

**BIOLOGY AND DIVERSITY OF ALGAE,
BRYOPHYTES, PTERIDOPHYTES AND
GYMNOSPERMS
(DBOT01)
(MSC BOTANY)**



ACHARYA NAGARJUNA UNIVERSITY
CENTRE FOR DISTANCE EDUCATION
NAGARJUNA NAGAR,
GUNTUR
ANDHRA PRADESH

ALGAE

LESSON-I

GENERAL CHARACTERS AND CLASSIFICATION OF ALGAE

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1. Introduction

The algae comprise a heterogeneous group of chlorophyll bearing lower plants with enormous diversity of form, structure, reproduction and life history. The plants may be microscopic as well as macroscopic inhabiting the fresh water and aquatic habitats. The science

that deals the study of algae is called Phycology (or Algology). The term 'Phycology' was derived from the Greek word **Phykos** means sea weeds. These plants are known to occur every place where there is light and moisture. It is true that they grow richly in the seas and in the freshwater reservoirs such as rivers, streams, lakes, ponds, damp soil, moist wall, wet tree trunks etc., and also in the extreme habitats such as deserts, snow-clad polar regions and hot water springs.

As in higher green plants, photosynthesis in algae is accompanied by oxygen evolution. However, unlike bryophytes and other higher plants, algae lack a covering or jacket of vegetative cells around their reproductive organs. An exception is the antheridium of the Charophyceae which has a sterile jacket around it. In the Phaeophyceae (Brown algae), some reproductive organs are multicellular and all the cells of such an organ are fertile. With the exception of the blue-green algae (Cyanophyta) and *Prochloron* all algal members are eukaryotic in nature.

Among the Indian Phycologists, Ghose (1919-1932) was pioneer who made significant contribution on blue-green algae of Punjab. His student Randhawa (1932-1959) published a series of papers on Zygnemaceae and Oedogoniales of Uttar Pradesh and Punjab. Prof. M.O.P. Iyengar established a strong school of algae at the University of Madras and discovered *Fritschiella tuberosa* (1932) and studied many aspects of Chlorophyceae. Randhawa (1959) rightly called him the 'Father of Modern Algology of India'. Desikachary (1959), a student of Iyengar, had written a monograph on 'Cyanophyta'. Another strong school of algae which is internationally reputed, was built by Bharadwaja, a student of Prof. F.E. Fritsch, at Banaras Hindu University (BHU), Varanasi. Y.S.R.K. Sarma (1960, 1974) worked on nuclear cytology of green algae at B.H.U. At Allahabad, Mitra (a student of Fritsch) contributed to the morphology, taxonomy and life histories of many green and blue-green algal species. Prasad (at Lucknow) worked with Prof. M.B.F. Godward of Queen Mary College (London) on cytogenetics of green algae. R.J. Patel (Vallabh Vidyanagar), another student of Prof. Godward, made a significant contribution towards the cytology of the Chlorophyceae and, algal flora of Gujarat and Maharashtra.

2. Classification

The classification of algae has been modified from time to time ever since Linneaus placed them in the class Cryptogamia. Till 20th century, it was customary to recognise four classes of algae namely Chlorophyceae, Phaeophyceae, Rhodophyceae and Myxophyceae. Diatoms were placed in Phaeophyceae. All motile unicellular and colonial flagellated organisms with chlorophyll are placed in the class Mastigophora of phylum Protozoa. The classification was based on vegetative structures and reproductive processes. In modern systems of classification many criteria has been taken into consideration so that it is possible to understand the interrelationships and phylogeny. Some of these criteria taken into account for classification are: (1) Photosynthetic pigments, (2) the nature of storage products, (3) the nature of cell wall components, (4) details of cell structure, and (5) the type of flagella.

(i) Fritsch's system

According to F.E. Fritsch (1935, 1944, 1945), the algae have been divided into following eleven classes.

- | | |
|----------------------|-----------------------|
| (A) Chlorophyceae | (B) Xanthophyceae |
| (C) Chrysophyceae | (D) Bacillariophyceae |
| (E) Cryptophyceae | (F) Dinophyceae |
| (G) Chloromonadineae | (H) Euglenophyceae |
| (I) Phaeophyceae | (J) Rhodophyceae |
| (K) Myxophyceae | |

Fritsch classification is mainly based on the pigmentation, the assimilatory food products (metabolic products) and type of flagella. Some important classes are given below:

A. Chlorophyceae

The class Chlorophyceae is characterized by following features:

- The pigments such as chlorophyll **a**, chlorophyll **b**, xanthophyll and carotenes, are localized in definite plastids or chromatophores.
- The reserved food material is starch, rarely oil in very few cases. Usually in chromatophores pyrenoids are present. A part of pyrenoid converts into starch.
- The flagellation is isokontae type, i.e., both of the flagella are equal in length.
- Vegetative body may be one to many-celled.
- Cellulosic cell wall is present.
- Sexual reproduction ranges from isogamy to oogamy.
- The life-cycle is mostly of haplontic type.
- Most of the species are fresh water and few are marine.

e.g. *Chlamydomonas*, *Volvox*, *Ulva*, *Draparnaldia*, *Oedogonium*, *Spirogyra*, *Chara* etc.

B. Xanthophyceae

- The chromatophores are yellow green, containing chlorophyll **a**, carotenes (β -carotene) and xanthophylls in them.
- Pyrenoids are absent and starch is not found. The chief food products are oils.
- The flagellation is of heterokontae type, i.e., one flagellum is short and other long.
- The cell wall consists of pectin, and in majority of cases two overlapping halves are present, e.g., *Tribonema*.
- The sexual reproduction is rarely found.
- The walls are silicified.

- (g) The life-cycle is mostly of haplontic type.
- (h) Majority of species are fresh water, some are marine.
e.g., *Botrydium*, *Vaucheria* etc.

C. Bacillariophyceae

- (a) Golden brown or yellow colour of the thallus is due to the presence of a pigment called diatomin. The other pigments are chlorophyll **a**, carotenes (β carotene) and xanthophylls. The members of Bacillariophyceae are known as diatoms.
- (b) Reserved food materials are fats or volutins.
- (c) The flagellate bodies are 1 or 2 flagellated.
- (d) Majority of them are unicellular, some are colonial.
- (e) The sexual reproduction is of special type resulting in the formation of auxospores.
- (f) They are diplontic.
- (g) They are widely distributed in sea and fresh waters.
e.g. *Pinnularia*, *Navicula*, *Synedra* etc.

D. Phaeophyceae

- (a) Brown or yellowish brown colour of the thallus is due to the abundance of carotenoids, especially fucoxanthin. Other pigments are chlorophyll **a**, chlorophyll **c**, β carotene, violaxanthin and other xanthophylls.
- (b) The reserved food materials are laminarin, mannitol and alcohols.
- (c) The plant body is multicellular but motile reproductive structures are unicellular. These motile reproductive cells are pyriform with two laterally inserted flagella; anterior flagellum is longer and pantonematic while the posterior one is short and acronematic.
- (d) The sexual reproduction ranges from isogamy to oogamy.
- (e) The life cycles indicate clear alternation of generations.
- (f) Most of them are marine.
e.g., *Ectocarpus*, *Dictyota*, *Sargassum*, *Laminaria*.

E. Rhodophyceae

- (a) They are red algae due to presence of γ -phycoerythrin and c-phycoerythrin pigments. The other pigments are chlorophyll **a**, carotenes (β carotene) and xanthophylls.
- (b) Reserved food materials are polysaccharides, floridean starch and a soluble sugar called floridoside.
- (c) The flagellation is absent.
- (d) Prominent plasmodesmata are present.
- (e) An advance type of oogamous sexual reproduction is found.
- (f) Life-cycles show clear alternation of generations.
- (g) Most of the species are fresh water and the rest are marine.
e.g., *Batrachospermum*, *Polysiphonia*.

F. Myxophyceae (Cyanophyceae)

- (a) Excess amount of phycocyanin gives blue-green colour to the thallus. Definite chromatophores are absent but pigments are localized in the peripheral portion of the protoplast. Other photosynthetic pigments are c-phycoerythrin, carotenes and xanthophylls.
- (b) Reserved food materials are sugars and cyanophycean starch.
- (c) They are prokaryotic in nature.
- (d) Sexual reproduction is unknown.
- (e) Majority of them are fresh water forms. Some are found in sea water.

(ii) Round's (1973) system

F.E. Round (1973) classified algae into two major groups, i.e., Prokaryota and Eukaryota.

Group-A : Prokaryota – Phylum Cyanophyta

Group-B : Eukaryota – 12 phyla

- | | |
|-----------------|--------------------|
| a. Euglenophyta | g. Dinophyta |
| b. Chlorophyta | h. Bacillariophyta |
| c. Charophyta | i. Chrysophyta |
| d. Prasinophyta | j. Phaeophyta |
| e. Xanthophyta | k. Rhodophyta |
| f. Haptophyta | l. Cryptophyta |

(iii) Whittaker and Margulis (1978) system

Whittaker and Margulis (1978) opined that most of the algal groups may have closer affinities with other protist groups than with each other. On the basis of this idea, they classified all prokaryotes under kingdom Monera, and all algae under superkingdom Eukaryota and kingdom Protista or Proctista.

- | | | |
|---------------|---|--|
| Kingdom | : | Monera (Prokaryotic cells) |
| Superphylum | : | Photomonera (Photosynthetic prokaryotes) |
| Phylum | : | Photobacteria |
| Phylum | : | Prochlorophyta (green oxygenic prokaryotes) |
| Phylum | : | Cyanophyta or Cyanobacteria (Blue-green algae) |
| Superkingdom: | | Eukaryota |

Kingdom : Protista or Proctista

There are 3 super phyla – Chromophyta (8 phyla – yellow and brown algae), Chlorophyta (6 phyla--green algae) and Rhodophyta (red algae).

(iv) Larkum and Barret (1983) system

Larkum and Barret (1983) adopted the views of Whittaker and Margulis with some modifications:

Kingdom : Monera (Prokaryotic cells)

Superphylum : Photomonera (Photosynthetic prokaryotes)

Phylum : Photobacteria (non-oxygen evolving photosynthetic bacteria)

Phylum : Prochlorophyta (green, oxygenic prokaryotes)

Phylum : Cyanophyta or Cyanobacteria (Blue-green algae)

Superkingdom: Eukaryota

Kingdom : Protista or Protoctista [eukaryotic cells with solitary and colonial unicellular organization (Protista) or also including simpler multicellular form (Protoctista)].

Superphylum : Chromophyta (yellow and brown flagellate algae)

Phylum : Chrysophyta (golden algae, including Prymnesiophyta and Chloromonandophyta)

Phylum : Bacillariophyta (Diatoms)

Phylum : Xanthophyta (yellow-green algae)

Phylum : Haptophyta

Phylum : Eustigmatophyta

Phylum : Dinaflagellata

Phylum : Cryptophyta

Phylum : Phaeophyta (Brown algae)

Superphylum : Chlorophyta (Green algae)

Phylum : Chlorophyta (Grass-green algae)

Phylum	:	Siphonophyta (Siphonaceous green algae)
Phylum	:	Prasinophyta
Phylum	:	Zygnematophyta (conjugating green algae)
Phylum	:	Charophyta (Stoneworts)
Phylum	:	Euglenophyta
Superphylum	:	Rhodophyta

(v) Corliss (1987) system

Corliss (1987) classified the algal protists in the following 6 series.

Series I - Chlorophyte

This series comprises both motile (flagellated) and non-motile groups of green algae including unicellular, coenobial, filamentous and multicellular forms.

This series contains 5 phyla, these are: (1) Chlorophyta, (2) Prasinophyta, (3) Conjugatophyta, (4) Charophyta and (5) Ulvophyta.

This series is characterized by:

- (a) The presence of chlorophyll **a** and chlorophyll **b**.
- (b) Flattened mitochondrial cristae.
- (c) Cellulosic cell walls.
- (d) Motile cells.
- (e) Arrangement of thylakoids in several layered grana.
- (f) Chloroplast bounded by double membrane.
- (g) Most of these are fresh water ones.
- (h) Except for the Charophyta, the other phyla typically form a phycoplast in cytokinesis; in Charophyta phragmoplast is formed.

Series II - Chromophyte

This series is larger than the chlorophyte. The motile members are typically biflagellated with one smooth and other hairy flagellum, except diatoms and haptophytes in which flagellated stage is lacking in their life cycle.

The phyla included in this series are: (1) Chrysophyta, (2) Haptophyta, (3) Bacillariophyta, (4) Xanthophyta, (5) Eustigmatophyta, (6) Phaeophyta, (7) Raphidophyta.

The above phyla have some common characters. These are as follows:

- (a) Presence of chlorophyll **a** and chlorophyll **c** (chlorophyll **a** in Eustigmatophyta only).
- (b) Tubular mitochondrial cristae.
- (c) Typically no cell walls (except Phaeophyta) but often scales.
- (d) Often silicified cysts.
- (e) Pair of heterokont flagella.
- (f) Thylakoid grouped in threes.
- (g) Chrysolaminarin is main storage reserved food material.
- (h) Plastids bounded by 3 or 4 membranes.
- (i) Uncommon sexual reproduction.
- (j) Predominantly marine in distribution.

Series III – Euglenophyta

This series is characterised by the following features:

- (a) Presence of chlorophyll **a** and chlorophyll **b**.
- (b) Unique pellicle underlaid by interlinked microtubules.
- (c) Single large mitochondrion with discoidal cristae.
- (d) Nucleus with prominent endosome.
- (e) Permanently condensed chromosome.
- (f) Intranuclear spindle.
- (g) Presence of cytosome and a contractile vacuolar system.
- (h) Absence of cellulosic cell wall.
- (i) Storage of starch.

Series IV - Pyrrhophyte

This series includes the dinoflagellates and pyrrhophytes. these are characterized by the following features:

- (a) Presence of distinctive nuclear apparatus.
- (b) Presence of cortical alveoli (membrane bound vacuoles lacking contractile activity).
- (c) Presence of chlorophyll **a** and chlorophyll **c**.
- (d) Plastids generally covered by three membranes.
- (e) Uniquely positioned two heterodynamic flagella.
- (f) Tubular mitochondrial cristae.

Series V – Rhodophyte (Red algae)

Red algae are characterized by the following features:

- (a) Presence of phycoerythrin and phycocyanin and chlorophyll **a**.
- (b) Plastid is bounded by two layers containing single thylakoid.
- (c) Presence of floridean starch.
- (d) Mitochondrial cristae are lamellar.
- (e) Presence of gelatinous and microfibrillar cell walls.
- (f) Sexuality is common.
- (g) Distributed both in fresh water and marine habitats.

Series VI - Cryptophyte

- (a) Presence of chlorophyll **a** and chlorophyll **c** and phycobillins.
- (b) Biflagellate with both flagella bearing tubular hairs.
- (c) Presence of lamellar mitochondrial cristae.
- (d) Cryptomonads have a distinct gullet (invaginated cell surface functioning as a means of ingestion of food materials) and ejectisomes (extrusomes).
- (e) Mitosis is usually open.
- (f) Starch is the reserved food material.

3. Ultrastructure of algal cell

Basically there are two types of cells in Algae. They are prokaryotic and eukaryotic.

(i) Prokaryotic Algae

The blue-green algae (Cyanophyceae or Myxophyceae) show the prokaryotic cell organization (Fig. 1.1). Nuclear envelope around the nuclear material is absent. The DNA (Deoxyribonucleic acid) material representing the nuclear body consists of fibrils which may extend through out the cell or concentrated in the central part. The membrane-bound plastids are absent; the photosynthetic lamellae occur freely in the cytoplasm. The endoplasmic reticulum, mitochondria and golgi apparatus are also absent.

The cells of a planktonic blue-green algae, e.g. *Anabaena*, *Oscillatoria* etc., usually contain a large number of smaller bodies of irregular shape known as the gas vacuoles or pseudovacuaules. These vesicles are bounded by a single membrane, and contain metabolic gases. Gas vacuoles are more commonly produced under low light intensity and they suddenly collapse under higher light intensity. The most important feature of gas vacuoles is that they vanish completely when subject to pressure. Since they contain metabolic gases, the presence of gas vacuoles in a cell makes it buoyant, i.e., float on the surface of the water. Likewise, disappearance of the vacuoles makes the organism sink down.

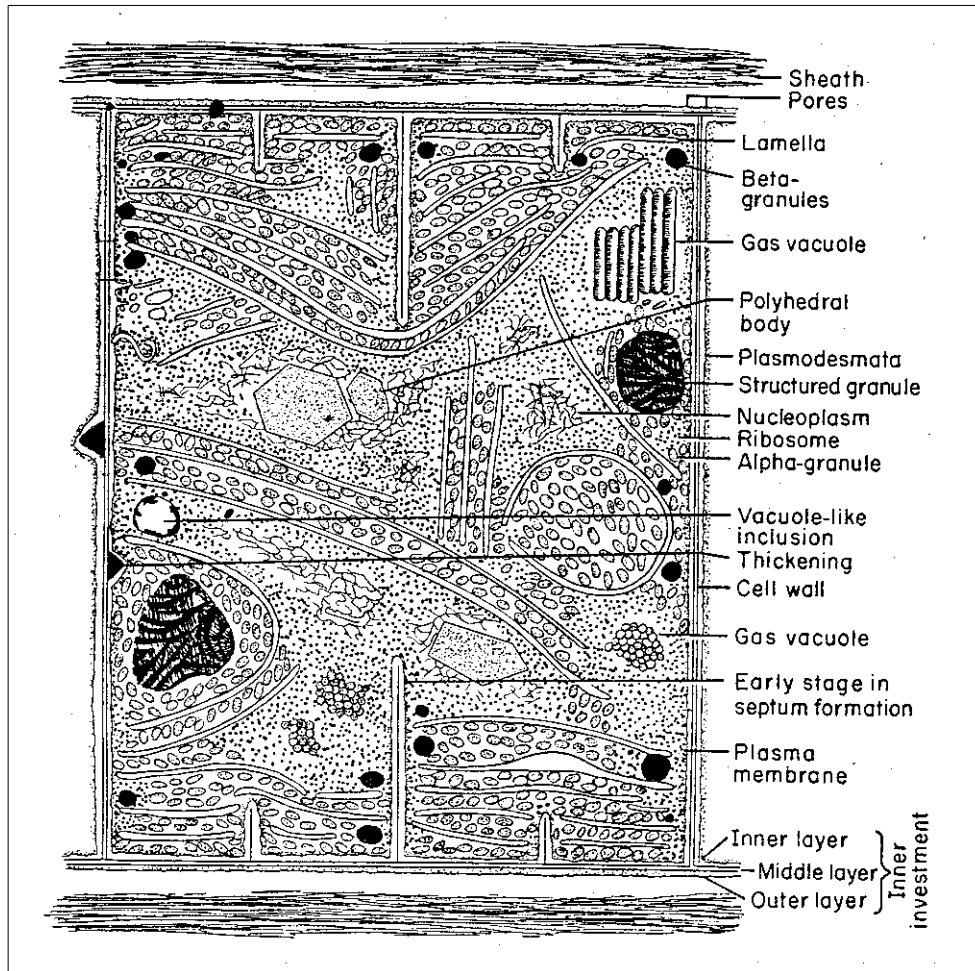


Fig.1.1 Diagrammatic sketch of a typical cyanobacterial vegetative cell to illustrate its fine structure (adopted from Kumar, 1985)

The central part of the cell consisting of nuclear material which is transparent having lower electron opacity, is known as nucleoplasm. It has numerous randomly disposed fine strands of DNA microfibrils. In some forms, the nucleoplasm is traversed by a few photosynthetic lamellae. There is no nucleus. DNA microfibrils lack histones and protamines; essential proteins are responsible for the composition of chromosomes.

Besides the above organelles, the ultrastructure of the cell reveals the presence of some granular bodies: (1) Polyglucoside granules (α granules) occur commonly associated with the thylakoids. They are less dense and longer than the ribosomes and represent glycogen granules. (2) The structural granules are large and dense and probably represent the areas of cyanophycean granules. (3) Ribosomes, the tiny granules (100-150 nm) distributed in the entire cytoplasm and mostly around the nucleoplasm provide the sites for protein synthesis. (4) Polyhedral bodies (carboxysomes) occur in the central region of the cell and contain the important enzyme ribulose biphosphate carboxylase oxygenase. (5) Poly-beta-hydroxybuterate granules which may be

distinguished from the closely resembling polyphosphate granules by the presence of a 3 nm limiting monolayer are present in some blue-greens such as *Chlorogloea fritschii*, *Microcystis* etc.

(ii) Eukaryotic cell

All other algae (except blue-greens) show eukaryotic cell organization. The eukaryotic cell has the same structure as is the typical of the higher plants (Fig. 1.2A). The nucleus is separated from the cytoplasm by a distinct nuclear membrane. It is divided by mitosis. The membrane-bound organelles such as chloroplasts, mitochondria, golgi bodies and endoplasmic reticulum, are present in cytoplasm.

Cell wall

Basically an eukaryotic cell of algae is chiefly composed of cellulosic or silicified materials. In green algae, the cell wall is cellulosic; in yellow green algae it is chiefly pectic while in brown algae, certain additional compounds like alginic acid, fucoidin, fucin and hemicellulose occur very prominently. In red algae, the cell wall is made up of cellulose and pectin but in the diatoms the valves are composed of hydrated amorphous silica within a pectin like matrix.

Plastids

In eukaryotic cell of *Chlamydomonas*, there is a single double membrane –bound cup-shaped chloroplast occupying two-third of cell at posterior end. In all green algae, these photosynthetic organelles contain chlorophyll **a** and chlorophyll **b**. In some cases, chlorophyll **b** is replaced by chlorophyll **c**, **d** or **e**. Chloroplast contains photosynthetic lamellae and colourless granular stroma. In red algae, the single lamella is widely separated while in other groups, the lamellae are stacked into bands. Brown algae usually possess 3 thylakoids in a band while in green algae, the range varies from 4-6 thylakoids per band. Recent studies showed that histone-free DNA, messenger and transfer RNA, ribosomes also occur in the chloroplasts and other chromatophores.

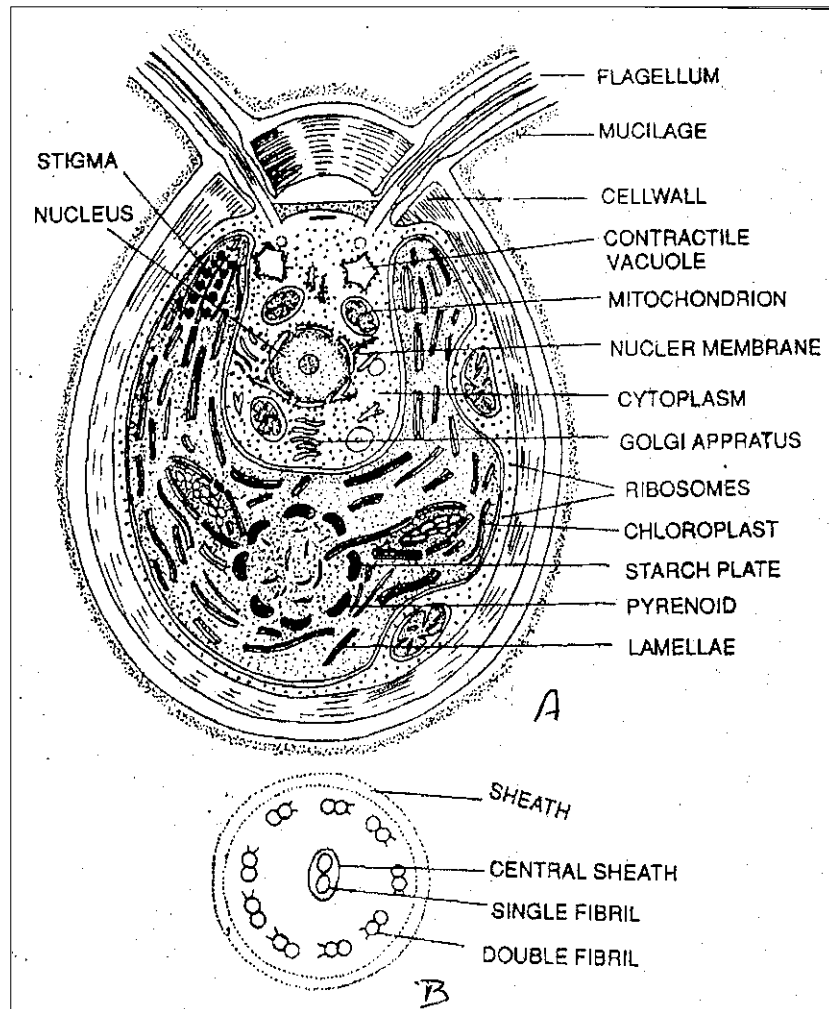


Fig. 1.2. A. Ultrastructure of eukaryotic cell (*Chlamydomonas*); B. Transverse section of flagellum seen under the electron microscope.

The number, position and shape of the chloroplast or chromatophore vary in different group of Algae. A single chloroplast occurs in Zygnematales and Charales while in many others, the number is usually more than one cell. The plastids may be cup-shaped, girdle-shaped, spiral, stellate, discoid or plate-like in different species of algae.

Pyrenoids with starch sheath occur commonly in a number of genera of green algae such as *Chlamydomonas*, *Hydrodictyon*, *Oedogonium*, *Spirogyra*, *Ulothrix*, *Volvox*, *Zygnema*, etc. These structures are found lying within or on the surface of a plastid and contain densely packed proteinaceous fibrils in the central core.

Stigma (Eye-spot)

Stigma occurs usually within the plastid in the anterior part of the motile cell (*Chlamydomonas*) or near the base of the flagellum. It is a reddish streak or a small dot-like body. It is served as photoreceptive organ and involved in phototactic movement of the cell.

Nucleus

In eukaryotic cells, the genetic apparatus is represented in the form of a well organized nucleus with outer and inner membranes. In *Euglena*, the two nuclear membranes are widely separated by a perinuclear space. Within a nucleus, there are chromosomes but no organized chromosomes occur in dinoflagellates. Majority of green algae are uninucleate; however the taxa belong to orders Cladophorales, Siphonales and Charales are multinucleate (coenocytic).

Mitochondria

Mitochondria are sites for the localization of the chief respiratory enzymes. A mitochondrion is bounded by a double membrane, of which inner one is folded and projects into the central cavity. The mitochondria also possess DNA, RNA and ribosomes as in the chloroplast.

Dictyosomes (Golgi apparatus)

Dictyosomes occur in stacks of 2-20 smooth lamellae (cisternae) and collectively form the golgi apparatus. Generally, they are found associated with the nucleus, chloroplast or the base of the flagella. There are evidences shown that golgi apparatus in Algae play an important role in the formation of wall and also scales in Haptophyceae and Prasinophyceae.

Endoplasmic reticulum

In eukaryotic algal cell, the entire cytoplasm is traversed by a well-organized system of tubules and vesicles, commonly referred to endoplasmic reticulum. These structures are associated with the protein synthesis.

Vacuoles

Eukaryotic algal cell commonly possesses one or two vacuoles bounded by tonoplast membrane. They play an important role in osmo-regulation of water and solutes. In motile cells of the green algae, there are usually two contractile vacuoles which alternate contraction and expansion, and expel out the excess water and waste materials.

Table 1.1 Some properties of Prokaryotes and Eukaryotes

	Characters	Prokaryotic cell	Eukaryotic cell
1.	Size	upto 10 μm	upto 100 μm
2.	Membrane-bound organelles	Absent	Present
3.	Cell wall	Generally present	Present or absent
4.	Endoplasmic reticulum	Absent	Present
5.	Golgi bodies	Absent	Present
6.	Ribosomes	70s (50s + 30s)	80s (60s + 40s)
7.	DNA genome	Usually single, circular DNA molecule	Many DNA molecules associated with histones in definite chromosomes
8.	Spindle or mitotic figures	Absent	Present
9.	Location of phosphorylative cell respiration	Cell membrane	Mitochondria
10.	Location of photosynthesis	Cell membrane (or) thylakoids	Chloroplasts
11.	Reproduction	Fission, fragmentation, parasexual phenomenon (amitosis)	Mitosis, meiosis, true sexuality
12.	Chloramphenicol inhibits protein synthesis	Yes	No
13.	Cyclohexamide inhibit protein synthesis	No	Yes

Flagella

Many unicellular and multicellular colonial forms are motile through out their life cycle. There are motile sexual zoospores and gametes in a large number of eukaryotic algal groups except red algae. Motility is brought about by the lashing action of flagella.

Depending on their morphology, motile bodies possess two types of flagella viz., (I) acronematic or whiplash type which are smooth (Fig. 1.3A), and (ii) pantonematic or tinsel or flimmer type which bear longitudinal small hairy or filamentous appendages (Fig. 1.3B).

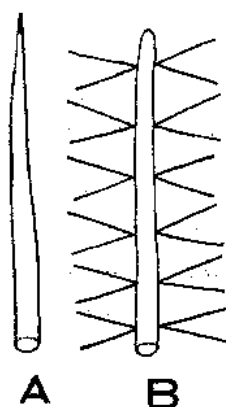


Fig. 1.3. A, Acronematic type (common in Chlorophyta); B, Pantonematic type (common in Chrysophyceae and Phaeophyceae)

The flagellum arises from blepharoplast, a granular structure situated usually anteriorly in the cytoplasm at the margin. The inner core of the flagellum is composed of a pair of singlet fibrils. These are surrounded by a peripheral cylinder formed of 9 doublet fibrils. So the flagellum has got 9+2 configuration of fibrils enveloped by a sheath (Fig. 1.2B).

In Chlorophyta, the flagella are 2,4 or many in a whorl, which arise anteriorly and are smooth and equal in length. In Xanthophyta and Phaeophyta, each motile cell possesses two unequal flagella of which one is acronematic and other pantonematic type. The former type arises anteriorly and latter one posteriorly or laterally.

Range of thallus organization

Algae show a wide range of variation in thallus organization. Basically, thallus organization is of two types, the unicellular and the multicellular. The wide range of forms that algae exhibit arises from a modification or elaboration of these types.

(i) Unicellular Algae

Large number of unicellular forms are found in major groups of algae such as Cyanophyta, Chlorophyta, Bacillariophyta and Rhodophyta. However, unicellular forms may be motile or non-motile.

(A) Unicellular Motile: The motile forms are of two types, the flagellated type, moving by means of flagella (found in all phyla except the Cyanophyceae, Prochlorophyceae and Rhodophyceae) and, the rhizopodia kind, having the fine protoplasmic projections (rhizopodia) and showing an amoeboid movement (Tribophyceae).

The flagellated cells may have a rigid cell wall or periplastic as in *Euglena*. The flagella may be one in *Chromulina* or two and equal as in *Chlamydomonas* (Fig. 1.4A), or two and unequal, e.g., *Cryptomonas*.

In some flagellates, external to the periplast there is a calcareous envelope and they are called encapsulated forms, e.g. *Chrysococcus*.

(B) Unicellular Non-motile: Unicellular non-motile algae are coccoid genera which lack both flagella and pseudopodia. However, these forms usually bear a thick cell wall as in *Chlorella* (Fig. 1.4B) and *Chroococcus* (Cyanophyta). Unicellular non-motile forms also found in Bacillariophyceae, Xanthophyceae (*Characiopsis*) and Rhodophyceae (*Porphyridium*). The smallest known eukaryotic algae is *Micromonas pusilla*.

(ii) Multicellular Algae

Depending on the manner in which cells are produced and arranged during vegetative phase, three principal types are recognized. These are colonial, filamentous and siphonous.

A. Colonial forms: A colony is a group of separate cells generally similar in structure and function and aggregated by a mucilaginous envelope. There are four main types of colonial organization – coenobial, palmelloid and dendroid.

Coenobial type – A coenobium is known to possess a definite shape of the colony and a constant number of cells arranged in a specific manner. The coenobium may be motile or non-motile. There is no division of cells during vegetative phase of the colony and the cells are embedded in the mucilaginous matrix. In the motile forms, the cells are flagellated, e.g., *Volvox* (Fig. 1.4C). In the non-motile, the cells are coenocytic, e.g., *Hydrodictyon* (Fig. 1.4D).

Palmelloid type – Contrary to the coenobium type, in palmelloid forms, neither the number of cells nor the shape and size of the constituent cells, are constant. All the cells are held together in the mucilaginous matrix and give the irregular outline of the thallus, e.g. *Tetraspora* (Fig. 1.4E), *Aphanocapsa* (Cyanophyta).

Dendroid type – In the dendroid forms, cells are united in a branching manner by the localized production of mucilage at the base of each cell. The whole colony looks like a tree in habit, e.g., *Ecballocystis* (Fig. 1.4F) and *Ecballocystopsis*, both belong to Chlorophyta.

B. Filamentous forms: A uniseriate row of cells joined end to end in a transverse plane through middle lamellae constitute a trichome. When this trichome surrounded by sheath, is referred to as a filament.

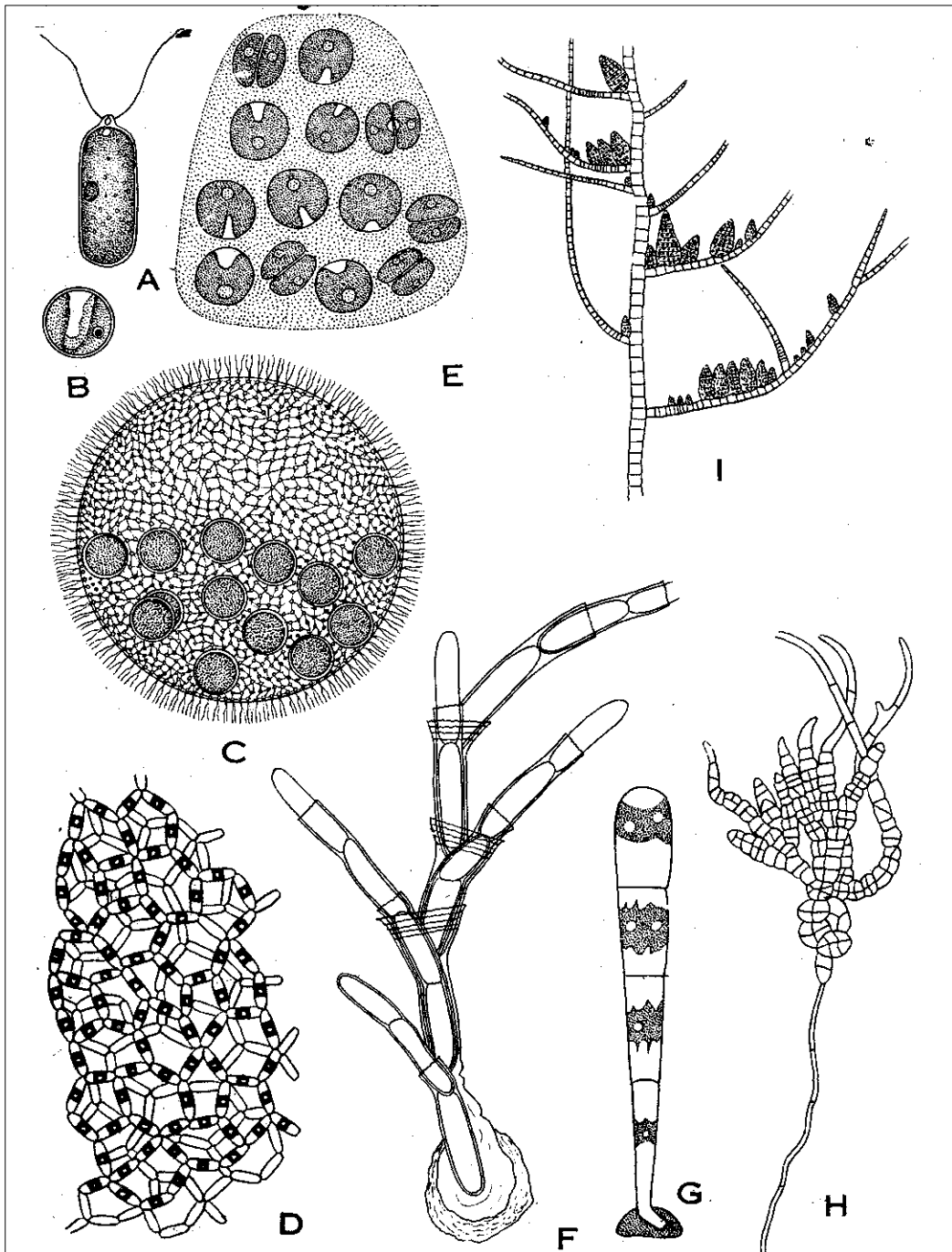


Fig.1.4. Range of thallus structure in algae.

A. *Chlamydomonas*, unicellular flagellated motile cell; B. *Chlorella* unicellular, non-motile coccoid cell; C. *Volvox*, multicellular flagellated motile coenobium; D. *Hydrodictyon* multicellular non-motile coenobium; E. *Tetraspora*, palmelloid colony; F. *Ecbellocystopsis*, dendroid colony; G. *Ulothrix*, unbranched filament; H. *Fritschella*, branched heterotrichous filament; I. *Ectocarpus*, branched filament. (Based on Fritsch, 1935).

Unbranched filaments – A filament may be unbranched, e.g., *Anabaena*, *Nostoc*, *Oscillatoria* of Cyanophyta and *Oedogonium*, *Ulothrix* (Fig. 1.4G) of Chlorophyta. Some filamentous taxa exhibit distinct polarity with the trichomes tapering towards the tip, e.g., *Rivularia*.

Branched filaments – The branching of the filaments is of two kinds – false and true. In false branching, which occurs in Scytonemataceae (Cyanophyta), the trichome generally fragments due to the degeneration of an intercalary cell (or by the formation of biconcave separation discs), after which one or both of its ends adjacent to the dead cell grow out of the parent sheath, giving the resemblance of branching, e.g. *Scytonema*.

True branching results from repeated transverse divisions of the lateral outgrowth produced on the main filament. The truly branched thalli are of following types: (1) simple branched filament, e.g. *Cladophora*; (2) heterotrichous, in which the thallus is differentiated into an erect and prostrate system of branched filaments, e.g., *Coleochaete*, *Fritschiella* (Fig. 1.4H), and *Draparnaldiopsis* of Chlorophyta, *Ectocarpus* of Phaeophyta (Fig. 1.4I), *Batrochospermum* of Rhodophyceae and *Stigonema* of Cyanophyta. In *Draparnaldiopsis*, the prostrate system is well developed. Fritsch opined that the first land plants might have arisen from the algae exhibiting heterotrichous habit; and (3) Pseudoparenchymatous in which the thalli show uniaxial or multiaxial construction, e.g., *Batrochospermum* (uniaxial), *Polysiphonia* (multiaxial) (Fig. 1.5B) etc. In multiaxial pseudoparenchyma, the branches of many axial filaments aggregate in juxtaposition, e.g. *Nemalion*. The central filaments give rise to lateral branches. The branches become compact and is called cortex, e.g., *Codium*, *Polysiphonia*.

C. Siphonous forms: The filamentous habit without occurrence of septa and presence of coenocytic condition constitute the siphonous structure of the thallus. Such condition results into larger thalli in some genera. Many workers considered these genera as acellular or unicellular forms, e.g., *Dichotomosiphon* of Chlorophyta (Fig. 1.5A) and *Vaucheria* of Xanthophyta (Fig. 1.5D).

D. Parenchymatous forms: Parenchymatous condition of a thallus results when uniseriate filaments show potentiality of cell division in more than one plane. In these forms growth takes place in four ways – diffuse, intercalary, trichothallic and apical. In simple filamentous forms such as *Ulothrix* and *Nostoc*, the growth of thallus is diffuse because each vegetative cell is potentially capable of growth and division. In trichothallic growth, the cells at the base of a hair-like branch are meristematic, e.g., *Rivularia*. A good example of intercalary growth is *Laminaria* in which growth of the thallus is brought about by the meristem located at the junction of the stipe and the blade. The thalli of the Charophyceae, Dictyotales and certain other algae grow by the activity of a single or a group of apical cells.

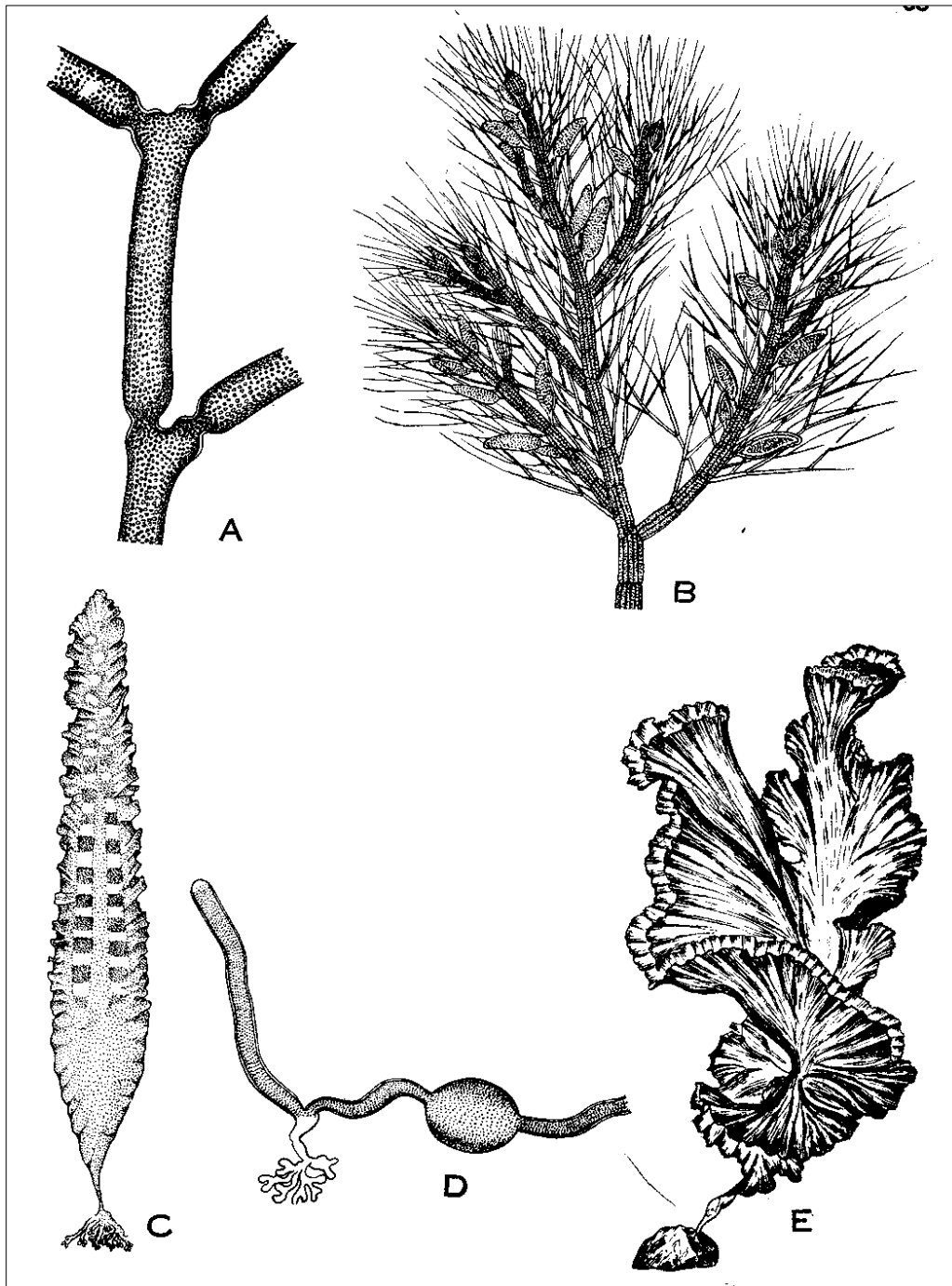


Fig. 1.5 A. *Dichotomosiphon*, B. *Polysiphonia*, C. *Laminaria*, D. *Vaucheria*, E. *Ulva*

The thallus in these forms may be foliage and flat (*Ulva*, *Porphyra*) or tubular (*Enteromorpha*). In brown algae parenchymatous habit is well-developed. The thallus is differentiated into central columella, middle cortex and outer meristoderm. Other examples are *Macrocystis*, *Fucus* etc.

5. Reproduction in Algae

Reproduction actually means the production of young ones similar to the parental individuals. The chief objective of the reproduction, therefore, is the perpetuation of the species and consequently its increase in number of the individuals in geometric ratio. The reproduction in algae is by vegetative, asexual and sexual methods.

(i) Vegetative Reproduction

(A) Fragmentation – The plant body breaks into several fragments and each such fragment develops into an individual. This is very common in filamentous forms belonging to the order Ulotrichales (Chlorophyta), i.e., *Hormidium* (Fig. 1.6A), *Stichococcus*, *Ulothrix* etc. The fragmentation of colonies also takes place in several blue-green algae, e.g., *Aphanocapsa*, *Aphanothece*, *Nostoc* etc.

(B) Budding – In some genera of Chlorophyta, i.e., *Protosiphon*, the vesicle gives rise a lateral bud (Fig. 1.6B). This small lateral bud becomes separated and develops into an adult individual.

(C) Hormogonia (hormogones) formation – The trichome breaks into small pieces of two or more cells. These small pieces are known as hormogones. Each hormogone develops into a new individual, e.g., *Anabaena*, *Lingbya* (Fig. 1.6C), *Nostoc*, *Oscillatoria*, *Scytonema* etc.

(D) By adventitious thalli – Certain special structures, known as propagules, formed from the thallus, are involved in vegetative reproduction, e.g., *Nereocystis*, *Sphacelaria* (Fig. 1.6D) etc.

(E) Akinetes (resting spores) formation – Akinetes are resting cells which mainly serve as a means of perennation rather than multiplication. The protoplasts of the vegetative cells become rounded and possess a thick cell wall. These thick-walled cells are separated from the parental plant and withstand unfavourable conditions. Thus they help in perennation. Akinetes are common in Cyanophyta members, such as *Anabaena*, *Gloetrichia*, *Nostoc* and also in *Pithophora* (Fig. 1.6E) of Chlorophyta.

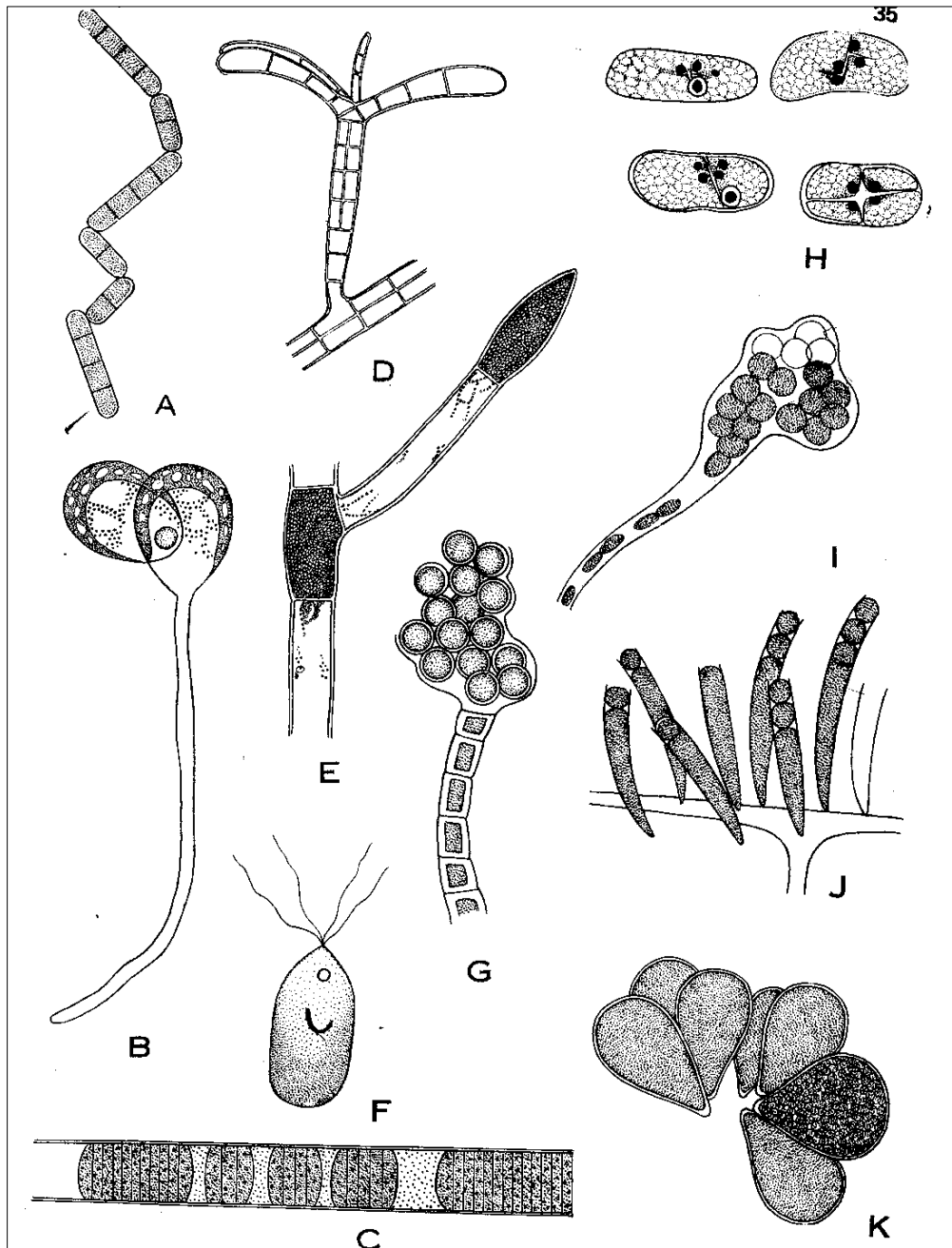


Fig. 1.6. Vegetative and asexual reproduction in algae.

A. *Hormidium*, fragmentation of a filament; B. *Protosiphon*, stage in budding of a vesicle; C. *Lyngbya*, filament with hormogonia; D. *Sphacelaria*, propagule; E. *Pithophora*, filament with a terminal and intercalary akinete; F. *Ulothrix*, quadriflagellate zoospore; G. *Ulothrix*, aplanospores; H. *Scenedesmus*, showing production of autospores; I. *Protosiphon*, vesicle with hypnospores; J. *Chamaesiphon*, exospores; K. *Dermocarpa*, endospores; (C-After Smith, 1955; rest after Fritsch, 1935).

(ii) Asexual Reproduction

Asexual reproduction takes place by several methods.

Motile spore (zoospore) formation: The spores are reproductive units specialized for asexual reproduction. During favourable conditions, each spore can grow into a new organism. These spores with flagella are capable of swift movement. The factors which influence the zoospore formation are: (1) temperature changes, (2) light intensity variation, (3) water flow, and (4) concentration variation of culture medium.

The zoospores are tiny, naked masses of protoplast furnished with fine protoplasmic threads, the flagella. In some genera, e.g., *Ulothrix* (Fig. 1.6F), *Drepanaldiopsis* and *Fritschiella* zoospores are quadriflagellate while in others, e.g., *Oedogonium* they bear a crown of flagella. After a brief swimming, zoospore settles down on a suitable substratum, regenerates its cell wall and develops into a new individual.

Non-motile spores: Asexual reproduction takes place by variety of non-motile spores, such as aplanospores, autospores, hypnospores, exospores, endospores and tetraspores.

Aplanospores – They are produced in the same manner as zoospores. They are non-flagellate and non-motile, and produced during the drier conditions of the environment. The protoplast of vegetative cell divides repeatedly and gives rise aplanospores. These are liberated out and germinate to give rise new individual during favourable conditions. Aplanospores are common in Chlorophyta, e.g., *Chlamydomonas*, *Ulothrix* (Fig. 1.6G) etc.

Autospores – They are the non-motile spores similar to the parent cells but smaller in size, e.g., *Chlorella*, *Scenedesmus* (Fig. 1.6H) etc. The contents of cell divide into 2, 4, 8 sometimes 16 daughter protoplasts. Each daughter protoplast rounds-off to form a non-motile autospore.

Hypnospores – They are nothing but very thick-walled aplanospores and produce during adverse conditions, e.g., *Protosiphon* (Fig. 1.6I).

Exospores – They are the exogenously formed naked spores. In certain epiphytic Cyanophyta, e.g., *Chamaesiphon* (Fig. 1.6J), the cell membrane bursts up at the apex, and the exposed protoplast becomes fragmented to give rise spherical spores known as exospores. They are surrounded by a delicate membrane. They germinate whenever the host is available.

Endospores – They are endogenously formed spores. In some genera of Cyanophyta, endospores are formed by successive divisions of cell contents in three planes. These fragments of protoplast increase in size and on liberation they regenerate the cell wall. In *Dermocarpa* (Fig. 1.6K) the entire protoplast of a cell forms a single endospore.

Tetraspores – In *Polysiphonia* (Rhodophyta) tetraspores are produced on tetrasporophyte (Fig. 7.5E, F). The nucleus of tetrasporangium undergoes meiosis and gives rise

4 haploid, motionless spores. The resultant tetraspores germinate to produce two kinds of sexual plants of the gametophytic generation.

