-5 forming **sori** that are surrounded by many single-called delicate **hairs** (Fig. 1.17D). Each sporangium is oval or circular in shape having a very short massive stalk. The dehiscence of sporangia takes place by longitudinal slit (Fig. 1.17D). The development of sporangia is of **eusporangiate** type. The sporangial wall is multilayered with a thickened epidermis and a ill-defined tapetum enclosing numerous microspore (pollen) mother cells. Further, microspore mother cells through meiotic division produce numerous microspores or pollen grains. The pollen grain is oval-shaped having a large rounded monosulcate aperture. The pollen is bounded by two concentric wall layers; the outer thick **exine** and the inner thin **intine** (Fig. 1.20A).

Female fructification

The megasporophylls of *Cycas* are not organised into a definite cone. Instead, they arise at the stem apex spirally and acropetally forming a loose crown. The **megasporophylls** are pinnate in nature and are covered with brown hairs called **rementa.** Hence the megasporophylls of *Cycas* are considered to be the modified foliage leaves. **Megasporophylls** are produced every year like the foliage leaves, though they are produced more in numbers than the foliage leaves. A single megasporophyll is a flat dorsiventral structure, measuring up to 30 cm in length. It is differentiated into an upper pinnate lamina and a basal stalk that bears two rows of opposite or sub-opposite, one to six pairs of ovules (Fig. 1.18A–F). There is a great variation in structure of megasporophylls and in number of ovules per megasporophyll in *Cycas* and these criteria can be applied to identify the species of *Cycas.* There is a great reduction in the structure of megasporophylls and in number of ovules among the various species of *Cycas.* *C. revoluta* is the most primitive species where the megasporophyll lamina is much dissected and tapers into a point, bearing 3-4 pairs of ovules (Fig. 1.18A). In *C. pectinata,* the mere

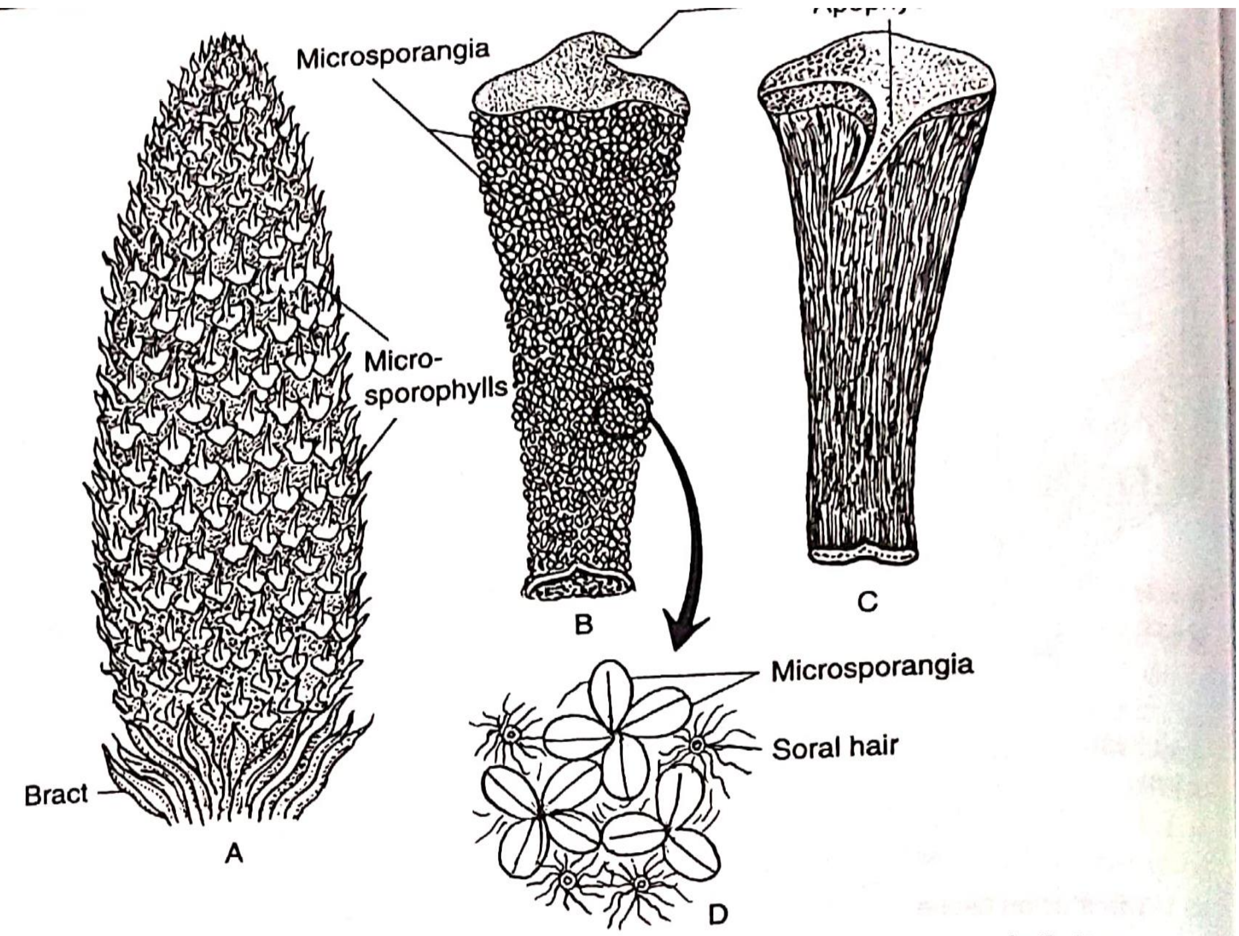


Fig. 1.17 : *Cycas* : A. A male cone, B. A microsporophyll (Abaxial view), C. A microsporophyll (Adaxial view), D. Microsporangia arranged in sori