(iii) Sexual Reproduction

Sexual reproduction involves the union of two gametes of opposite sex to produce the zygote. Such condition is not prevailed in the prokaryotes, such as bacteria and blue-green algae. However, in bacteria, there are definite records of genetic recombination. Parasexuality or genetic recombination of similar nature appears to take place in a few genera, viz., *Anabaena*, *Anacystis* and *Cylindrospermum*, among Cyanophyta under certain controlled conditions in culture (Kumar, 1999). Thus, the sexual reproduction among algae indicates a comparatively advanced phase in the process of sex.

Sexual reproduction may be: (A) isogamous, (B) anisogamous, and (C) oogamous.

(A) Isogamous: It is the simplest and primitive type of sexual reproduction. The two opposite gametes possess similar or identical morphological features (Fig. 1.7A). These gametes are normally naked and non-flagellated or non-motile. The non-motile ones show amoeboid movement and are known as aplanogametes. The gametes are ordinarily produced as the zoospores by the divisions of the protoplast in the ordinary vegetative cells but these are always smaller in size than the zoospores.

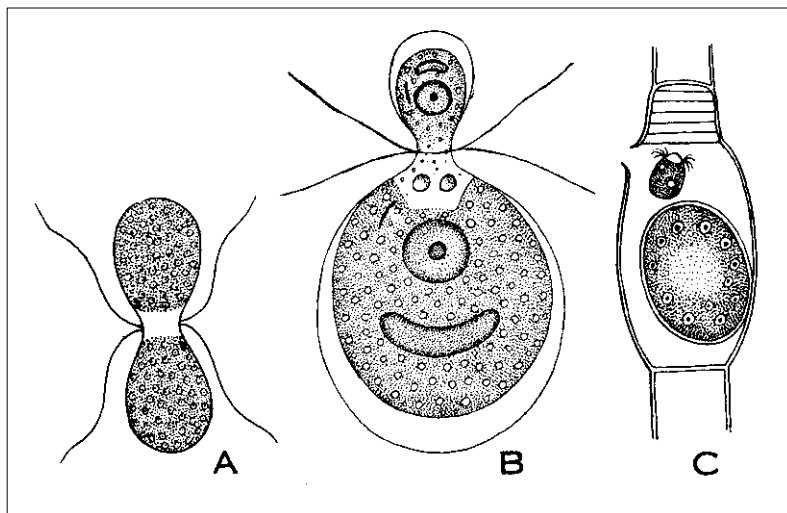


Fig. 1.7. Sexual reproduction in algae

A, B. *Chlamydomonas*. A, fusion of two opposite isogametes; B, fusion of two opposite anisogametes; C. *Oedogonium*, oogamous sexual reproduction, a spermatozoid seen near a non-motile female gamete, ovum (egg) within oogonial wall (All based on Fritsch, 1935).

Among isogamous forms, these two fusing gametes come from two different individual thalli, i.e., functionally they are dioecious, they are termed as plus (+) or minus (-) strains or mating types. It is very common in Siphonales of green algae and in Phaeophyta. In some unicellular Chlorophyta, e.g., *Chlamydomonas*, the mature adult cell may turn into a single gamete. Such condition is known as hologamy.

In *Spirogyra*, the fusing gametes are morphologically similar but dissimilar in their behaviour, such a physiological anisogamy is a step towards anisogamy.

In *Ectocarpus siliculosus* (brown algae), gametes are identical but at the time of fusion one gamete becomes passive and is surrounded by a large number of so called male gametes. The passive gamete may be designated as female. This mode of fusion is called clump formation (Fig. 6.7C).

It has been suggested that in isogamous sexual reproduction each strain secretes its own specific type of chemotactic substance. The act of fusion in isogamy is called conjugation and the fusion product is known as zygospore.

(B) Anisogamous: In some algae, the two opposite gametes are not only genetically distinct, but they also differ in size, motility and behaviour. Large number of small size gametes are active (male gametes) whereas fewer number and larger in size gametes are more passive (female gametes). They are derived from different thalli. Fusion of these two dissimilar gametes is known as anisogamy, e.g., *Chlamydomonas* (Fig. 1.7B), *Pandorina* etc., and members of Phaeophyta.

(C) Oogamous: It is the highest and most advanced stage of sexual reproduction and it is found in the filamentous forms. The gametes are produced in special sexual organs which are sharply differentiated from the ordinary vegetative cells. The female sex organ, known as oogonium, produces a single ovum and male reproductive structure, antheridium, produces one or more male gametes furnished with flagella (Fig. 1.7C).

The most complex reproductive structures are present in *Chara* and *Nitella*. Male and female reproductive structures are called globule and nucule respectively (Fig. 3.20A). In Rhodophyta, non-motile, male gametes are called spermatia; female reproductive structure is known as carpogonium (Fig. 7.5A).

The ovum, with the exception of Fucales, is retained within the oogonium. The male gamete gains entrance into the oogonium through an aperture in its wall. As a result of fusion of two gametes, zygote is formed. This zygote develops either directly or undergoes meiosis to give rise new adult individual.

In Cyanophyta true sexuality is absent but genetic recombinations take place.

The reproduction in algae indicates that there has been a progressive change from isogamy to anisogamy and from anisogamy to oogamy. This progression appears to have evolved independently in different groups of algae including Chlorophyta, Xanthophyta, Bacillariophyta and Phaeophyta.

6. Origin and Evolution of Sex

Sexual reproduction involves the union and fusion of two haploid gametes. These gametes are called male and female or plus and minus gametes. They may be isogametes (morphologically similar) or anisogametes (morphologically dissimilar). The gametes are usually naked and products of the reduction division. As a result of fusion, zygote is formed. This zygote germinates to give rise the offspring. In some cases, in which plant body is haploid, zygote undergoes meiosis, e.g., *Chlamydomonas*, *Oedogonium*, *Ulothrix* etc. In Cyanophyta, sexual reproduction is absent. However, genetic recombinations have been reported in this phylum. The Cyanophyta may be considered as the most primitive group among algae. Also in Chlorophyceae, some primitive forms, such as *Chlorella*, *Scenedesmus* etc., reproduce exclusively by asexual bodies; others such as *Chlamydomonas* and *Ulothrix* form asexual motile zoospores as the chief reproductive structures under favourable conditions and sexual reproduction takes place in the later stage of the life-history.

From the above discussion, it is quiet evident that the most primitive algae lack sexual reproduction and asexual reproductive bodies might have given rise to sexual reproductive structures during the course of evolution. This supports the fact that in some algae such as *Chlamydomonas*, *Ulothrix* etc., the isogametes are similar to asexual zoospores which are slightly larger; the unfused isogametes some times may also function as zoospores. In *U. zonata*, there are 4 kinds of swimmers viz., quadriflagellate macrozoospores, quadriflagellate microzoospores, biflagellate microzoospores and biflagellate gametes. Except biflagellate gametes, all the swimmers are able to germinate to give rise the new individuals. Apparently they have some quantity of factors responsible for growth into a new individual. But the smallest swimmer, i.e., gamete usually do not possess sufficient quantity of factors for growth and usually fail to germinate; they have to fuse in pairs to give rise a zygote. The division product of zygote ultimately gives rise to a new plant. During the sexual fusion of the two gametes, the zygote gains enough quantity of factors responsible for the development of the new plant. The nature of growth factors is, of course is not known so far. Generally, in zoospore production, the protoplast of parent cell undergoes a lesser number of divisions and therefore, the division-products (zoospores) are larger in their size than gametes. But gametes are formed as a result of a large number of divisions of parent protoplast. Zoospores are able to give rise the new plant upon germination but rarely gametes may produce weak filaments. So the pairing of gametes is necessary and it is an adaptation to supplement the quantity and level of growth factors.

As far as **evolution of sexual reproduction** is concerned, isogamous is considered to be the primitive type found in primitive taxa such as *Chlamydomonas*, *Hydrodictyon*, *Ulothrix* etc. The next size in the evolution of sexual reproduction is heterogamous in which two morphologically dissimilar gametes fused together, forming the zygote; the smaller gametes behave as the male (active) and larger one as the female (sluggish). In *Chlamydomonas monoica*, the female receives the cytoplasmic contents of the male gamete. In *C. braunii*, the two fusing gametes are of different sizes.

The next step after the heterogamous type is the oogamous which is considered as the most advanced type of sexual reproduction. The female gamete is completely passive and is known as egg (ovum). Male gamete is much smaller and very active, and it is known as antherozoid. The process is well marked in *Chlamydomonas coccifera*. Oogamy is rare in the unicellular forms and more common in the filamentous algae. The egg is produced in the oogonium, e.g., *Oedogonium* (Fig. 1.6C), *Vaucheria* etc. In Rhodophyta highly specialized type of oogamy is found. Both male and female gametes are non-motile, and are known as spermatia and carpogonia respectively. The carpogonium possesses a long projectile structure, known as trichogyne which serves to receive the spermatia (male gametes), e.g., *Batrachospermum*, *Polysiphonia* etc.

7. Life Cycles

On the basis of number of generations, the life cycles are of three types:

(i) **Monophasic (monogenetic):** Single phase is dominant and distinct, e.g., *Chara*, *Chlamydomonas*, *Volvox* etc.

(ii) **Diphasic (digenetic):** Morphologically two distinct generations are present, eg., *Ectocarpus*, *Ulva* etc.

(iii) **Triphasic (trigenetic):** Morphologically three distinct phases or generations are present, e.g., *Batrachospermum*, *Polysiphonia* etc.

On the basis of cytology and morphology, 5 types of life cycles are found in the algae. They are as follows:

(i) **Haplontic:** Haploid gametophytic phase is dominant one, whereas the diploid stage is represented by the zygote. Majority of Chlorophyceae members represents the haplontic life cycle.

(ii) **Diplontic:** The plant body is diploid and it is dominant phase in the life cycle. Meiosis takes place at the time of formation of gametes; so gametes are haploid. The union of two gametes results in the formation of diploid zygote which in turn develops into the adult

plant. Diplontic life cycle is common in Bacillariophyta (diatoms), some Siphonales and in Fucales of Phaeophyta.

(iii) Diplohaplontic: There are two distinct individuals of haploid and diploid generations, alternating each other in the life cycle. These are two types again.

(A) Isomorphic – In isomorphic diplohaplontic life cycle, both diploid and haploid plants are morphologically similar, and alternation of generations take place in between these two plants. The zygote directly gives rise to diploid sporophyte. It produces zoospores only after meiosis and they germinate to give haploid, gametophytic plants. Haploid plants are similar to sporophytes and give rise the gametes, e.g. *Ectocarpus*.

(B) Heteromorphic – When the diploid and haploid plants are morphologically dissimilar, the life cycle is called heteromorphic, e.g., *Laminaria*, in which the sporophyte is macroscopic whereas gametophyte is microscopic. In *Urospora*, the gametophyte is large and dominant while the sporophyte is small in size.

(iv) Haplobiontic: In this life cycle, two haploid generations alternate with one diploid zygote stage, e.g., *Batrachospermum* in which two haploid phases, the haploid gametophyte and carposporophyte, are present.

(v) Diplobiontic: In this life cycle, there are two diploid phases and one haploid phase. In *Polysiphonia*, both carposporophyte and tetrasporophyte are diploid in nature. Tetraspores are produced on tetrasporophyte after meiosis. The haploid tetraspores give rise the gametophyte. Both the diploid tetrasporophyte and haploid gametophyte are morphologically similar.

8. Economic Importance of Algae

Since algae are the simple photosynthetic plants, they perform 90% of the total photosynthetic activity globally. They are intimately connected with human beings as a source of food, manure and fodder. They have been exploited in the cleaning of the environment (bioremediation of the environment) and also in the urban sewage treatment plants.

(1) Algae as food

Algae and their products have been eaten in the most maritime countries. They are rich in proteins, vitamins and minerals. In the Far East and the Pacific Islands, people eat seaweeds such as *Porphyra*, *Laminaria*, *Undaria*, *Gracillaria*, *Alaria* and *Asparagopsis*. In Japan, about 20 species of green, brown, red and blue-green algae are eaten and total sales of *Porphyra tenera* (a red alga) alone amounts to more than 80 million U.S. Dollars per year. Chemical analysis show that *P. tenera* has 30-35% proteins, 40-45% carbohydrates and a high percentage of vitamins A, B, C and E. Another alga, *Laminaria* growing on stones, cylinders and ropes, yields

a product known as '**Kombu**' or '**Konbu**'. Besides, *Monostroma* (a green alga) cultivating in Japan, yields a product known as '**Aonori**'. All these algal products can be served as a staple food for human beings. Some brown algae such as *Sargassum* and *Undaria*, and larger balls of the terrestrial species of *Nostoc* have been used as food by the Chinese and the South Americans (Peru).

Among red algae *Porphyra*, *Chondrus*, *Palmeria*, *Gelidiella* and *Gracillaria* are important edible algae in Canada, Japan, Philippines and Korea. They are used in salads, soups and vegetables. The unicellular algae such as *Chlorella*, *Scenedesmus*, *Spirulina* etc., have been mass cultured on large scale in many countries.

Chlorella and *Scenedesmus* have been exploited in the spaceships and nuclear submarine programmes as oxygen regenerating and, food and water recycling organisms.

(ii) Algae as fodder and biofertilizer

Sea weeds are rich in copper, iron, manganese, boron, cobalt, vanadium and molybdenum. They are used as fodder for livestock and poultry. *Gracillaria* is used as poultry feed. Algae such as *Ascophyllum*, *Laminaria* and *Fucus* are used as livestock feed. *Spirulina* when feed to fishes, poultry and cattle, their productivity is improved. Mass culture of *Spirulina* is gaining importance and this can be used as feed for fish, poultry and cattle.

Blue-green algae grow luxuriantly in the paddy field soils and contribute significantly in enriching the nitrogen content of the soils. More common nitrogen-fixing genera in the Indian rice fields are *Aulosira*, *Anabaena*, *Calothrix*, *Cylindrospermum*, *Gloeotrichia*, *Nostoc*, *Scytonema*, *Stigonema*, *Tolypothrix* etc. It has been estimated that about 15-48 kg nitrogen per hectare is fixed in the rice fields by the activity of these algae. They are known as biofertilizers. Nitrogen fixed by these algae is utilized by the crop plants. The soil also becomes rich in amino acids, vitamins and auxin-like compounds. These ingredients serve to improve the growth of the crop plants.

(iii) Commercial products from Algae

(A) **Alginates:** Alginic acid (carbohydrate) is extracted from the cell walls of several brown algae including *Ascophyllum*, *Durvillea*, *Echlonia*, *Fucus*, *Laminaria*, *Lessonia*, *Macrocystis*, *Nereocystis*, *Sargassum*, *Turbinaria* etc. Alginates have been used in the preparation of flame-proof fabrics and in plastic industries. Alginates are extensively used in pharmaceutical industry, especially in the preparation of dental impressions, gauze material in surgical dressing, and also used as an agent to stop the bleeding. Since alginates are non-toxic and possess colloidal properties, they are commonly used in the preparation of creams, jellies, soups, sauces and antibiotic capsules.

- (B) **Agar Agar:** Agar agar is a non-nitrogenous gel like substance extracted from the red algae, such as *Gelidium*, *Gracillaria*, *Gigartina*, *Chondrus*, *Ceramium* etc. Agar is used as gelling and solidifying agent in the preparation of culture media for culturing bacteria, fungi and algae. Besides, it is used as stabilizer and emulsifier in food, cosmetics, leather and pharmaceutical industries.
- (C) **Carrageenin:** This is a polysaccharide extracted from the cell walls of some red algae. Carrageenin forms colloidal solution with water. It is widely used in the bakery and confectioneries and also in preparation of creams, soups, sauces, cheese, fruit juice and also in the clarification of beer.
- (D) **Diatomite (Kieselgurh):** It is the cell wall material of diatoms, forming extensive deposits and it is called as diatomaceous earth or kieselgurh. It is insoluble, porous and chemically inert material. It is used in insulating the boilers as it can resist very high temperature. Alfred Nobel used diatomite as an absorbant for nitroglycerine in the manufacture of dyanamite. It is also used as industrial filter in sugar refining and brewing industries (see also Lesson V).

(IV) Antibiotics and medicine: The well known antibiotic, chlorellin obtained from *Chlorella* is effective against a number of pathogenic bacteria. Extracts from *Cladophora* and *Lingbya* can kill the pathogenic *Pseudomonas* and *Mycobacterium*. Sodium laminarin sulphate extracted from *Laminaria* can be used as blood anti-coagulant. It has been found that the extracts of *Digenia simplex* can be served as antihelmitic.

9. Fossil Algae

Very few fossil algae have been reported till date. Most coccolithophorids belonging to phylum Chrysophyta are well preserved as fossils and are known from the lower Jurassic. They occur abundantly in many Mesozoic and Tertiary rocks. The group coccolithophorids are characterized by the presence of coccoliths, i.e., the external calcitic microcrystalline plate or disc (Fig. 1.8). These coccoliths are much larger than the scales present in members of Chrysophyta. In fact, ordinary chalk often contains numerous little rosettes of calcite crystals (about 1 μm diameter); those crystals represent the fossil *Cocoliths*. The Cretaceous species, *Braarudosphaera bigelowi* is unique having survived to the present day; most other Cretaceous coccolithophorids must have become extinct by the end of Cretaceous itself, with various new species evolving in the Tertiary. The Tertiary rocks often harbour a very interesting group known as 'diacoasters' that are believed to be closely related to coccoliths.

Due to the siliceous nature of cell walls, diatoms (Bacillariophyta) are well preserved in the form of fossils. The Centrales have been reported from the Jurassic and the Pennales from the early tertiary. The first deposits of the Pennales appeared in the late Cretaceous after the Centrales appeared in the early Jurassic.



Fig. 1.8 *Cricosphaera roscoffensis*, coccoliths (x20,000) Courtesy P. Gayral

10. Summary

Classification: In modern systems of classifications many criteria have been taken into consideration, so that it is possible to understand the interrelationships and phylogeny of algae. Some of these criteria are: (1) photosynthetic pigments, (2) nature of storage products, (3) nature of cell wall components, (4) cell ultrastructure, (5) type of flagella.

Fritsch (1935) had divided the algae into eleven classes. Round (1973) classified the algae into two major groups, viz., Prokaryota and Eukaryota. Cyanophyta was included in the Prokaryota. Eukaryota again divided into 12 phyla. He had raised the Charales of Fritsch (1935) to the rank of phylum.

Range of thallus organization: Algae show a wide range of variation in thallus organization. They may be unicellular motile or non-motile ones; multicellular algae include the colonial, palmelloid, filamentous and siphonous forms and also highly advanced parenchymatous forms such as *Ulva*, *Porphyra*, *Macrocystis*, *Fucus* etc.

Reproduction: The reproduction in algae is by vegetative, asexual and sexual methods. Algal reproduction indicates that there has been a progressive change from isogamy to anisogamy and

from anisogamy to oogamy. This progression appears to have evolved independently in different groups of algae including Chlorophyta, Xanthophyta, Bacillariophyta and Phaeophyta.

Life Cycles: On the basis of number of generations, the life cycles are of three types, these are: (1) monophasic, (2) diphasic, and (3) triphasic. On the basis of cytology and morphology, the life cycles are: (1) haplontic, (2) diplontic, (3) diplohaplontic (isomorphic or heteromorphic), (4) haplobiontic, and (5) diplobiontic.

Model Questions

(1) Essay Questions

- (i) Give an account on thallus organization in Algae.
- (ii) Describe the ultrastructure of prokaryotic algal cell and, compare and contrast with the eukaryotic algae.
- (iii) Describe the reproduction in Algae and trace out the evolution of sex in algae.
- (iv) Describe the life cycles in Algae.
- (v) Give an account on economic importance of algae.

(2) Short Questions

- (i) Fritsch's system of algal classification
- (ii) Round's system of algal classification
- (iii) Filamentous forms of algae
- (iv) Coenobium
- (v) Heteromorphic alternation of generations in algae
- (vi) Algae as biofertilizers
- (vii) Single-cell proteins
- (viii) Kieselgurh
- (ix) Fossil algae

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Dr. S.M. KHASIM

ALGAE

LESSON-II

CYANOPHYTA (Blue-Green Algae) and PROCHLOROPHYTA (Prochlorobacteria)

OBJECTIVES

- 1 CYANOPHYTA
 - (i) Introduction
 - (ii) Occurrence and distribution
 - (iii) Range of thallus organization
 - (iv) Cell structure
 - (v) Nitrogen fixation
 - (vi) Reproduction
 - A. Vegetative reproduction
 - B. Asexual reproduction
 - (vii) Parasexual phenomenon (Genetic recombination)
 - (viii) Classification
 - (ix) Phylogeny and interrelationship
- 2 PROCHLOROPHYTA
- 3 Summary

1. CYANOPHYTA (Blue-green Algae)

(i) Introduction

The blue-green algae differently known as Cyanophyceae (Cyano=blue) or Myxophyceae (myxo=slime) or Schizomyceae (Schizo=fission) are generally called Cyanobacteria due to their similarity with eubacteria. The members of phylum Cyanophyta have some characteristics differ from other algae in (1) having the prokaryotic cell organization, i.e., lacking double membraned nucleus, chromatophores and mitochondria; (2) Presence of characteristic photosynthetic pigments such as chlorophyll **a** and β -carotene, biliproteins and myxoxanthophyll; (3) no flagella but motility is brought about by characteristic gliding action; (4) presence of specialized cells, known as heterocysts; (5) true sexuality is absent but genetic recombination occurs; (6) they involve in nitrogen fixation and convert the molecular nitrogen found in the atmosphere into useful nitrogenous compounds; (7) the unique reserve food materials are the **myxophycean starch** and a proteinaceous material **cyanophycin**; and (8) free-floating population of microscopic blue-green algae constitute the plankton of eutrophic (organic rich) lakes, and also oceans.

(ii) Occurrence and Distribution

The members of Cyanophyta are cosmopolitan in distribution, occurring throughout the world. However, they are more common in the tropical part of the world than in the temperate regions. The blue-green algae form a significant part of the free floating population which constitute the plankton of eutrophic fresh water bodies and also oceans. The rice fields in tropical and subtropical regions provide a very hospitable habitat for the luxuriant growth of nitrogen-fixing genera such as *Aulosira*, *Anabaena*, *Cylindrospermum*, *Scytonema*, *Tolypothrix* etc.

There are about 1600 species spreading over to 150 genera. The blue-green algae can withstand and grow in adverse and harsh environment, e.g., *Colteronema* and *Synechococcus* are grown in hot springs. The species of *Gloeocapsa*, *Nostoc*, *Plectonema*, *Rivularia*, *Calothrix* etc., are grown in fresh water habitats. Some are endophytic, e.g., *Nostoc symbioticum*, *Richelia intracellularis* etc., *Nostoc* is associated with the thalli of *Anthoceros* and *Anabaena* species, and also with the *Azolla*. Symbiotic nature is well represented in lichens in which major components of the thalli are blue-green algae such as *Nostoc*, *Gloeocapsa*, *Scytonema* etc.

Ecological studies on the bare rocks and virgin areas show that the blue-green algae are the pioneer colonizers. They develop the substratum on the rock for the growth of other algae and higher plant communities.

(iii) Range of Thallus Organization

The organization of plant body ranges from unicellular forms (*Synechococcus*) to relatively large branched heterotrichous filamentous forms (*Stigonema*).

Unicellular forms: They are spherical or oval in shape, e.g., *Anacystis*, *Chroococcus* (Fig. 2.1), *Gloeocapsa*, *Synechococcus* etc.

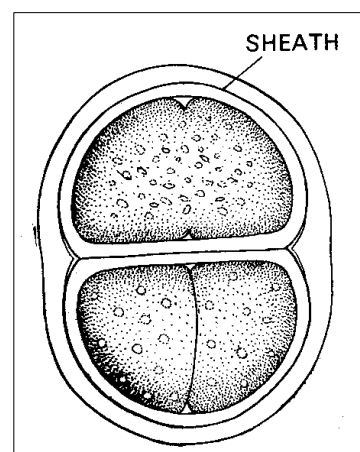


Fig. 2.1 *Chroococcus*, (After Geitfer, 1932)

Colonial forms: In most members, the cells after divisions held together in a common gelatinous matrix to form a loose organization which is termed as **colony**, e.g., *Aphanocapsa*, *Aphanothece* etc.; colonies may be cubical (*Eucapsis alpina*), spherical, square and irregular (*Microcystis*, Fig.2.2) depending upon the plane and direction in which the cells divide.

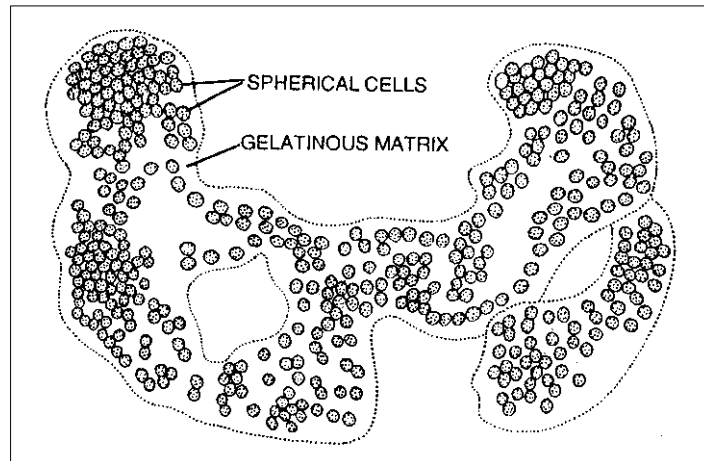


Fig. 2.2 *Microcystis*. A colony containing hundreds of cells

Filamentous forms: The filamentous form is the result of repeated cell divisions in a single plane forming a chain thread surrounded by gelatinous sheath.



Fig. 2.3 *Anabaena variabilis* (x400; adopted from Kumar, 1999)

Here the term 'filament' includes the row of cells as well as the surrounding gelatinous sheath; if it consists of cells without a distinct sheath, it is designated 'trichome'. These filaments are simple and unbranched, e.g., *Arthrospira*, *Calothrix*, *Gloeotrichia*, *Lyngbya* (Fig. 2.4C), *Oscillatoria* (Fig. 2.4B), *Pseudanabaena* (Fig. 2.4D), *Rivularia* (Fig. 2.5) etc.

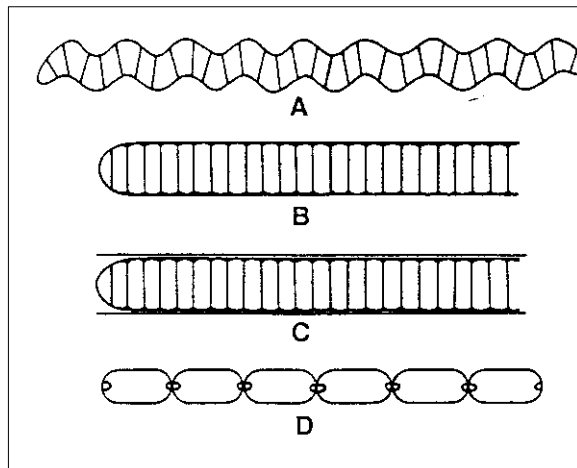


Fig. 2.4 Unbranched filamentous Cyanobacteria.
A. *Spirulina*, B. *Oscillatoria*, C. *Lyngbya*,
D. *Pseudanabaena* (After Rippka *et al.*, 1979).

Among the filamentous forms, *Oscillatoria* (Fig. 2.4) possesses the simplest unbranched filaments without heterocysts and akinites. *Lyngbya* (Fig. 2.4C) is similar to *Oscillatoria*, but the trichome is conspicuously enveloped within a mucilage sheath. In *Spirulina*, the cells are elongated and spirally coiled (Fig. 2.4A).

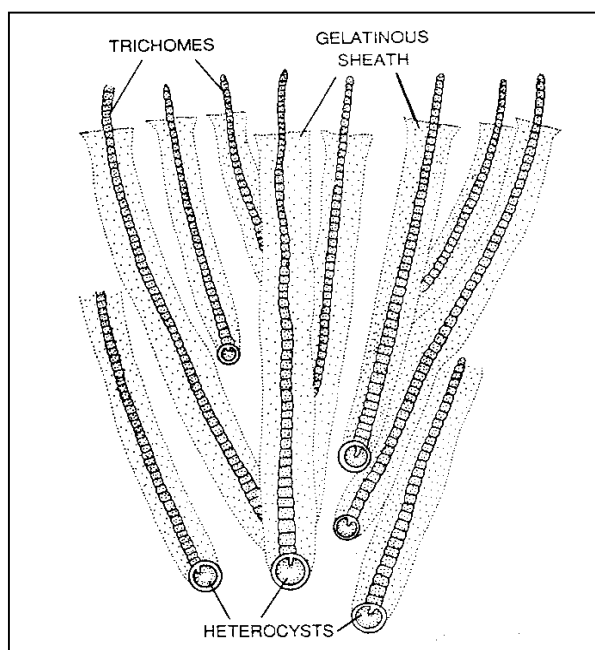


Fig. 2.5 *Rivularia*. Trichome attenuated from base to apex and possess basal heterocysts

(adopted from B.P. Pandey, 2004).

Some unbranched filamentous species possess heterocysts and they involve in nitrogen fixation, e.g., *Anabaena*, *Nostoc* etc. In *Anabaena* (Fig. 2.6A), filaments are uniseriate and usually straight but in planktonic species, they may be coiled, circinate or irregularly contorted. They don't form the gelatinous colony (Fig. 2.3). But in *Nostoc*, gelatinous colonies appear as ball-like structures. Filaments are twisted and contorted embedding in the gelatinous matrix. Gliding movement is absent in *Nostoc*.

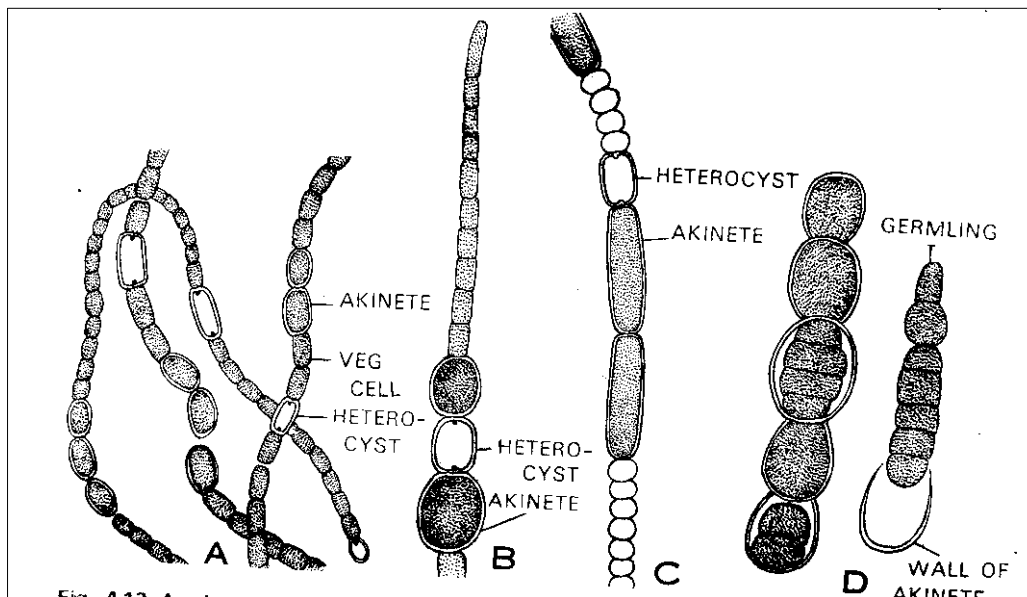


Fig. 2.6. *Anabaena*. A. B. C. Filaments with heterocysts and akinetes. D. Germination of akinetes (based on Desikachary, 1959)

In another series of blue-greens, the heterocystous filaments show a differentiation into base and an apex, e.g., *Rivularia* (Fig. 2.5) and *Gloeotrichia* (Fig. 2.7).

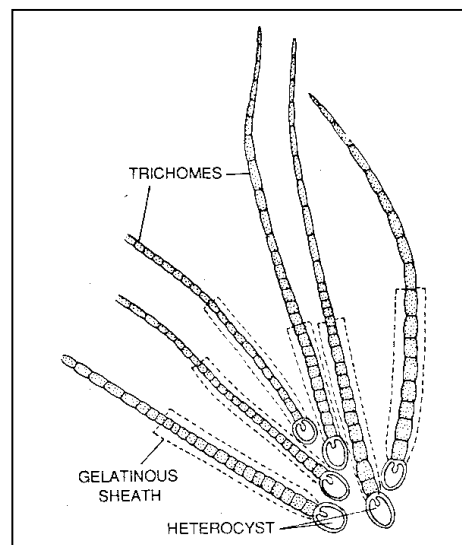


Fig. 2.7 *Gloeotrichia echinulata*. Portion of a sterile colony

Among branched filamentous forms, e.g., *Hapalosiphon*, *Mastigocladus* and *Stigonema* have the most highly evolved thallus which is with true branches and usually possessing heterocysts and akinetes. In *Scytonema* and *Tolypothrix*, filaments possess false branches and also heterocysts.

The cells in the colonies are independent of one another. There is little coordination of activity among them and no division of labour. It is obvious that the organization of thallus in the Cyanophyta has not progressed well. They are considered just at the colonies of individuals rather than the true multicellular organisms.

(iv) Cell Structure

The cyanophycean cell is characterized by the prokaryotic cell organization (Fig.1.1). There are no organized nuclei, chromatophores, pyrenoids, mitochondria or true vacuoles.

Cell Wall – The major constituent of cell wall is peptidoglycan. Cell wall is surrounded by a sheath of mucilage. This sheath functions in protecting the cells from drying and in gliding movement of the cell.

Protoplasm – Fibrils of DNA which are not associated with basic proteins (histones), are located in the central protoplasm. Photosynthetic lamellae (thylakoids) are restricted to the peripheral region of chromoplasm (Fig. 2.8A). They contain photosynthetic pigments, such as chlorophyll *a*, carotenes, xanthophylls and phycobilins.

Gas vacuoles – Abundant gas vacuoles are distributed through out the cytoplasm. They are pseudovacuoles without having true-protein-lipid membranes and they are filled with metabolic gases. The gas vacuoles are of great ecological importance and served to regulate the buoyancy of the planktonic forms.

Lamellosomes – Lamellosomes are the semicircular group of coiled membranes, similar to mesosome in bacteria. It is attached to the plasma membrane and plays an important role in the septum formation during cell division.

Food reserves – The important reserve food materials are mixophycean starch and a proteinaceous material, Cyanophycin.

Heterocysts – Heterocysts are larger than the vegetative cells with thickened walls and one or two pores. Each heterocyst is connected with vegetative cell with protoplasmic strands. In heterocyst, only photosystem-I persists which is able to perform cyclic photophosphorylation and produce ATP without photolysis and evolution of oxygen. Heterocysts also involve in nitrogen fixation, as the enzyme, nitrogenase is invariably present only in heterocysts.

Other functions of heterocysts are the fragmentation of filaments, storage of food materials, secretion of substances stimulating the growth and cell division, and control of sporulation.

(v) Nitrogen fixation

Numerous blue greens (Cyanobacteria) have got potentiality to fix the elementary nitrogen present in the atmosphere and convert it into useful nitrogenous compounds which can be assimilated in them. The Cyanobacteria which fix nitrogen, can be broadly classified into following three types:

- (i) Unicellular forms, such as *Aphanothece* and *Gloeocapsa*, can fix atmospheric nitrogen both in aerobic and anaerobic conditions.
- (ii) Certain non-heterocystous forms, i.e., *Oscillatoria* can fix elementary nitrogen only under anaerobic conditions.
- (iii) Heterocystous filamentous forms, such as *Anabaena*, *Aulosira*, *Cylindrospermum*, *Mastigocladus*, *Nostoc*, *Tolypothrix* etc., can fix atmospheric nitrogen in both aerobic and anaerobic conditions.

The enzyme involved in nitrogen fixation is nitrogenase which is a multi-subunit iron, sulphur and molybdenum containing enzyme complex. This enzyme catalyzes the reduction of N_2 into Ammonia. It is composed of two chief protein types, viz., Protein I contains iron, sulphur and molybdenum and protein II has only iron and sulphur. It is sensitive to oxygen. Its activity requires anaerobic conditions, an electron donor (ferredoxin), magnesium ions, and fairly high amounts of ATP.

The blue-green algae liberate the nitrogenous compounds into their surroundings and enrich the soil fertility. They are the promoters of soil fertility, especially *Anabaena* and *Tolypothrix* play a very significant role in increasing the fertility of rice fields in tropical and subtropical regions.

(vi) Reproduction

Blue-green algae reproduce by various means. The true sexual reproduction is absent but parasexual phenomenon is observed in few cases.

(A) Vegetative Reproduction

This takes place by various methods.

(i) **Fission** – It takes place by the formation of a ring like outgrowth which grows inwards and divides the cell into two daughter cells and eventually they become adult individuals.

(ii) **Fragmentation** – The filament or colony breaks into small fragments and each fragment develops into adult individual, e.g., *Chroococcus*, *Polycystis* etc.

(iii) **Hormogonia** – In filamentous genera, the main filament breaks into small pieces called 'hormogonia'. The hormogonia separate from the parental filament by 'separation discs' between two adjoining cells (Fig. 2.8B, C).

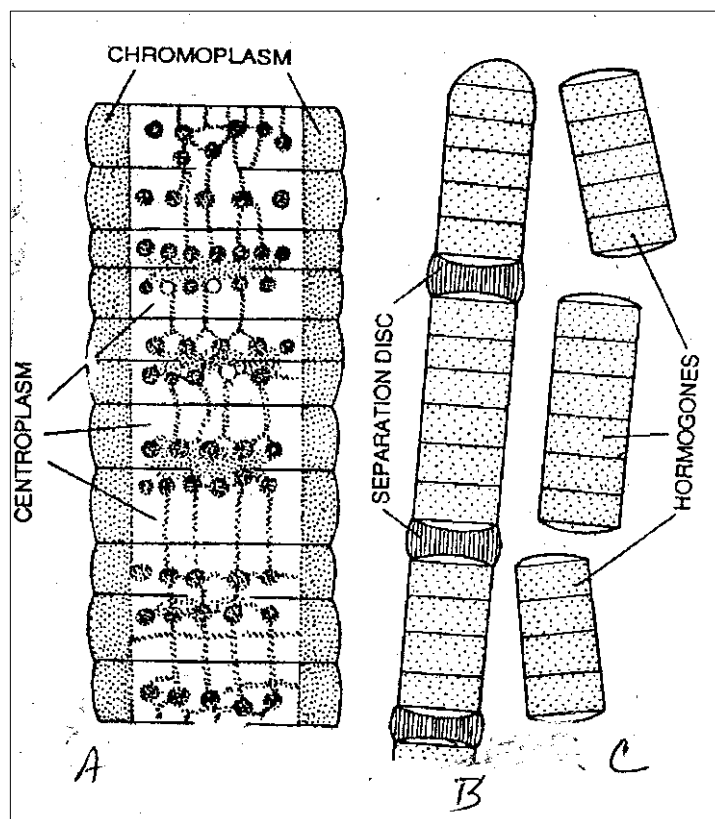


Fig. 2.8. *Oscillatoria* sp. Vegetative reproduction. A, Cell structure (detailed); B, formation of hormogones; C, hormogones (adopted from B.P. Pandey, 2004)

(iv) **Hormospores or hormocysts** - In some forms, e.g., *Westiella*, hormogonia develop thick, laminated, pigmented sheath around them during unfavourable conditions. Such multicellular spore-like structures are called hormospores or hormocysts or pseudohormogonia (Fig. 2.9B). Each hormospore germinates during favourable conditions and gives rise adult individual.

(B) Asexual Reproduction

This takes place by following ways.

(a) **Akinetes (resting spores)** – Akinetes (Fig. 2.9A) are thick-walled cells meant for perennation. They may be discoidal (*Nodularia*), spherical (*Anabaena*, Fig. 2.6B, C) or elongated (*Gloeotrichia*, *Cylindrospermum*). Mature akinetes are larger than vegetative cells and they are rich with reserve food materials (Fig. 2.9A). They possess thick wall and can withstand desiccation and, extremes of low and high temperatures.

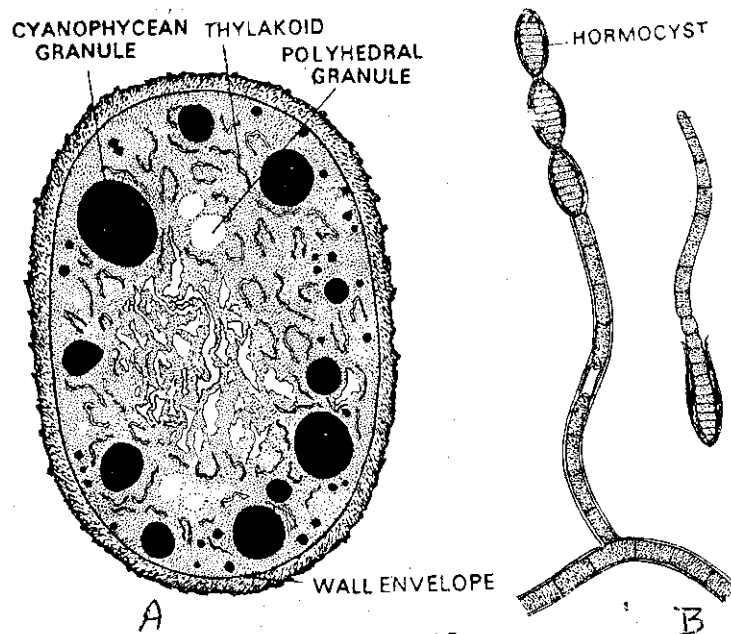


Fig. 2.9 A. *Cyanophycean akinete*; B. *Westiellopsis* with hormocysts.

(b) **Endospores** – Endospores are produced inside the cell (Fig. 2.10). During their formation, the cytoplasm of the cell cleaved into several bits. These bits later become endospores and are liberated. Each endospore germinates and gives rise new adult individual e.g. *Dermocapsa*.

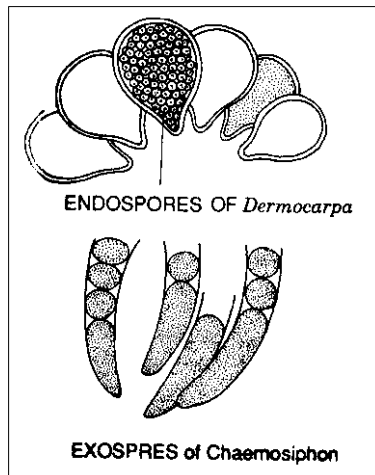


Fig. 2.10 Asexual reproduction in Cyanophyceae

(iii) **Exospores** – Exospores are produced outside the cell by constriction (Fig. 2.10). In *Chamaesiphon* (epiphytic on *Oedogonium*), the exospores are developed from the terminal end of the plant in continuous succession.

(vii) Parasexual Phenomenon (Genetic Recombination)

True sexuality is absent but a kind of parasexual phenomenon, known as genetic recombination was first reported in *Anacystis nudulans* by Kumar (1962). Since then it has been confirmed by other workers. Genetic transformation (gene transfer leading to genetic recombination) for antibiotic resistance characters have been demonstrated in *A. nudulans* by others. Genetic recombination differs from true sexuality in that it does not show syngamy or meiosis, however, the function of true sexuality (i.e., to bring about gene recombination) is achieved. Besides *A. nudulans*, genetic recombination has been reported in *Cylindrospermum majus* and *Anabaena doliolum*.

(viii) Classification

Fritsch (1945) divided the blue-green algae into 5 orders.

(i) **Chroococcales** – Unicellular or colonial (palmelloid) forms; reproduction by cell division and by endospore formation, e.g., *Gloeotheca*, *Microcystis*, *Synechococcus*, *Synechocystis* etc.

(ii) **Chamaesiphonales** – Unicellular or colonial lithophytes or epiphytes exhibiting marked polarity; reproduction by endospores or exospores, e.g., *Chamaesiphon*, *Dermocarpa* etc.

(iii) **Pleurocapsales** – Heterotrichous filamentous species lacking heterocysts; reproduction by endospores; hormogonia absent, e.g., *Pleurocapsa*.

(iv) **Nostocales** – Non-heterotrichous filamentous forms often showing false branching; heterocysts commonly present; reproduction through hormogonia and akinetes, e.g. *Anabaena*, *Aulosira*, *Calothrix*, *Hydrocoleus Lingbya*, *Nostoc*, *Rivularia*, *Spirulina* etc.

(v) **Stigonematales** – Heterotrichous filamentous forms, mostly with heterocysts, showing true branching and pit-connections between adjacent cells; Reproduction by hormogonia and rarely by hormocysts and akinetes, e.g., *Stigonema*.

(ix) **Phylogeny and interrelationship**

The blue-green algae are the most primitive among the all algal groups. Fossil evidence indicates that unicellular cyanophytes had originated in the early Precambrian and the filamentous forms (including heterocystous forms) probably developed in the middle Precambrian.

Most scheme of algal evolution show that all the algal groups probably had evolved from an ancestral cyanobacterium. In their general cytology, genetics and prokaryotic nature, blue greens seem to be closely related to bacteria, but differ from them in their photosynthetic metabolism and absence of flagellated stages. Some affinity with the red algae is indicated by the presence of phycoerythrin and pit-connections and the lack of flagellated cells.

As a whole, blue-green algae are closely related to photosynthetic bacteria in having the similar chemical composition of cell wall, organization of photosynthetic apparatus and also in the aspects of hydrogen, nitrogen and sulphur metabolism. Clearly, the blue-greens and the bacteria are two groups of the same kingdom, Prokaryota (Klein and Cronquist, 1967).

(x) **Economic importance**

In China and Japan *Nostoc commune* is used as food, locally called as Yuyuchu. Some blue greens such as *Anabaena*, *Nostoc* etc., are useful in reclamation of usar (alkaline) soils. Their capacity to fix atmospheric nitrogen is utilized in increasing the soil fertility. *Tolypothrix* has potential to fix atmospheric nitrogen at the rate of 906 kg/acre/yr. In rice fields, the productivity increased due to cultivation of *Aulosira* and *Tolypothrix*.

2. PROCHLOROPHYTA (Prochlorobacteria)

A typical prochlorophyte, *Prochloron didemni* resembles the Cyanobacteria in its general cell structure but differs in lacking phycobiliproteins as well as phycobilisomes. It contains both chlorophyll **a**, chlorophyll **b**, in addition to β -carotene. In this way, it resembles the eukaryotic green algae.

Prochloron is one of the largest known unicellular prokaryotes, spherical in shape and 30 µm in diameter. It appears to be obligate symbionts in colonies of some tropical and subtropical didemnid ascidians (prochordates). It is not normally found as free-living cells in nature but survive in association with the larvae of symbiotic didemnids. *Prochloron* is also quite abundant in coral reefs where it is associated with colonies of *Lissoclinum potella* (largest symbiotic didemnid).

Prochloron cell has one or more vacuoles occupy major part of the cells and stacked thylakoids which again reminiscent of green algal and plant chloroplasts. When alive, the cells are highly turgid and highly refractile. Upon death, they shrink, become translucent, and release a pinkish exudate and also show the refractive index higher than that of sea water.

Recent molecular analyses indicate that prochlorophytes may have evolved chlorophyll **b** and stalked thylakoids independently of the green algae and land plants. However, some phycologists opined that *Prochloron* has no evolutionary significance. It is a part of the cyanobacteria, and evolved chlorophyll **b** and lost phycobillins in the course of evolution.

Lewin (1979) had made distinctions among Cyanophyta, Prochlorophyta and Chlorophyta (Table 2.1).

Table 2.1. Comparison of characters among Cyanophyta, Prochlorophyta and Chlorophyta

Characters	Cyanophyta	Prochlorophyta	Chlorophyta
1) Cell organization	Prokaryotic	Prokaryotic	Eukaryotic
2) Plastids	Absent	Absent	Present
3) Thylakoids	Single	Paired	Paired
4) Chlorophyll b	Absent	Present	Present
5) Phycobilisomes	Present	Absent	Absent
6) Biliproteins	Present	Absent	Absent

(3) Summary

1. Cyanophyta

The blue-green algae are generally known as Cyanobacteria due to their similarity with eubacteria. They possess prokaryotic cell organization, lacking double membrane nucleus, chromatophores and mitochondria.

The blue-green algae form a significant part of the floating population which constitute the plankton of eutrophic fresh water bodies and oceans.

Thallus organization: The organization of plant body ranges from unicellular forms (*Synechococcus*) to relatively large branched heterotrichous filamentous forms (*Stigonema*). Trichomes surrounded by gelatinous sheath are called filaments. Some of these filamentous forms are simple, unbranched, e.g., *Oscillatoria*, *Spirulina*, *Lingbya*, *Gloeotrichia* etc., and some are branched, e.g., *Haplosiphon*, *Mastigocladus* etc. These filamentous forms possess heterocysts which are responsible for nitrogen fixation.

Cell Structure: The cyanopycean cell is characterized by the prokaryotic cell organization. Photosynthetic lamellae (thylakoids) are restricted to the peripheral region of chromoplasm. Gas vacuoles (pseudovacuaes) present in cytoplasm serve to regulate the buoyancy of the phytoplanktonic forms.

Nitrogen fixation – Numerous blue-greens have got potentiality to fix the elementary nitrogen present in the atmosphere and convert it into useful nitrogenous compounds. These compounds are liberated into surroundings and enriching the soil fertility. They are the promoters of the soil fertility, e.g., *Anabaena*, *Tolypothrix* etc.

Reproduction – Blue-greens reproduce by various means, such as fragmentation, hormogonia, akinetes, endospore and exospore formation. True sexuality is absent, however, parasexual phenomenon has been observed in few cases, e.g., *Anabaena doliolum*, *Anacystis nudulans* and *Cylindrospermum majus*.

Phylogeny – The blue-green algae are the most primitive among the all algal groups. In their general cytology, genetics, prokaryotic nature and cell wall chemical composition, blue-green algae are closely related to the bacteria.

2. Prochlorophyta

Prochloron is one of the largest known unicellular prokaryotes associated with the colonies of some tropical and subtropical didemnid ascidians (Prochordates). It is also associated with coral reefs. It resembles the cyanobacteria and eukaryotic green algae in possessing the chlorophyll **a**, chlorophyll **b** and β -carotene but differs in lacking phycobilisomes and phycobiliproteins.

Model Questions

(1) Essay Question

(i) Write comprehensive account on thallus organization and reproduction in blue-green algae.

(2) Short Notes

- (i) Nitrogen fixation in blue-green algae
- (ii) Ultrastructure of Cyanophycean cell
- (iii) Occurrence and distribution of blue-green algae
- (iv) Phylogeny and interrelationships in Cyanophyta
- (v) Classification of Cyanophyta
- (vi) *Prochloron*
- (vii) Compare the Cyanophyta with that of Prochlorophyta and Chlorophyta.

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Dr. S.M. KHASIM

ALGAE

LESSON-III

CHLOROPHYTA AND CHAROPHYTA

CHLOROPHYTA (Green-Algae)

Objectives

1. Introduction
2. Occurrence
3. Range of thallus organization
4. The Cell Structure
5. Cell Division
6. Reproduction
7. Classification
8. Phylogenetic Relationships
9. Life Cycles

CHAROPHYTA (Stoneworts)

1. Thallus Structure
2. Cell Structure
3. Reproduction
4. Life cycle

Summary

CHLOROPHYTA (Green-Algae)

1. Introduction

The class Chlorophyceae of division Chlorophyta is characterized by the presence of eukaryotic cell organization. The green colour of thallus is due to same pigments as in higher plants. The chloroplasts in which these pigments located, are of different shapes. The pigments are chlorophyll **a**, chlorophyll **b**, various carotenes and xanthophylls including lutein, violaxanthin, neoxanthin, astaxanthin and fucoxanthin. Starch is the reserve food material in this group of algae. The cell wall is chiefly composed of cellulose. The motile cells, if present, possess acronematic type of flagella (smooth and whiplash type) of equal length.

2. Occurrence

Green (or grass-green) algae occur widely in fresh and marine water habitats. About 90% of Chlorophyceae are fresh water and the remaining 10% are marine. Most of the Ulvaceae and Siphonales grow in sea water. The order Conjugales is exclusively fresh water. The members of Volvocales and Chlorococcales are the components of planktonic flora. The species of *Vaucheria* are commonly attached to rocks in mountain cataracts. *Coleochaete* grows on aquatic plants and grasses. The species of *Cladophora* grow on mollusc shells. The cryo algae are found upon ice and snow. *Chlamydomonas nivalis* is the main cause of red snow in U.S.A. *Chlorella* is endophytic and grows inside the tissue of *Hydrilla*. *Cephaleuros virescens* causes 'Tea Rust' on tea plants in Assam and other parts of North-Eastern region.

Some of the green algae grow symbiotically in the thalli of lichens along with fungi, these are *Treboxia*, *Chlorella*, *Coccomyxa* etc.

3. Range of thallus organization

The thallus exhibit a great variation in its habit and structure, ranging from a motile or non-motile cell through colonial, filamentous, parenchymatous and siphonous habits to the highly evolved heterotrichous filament. This highest type of specialization seems to be attained in the genera such as *Draparnaldiopsis* and *Chara* (Charophyta) which have highly differentiated and complicated thallus. In general, the plant body does not show any differentiation into true root, stem and leaves. For this reason, the plant body of the algae is called thallus.