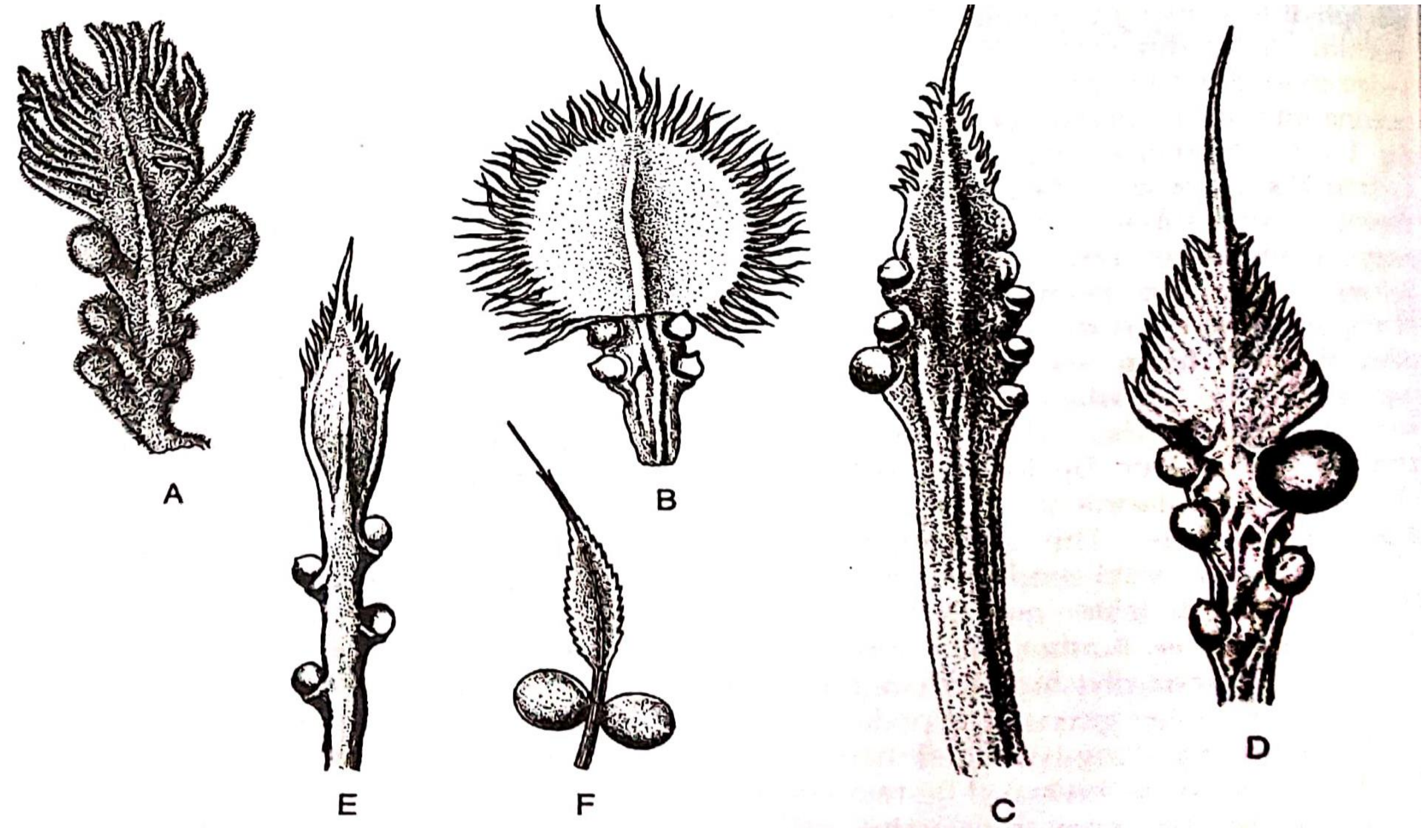


Fig. 1.18 : Megasporophylls : A. *Cycas revotuta*, B. *C. pectinata*, C. *C. circinalis*, D. *C. rumphii*, E. *C. beddomei* F. *C. normanbyana*

serrated lamina is orbiculate with pectinate margins, bearing 2-3 pairs of ovules (Fig. 1.18B). In *C. circinalis*, the lamina is lanceolate with dentate margins and acuminate apex, bearing 4-6 pairs of ovules (Fig. 1.18C). The further reduction in lamina has been observed in *C. rumphii* (Fig. 1.18D) and *C. beddomei* (Fig. 1.18E) where lamina is ovate-lanceolate with acuminate apex, bearing 2–3 pairs of ovules. The maximum reduction in megasporophyll has been noted in *C. normanbyana*. Its lamina shows a mere serrated margins bearing only one pair of ovule (Fig. 1.18F).

Ovule

The ovules of *Cycas* are **orthotropous** and shortly stalked. The ovules are large, attaining a length of about 6-7 cm with a diameter of 4 cm and is perhaps the largest amongst the plant kingdom. The mature seeds are elliptical, bilobed and slightly flattened — they become fleshy and bright orange or red in colour. There is a single integument which is fused with the nucellus except the top (Fig. 1.19). The integument is differentiated into three layers. The **outer layer** is fleshy and pulpy and becomes variously coloured at maturity. The **middle layer** is very hard and stony, while the **inner layer** is fleshy and becomes papery before maturity. There are frequent mucilage canals and tannin cells in the integument.