(i) Unicellular forms:

They may be unicellular motile, e.g., *Chlamydomonas* and unicellular non-motile, e.g., *Chlorella*, *Chlorococcus* etc. Non-motile unicellular forms are called coccoid forms.

(ii) Colonial forms:

Thallus consists of loose assemblage of cells, mechanically held together in the gelatinous matrix, forming the colony. The colony may be plate like or hollow sphere and it may be motile or non-motile.

In motile colonial forms, definite number of cells held together in the mucilaginous sheath and motility is brought about by lashing movement of flagella, e.g. *Gonium sociale* is a 4-celled colony and *G. pectorale* is 16-celled; *Pandorina* is 8-celled, *Eudorina* 32-celled (Fig. 3.1) and *Pleodorina* 32-128-celled (Fig. 3.2) colonies. *Volvox* is the highest evolved colonial form and consists of 500-50,000 cells. Only a few cells are reproductive and the rest are vegetative colony of definite number of cells arranged in a specific manner and forming an integrated thallus and it is also called *Coenobium*.

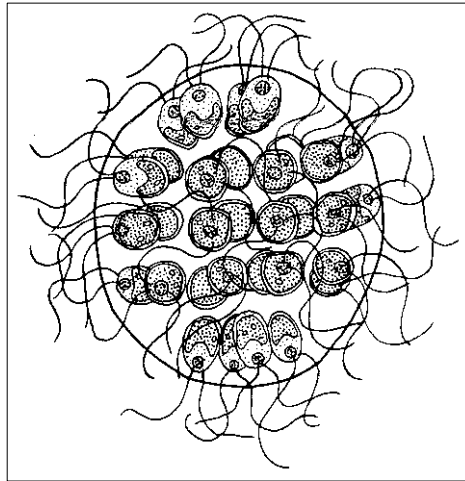


Fig. 3.1 *Eudorina elegans*

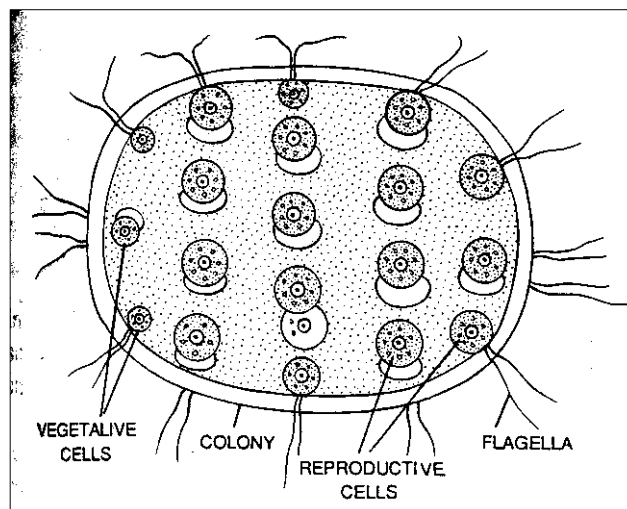


Fig. 3.2 *Pleodorina* mature colony.

Non-motile colonial forms are: *Hydrodictyon*, *Pediastrum*, *Tetraspora*, *Scenedesmus* etc. They are also called pameloid forms. In *Chlamydomonas*, the pameloid phase prevails temporarily.

(iii) Siphonous or Coenocytic thallus

In this case, the unicellular thallus is enlarged to form a non-septate multinucleate (coenocytic) sac-like or tubular structure. In *Acetabularia* and *Characium*, single nucleus lies in the base of the stalk; in both the cases as the unicell reaches maturity and enters the reproductive phase, the nucleus undergoes division to form coenocytic condition. It happens for a short time only. Contrary to this, *Protosiphon* is permanently coenocytic.

In *Caulerpa*, the thallus is differentiated into a creeping structure resembles the rhizome and erect leafy shoots (Fig. 3.3). The rhizoids anchor the plant to the substratum. The stolons produce upright fronds which may be leaf-like or cylindrical or in clusters. Both the creeping and upright parts contain mechanical tissues in the form of trabeculae.

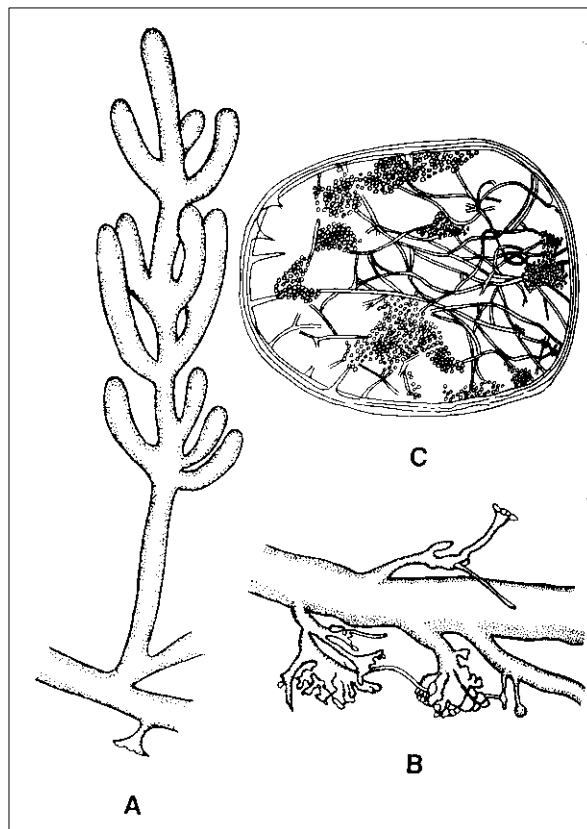


Fig. 3.3 *Caulerpa fastigiata*. **A**, a part of stolon with attaching disc; **B**, stolon with rhizoids terminating in coralloid discs; **C**, t.s. of stolon showing trabeculae, stratified wall, and starch grains (adopted from Kumar, 1999).

(iv) Multicellular filamentous forms

In these forms, cells are arranged in a linear rows, called the threads or filaments; repeated cell divisions take place in a single plane, resulted into filament. They may be simple unbranched and branched filamentous.

A. Simple unbranched filamentous forms: They possess a long, thread-like, unbranched filamentous thallus. Like the colonial thallus, all the cells in the filament are alike, self-sufficient and independent of one another, e.g., *Spirogyra*, *Ulothrix*, *Oedogonium* etc.

The thallus of *Ulothrix* illustrates a step further in the development of a multicellular filamentous forms. As in *Spirogyra*, the simple filament of *Ulothrix* consists of similar cells but it is attached to the substratum at one end by a rhizoidal cell. Like this, there is a beginning of differentiation of cells accompanied by slight division of labour.

In *Oedogonium*, thallus represents a step still further in the differentiation of cells accompanied by division of labour. It is a simple multicellular filament with a branched or lobed rhizoidal cell. The rhizoidal cell is modified to form a more complex holdfast than the *Ulothrix*. The holdfast is expanded into a flattened disc with outgrowths. Besides, the filament consists of green vegetative cells for nutrition, cap cells for cell division, zoospore formation, and highly specialized reproductive organs, such as antheridia and oogonia (Fig. 3.4; 3.5).

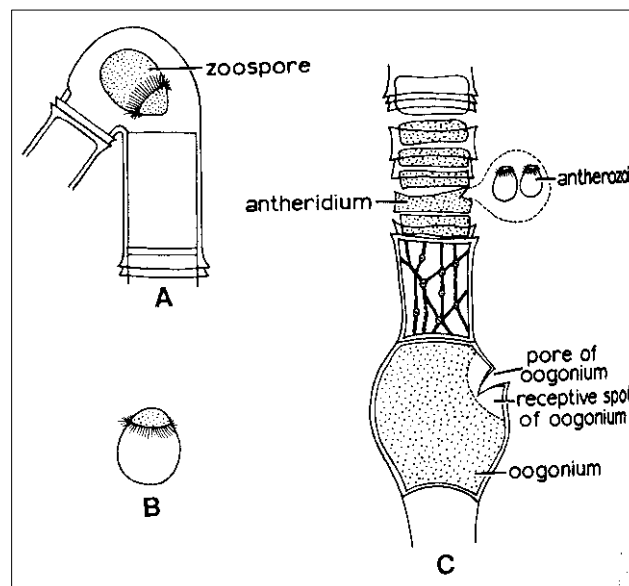


Fig. 3.4 *Oedogonium*. **A**, Zoospore formation; **B**, Zoospore with crown of flagella; **C**, oogamous reproduction in homothallic macrandrous form (adopted from Kumar, 1999).

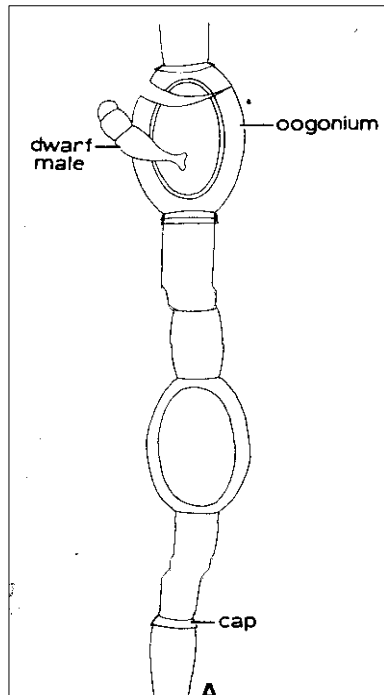


Fig. 3.5 Nanandrous species of *Oedogonium*.

B. Branched filamentous forms: In these forms, thallus is branched filament e.g., *Bulbochaete*, *Chaetophora*, *Cladophora* etc. It is considered as much more advanced multicellular thallus among green algae. The cells in the main filament undergo divisions and give rise branches.

Cladophora is profusely branched and attached to the substratum by septate rhizoid growing down from the basal part of the filament. The cells are large, cylindrical, multinucleate and have an elaborate chloroplast which may form a continuous reticulate network in younger cells but may become parietal in older ones (Fig. 3.6).

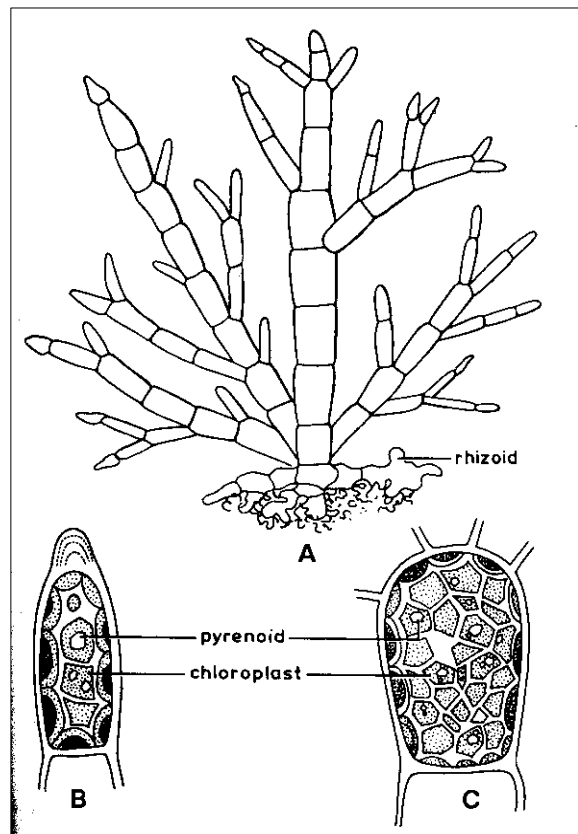


Fig. 3.6. *Cladophora jongianum*. A, habit; B,C, apical and intercalary cells with parietal chloroplasts (adopted from Kumar, 1999).

C. Foliaceous forms: In these forms, the cells divide in more than one plane and give rise thin, flate and plate - like thallus, e.g., *Ulva* (Fig. 3.7A, B, C). The thallus is macroscopic and composed of two layers of parenchyma cells. Several multinucleate rhizoids arise from the lower cells of the thallus and attach to the substratum. These rhizoids may penetrate between two layers of the thallus (Fig. 3.7B) and finally attach to the substratum.

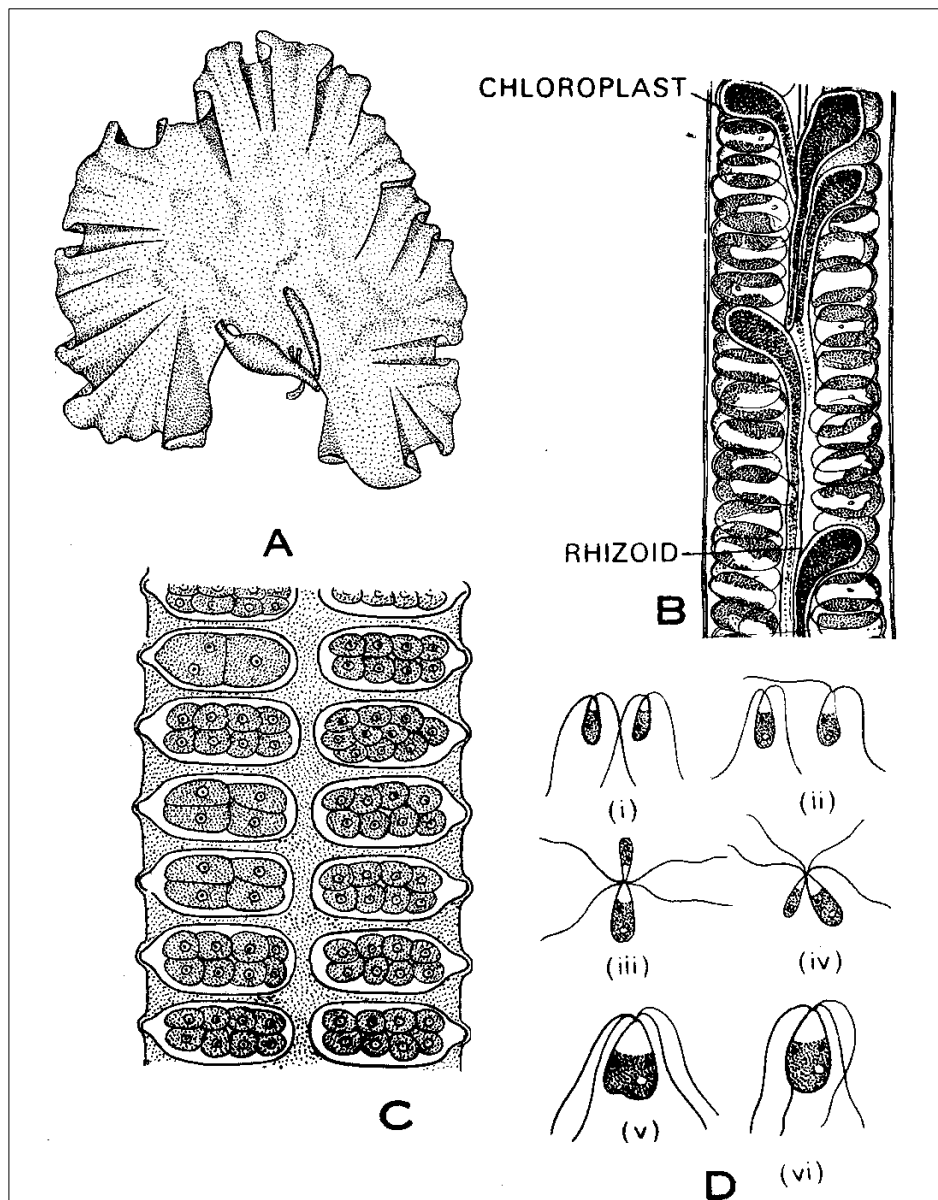


Fig. 3.7. *Ulva*. A. thallus, B. longitudinal section; C, *U. lobata* formation of gametes; D, male and female gametes, fusion and formation of quadriflagellate zygote (A, after Bold, 1957; B after Fritsch, 1935; C, D, after Smith, 1955).

D. Heterotrichous filamentous forms: Heterotrichous filamentous thallus is highly evolved habit in Chlorophyta. The members of Chaetophorales possess heterotrichous filamentous thallus, e.g., *Coleochaete*, *Draparnaldia*, *Draparnaldiopsis*, *Stigeoclonium* etc. In the heterotrichous habit, the thallus is distinguishable into a basal prostrate system and an erect system (upright system) composed of branched threads.

In *Stigeoclonium* and *Fritschiella*, both prostrate and erect systems are well developed. In *Stigeoclonium*, the prostrate system is generally formed of short cells (Fig. 3.8) and filaments exhibit apical growth. Sometimes prostrate system is profusely branched to form a compact pseudo-parenchymatous disc of one layered stratum. The erect system composed of alternate or opposite, profusely or sparsely branched filaments (Fig. 3.8). The lateral branches alternate and terminate into long, multicellular and hyaline hairs. In *Fritschiella*, the thallus remains differentiated into rhizoidal system, prostrate system, primary projecting and secondary projecting systems.

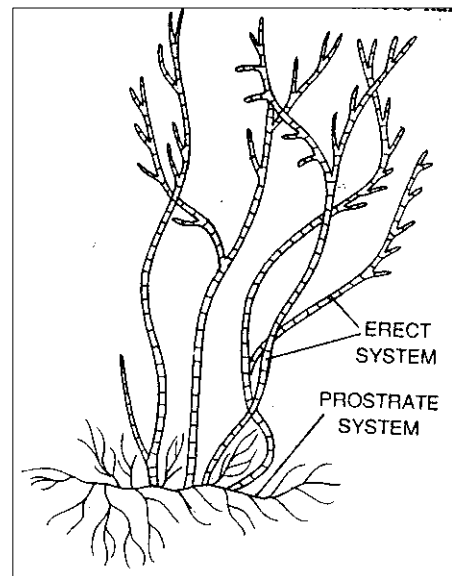


Fig. 3.8. *Stigeoclonium*, thallus showing prostrate and erect systems.

The heterotrichous habit has undergone a variety of modifications by reduction or elimination of one or other of the system.

In *Coleochaete*, there is a disappearance of erect system resulted in the discoid type of thallus, e.g., *C. orbicularis*, *C. scutata* (Fig. 3.9A, B), *C. soluta* etc. Discoidal thallus consists of loosely arranged branched filaments distinct from one another. However, in *C. pulvinata*, the thallus is a typical heterotrichous.

In both *Draparnaldia* and *Draparnaldiopsis* there is complete disappearance of prostrate system and a corresponding elaborate development of the erect (projecting) system. In these genera, the prostrate system is vestigial and represented by a holdfast. *Draparnaldia* is characterized by the (i) presence of a central axis consisting of large barrel-shaped cells, (ii) highly branched whorls of laterals (limited growth) consisting of much shorter cells, (iii) branches terminating into pointed cells or long, hair-like setae, (iv) parietal, plate-like chloroplast with a single pyrenoid and the soft copious mucilage around the entire thallus.

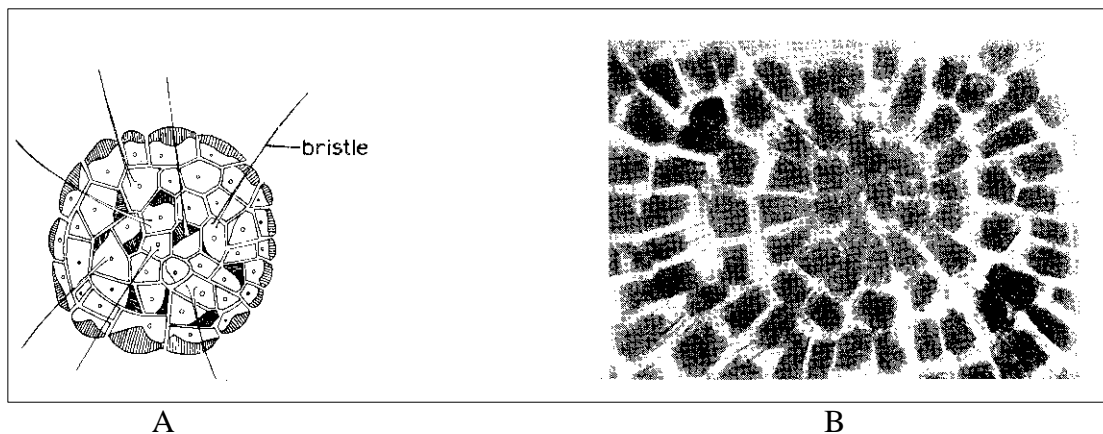


Fig. 3.9 *Coleochaete scutata*. **A**, habit; **B**, part of thallus showing sheathed setae (adopted from Kumar, 1999)

The thallus of *Draparnaldiopsis* shows further advancement than the *Draparnaldia*. The main filament of *Draparnaldiopsis* is made up of two kinds of cells, long internodal cells and short nodal cells. Nodal cells alone bear the laterals of limited growth and also lateral of unlimited growth. The cell possesses a single parietal chloroplast with several pyrenoids.

4. THE CELL STRUCTURE

The cells of Chlorophyta are eukaryotic in nature having definite nucleus, chloroplasts and mitochondria. Definite cell wall is present and usually consists of two or three layers. The innermost layer is made up of cellulose and encircles the protoplast. The outer layer is amorphous and made up of pectic substances. In planktonic forms, more pectic material is secreted and dissolved in water resulting into a mucilaginous envelop around the cell. Sometimes, the outer layer is encrusted with calcium carbonate as in Siphonales and Charales. A third layer is chitin outside the pectic layer as in *Cladophora* and *Oedogonium*.

The protoplast is covered by a thin plasma membrane. Usually the cells are uninucleated but in Cladophorales, Siphonales, *Sphaeroplea* and Charales, the cells are coenocytic (multinucleated cells). The nucleus is bounded by double-layered porous nuclear membrane. Inside the nucleus, one or more nucleoli and chromosomes are present.

Chloroplast – There is a great diversity in number, morphology and arrangement of the chloroplasts (Fig. 3.13 A, B); this has been interpreted to suggest the evolutionary tendencies among different orders of phylum Chlorophyta. The order Volvocales is characterized by the presence of a single, cup-shaped or bowl-shaped chloroplast per cell with one or more pyrenoids; rarely an axile and stellate (*Chlamydomonas arachne*, *C. eradians*) or reticulate (*Sphaerella lacustris*) chloroplast may be found. In Chlorococcales, a single parietal chloroplast with usually a single pyrenoid is present. A reticulate chloroplast with several pyrenoids is characteristic of *Cladophora*, *Hydrodictyon* (Fig. 3.11) and *Oedogonium*. A parietal ring, collar or girdle shaped

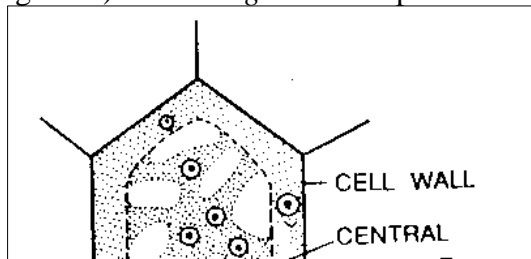
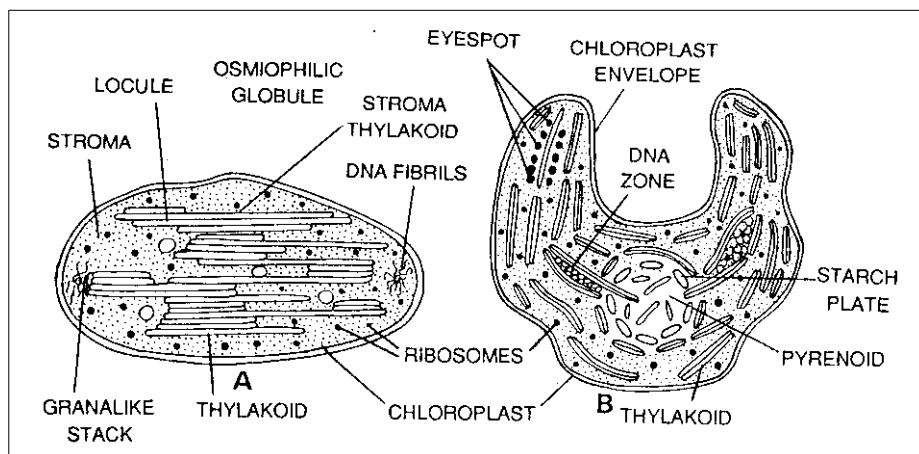
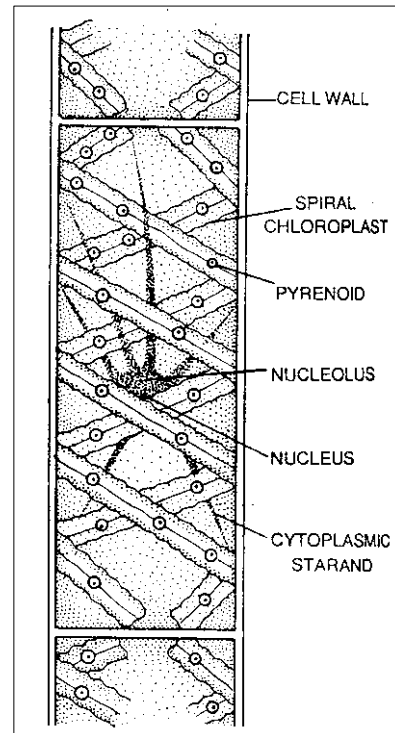


Fig. 3.11 *Hydrodictyon*, an enlarged cell

chloroplast containing a few pyrenoids is found in many Ulotrichales. In Chaetophorales, a parietal chloroplast having a variable number of pyrenoids is found. In more advanced members of this order, e.g., *Draparnaldia* and *Draparnaldiopsis*, the central cells of the main axis have a diminutive chloroplast restricted to the middle of the cell. In Conjugales, three basic types of chloroplasts are found, viz., (1) a flat axile plate with several pyrenoids, e.g., *Mesotaenium* and *Mougeotia*. (2) a pair of axile stellate chloroplasts, each with a single pyrenoid, e.g., *Zygnema* (Fig. 3.12) and (3) one or few spiral, ribbon-shaped chloroplasts, each with many pyrenoids, e.g., *Spirogyra* (Fig. 3.12). In Siphonales and Charales, many discoidal chloroplasts with or without pyrenoids are found.

The chloroplast consists of numerous tube-like paired lamellae. These lamellae are arranged one above the other to form the stacks. In between the stacks, ribosomes are located and these ribosomes are smaller in size than that of cytoplasmic ribosomes. The pyrenoid of the green algae commonly consists of a proteinaceous core which is surrounded by minute plates of starch.

Fig. 3.12 *Spirogyra*, an enlarged cellFig. 3.13 Ultrastructure of chloroplasts of *Chlamydomonas*.
A, discoidal chloroplast; B, cup-shaped chloroplast.

The Pigments – The most important pigment of Chlorophyceae is chlorophyll a. Other pigments such as chlorophyll b, carotenoids and xanthophylls are also present. Phycoporphylin is recorded from several Conjugales. Fucoxanthin has been found in *Zygnema pectinatum*.

Contractile vacuoles – Usually there is a single large central vacuole bounded by a thin membrane. However, in motile genera there are two contractile vacuoles at the anterior end of

the cell just near the base of the two flagella. The vacuoles are involved in osmoregulation, removing excess of water and excretory wastes of the cells.

The other cell organelles such as mitochondria, endoplasmic reticulum and golgi bodies are also present. The eye-spot (stigma) is present near the anterior end of the cell. It is light sensitive and directs the movement of swimming cells. The flagella may be 2 or 4 or rarely many and they are inserted at the anterior end. Equal length of flagella are acronematic type, i.e., they are smooth and whiplash type. The flagella arise from the granules called blepharoplast granules. They show the 9+2 fibrillar organization. Generally starch is the reserve food material in Chlorophyta. Some Chlorococcales accumulate starch and lipid, whereas majority of Siphonales and some Conjugales store fat.

5. CELL DIVISION

There are two modes of nuclear cell division in the green algae.

- (i) The mitosis is intranuclear, i.e., with the nuclear envelope remains closed at the metaphase. Apart from spindle microtubules, a characteristic additional set of microtubules disposed transversely to the long axis of the spindle occurs in telophase and it is known as *phycoplast*. This structure facilitates the cytokinesis either by furrowing (*Tetrahedron*) or by cell plate formation (*Oedogonium*). At telophase, the daughter nuclei tend to lie close together, e.g., *Ulothrix*, *Oedogonium*, *Draparnaldia*, *Volvox*, *Ulva* etc.
- (ii) The spindle and nuclear envelope are open. At telophase, the microtubules of the intranuclear spindle are persistent and phragmoplast is formed during the cytokinesis, e.g., *Chara*, *Coleochaete*, *Spirogyra* and several land plants.

6. REPRODUCTION

The members of Chlorophyceae are represented by the vegetative, asexual and sexual types of reproduction.

(i) Vegetative reproduction

A. Fission: Unicellular organisms produce their progeny through fission, e.g., *Chlamydomonas*, *Pleurococcus* etc.

B. Fragmentation: It is very common in filamentous forms, such as *Oedogonium*, *Ulothrix*, *Sphaeroplea*, *Spirogyra* etc.

C. Akinetes (Resting spores): In some green algae, e.g., *Cladophora*, *Pithophora*, *Ulothrix* etc., the protoplast is rounded-off and covered with very thick cell wall. These cells with abundant reserve food materials are called akinetes. They are capable of withstanding unfavourable environmental conditions. During favourable conditions, akinete germinates liberating a young germling.

(ii) Asexual reproduction

A. Zoospore formation: Zoospore production is more common in Chlorophyceae. Zoospore is biflagellate in *Chlamydomonas* and quadriflagellate in *Draparnaldiopsis*, *Fritschiella*, *Ulothrix* etc. In *Oedogonium* a crown of flagella are present (Fig. 3.4 A, B). Zoospores may be produced singly (*Oedogonium*) or in twos, or in still larger number within a vegetative cell or sporangium. Zoospores possess eye spot and chloroplast, and motility is brought about by the lashing movement of flagella. Each zoospore on coming in contact with a suitable substratum and under favourable conditions, develops into a new adult individual.



B. Aplanospore: In certain cases, aplanospores (non-motile) are formed singly within a cell (Fig. 3.14). Unlike zoospores, protoplasts become rounded, secrete a wall of their own and are non-flagellate and non-motile. Aplanospores occur in *Ulothrix* and also in other genera.

Fig. 3.14 *Spirogyra*, aplanospores

C. Autospores: In a few genera, aplanospores have almost similar distinctive shape as the parent cell and are called autospores. These are commonly found in the order Chlorococcales.

(iii) Sexual reproduction

Sexual reproduction is of three types, (A) isogamy, (B) anisogamy, and (C) oogamy.

(A) Isogamy – In majority of Chlorophyta, sexual reproduction is isogamous in which the two fusing gametes are equal in size and have identical morphology and physiology, e.g., *Chlamydomonas*, *Spirogyra*, *Ulothrix*, *Zygnema* etc. The resultant fusion product is known as zygospore.

(B) Anisogamy – In this, the fusing gametes are not identical morphologically and physiologically. Active male gametes are of smaller in size as compared to the larger female gametes which are less active, e.g. *Chlamydomonas braunii*.

(C) **Oogamy** – Oogamous reproduction involves the fusion between a small flagellate, actively motile male gamete (antherozoid) and, a large, non-motile, passive female gamete, the ovum or oosphere. The ovum is generally produced singly within a specially differentiated and enlarged cell called the oogonium, e.g., *Oedogonium* and *Coleochaete*. The antherozoids are many and produced within an antheridium.

In *Oedogonium*, there are two forms, viz., (1) macrandrous (Fig. 3.4C), and (2) nanandrous (Fig. 3.5). The macrandrous forms may be monoecious producing antheridia and oogonia on the same plant (Fig. 3.4C), or dioecious, producing antheridia and oogonia on different individuals. In the nanandrous forms, the sexual plants are dimorphic; the oogonia are formed on filaments of normal size, whereas the antheridia are produced in filaments known as dwarf males or nanandria. The nanandria are extremely small and are always found attached to oogonia proper or to the underlying cell. These nanandria are derived from antherozoid-like zoospores, known as androspores, which are formed singly within the androsporangia. A species that bears both oogonia and androsporangia is described as gynandrosporous, whereas the one that bears them on different filaments are called idioandrosporous. After their liberation and brief swimming, androspores settle on an oogonium or a suffultory cell, and then germinate to give rise nanandria. Each antheridium of the dwarf male generally produces two antherozoids.

There has been a evolutionary advancement in sexual reproduction from isogamy through anisogamy to oogamy, accompanying the reduction in number and an increase in the size of the female gametes. This evolution perhaps occurred independently in different orders of the Chlorophyta. Progressive evolutionary series illustrating the transition from isogamy to oogamy are met within the coenobial Volvocales and in certain Chaetophoraceae, e.g., *Aphanochaete*, *Chaetonema*, *Coleochaete* and *Stigeoclonium*.

7. CLASSIFICATION

Fritsch (1935) had divided the Chlorophyta into nine orders under only one class Chlorophyceae.

Phylum	: Chlorophyta	
Class	: Chlorophyceae	
Orders	: (1) Volvocales	(6) Oedogoniales
	(2) Chlorococcales	(7) Conjugales
	(3) Ulotrichales	(8) Siphonales
	(4) Cladophorales	(9) Charales
	(5) Chaetophorales	

Bold (1967) had raised the Charales to the rank of phylum, the Charophyta. The division Chlorophycophyta includes only one class, the Chlorophyceae having ten orders as follows:

Phylum	: Chlorophycophyta	
Class	: Chlorophyceae	
Orders	: (1) Volvocales	(6) Cladophorales
	(2) Chlorosphaerales	(7) Siphonales
	(3) Chlorococcales	(8) Dasycladales
	(4) Ulotrichales	(9) Oedogoniales
	(5) Ulvales	(10) Zygnematales

Round (1971) had divided the green algae (Chlorophyta *sensu* Fritsch) into three phyla, containing six classes and 37 orders as follows:

I. Phylum	: Chlorophyta	
(1) Class	: Chlorophyceae	
Orders	: (1) Chlamydomonadales	(10) Ulvales
	(2) Volvocales	(11) Prasiolales
	(3) Polyblepharidales	(12) Cylindrocapsales
	(4) Tetrasporales	(13) Microsporales
	(5) Chlorodendrales	(14) Chaetophorales
	(6) Chlorosarcinales	(15) Trentepholiales
	(7) Chlorococcales	(16) Pleurococcales
	(8) Ulotrichales	(17) Ulvellales
	(9) Codiolales	
(2) Class	: Oedogoniophyceae	
Order	: Oedogoniales	
(3) Class	: Zygnemaphyceae	
Orders	: (1) Mesotaeniales	(3) Gonatozygales
	(2) Zygnematales	(4) Desmidiiales
(4) Bryopsidophyceae		
Orders	: (1) Cladophorales	(7) Derbesiales
	(2) Sphaeropleales	(8) Codiales
	(3) Acrosiphonales	(9) Caulerpales
	(4) Dasycladales	(10) Dichotomosiphonales
	(5) Siphonocladales	(11) Phyllosiphonales
	(6) Chlorochytriales	
II. Phylum	: Prasinophyta	
Class	: Prasinophyceae	
Orders	: (1) Pyramimonadales	
	(2) Prasinocladales	
	(3) Halosphaerales	
III. Phylum	: Charophyta	

Class : Charophyceae
Order : Charales

8. PHYLOGENETIC RELATIONSHIPS

In Chlorophyta, three phylogenetic lines have been taken into consideration, these are (1) *Volvocine*, (2) *Chlorococcine* and (3) *Tetrasporine* lines (Fig. 3.15).

Volvocine line had evolved from a simple flagellated unicell, probably similar to *Chlamydomonas*, to a larger colonies of differentiated cells, e.g., *Volvox*.

Chlorococcine (siphonous) line had evolved again from the simple flagellated chlamydomonad type of cell to the coenobial (Chlorococcales) and siphonous (Siphonales) forms, the latter is coenocytic in nature with few or no cross walls.

Tetrasporine (Ulotrichalean) line also thought to have evolved from uninucleate unicellular organism into relatively complex filaments and thalli differentiating into branches and rhizoids, e.g., *Fritschiella*. As the ulotrichalean line has the most complex thallus organization, probably it is the ancestor of present day land plants.

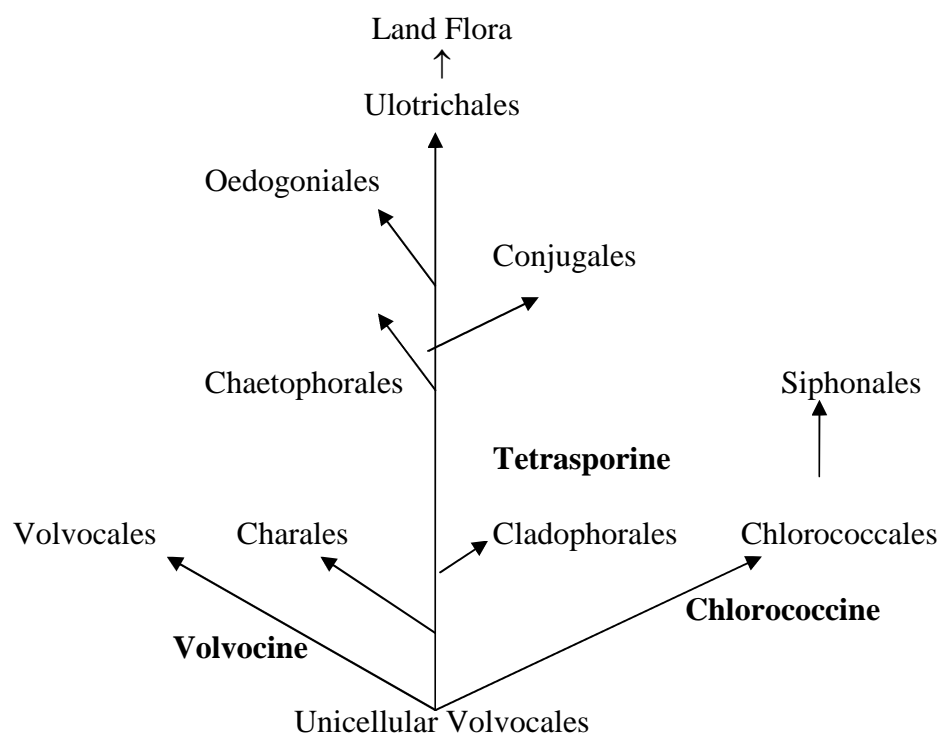


Fig. 3.15 Evolution in Chlorophyceae
(adopted from B.P. Pandey, 2004)

9. LIFE CYCLES

The following types of life cycles are encountered in Chlorophyceae.

1. Haplontic Life Cycle

The Chlorophyceae members, such as *Coleochaete*, *Oedogonium*, *Pandorina* and *Ulothrix* (Fig. 3.16) are haploid, with the zygote representing the only diploid phase in the life cycle. In these, meiosis occurs during the first division of the zygote nucleus.

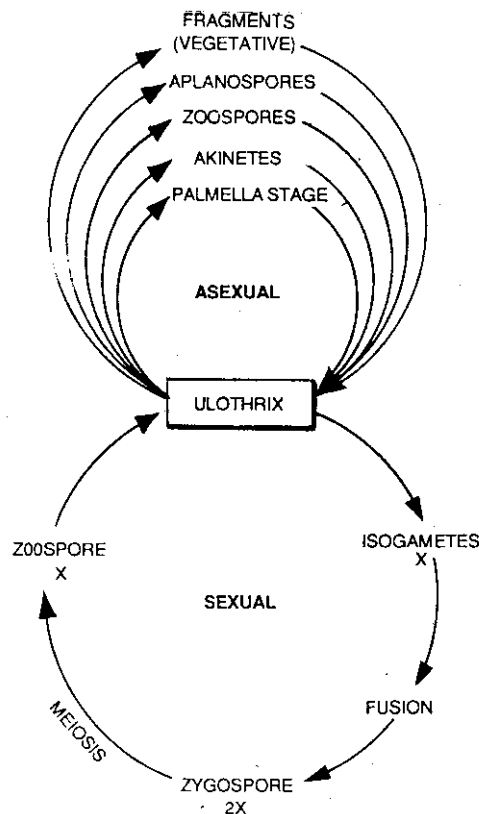


Fig. 3.16 Haplontic life cycle of *Ulothrix*.

2. Diplontic Life Cycle

In the diploid forms belonging to Siphonales and Chlorococcales, the vegetative plant is diploid and meiosis occurs during the formation of gametes which represent only haploid stage. The zygote germinates directly into the diploid plant (Fig. 3.17).

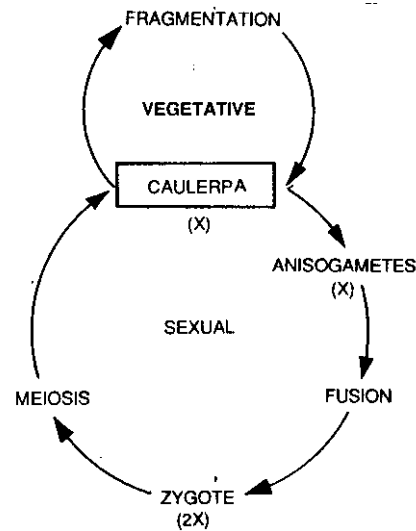


Fig. 3.17. Diplontic life cycle of *Caulerpa*

(3) Isomorphic Life Cycle

This involves an alternation between the haploid gametophyte and the diploid sporophyte, both of which are morphologically indistinguishable from each other. The haploid phase produces gametes that fuse to form a zygote which in turn germinates into a diploid sporophytic plant. This sporophyte produces zoospores. Prior to zoospore formation meiosis takes place, e.g., members of Chaetophoraceae, Cladophoraceae (Fig. 3.18) and Ulvaceae.

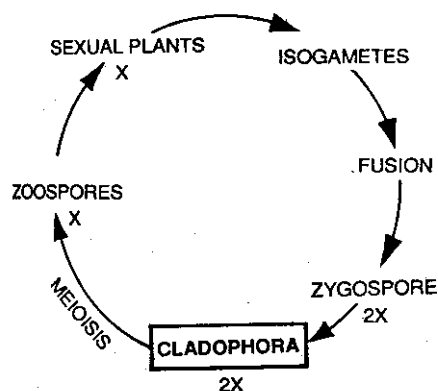


Fig. 3.18 Isomorphic life cycle of *Cladophora*

(4) Heteromorphic Life Cycle

This involves an alternation between the morphologically dissimilar haploid gametophyte and diploid sporophyte, e.g., *Urospora*. In *Urospora* gametophyte is dominant and the sporophyte is known as *Codiolum*.

CHAROPHYTA (Stoneworts)

The class Charophyceae under Charophyta includes a single order Charales having six living genera and all these placed in the family Characeae, popularly known as stoneworts. This constitutes a distinctive and isolated group of highly differentiated and elaborately organized green thallophytes. It is characterized by the presence of thallus with regular differentiation of nodes and internodes and with the deposition of calcium carbonate; and also the presence of highly specialized male and female reproductive structures, known as 'globule' and 'nucule' respectively.

The genus *Chara* grows more commonly in stagnant and clean freshwater bodies. It prefers a substratum of decaying organic matter. It forms a submerged vegetation in the fresh water habitats. Some are occurred in hot water springs, e.g. *C. fragilis*. Some species viz., *C. nuda* and *C. vandalurensis* are endemic in India.

(i) Thallus structure

The main axis and branches of *Chara* are differentiated into nodes and internodes (Fig. 3.19A). Each node bears a whorl of several branches of limited growth and consists of pair of central cells surrounded by a peripheral group of 6-20 cells. The species having nodes with cortical cells are known as corticated species, e.g., *C. zeylanica*; some are ecorticated, e.g., *C. braunii*, *C. corallina*, *C. wallichii* etc. Branched multicellular rhizoids are formed from the lowermost one or two nodes and they are attached to the substratum.

The branches of the first order, produced from the nodes of the main axis are known as primary laterals of limited growth. Single celled branches called secondary laterals arise from the nodes of primary laterals. In addition to these, the stem node may also bear one or more branches of unlimited growth. These branches are located at the axillary position of the oldest primary lateral in the whorl.

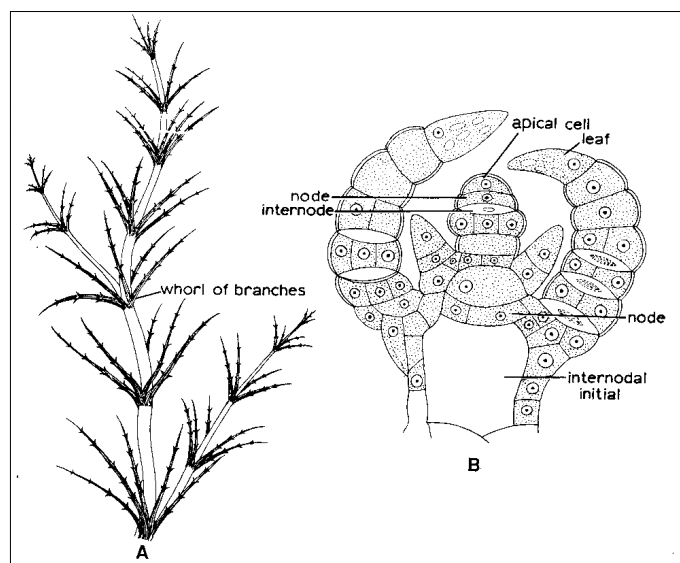


Fig. 3.19 *Chara*. A. Habit, B. Apex of the thallus

The main axis and primary laterals grow by means of a dome-shaped apical cell (Fig. 3.19B) and cuts off a transverse segment at its posterior end. The resultant segment divides transversely into an upper nodal initial and a lower internodal initial. The latter remains undivided and elongates considerably to form the internode. The nodal initial divides repeatedly in such a way that it gives a pair of central cells surrounded by peripheral cells. The peripheral cells in the node protrude and function as apical cell of the branches (primary laterals). These primary laterals exhibit the same type of apical growth but of limited activity.

Cell structure

The nodal cells contain dense cytoplasm, a single nucleus and a few discoid or elliptical chloroplasts. In the central cell, there is a large vacuole, multi-nucleate, and many discoid chloroplasts. The chloroplast lacks a pyrenoid. Cytoplasmic streaming is very conspicuous in *Chara*.

(ii) Reproduction

(A) Vegetative reproduction

Vegetative reproduction takes place by amylum stars and bulbils. Amylum stars are star-shaped aggregations of cells developed on the lower nodes of the main axis. These cells are filled with amylum starch. The amylum star grows into a new individual. Bulbils are rounded tuber-like structures; these are perennating bodies, when detached it forms a new plant.

(B) Sexual reproduction

All species of *Chara* show a highly advanced type of oogamy. Male reproductive structure is called '**globule**' whereas female reproductive structure is '**nucule**'. Both reproductive structures are situated at the base of secondary laterals (Fig. 3.20A, B).

Globule (Male reproductive structure): Mature globule is a hollow spherical body and consists of outer shield cells, middle manubrial cells and inner capitulum cells (Fig. 3.20B). Primary capitulum cells divide and give rise to secondary capitulum cells. Each cell of secondary capitulum produces a pair of antheridial or spermatogenous filaments. Each cell of the spermatogenous filament forms a biflagellate sperm (Fig. 3.20D).

Globule development (Fig. 3.21A-C) – Both the sex organs in *Chara* develop from an adaxial peripheral cell at the node of a primary lateral. Antheridial initial differentiates and divides transversely into a basal pedicel cell and a terminal antheridial mother cell. The antheridial mother cell divides and gives rise quadrantly arranged cells. Each of these cells divides transversely to give rise to the octant stage. Each octant cell undergoes periclinal

divisions resulting in a radial row of three cells with the outer cell functioning as the shield cell, the middle as the manubrium, and the inner as the primary head cell. Subsequently, the shield cells expand laterally and the manubria elongate vertically. By this time, the primary head cell has already divided and the resulting head cells bifurcate vertically into a pair of cells, each developing into a spermatogenous filament.

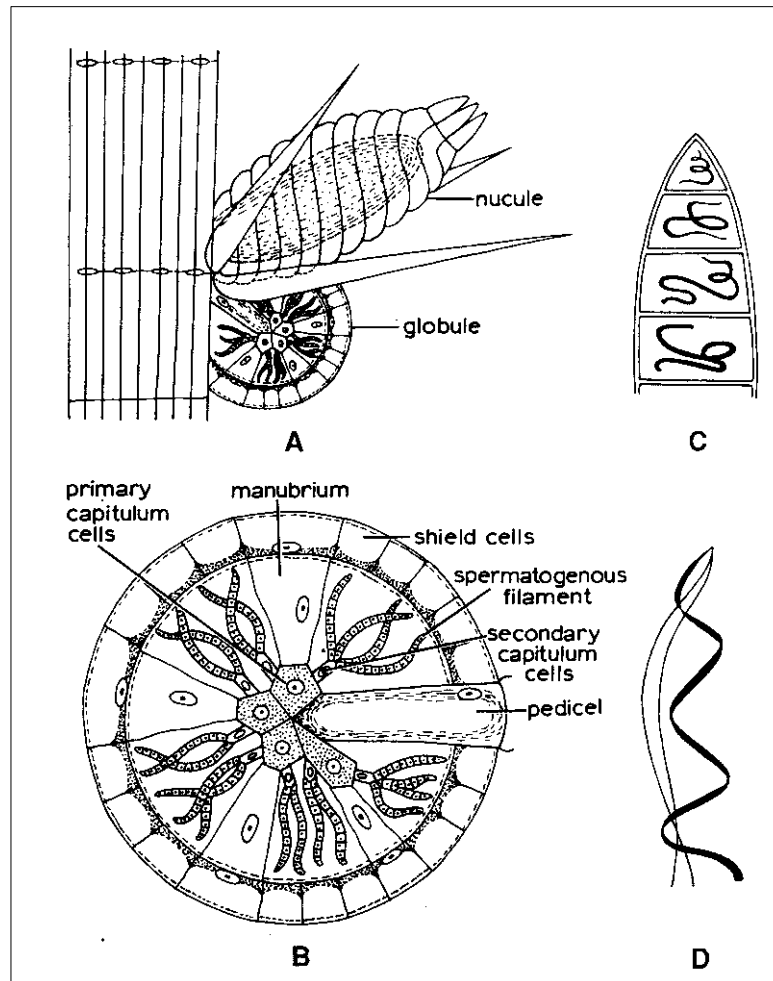


Fig. 3.20 *Chara*. A, portion of plant bearing nucule and globule; B, structure of mature globule; C, spermatogenous filament; D, spiral spermatozoid.

Nucule (Female reproductive structure): It is an oblong structure located just above the globule. It consists of spirally coiled tube cells which form a sterile envelope around the oogonium and five-lobed corona cells that project beyond the apex of the oogonium.

Nucule development – Nucule is also produced from a peripheral cell close to the antheridial initial. Oogonial initial divides to give rise a row of three cells, of which the lower

forms the pedicel, the middle the sterile jacket (sheath cells) and the upper the oogonial mother cell. The middle cell divides repeatedly to form a group of five sheath cells enclosing a central cell. The oogonial mother cell divides and form a stalk cell and upper oogonium. The five sheath cells undergo a transverse division resulting into 5 lower tube cells and upper coronal cells; the tube cells elongate and coil spirally around the oogonium. In this process, the coronal cells are pushed to the top of the oogonium (Fig. 3.21 D-E).

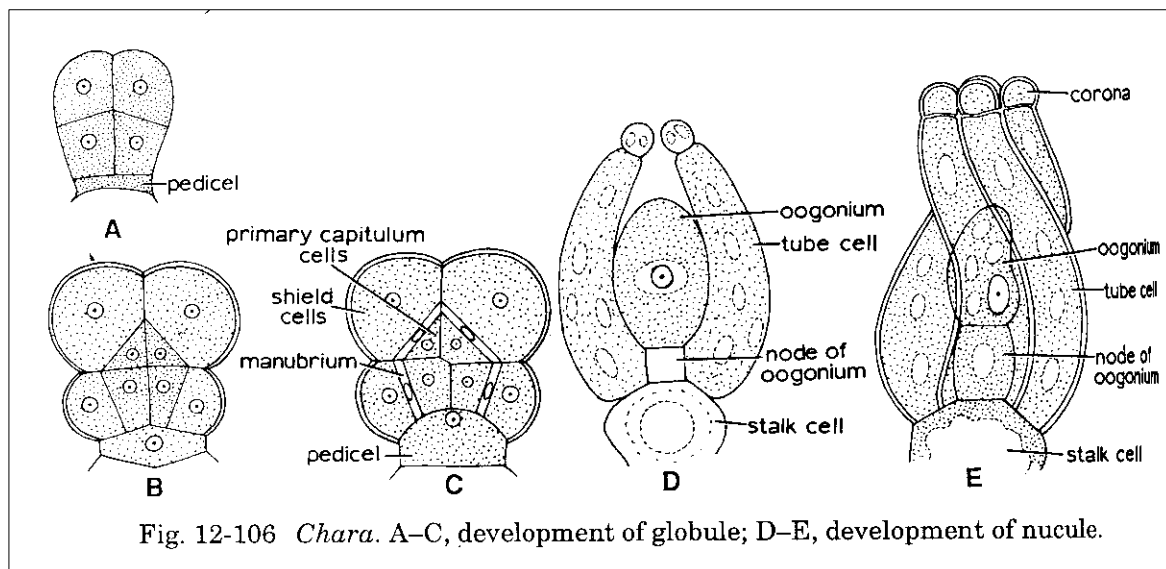


Fig. 12-106 *Chara*. A–C, development of globule; D–E, development of nucule.