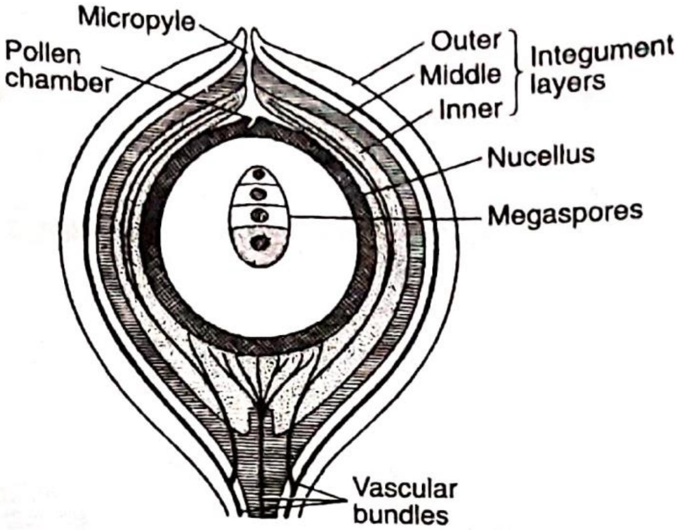


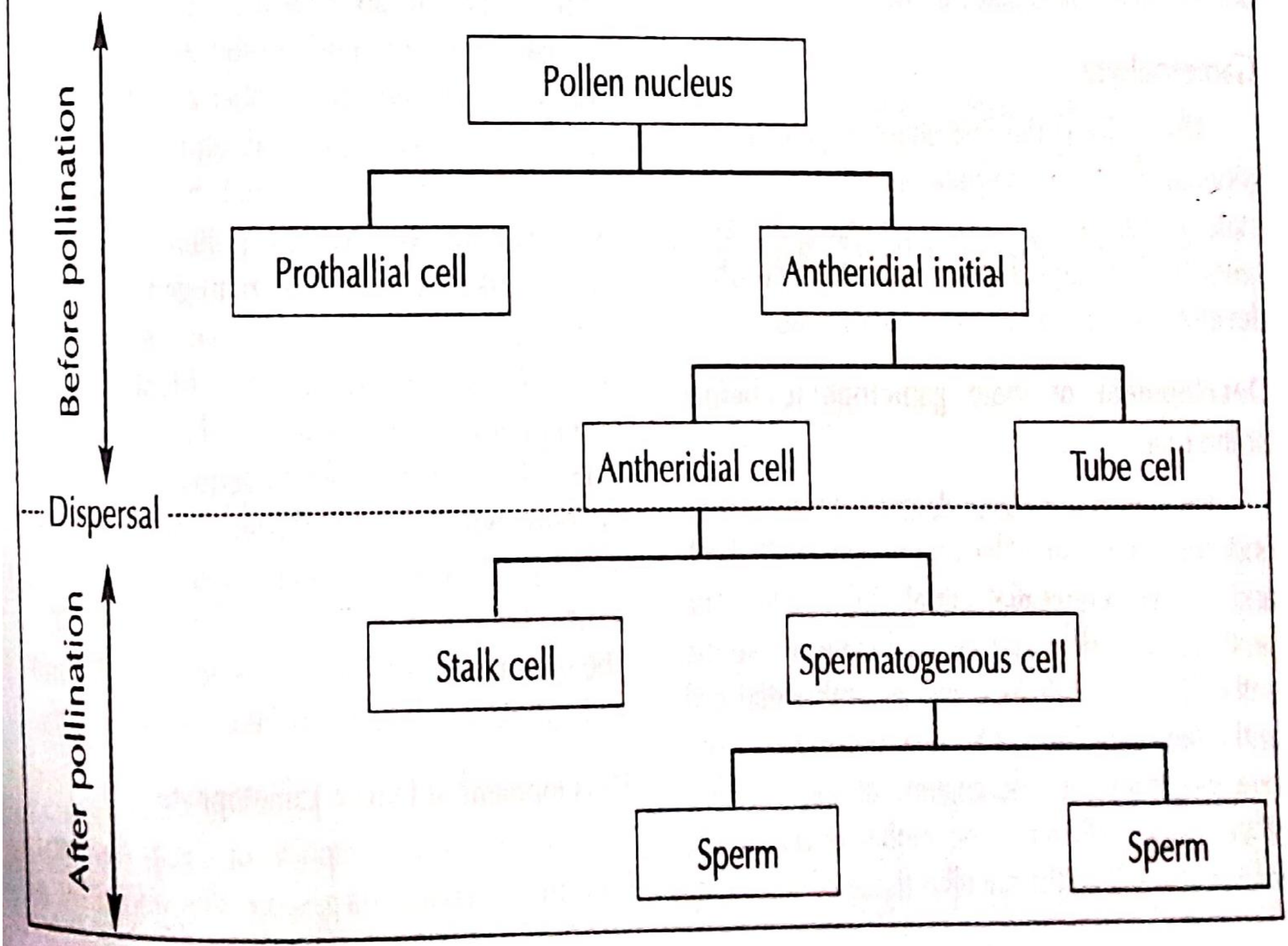
Fig. 1.19 : Vertical median section of *Cycas* ovule

The ovule is supplied with three vascular traces (Fig. 1.19). The median strand supplies the base of the integument, which extends up to the chalazal end of the nucellus and further ramifies abruptly. The two side strands pass to the integument which again divide — one branch supplies to the outer pulpy layer and the other to the inner soft layer.

Megasporogenesis

A deeply situated cell of the nucellus is differentiated into a large megaspore mother cell which undergoes meiotic division to form a **linear tetrad** of four megaspores. Out of the four megaspores the outer three degenerate, while the

Schematic representation in the development of male gametophyte of *Cycas*



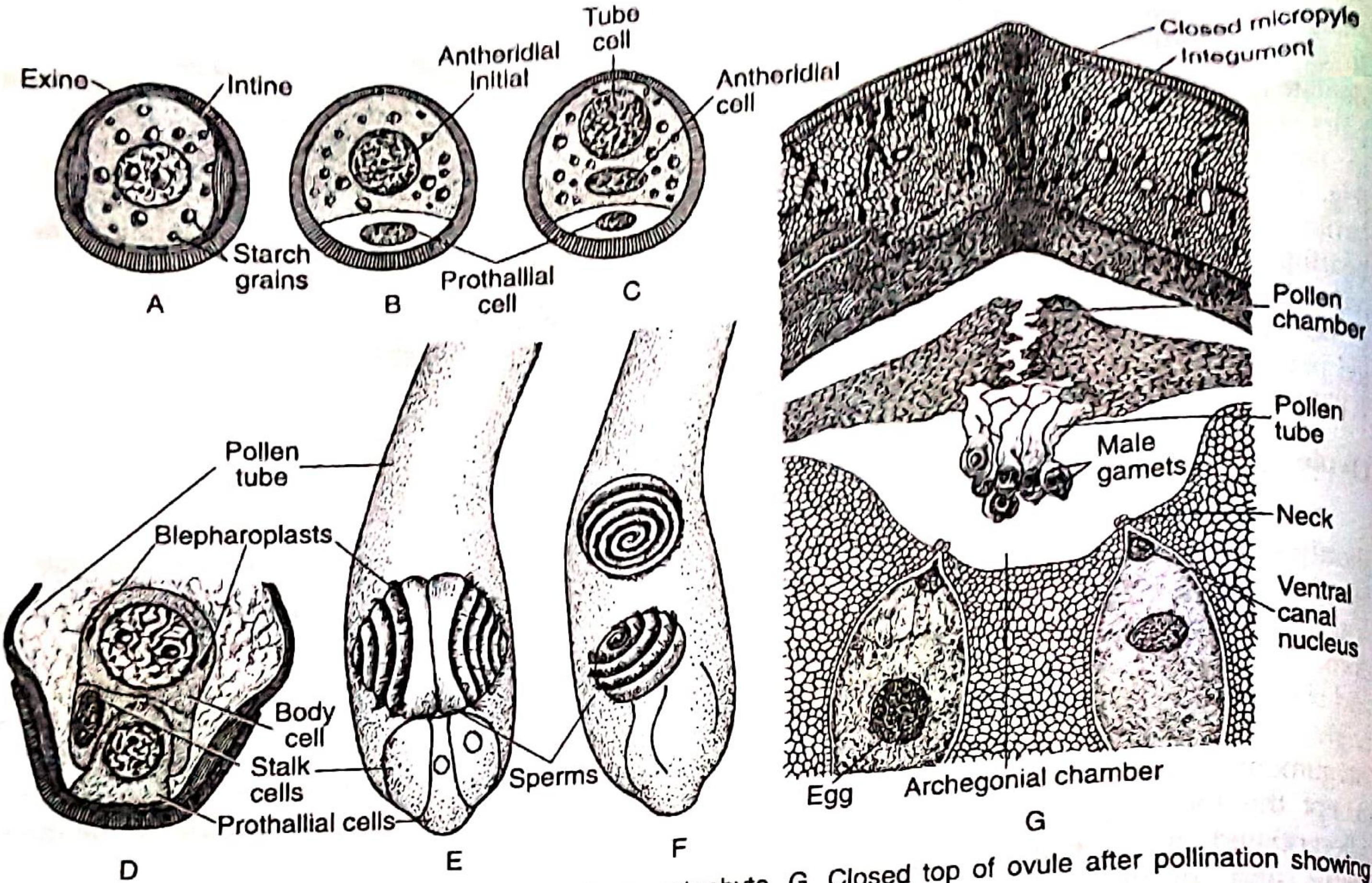


Fig. 1.20 : *Cycas* : A–F. The development of male gametophyte, G. Closed top of ovule after pollination showing course of pollen tubes

lowermost megaspore becomes functional (Fig. 1.21A). The upper free opening of the integument forms the micropyle and a concavity in the top of the nucellar tissue forms the pollen chamber. After pollination, the pollen grains are collected in the pollen chamber and the development of pollen grains takes place in the nucellar tissue.

Gametophyte

The spore is the first phase of gametophyte generation. The microspore or pollen grain is the male gametophyte, while the megaspore represents the first stage of female gametophyte which develops to form a female gametophyte.

Development of male gametophyte before pollination

The pollen nucleus undergoes mitosis to form endosporically a small lens-shaped **prothallial cell** and a large **antheridial initial** (Fig. 1.20B). The prothalial cell does not divide further, while the antheridial initial divides into an **antheridial cell and a tube cell** (Fig. 1.20C). The pollen grains are released from the sporangium at the 3-celled stage. After pollination, the further development takes place within the nucellus tissue of the ovule.