Fig. 3.21 *Chara*. A–C, development of globule; D–E, development of nucule (adopted from Kumar, 1999)

When nucule matures, the spiral tube cells separate from one another and the resulting space in between them provides an opening for the entrance of spermatozoids. One of the spermatozoids fuses with ovum resulting into formation of zygote (oospore).

Zygote germination: After a brief rest, zygote germinates and gives rise a new plant. Before germination, the nucleus migrates to the anterior region where it divides meiotically. A septum is laid down forming a uninucleate upper cell and a degenerative trinucleate lower cell (Fig. 3.22A,B). The upper cell undergoes one mitotic division in a vertical plane. Of the two daughter cells, one acts as the protonemal initial and other as the rhizoidal initial. These initials form the filamentous protonema and the colourless rhizoids respectively, both with nodes and internodes. The plant arises from one of the appendages borne on the second node of the protonema.

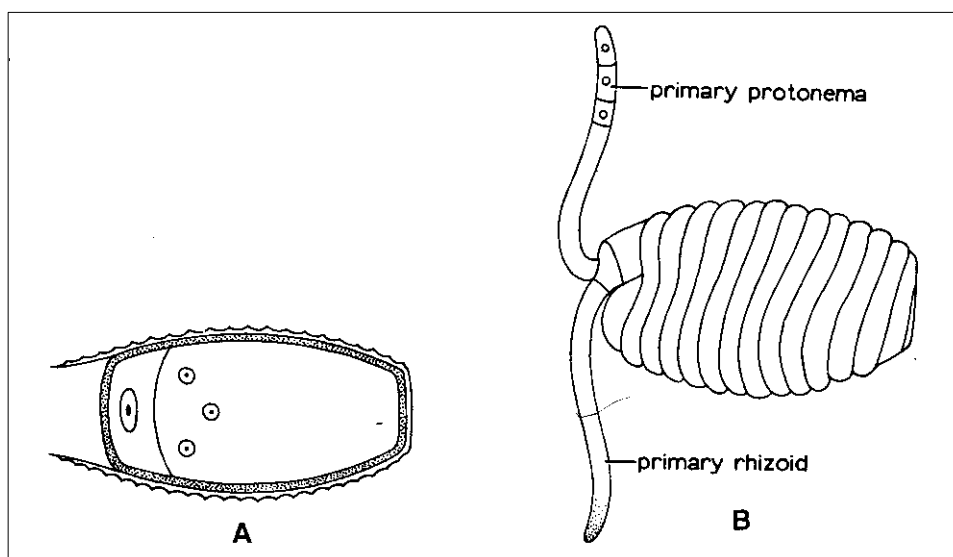


Fig. 3.22 *Chara*. A. germinating division; B, surface view of germinating oospore (after Smith, 1955)

(iii) Phylogeny

Charophyta resembles the Chlorophyta with respect to photosynthetic pigments, food reserves, cell wall composition, flagella and zygote germination. Some of the features of Charophyta are shared by the chaetophorean genus *Draparnaldiopsis*, these are the (1) differentiation of main filament into node and internodal cells, (2) formation of corticating filaments, (3) production of lateral branches of limited growth, and (4) participation of laterals of limited growth in reproduction. Desikachary and Sunderalingam (1962) opined that Charophyta were derived from Chaetophorales. But the apical growth and the complex nature of the sex organs discount any possible origin of the Charophyceae from the Chaetophorales.

Papenfuss (1955), on the basis of parallelism in the development of sex organs has emphasized an affinity between bryophytes and charophytes. Bold (1967) considers that morphologically the sex organs of the Charophyceae are in no way different from these bryophytes.

Origin of land plants: According to Stewart and Mattox (1975), the ancestry of archegoniate plants should be traced from the Charales and also possibly from *Coleochaete* like alga. This view is based on the following points of resemblance between Charales and archegoniate plants: (1) presence of phragmoplast, (2) presence of similar type of antherozoids (identical

microtubular cyto-skeleton), (3) occurrence of glycolate oxidase, (4) protection of gametangia by sterile cells, and (5) apparent similarity between the plant bodies.

(iv) Life cycle

The genus *Chara* is haploid plant representing the gametophytic stage while the zygote is the diploid stage (Fig. 3.23). It undergoes meiosis and germinates to give rise the haploid plant.

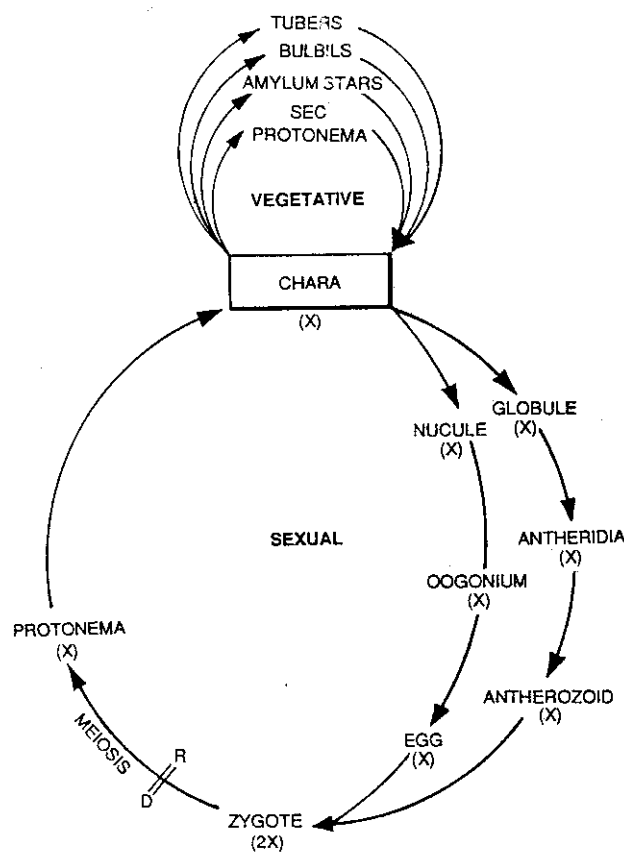


Fig. 3.23. Life cycle of *Chara*.

3.3 SUMMARY

Chlorophyta: The class Chlorophyceae of division Chlorophyta is characterized by the presence of eukaryotic cell organization and presence of pigments such as chlorophyll **a**, chlorophyll **b**, various carotenes and xanthophylls. Green algae occur widely in fresh and marine water habitats. The thallus exhibit a great variation in its habit and structure, ranging from a motile or non-motile cell through colonial, filamentous, parenchymatous and siphonous

habits to the highly evolved heterotrichous filament (e.g., *Coleochaete*, *Draparnaldia*, *Draparnaldiopsis*, *Stigeoclonium* etc.)

Usually, the cells are uninucleated but in Cladophorales, Siphonales, *Sphaeroplea* and Charales, the cells are coenocytic. There is a great diversity in number, morphology and arrangement of chloroplasts. The pyrenoid of the green algae commonly consists of a proteinaceous core which is surrounded by minute plates of starch.

There has been an evolutionary advancement in sexual reproduction from isogamy through anisogamy to oogamy, accompanying the reduction in number and an increase in the size of the female gametophytes.

Charophyta: Bold (1967) and Round (1971) had raised the Charales of Fritsch (1935) to the rank of phylum, the Charophyta. The division Charophyta includes a single order Charales, popularly known as 'stoneworts'. It is characterized by the presence of thallus with regular differentiation of nodes and internodes with the deposition of calcium carbonate; and also presence of highly specialized male and female reproductive structures, known as 'globule' and 'nucule' respectively.

Charophyta resembles the Chlorophyta in many respects. Some of the features of Charophyta are shared by the chaetophorean genus *Draparnaldiopsis*. Desikachary and Sunderlingam (1962) opined that Charophyta were derived from Chaetophorales. Papenfuss (1955), on the basis of parallelism in the development of sex organs has emphasized an affinity between bryophytes and charophytes.

Model Questions

(1) Essay Questions

- (i) Discuss the range of thallus organization in Chlorophyta.
- (ii) Give an account on Reproduction in Chlorophyta.
- (iii) Give an account on Life cycles of Chlorophyta.
- (iv) Discuss the general features of Charophyta and its phylogenetic significance.

(2) Short notes

- (i) Structure of Chlorophyte cell
- (ii) Classification of Chlorophyta
- (iii) Phylogenetic relationships of Chlorophyta
- (iv) *Oedogonium*
- (v) *Draparnaldia*
- (vi) Globule
- (vii) Nucule

(viii) Phylagenetic importance of *Chara*.

Reference Books

- (1) Kumar, H.D. 1999. **Introductory Phycology**. Affiliated East-West Press Pvt. Ltd., New Delhi.
- (2) Pandey, D.C. 1981. **Algae**. Kitab Mahal, Allahabad.
- (3) Round, F.E. 1963. **The Biology of the Algae**. Edward Arnold, London.

Dr. S.M. KHASIM

M.Sc. BOTANY (First Year)**Paper-I : Biology and Diversity of Algae, Bryophytes and Gymnosperms****Unit-IV : GYMNOSPERMS****Lesson 1****GYMNOSPERMS – CLASSIFICATION, DISTRIBUTION AND ECONOMIC IMPORTANCE**

- 1.0 **AIM**
This lesson deals with the general characteristics, classification, distribution and economic importance of gymnosperms
- 1.1 **INTRODUCTION**
- 1.2 **ANTIQUITY AND FOSSIL HISTORY**
- 1.3 **GYMNOSPERMS AND PTERIDOPHYTES**
- 1.4 **GYMNOSPERMS AND ANGIOSPERMS**
- 1.5 **CLASSIFICATION OF GYMNOSPERMS**
- 1.6 **DISTRIBUTION OF GYMNOSPERMS:**
 - a) Worldwide distribution
 - b) Distribution in India
- 1.7 **ECONOMIC IMPORTANCE**
 - A) Wood
 - B) Paper and Board
 - C) Resins
 - D) Tannins
 - E) Essential oils
 - F) Fatty oils
 - G) Food supplements
 - H) Drugs
 - I) Other uses
- 1.8 **SUMMARY**
- 1.9 **KEY TERMS**
- 1.10 **MODEL QUESTIONS**
- 1.11 **REFERENCE BOOKS**

1.1 INTRODUCTION

Spermatophyta division includes all those plants which bear seeds. This division is divided into gymnosperms and angiosperms. The word gymnosperm was first used by Theophrastus (in 300 B.C.) to describe plants whose seeds are unprotected. In gymnosperm (Gr. gymnos = naked;

Sperma = seed), the ovules are exposed, where as in angiosperms (Gr. angios = closed; sperma = seed), ovules are enclosed in an ovary. Thus the gymnosperms are seed plants, whose ovules are borne directly on the sporophyll or an equivalent structure and are exposed. In some gymnosperms, overlapping scales and sporophylls protect the ovules but they are freely exposed at pollination.

Some of the typical features of gymnosperms are: They are mostly woody and ever green trees, shrub or lianes. They have a tap root which usually persists for a long time. Stems contain conjoint, collateral, open and endarch vascular bundles usually arranged in a ring. The xylem consists of trachieds, parenchyma and rays. Vessels are absent (except in *Ephedra*, *Welwitschia* and *Gnetum*). Phloem consists of sieve tubes and phloem parenchyma. Companion cells are absent. Secondary growth takes place in all gymnosperms. Numerous light pollen grains are produced in the microsporangia which develop in eusporangiate type. Prothallial cells are formed in the male gametophyte. The ovule is unitegmic and orthotropous. Gymnosperms are wind-pollinated. Insect pollination, common in angiosperms is nearly absent in gymnosperms. There is a prolonged free nuclear phase in the development of the female gametophyte, a long interval between pollination and fertilization and a free-nuclear phase in the development of the pro-embryo. Double fertilization, a feature unique to angiosperms is absent in gymnosperms (with exception in *Ephedra*). The nutritive storage tissue (endosperm) in post-fertilization stages is gametophytic in nature and it is haploid.

1.2 ANTIQUITY AND FOSSIL HISTORY

The gymnosperms are an ancient heterogenous group of seed plants. They constituted most of the world's dominant vegetation throughout the late Paleozoic and Mesozoic eras and steadily declined there after. The occurrence of gymnosperms dates back to the Devonian (395 my B.P. = million years before present). During the Carboniferous (345-280 my B.P.) a large variety of pteridosperms and cordiales existed. In the Permian and Triassic (280-225 my B.P.) the carboniferous pteridosperms became extinct. The early conifers (vultziales) diversified and the cycads and cycadeoides became evident for the first time. Glossopteridales formed a conspicuous flora of the Southern Hemisphere during the Permian. The ginkgophytes appeared some time during the permian, and became more widely spread in the Triassic. In the Jurassic (195-141 my B.P.), the cycads, cycadeoids conifers and ginkgophytes reached their peak of diversification and the glossopterids became extinct. During the upper Carboniferous (141-65 my B.P.), the angiosperms appeared and diversified rapidly. They began to replace the already declining cycads, cycadeoids, conifers and ginkgophytes. Mesozoic pteridosperms and other smaller groups became extinct. However, the majority of the conifers have continued upto the present. In the Tertiary (65 my B.P.) the angiosperms evolved steadily while the conifers declined in diversity. The gymnosperms occupied a second position, although they still dominated landscapes. At present, the gymnosperms comprise only 69 genera and 760 species.

1.3 GYMNOSPERMS AND PTERIDOPHYTES

These two groups of plants share some common features like: a) both have independent sporophyte mostly differentiated into stem, root and leaf, b) a well-developed vascular tissue, the xylem lacks true vessels and phloem is without companion cells, c) the leaves of cycads are compound with circinate vernation like many ferns, d) motile male gametes of cycas and *Ginkgo*, and e) archegonia are present in the female gametophyte except in *Gnetum* and *Welwitschia*.

At the same time, gymnosperms show a definite advance over pteridophytes: a) long-lasting tap root system provides better anchorage to the gymnosperm plant. In pteridophytes, the roots are mostly adventitious. b) The gymnosperm stems are mostly mono stelic but pteridophytes have a wide range of primary vascular system. c) All gymnosperms show secondary growth, but it is absent in pteridophytes. In *Isoetes* and *Botrychium*, secondary growth occurs but is not extensive. d) The mature metaxylem in gymnosperms shows bordered pits, but in pteridophytes the xylem is typically scalariform. e) Gymnospermous sieve cells are shorter, where as pteridophytic sieve elements are longer. f) All gymnosperms are heterosporous, where as the majority of pteridophytes are homosporous. g) Wind pollination is a rule in gymnosperms except in Gnetopsida in which entomophily is reported. h) Gymnosperms are seed bearing plants and seed formation is absent in pteridophytes.

1.4 GYMNOSPERMS AND ANGIOSPERMS

Both gymnosperms and angiosperms are seed plants. There are many differences in vegetative and reproductive structures between the two groups of plants: a) The gymnosperms are slow growing perennials with limited vegetative reproduction. In angiosperms, the plants are annual, biennial or perennial and have varied means of vegetative reproduction. b) In angiosperms both tracheids and vessels are present and in gymnosperms tracheids are present (except in Gnetopsida). Companion cells in phloem of angiosperms are present and they are absent in gymnosperms. c) Gymnosperm wood is of either manoxylic or pycnoxylic type and angiosperms do not show such distinction. d) Pollination and seed dispersal in gymnosperms is mostly anemophilous but in angiosperms entomophilous, hydrophilous and zoophilous. e) The ovules are naked and unitegmic in gymnosperms where as in angiosperms ovules are inside carpels and are uni- or bitegmic. f) Pollen grains directly rest on the nucellus of ovules in gymnosperms but the angiosperm pollen land on the stigma. g) Monosporic type of female gametophyte development is characteristic of gymnosperms (except in *Gnetum* and *Welwitschia*) but mono-, bi-, or tetrasporic types of female gametophyte development are observed in angiosperms. h) The haploid female gametophyte in gymnosperms functions as endosperm after fertilization. In angiosperms the endosperm is triploid formed by double fertilization. i) The zygote division is invariably followed by wall formation in angiosperms (except in *Paeonia*) where as in gymnosperms the zygote undergoes free nuclear division with exception in *Sequoia*, *Gnetum* and *Welwitschia* followed by wall formation. j) Cleavage polyembryony is prevalent in gymnosperms and it is absent in angiosperms. k) Prothallial cells are present in male gametophytes of gymnosperms and archegonia

present at the micropylar end of female gametophytes of gymnosperms. In angiosperms prothallial cells and archegonia are lacking.

The fascinating group of Gymnospermous plants stands between cryptogams and flowering plants.

1.5 CLASSIFICATION

Gymnosperms have been variously classified by different taxonomists. The evolutionary history of gymnosperms extends back in geological time scale and its fossil record begins in upper Devonian and spreads over nearly 350 million years before present. There is only fragmentary fossil record on many of the branches and several presumed gymnospermous remains have been described from upper Devonian and lower carboniferous periods. It is therefore, natural that there will be diversity of opinion on the phylogenetic relationships and classification of gymnosperms. In most instances, the evolutionary relationships of fossil plants are not completely known (Miller, 1985). Sporne (1965) stated that until reproductive organs are discovered in organic connection with the vegetative parts, their taxonomic placement is entirely optional.

The smallest unit of classification is the *species*. Similar species are grouped into a *genus*. Various genera are grouped into a *family*, various families into an *order*, orders into a *class*, classes into a *division* or *phylum* and various *divisions* or *phyta* into a *kingdom*. Many different positions have been assigned to gymnosperms in the plant kingdom.

Bentham and Hooker (1883) in their *Genera Plantarum* placed gymnosperms between monocotyledons and dicotyledons. Van Tieghem (1898) was first to recognise gymnosperms as one of the two major divisions of Spermatophyta (seed plants): the Gymnosperms (Astigmatae) and Angiosperms (Stigmatae). Coulter and Chamberlain (1917) straightway divided gymnosperms into orders namely – Cycadoflicales, Bennettitales, Cycadales, Cordaitales, Ginkgoales, Coniferales and Gnetales. Later Chamberlain (1935) accommodated these orders in two divisions viz., Cycadophytes (including Cycadofilicales, Bennettitales and Cycadales) and Coniferophytes (including Cordaitales, Ginkgoales, Coniferales and Gnetales). Sahni (1920) divided gymnosperms into two divisions, based on the origin of ovules either on the leaves or sporophylls (Phyllospermae) or on the stems (Stachyospermae). Phyllospermae includes Pteridospermales (Cycadofilicales), Cycadales and Bennettitales. Stachyospermae includes Cordaitales, Ginkgoales, Coniferales and Taxales. The class cycadophytes of Chamberlain is similar to the phyllospermae of Sahni. Also Stachyospermae of Sahni is similar to coniferophytes of Chamberlain except that Sahni recognised Taxales as a separate order and Chamberlain included Gnetales as separate order in the class.

Arnold (1948) recognised three separate phyta (classes) viz., i) Cycadophyta (Pteridospermae, Cycadeoidales and Cycadales), ii) Coniferophyta (Cordaitales, Ginkgoales, Taxales and Coniferales) and iii) Chlamydospermophyta (Ephedrales and Gnetales). Arnold (1948) opined that the seed habit arose independently in different classes, thus the gymnosperms

representing a polyphyletic group. Florin (1948) upheld the separation of Taxales as an order coordinate in rank with the Cordaitales, Ginkgoales and Coniferales. However, he included only *Taxus*, *Torreya*, *Amentotaxus*, *Nothotaxus*, *Austrotaxus* and their fossil relatives and retained *Cephalotaxus* within Coniferales. Pilger and Melchior (1954) recognized three classes viz., a) Cycadopsida (Pteridospermales, Bennettitales, Pentoxylales, Cycadales), b) Coniferopsida (Cordaitales, Coniferales, Taxales and Ginkgoales) and c) Gnetopsida (Gnetales).

Bierhost (1971) proposed a slightly different classification:

Cycadopsida: Pteridospermales, Caytoniales, Cycadales, Cycadeiodales, Pentoxylales and Glossopteridales.

Coniferopsida: Cordaitales, Protopityales, Coniferales, Taxales and Ginkgoales.

Gnetopsida: Ephedrales, Gnetales and Welwitschiales.

He proposed separate orders Caytoniales, Glossopteridales in Cycadopsida and protopityales in Coniferopsida. Ephedrales, Gnetales and Welwitschiales in Gnetopsida.

Beck (1981) and Rothwell (1982) proposed a scheme of classification to account for the role of progymnosperms. The progymnosperms show a combination of pteridophytic (spore producing reproductive structure) and gymnospermic (arborescent, abundant secondary xylem, bordered pits on xylem tracheids and leaf traces without leaf gaps) characters. This group is considered to be the progenitor of gymnosperms.

Stewart (1983) proposed a classification which is synthesis of several different natural systems. He used the fossil record to establish the natural relationship within the major groups of vascular plants. His classification is as follows:

1. **Progymnospermopsida (Ancestors of Gymnosperms):**

a) Aneurophytales, b) Archaeopteridales, and c) Protopityales.

2. **Gymnospermopsida:** Pteridospermales, Cycadales, Cycadeiodales, Caytoniales, Glossopteridales, Pentoxylales, Czekanowskiales, Ginkgoales, Cordaitales, Voltziales, Coniferales and Taxales.

3. **Gnetopsida:** Gnetales, Ephedrales and Welwitschiales.

Meyen (1984 & 1986) recognized three classes namely, Ginkgoopsida, Cycadopsida and Pinopsida. Under Ginkgoopsida he placed nine orders, Cycadopsida had six orders and Pinopsida had two orders. Meyen treated Gnetales and Welwitschiales in the Cycadopsida and Ephedrales in the Ginkgoopsida which appears highly unsatisfactory.

Rothwell (1985) commented that during the past 50 years, new taxa have not been described and the inter-relationships between the existing taxa have also not changed significantly. Hence, the different classifications which are in vogue, differ mainly in their content and placement of various orders and families. The classification in this book is based on Pilger and Melchior (1954) adopted by Sporne (1974).

Gymnosperms

A. Cycadopsida

1. Pteridospermales*
2. Bennettitales*
3. Pentoxylales*
4. Cycadales

B. Coniferopsida

1. Cordaitales*
2. Coniferales
3. Taxales
4. Ginkgoales

C. Gnetopsida

1. Gnetales

1.6 DISTRIBUTION OF GYMNOSPERMS

Of the living (extant) gymnosperms, cycadales and Ginkgoales are very ancient with a long fossil history and they are often referred as “living fossils”. The living gymnosperms are represented by 69 genera and 760 species. In India, gymnosperms are represented by 14 genera and 50 species (Raizada & Sahn, 1960). Such a low representation of gymnosperms in India is due to the fact that these plants require mainly temperate climate and such climate in our country is available chiefly in Himalayas. Therefore, gymnosperms distributed in Himalayan ranges only.

1.6. (a) Worldwide Distribution of Gymnosperms

Cycadales: Of the 11 taxa of cycadales, six taxa occur in Eastern hemisphere and five taxa in western hemisphere. No single genus is represented in both hemispheres. Of the eastern cycads, *Macrozamia*, *Lepidozamia* and *Bowenia* are confined to Australia and *Encephalartos* and *Stangeria* exclusively to South Africa. The genus *Cycas* occurs from Australia to Japan, touching India and China. Of the western genera *Dioon* and *Ceratozamia* are confined entirely to Mexico, *Microcycas* to Western Cuba, *Zamia* to both areas and *Chigua* in Columbia only.

Ginkgoales: All members of the order Ginkgoales except *Ginkgo* became extinct by Cretaceous period. The sole surviving member *Ginkgo biloba* is restricted in its geographical distribution. At present, it is confined to a small in accessible region in South-eastern China. The reason for its survival is probably its immense vigour that enabled it survival. *Ginkgo* is to be regarded as one of the wonders of the world because it has persisted with very little change through a very long succession of ages. The remarkable unchangedness of cycads and *Ginkgo biloba* is that still they produce motile sperms, though they have been in existence for at least 200,000,000 years.

*Extinct and represented by fossil genera only

Coniferales: Coniferales are the most conspicuous group and constitute more than three fourths of the total living gymnosperm flora. They occupy vast areas of the temperate regions of both Northern and Southern hemispheres. Western North America, Eastern and Central China, parts of Australia and New Zealand have abundant conifers. There are 52 genera and 566 species of conifers (Mehra, 1988). Of the six families, Pinaceae, Taxodiaceae are distributed in Northern hemisphere and Podocarpaceae, Araucariaceae are represented in Southern hemisphere. Cupressaceae is an interesting family in that half the genera northern and half southern in distribution.

The taxa of Pinaceae i.e., *Abies*, *Cedrus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga* are distributed mainly in Northern Europe, North and Central America, Subtropics of North America, the Canary Islands, Afghanistan, Pakistan, India, Myanmar and the Philippines. They spread upto Indonesia after crossing the equator.

Of the ten genera of Taxodiaceae seven are monotypic and remaining three have 8 species. *Taxodium* is native to North America and Mexico. *Taxodium* has three species of which *T. ascendens* is common in wet grounds from Florida to Mexico. *T. mucronatum* specimen present in Tule about 400 km South of old city of Mexico is 5,000 years old and probably the oldest living thing in the world. The tallest living tree *Sequoia sempervirens* (Californian redwood) is restricted to a narrow coastal belt in California (USA) and *Sequoiadendron giganteum* (big tree) in central California. *Cryptomeria japonica* and *Cunninghamia* spp. are distributed in Japan and parts of China. *Sciadopitys verticellata* is present in Japan, *Glyptostrobus* in **China** and *Taiwania* in Formosa. *Athrotaxis* is the only Southern taxa confined to Tasmania.

Cupressaceae is the largest family of conifers. There are about 22 genera and 150 species in this family that occur both in Northern and Southern hemisphere. *Cupressus*, *Chamaecyparis*, *Retinospora*, *Thuja* and *Juniperus* are distributed in Northern hemisphere while southern taxa such as *Callitris* is confined to Australia, Tasmania and New Caledonia, *Libocedrus* to New Zealand and *Popuacedrus* to New Guinea extending across the equator into Northern hemisphere.

Podocarpaceae consists of seven genera namely *Acmopyle*, *Dacrydium*, *Microcachrys*, *Microstrobus*, *Phyllocladus*, *Podocarpus* and *Saxegothea*. These are mainly distributed in Africa, South East Asia, Australia and South America. The largest genus *Podocarpus* (106 species) occurs in the mountain forests of warm temperate and subtropical regions of Southern hemisphere. Some species occur in Japan, China, India, Malaya and the Philippines. *Dacrydium* and *Phyllocladus* are chiefly distributed in New Zealand and Tasmania. *Saxegothea* is confined to Chile and *Microstrobus* to Tasmania. *Acmopyle* is restricted to New Caledonia and Fiji.

Araucariaceae is with two taxa viz., *Araucaria* and *Agathis*. They are restricted to Southern hemisphere. *Araucaria* is distributed in South America, Australia, New Guinea and New Caledonia. *Agathis* is exclusively eastern extending from the Philippines to New Zealand and Malaya to Fiji.

Cephalataxus is the only genus of the family. *Cephalotaxaceae* is distributed from Eastern Himalayas to Japan in subtropical forests.

Taxales: The order Taxales includes a single family, Taxaceae with five genera viz., *Taxus*, *Austrotaxus*, *Pseudotaxus*, *Torreya* and *Amentotaxus*.

The principal genus *Taxus* is distributed in North America, Europe and Asia and extends upto Malaya. *Amentotaxus* presently occurs in East Asia. *Torreya* occurs only in California, Florida and Eastern Asia. *Austrotaxus* is confined to New Caledonia.

Gnetales: This order includes three genera i.e., *Gnetum*, *Welwitschia* and *Ephedra*. *Gnetum* inhabits moist tropical forests in parts of Asia, Africa, Northern South America and certain islands between Asia and Australia. Most of the species of *Gnetum* (30 spp) are endemic. The monotypic *Welwitschia* is confined to only narrow belt in South-West Africa. *Ephedra* comprises nearly 40 species widely distributed in the arid regions of New world and old world from Mediterranean and Black Sea shores upto China including northern and north-eastern India. The old world (France, Canary islands, around the Mediterranean east to Persia, India and China) accounts for about 18 species whereas 22 species are confined to the New World (North and South America).

1.6 (b) Distribution of Gymnosperms in India

The gymnosperm flora of India comprises **14** genera and **50** species (Raizada and Sahni, 1960).

Cycadales: Five species of *cycas* occur mainly in South India. These are *Cycas beddomei* (Madras and Cuddapah district in Andhra Pradesh), *C. circinalis* (Andaman and Nicobar Islands and some dry deciduous forests of South India), *C. rumphii* (Andaman and Nicobar Islands), *C. griffithii* (Manipur and Nega Hills) and *C. pectinata* (Assam, Bihar, Sikkim and several parts of Eastern India). *C. revoluta*, a Japanese species is cultivated commonly in Indian gardens.

Coniferales: Ten different genera of coniferales are reported from India. The distribution of majority of these members is restricted to Himalayas (Table 1).

Table 1. Distribution of coniferales and taxaes in India

S.No.	Species	Family	Place of occurrence
1	<i>Abies delavayi</i>	Pinaceae	Eastern Himalayas (2750-3350 m)
2	<i>A. densa</i>	„	Eastern Himalayas
3	<i>A. pindrow</i>	„	Western Himalayas (2500 m)
4	<i>A. spectatbilis</i>	„	Western Himalayas
5	<i>Cedrus deodara</i>	„	Western Himalayas (1200-3300 m)
6	<i>Cephalotaxus griffithi</i>	Cephalotaxaceae	Eastern Himalayas
7	<i>Cephalotaxus mannii</i>	„	Eastern Himalayas
8	<i>Cupressus tortulosa</i>	Cupressaceae	Chamba Hills (H.P.) to Akai Hills - Assam (1800-2800 m)
9	<i>Juniperus communis</i>	„	Garhwal Himalayas (2900-4250 m)
10	<i>J. coxii</i>	„	Eastern & Western Himalayas
11	<i>J. macropoda</i>	„	Laddakh, Kanawar and Alaknanda Valley (2500-4300 m)
12	<i>J. squamulata</i>	„	Eastern Himalayas (3000-5000 m)
13	<i>J. wallichiana</i>	„	Himalayan ranges (3000-4200 m)
14	<i>Larix griffithiana</i>	Pinaceae	Sikkim, Chumbi valley of Tibet, Mishmi Hills (Assam)
15	<i>Picea smithiana</i>	„	Western Himalayas
16	<i>Pinus</i> 6 species (<i>P. roxburghii</i> , <i>P. insularis</i> <i>P. gerardiana</i>)	„	Himalayas
17	<i>Podocarpus neerifolia</i>	Podocarpaceae	Andaman Islands & Eastern Himalayas
18	<i>Podocarpus wallichiana</i>	„	Nilgiri Hills, Assam
19	<i>Tsuga dumosa</i>	Pinaceae	Darjeeling
20	<i>Taxus baccata</i>	Taxaceae	Khasi-Jaintia hills in Assam & Naga Hills, Manipur, Simla

(Numbers in parentheses indicate meters above sea level).

Gnetales: The five species of *Gnetum* and six species of *Ephedra* occur in India (Table 2).

Table 2. distribution of Gnetum species in India

S.No.	Species	Place of occurrence
1	<i>Gnetum ula</i>	Western Ghats, Kerala, Nilgiris, A.P. and Orissa
2	<i>G. contractum</i>	Nilgiri Hills, Coonoor & Hills of Kerala
3	<i>G. gnemon</i>	Assam
4	<i>G. montanum</i>	Assam, Sikkim and Orissa
5	<i>G. latifolium</i>	Andaman Nicobar islands

Ephedra foliata, *E. gerardiana*, *E. intermedia*, *E. nebrodensis*, *E. regiliana* and *E. saxatilis* are widely growing in dry parts of Haryana, Punjab, Rajasthan and parts of Sikkim, Kashmir and also at high altitudes of Himalayas.

1.7 Economic Importance of Gymnosperms

The gymnosperms constitute an economically important group of plants. They are being used throughout the world for various purposes including landscaping, timber, building construction, paper manufacturing, resin, varnishes, perfumes, essential oils and medicines. Some of such aspects are dealt in brief here.

(A) Wood: The coniferous wood is generally straight-grained, light-coloured and light-weighted. Its texture is softer than angiosperm wood, due to presence of more cellulose. The wood finds great use where strength and durability are not required. It is much valued for cabinet and furniture making, joinery work and interior decoration. The wood of *Abies alba* an important timber of Europe is used in general carpentry, musical instruments, boards and boxes. Different species of *Abies* form important timber yielding trees of different countries. *A. delavayi* is an important timber tree of China, *A. grandis* in Canada, *A. firma* in Japan, *A. procera* in America and *A. pindrow* in India. *Agathis australis* (Kauripine) is the chief timber tree of New Zealand. *Araucaria angustifolia* occurs mainly in Brazil, yielding uniformly textured wood useful in making doors, bus chassis, plywood and in joinery work. The wood of *Callitris* is hard, close grained and fragrant. It polishes and finishes well and is resistant to white ants due to the presence of phenol and other chemicals.

Cedrus atlantica (Algeria, Morocco), *C. deodara* (India) and *C. libani* (Lebanon) are much valued among conifers, as their wood is very durable, oily, sweet scented and without resin ducts. The cedar of Lebanon (*C. libani*) was called 'Tree of God' by the ancients as its wood was used as roof beams in all the sacred and celebrated temples of Egypt. *Cedrus deodara* is one of the most important timbers of North India. It is considered strongest among the Indian coniferous woods and as strong as teak. It is resistant to insect attack and used for making doors, poles, furniture, beams,

ceilings, columns, carriages, wagons, boats, flooring and wood carving. *Cryptomeria japonica* yields, one of the most utilized timbers of Japan and is used for furniture, building construction and panelling. The wood of *Juniperus* species is used for pencil making, ship building, ports, carpentry and furniture. Good quality furniture is made from the wood of *Juniperus chinensis* in China, Japan and Mongolia. *Cupressus sempervirens* wood is considered an excellent furniture wood in France and Italy. The doors of St. Peter's in Rome were made from this wood which lasted for nearly 1000 years and this wood is reputed to be one of four woods used in the construction of the cross upon which Christ was crucified. The wood of *Larix* is one of the heaviest, strongest and toughest of the softwoods.

The wood of *Picea sitchensis* is the most valuable of all spruce woods because of its combined qualities of strength and lightness. It is used for plywood for special laminates in aeroplane and glider construction. Different species of *Pinus* yield commercially important and valuable timber. The wood of *Taxus* is also strong, oily, elastic and very durable. *Ginkgo biloba* wood is light and brittle. In China and Japan, it is used for chess boards.

(B) Paper and Board

Paper is made from fibrous material of plant wood. The largest paper producers USA and Canada get 85% of the wood pulp from coniferous wood that contains greater average length of fibres and large percentage of long fibres per unit volume of wood. The wood is converted into pulp or fibrous mass by either mechanical process or chemical process. The important conifers used extensively for the manufacture of paper and board are: *Pinus* sp, *Picea*, *Abies*, *Tsuga*, *Thuja*, *Agathis*, *Araucaria* and *Larix*.

(C) Resins

The conifers are amongst the major resin yielders in the world. Resins are plant exudates and insoluble in water. They are chemically related to terpenes or essential oils. The superior grade resins have invaluable application in industries like paints and varnish, lacquers, paper sizing and medicine. The inferior grades go in the manufacture of yellow laundry soap, printing ink, oil cloth, insulators, insecticides, adhesives, plastics, disinfectants and shoe polish.

In most conifers, the resin remains mixed with either abundant essential oil (oleo-resins) or very little of it (hard resins). In some others the resin is mixed with gum (gum-resin). The hard resin obtained from *Agathis australis* is known as '*Kauri copal*' and from *Agathis alba* is called *Manila copal*. *Amber* is another hard resin produced from the extinct conifers of which *Pinus succinifera* is the main source. Sandarac is also a hard resin obtained from *Tetraclinis articulata* and *Callitris* sps.

Turpentine is an oleo-resin obtained exclusively from conifers. On distillation turpentine yields essential oil (spirits of turpentine) and rosin, both of them are immensely useful. The oleo-resin obtained from *Abies balsamea* is called '*Canada Balsam*' which is a viscid, yellowish

substance with high refractive index. It does not crystallize or granulate on drying. So it is preferred as mounting medium for microscopic objects.

(D) Tannins

The bark of *Tsuga canadensis* has 4-18% of tannins. The other conifers that yield tannins are *Larix decidua*, *Picea abies* and *Phyllocladus trichomanoides*. Tannins are organic compounds, glucosidal and are astringent. They are useful in leather industry, medicine and common inks.

(E) Essential oils

Almost all those conifers that yield resin produce essential oils. Steam distillation of the young branches, leaves and wood yields the oil, which is used extensively in preparations of deodorants, room sprays, disinfectants, perfumery and medicine. Oil of juniper (*Juniperus communis*) is used as an essence for flavouring several European liquors such as gin. Oil of cade (*J. oxycedrus*) is used in the treatment of chronic eczema. In India, the oil extracted from *Cedrus deodara* is used in perfumery and scented soaps.

(F) Fatty Oils

The seeds of several gymnosperms have fatty oils. *Cephalotaxus drupacea* seeds yield a fatty oil which is used as an illuminant in Japan. The fatty oil yielded from the seeds of *Torreya nucifera* is edible. The seed kernels of *Gnetum ula* yield a fatty oil which is used for massage in rheumatism.

(G) Food supplements

Young succulent leaves of *Cycas* spp. and *Gnetum* are cooked and eaten as vegetable. The starch extracted from the cortex and pith of *cycas* stem and seeds is used as a food. The pith of *Encephalartos* is used to make kaffir bread by the aborigines of South Africa. The seeds of *Torreya nucifera* are an important article of food in Japan. The seeds of *Gnetum ula* and *G. gnemon* are eaten roasted or cooked. Pine (*Pinus* spp.) seeds are rich in fats and proteins. They have a good flavour and are edible. The nut is referred to as pignolia (England), Pinone (Italy) and Pignon (France). The ripe seeds of *Araucaria bidwilli* are used for food in Queensland by the aborigines and similarly natives of Chile. In India, starch is extracted from the dried seed kernels of *Cycas* and *Dioon*.

(H) Drugs

The alkaloid 'ephedrine' is extracted from the green branches of *Ephedra* spp. (*E. sinica*, *E. equisetina*, *E. intermedia*, *E. gerardiana* and *E. major*). The plants of *Ephedra* contain up to 2% of alkaloids of which 30-90% is ephedrine and pseudoephedrine. Ephedrine resembles adrenaline,

a hormone-like substance with a stimulating action on sympathetic nervous system. Ephedrine is an important ingredient in the cough mixtures, in nasal drops and inhalants. In China, *Ephedra* (Ma-huang) has been a common medicine for over 5000 years. It is prescribed for typhoid, bad colds, fever without sweat, pains of body and joints, swelling of ankles and short breath.

An extract of *Ginkgo biloba* leaves is useful in the treatment of cerebral insufficiency and vertigo. The extract is chief source of C₂₀ trilactone ginkgolide compounds which antagonize platelet activating factor (PAF) in vertebrate blood systems. The leaves of *Taxus baccata* are used in asthma, bronchitis, hiccup, epilepsy and for indigestion.

Taxol is a drug obtained from the dried inner bark (phloem-cambial tissues) of *Taxus brevifolia*. *Taxol* is considered to be the most effective natural anti-cancer drug and approved for clinical treatment of ovarian cancer, breast cancer, non-small-cell lung cancer, melanoma and colon cancer. *Taxol* has two tumour fighting mechanisms: a) it freezes the mitotic spindle, preventing depolymerization and subsequent division of tumour cells, b) it inhibits cell migration and spread of metastatic cancer cells. The amount of *taxol* in the bark is relatively low (0.01%) and 7000 kgs bark from 3 or 4 trees of 60 years old produce 1 kg of *taxol*. Hence, *Taxus* species may become extinct if its exploitation continues and scientists take long time to explore alternative sources of *taxol*.

A mucilaginous and transparent gum exudated from *Cycas* is used for curing ulcers and as antidote for snake and insect bites. Powdered stem of *Cycas pectinata* is used as a hair wash in Assam. The juice of young leaves of *C. revoluta* finds its use for flatulence and vomiting blood. *Cycas* seeds are used as an emetic and cure for boils, sores, wounds etc.

(I) Other uses

Conifers constitute important group that heightens the beauty of any hill resort, due to their stately appearance, symmetrical growth, evergreen habit and they are undoubtedly a treat to the eye. They are used frequently in landscaping of parks and gardens. Gymnosperms offer a good source material for developing 'bonsai' plants.

Wood wool and leaf wool are obtained from conifers by cutting wood or leaves into tiny small pieces. the wool is used for stuffing pillows, cushions etc. Wood wool of oil-yielding conifers is in demand as it emits a very faint and pleasant pine smell. Conifers are used as Christmas trees and *Ginkgo biloba* is worshipped by buddhists.

The symbiotic association of blue green algae with *Cycas* coralloid roots that assists nitrogen fixation and mycorrhizal association of conifer roots (e.g. *Pinus*) are the two important areas to be understood thoroughly for their use in gymnosperm tree improvement programmes. Indeed there is a need to study this fascinating group of plants – Gymnosperms.

1.8 SUMMARY

Seed plants are divided into Gymnosperms and Angiosperms. The plants whose seeds are afforded less protection, borne directly on sporophyll like structure and exposed vividly are included in Gymnosperms. These are mostly woody and evergreen trees, shrubs or lianes. The gymnosperms constituted once world's most dominant vegetation during Palaeozoic and Mesozoic eras and steadily declined thereafter. Taxonomists classify gymnosperms into three major classes viz., Cycadopsida, Coniferopsida and Gnetopsida, each one of them variously divided into different orders and families. The living gymnosperms are at present represented by 69 genera and 760 species, distributed throughout the world. In India, 14 genera and 50 species are present. Gymnosperms constitute an economically important group of plants used for various purposes including landscaping, timber, building construction, paper and board manufacturing, resin, varnish, perfumes, essential oils and drugs.

1.9 KEY TERMS

Angiosperms: Seed plants whose seeds or ovules are enclosed in an ovary.

Ephedrine: An alkaloid extracted from the plants of *Ephedra*.

Gymnosperms: Seed plants whose seeds are unprotected and ovules exposed.

Hard-resin: Resin with little amount of essential oil in it.

Manoxylic wood: Soft and sparse secondary wood of gymnosperms with very wide parenchymatous rays. Commercially less useful wood.

Oleo-resin: Resin with abundant amount of essential oil in it.

Pycnoxylic wood: Dense and bulky secondary wood of gymnosperms with very small narrow wood rays and an important source of world's timber.

Resin: Plant exudate insoluble in water and soluble in organic solvents.

Spermatophyta: The division representing plants with seeds.

Taxol: A drug obtained from the inner-bark (Phloem-cambial tissues) of *Taxus* spp.

1.10 MODEL QUESTIONS

- i. Write an essay on the classification of Gymnosperms.
- ii. Describe the distribution of living gymnosperms.
- iii. Write an account on the economic importance of Gymnosperms.
- iv. Write short notes on the following:
 - Ephedrine
 - Taxol
 - Oleo-resins
 - Timber yielding conifers

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■ Prof. Z. VISHNUVARDHAN

M.Sc. BOTANY (First Year)

Paper-I : Biology and Diversity of Algae, Bryophytes and Gymnosperms

Unit-IV : GYMNOSPERMS

Lesson 2

PTERIDOSPERMALES

- 2.0 **AIM**
A comprehensive account on seed ferns (Pteridospermales) is presented in this lesson.
- 2.1 **INTRODUCTION**
- 2.2 **GENERAL CHARACTERISTICS OF PTERIDOSPERMALES**
- 2.3 **CLASSIFICATION OF PTERIDOSPERMALES**
- 2.4 **LYGINOPTERIDACEAE**
 - A. General characteristics
 - B. Stems
 - C. Fronds
 - D. Seeds
 - E. Pollen-bearing organs
- 2.5 **SALIENT FEATURES OF**
 - A. Medullosaceae
 - B. Calamopityaceae
- 2.6 **GLOSSOPTERIDACEAE AND MESOZOIC PTERIDOSPERMALES**
 - A. Glossopteridaceae
 - B. Peltaspermaceae
 - C. Corystospermaceae
- 2.7 **SUMMARY**
- 2.8 **KEY TERMS**
- 2.9 **MODEL QUESTIONS**
- 2.10 **REFERENCE BOOKS**

2.1 INTRODUCTION

Fossils are vestiges or traces of plants and animals of the past. The study of fossil plants (Palaeobotany) is such an important branch of science that much of our understanding on past plant life depends on it. One of the most significant contributions that palaeobotany has made to enhance the knowledge of plant history is the discovery of a large and diverse assemblage of fossil plants known as the '**Pteridospermales** or **Seed ferns**'. Our present day knowledge on gymnosperms

support the fact that all gymnosperms except **Gnetopsida**, have originated from Middle Devonian Aneurophytales. The two divergent lines have given rise to **Cycadopsida** and **Coniferopsida** each with distinctive features. The Cycadopsida comprises four orders viz., **Pteridospermales**, **Bennettitales**, **Pentoxylales** and **Cycadales**.

Pteridospermales (Seed ferns) possessed fern-like foliage and seeds, the features that led to coin the name 'Pteridosperms'. As they contain the characters that combine both the characters of cycads and ferns, the group was also named as 'Cycadofilicales'. Pteridospermales are a large and diverse assemblage of plants which first appeared in the Upper Devonian times and extended through the Carboniferous and Permian to the Mesozoic era. The fossil remains of most of these plants are however of fragmentary nature and hence very difficult to define them.

The nature of ovule and seed habit in the seed-ferns and seed plants can be explained from the comparison of similar structure in ferns. For example, a fern species of *Selaginella* have only one megaspore in each sporangium that retains within sporangium for long time. The megaspore may exhibit *in situ* germination, formation of archegonia, their fertilization in the female prothallus and young sporeling may begin to develop while still on the parent sporophyte. This behaviour forms a close parallel with that of seed-plants. But in seed-plants the megasporangium does not dehisce and it is completely enclosed in one or more envelopes (integuments). Upto the stage of fertilization this compound structure consisting of megasporangium and integuments is termed as ovule, which after fertilisation develops into a seed and sheds from the parent plant. Thus an ovule may be defined as an indehiscent integumented megasporangium containing a single functional megaspore.

2.2 GENERAL CHARACTERISTICS OF PETRIDOSPERMALES

1. Plants with relatively slender stems.
2. Primary xylem mesarch (rarely exarch).
3. Primary wood in the form of solid or medullated protostele. Sometimes reduced to circum-medullary strands.
4. Stems are sometimes polystelic.
5. Secondary wood is manoxylic type, very limited in amount and consists of tracheids with multiseriate pitting on the radial walls.
6. Leaves mostly large, fern-like and often multi-pinnate.
7. Ovules and seeds borne on frond (megasporophyll) which is not part of the cone.

2.3 CLASSIFICATION OF PTERIDOSPERMALES

This group is divided into seven families (Sporne, 1965), namely: i) Lyginopteridaceae, ii) Medullosaceae, iii) Calamopityaceae, iv) Glossopteridaceae, v) Peltaspermeaceae, vi) Corystospermaceae, and viii) Caytoniaceae. Stewart (1983) separated the last three families from the rest to include them into an order 'Caytoniales'. In some other classifications Caytoniaceae is separately described as a distinct order 'Caytoniales'. Hence, in this chapter only details of the six

families included. Based on the distribution of the fossils the four families viz., Lyginopteridaceae, Medullosaceae, Calamopityaceae, Glossopteridaceae considered as palaeozoic pteridospermales and the other two families viz., Peltaspermaceae and Corystospermaceae constitute, Mesozoic pteridospermales.

The fossil remains of pteridospermalean plants are, however, of fragmentary nature and therefore the description is based on isolated parts which are assigned to a large number of form-genera.

2.4 LYGINOPTERIDACEAE

(A) General characteristics

Taylor and Millay (1981) and Stewart (1983) listed the following distinguishing features of Lyginopteridaceae.

1. Fossil specimens have been found from both the lower and Upper Carboniferous periods of Palaeozoic era.
2. The plants were lianes or vine-like in habit.
3. Fronds large and usually had a bifurcate rachis.
4. Leaves were highly dissected.
5. Petioles had a V- or W-shaped trace formed from the fusion of several smaller traces.
6. Stems were monostelic.
7. Due to monostelic stems, it was always difficult for the stems to support their large fronds. Therefore, the plants must have had a straggling growth habit.
8. Cortex was with anastomosing longitudinal bands (dictyoxylon or Sparganium cortex) of sclerenchyma.
9. Ovules radially symmetrical and borne in cupules.
10. A structurally complex pollen chamber or pollen-receiving device was present in the ovule.
11. The apex of the nucellus elaborated into a lagenostome or salpinx.
12. Pollen-producing organs were in clusters (synangia) on the branches of fronds.

B. Stems:

The stems of Lyginopteridaceae have been described by different generic names viz., **Tetrastichia**, **Tristichia**, **Rhetinangium**, **Heterangium**, **Lyginopteris**, **Schopfiastrum** etc.

Tetrastichia and **Tristichia** are monotypic genera, whose primary stem structures would almost certainly have placed them with ferns, were it not for their secondary wood and cortical bands of sclerenchyma, which are typical of pteridosperm stems. The stem of **Tetrastichia** was less than 1 cm in diameter and branched in an opposite and decussate fashion (Fig. 2.1A). The primary xylem was cruciate (four-armed) and consisted of a solid protosteles. This consisted of reticulately pitted tracheids, without any admixture of parenchyma. In each arm of the protosteles,

there was a mesarch protoxylem from which the branch trace protoxylems had their origin. The branch-traces were butterfly shaped. A narrow zone of secondary wood (manoxylic) was present that followed the outline of the primary wood. This was made up of tracheids with reticulate thickenings and both uniseriate and multi-seriate wood-rays. In the inner cortex there were scattered groups of stone-cells (Sclerotic nests) and in the outer cortex a network of plates of fibres (Spharganum cortex). **Tristichia** was similar to **Tetrastichia**, differing mainly in its 1/3 phyllotaxy and its primary wood had three radiating arms (Fig. 2.1 B). **Rhetinangium** stem was about 2 cm in diameter with a central stele about 7 mm across. The primary xylem was exarch. The stele consisted of numerous strands of tracheids separated by a meshwork of parenchyma. Cortex was similar to other stem genera in having network of fibrous plates. Petiole received several xylem strands that arranged in U-shaped corrugated band. **Heterangium** is the commonest stem genus. Some twelve species of **Heterangium** are known from the upper carboniferous period. Scott (1923) placed them in three sub-genera, **Eu-Heterangium**, **Polyangium** and **Lyginangium**, which are believed to represent successive levels of evolution. Eu-Heterangium subgenus includes the species like *H. grievii* in which the leaf trace was single at its point of origin. In other species (*H. schusteri*), the leaf trace divided into two. In **Polyangium** group (*H. tiliaeoides* and *H. shorensis*), the leaf trace was a double structure from the start. **Lyginangium** group contains species (*H. andrei*) in which some degree of medullation had taken place. The primary xylem was mesarch and manoxylic secondary wood consisted of tracheids with multiseriate pits on the radial walls. Both the outer and inner cortex of the stems contained sclerotic cells and bands of fibres.

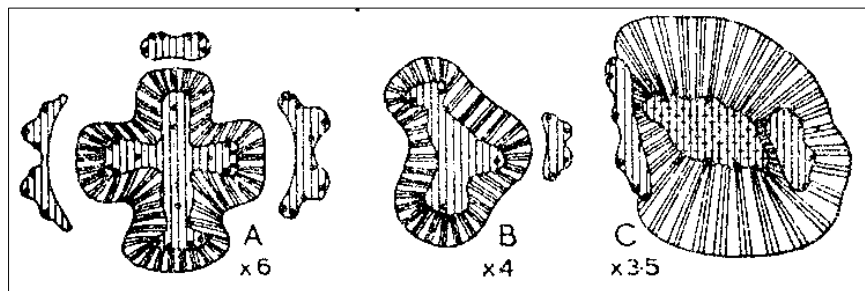


Fig. 2.1 Vascular systems of primitive pteridosperms
 A. Tetrastichia. B. Tristichia. C. Schopfiastrum
 (A, based on Gordeon; B, on Long; C, on Andrews)

Another common stem genus **Lyginopteris** was studied in greater detail. This was represented an example where the process of medullation was complete resulting central pith and primary wood remained nearly by the peripheral leaf-trace system. A reconstruction of the transverse section of the stem of *L. oldhamia* shows a mesarch siphonostele with a well developed centrally located pith (Fig. 2.2). Primary wood consisted of 5-10 mesarch circum-medullary xylem strands surrounding a central pith. Outside to this, a narrow zone of secondary wood was present, which was very loose because of the multiseriate rays. Xylem tracheids of the secondary wood are with multiseriate bordered pits on the radial walls. Sclerotic nests are present both in the pith region and pericycle also. The outer cortex is with a very well-marked network of longitudinal

plates of fibres (dictyoxylon cortex) which in transverse section give the general impression of the Roman numerals on a clock face. This makes the stem of *Lyginopteris* one of the easiest fossils to recognise. Leaves on the *Lyginopteris* stem were borne in a $2/5$ phyllotaxy. One of the peripheral xylem strands in the stem splits into two and sends-out the leaf trace strand which on entering into the leaf base divides to form V-shaped strand.