Development of male gametophyte after pollination

The further development of male gametophyte takes place within a week after pollination. The tube cell of 3-celled male gametophyte comes out through the pollen aperture in the form of a pollen tube which penetrates into the nucellar tissue. The pollen tube destroys all the tissues between pollen chamber and the female gametophyte. Thus, the fertilisation is siphonogamous, though it is haustorial in nature. Now, the antheridial cell within the pollen tube divides into a **stalk cell** and a **spermatogenous (body) cell** (Fig. 1.20D). The spermatogenous cell enlarges considerably and two **blepharoplasts** develop at the opposite end of the spermatogenous cell. Then the spermatogenous cell divides to form two large, top-shaped, motile sperms with spiral band bearing numerous flagella around the distal end of the sperm (Fig. 1.20E). The sperms of *Cycas* are very large (180-210 μm) and can be visible to the naked eye (Fig. 1.20F).

Development of female gametophyte

The female gametaphyte of *Cycas* develops from the functional megaspore surrounded by a tough membrane that persists in the gametophyte (Fig. 1.21B). The nucleus of the megaspore divides by free nuclear divisions forming a large number of nuclei unaccompanied by wall-formation. In the mean time, the megaspore increases in size and develops a vacuole in the centre which forces the cytoplasm along with nuclei towards the periphery. Thus the nuclei lie in a thin film of cytoplasm around the vacuole (Fig. 1.21B). The cell wall formation starts in a centripetal fashion, from periphery inwards. The wall formation proceeds very rapidly and as a result the central vacuole in obliterated (Fig. 1.21C). The entire gametophyte becomes cellular and the tissue thus formed is called **endosperm**. The peripheral cells of the gametophyte are small, isodiametric devoid of any food reserves, while the inner cells are large, irregular and filled up with starch grains.

Development of archegonia

Two to eight cells of the female gametophyte at the micropylar end enlarge in size and have dense cytoplasm and prominent nuclei. These cells function as **archegonial initials** (Fig. 1.21D). Each archegonial initial divides periclinally to form an outer small **neck initial** and a large **central cell** (Fig. 1.21E). The neck initial divides by a vertical (anticlinal) wall to form two **neck cells** (Fig. 1.21F). A second division takes place prior to fertilisation, thus the neck actually comprises of four cells. The central cell enlarges considerably in size and its nucleus divides into a small ephemeral **ventral canal nucleus** and a large **egg cell** (Fig. 1.20G). The egg of *Cycas* is reported to be the largest among the living plants, thus it can be seen with naked eyes. The nucellar tissue above the archegonia disorganises to form an archegonial chamber (Fig. 1.21G).

Pollination

Cycas is anemophilous i.e., wind pollinated. The airborne pollen grains remain suspended in the air and at the same time some cells of the nucellar beak in the ovule are disorganised to form a viscous fluid. This fluid comes out through the microphyle in the form of a '**pollination drop**'. Thus, some of the airborne pollen grains come in contact with the fluid and are sucked into the pollen chamber through the micropylar canal. The pollen grains are then deposited and concentrated within the pollen chamber as a result of drying off the fluid (Fig. 1.20G). At this stage, the ovule increases in size.

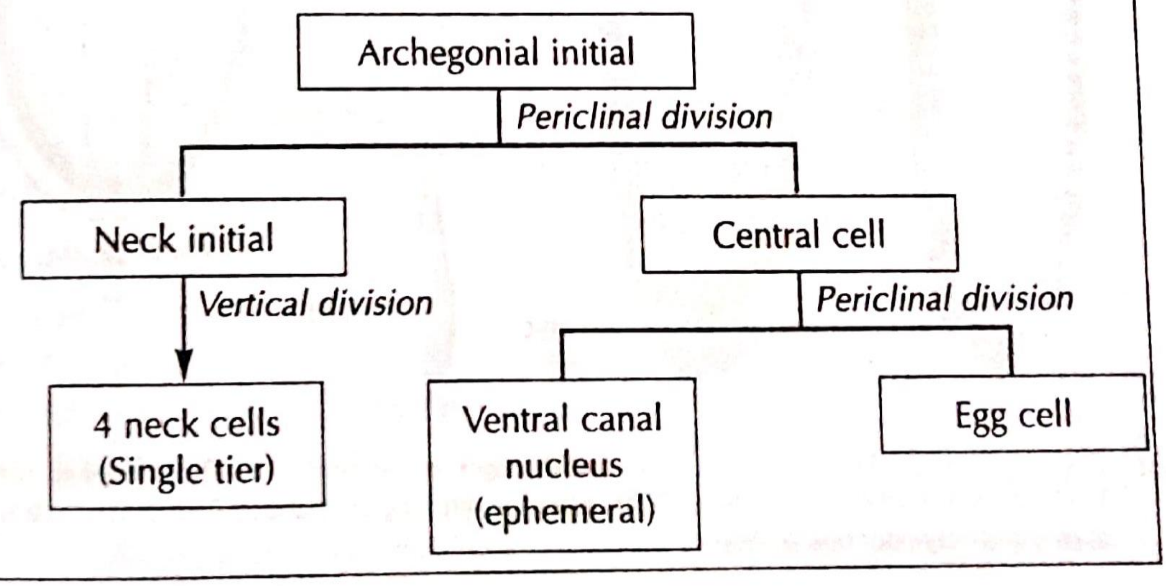
Fertilisation

The sperms and the cytoplasm of pollen tube are released in the archegonial chamber by the rupture of the basal end of pollen tube. The osmotically rich pollen tube cytoplasm causes the rupture of neck cells. The motile sperms enter into the archegonium with a forward and circular motion, ciliary band forming the anterior end. The archegonial chamber is flooded with the fertilisation fluid produced by nucellar cells. The ciliary band of the sperm is left behind on the top of the egg cell. The sperm nucleus fuses with the egg nucleus and thus a **zygote** in formed.

Embryogeny

The zygote enlarges considerably and undergoes numerous free nuclear divisions. As much

Schematic representation in the development of archegonia of *Cycas*



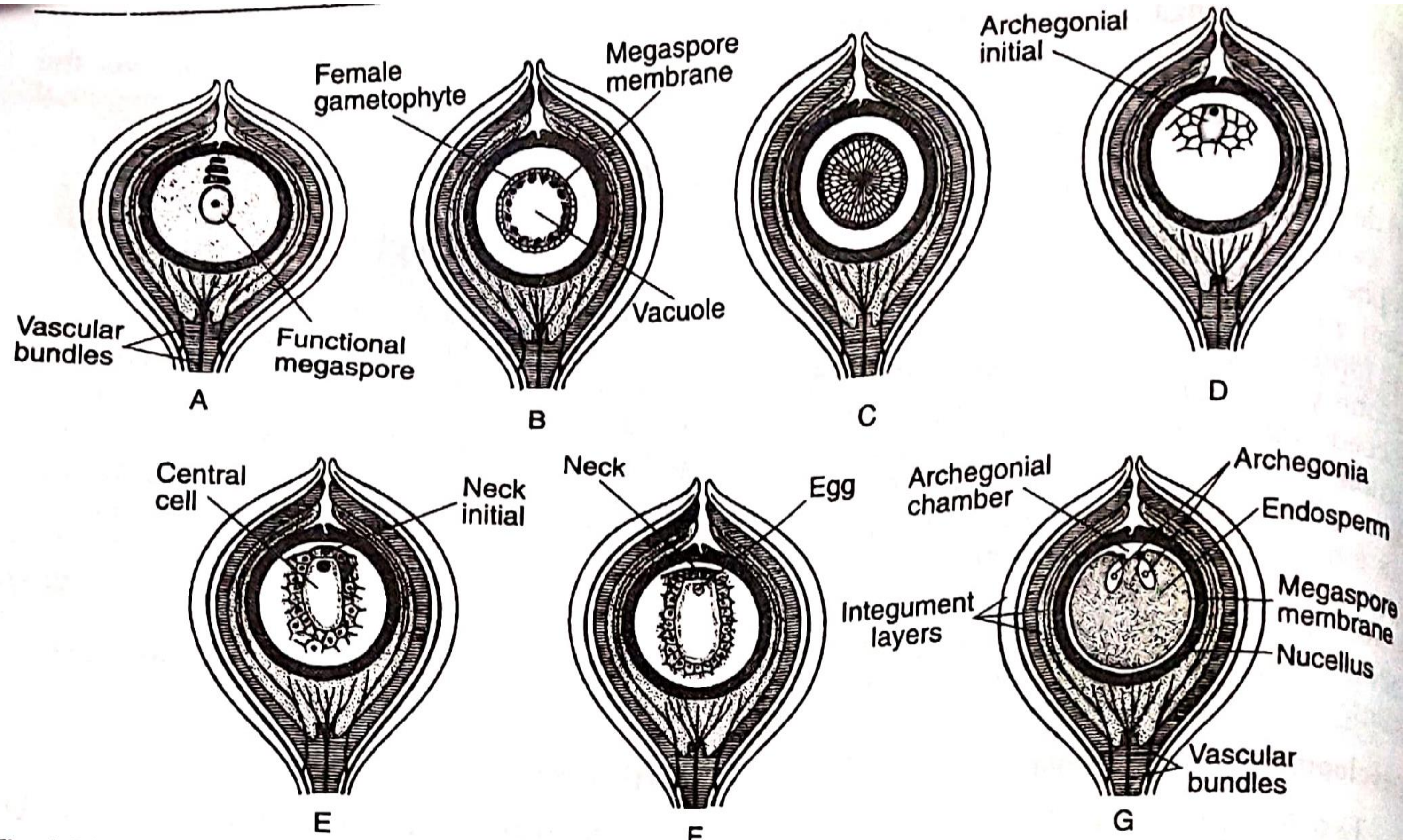
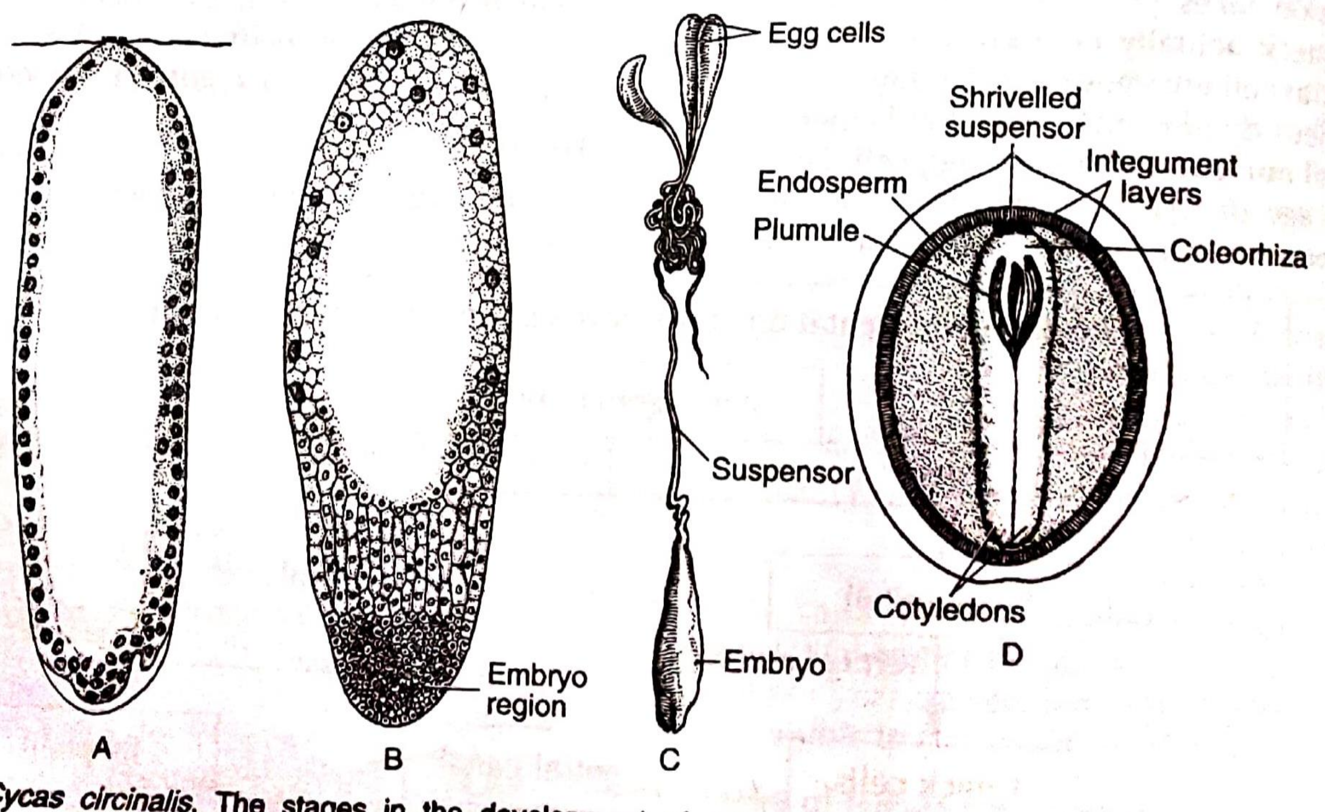