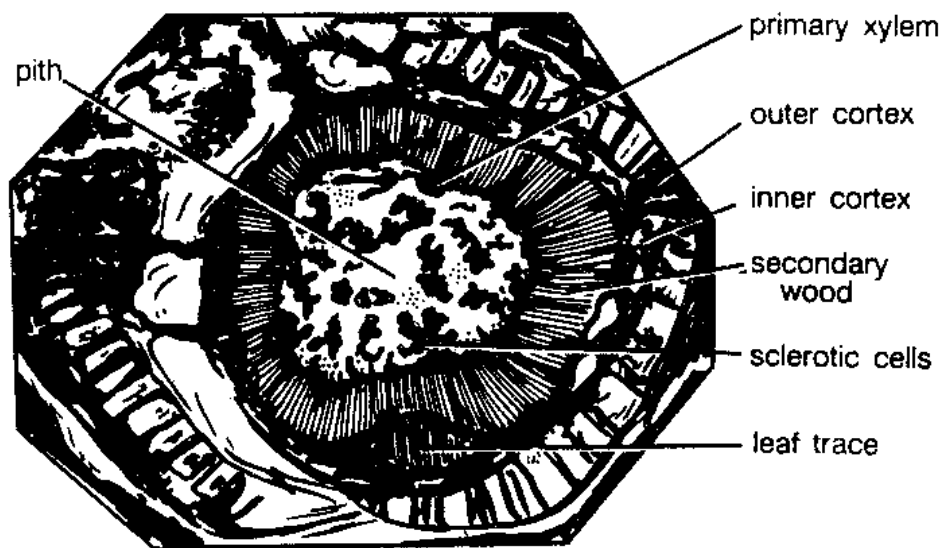


Fig. 2.2 *Lyginopteris oldhamia*. T.S. stem (modified after Kidston)

The stem of *Schopfiastrum decussatum* (Fig. 2.1C) resembles *Rhetinangium* and *Heterangium* in that a few parenchyma cells present mixed with primary xylem trachieds of the centrally located stele. But the protoxylem was exarch. Leaf traces were large-sized and given off in an opposite fashion. The outer cortex was with a network of fibrous strands.

C. Fronds:

Most of the pteridosperm fronds were so large that their fossils are rarely found intact. Hence, minute details of shape and venation of the pinnules are the only available characters. When the complete frond is found, it is frequently seen to have forked near the base into two equal halves. This seems to be the characteristic of pteridosperm fronds.

Pecopteris, *Alethopteris*, *Callipteridium*, *Odontopteris*, *Neuropteris*, *Sphenopteris*, *Sphenopteridium*, *Diplopteridium*, *Adiantites* are some of the frond-genera (Fig. 2.3) of Pteridospermales.



Fig. 2.3 Fronds of some Lower (A to D) and Upper (E to M) Carboniferous Pteridosperms
 A, A complete frond of *Diplopteridium tellianum*; B, A part of frond of *Sphenopteris affinis*; C, A complete frond of *Sphenopteridium capillare*; D, A part of the frond of *Adiantites machanekii*; E, A pinna of *Meriopteris* showing double dichotomy; F, A complete frond of *Odontopteris*; G, Upper part of frond of *Alethopteris*; H, Upper part of the frond of *Neuropteris*; I, A pinnule of *Sphenopteris*; J, Pinnule of *Pecopteris armasii*; K, Pinnule of *Lonchopteris*; L, Pinnule of *Neuropteris*; M, Pinnule of *Linopteris*.

Pecopteris had pinnules with parallel or slightly curved margins attached by the whole width at the base. The pinnules were free from each other (*P. dauberii*) or partly joined (*P. armasi*) resulting pinnatifid condition, rather than pinnate. In *Alithopteris*, the concurrent portion received veins from the rachis as well as from the pinnule midrib. *Odonopteris* had decurrent pinnules with arched veins entering directly from the rachis. The form-genus *Callipteridium* resembles *Pecopteris* and *Alethopteris* on one hand and *Odontopteris* on the other. In some other genera like *Neuropteris* pinnule morphology varied from place to place in the same frond. The pinnae become progressively less compound towards apex, often changing from pinnate through pinnatifid to entire.

The frond known as *Sphenopteris Hoeninghausii* was forked once at a point just above the basal pinnae and with W-shaped trace in the petiole. It was confirmed to have borne on *Lyginopteris* stem, not only by the continuity of the dictyoxylon cortex into the petiole but also because of the occurrence on both the stem and petiole of peculiar glandular spines.

The lower carboniferous pteridosperm fronds are with much branched pinnules and the ultimate segments were still narrow and axis like. But the upper carboniferous genera had a well-marked midrib with lateral veins and some with reticulate venation.

D. Seeds:

Many seed genera have been described from lower and upper carboniferous deposits, of which *Sphaerostoma*, *Salpingostoma*, *Calathospermum*, *Genomosperma*, *Hydrasperma*, *Stannostoma*, *Eosperma*, *Lyrasperma*, *Eusystema*, *Camptosperma* are of Lower Carboniferous and *Lagenostoma*, *Physostoma*, *Conostoma*, *Tyliosperma* are upper Carboniferous age (Fig. 2.4). The details of two seed-genera (*Sphaerostoma* and *Lagenostoma*) representing lower and upper carboniferous period are presented here along with some distinguishing features of other seeds.

Sphaerostoma ovale (Fig. 2.4A), believed to be the seed of *Heterangium grievii* was like all the seeds of *Lyginopteridaceae*, it was relatively small (3.5 mm x 2 mm) and closely invested by a cupule. The cupule had eight vascular bundles running vertically within it. The integument also had eight vascular bundles and it was fused with the nucellus except right at the apex where it formed a canopy over nucellar cap. Eight crested lobes of integument, corresponding to eight vascular bundles, constitute the canopy round the micropyle. The nucellar cap was modified into a pollen capturing device called 'lagenostome' (Fig. 2.4 A-D) Of the hundreds of seeds examined, none has been found with an embryo inside, lending support to the view that fertilization must have taken place after the pollinated seed shed from the parent plant, as in all palaeozoic seeds.

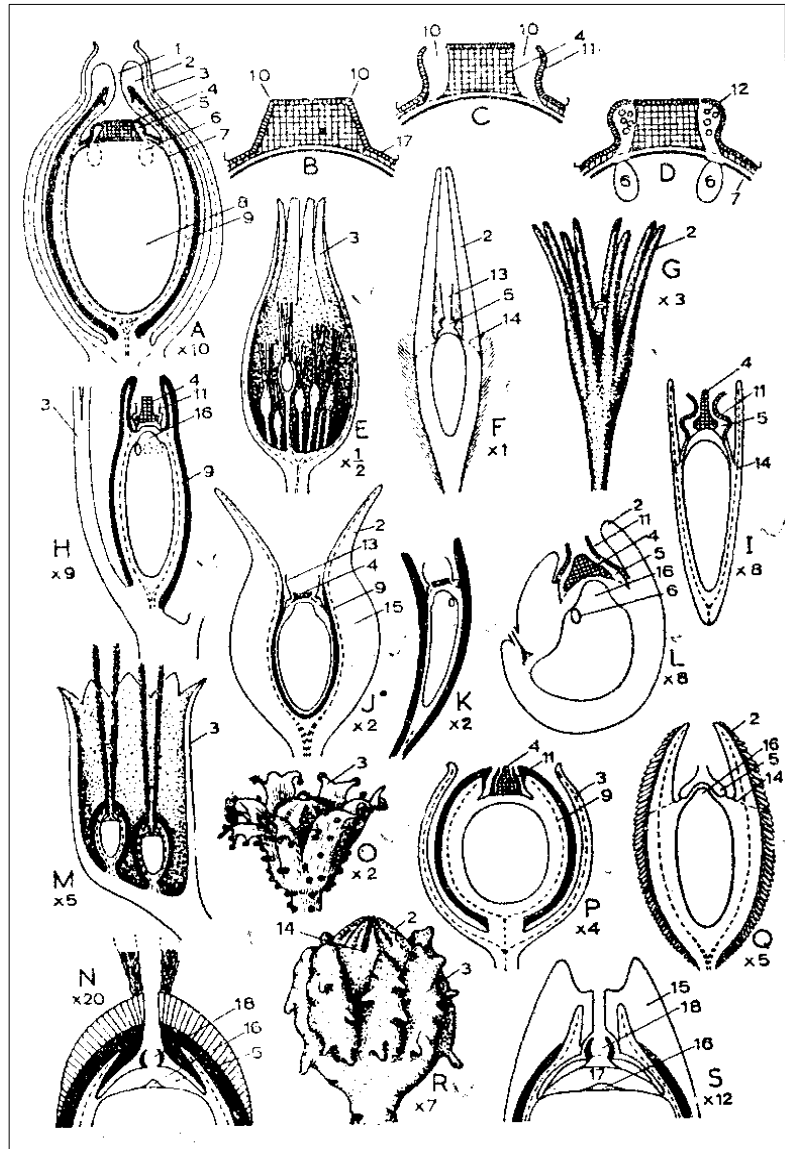


Fig. 2.4 Seeds of Lyginopteridaceae. (A-L from Lower Carboniferous; M-S from Upper carboniferous)
 A, *Sphaerostoma* ovule, l.s. seed in cupule (B, C, D, stages in development of the nucellar cap). E, *Calathospermum scoticum*, cupule cut in half to show stalked seeds inside. F, *Salpingostoma dasu*, l.s. G, *Genomosperma kidstonii*, reconstruction to show free integument-lobes. H, *Stammnostoma huttonense*, l.s. showing part of cupule-lobes. I, *Hydrasperma tenuis*, l.s. J, K, *Lyrasperma scotica*, l.s. seed in planes at right angles. L, *Camptosperma berniciense*, l.s. showing campylotropous shape. M, *Gnetopsis elliptica*, l.s. cupule with two seeds, partly hypothetical (N, l.s. micropylar region), O, *Lagenostoma lomaxii*, reconstruction of seed in cupule (P, l.s. of seed and cupule), Q, *Physostoma elegans*, l.s. R, *Tyliosperma orbiculatum*, reconstruction of seed, showing fleshy cupule-lobes. S, *Conostoma anglo-germanicum*, l.s. micropylar region.

(1, micropyle; 2, integument-lobes; 3, cupule; 4, central plug; 5, pollen-chamber; 6, archegonium; 7, megaspore-wall; 8, female prothallus; 9, integumentary vascular supply; 10, line of circumscissile dehiscence; 11, wall of pollen-chamber; 12, pollen-grains; 13, salpinx; 14, level at which integument-lobes become free from each other; 15, wing-like flange of integument; 16, papilla, or tent-pole; 17, plinth; 18, barrel-shaped lagenostome).

In *Sphaerostoma* each cupule contained just one seed and this was presumably true of many lower carboniferous pteridosperms. Cupule of *Calathospermum scoticum* was rather tulip-flower shaped and contained as many as 70 stalked seeds (Fig. 2.4E). Nine tentacle like lobes were formed from the integument. In *Salpingostoma dasu* each seed contained six tentacles formed from integument. In addition, extending beyond the lagenostome, a trumpet-shaped extension (salpix) was present (Fig. 2.4F). The free lobes (8-10) of integument in *Hydrasperma tenuis* were diverging type. The pollen chamber of *Salpingostoma* seeds contained a central plug of tissue extending up into it. The integument of *Genomosperma* seed was free from the nucellus right to the chalazal end of the seed. The seeds of *Lyrasperma* and *Eosperma* are platyspermic. Campylotropous ovules are present in *Camptosperma*. The cupule of *Stamnostoma* consisted of simple cylindrical axes that branched and folded round the seeds. The integument of *Eurystoma angulare* had four lobes and the seed was quadrangular.

Lagenostoma was an upper carboniferous seed genus. The seed was enveloped by its own cupule. Another seed genus of the same age, *Gnetopsis* contained more than one seed was invested by one cupule. The 'salpix' was absent in these seeds and pollen chambers were barrel shaped without central plug of tissue (Fig. 2.4M).

Lagenostoma lomaxii seed was about 5.5 x 4.25 mm in size and borne inside cupule. The integument was fused with the nucellus except at the apex. It did not form any free lobes around the micropyle, at the apex of the seed. Nine vascular bundle were observed extending in the integument. The lagenostome was bottle-shaped with a central plug (Fig. 2.4 P). In well preserved specimens, prothallus containing archegonia and a well-marked tent-pole were described.

Physostoma seeds had ten integument lobes and covered by large club-shaped epidermal hairs. Another upper carboniferous seed *Tyliosperma* shows an interesting feature that the cupule which was divided to the base into 7-8 fleshy lobes.

It would seem, from the aforesaid information, that there may well have been two quite different kinds of cupule among the Lyginopteridaceae. Radially symmetrical ones that could have resulted from the phylogenetic fusion of a number of separate lobes, while bilaterally symmetrical ones from the folding round of the ultimate segments of the frond. So also in the case of integument, some regarded it as a part of the frond wrapped round the seed and others regarded it as having formed by the fusion of a number of branch tips.

E. Pollen-bearing organs:

It is felt that no pollen bearing organs have been found in organic connection with stems or seeds of Lyginopteridaceae and not a single species can yet be said completely known. However, circumstantial evidence strongly supports the belief that *Telangium*, *Schutzia*, *Alcicornopteris*, *Diplothea*, and *Crossotheca* all represent such pollen bearing organs. These were much more uniform than their seeds. All of them have similar arrangement (synangium) of sporangia (Fig. 2.5). *Telangium affinae* is found with *Sphenopteris affinis* and it is believed that they belonged to

Tetrastichia stems. *Telangium* consisted of a group of 6-8 elongated bilocular sporangia united near the base into a synangial disc. There were upto 25 spore in *T. bifidum* (Fig. 2.5 B-C). Similar synangial discs borne on a slender rachis, with wide-angled forkings attached in the main angle of the forked frond were present in *Diplopteridium* (Fig. 2.5A). *Schuetzia* had pedicellate companulate synangia arranged spirally on a fertile axis (Fig. 2.5H). The number of spore in each synangium is difficult to determine in it. *Alcicornopteris* had about 15 spore attached to a peltate disc and in *Diplothea*, synangial disc bore ten spore united in pairs at the base. *Crossothea* which is believed to be the pollen-bearing organ of the plant *Lyginopteris oldhamia*, contained a number of boot-shaped bilocular spore arranged radially on the underside of the disc (Fig. 2.5E-F). These discs were borne terminally on the segments of fertile frond (Fig. 2.5G) and look like minute hair brushes.

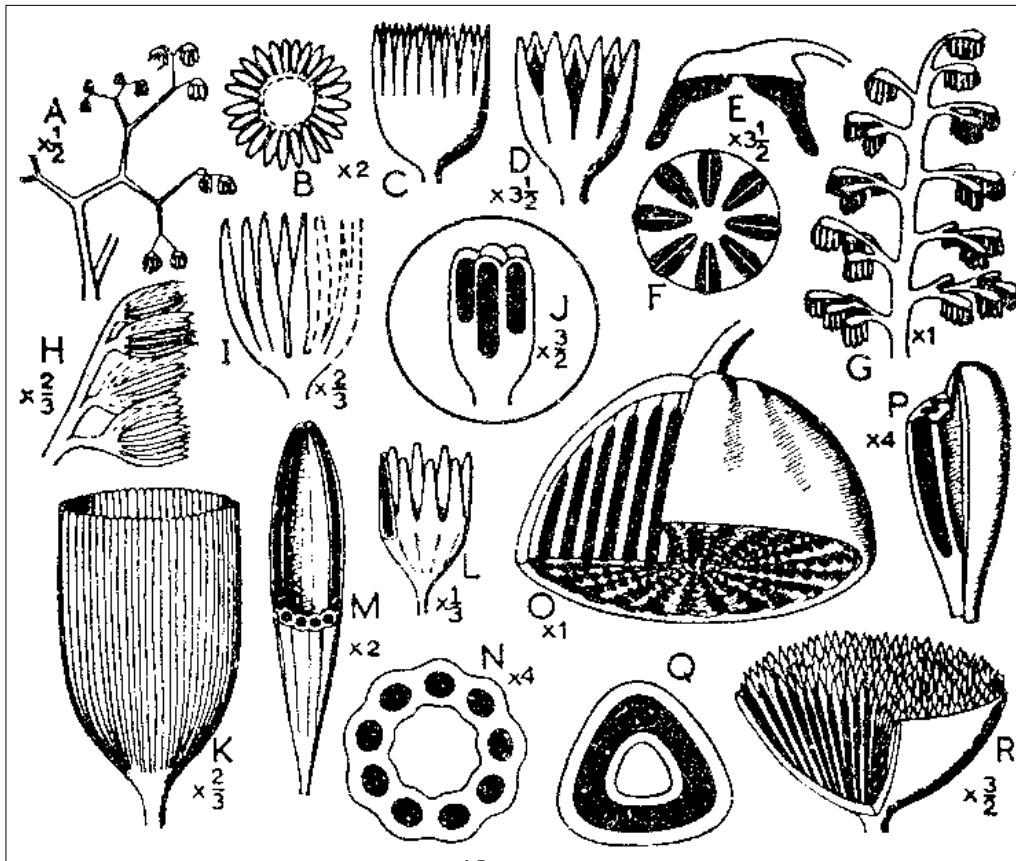


Fig. 2.5 Pollen-bearing organs of Carboniferous pteridosperms
(A-I, Lyginopteridaceae; K-Q, Medullosaceae; J, possible ancestor)

A, *Diplopteridium teilianum*, B, C, *Telangium bifidum*, D, *Telangium affine*, E, F, *Crossothea hoeninghausii*, G, *Crossothea* sp. H, *Schuetzia* sp. I, *Alcicornopteris*, J, *Yarravia oblonga*, a member of the Psilophytales, from the Upper Silurian/Lower Devonian, K, *Whittleseya elegans*. L, *Codonotheca caduca*, M, N, *Aulacotheca elongata*. O, *Dolerotheca formosa*. P, *Goldenbergia glomerata*, Q, *Boulaya fertilis*, R, *Potoniea adiantiformis*.

The characteristic features of other families of Pteridospermales are given hereunder:

2.5 SALIENT FEATURES

(A) Medullosaceae

- i) Medullosaceae members occurred between Upper Carboniferous and Permian periods of palaeozoic era.
- ii) Stems and seeds were large and massive than Lyginopteridaceae.
- iii) Stems were polystelic. Some contained more than forty steles in their stems.
- iv) Each stele had its own cambium that produce secondary wood.
- v) *Medullosa* and *Sutcliffia* are the examples of stem-genera. *Sutcliffia* stem contained a single large stele with exarch protoxylem. A ring of manoxylic secondary wood is present around the main stele. The petiole traces contain concentric cylinder of secondary wood. *Medullosa* stem contained varied number of steles in different species. In advanced forms, secondary wood is absent in the leaf trace bundles. In some stem species of *Medullosa*, the steles expanded tangentially and fused to form a ring of primary wood surrounded on either sides by a ring of secondary wood.
- vi) *Pachytesta* and *Stephanospermum* are the seed genera of medullosace.
- vii) The pollen-bearing organs are described as *Whittleseya*, *Aulacotheca*, *Boulaya* and *Dolerotheca*. The sporangia are found to be fused side-by-side to constitute a wine-glass like structure in *Whittleseya*, an half-orange like structure in *Dolerotheca* and a club-shaped structure in *Aulacotheca*.

(B) Calamopityaceae [General characters]

1. It contains three manoxylic stem genera (*Calamopitys*, *Diichnia* and *Stenomyelon*).
2. *Stenomyelon* stem contained a solid protostele with exarch protoxylem. *Calamopitys* stem contained a mixed pith, round which a ring of mesarch strands present. *Diichnia* stem had a five angled mixed pith with a single mesarch protoxylem strand in each arm.
3. Secondary wood contained tracheids with multi-seriate pits on radial walls and wood rays that ranged from 1-6 cells in width.
4. 'Sparganum' cortex was observed in stems.
5. Petioles contained a large number of traces that arranged in a ring and described by the generic name *Kalymma*.
6. No reproductive organs or leaves have been found in association with stems and petiole.

2.6 GLOSSOPTERIDACEAE AND MESOZOIC PTERIDOSPERMALES

This group consisted of three families viz., Glossopteridaceae, Peltaspermeaceae and Corystospermaceae, the general features of which are described here.

(A) Glossopteridaceae

Australia, South Africa, South America, Antarctica and the Indian Peninsula together constitute the supposed continent of “**Gondwana land**”, separated by the Tethys Sea from other continents of Northern hemisphere. A peculiar and completely different flora had come to occupy the Gondwana land, by Upper Carboniferous and Lower Permian times. This flora is often called the *Glossopteris* flora because of the widespread occurrence of the leaves known as *Glossopteris*. These were tongue shaped, as the name suggests and their venation was reticulate, with prominent midrib (Fig. 2.6B).

Over a period of hundred years about 50 species of *Glossopteris* leaves, and the cuticular details of these have been studied. This led to the splitting of *Glossopteris* into three genera viz., *Gangamopteris*, *Palaeovittaria* and *Rhabdotaenia*.

Gangamopteris lacked the prominent midrib, *Palaeovittaria* had a midrib in the proximal half of the leaf, but none in the distal half and there was no anastomosis of lateral veins. Leaves of *Rhabdotaenia* had a strong midrib and forked lateral veins, between which anastomosis was extremely rare.

The anatomy of *Glossopteris* leaf was worked out by Pant (1958). The leaves had haplochielic stomata, sunken and irregularly dispersed between veins. Both palysade and spongy parenchyma were present in the mesophyll. The midrib showed many longitudinally extended veins that may either separate or fused. The tracheids of the veins contained scalariform thickenings and rarely bordered pits.

The probable plant that bore *Glossopteris* leaves has long been a matter of debate. Pant (1977) and Gould and Delevoryas (1977) reconstructed the plant as a large tree having trunk of 6 m high (Fig. 2.6A).

Verterbraia is the name given to some peculiar axes that are commonly associated with *Glossopteris* leaves. These axes had the xylem tissue that inturn had a number of vertical radiating flanges separated by very broad parenchymatous rays that were interrupted at regular intervals by horizontal plates of xylem. The pitting of tracheids was more like that of coniferopsida members. These axes were treated as root.

Several male, female and bisexual fructifications have been reported. Reproductive structures attached to the leaves of Glossopteridaceae have been described that were in the form of compressions whose internal structure is not preserved.

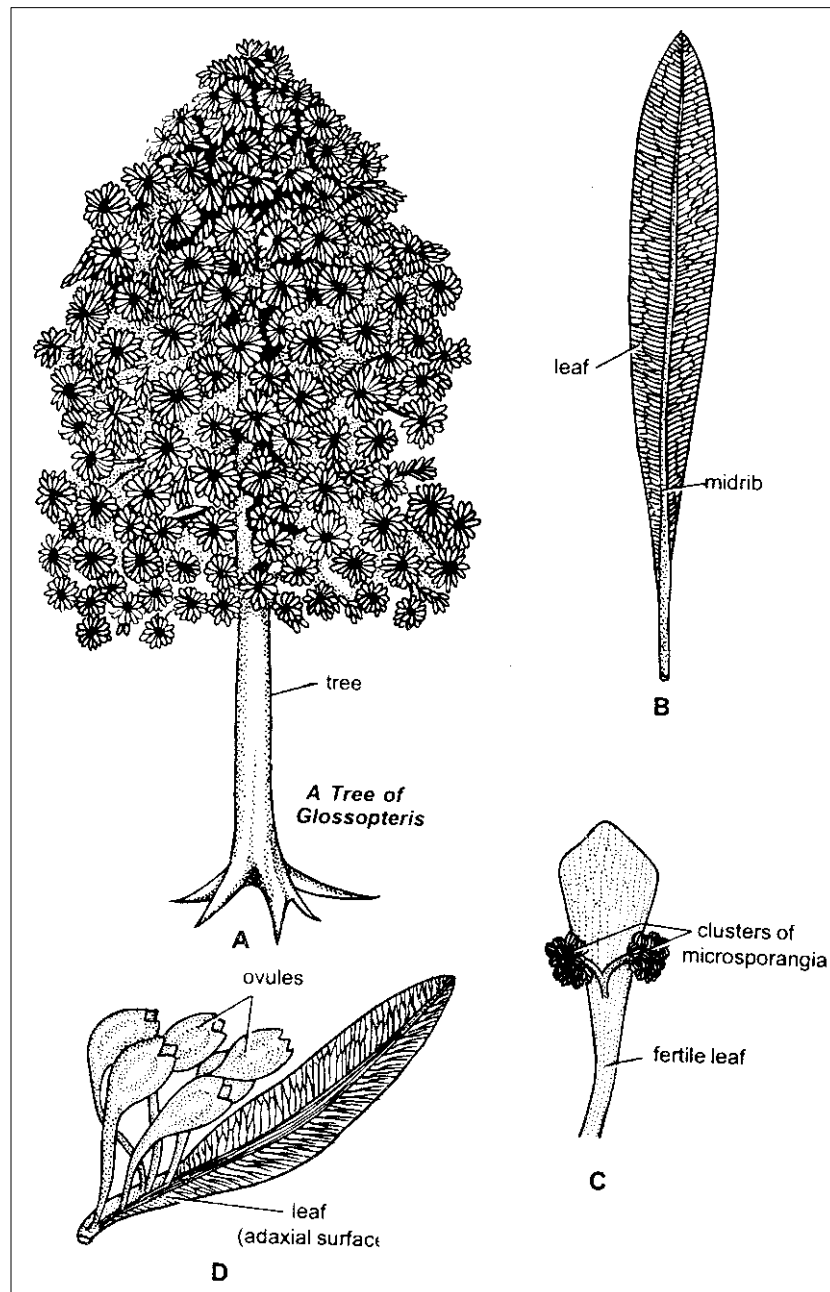


Fig. 2.6 A, Reconstruction of *Glossopteris*; B, A leaf of *Glossopteris*; C, A fertile leaf of *Eretmonia*; D, Ovules of *Denkania indica* developing in a row on the adaxial surface of leaf.

The male fructifications are described by the generic names viz., *Eretmonia*, *Glossotheca* and *Nesowalesia*, *Eretmonia* consists of a stalked lamina triangular in outline. On the upper half of lamina are borne two branches which bear whorls of purse shaped sporangia (Fig. 2.6C). *Glossotheca* is basically similar to *Eretmonia* except that it contains more sporangia-bearing pedicels

Female fructifications are included in form genera like *Ottokaria* and *Denkania*, whose structural details could not be confirmed. *Denkania* shows (Fig. 2.6D) a large number of long stalks (pedicels) attached to the adaxial surface of the midrib of *Glossopteris*-like leaf. These stalks carry uniovulate cupules at their ends.

The significance of Glossopteridaceae is not yet fully understood. Plumstead (1958) suggested that they may have been the ancestors of flowering plants. But Thomas (1958) concluded that this form of leaf may well have evolved by parallel or even convergent evolution.

(B) Peltaspermaceae

This family was established in 1933 by Thomas (1933). He reported some specimens of Triassic (Mesozoic era) age from Natal and proposed this family. Later, the similar specimens have been described by others from Sweden, Greenland, Argentina, Australia and China. Fronds (*Lepidopteris*), seed-bearing organs (*Peltaspermum*) and pollen-bearing organs (*Antevsia*) have been reported in this family.

Lepidopteris consisted of fronds with lanceolate pinnules borne on 30 cm long bipinnate or tripinnate unforked rachis. The ultimate pinnules had a prominent midrib and forking secondary veins. Stomata occurred on both surfaces of pinnules, sunken and surround by 5-6 radially arranged subsidiary cells. The rachis had a very uneven surface because of raised lumps or blisters. The occurrence of similar blisters on the axes of reproductive axes support that they belonged to one and the same plant.

Antevsia, the pollen bearing organs were bipinnate bodies with alternate primary branching. The ultimate branches possessed 10-12 pollen sacs of 2 mm long. Pollen sacs contained unwinged pollen grains.

Peltaspermum, the seed bearing organs were present on leaves. There are several stalked peltate heads each with two seeds. The integument is free from nucellus in the seeds. Peltaspermaceae represents probably a link between primitive ferns and angiosperms.

(C) Corystospermaceae

This family was also created by Thomas (1933) to accommodate some frond genera (*Dicroidium*, *Xylopteris*), seed-bearing organs (*Unkomasia*) and pollen bearing organs (*Pteruchus*), of Triassic age (Mesozoic era).

Dicroidium and *Xylopteris* fronds had forked rachis near the base as in many palaeozoic pteridosperms. The rachis was once pinnate in *D. odontopteroides* and about 10 cm long, where as it was bipinnate in *D. feistmantelii* which was about 100 cm long. *Xylopteris* had narrow linear pinnules, each with single unbranched vein.

The pollen-bearing organs (*Pteruchus*) had a central axis with short lateral branches. At the tip of each branch was present a peltate head bearing upto 30 sporangia.

Umkomasia, the seed bearing organ was a pinnate structure, contained number of branches that bear terminally single helmet shaped cupules. The cupules were split into two halves. A long bifid micropyle was present in seeds.

2.7 SUMMARY

A large and diverse assemblage of fossil plants known as the Pteridospermales or seed-ferns or Cycadofilicales are described in this lesson. They were in existence during Palaeozoic era and extended to the Mesozoic era. The Pteridosperms possessed fern-like foliage and seeds. The pteridosperms have not been preserved as intact fossils and the various parts have been described under different form-genera. This order contained six families out of which four confined to Palaeozoic era and two to the Mesozoic era. The characteristic features of these families, along with the description of fronds, pollen bearing organs and seed bearing organs have been presented in this lesson.

2.8 KEY TERMS

Fossil: Anything which gives evidence that an organism once existed at some time in the past.

Medullation: Formation of a parenchymatous pith in the stem.

Pinnate leaf: A compound leaf with leaflets (pinnules) arranged in two ranks on opposite sides of the rachis.

Polystely: A condition of an axis which is having a number of independent steles.

Primary wood: The xylem that is formed from a procambium and present in a primary vascular strand. It consists of protoxylem and metaxylem.

Protostele: Most simple and primitive form of stele consisting of a solid mass of xylem surrounded by a ring of phloem.

Proximal: Situated towards the point of attachment.

Seed-fern: A plant with fern-like foliage and possessed seeds.

2.9 MODEL QUESTIONS

1. Write an account on the Lyginopteridaceae.
2. Describe the stem genera of Palaeozoic pteridospermales.
3. Give a detailed account on Mesozoic pteridospermales.
4. Explain the salient features of Pteridospermales.
5. Give an account on Glossopteridaceae.

2.10 REFERENCE BOOKS

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Prof. Z. VISHNUVARDHAN

M.Sc. BOTANY (First Year)

Paper-I : Biology and Diversity of Algae, Bryophytes and Gymnosperms

Unit-IV : GYMNOSPERMS

Lesson 3

CAYTONIALES

- 3.0 **AIM**
The salient features of Caytoniales are presented in this lesson.
- 3.1 **INTRODUCTION**
- 3.2 **CAYTONIALES : CAYTONIACEAE**
 - 3.2.1 **Leaves**
 - 3.2.2 **Seed-bearing organs**
 - 3.2.3 **Pollen-bearing organs**
- 3.3 **SUMMARY**
- 3.4 **KEY TERMS**
- 3.5 **MODEL QUESTIONS**
- 3.6 **REFERENCE BOOKS**

3.1 INTRODUCTION

Few fossils have created such a stir among morphologists as did the Caytoniales when they were first discovered. They are considered controversial and highly interesting group of plants which because of their supposed affinity with angiosperms, attracted the attention of botanists. The fossil form-genera that have been found in rocks ranging from the Upper Triassic to the Lower Cretaceous were assigned to a family (Caytoniaceae) in the order Pteridospermales. But in some classificatory systems this family was elevated to an order called caytoniales.

3.2 CAYTONIALES : CAYTONIACEAE

3.2.1 Leaves

Sagenopteris is the name given to a very characteristic type of leaf which has been known since 1828. The leaves known for over a century are scattered geographically and stratigraphically from Upper Triassic to Lower Cretaceous rocks. They had a slender petiole and typically four terminal leaflets arranged in two pairs (Fig. 3.1A). The leaflets are lanceolate and palmately compound. Each leaflet had a prominent midrib and reticulate venation (Fig. 3.1B). The lateral arched forking veins formed anastomosing system like that of *Glossopteris*. Haplocheilic stomata

were scattered on the lower surface. Harris (1951) has pointed out the curious fact that the leaf as well as leaflets shed by means of an absciss-layer which is an angiospermic feature. The leaves of *Sagenopteris* have been compared to angiosperms by Thomas (1925) on the basis of epidermal structure. Harris (1951) also compared them with dicotyledonary leaves by referring to the formation of abscission layer during the shedding of the leaves.

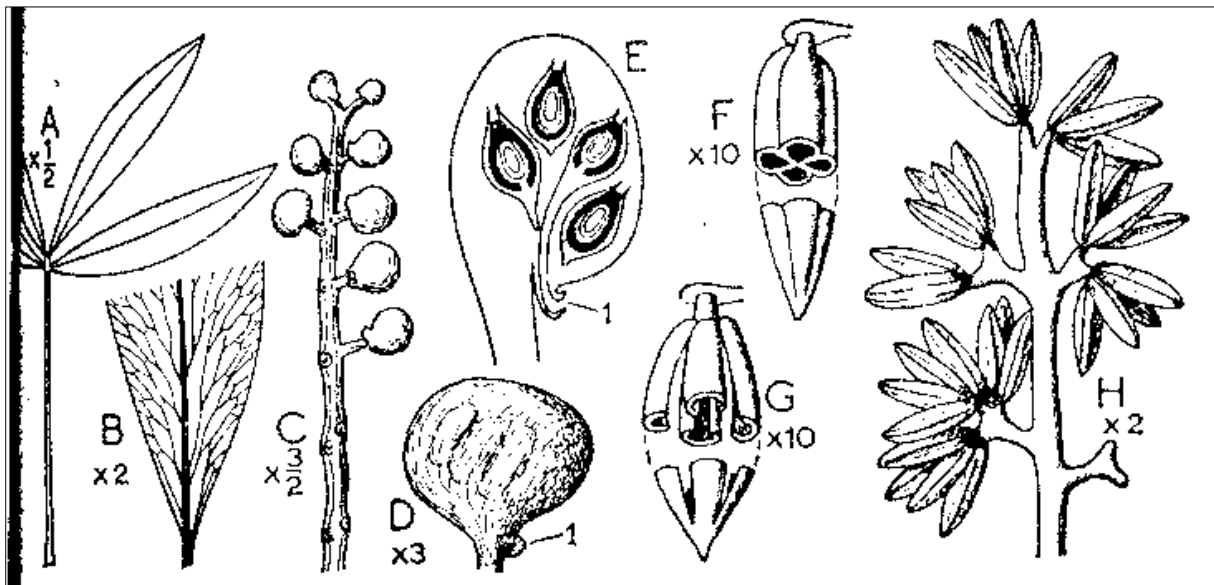


Fig. 3.1 Caytoniaceae. **A.** *Sagenopteris phillipsii*, leaf with four leaflets. **B.** *S. colpodes*, showing reticulate venation of leaflet, **C.** *Caytonia nathorstii*, fruiting rachis, from which the lower 'fruits' have been shed. **D.** *C. seawardii*, external appearance of 'fruit'. **E.** *Caytonia* 'fruit' in l.s., as interpreted by Harris, **F.** **G.** *Caytonanthus arberi*, restoration of synangia, cut across so as to show the loculi (**F.** before and **G.** after dehiscence). **H.** *Caytonanthus arberi*, male sporophyll. **I.** flange, or lip, of 'fruit'

Till 1925, hardly anything is known of the plant which bore *Sagenopteris* leaves. Even now also, there is a fragmentary information about the stem except for a tiny branched twig bearing the characteristic bud scales of *Sagenopteris phillipsii*. It shows a single scar with a C-shaped trace. It brings home one point that the stem was not thick and atleast we know that leaves were not borne directly on the tree trunk as found in cycads and tree ferns.

Thomas (1925) described the reproductive organs (male & female) from the Mid-Jurassic rocks of Yorkshire and Edwards (1929) described some seed-bearing organs from Sardinia. Later, Harris (1933) described both types of reproductive structures from Lower Jurassic rocks of Greenland.

3.2.2 Seed-bearing organs

Caytonia is the name given to seed-bearing organs. It consists of an axis which is about 5 cm long and strongly dorsiventral. The rachis bears two rows of stalks on which borne fruit-like bodies or ovule containing cupules (Fig. 3.1C). The seeds were almost completely enclosed within them. Each fruit-like body or cupule is a small, sac-like structure, with a conspicuous outgrowth (lip or flange) situated near the stalk (Fig. 3.1D). In between the lip and stalk is a minute opening or mouth. The lip or flange bears about the same number of ridges as there were seeds inside. Three species have been described in *Caytonia* viz., *C. Sewardii*, *C. Nothorstii* and *C. Thomasii*, which differ in the number of seeds in the fruit-like bodies.

In *C. Sewardii* there were eight seeds in each fruit in a single arched row, in *C. Nothorstii* about fifteen, and in *C. Thomasii* about thirty in a double row. Thomas (1925) reported the presence of pollen grains on the lip of *C. Nothorstii*. He believed that this part (flange) to be functioning as stigma as in angiosperms. But it is now known that pollen grains reached the micropyle of the seeds. Harris (1951) interprets the fruit (Fig. 3.1E) as having had a separate channel leading from flange to each seed. He supposes that there was a drop 'mechanism' as in many living gymnosperms, the pollen grains trapped in the drop, floating and reach through channels to the seeds.

Each seed, about 2 x 1 mm, is flattened, oval in shape and unitegmic. The integument is free from the nucellus. The nucellus was covered by a thick cuticle. The seeds lack a micropylar beak which is so prominent in Peltaspermaceae and Corystospermaceae. There is no trace of any vascular bundle in the integument.

3.2.3 Pollen-bearing organs

These were described under the name *Caytonanthus*. This is an unusual structure. Thomas and Harris has made it clear that in structure, *Caytonanthus* was quite unlike any other microsporophyll. There was a dorsiventral rachis (the upper and lower epidermis differing from each other) bearing opposite, sub-opposite pinnae (Fig. 3.1 H). The pinnae branched irregularly and each terminal branchlet bore a single synangium. Each synangium is pendent, tubular and quadrilocular (Fig. 3.1 F). The four pollen sacs or sporangia on dehiscence separate out except at the tip thus releasing the pollen grains (Fig. 3.1 G). The pollen of *Caytonanthus* are small, nearly 25-35 µm, bisaccate (winged) with an elongated terminal aperture. The surface of pollen grain is smooth with irregular pits. The sporoderm is two layered; the inner lamellate and outer alveolate. SEM and TEM studies on pollen revealed their distinction from the angiosperms.

Caytonia when first described in 1925 by Thomas, was compared with the angiosperms. It was considered as the Jurassic representative of the angiosperms and Thomas believed that the family provided important clues to the origin of angiosperms. He believed the fruit to be a carpel, the lip (flange) to be a stigma and compared the synangium to the stamen. *Caytonia* was interpreted as showing an early stage in the evolution of the carpel. Besides this, the reticulate

venation of leaves, formation of abscission layer, presence of bud scales and microsporophyll bearing tetralocular synangia were considered characters closer to angiospermous group.

However, it is clear now that *Caytonia* is still at the level of a gymnosperm. Some of the gymnospermous characters which are strongly non-angiospermic are:

- i) Radial symmetry of the male fructification, lack of filament and connective tissue in *Caytonanthus*.
- ii) Winged pollen grains.
- iii) Absence of blind vein end in leaf, and
- iv) Pollen germinate inside the micropyle and at the tip of the nucellus.

These characteristic features of **Caytoniaceae** prompted Harris (1933) to classify them with Gymnosperms. The decisions as to its phylogenetic relationship should be withheld, until we know more about this group.

3.3 SUMMARY

A detailed description of the order Caytoniales, an interesting group of mesozoic pteridopsperms is made here. Leaves, seed-bearing organs and pollen-bearing organs are described under different form-genera namely *Sagenopteris*, *Caytonia* and *Caytonanthus*. They possessed characters having supposed resemblance with angiosperms, which created lot of interest among botanists. Caytoniales are still at the level of Gymnosperms and their correct phylogenetic relationship is yet debatable.

3.4 KEY WORDS

Abscission layer: Layer of cells present at the base of leaf-stalk in angiosperms, in connection with leaf shedding.

Haplocheilic stomata: Stomata in which the subsidiary cells and guard cells are not originating from the same initials.

Orthotropous ovule: Ovule in which the micropyle is in a straight line with the funicle.

Synangium: A compound structure which is formed from the fusion of sporangia.

Tetralocular: A synangium with four compartments.

3.5 MODEL QUESTIONS

1. What are Carlytoniales? Describe their leaves and reproductive organs.
2. Give a detailed account on resemblances of caytoniales with angiosperms.
3. **Write short answers:**
 - A. *Caytonanthus*
 - B. *Sagenopteris*
 - C. *Caytonia*

3.6 REFERENCE BOOKS

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■ Prof. Z. VISHNUVARDHAN

M.Sc. BOTANY (Previous)**Paper-I : Biology and Diversity of Algae, Bryophytes and Gymnosperms****Unit-IV: GYMNOSPERMS****Lesson 4****B E N N E T T I T A L E S**

- 4.0 OBJECTIVES
- 4.1 INTRODUCTION
 - 4.1.1 General Features
- 4.2 WILLIAMSONIACEAE
 - 4.2.1 Stem
 - 4.2.2 Leaves
 - 4.2.3 Male fructification
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- 4.3 WIELANDIACEAE
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- 4.4 CYCADEOIDACEAE
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4.1 INTRODUCTION

Bennettitales or Cycadeoidales are an important group of fossil gymnosperms which resemble cycadales in leaf form, structure and venation. However, they can be distinguished from cycadales in having syndetocheilic stomata instead of haplocheilic stomata as in cycads. They co-existed with cycadales during mesozoic era from jurassic to cretaceous period hence this period was designated as the 'age of the cycads'.

4.1.1 General features

The general characteristic features of the order Bennettitales are:

- a) plants with either columnar (Williamsoniaceae or Wielandiellaceae) trunks of nearly 2 m height or short tuberous branched or unbranched, spherical, conical or irregular trunk upto 50 cm in diameter (Cycadeoidaceae). The surface of the trunks is covered with rhomboidal leaf bases with or without hairs in between with a crown of pinnately compound leaves present at the apex.
- b) Stems are stout or slender forking bearing large compound (rarely simple) leaves with parallel venation and syndetocheilic stomata.
- c) The reproductive structures are either uni or bisexual cones or flowers protected by many bracts. The receptacle is either cylindrical or dome-shaped having numerous stalked or sessile ovules, interspersed with interseminal scales with their distal ends fused to form a shield through which micropyles protrude. The microsporophylls are arranged in whorls, free or united, pinnate or entire with numerous microsporangia usually fused in a synangium or capsules. Pollen grains are monocolpate and the embryo is dicotyledonous.

The order Bennettitales has been divided into three families viz., (i) Williamsoniaceae, (ii) Wielandiellaceae, (iii) Cycadeoidaceae. However some authors prefer to merge Wielandiellaceae into Williamsoniaceae.

4.2 WILLIAMSONIACEAE

The genus *Williamsonia* was first described by Williamson in 1870, as *W. gigas* from Jurassic of Yorkshire. Although it was first placed under cycads, the presence of flower-like fructifications made it possible to be grouped under Bennettitales or cycadeoidales. In India, five species were discovered from Rajmahal hills in Bihar they being, *W. indica*, *W. microps*, *W. sahnii*, *W. santalensis* and *W. sewardiana*. They differ from cycadeoidaceae members in having slender, taller, considerably branched (*W. sewardiana*) or unbranched (*W. gigas*) stems.

The plant *W. sewardiana* (Fig. 4.1) was the first reconstruction of a fossil from India by Sahnii (1932) from the Jurassic material collected from Rajmahal Hills. It consists of a columnar stem (*Bucklandia indica*) about 2 m long with prominent spirally arranged rhomboidal leaf bases and a crown of unipinnately compound leaves (*Ptilophyllum cutchense*). The plant appears to be a miniature cycas.

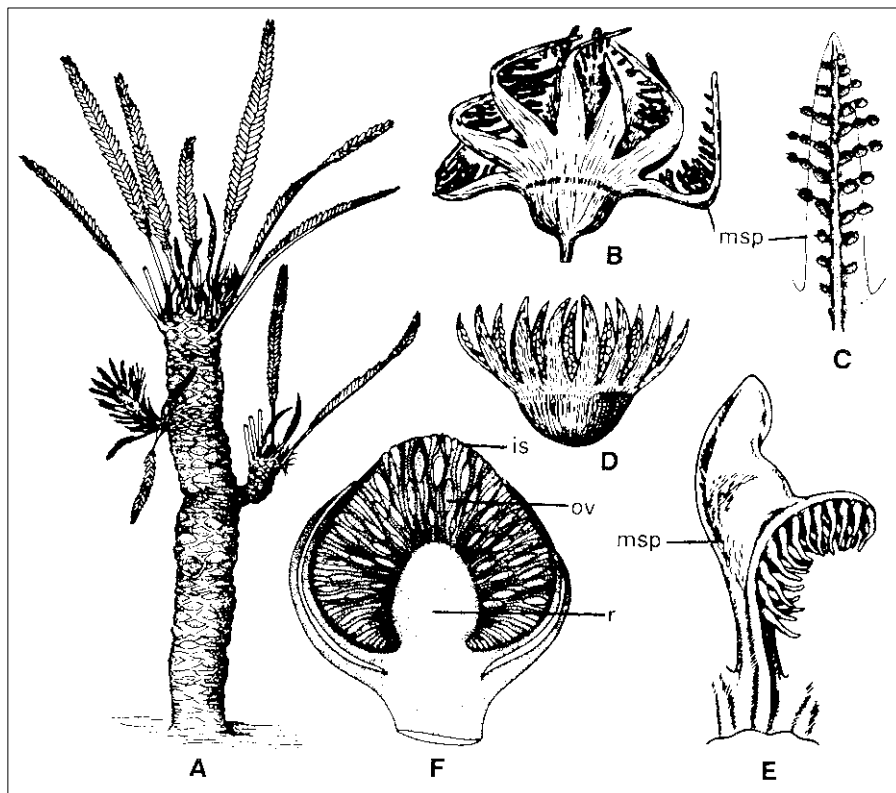


Fig. 4.1 *Williamsonia seawardiana*; **B, C**, *Weltrichia spectabilis*; **D**, *W. whitbiensis*; **E**, *W. santalensis*, **F**, *Williamsonia harrisiana* (**is**, interseminal hairs; **m**sp, microsporophyll; **ov**, ovule; **r**, receptacle). **A**. Reconstruction of the plant. **B, D** and **E**. Reconstruction of male fructification (**B, D**) and microsporophyll (**E**). **C**. Microsporophyll with attached synangia. **F**. LS female cone showing position of receptacle, ovules and interseminal hairs. (**A**, after Sahni, 1932; **B**, after Thomas, 1913; **D**, after Nathorst, 1911, **B, D** redrawn from Andrews, 1961; **C**, redrawn from Stewart, 1983; **E**, after Sitholey & Bose, 1953; **F**, after Bose, 1968, redrawn from Stewart, 1983).

4.2.1 Stem

Stems are simple or monopodially or dichotomously branched. The stem shows a rough and wavy outline due to the presence of numerous leaf bases. The shape, size and arrangement of leaf bases are of taxonomic importance for the stem genus *Bucklandia*. Two types of branches have been described: i) the sterile or vegetative shoots, and the ii) fertile shoots which terminate in a flower or cone. Only pinnately foliate leaves are present on lateral shoots. The main shoot bears in addition, small scale like pointed leaves. The lateral shoots show a prominent constriction at the base. It is presumed that they get detached and serve as a means for vegetative propagation.

Anatomically the stem shows a narrow pith with a wide parenchymatous cortex. Secretory ducts are present both in the cortex and the pith. Conjoint, collateral and endarch vascular bundles are embedded in pith. A distinct cambium is present. The secondary wood is monoxyletic and consists of scalariform tracheids with bordered pits. Medullary rays are uni, bi or triseriate.

Numerous leaf traces are present. *Williamsonia* differs from *Cycas* in the absence of girdling leaf traces.

4.2.2 Leaves

The leaves belong to the type genera *Pterophyllum*, *Ptilophyllum*, *Dictyozamites* and *Otozamites*. *Pterophyllum*, the most common leaf form is characterised by long slender pinnae with parallel margins attached to the rachis by full width of its base. Pinnae exhibit parallel venation (rarely dichotomous). *Ptilophyllum* is similar to *Pterophyllum* except for the difference that the pinnae are sickle-shaped and are attached to the adaxial surface of the rachis. The broad bases of pinnae almost cover the entire upper surface of the rachis. In *Otozamites* the pinnule bases are lobed and they are attached to the adaxial side of the rachis. Veins are spreading. *Dictyozamites* is like *Otozamites* except that the pinnae have broad bases and reticulate venation. The leaves of *Williamsoniaceae* show syndetocheilic stomata with rachis having collateral, endarch bundles arranged in a double U manner (Sharma, 1991).

4.2.3 Male Fructification

The male fructifications were referred under the genus *Weltrichia* which is represented by several species. Actually, they are never found in connection with the plant. Some authors grouped them under the genus *Williamsonia*. The microsporophylls are arranged in a whorl and fused at the base to form a cup-like structure. According to Sharma (1991) nearly 20 twisted microsporophylls alternate with similar number of bracts. The shape of the microsporophylls may vary from species to species (Fig. 4.1 B & D). In *Neltrichia companulatiformis*, the receptacle is bell-shaped, bearing broken microsporophylls. In *W. spectabilis* (Fig.4.1), the male cones measure 9 cms in diameter in the centre and 3 cm in the region of the basal cup. The microsporophylls extend out horizontally and then bend upward. They bear numerous minute appendages on the inner surface, each bearing two rows of synangia *W. whitibiensis* (Fig. 4.1 C & D) shows sessile male cones and total absence of appendages on the inner surface of microsporophylls. The microsporophylls are forked or bifid in *W. santalensis* with one portion sterile and the other fertile (Fig. 4.1C). The fertile part bears figure-like synangia. Each synangium contains two rows of chambers enclosing microsporangia. the pollen grains are monocolpate (Harris, 1969).

4.2.4 The Female fructification

The plants of *Williamsonia* were found to be dioecious. Seed bearing organs were described under different genera (Fig. 4.1 E & F). Lateral shoots with cones arise from the axil of a leaf. these shoots bear both scales and foliage leaves and a terminal cone. In *W. seawardiana*, *W. harrisiana* and *W. gigas*, the female cones are made up of a well developed central, conical receptacle bearing stalked ovules interspersed with interseminal scales in a spiral fashion. Interseminal scales are fleshy, club-shaped with stomata on their distal exposed surfaces. Each scale is traversed by a single vascular trace. The cone is covered by perianth like bracts with scales at their base and hairs above. The tip of central conical receptacle is anked. Each orthotropous ovule

consists of a short stalk through which it is attached to the receptacle. the nucellus is fused with the single vascularized integument (non-vascularized according to Sharma) except at the tip where it is prolonged beyond the surface layer formed by the enlarged tips of the interseminal scales. The tip of the nucellus extends to form nucellar beak and pollen chamber. The micropyles project through small openings formed by dotting of interseminal scales. The micropylar canal in young ovules of *Williamsonia* is long and narrow and is lined with large thin walled cells. As the ovule matures, the canal becomes wide because of the formation of the nucellar plug and disappearance of transversely oriented interlocking cells. Sharma (1979) has observed 2, 3 or even more archegonia in a ring in the apical part of the endosperm in the ovules of *Williamsonia*. Cellular endosperm and dicotyledonous embryos are reported from some nucellar cavities.

Harris (1932) included female cones studied from Greenland in the form genus *Benetticarpus* instead of *Williamsonia*. *Westershemia* and *Vardekloeftia* are some other reproductive fructifications of the family Williamsonsiaeeae.

The mature seeds of *Williamsonia* are stalked, dicotyledonous and endospermic. The seed coat is differentiated into three zones viz, the outermost zone composed of tubular cells, the middle zone of parenchymatous cells and the innermost parenchymatous and vascularized zone.

The reproductive fructifications of Williamsonsiaeeae so far studied are unisexual. The only reports of bisexual flowers are *Sturiella laugeri* by Krausel (1948) from Triassic of Lun, Australia and that of *Amarjolea dactylota* (Benerjee, 1991 and Sharma, 1991). In *Sturiella*, the club-shaped receptacle consists of 25-30 radiating ray-like lobes with central ovuliferous structures and microsporophylls around the lobes. *Amarjolea* resembles *Williamsonia*, but it is bisexual (as in cycadeoidea) because of the presence of microsporophylls. Since *Amarjolea* is associated with columnar stems, it is placed along with *Williamsonia* and is separated from Cycadoidea (Fig. 4.2).