Fig. 1.21 : *Cycas*. Development of female gametophyte within ovule : A. Linear tetrad with one functional megaspore, B. Free nuclear stage, C. Cellular stage, D–F. Stages in development of an archegonium, G. A mature female gametophyte containing two archegonia

as 256 (*C. revoluta*) to 512 (*C. circinalis*) free nuclei have been reported. A large central vacuole is formed and the nuclei are arranged around the central vacuole (Fig. 1.22A). Most of the free nuclei move to the base of the **proembryo**. The cell formation in the proembryo begins from the basal part and extends up the periphery. The entire embryo never becomes cellular. The basal cells are smaller with dense cytoplasm forming the **embryo** (Fig. 1.22B). A dicotylede-



g. 1.22 : *Cycas circinalis*. The stages in the development of embryo : A. Free nuclear stage in proembryo, B. Organisation of embryo region, C. An embryo with long suspensor, D. Median vertical section of a seed showing dicotyledonous embryo nous embryo is developed at the tip. The upper cells elongate greatly to form the **suspensor** which may be coiled and twisted (Fig. 1.22C). Several egg cells may be fertilised to form many zygotes, but ultimately only one embryo in an ovule attains maturity. The layer of cells covering the outer curved face of the embryonal mass is called the **cap**.

Seeds

Cycas seeds are fleshy and remain covered with an orrange red-coloured thick seed coat. The embryo in the seed enlarges much. The nucellus is used up and the seed is covered with the three-layered seed coat (Fig. 1.22D). The coleorrhiza is the first region to differentiate in the embryo proper which is quite hard. The plumule develops later inside the base of the cotyledons. Subsequently the suspensor dries up. The growth of the embryo in seeds is very slow, taking over a year to mature. *Cycas* shows three years reproductive cycle where pollination in first year winter, fertilisation in second year summer and seed shedding in third year summer. The development of embryo continues even after the seeds are shed.

The seeds are dispersed by birds due to their attractive fleshy outer pulp. The germination of the seed is **epigeal**. The first leaves come out at right angle to the cotyledons in a decussated fashion, although the remaining leaves develop spirally (Fig. 1.23).

Figure 1.24 shows the life-cycle of *Cycas*.

Origin and relationships

Cycads probably originated from the Pteridosperm ancestor (*Palaeocycas* megasporophyll with *Taeniopteris* leaf) in the Upper Carboniferous period. Among the order Cycadales, *Cycas* is the most primitive genus because of the absence of female cone. *Cycas* shows relationship with different groups of plants based on their morphological and anatomical features.

Relation to Ferns (Filicopsida)

Cycas resembles ferns in exhibiting the following characteristics :

1. The young rachis as well as leaflets are circinately coiled like those of ferns.
2. Microsporangia are borne in sori on the abaxial surface of the microsporophylls like those of ferns.