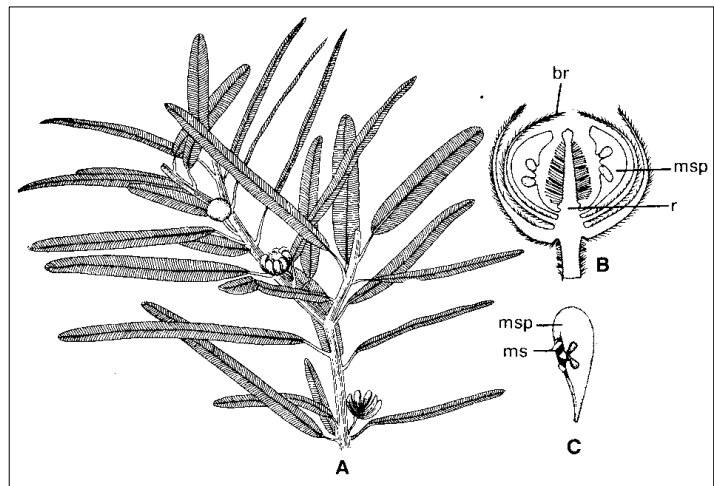


Fig. 4.2 **A**, *Williamsoniella*; **B**, **C**, *W. coronata* (**br**, bract; **ms**, microsporangium; **msp**, microsporophylls; **r**, receptacle). **A**. Reconstruction of a part of the plant. **B**. LS bisexual cone showing two microsporophylls and central receptacle bearing seeds (solid black) and interseminal scales (pin heads) surrounded by hairy bracts. **C**. Embedded microsporangia in a microsporophyll. (**A**, **C**, redrawn from Stewart, 1983; **B**, after Harris, 1944; redrawn from Andrews, 1961).

4.3. WIELLANDIACEAE

This family includes two genera namely *Williamsoniella* (recovered from Jurassic of Yorkshire by Thomas, 1915) and *Wielandiella* from Rhaetic of Scania in Sweden by Nathorst, 1911.

4.3.1 *Williamsoniella*

This genus consists of four species, of which *W. coronata* is best studied. It consists of a long trunk upto 1.5 m, dichotomously branched or pseudodichotomously branched bearing simple, entire, petiolate and linear lanceolate leaves. Leaves are 20 cm long and 2 cm wide with a prominent midrib and parallel venation (Fig. 4.2A). The leaves are placed under the form genus *Nilssoniopteris*. The stem consists of a large parenchymatous cortex with a comparatively much smaller pith. The primary xylem is endarch with tracheids showing circular bordered pits on radial walls. Medullary rays in secondary wood are uni, bi or triseriate. Many leaf traces could be seen.

The bisporangiate flower is present at the tip of a peduncle which itself arises in the axil of a leaf. Later two branches arise from below giving the appearance of a false or a pseudodichotomy. Arising from the base of each flower are several, hairy, sterile perianth lobes which enclose the reproductive structures. On the columnar receptacle, the pollen bearing region is below the ovuliferous zone. Attached to the base of receptacle or central column are a whorl of 12-14 microsporophylls which are independent of each other (Fig. 4.2). Each microsporophyll is a fleshy structure being made up of parenchymatous tissue and appears like the segments of an orange fruit. A finger like out growth arising from the middle of the microsporophyll encloses two synangia or pollen capsules (Fig. 4.2 B & C). The term capsule has been preferred to synangium because the latter would imply that it evolved as a result of fusion of separate sporangia. Each capsule contains many sporangia which in turn contain monocolpate pollen grains. The pollen capsules split longitudinally and dehisce pollen grains, following this the microsporophylls are shed.

In the same flower just above the microsporophylls is the ovulate receptacle. The ovulate columnar column is about 10 cm long, tapering towards a sterile and naked tip. The column bears about 300 ovules and 1200 interseminal scales in a spiral manner. The interseminal scale have a thin stock and bulbous tip. The integument is free from the nucellus.

4.3.2 *Wielandiella*

This second genus of the family Wielandiaceae, *W. augustifolia* resembles the first in showing false dichotomy of stems. However, they differ in being more slender (Fig. 4.3) and herbaceous measuring upto 1.5 cm in diameter. The leaves are placed under the form genus *Anamozamites* minor are unipinnately compound 8 cm long with a widened petiole and tend to concentrate in the region of the bifurcation (Fig. 4.3). Anatomical details are unknown as they are recovered as compressions.

The basic pattern of flowers also appears to be similar in being bisporangiate and having a club-shaped receptacle bearing numerous ovules and interseminal scales, perianth like leaves and microsporophylls. The tip region of the central column appears to be sterile. The ovules show the typical nucellus which is free from the integuments except at the base. The integument extends to form a well developed micropylar canal. There is not much information on the microsporangiate organs because of poor preservation.

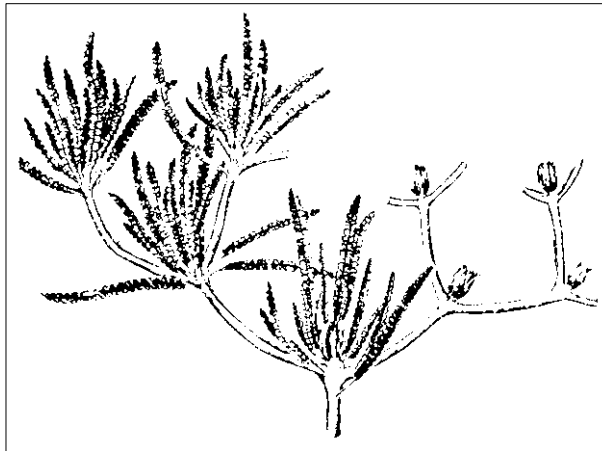


Fig. 4.3 *Wielandiella angustifolia*. Reconstruction of a part of the plant (redrawn from Andrews, 1966)

4.4 CYCADEOIDACEAE

This is the third family of the order Bennettitales and contains a single genus *Cycadeoidea* (Fig. 4.4).

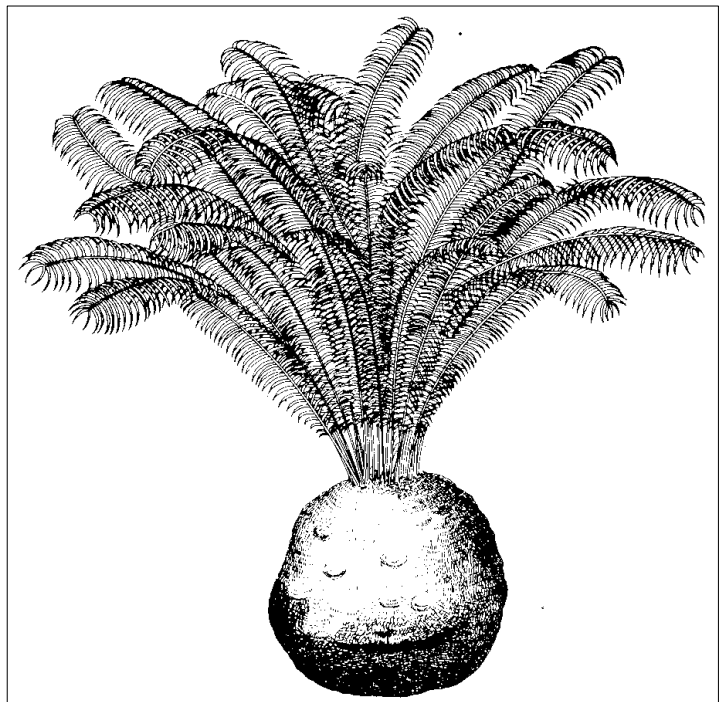


Fig. 4.4 *Cycadeoidea*. Reconstruction of the plant (after Delevoryas, 1971; redrawn from Stewart, 1983)

4.4.1 Cycadeoidea

This genus exists in upper Jurassic to upper Cretaceous comprising of about 30 species. The major species are recovered as petrified trunks from America and a few from Europe and India. The Cycadeoidean members have ovoid or short columnar trunks which are unbranched or apparently branched. The trunks are massive not more than 1 m in length and about 60 cm in diameter. The surface of the stem is covered with prominent rhomboidal leaf bases and multicellular hairs in between them. These short, stout trunks are much different from members of the first two families (Delevoryas, 1971).

Anatomical study of trunk shows large parenchymatous pith (Fig. 4.5A) surrounded by a thin zone of primary wood with endarch protoxylem and secondary wood with scalariform tracheids (circular bordered pits on radial walls) and small wide rays. The wood is thus typically manoxylic. The rays may be entirely uniseriate or biseriate (in part) and extend upto the phloem. The parenchymatous cortex is interspersed with gum canals (also present in pith) and leaf traces. The leaf traces are single and C-shaped at the point of origin but as they pass through the cortex they divide into several mesarch units and get arranged in a horse-shoe shaped manner. They enter the leaf without circling around the stem i.e. there are no girdling leaf traces.

4.4.2 Leaves

The mature leaves are not found attached to the trunks. However, it is assumed on good evidence that leaves were borne in a crown at the apex of the trunk. The study of young fronds still folded in the terminal buds revealed their close similarity to the present day Cycadaceae members such as *Macrozamia*, *Encephalartos* and *Bowenia*. The size of the mature frond is unknown but it is around 3.3 m long in *Cycadeoidea ingens* (Fig. 4.5).

Anatomical study of pinnule shows distinct upper and lower epidermal layers of thick walled cells, mesophyll with spongy and palisade parenchyma and vascular bundles with a prominent bundle sheath (Fig. 4.5C).

4.4.3 Reproductive fructifications

The reproductive fructifications of the Cycadeoidian members were axillary in position. In a few species only all the leaf axils were fertile while in most species only a portion of leaves subtended fertile shoots. In six species, flowers are monocarpic (flower only once during their life time) as in some palms and bamboos. The flowers are bisexual in *Cycadeoidea* (Crepet, 1972, 74). These are borne on a small pedicel and are protected by about 100 spirally arranged pinnate bracts which are covered by a ramentum of scales. The bracts on maturity open up to form a broad saucer-shaped structure. The pollen bearing organs consists of about 20 pinnate microsporophylls arranged in a whorl at the base of ovuliferous receptacle (Fig. 4.5B).

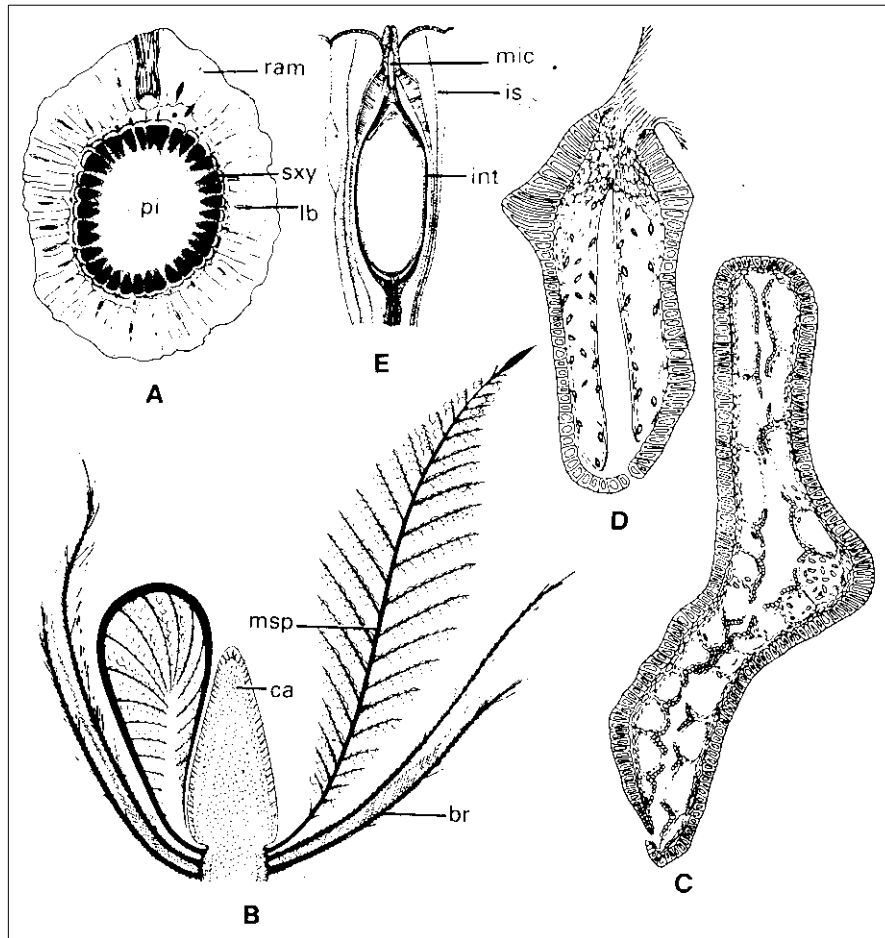


Fig. 4.5 (**br**, bract; **ca**, cone axis; **int**, integument; **is**, interseminal scale; **lb**, leaf base; **mic**, micropyle; **msp**, microsporophyll; **pi**, pith, **ram**, ramentum; **sxy**, secondary xylem). **A**. TS *Cycadeoidea* trunk showing large pith surrounded by poorly developed secondary xylem. The cone and leaf bases are embedded in thick ramentum. **B**. *Cycadeoidea dacotensis* cone (diagrammatic) showing central axis bearing numerous interseminal scales. Of the two microsporophylls, one on the left is immature whereas other on the right is mature and expanded. Two rows of synangia are arranged on each branch. **C**, **D**. LS and TS of synangia of *C. dacotensis*. **E**. LS *Cycadeoidea morierei* ovule showing well developed integument surrounded by vascularized interseminal scale (**A**, **E**, redrawn from Stewart, 1983; **B-D**, redrawn from Andrews, 1961).

The pollen bearing structures were bean-shaped and arranged in two rows on the inner surface of each pinnule of a microsporophyle. These synangia (Fig. 4.5D) were about 3.5 x 2.5 mm long and bore 20-30 tubular pollen sacs or sporangia which contain monocolpate pollen grains. The dehiscence of synangia is by means of an apical slit which cleave the synangium into two equal halves.

In Cycadeoidales, the protection of sporangia is by grouping of microsporophylls into a flower or cones. Pollination was accomplished by boring insects. Since the cone is bisporangiate, self pollination is ensured which leads to increasing homozygosity and presumably resulted in the ultimate extinction of the group.

On the conical or dome shaped apex of the fertile shoot, there are numerous, tiny, stalked orthotropous ovules of 1 mm long interspersed with the same number of interseminal scales. The heads are enlarged into a club which becomes fused with the adjoining interseminal scales in a way that it forms a continuous surface layer with openings through which the micropyles project. This continuous surface layer constitutes an external protective covering (or pericarp) over the developing seeds. Harris (1932) studied the macerated seeds and found that the integument is completely fused with the nucellus except at the apex. Each ovule consists of a two layered integument, nucellus with a beak and a prominent pollen chamber (Fig. 4.5E). The cells of nucellus are thin walled and are much smaller at the chalazal end than at the micropylar end. Embryo is dicotyledonous.

A discovery of special interest made by Crept and Delevoryas (1972) is the presence of linear megaspore tetrads and the tetrad showing the first three aborted megaspores and the lower functional megaspore as in the case of most living gymnosperms. A nucellar plug is observed in *Cycadeoidea morierei* similar to that reported in *Williamsonia*. The presence of archegonia has also been reported in the female gametophytes of *Cycadeoidea*. In the ovules of cycadeoids, the nucellus is fused with the integument through out except at the apical region. The integument is composed of two thin layers without vascular supply. The ovule is surrounded by five or six interseminal scales each having its own vasculature. According to Delevoryas (1968) these scales represent the fertile and sterile fronds of pteridophytes in a reduced state. The termination of some interseminal scales in abortive ovules suggest that the interseminal scales and the stalked ovules are homologous structures.

4.5 RELATIONSHIPS WITH OTHER GROUPS

Bennettitales exhibit similarities with many groups but are unique in having stalked ovules. The relationships with other groups are given below.

4.5.1 With cycadales

Both of them have similar habit and similar fronds. Anatomically they both have monoxyle wood. Other similar features include monocolpate pollen grains, orthotropous ovules and dicotyledonous embryos.

The two groups mainly differ in the anatomical details of the frond, haplochelic stomata in cycadales and syndetochele in Bennettitales, girdling leaf traces which are prominently displayed in a cycad stem are absent in the members of Bennettitales. Cones are monosporangiate in

cycadales, whereas in Bennettitales they are bisporangiate also. The microsporophylls are arranged in whorls in Bennettitales while they are spirally arranged in cycadales. Based on these differences Andrews (1961) opined that both the groups have evolved along two different and independent lines.

4.5.2 With Pteridospermales

The common features between these two groups are presence of ramental hairs, similar internal structure; syndetochelic stomata, direct leaf traces, presence of leafy microsporophylls bearing synangia and the presence of cupule. The bisporangiate 'flower' of Bennettitales could be compared to bisporangiate fronds of Cycadofilicales (pteridosporus). According to some authors there are two independent lines of evolution from Pteridospermales. One gave rise to monosporangiate forms like cycads and the other to Bennettitales which possess both mono and bisporangiate forms. The major differences are the organization of ovules as they are smaller and stalked in Bennettitales and exhibit prominent vascular supply to the nucellar tissue (absent in Pteridospermales).

4.5.3 With Angiosperms

The similarity in flower structure of Bennettitales and some angiosperms groups such as Ranales and Magnoliales which have primitive flowers with numerous floral parts arranged spirally lead a few morphologists (Bessey, Hallier Hutchinson etc.) to believe that the angiosperms might have originated from mesozoic Bennettitales. The bracts around reproductive organs of Bennettitales could be compared to the perianth of angiosperms. Other similarities include the mesoparacytic stomata of Magnoliales and the syndetochelic stomata of Bennettitales, homoxylous (without vessels) wood comparable to few angiosperms like *Drimys*, *Trochodendron* and *Tetracentron* and the presence of dicotyledonary embryos in both groups. Bennettitales, however, differ from angiosperms in having naked ovules (characteristic feature of gymnosperms) intermixed with sterile scales. The stamens are large compound structures with simple synangia which are quite different from angiosperm stamens. The wood rays in Bennettitales lack marginal cells whereas in angiosperms prominent marginal cells are present. Pant and Kidwai (1977) observed that the flower of Bennettitales may represent a parallel line of evolution to angiosperms. This view is substantiated by the fact that the group Bennettitales disappeared during Cretaceous whereas the angiosperms were already established by them.

4.6 SUMMARY

Bennettitales is an important group of fossil gymnosperms which co-existed with cycadales during Mesozoic era from Jurassic upto Cretaceous. It consists of three families: (1) Williamsoniaceae, (2) Wielandiellaceae, and (3) Cycadeoidaceae.

Plants are with columnar trunks with 2 m height in the first two families while the plants are short tuberous branched or unbranched spherical, conical or irregular trunk of 50 cm diameter in

Cycadeoidaceae. But all the three families are characterized by rhomboidal leaf bases and a crown of pinnately compound leaves present at the apex. The stomata are syndetochealic, flowers or uni or bisexual cones are the reproductive structures. Numerous stalked or sessile ovules are present on conical, cylindrical or dome shaped receptacle interspersed with interseminal scales with their distal ends fused to form a shield through which the micropyles protrude, microsporophylls in whorls free or united, pinnate or entire with numerous microsporangia fused into synangia or capsules. Pollen grains monocolpate and embryo dicotyledonous. The interrelationships of Bennettitales with cycadales, pteridospermales and angiosperms are discussed.

4.7 MODEL QUESTIONS

1. Give a general account of Bennettitales.
2. Briefly describe the salient features of the three families of Bennettitales and discuss their interrelationships with Cycadales, Pteridospermales and angiosperms.
3. Write short notes on:
 - a) *Williamsonia*
 - b) *Williamsoniella*
 - c) *Wielandiella*
 - d) *Cycadeoidea*.

4.8 REFERENCE BOOKS

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Prof. N. Lakshmi

M.Sc. BOTANY (First year)

Paper-I : Biology and Diversity of Algae, Bryophytes and Gymnosperms

Unit-IV : Gymnosperms

Lesson 5

C Y C A D A L E S

- 5.0 AIM:
The morphological and reproductive details of the order Cycadales (class: Cycadopsida) are presented in this lesson.
- 5.1 INTRODUCTION
- 5.2 GENERAL CHARACTERS OF CYCADALES
- 5.3 CLASSIFICATION OF CYCADALES
- 5.4 NILSSONIACEAE*
Leaves: *Nilssonia*
Pollen-bearing organs: *Androstrobus*
Seed-bearing organs: *Beania*
- 5.5 CYCADACEAE
- 5.5.1 Morphology
- 5.5.2 Anatomy of stem, leaf and root
- 5.5.3 Reproduction
- 5.6 PHYLOGENY
- 5.7 SUMMARY
- 5.8 KEY TERMS
- 5.9 MODEL QUESTIONS
- 5.10 REFERENCE BOOKS

5.1 INTRODUCTION

Of the different orders of Cycadopsida, the order Cycadales is the only order in which the extant (living) genera are present, while the other orders contained no living genera and all extinct.

The Cycadales first appeared in Upper Triassic times of Mesozoic era and are surviving until the present day. Hence, among living plants, the cycadales constitute the most ancient group. They exhibit a number of primitive features. The order Cycadales is divided into two families i.e., Nilssoniaceae and Cycadaceae, of which the latter only contained living genera.

5.2 GENERAL CHARACTERS OF CYCADALES

1. Plants are woody and with unbranched stems or occasional adventitious branching.
2. Wood is manoxylic and some genera are with co-axial vascular cylinders.
3. Mucilage canals present in the cortex and pith.
4. Leaves are large, frond-like and pinnate.
5. Leaf traces are diploxylic (except in Nilssoniaceae)
6. Plants are dioecious
7. Reproductive organs are in the form of cones (except in female *Cycas*).
8. Cones are terminal or lateral.
9. Megasporophylls with serile tips and 8-2 orthotropous ovules.
10. Seeds are large.
11. Microsporophylls are sac-like or peltate with pollen sacs on the abaxial side.
12. Sperms are with spiral band of flagella. Cycadaceae and Ginkgoaceae are the only two families of seed plants which have retained the ciliate sperms, so characteristic of lower plants.
13. The sperms are very large (200 μm in *Cycas* and 400 μm in *Chigua*).
14. In all cycads apical meristem is extremely massive.

5.3 CLASSIFICATION OF CYCADALES

Johnson (1959) and Bierhorst (1971) divided the order into three families i.e., *Cycadaceae*, *Stangeriaceae* and *Zamiaceae*. Stevenson (1981) removed *Bowenia* from and placed in a separate family *Boweniaceae* by which the number of families is increased to four. But in this present text the classification proposed by Sporne (1965) is followed. He included all fossil forms in a family *Nilssoniaceae* and living cycads in *Cycadaceae*.

5.4 NILSSONIACEAE*

This family is represented by all fossil forms in which leaves, and reproductive organs were described under different form genera.

- (i) Leaves: *Nilssonia*, *Pseudoctenis*
- (ii) Pollen-bearing organs: *Androstrobus*
- (iii) Seed-bearing organs: *Baenia*

Nilssonia: In the Jurassic rocks, one of the most common leaf type observed was about 60cm long and 10cm wide. The lamina is entire or dissected into pinnule like segments and supported on a strong mid rib. Simple veins pass obliquely or at right angles from mid rib to leaf margin. The veins were rarely forked, such leaves were described by the name *Nilssonia* and these are worldwide in distribution from Triassic to Cretaceous (Fig. 5.1A). Another fossil leaf that looked like cycad frond from Upper Triassic deposits was described by the name *Pseudoctenis*.

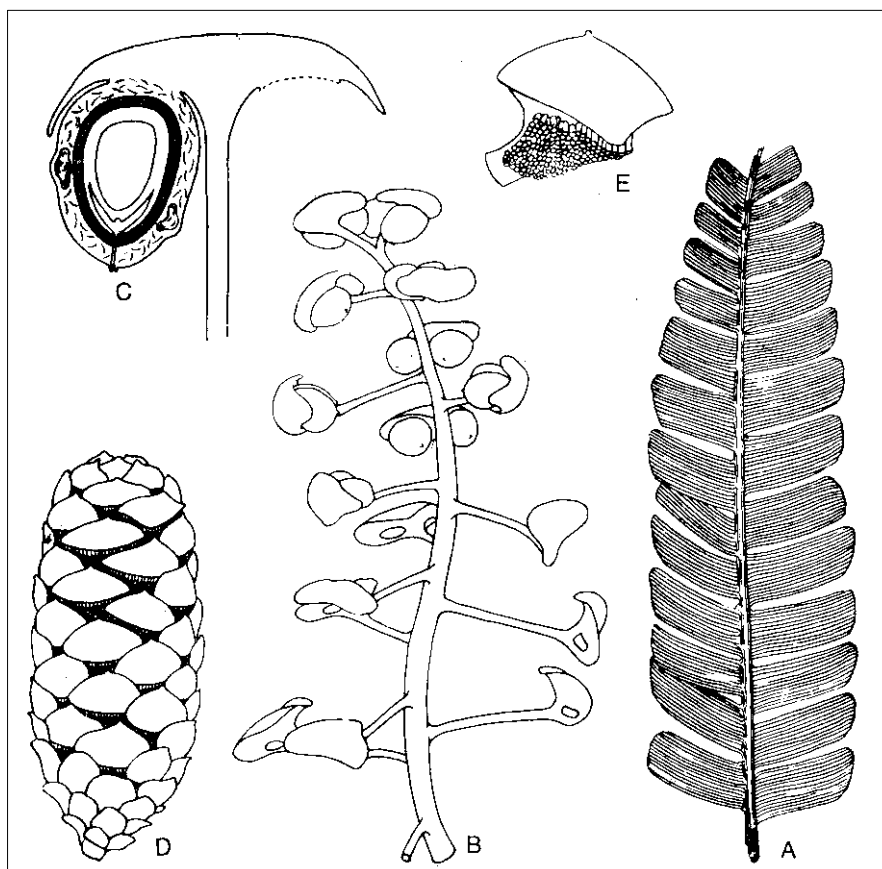


Fig. 5.1 A-E. Fossil cycads. A. *Nilssonia compta*, leaf; B, C *Baenia gracilis*. B Seed "cone". C Megasporophyll with one seed in longisection. D, E *Androstrobus manis*. D. Microsporangiata cone. E. Microsporophyll. (A After Andrews 1961, B-E after Harris 1941, 1964).

Androstrobus: Thomas and Harris (1960) describes pollen-bearing organs (cones) under the name *Androstrobus*. In *Androstrobus manis*, male cones were compact (5 x 2 cm) and had several spirally arranged peltate microsporophylls (Fig. 5.1D). Each microsporophyll contained several finger-like pollen sacs, on its abaxial side (Fig. 5.1E).

Baenia: Harris (1961) described seed bearing structures from the Jurassic of Yorkshire, under the name *Baenia*. In it peltate sporophylls were loosely arranged spirally around the central cone axis (Fig. 5.1 B). Each sporophyll bore two ovules. (Fig. 5.1C). The integument was fused with the nucellus except at the apex.

Megasporophylls, with terminal leaf like sterile portion and basal fertile portion representing the scars left by the detached ovules, were described as *Palaeocycas*; the only fossil genus of Cycadaceae. Florin (1933), Harris (1961), Delevoryas and Hope (1971) prepared reconstructions of extinct cycads, by making use of imaginary trunks. Florin (1933) named the reconstruction as

Bjuvia simplex, where *Palaeocycas* megasporophylls which crowned the apex of an imaginary unbranched stout trunk, of 3 m tall (Fig. 5.2B). Harris (1961) in his reconstruction showed *Nilssonia* (leaves) *Beania* and *Androstrobus* (reproductive organs) on an imaginary branched stem (Fig. 5.2D). Delevoryas and Hope (1971) in their reconstructions (*Leptocycas*) depicted a slender stem (1.5 m tall), with crown of *Pseudoctenis* type of fronds (Fig. 5.2A).

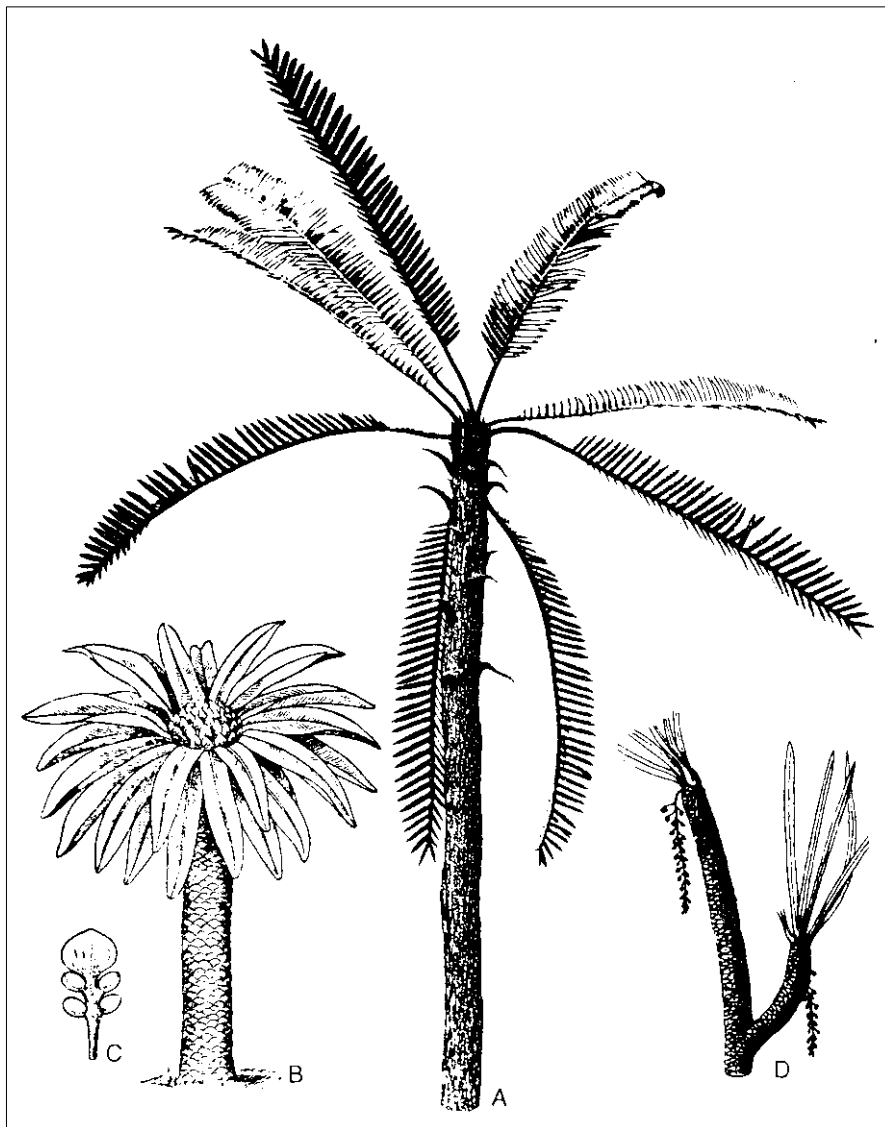


Fig. 5.2 A-D. A, B, D Reconstruction of extinct Cycad plant. A *Leptocycas gracilis*. B *Bjuvia simplex*, C. *Palaeocycas*, an ovule-bearing organ. D Cycad bearing *Beania* ovulate cones and *Nilssonia* type foliage. (A After Delevoryas and Hope 1971, B, C after Florin 1933a, D after Harris, 1961).

5.5 CYCADACEAE

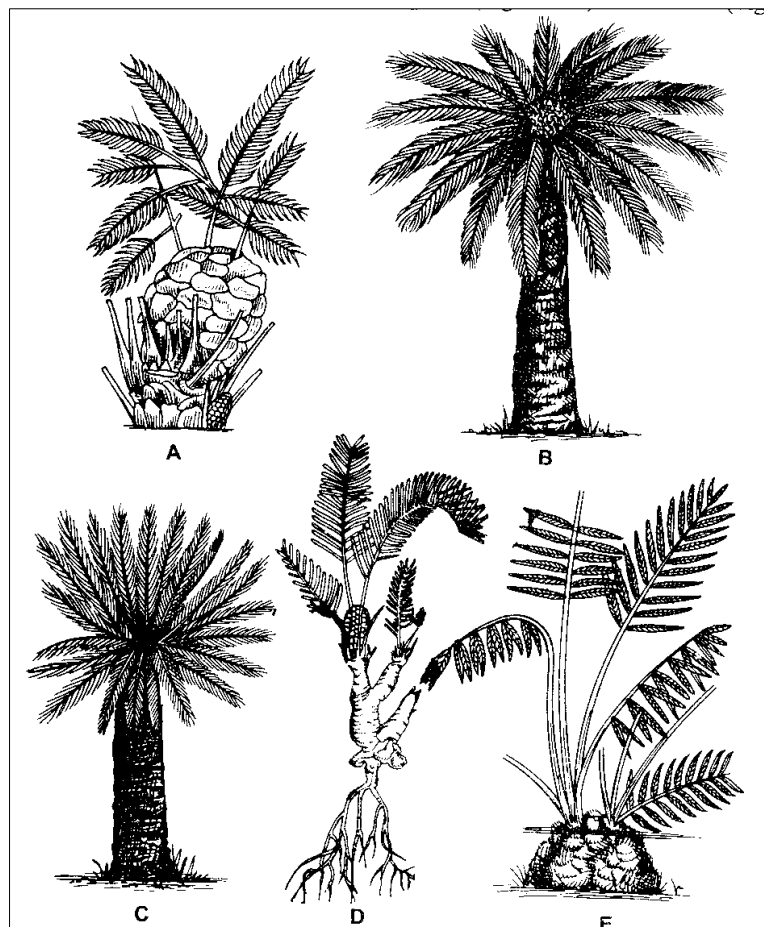
This family represents all the eleven living (extant) genera with about 100 spp. They exhibit a disconnected distribution. Of the 11 genera, five namely, *Dioon*, *Ceratozamia*, *Zamia Chigua* and *Microcycas* are distributed in Western Hemisphere, and the remaining six genera viz., *Cycas*, *Macrozamia*, *Lepidozamia*, *Encephalartos*, *Stangeria* and *Bowenia* occur in Eastern Hemisphere. The details of cycads distribution are given in lesson 1. There is considerable uniformity among all genera in respect of their morphology, anatomy and reproductive biology. Hence, the present comparative description rests mainly on the type genus *Cycas* and relevant information on other genera has also been provided wherever necessary.

5.5.1 Morphology

The cycads usually grow in exposed habitats and are considered xerophytes. The adaptive features of their xerophytic nature include short, slow growing unbranched stems or tuberous underground stems and persistent leaf bases which combined with cortex to give the trunk excellent insulating qualities. A plant of *Encephalartos* takes 200-300 years to grow 1.5 -1.75 m tall and *Dioon* grows to 2 - 25 m in 1000 days.

The cycads generally look like a palm with columnar aerial trunk, and a crown of pinnately compound leaves. The natives call them as palms. Adult plants of *Dioon*, *Ceratozamia*, *Microcycas* and *Cycas* are always arborescent (Fig. 5.3). The tallest cycad (18 m) is *Macrozamia hopei*. The plants of *Dioon* and *Microcycas* attain a height of 10–15 m. The stems of *Stangeria* and *Bowenia* are tuberous and subterranean, while in *Zamia*, *Macrozamia* and *Encephalartos* some species are arborescent and others tuberous.

Fig. 5.3 Some Cycadales. A. *Bowenia spectabilis*, B. *Cycas revoluta*; C. *Dioon spinulosum*; D. *Zamia floridiana*; E. *Stangeria paradoxa*.



Cycads produce two types of leaves (leaf-dimorphism). There are large green foliage leaves and small scale leaves or cataphylls. The two types alternate regularly. Scale leaves are brown in color due to a heavy coating of ramental hairs.

The green foliage leaves are frond-like and pinnate in all genera except *Bowenia* in which they are bipinnate. The largest fronds (3 m long) are found in *Cycas circinalis*, while the smallest (5 cm long) are in *Zamia Pygmaea*. The rachis as well as pinnae of young fronds show circinate vernation in *Bowenia* and *Ceratozamia*. In *Cycas* only leaflets and in *Stangeria* and *Zamia* only rachis exhibit circinate vernation. The pinnae of *Cycas* and *Stangeria* have a prominent midrib while in other genera pinnae are without midrib. Leaflets of *Cycas* have only midrib without any side veins, while in *Stangeria* there are lateral veins from the midrib. The pinnae of other genera are with parallel veins only.

The trunk in all arborescent forms is covered by an armor of leaf bases (Fig. 5.4). Alternating bands of large and small rhomboidal leaf bases cover the aerial stem in a spiral manner. The large leaf bases belong to foliage leaves and the small ones to the scale leaves. The stems of tuberous form do not have persistent armor of leaf bases.



Fig. 5.4 *Dioon edule*: portion of trunk of an old plant, showing armor of leaf bases. The trunk is smaller below than above. It also shows three zones, marking prolonged dormant periods.

The primary root in the cycad seedlings is much larger than the stem and in the adult plants the reverse is the case (Fig. 5.5). The normal tap root system is replaced by strong unbranched adventitious roots, which develop a number of apogeotropic corolloid roots. These roots grow up instead of down, branch dichotomously and profusely forming corolloid masses above ground. Rienke (1872) discovered corolloid roots in *Cycas revoluta*. Since then, it has been recorded in all cycads including the new genus *Chigua* (Stevenson, 1990).

5.5.2 Anatomy of stem, leaf and root

Stem: The stem of *Cycas* and allied genera (Fig. 5.6) has an irregular outline because of numerous persistent leaf bases. The stem shows a larger central parenchymatous pith surrounded a ring of numerous small vascular bundles which are followed by a wide parenchymatons cortex. Broad medullary rays connect pith with the cortex. The parenchymatous cells are full of starch which is commercially exploited as 'sago'. Both the cortex and pith are with full of mucilage ducts. The outermost layer consisting of compactly arranged thick walled cells constitutes an epidermis. But the persistent leaf bases makes the epidermis a discontinuous and ruptured layer. The vascular bundles are arranged in a ring. Each vascular bundle is conjoint, collateral, open and endarch. The protoxylem elements contain spiral thickenings, while the metaxylem elements exhibit either scalariform thickening or with multiseriate pits. The phloem consists of sieve cells, phloem parenchyma and fibres.

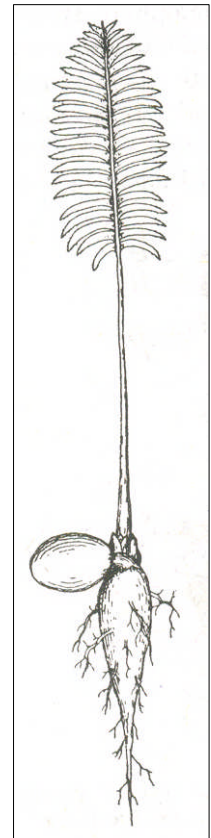


Fig. 5.5 *Dioon edule*: seedling; all the part bearing secondary roots is the primary root. The stem, bearing the leaf and scale leaves, is so small at this stage that it is hidden by the emergent part of the cotyledons.

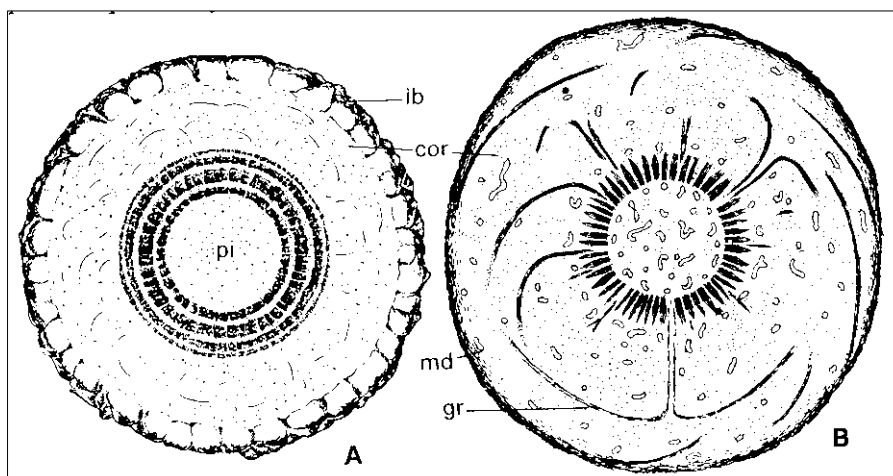


Fig. 5.6 **A.** *Cycas circinalis*; **B.** *Zamia floridana* (**cor**, cortex; **ib**, leaf base; **gr**, girdling leaf trace; **md**, mucilage duct, **pi**, pith). **A.** TS stem showing polyxylic condition, armour of leaf bases and a large cortex and pith. **B.** Same, *Zamia* showing prominent girdling leaf traces and manoxylic wood. Both cortex and pith are full of mucilage ducts (**A**, after Maheshwari, 1960; **B**, after Chamberlain, 1935).

Secondary growth of stem is similar to that of dicotyledons. It takes place very early in the life of the plant. The interfascicular cambium and intra fascicular cambium join to form a cambium ring. It cuts off radially seriated secondary xylem towards the pith and secondary phloem towards outside. After a short while this cambium ring stops functioning and additional cambium rings develop either in the parenchymatous cortex or in the region of pericycle. This cambium also functions in the similar fashion. In this way as many as 14 rings of vascular tissue may develop in the stem of *Cycas pectinata*. The cork cambium arises in the outer region of the cortex and produces secondary cork toward inner and outside. The secondary wood is manoxylic type and is surprisingly small in amount. A mature stem of *Zamia floridana* (6 cm in diameter) had a zone of xylem 2 mm wide. Similarly *Ceratozamia mexicana* stem (15 cm in diameter) had a zone of xylem 3 mm. Stems of *Zamia*, *Stangeria* and *Ceratozamia* which may be more than 50 years old, show no trace of growth rings. On the other hand, species of *Dioon* exhibit growth rings. Stems in which a single persistent cambium is present produce a single vascular cylinder (monoxylic). *Cycas*, *Macrozamia* and *Encephalartos* species produce polyxylic stems in which many concentric rings of secondary xylem and phloem are present. The secondary xylem consists of trachieds with multiseriate bordered pits, except in *Zamia* and *Stangeria*, which still retain the scalariform trachied of their remote fern ancestry. Inter mingled with the trachieds are some times rows of thin walled cells, as in *Dioon spinulosum* (Fig. 5.7). The vascular rays are conspicuous and of three types viz., a) uniseriate rays 1-10 cells high, b) multiseriate rays which are 2-5 cells in width and much higher and c) foliar multiseriate rays which are continuous from the pith to the phloem.

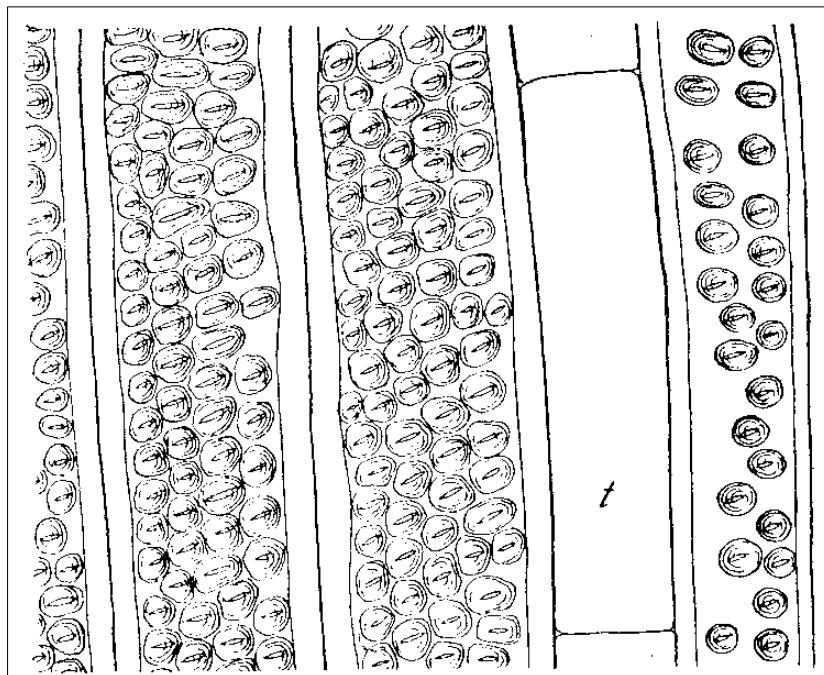


Fig. 5.7 *Dioon spinulosum*: longitudinal section of mature wood, showing multiseriate bordered pits, and also one of the thin walled cells (t); x 300 – After Chamberlin.

The leaf trace, as it appears near the base of the leaf gap, is small but in the cortex of the stem it is very conspicuous. The girdle traces are characteristic of cycadales. A leaf trace, after arising from the stelar cylinder, usually does not pass directly into the nearest leaf but turns round a semi circle (or girdles) in the stem horizontally and enters the leaf almost opposite to its point of origin. It joins at intervals by other traces, so that a number of traces enter each rachis. Such a girdling of a trace is also found in many angiosperms which have radial leaves. Leaf trace bundles exhibit endarch protoxylem and the metaxylem elements are centrifugally placed, such bundles are described as '*diploxylic*' as they show both centripetal and centrifugal xylem.

Another curious feature of the stem, that in the longitudinal section of the trunk of a genus which has terminal cones, is the '*cone dome*'. The meristem is entirely used in the formation of the cone, and a new meristem appears at the base of the peduncle and from the new meristem a crown of leaves are formed, until another cone is produced and the process is repeated every time a new cone produced alternately with a crown of leaves. Thus each cone dome represents the vascular tissue crossing the central pith, belonging to apical meristem that formed a cone which was pushed aside by a new meristem at the apex of the plant indicating sympodial system. Cone domes are absent in female *Cycas* and in those species of *Macrozamia* and *Encephalartos* which have axillary cones.

Leaf: The green foliage leaves usually pinnate or bipinnate. The rachis is cylindrical and pinnae are inserted on it. The epidermis of rachis consists of cuticularized thick-walled cells interrupted by stomata. The hypodermis contains a mixture of chlorenchyma and sclerenchyma followed by a parenchymatous ground tissue. The vascular bundles are arranged in an arc in the ground tissue, like the inverted Greek letter omega (Fig. 5.8). Mucilage canals are present both on the outer and the inner side of the arc. The vascular bundles show an interesting feature in that the two endarch bundles which enter the leaf base from stem split into numerous bundles which arrange themselves in the fashion of inverted omega. Towards the tip of the rachis the number of bundles arranged in a C-shaped arc. Each vascular bundle is surrounded by a fibrous sheath. The vascular bundles are mesarch and with diploxylic xylem elements.

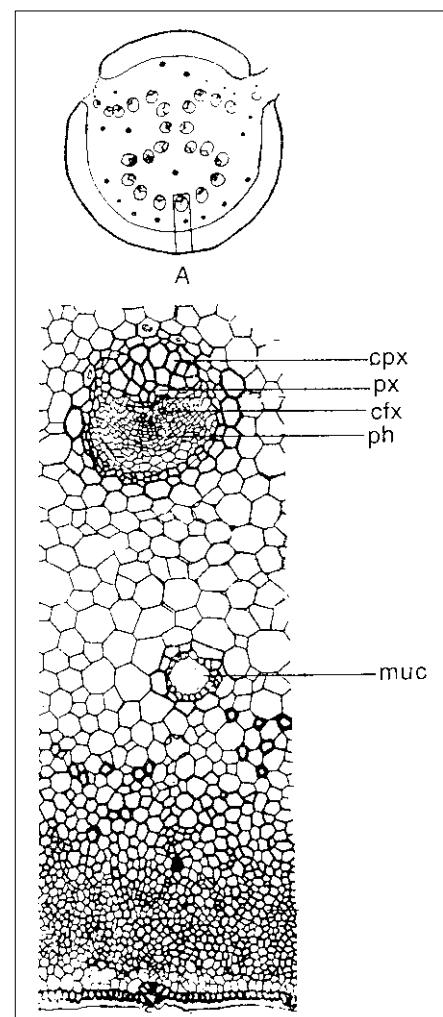


Fig. 5.8 A, B. *Cycas revoluta*. A. Transection rachis shows inverted omega arrangement of bundles, B. Enlargement of part of A. *cfx* centrifugal xylem. *cpx* centripetal xylem. *muc* mucilage canal, *ph* phloem, *px* protoxylem (After Pant, 1973).

The leaf-lets exhibit xerophytic characters. The upper and lower epidermis are heavily cutinized and interrupted by deeply sunken haplocheilic stomata. The stomata are mostly confined to lower epidermis except in *Bowenia* and *Macrozamia* (Fig. 5.9A,C,D). There is sclerenchymatic hypodermis beneath the upper epidermis followed by a palisade tissue and spongy parenchyma. In *Encephalartos* hypodermal region is several cells thick. Between the palisade and the spongy tissue there are several layers of transversely elongated thin-walled colorless cells called the transfusion tissue. Additionally, a few layers of empty thick-walled, trachied like cells with bordered pits are present. These cells are at right angles to the longitudinal axis of leaf and run from either side of the midrib to the margins of the lamina, forming accessory transfusion tissue. It probably functions as lateral conducting tissue in the leaflet which lacks veins (Fig. 5.9B). The vascular bundle is diploxylic and with mesarch xylem. The phloem lies below the xylem.

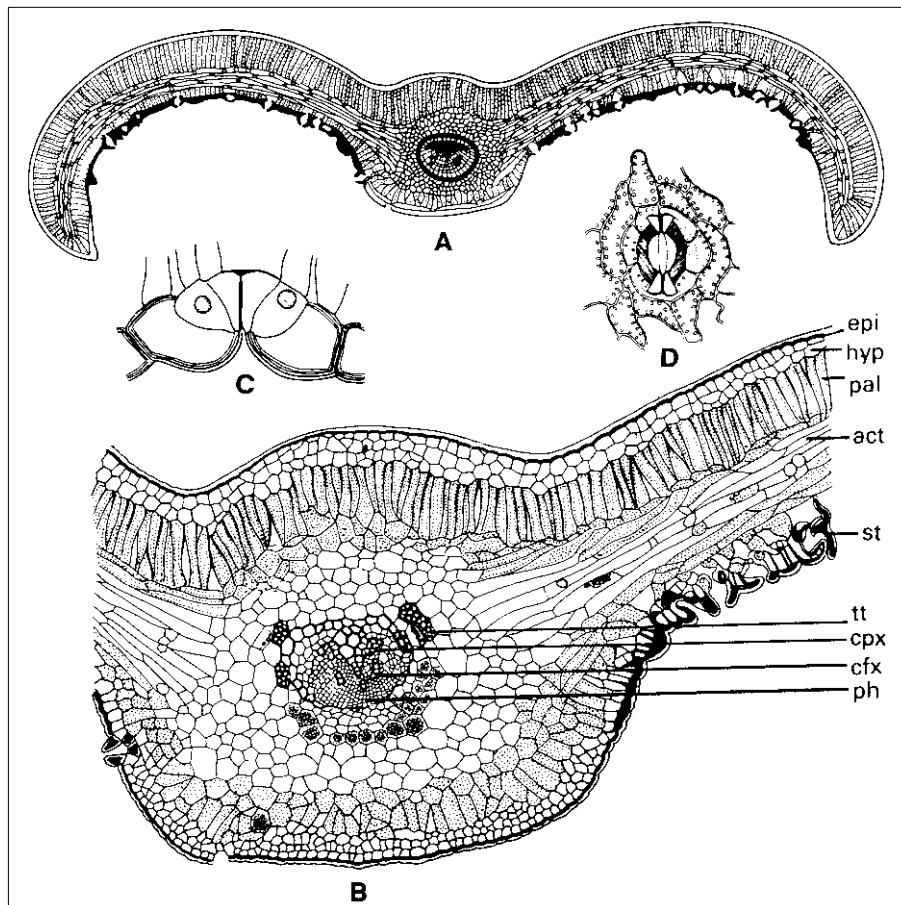
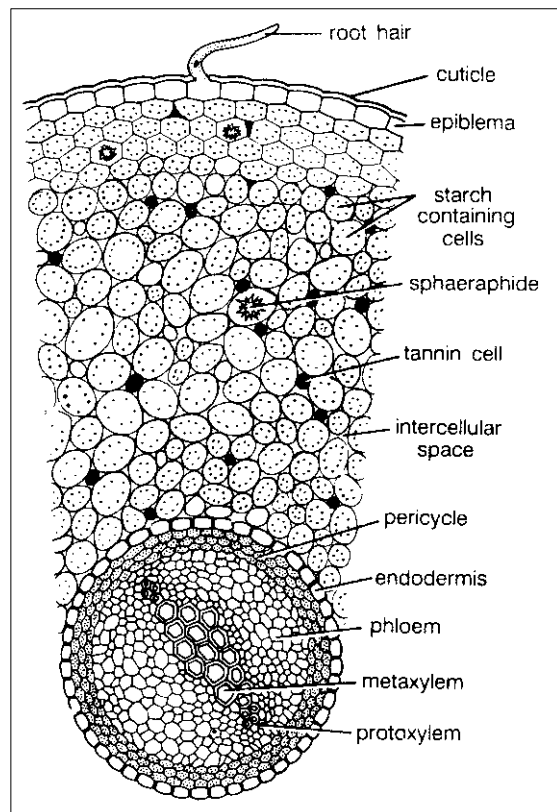


Fig. 5.9 **A, B**, *Cycas revoluta*; **C, D**, *C. circinalis* (**act**, accessory transfusion tissue; **cfx**, centrifugal xylem; **cpx**, centripetal xylem; **epi**, epidermis; **hyp**, hypodermis; **pal**, palisade layer; **ph**, phloem; **st**, stomata; **tt**, transfusion tracheid). **A**. VS leaflet; note the thick cuticle, revolute margins and stomata on lower surface only. The single vascular bundle is diploxylic showing both centripetal and centrifugal xylem. The accessory transfusion tissue is prominent running into both the arms of the leaflet. **B**. Portion of leaflet showing details. **C**. Stomata enlarged to show sunken nature. **D**. Epidermal peel of leaf to show stomata and surrounding cells. (**A,B**, after Pant, 1973; **C,D**, after Maheshwari, 1960).