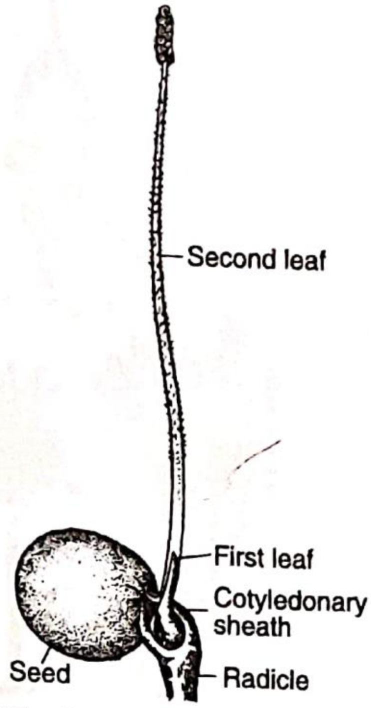


Fig. 1.23 : *Cycas* : The germinating seed

3. The sperms are very large and motile with spiral band, bearing countless cilia like those of ferns.

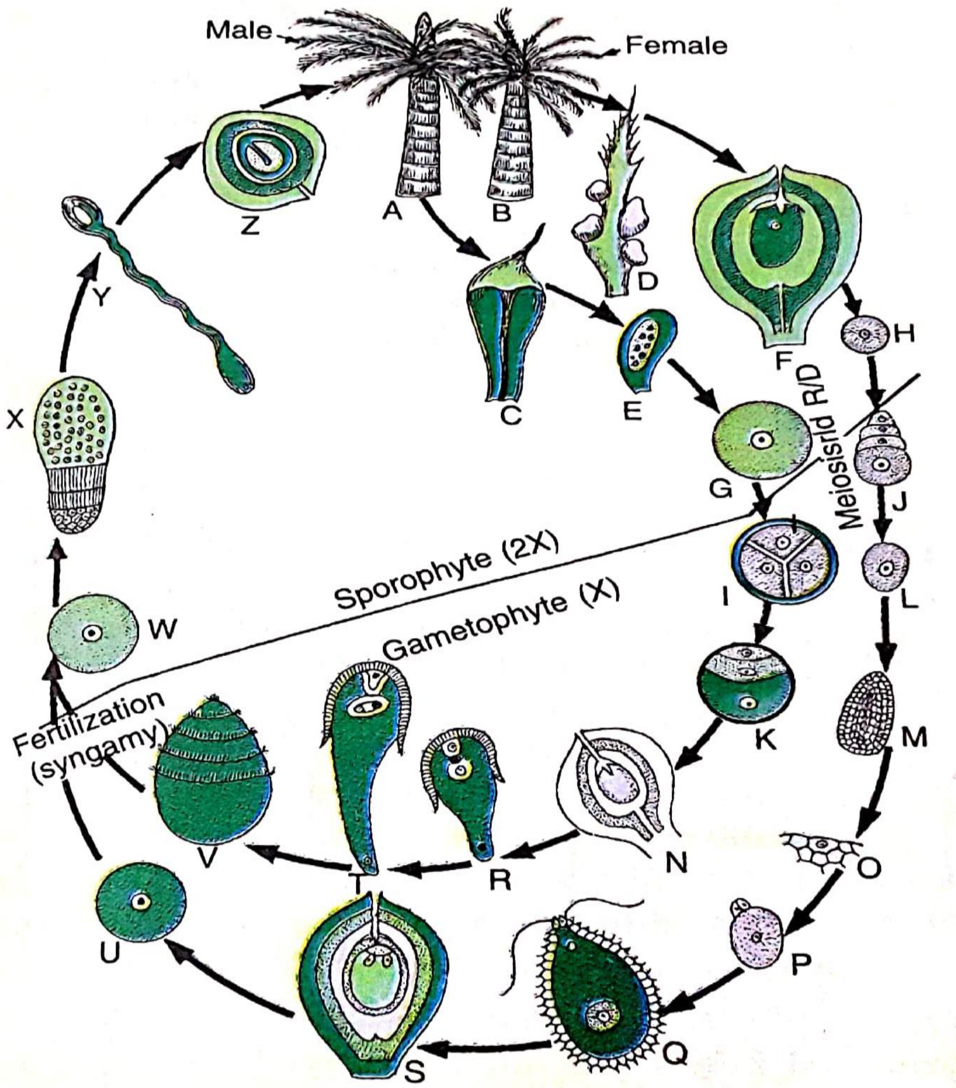
Relation to Pteridosperms

1. Most of the pteridosperms have stout unbranched columnar stem like those of *Cycas*.
2. Presence of manoxylic wood with large pith and extensive cortex in stem.
3. The leaves are pinnately compound.
4. The ovules have three-layered integument with two systems of vascular bundles.
5. The presence of nucellar beak with a distinct pollen chamber.

Relation to Bennettitales

The points of similarity between *Cycas* and Bennettitales are :

1. The plants are small trees with a barrel-shaped trunk.
2. The stem anatomy shows a very thick cortex, relatiively thin vasculature and large pith. Stele is of siphonostelic with exarch xylem.
3. Presence of manoxylic wood.
4. Leaves are pinnately compound with striking similarities in form, size and venation.
5. The presence of dicotyledonous embryo.
6. The presence of monocolpate (monosulcate) pollen grains.



33. *Cycas* sp. Diagrammatic life-cycle; A, male plant; B, female plant; C. microsporophyll; D, female strobilus; E, microsporangium; F, ovule; G, microspore mother cell; H, megasopore mother cell; I, microspore tetrad; J, megaspore linear tetrad; K, male gametophyte; L, megaspore; M, female gametophyte; N,ovule; O, archegoinal initial; P, young archegonium; Q, mature archegonium; R, germinating pollen; S, germinating pollen in pollen chamber; T, germinating pollen; U, egg; V, spermatozoid; W, oospore; X, young embryo; Y embryo; Z, seed.

Plate XII : Megasporophyll of *C. revoluta*.