Root: A normal young root is mostly diarch. Outer most layer is epiblema consisting of tangentially elongated cells. From some of these cells arise root hairs. A wide zone of parenchymatous cortex is present beneath the epiblema. Cells of the cortex are filled with starch, and some cells are filled with tannins, mucilage and sphaeraphides. The cortex is delimited by one layered endodermis and pericycle. The exarch protoxylem elements are with spiral thickening, while the metaxylem elements are with scalariform thickenings. Phloem tissue with sieve tubes and phloem parenchyma is present (Fig. 5.10) alternately with xylem tissue.

Fig. 5.10 *Cycas revoluta*. T.S. normal root (young)



The older roots exhibit secondary growth. The cambium produces secondary phloem towards the outer side and secondary xylem towards inner side. Some times the pericycle cells become meristematic and produce xylem and phloem tissues. The secondary xylem is manoxylic type consisting of radial rows of trachieds separated by parenchymatous rays. Some of the cells of the outer cortex become meristematic and function as cork cambium which produces secondary cortex towards inner side and cork towards outer side. Epiblema is ruptured and no root hairs present on the older roots.

Corolloid root

The apogeotropic corolloid roots represent the only known naturally occurring symbiosis between plant roots and nitrogen fixing cyanobacteria. The anatomy of a corolloid root is similar to that of a normal root, except that: a) the development of vascular tissue is poor, b) the secondary growth is absent, and c) the cortex has a conspicuous greenish zone of radially elongate thin-walled cells with large inter cellular spaces and cells filled with blue green algae (Fig. 5.11)

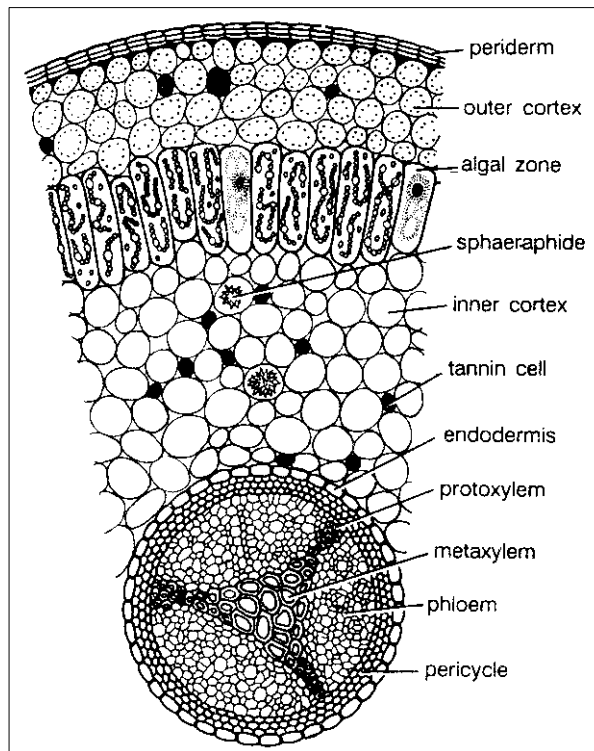


Fig. 5.11 *Cycas revoluta*. T.S. coralloid root

5.5.3 Reproduction

All cycads are absolutely dioecious, i.e. male and female plants are separately present. The sex is determined by X and Y chromosomes. Sporophylls are organized into male and female cones (strobili) except in female *Cycas*, where megasporophylls remain loose and do not form a cone. Male cones are not usually so large as the female cones.

Male Cone

The short-stalked male cone is generally terminal and compact. In *Macrozamia* cones are axillary in position. The apical meristem of stem exhausts itself during cone production. Then the growth of the trunk is continued by a new meristem arising from the base of the peduncle, pushes the cone to one side and takes its place. This new shoot apex appears terminal, forms fresh crown of scales, leaves, and later a cone. This process repeats with the production of each new cone. Male cones of cycads are the largest among the gymnosperms.

The largest cone described is that of *Macrozamia denisonii* which measures 80 cm long and 20 cm in diameter. The size of male cones of other cycads is, *Encephalartos altenstenii*, 60cm; *Cycas circinalis*, 45 cm; *Dioon spinulosum* 40 cm; *Zamia floridana*, 10cm; *Bowenia serrulata*, 5 cm and *Zamia pygmaea*, 2 cm (Fig. 5.12).

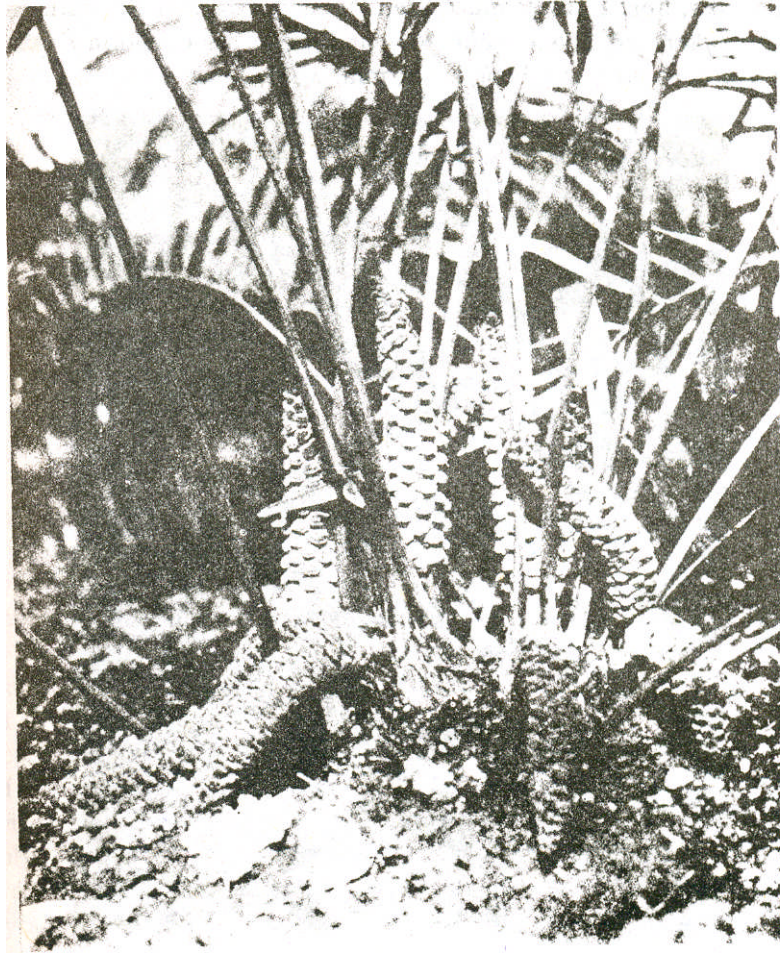


Fig. 5.12 *Zamia portoricensis*: male cones of various ages on one plant. The microsporophylls, although in strictly spiral arrangement, look as if they were in vertical rows. The University of Chicago greenhouse (January, 1933).

A male cone is an oval or conical structure with numerous spirally arranged microsporophylls, which are almost perpendicularly attached to the cone axis. The arrangement of sporophylls is so regular that in surface view they look as if they were in vertical rows like the grains of corn. The size of the microsporophyll also varies from 5 cm (*Cycas circinalis*) to 4 mm (*Z. pygmaea*) in length. A mature sporophyll is hard and woody. It has a wedge shaped distally expanded fertile portion which bears microsporangia on its lower (abaxial) surface and sterile end portion which has a pointed upcurved apex. The number of microsporangia on a sporophyll is the largest in *Cycas* (more than 1100) and decreases to 5-6 in *Zamia*. The sporangia arranged in definite groups (sori) like those of ferns. The number of sporangia in each sorus ranges from 5 in *Cycas* to 1 in *Zamia*. The strobili of cycads release odours that are sweet, resinous or musty. Thermogenesis (temperature mediated circadian rhythm related to insect pollination) is a widespread phenomenon in the group. Heat production helps in volatize odours that attract insects

for pollination. The male strobili have a high concentration of starch that may help the supply of energy for thermogenesis.

Microsporangium

Microsporangia development is eusporangiate type and have striking resemblance to those of ferns. In both, the stalk is massive and there are several layers of wall cells between epidermis and tapetum. The ramentum is unicellular, while in the ferns, two or three cross walls are common. The tapetum consists of very small cells in cycads and rather large ones in ferns. (Fig. 5.13). In the development of the microsporangium, one or several hypodermal cells divide to give rise to a primary wall cell or cells, from which wall layer cells form and a primary sporogenous cell or cells, that produce sporogenous cells. Tapetal cells break down into plasmodium. The sporogenous cells divide to produce microspore mother cells which divide meiotically to give rise to pollen grains or microspores. The epidermal cells become very thickened especially at the bottom and along sides, while other areas remain thin at the top, where the cell contents break through and escape. Each microspore develops a thick exine and a thin intine. They show an oval germinal furrow or sulcus on their distal face. The microsporangium has a radial line of dehiscence, which helps in the spore release from the sporangium. After the sporangia open, the cone *axis* elongates separating the sporophylls and this enables the pollen to release.

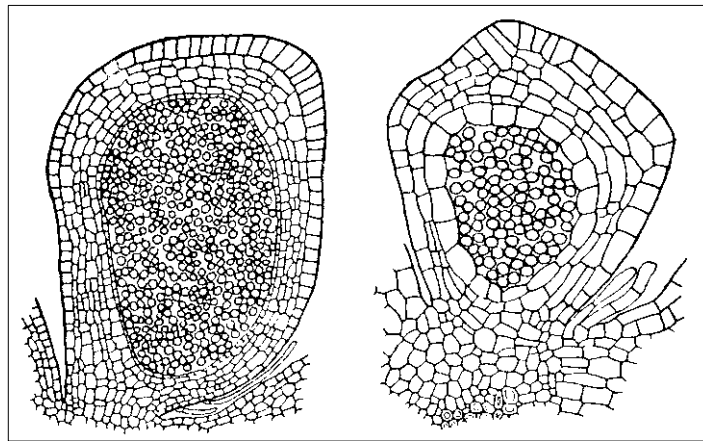


Fig. 5.13 *Dioon edule*: longitudinal section of microsporangium, showing numerous microspores and typical structure of a eusporangiate sporangium. Two ramental hairs, each with one transverse wall, are shown on the lower left part of the sporangium – From Chamberlain, *The Living Cycads* (University of Chicago Press).

Male gametophyte

Microspore is the first cell of the male gametophyte. Microspore nucleus divides into two unequal cells while still inside the microsporangium (*in situ* germination). The smaller one is called prothallial cell, while the large one represents antheridial initial cell. The antheridial initial cell divides to produce a tube nucleus and one generative cell. The microspores are released from

the microsporangium at this three celled stage. (Fig. 5.14C). Further development of the male gametophyte takes place after pollination when the microspores reach the nucellar surface of the ovules. The microspores are blown away by wind for pollination. Niklas and Norstog (1984) opined that wind alone is not sufficient to effect pollination in some of the cycads. Tang (1987) reported insect pollination in *Zamia pumila*. Wilson (1993) reported amphiphilous pollination where pollen being transferred by the weevil (*Tranes subopaca*) in *Bowenia serrulata*. Microspores trapped in mucilaginous drop of the micropyle are withdrawn into the micropylar chamber of the ovules.

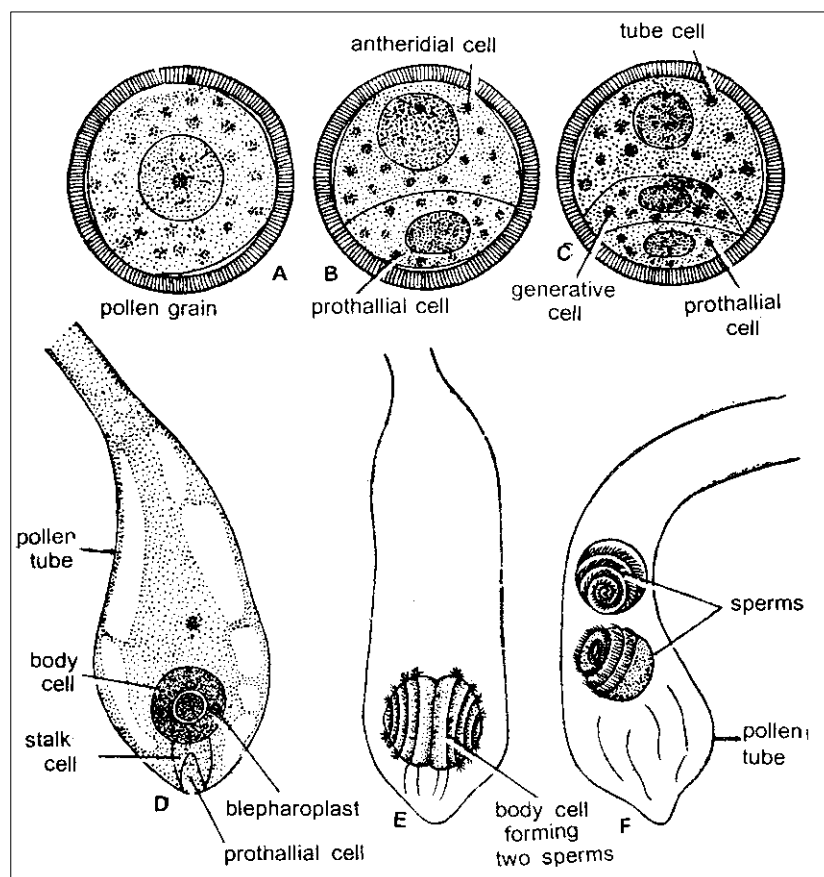


Fig. 5.14 A-F. *Cycas*. Development of male gametophyte

The exine breaks up and intine comes out in the form of a pollen tube. The latter penetrates the nucellar tissue. The generative cell divides soon to form a sterile cell (stalk cell) and a spermatogenous cell (body cell). The stalk cell does not divide further, but enlarges in size. The prothallial cell pushes into the stalk cell and presses it against the cell (Fig. 5.14D). Then, there will be gap of 4 months in *Cycas* sp, five months in *Zamia floridana* and six months in *Dioon edule*, for further development of the male gametophyte. Immediately before fertilization the body cell enlarges and elongates. It gradually becomes spherical. Two blepharoplast appear in the body cell, that lie perpendicular to the long axis of the pollen tube, one each on either sides of the body cell nucleus. Then body cell divides resulting into two cells from each one a single sperm is

developed (Fig. 5.14 E-F). The male gametophyte development in all cycads is similar except in *Microcycas* (Fig. 5.15).

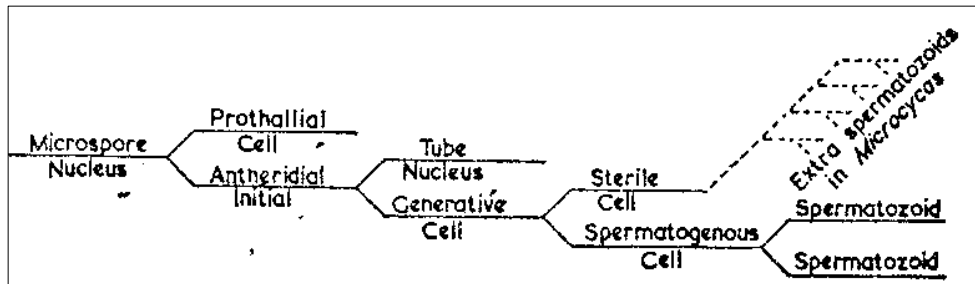


Fig. 5.15 Stages in the formation of the male prothallus in cycads

A mature spermatozoid contains 5-6 turns of spiral bands with thousands of cilia. Twists of spiral bands are directed from left to right. Sperms of cycads are remarkably large. In *Dioon edule* sperms are 300 microns in length and 230 microns in diameter. Consequently, they are visible to the naked eye. The largest ever reported spermatozooids of size 400 microns are of the cycad, *Chigua*. In all of the cycads, except in *Microcycas*, there are two sperms in each pollen tube. In *Microcycas*, there are usually 16 or 32 sperms, produced by the division of stalk cell (Fig. 5.15).

Female Cones

In *Cycas*, instead of female cone, the individual megasporophylls form a loose crown at the stem apex. Each megasporophyll is a leaf-like structure, 15-30 cm long, and pinnately dissected in its upper region. In the lower portion one to five pairs of ovules are borne on either side of the sporophyll.

In other genera, the megasporophylls are organized into female cones and some of these are the largest cones that have ever existed. Female cones of *Macrozamia denisonii* are 70 cm long and weigh about 30 kg. The cones of *Dioon spinulosum* are 50 cm long, in *Ceratozamia* 26 cm in length and *Zamia pygmaea* has the smallest cones about 2 cm long. The sporophylls are spirally arranged on the cone axis, each bearing two orthotropous ovules, the number characteristic of all genera except *Cycas*. In various species of *Cycas*, there is a gradual reduction in the expanded part of sporophyll, from large elongated pinna in *C. siamensis* to a highly reduced to almost mere serrations in *C. normanbyana*. Similarly the number of ovules reduced from 8 to 2 in different *Cycas* species (Fig. 5.16). The megasporophylls of some genera have some characteristics that enable the easy identification of the genus. In *Dioon edule*, the sporophylls have lost even the serration. The rachis of sporophyll remains as prolonged tapering spine in *Macrozamia*, the terminal part is totally suppressed in *Encephalartos* and in others it is merely a thick peltate structure. In *Ceratozamia*, two strong horns are formed from the terminal part of sporophyll.

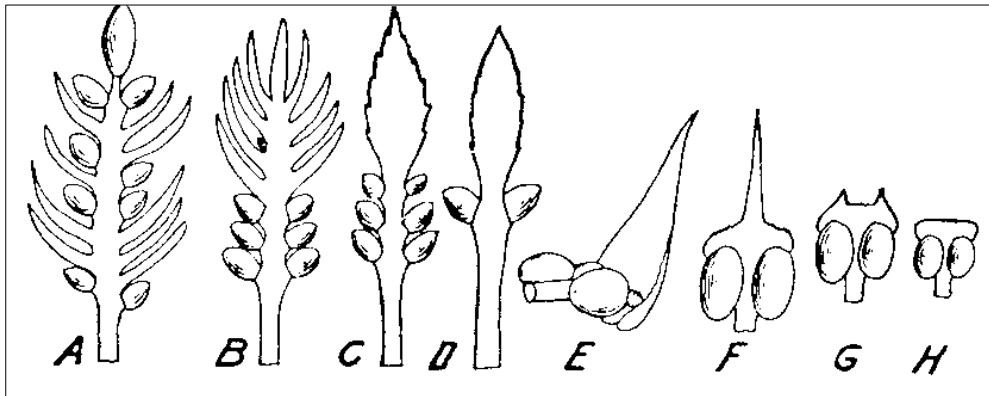


Fig. 5.16 Reduction of the megasporophyll in Cycadales: **A**, theoretical ancestor of *Cycas*; **B**, *Cycas resoluta*; **C**, *Cycas circinalis*; **D**, occasionally in *Cycas media*, and usually in *Cycas normanbyana*; **E**, *Dioon edule*; **F**, *Macrozamia*; **G**, *Ceratozamia*; **H**, *Zamia*.

Megasporangium or ovule

The ovules are all erect and have a single integument. In *Cycas circinalis* and *Macrozamia denisonii* ovules are about 6 cm in length and *Zamia pygmaea* has the smallest which measure about 5 to 7 mm in length. The integument is fused with the nucellus and free from it only at the apex. The principal features of the ovule are well illustrated by a longitudinal section (Fig. 5.17). The integument is massive and differentiated into three layers: a) The outer fleshy layer which become variously colored at maturity, b) middle stony layer, and c) an inner fleshy layer which is reabsorbed and become papery even before maturity. The vascular supply at the base of the ovule divides into three strands, the middle one supplies the base of the sporangium and the lateral two enter the integument and divide again. The integument is open at the tip to form the micropyle. The nucellus grows out into a beak which protrudes into micropyle. Certain cells at apex of the nucellus disorganize to form a cavity called pollen-chamber. The epidermal cells of the nucellus divide periclinally to form nucellar cap. The epidermal cells of the nucellus are heavily cutinized and has stomata. In the ripe seeds, the outer fleshy integument is bright red in *Encephalartos altensteinii*, pale yellow in *E. horridus*, orange-red in *Zamia floridana*, salmon pink in *Microcycas* and nearly white in *Dioon* and *Ceratozamia*.

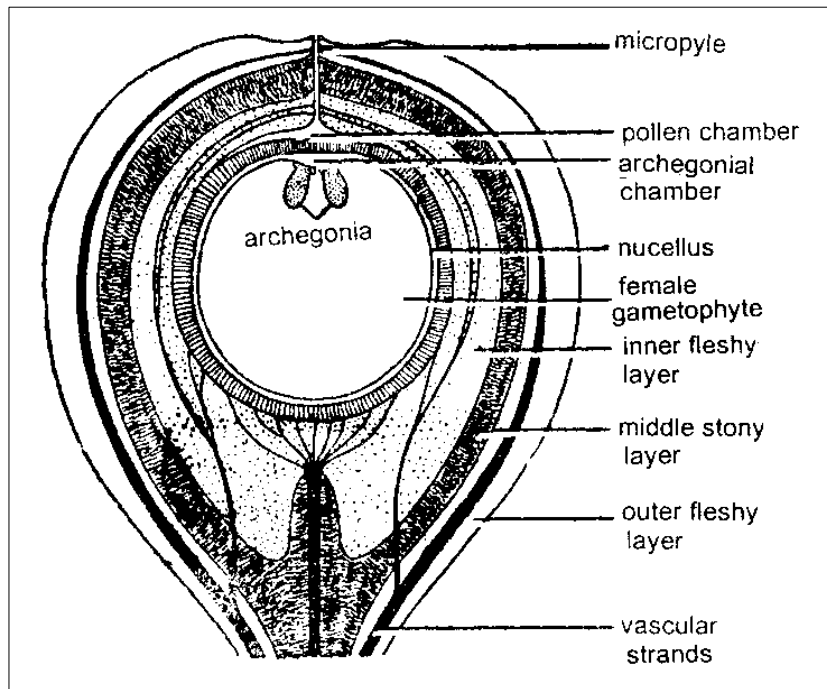


Fig. 5.17 Reduction of the megasporophyll in Bennettitales: **A, B, C**, stages in the reduction in some hypothetical ancestor; **D**, the usual condition found in fossils; **E**, the sporophyll has become entirely sterile; **F**, fertile and sterile sporophylls with about the arrangement found in *Bennettites gibsonianus*.

Megasporogenesis: In the nucellus one to several hypodermal archeserial cells differentiate. They divide periclinally to produce an outer primary perietal and inner primary sporogenous layer. Above the sporogenous cells, primary perietal cells divide to produce a massive perietal tissue. Sporogenous tissue increase in amount by the divisions in it. One of the cells of sporogenous tissue functions as the megaspore mother cell. It under goes meiotic division producing a linear tetrad of four megaspores. The chalazal megaspore is functional from which female gametophyte develops. (Fig. 5.18A-C).

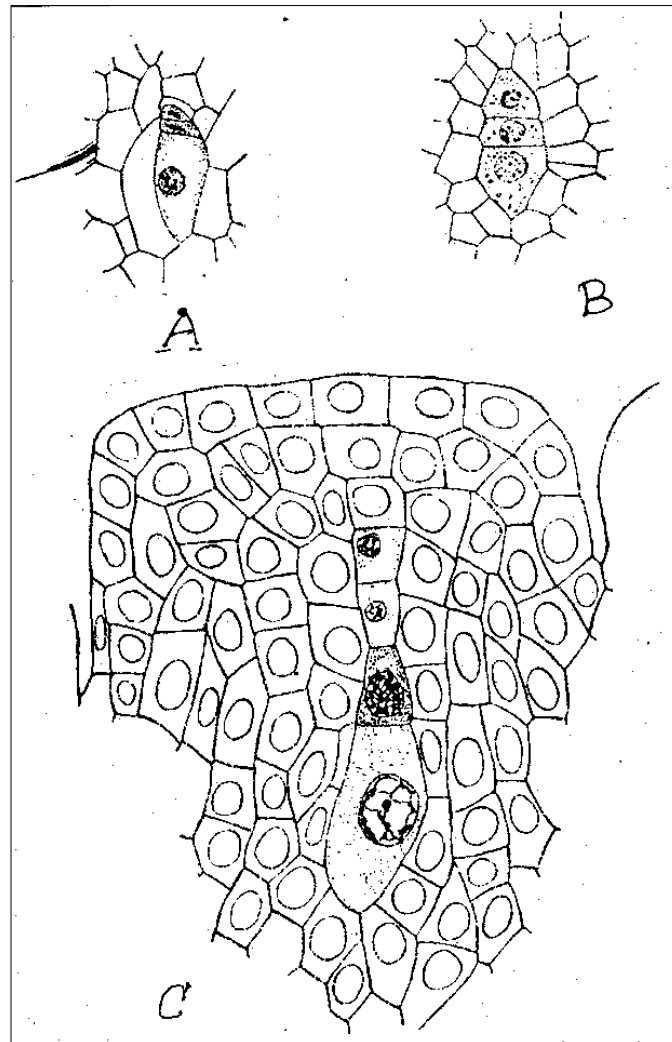


Fig. 5.18 Megaspores of cycads. **A.** *Stangeria paradasa*; the lower cell of the row of three is the functioning megaspore; X 230 – After Lang. **B.** *Ceratozania mexicana*, similar stage; X 266 – After Treub. **C.** *Zamia floridana*, row of four megaspores; X 930 – After Dr. F. Grace Smith.

Female gametophyte

Repeated free-nuclear divisions occur in the functional chalazal megaspore, forming about 1000 free-nuclei. The megaspore in the meantime enlarges rapidly and nuclei become distributed in the peripheral layer of cytoplasm around a central large vacuole (Fig. 5.19A). Then cell walls are laid down in a centripetal fashion to result a cellular gametophyte. The arrangement of cells in the young gametophyte is extremely regular radiating from the centre to the periphery (Fig. 5.19B). Soon after this stage, some of the cells at the micropylar end become larger and their nuclei move from central position to the peripheral end of the cell. These are archegonia initials (Fig. 5.20A). Each of these divide to form a primary neck cell and a central cell. The former anticlinally

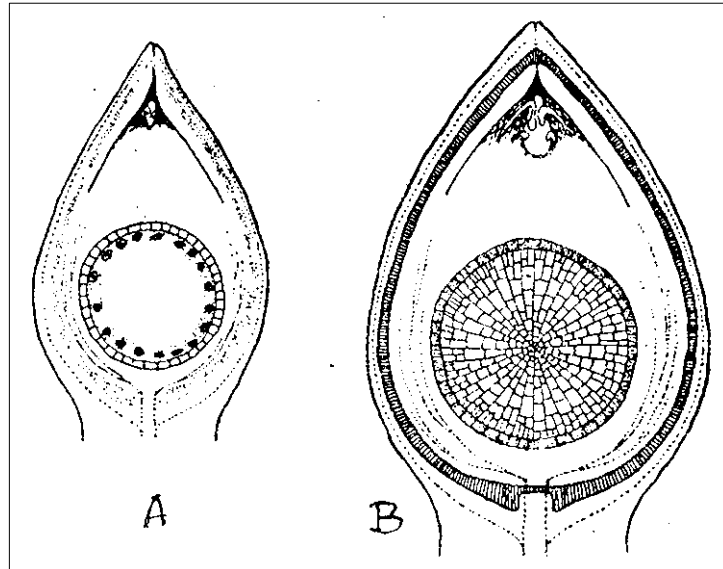


Fig. 5.19 **A.** *Dioon edule*; ovule soon after pollination, free nuclear stage of the female gametophyte – From Chamberlain, *The Living Cycads* (University of Chicago Press). **B.** *Dioon edule*; the female gametophyte has become cellular throughout – From Chamberlain, *The Living Cycads* (University of Chicago Press).

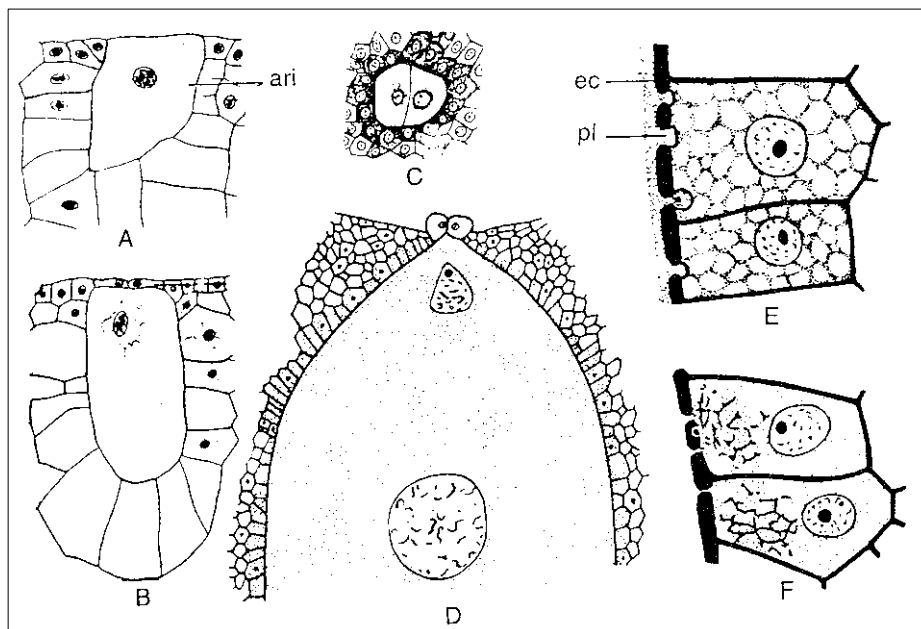


Fig. 5.20 **A-F.** Archegonium. **A-C.** *Cycas rumphii*. **A.** Archegonial initial (*ari*). **B.** Archegonium. **C.** Two neck cells of archegonium in transection. **D-F.** *C. circinalis*, **D.** Longisection (part of) archegonium. **E.** Plugs (*pl*) of egg cytoplasm (*ec*). **F.** Cells (devoid of contents) show dark-staining bodies (**A-C** After De Silva and Tambiah 1952, **D-F** after Rao, 1961).

divides to form a neck of two cells. Just before fertilization, two neck cells again divide to form four neck cells. The central cell grows for several months before its nucleus divides. The central cell nucleus divides into a small ephemeral ventral canal nucleus and a large egg cell. A mature archegonium consists of two to four neck cells, one ventral canal nucleus and an egg (Fig. 5.20 B,C). The ventral canal nucleus soon disorganized and usually unrecognizable. Three to five such archegonia are produced on a gametophyte. The nucleus of the cycad egg may reach a size of 500 microns, and is reported as the largest among in living plants. The cells in the immediate vicinity of the developing archegonium maintains a link with the jacket cells by means of large pores through which an inflow of food materials takes place (Fig. 5.20 D-F).

Pollination and Fertilization

The wind dispersed pollen grains are caught in the pollination drop secreted at the micropyle of the ovule and are sucked in through micropyle to the pollen chamber. Insect pollination is reported in *Zamia pumila*.

The pollen grains germinate immediately with the rupture of exine at the tube cell end. The tube nucleus passes into the pollen tube, which penetrates the nucellar tissue and becomes highly branched. The branches of pollen tube also produce haustorial growths in *Zamia furfuracea*. The pollen tube thus acts more as a haustorium.

The sperms and pollen tube cytoplasm are released into the archegonial chamber by the rupture of pollen tube. The neck cells of archegonium are plasmolysed, facilitating the entry of motile sperms. The sperm casts off its ciliary band and its nucleus approaches the egg. It makes contact with the egg nucleus and gradually sinks into it, thus completing fertilization and zygote formation.

Embryogeny: The zygote is the first cell of sporophyte. The zygote nucleus moves towards the base of archegonium and there is a period of free nuclear division (Fig. 5.21 A,C). The divisions are simultaneous and the number of nuclei is 512 and in some cases 1024. They lie scattered throughout the cytoplasm. A vacuole appears in the centre after some time. The early divisions are regular, but in *Dioon edule*, 8th, 9th and 10th divisions especially in the upper part of the embryo are irregular. In *stangeria* there is often a distinct polarity, the nuclei being in two groups. In *Zamia floridana*, the free nuclei number is quite regularly 256. In *Bowenia serrulata*, it is 64, the lowest number ever recorded in a cycad. In *Cycas* and *Stangeria* the nuclei at the base of the embryo undergo a vigorous simultaneous division, while the rest of the nuclei in the other parts of embryo have ceased to divide.

Following the free nuclear period, cell wall formation takes place, which starts from the base and progresses towards upper side (Fig. 5.21 D). The embryo becomes cellular throughout in species of *Cycas*. *Encephalartos* and *Macrozamia*, which is regarded as primitive type of embryogeny. In others, basal region becomes cellular and upper region contain free nuclei.

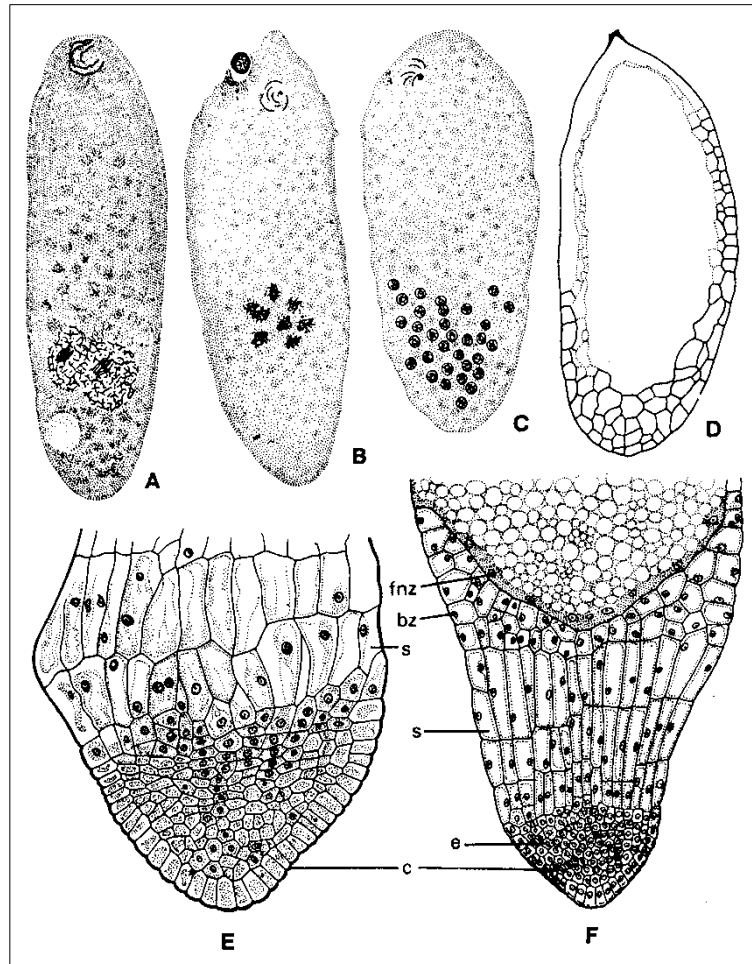


Fig. 5.21 (**bz**, buffer zone; **c**, cap cells; **e**, embryonal mass; **fnz**, free nuclear zone; **s**, suspensor). Development of proembryo in *Cycas* (A-E) and *Zamia* (F). A-C. Two-, eight-, and thirty-two nucleate proembryos. Relics of sperm are still seen in upper end of archegonium. D. Wall formation has started at the basal end of the proembryo. E. Later stage showing outer layer of 'cap cells', embryonal cells and suspensor cells. F. Developing embryo showing free nuclear zone, buffer zone, suspensor, embryonal mass and cap cells. (A-C, after Swamy, 1948; D, E, after Maheshwari, 1960; F, after Bryan, 1952).

The free nuclei and surrounding cytoplasm degenerate to form a plug. Initially the cells at the base divide and function as embryonal cells. The upper cells just above the embryonal cells differentiate into a suspensor. The zone of cells separating the suspensor cells and still free nuclear zone is called buffer zone. (Fig. 5.21F). The suspensor elongates pushing embryonal cells deep into the nutrient-rich female gametophyte. The layer of cells covering the outer curved face of the embryonal mass forms the cap (Fig. 5.21E,F). The cells of the embryonal mass develop into embryo proper by further divisions. There is cessation of growth in the centre and its continuance at the margins. The cotyledons develop as a result of meristematic activity very near the cylindrical shoot apex which itself develops at the tip of the embryonal region.

Normally, the eggs of all archegonia in a gametophyte get fertilized. More than one embryo starts developing at the same time, but one which is centrally placed and most vigorous takes the lead and matures. The growth of the embryo in the seed is very slow and takes over an year for the embryo to mature after fertilization. (Fig. 5.22). The mature embryo fills up the whole cavity inside the seed. It exhibits a leaf, one or more scale leaves and the stem tip between the cotyledons.

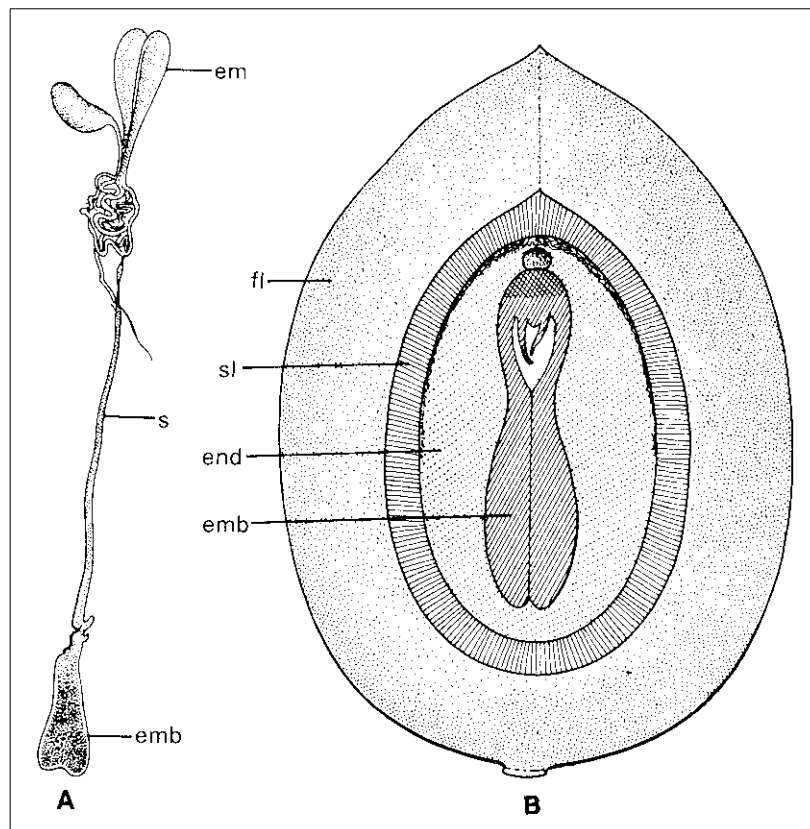


Fig. 5.22 *Cycas* (*em*, egg membrane; *emb*, embryo; *end*, endosperm; *fl*, fleshy layer; *s*, suspensor; *sl*, stony layer). **A.** Embryo showing long coiled suspensor and persistent egg membranes dissected from seed just before shedding. **B.** LS mature seed. (**A**, after Swamy, 1948; **B**, after Gifford & Foster, 1989).

Seed: In a mature seed, three-layered seed coat is present, of which the outer layer (sarcotesta) is pigmented. The attractive red or orange fleshy seeds are dispersed by birds and rodents. There is no resting period in the cycad seeds and viability is short.

The germination of the seed commences with the emergence of root tip from the micropylar end. The root tip as it elongates, protrudes through and goes deep in the ground. The cotyledons remain inside the seed and perform haustorial function. The seed germination is hypogeal. The plumule comes out and starts forming a few scale leaves and then a foliage leaf.

Haploid chromosome numbers that have been recorded for different cycad taxa are 13 in *Microcycas*; 11 in *Cycas*; 8 in *Stangeria*, *Ceratozamia* and *Zamia* spp and 9 in the rest. On the basis of asymmetrical karyotype and higher chromosome number, *Cycas* and *Microcycas* have been regarded as advanced and *Ceratozamia* and *Zamia* as primitive.

5.6 PHYLOGENY

The evolutionary history of an organism or a group of organisms (taxon) is known as its phylogeny. It is believed that cycadales have originated from pteridospermales (=cycadofilicales=seed ferns). This view was put forth by Worsdell (1909) and supported by Chamberlain (1935), Stewart and Delevoryas (1956) and Tailor (1969). There are several common characters between cycadales and pteridospermales. No living taxa of cycadales can be considered to be the forerunner, because every taxon shows primitive and advanced characters. According to Gaussen (1950) *Cycas* shows 12 primitive and 70 advanced features and *Zamia* shows 67 primitive and 33 advanced characters. The genus *Microcycas* is advanced in vegetative anatomy, cone structure and karyotype symmetry. But its male and female gametophytes are presumed to be the most primitive as they produce 16 to 20 male gametes and 64 to 200 archegonia from a single gametophyte. Therefore, the interrelationships in modern cycads are difficult to visualize. According to Chamberlain (1920), the cycads did not give rise to any other group and will probably become extinct in the next geological period.

5.7 SUMMARY

Out of all the Cycadopsida, the only group that appeared in Upper Triassic times and have survived until the present day, is the Cycadales. Therefore, the living cycads are the most ancient and exhibit a number of primitive features. There are eleven living genera in cycadales whose morphology, anatomy, male and females cones, gametophytes and embryogeny are presented in this chapter. All these taxa share some common features like manoxylic wood, diploxylic leaf traces leaf-like sporophylls, orthotropous unitegmic ovules, and motile sperms. This group is believed to have originated from pteridospermales.

5.8 KEY TERMS

1. **Circinate vernation:** Leaf primordium is rolled in on itself from its apical to basal end towards the adaxial surface so that apex lies in the middle of the coil.
2. **Cone domes:** Domes of vascular tissue crossing the central pith at intervals that represent the used-up apical meristem of the cones.
3. **Collateral bundle:** A vascular bundle in which xylem and phloem are one above the other lying on the same radius.

4. **Corolloid root:** Apogeotropic cycad roots that branch dichotomously and profusely forming corolloid masses above ground.
5. **Diarch Stele:** Stele with two separate strands of xylem with protoxylem points.
6. **Diploxylic trace:** A trace with two types of xylem (i.e. centripetal and centrifugal) elements.
7. **Haplocheilic stomata:** Stomata in which guard cells and subsidiary cells are not developed from the same initials.
8. **Hypogeal germination:** The cotyledons stay below the ground during the seed germination.
9. **Monotypic genus:** A genus which is exemplified in only one type i.e. contains only one species.
10. **Transfusion tissue:** A tissue that lies on either side of the vascular bundle and carries out the function of lateral veins.

5.9 MODEL QUESTIONS

1. What are the extant cycads? Write about their distribution.
2. Give an account on the fossil cycads.
3. Describe the male and female reproductive organs of cycadales.
4. Give a comparative account on the male and female gametophytes development in cycads.
5. Write a detailed account on the cycads embryogeny.
6. Write short answers on the following:
 - a. Diploxylic leaf traces
 - b. Megasporophyll of cycads
 - c. Primitive characters of cycads
 - d. Cycads archegonium.

5.10 REFERENCE BOOKS

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Prof. Z. VISHNUVARDHAN

M.Sc. BOTANY (First year)

Paper-I : Biology and Diversity of Algae, Bryophytes and Gymnosperms

Unit-IV : GYMNOSPERMS

Lesson 7**G N E T A L E S**

- 7.0 AIM:
General description of the order Gnetales and its relationship are provided in this lesson.
- 7.1 INTRODUCTION
- 7.2 DISTRIBUTION
- 7.3 ANATOMY
- Stem
 - Leaf
 - Root
- 7.4 REPRODUCTION
- Male Strobilus
 - Microsporangium and Microsporogenesis
 - Male gametophyte
 - Female strobilus
 - Megasporangium and Megasporogenesis
 - Female gametophyte
 - Pollination and Fertilization
 - Endosperm formation
 - Embryogeny
 - Seed and seed germination
- 7.5 COMPARISON OF CHARACTERS OF *GNETUM*, *EPHEDRA* AND *WELWITSCHIA*
- 7.6 INTERRELATIONSHIPS (Affinities)
- with Gymnosperms
 - With Angiosperms
- 7.7 SUMMARY
- 7.8 KEY TERMS
- 7.9 MODEL QUESTIONS
- 7.10 REFERENCE BOOKS

7.1 INTRODUCTION

The order Gnetales of class Gnetopsida comprise three genera, viz., *Gnetum*, *Ephedra* and *Welwitschia* belonging to families Gnetaceae, Ephedraceae and Welwitschiaceae respectively (Sporne, 1965). This group of plants have got immense importance showing a connected link between gymnosperms and angiosperms. Presence of naked ovules borne in cones is considered as

gymnosperm character whereas presence of flower-like shoot on which ovules and microsporangia are borne and presence of vessels in the xylem are considered to be angiosperm characters. However, the ovules are enclosed within coverings additional to the true integument, which are sometimes considered to be the equivalent to ovary walls. A common character found in all these three genera is the prolongation of inner integument into a long narrow tube with a pollen chamber in which pollen is collected.

General characters of Gnetales with special reference to *Gnetum* have been discussed in this chapter.

7.2 DISTRIBUTION

The genus *Gnetum* consists of 30-35 species which are trees, shrubs and woody climbers. The climbers are predominating in this genus. About four species are distributed in the tropical regions of the world, especially West Africa to the Amazon region. The species *G. scandens* is a large climber, growing in Asia and in the Western Ghats of India. The leaves are net-veined (Fig. 7.1), large, oval and entire and these are borne on the branches of unlimited growth. Branches of limited growth bear scale leaves on the shoot.

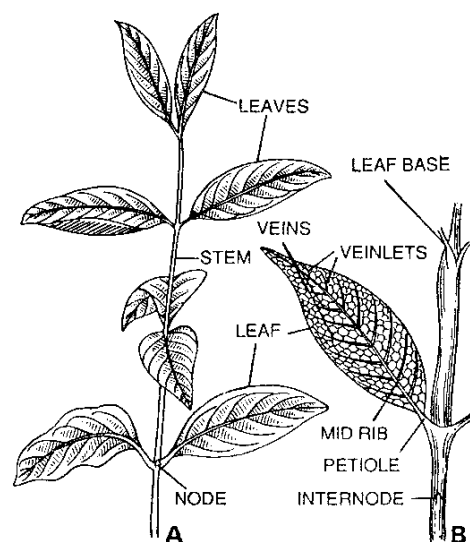


Fig. 7.1 *Gnetum gnemon*. A, a twig with opposite and decussate leaves; B, a leaf showing reticulate venation

The genus *Ephedra*, consists of 35 species distributed in the new and old world. In India, *E. intermedia*, *E. foliata*, *E. gerardiana* and *E. nebrodensis* are available in the Kashmir and North-West Himalayas, Punjab and Rajasthan. They are shrubby plants with green, long, jointed, slender branches bearing scale leaves (Fig. 7.2).

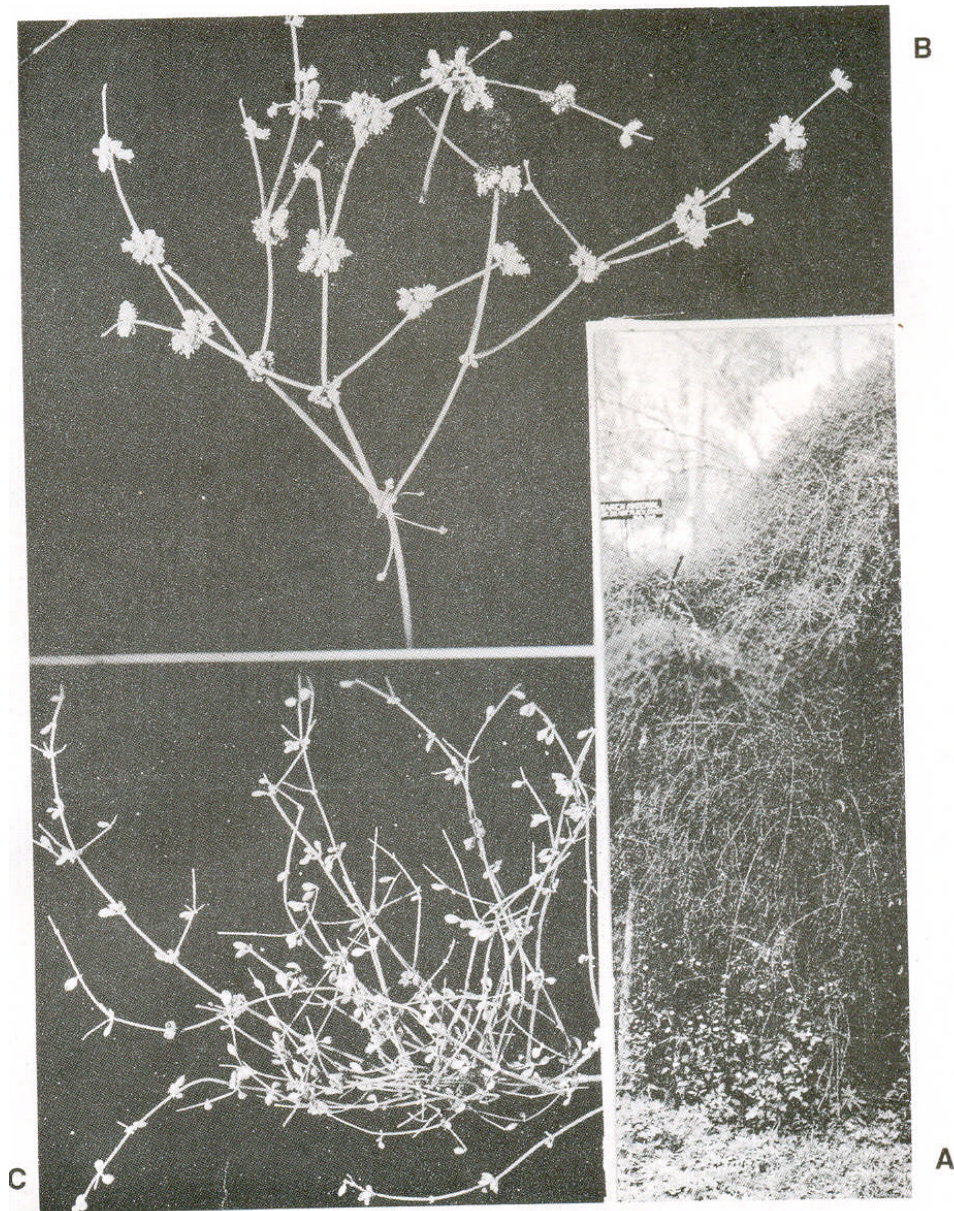


Fig. 7.2. A-C. *Ephedra foliata*

A, bushy nature of the plant; B, C, twigs bearing male and female cones respectively

The genus *Welwitschia* is a monospecific (*W. mirabilis*). It is a remarkable living plant confined to the desert region of South-West Africa. It was first discovered in Angola in 1860 by Frederic Welwitsch. Most of the stem is buried in the sandy soil; exposed portion is massive, woody, concave disc with two huge strap-shaped leaves (Fig. 7.3).

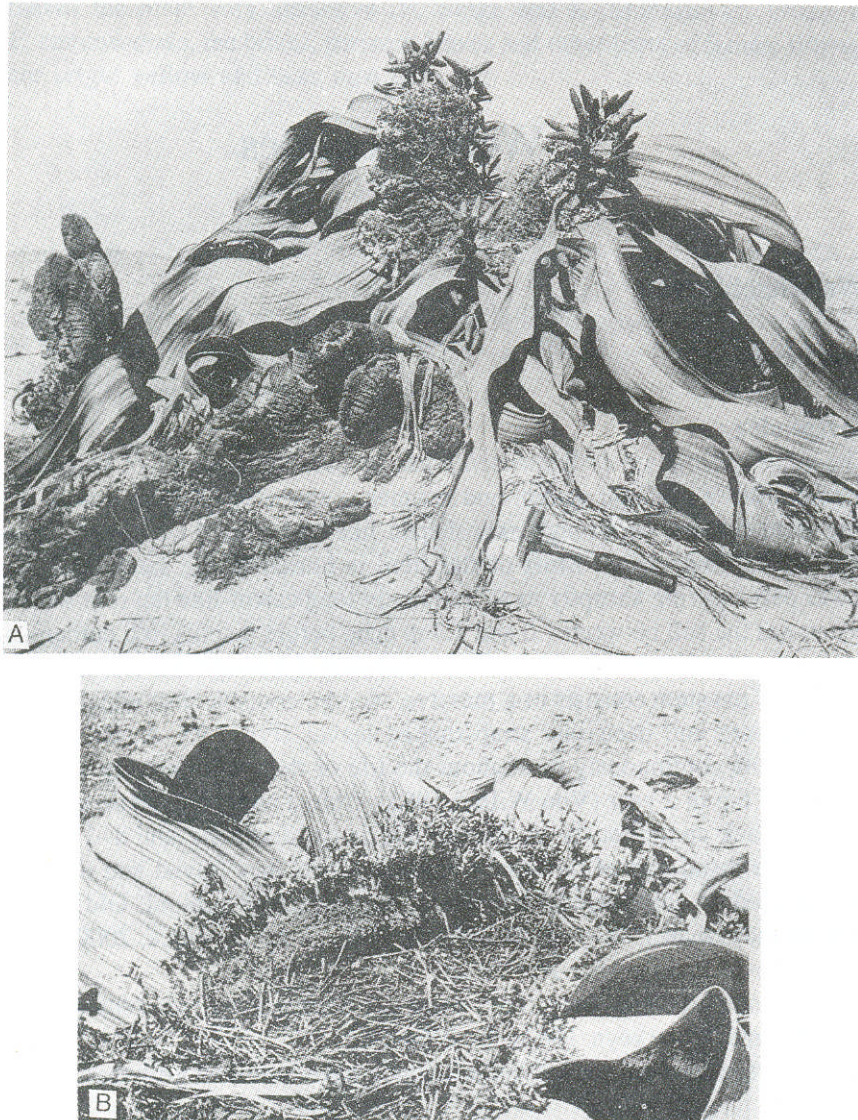


Fig. 7.3 A, B. *Welwitschia mirabilis*.

A. Plant with opposite strap shaped leaves.

B. Central part shows woody concave disc. (A After Von Willart 1985, B after Rodin 1953a).

7.3 ANATOMY

a) Stem

There is a distinct tunica-corporis organization of shoot apex found in *Gnetum*. Tunica undergoes anticlinal divisions only; whereas corpus divides periclinally, as a result, the volume is increasing. The corpus comprises 2-3 layers of sub-apical initials, central mother cell zone, flanking layers and rib meristem.

Anatomy of stem is similar to that of angiosperms. There is a ring of collateral endarch vascular bundles separated from one another by broad medullary rays. Towards outside there is a broad cortex (Fig. 7.4). The epidermis is single-layered with thick cuticle and sunken stomata. The endodermis and pericycle are inconspicuous. The wood is composed of a large number of tracheids and a few vessels. The phloem consists of sieve cells without companion cells and phloem parenchyma. The pith is parenchymatous and become lignified in older stems.

In tree species such as *G. gnemon*, the secondary growth is normal. In climbers such as *G. ula* and *G. africanum*, a new cambium differentiates from inner part of the cortex and gives rise a normally oriented ring of xylem and phloem wedge-shaped bundles separated by medullary rays. Like this new cambia are formed successively; some cambia may remain incomplete, which results in an eccentric arrangement of the rings (Fig. 7.4), or an eccentric position of the pith. In *G. ula*, these cambia are extrastelar in origin.

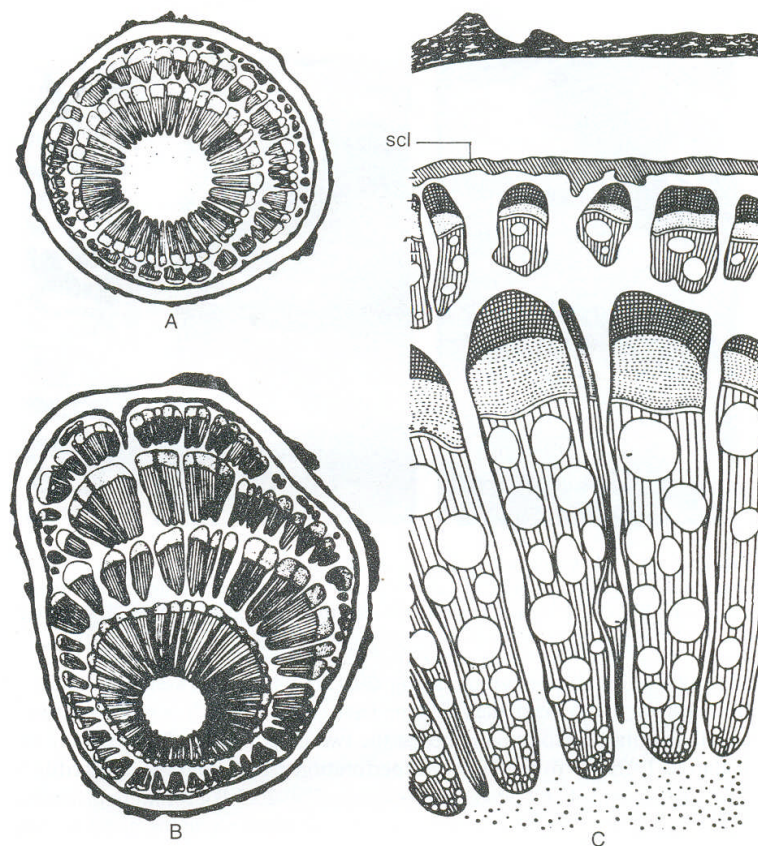


Fig. 7.4. A-C. *Gnetum ula*.

A, B Transverse section of young and old stem to show accessory (A) and eccentric (B) rings of vascular bundles. C. Vascular bundles from A. scl sclerenchyma. (After P. Maheshwari and V. Vasil 1961a).

The xylem consists of tracheids with highly tapering ends, vessels and xylem parenchyma. The vessel with simple perforation plate is more common in the late metaxylem, especially in the secondary xylem. Besides, vessels with scalaroid (vertical row of circular perforations in *G. montanum*), scalariform (row of transversely elongated perforations in *G. gnemon*) and foraminiate (round perforations in alternate or horizontal rows) perforation plates are found (Biswas and Johri, 1997).

The medullary rays are quite massive. They show considerable width and height. In T.L.S. multiseriate rays appear boat shaped with many lignified cells. Besides these, short biseriate or uniseriate rays, few to several cells deep, are also present (Fig. 7.5).

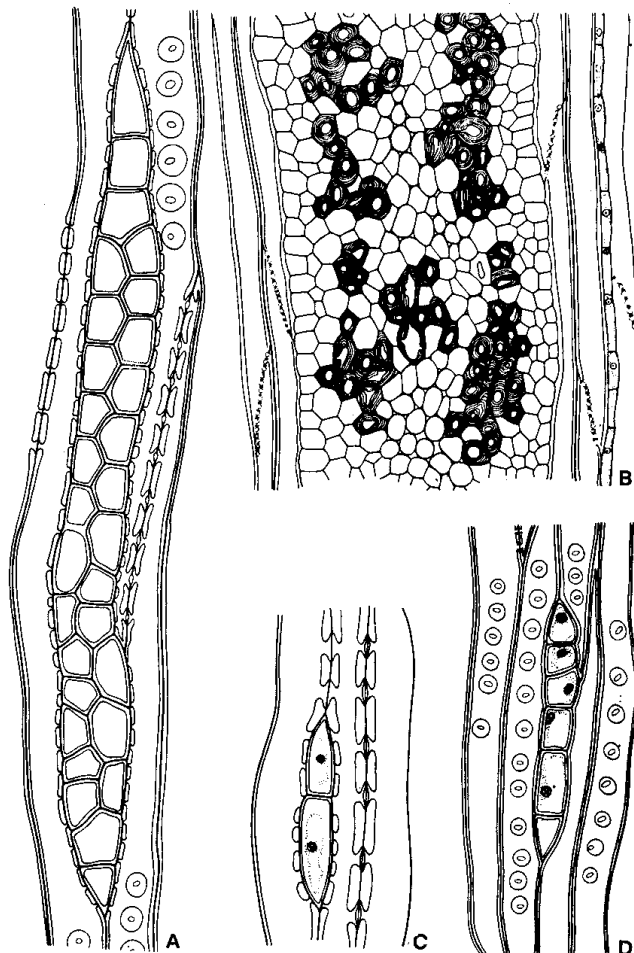


Fig. 7.5 *Gnetum ula*

- A. TLS part of stem showing a long, biseriate medullary ray,
 B. Portion of multiseriate ray showing lignified cells.
 C,D. Short uniseriate rays, two to several cells deep

In *Ephedra*, vessels with foraminate perforation plates have been observed. These vessels originate from the pitted tracheids.

In *Welwitschia mirabilis* vessels with simple perforation plates have been observed. Occasionally, vessel members have pores in pairs, or rarely a foraminate plate has three pores.

The presence of various types of vessels in Gnetales partially explains the connecting link between gymnosperms and angiosperms. There is a generally accepted view that angiosperm vessels have evolved from tracheids with scleriform thickenings whereas Gnetalean vessels have evolved from pitted tracheids. It is quite clear here by the occurrence of vessels that show intermediate stages between pits and perforations, or between many perforations and single perforation.

It is also quite evident that vessel with border pitted end wall has undergone many morphological specializations in the course of evolution and resulted into vessel with simple perforation plate. These morphological specializations are: (1) the vessel element increase in size, both length and breadth, (2) the bordered pits on the end walls increase in size, (3) the border of the pit reduces, (4) the middle lamella and torus disappear thus forming a circular perforation plate, and (5) these perforations enlarge and fuse to form a single large perforation.

(b) Leaf

The *Gnetum* leaf lamina is large, entire with reticulate venation and gives a typically dicotyledonous appearance. There is a well-marked cuticle on epidermis. Mesophyll is differentiated into palisade and spongy parenchyma. The vascular system consists of collateral bundles, the xylem faces the upper and the phloem the lower side of the leaf (Fig. 7.6). The sunken stomata with syndetocheilic development (both guard cells and subsidiary cells derived from a single meristemoid) are found in Gnetales (Fig. 7.7 A-C).

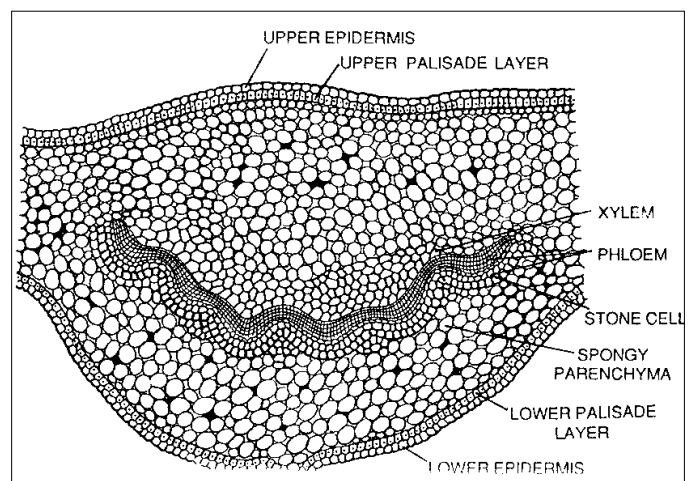


Fig. 7.6. *Gnetum* sp. T.S. of leaf.

c) Root

In cross section, the root shows epiblema, cortex, endodermis, pericycle and a diarch vascular region. The xylem elements in the roots are larger than those in the stem.

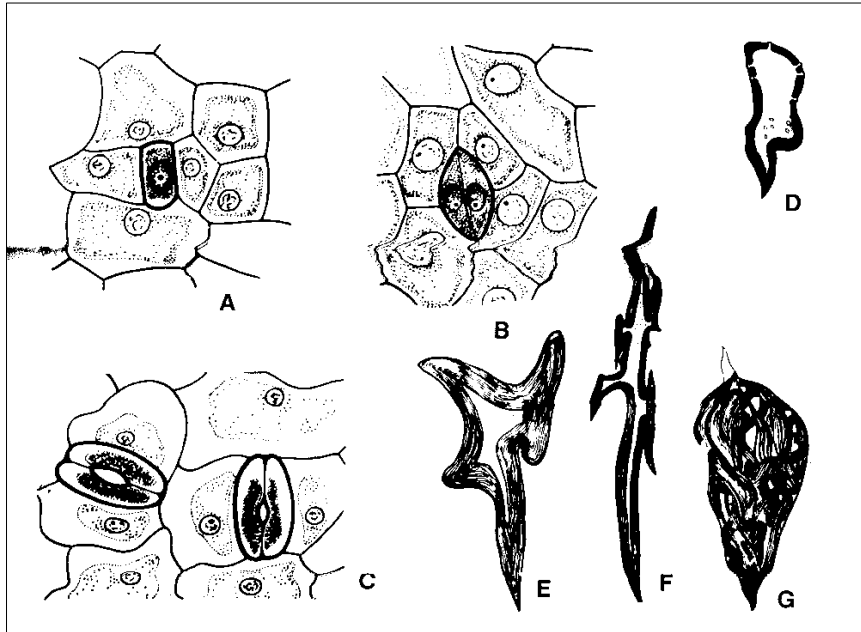


Fig. 7.7. *Gnetum ula*.

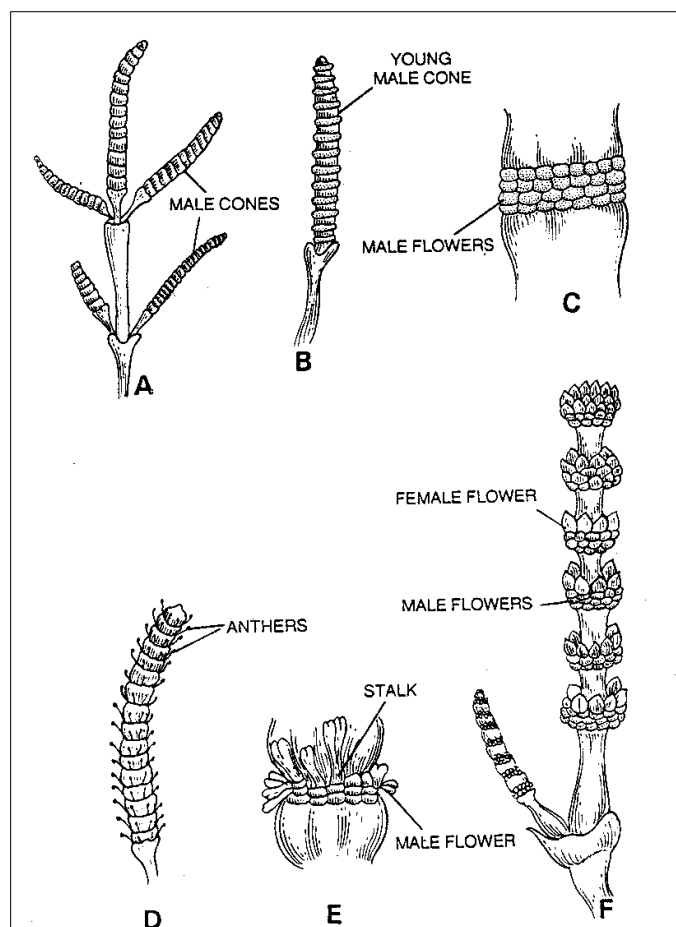
A-C. Epidermal peels from lower epidermis of leaf showing stomatal initial (A), division of stomatal initial to form guard cells (B) and mature stomata (C). D, E, G. Sclereids from outer envelope of an ovule. F. Same, from perianth of male flower (after Maheshwari & Vasil, 1961a).

7.4 REPRODUCTION

All the members of Gnetales are dioecious. The male and female strobili consist of a stout axis (inflorescence axis). This spike-like inflorescence axis contains nodes and internodes. At the node a pair of decussate bracts fuse together and form the cup-like structure known as cupule or collar. At the abaxial side of the collar, male and female flowers are arranged in whorls (Fig. 7.8).

Fig. 7.8 *Gnetum* sp. Structure and development of male strobili.

A, a twig with male cones; B, a young male cone; C, a portion of male cone showing male flowers; D, mature male cone; E, a portion of male cone with dehiscent flowers; F, enlarged cones with male flowers and ovular ring.



a) Male Strobilus

There are 3-6 male flowers develop basipetally above the collar. A single ring of abortive ovules also occur above the flowers. The male flowers in different rings are arranged alternatively (Fig. 7.8 C, E, F).

A male flower consists of a stalk (sporangiophore) bearing two unilocular anthers enclosed in a perianth. In *Ephedra* unilocular anthers are variable in number. In *Welwitschia* six sporangiophores are present. On maturity, the stalk elongates and pushes the anthers (through an opening in the perianth) beyond the collars of the cone (Fig. 7.9). Frequent presence of sclereids have been reported in the perianth (Fig. 7.7 D-G).

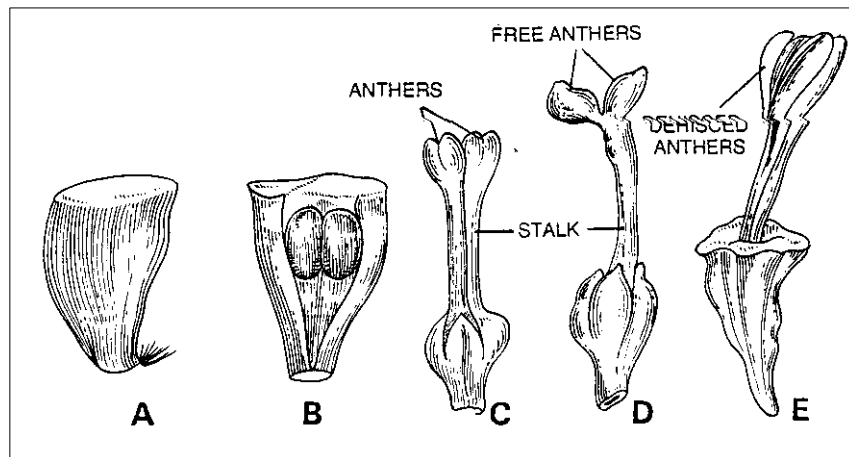


Fig. 7.9. *Gnetum* sp. Male flowers, A, B and D, male flowers of *G. ula* in different views; C and E, male flower of *G. gnemon*.

b) Microsporangium and Microsporogenesis

In a young anther, archesporial cells are differentiated in hypodermal position. They give rise multicelled archesporium (Fig. 7.10A, B, C) by undergoing repeated cell divisions. The outermost layer of archesporium divides periclinally and differentiates into the parietal cells and the inner layer cells into sporogenous tissue. The parietal cells again divide to produce an outer wall layer and the tapetum (Fig. 7.10 C). The narrow tangentially elongated wall layer cells become compressed during meiosis of the microspore mother cells. The tapetal cells rich in dense cytoplasm and binucleate nature, are increased in their size. Eventually, the wall layers and tapetum are absorbed for providing nourishment to the growing pollen grains.

The epidermis develops thickenings and it is persistent in the mature sporangium which dehisces by a median longitudinal slit. The epidermal cells living the slit are thin-walled.

The sporogenous cells undergo repeated divisions to form microspore mother cells that contain dense cytoplasm and prominent nuclei. Prior to meiosis, a special mucilaginous wall is

secreted between the protoplast and the mother cell. As a result of meiosis, microspore mother cells give rise tetrads. As the microspores enlarge, the callose wall is gradually absorbed, the original wall breaks down and finally young microspores are released. Gradually microspore wall differentiates into a thick, spiny exine and a thin intine (Fig. 7.10 D-G).

c) Male Gametophyte

The mature pollen grains are liberated at the 3-celled stage (Fig. 7.10 D-G). These three cells found in mature pollen grain are: (i) generative cell responsible for formation of two male gametes, (ii) tube cell which gives rise pollen tube, and (iii) prothallial cell. Microspore nucleus divides to give rise a small lens-shaped prothallial cell and a large antheridial initial. The prothallial cell rounds up and does not undergo any further division. The antheridial initial divides forming a antherial cell and tube cell. Since there is no stalk cell in *Gnetum*, the antheridial cell directly functions as generative cell. Tube cell gives rise tube in which generative nucleus enters and undergo division to give rise two male gametes in later stage. The prothallial cell eventually degenerates.

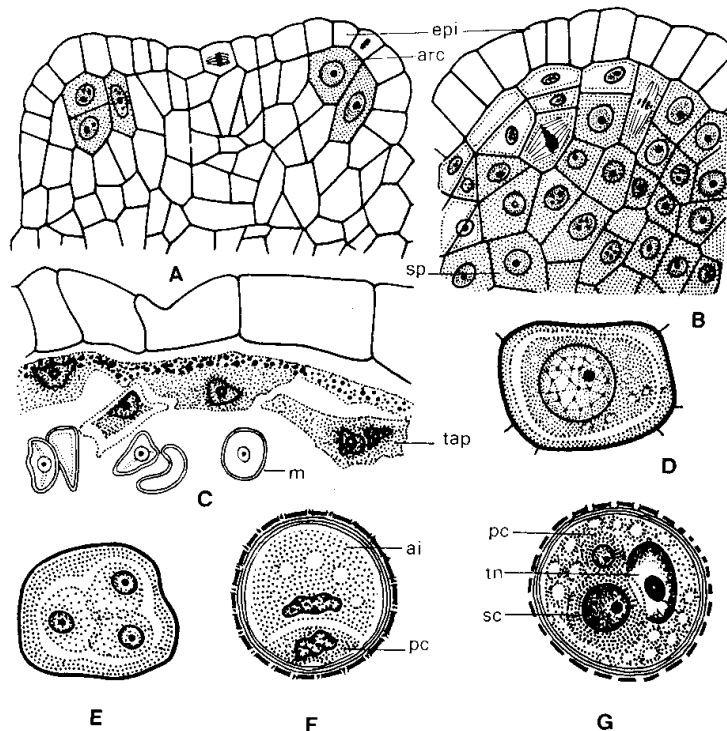


Fig. 7.10. *Gnetum gnemon* (ai, antheridial initial; arc, archesporial cell, epi, epidermis, m, microspore, pc, prothallial cell; sc, spermatogenous cell; sp, sporogenous tissue; tap, tapetum; tn, tube nucleus). Microsporogenesis and male gametophyte. A. LS very young male flower to show few hypodermal 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. Microspore mother cell. E. Microspore tetrad. F. Two-nucleate pollen grain. G. Mature, three-nucleate pollen grain at shedding stage.

d) Female Strobilus

Similar to male strobilus the female strobilus also possesses an axis which bears collars arranged one above the other. Just above the collar about 4-10 ovules are found, arranged in a ring (Fig. 7.11). The ovules are dimorphic. The smaller ones are eventually degenerated. a single large ovule is representing the female flower.

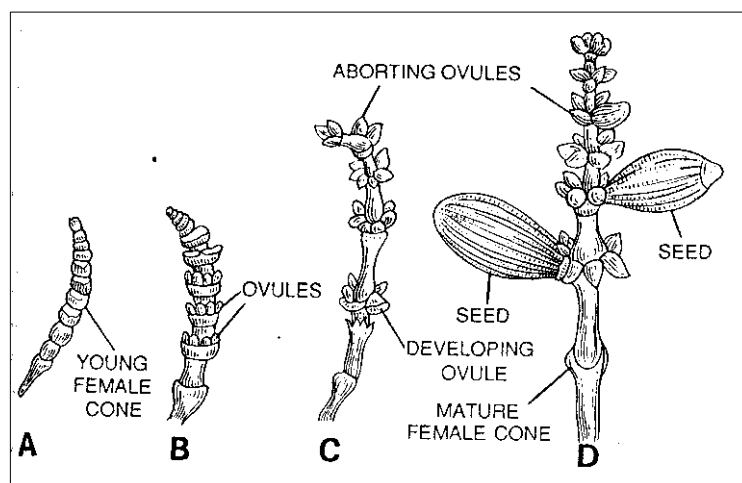
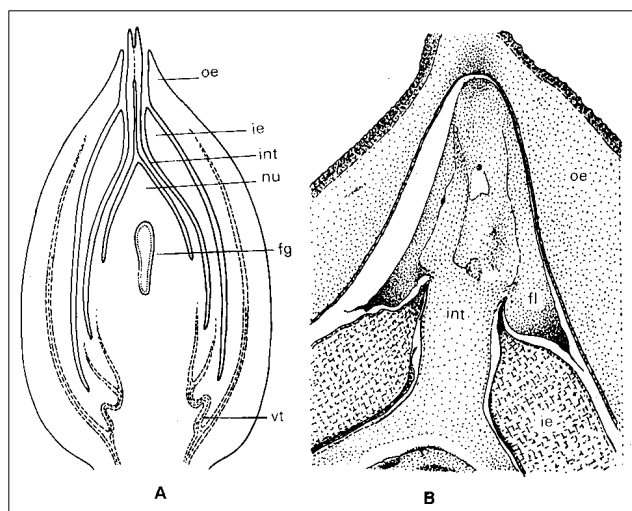


Fig.7.11 *Gnetum* sp. Structure and development of the female strobili and seeds.
A. young female cone; B, old female cone; C-D, still older female cones with seeds.

e) Megasporangium and Megaspороgenesis

The ovule is borne on a very short stalk. Ovule has got three envelopes; only the inner one is integument. The outer envelope differentiates first, often called perianth and it becomes succulent at maturity. It has got abundant Sclereids (Fig. 7.7 D-G). The inner envelope is next to arise and it is also called as inner integument (Fig. 7.12). The apical part is formed into tapering

Fig. 7.12. *Gnetum gnemon* (fg, female gametophyte; fl, flange; ie, inner envelope; int, integument; nu, nucellus; oe, outer envelope; vt, vascular trace). **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. **B.** Same, upper part only. The outer epidermal cells of the integument divide to produce a circular rim or flange around the tip of inner envelope (after Madhulata, 1960).



ring-shaped rim. The major part of the strong layer of the seed coat is formed by the fibrous elements and sclereids of this envelope. The inner integument is lastly formed and is fused with the nucellus in the lower part. It elongates considerably into micropylar tube (also called 'style') projecting beyond the apical cleft of the outer envelope. This exposed part of inner integument starts degenerating before or at the time of pollination.

Prior to meiosis in the megaspore mother cells, some nucellar cells below them divide to form a tissue, known as 'Pavement tissue' in which cells are arranged in radiating rows. The pavement tissue provides nourishment to the growing female gametophyte at the chalazal region. A pollen chamber develops at the apical portion of the nucellus.

In early stages of megasporogenesis, generally two to four archesporial cells are differentiated in the hypodermal region of the nucellus. These archesporial cells divide periclinally forming parietal cells towards outside and primary sporogenous cells towards inside. The parietal cells together with nucellar epidermis produce a massive nucellus. The primary sporogenous cells divide to form 8-16 sporogenous cells. These sporogenous cells are linearly arranged and function as megaspore mother cells (Fig. 7.13 A-E).

f) Female gametophyte

The megaspore mother cell gives rise to four megaspore nuclei by meiotic division. Since no walls are laid down after meiosis I and II (Fig. 7.13 F-J), a tetranucleate coenomegaspore is produced. All these four nuclei move towards the periphery of the coenomegaspore. Hence the development of the female gametophyte is tetrasporic. The only other gymnosperm showing tetrasporic development is *Welwitschia*.

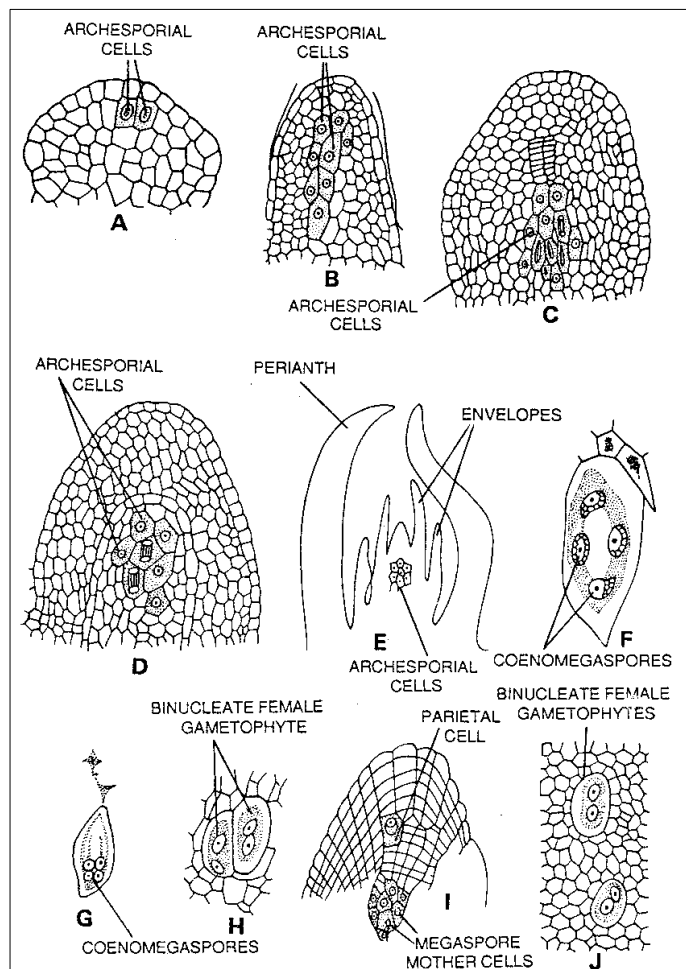


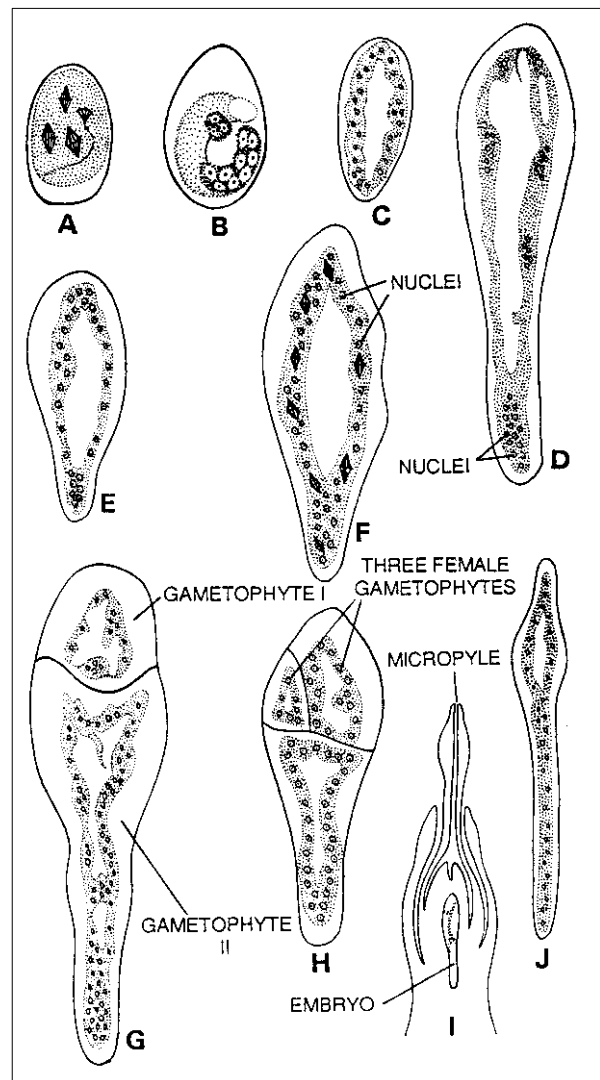
Fig. 7.13. *Gnetum* sp. A-J successive stages in the development of coenomegaspores, megaspore mother cells and female gametophyte.

As the female gametophyte develops, a large vacuole appears in the centre (Fig. 7.14 A-C) and nuclei in the periphery undergo repeated divisions. When the free-nuclear divisions continue, the gametophyte in the upper part widens and contains a vacuole, whereas in its lower

Fig. 7.14. *Gnetum* sp. Development of female gametophyte, A-F, free nuclear division stages; G-H, development of two and three female gametophytes respectively; I, V.S. of ovule; J, an abnormal female gametophyte. →

part accumulates cytoplasm. Later the gametophyte becomes elongated. In this process, female gametophyte acquires the shape of an inverted flask (Fig. 7.14 D-J).

An outstanding feature of the female gametophyte is the absence of archegonia, a feature *Gnetum* shares with *Welwitschia*. When the pollen tube makes contact with female gametophyte, one or more free nuclei in the dilated part become differentiated into eggs. These egg nuclei can be demarcated from other nuclei by their large size and dense staining. The gametophyte becomes cellular in its upper portion soon after one of the eggs is fertilized.



g) Pollination and Fertilization

The pollen grains germinate in the pollen chamber. The pollination takes place when the female gametophyte shows 250 nuclei in *G. ula* and 32 or 64 nuclei in *G. gnemon*. The pollination drop, rich in sugars, is exuded at the tip of the micropylar tube and collects pollen. Pollen grains are sucked into micropylar canal (Fig. 7.15) and lodged in the pollen chamber. At the time of pollen germination, the exine is cast off. The pollen tube is elongated and travelled almost half the length of the nucellus. The spermatogenous cell moves into the pollen tube and divides into two equal male gametes in *G. gnemon* and *G. ula* and come to lie near the tip of the pollen tube.

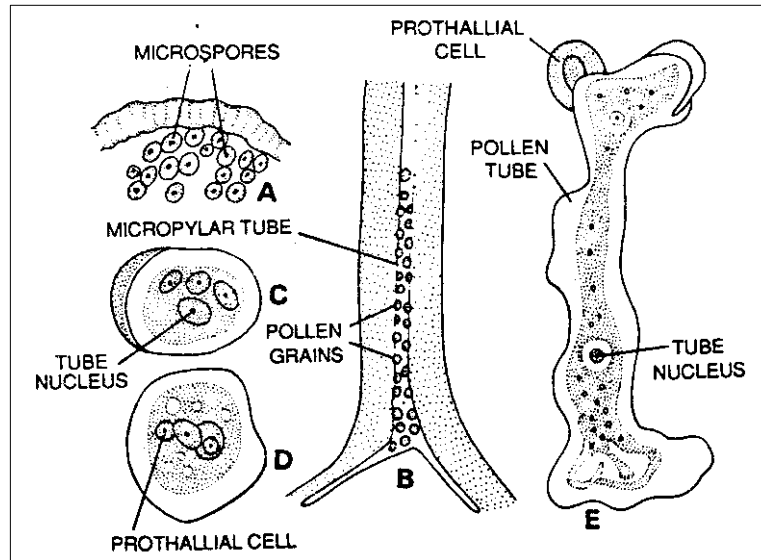
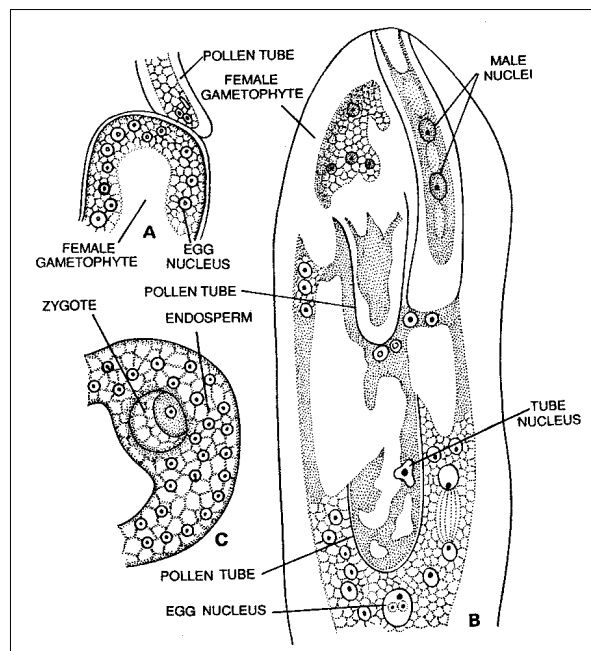


Fig. 7.15. *Gnetum* sp. Germination of pollen grains.

A, portion of anther with microspores; **B**, pollen grains germinating in micropylar canal; **C-D**, germinating pollen grains; **E**, germinated pollen grain showing pollen tube, prothallial cell and tube nucleus.

During fertilization, one of the male nucleus fuses with egg and forms the zygote. It is spherical in shape and densely cytoplasmic. The other male nucleus is non-functional and later degenerated (Fig. 7.16).

Fig. 7.16. *Gnetum* sp. Different stages of fertilization, **A**, male and female gametes in close contact; **B**, elongation of many pollen tubes, inside the female gametophyte; **C**, formation of zygote after fusion.



h) Endosperm formation

Although the cellularization begins before fertilization, a part of the gametophyte remains free nuclear. Wall formation results in multinucleate compartments (Fig. 7.17). The nuclei in each cell fuse to form a single polyploid nucleus. It is observed that polyploid cells are produced at the chalazal end of the gametophyte before fertilization, but only uninucleate cells are produced after

fertilization. Entire female gametophyte becomes cellular forming endosperm after fertilization. Cytologically this endosperm is haploid, quite different from the endosperm of the angiosperms in which endosperm is triploid.

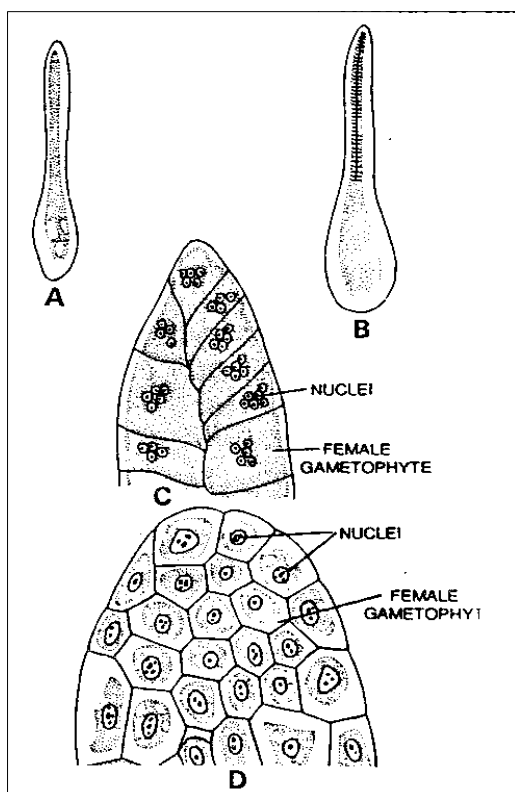


Fig.7.17. *Gnetum* sp. Development of endosperm. **A-B**, female gametophyte in longitudinal sections; **C**, a portion of multinucleate endosperm; **D**, uninucleate and multinucleate chambers.

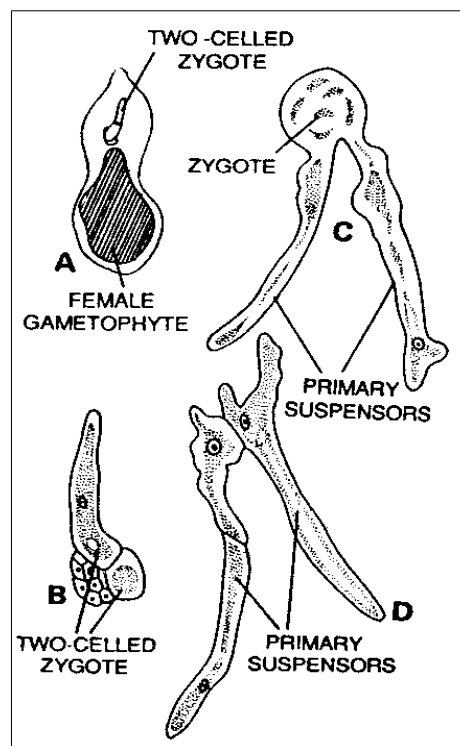


Fig. 7.18. *Gnetum* sp. Development of embryo (early stages). **A**, vertical section of female gametophyte; **B**, two celled zygote; **C**, a zygote with two primary suspensors; **D**, two zygotes developing together.

i) Embryogeny

Various researchers reported the both free-nuclear and nuclear divisions followed by a wall formation in the zygote. Several zygotes are usually formed in the female gametophyte. According to Madhulatha (1960) in *G. gnemon*, the zygote produces one or two protuberances which grow down towards the endosperm tissue. This protuberance further develops into a tubular structure and becomes septate to form several uninucleate cells. Later this tube becomes branched and develops the suspensor or proembryonal tubes which grow towards the endosperm tissue (Fig. 7.18).

According to Vasil (1959), the primary suspensor tube cuts a cell known as 'Peculiar cell' (Fig. 7.19). Generally the seeds are shed at this stage. Further development of embryo takes place in the soil after being detached from the plant. Now peculiar cell divides to form 2 cells. These two cells divide to form eight-celled embryo (Fig. 7.19 E, F). Later irregular divisions takes place and give rise a mass of cells. Some of the cells found towards the primary suspensor tubes become elongated and develop into secondary suspensor. The secondary suspensor system is very prominent and it pushes the developing embryo deep into the endosperm. After the formation of secondary suspensor system, the primary suspensor system becomes ceased to function.

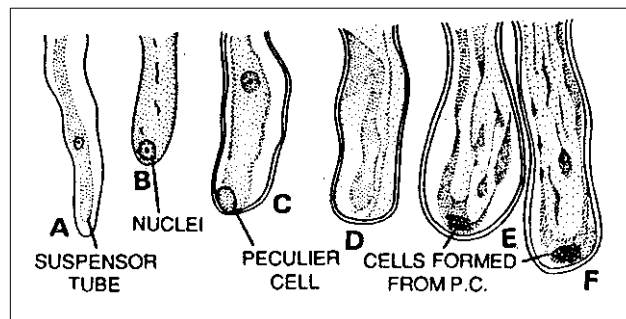


Fig. 7.19. *Gnetum* sp. A-F, formation of peculiar cell and its further division.

The growing embryo is conical in shape with shoot apex at the tip of the cone. On either side of it, two cotyledons are formed. The root tip is differentiated at the opposite end. After the differentiation of shoot and root apices, there is a 'feeder' developed in between the two apices (Fig. 7.20 C, D). It shows differentiation into epidermis, cortex, vascular bundles and pith. The feeder is very prominent in mature embryo and usually longer than the hypocotyl. Feeder is absent in *Ephedra*. Polyembryony is common feature in *Gnetum* (Fig. 7.20E). Polyembryony occurs due to the cleavage of the embryonal mass and budding of the primary and secondary suspensors. However, only one embryo survives and remaining ones degenerate.

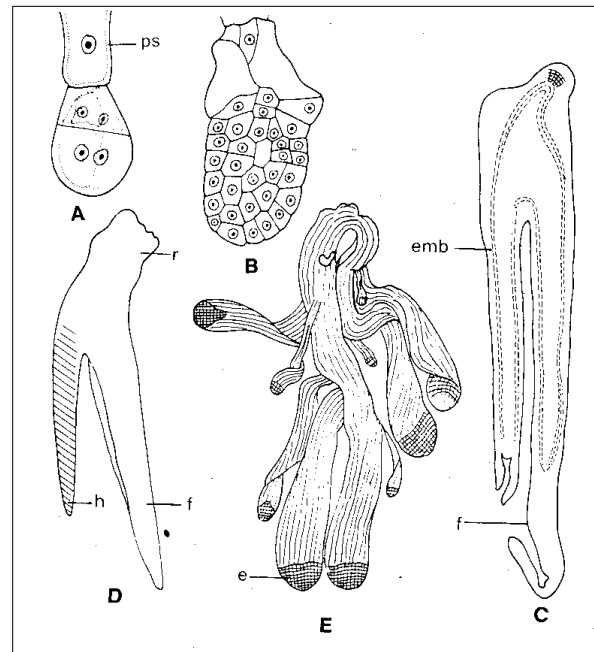
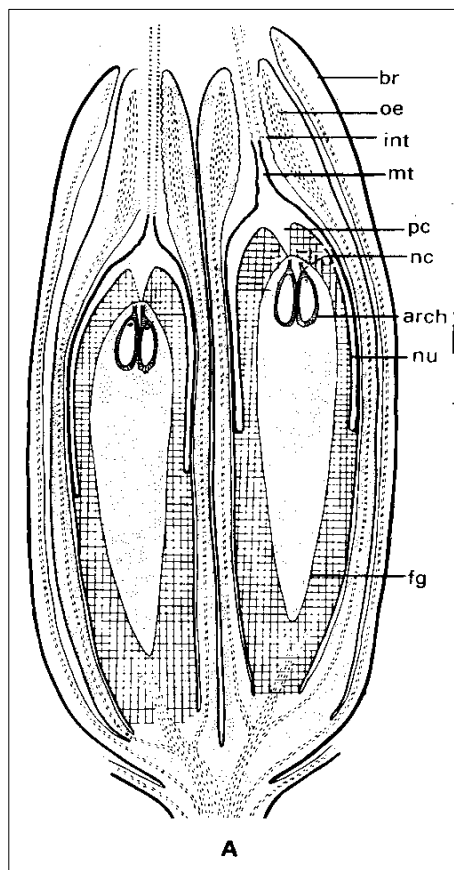


Fig. 7.20. *Gnetum gnemon* (e, embryonal cells; emb, embryo; f, feeder; h, hypocotyl; ps, primary suspensor tube; r, root). A,B. Formation of cellular mass at the tip of primary suspensor tube; the latter has also become multicellular. C. LS mature embryo showing a well developed feeder which is much longer than the embryonal axis. D. Embryo just prior to germination. E. Polyembryony; note the development of additional embryos from primary suspensor tube (after Sanwal, 1962).

j) Seed and Seed germination



The mature seed is oval or elongated and green to red in colour. The nucellus represents a thin strip at the apex; the endosperm is massive, surrounded by three-layered seed coat. The outermost envelope (sarcotesta) is green and succulent and it is free from base to apex. The middle envelope (sclerotesta) is hard and protective. The innermost integument (endotesta) is fused with the nucellus. It projects out beyond the nucellus. The endosperm lies with the innermost integument. All the three envelopes of seed coat are supplied with vasculature. However, seed has got two envelopes in *Ephedra* (Fig. 7.21) and *Welwitschia*.

Fig. 7.21 *Ephedra* sp. LS female cone showing two well developed ovules each showing two envelopes, a pollen chamber, long tapering female gametophyte bearing two archegonia with long, prominent necks. [after Narang, 1956] (*arch*, archegonium, *br*, bract; *fg*, female gametophyte; *hs*, hypostase; *int*, integument; *mt*, micropylar tube; *nc*, neck cells; *nu*, nucellus; *oe*, outer envelope; *pc*, pollen chamber).

The seed germination in *Gnetales* is epigeal. Initially root along with its cap comes out and gradually develops into a tap root system. Later hypocotyl elongates and pushes the two cotyledons out of the seed. The stem tip becomes enlarged and develop a pair of plumular leaves (Fig. 7.22). Feeder remains inside the seed.

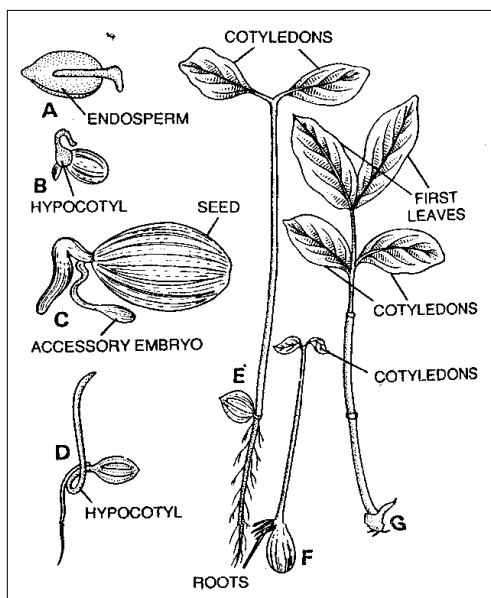


Fig. 7.22. *Gnetum* sp. A-G, successive stages in seed germination

7.5 COMPARISON OF CHARACTERS OF *GNETUM*, *EPHEDRA* AND *WELWITSCHIA*

A comparison of various characteristics of three genera (*Gnetum*, *Ephedra* and *Welwitschia*) is given in Table 7.1.

Table 7.1. Comparative account on *Gnetum*, *Ephedra* and *Welwitschia*

	<i>Gnetum</i>	<i>Ephedra</i>	<i>Welwitschia</i>
1	It grows in humid tropical and sub-tropical regions, especially West Africa to the Amazon region, Western ghats in India.	Usually grown in dry regions, distributed in new and old worlds; in India, Kashmir, North-West Himalayas, Punjab and Rajasthan	It confined to the desert region of South-West Africa
2	Angiosperm-like appearance	A xerophyte, bushy in appearance; stem shows ridges and furrows with minute scale leaves at the nodes	It resembles a giant turnip or an enormous woody carrot, or giant octopus
3	Stem shows abnormal secondary growth due to formation of accessory cambia, resulted into eccentric rings of vascular tissues	Stem shows normal secondary growth and annual rings in the secondary wood	Presence of accessory cambia resulted into several incomplete rings of secondary bundles
4	Photosynthesis carried out by leaves	Photosynthesis carried out by stem	Photosynthesis by leaves
5	Vessels are of angiosperm type with large simple perforation plates	Vessels with perforation plates (end wall) possessing both bordered pits and perforations	Vessels with simple perforation plate, rarely with foraminate plates
6	Leaves with reticulate venation (dicot like)	Leaves with parallel venation (monocot like)	Leaves with numerous longitudinal veins connected with smaller, obliquely oriented veins
7	Leaves large and photosynthetic	Leaves small and scale like; mesoparacytic (Rubiaceous) type stomata	Large strap-shaped leaves. Mesoparacytic (Rubiaceous) type stomata
8	Dorsi-ventral leaves with palisade and spongy parenchyma	Isobilateral leaves without photosynthetic tissue and vascular tissue	Isobilateral leaves with massive hypodermal fibre bundles
9	Dioecious, male and female strobili present	Normally dioecious but monoecious and even hermaphrodite flowers present	Dioecious
10	Each male flower bears two unilocular microsporangia	Each male flower bears 1-8 microsporangia.	Each male flower is bisporangiate

	<i>Gnetum</i>	<i>Ephedra</i>	<i>Welwitschia</i>
11	Microspores liberated at 3-nucleate stage (a prothallial cell, a generative cell and tube nucleus)	Microspores liberated at 5-celled stage (1 st prothallial cell, 2 nd prothallial, nucleus, a stalk nucleus, a body nucleus and a tube nucleus).	Microspores shed at 3-celled stage (ephimeral prothallial cell, a generative cell and a tube cell).
12	Female flower represented by a single ovule; it remains surrounded by three envelopes	Ovule surrounded by two envelopes	Ovule surrounded by two envelopes
13	Tetrasporic development of female gametophyte	Monosporic development of female gametophyte	Tetrasporic development of female gametophyte
14	Archegonia absent in female gametophyte	Archegonium with longest neck and massive; 2 or 3 archegonia per ovule	Archegonia absent in female gametophyte
15	After fertilization, female gametophyte remains free-nuclear in the upper part and becomes cellular in the lower part; pavement tissue occurs at the base of female gametophyte	Female gametophyte becomes completely cellular before the fertilization; pavement tissue absent.	Female gametophyte becomes cellular before fertilization; pavement tissue absent
16	Only one male gamete is functional and no double fertilization	In certain cases, the second male gamete fuses with the ventral nucleus causing double fertilization	Only one male gamete is functional and no double fertilization
17	Zygote nucleus undergoes divisions followed by wall formation	Zygote undergoes free-nuclear divisions upto 8-celled stage of embryo	Zygote undergoes divisions followed by wall formation
18	No proembryos formed; the zygote directly gives rise to several primary suspensors at the top of which develops the embryonal mass.	Zygote divides to form about 8 proembryos, they later develop into embryos; each of the embryo possesses its own primary and secondary suspensor	Proembryo later develops into embryo; primary and secondary suspensors are formed.
19	Embryo develops feeder which is nutritive in function and persistent for a long time	Feeder absent	Feeder present
20	Seed germination is delayed after being shed from the plant	No rest period during seed germination	Seed germinates and gives rise seedling which has been variously described as a persistent seedling, a seedling arrested in development, and adult seedling.

7.6 INTERRELATIONSHIPS (AFFINITIES)

A preliminary survey of 58 characters revealed that Gnetales share more than 60% of the characters with angiosperms and merely about 30% with gymnosperms.

The ovule of Gnetales has multiple nucellar envelopes, unlike other gymnosperms (possess a single integument only). These are interpreted as integumentary structures homologous with the outer integument of an angiosperm. Entomophily in Gnetales is rather an evolutionary progress from the primitive gymnospermous mode of anemophily. It is more economical and probably more effective and reliable form of pollination.

Eames (1952) opined that the *Ephedra* is nearer to *Cordiales* and conifers than to *Welwitschia* and *Gnetum*.

Ephedra also differs from *Gnetum* and *Welwitschia* in some embryological characters, such as: (1) presence of stalk cell in male gametophyte, (2) monosporic female gametophyte, (3) presence of alveoli during wall formation, (4) well-developed archegonia, (5) specialized type of proembryogeny, (6) absence of feeder. According to Sporne (1965) *Ephedra* occupies a position isolated from the other two taxa, and may have had a completely different origin.

Gnetum and *Welwitschia* are more closely related to one another though they are widely differed from each other in form and habitat. Both are shared some important features such as their general anatomy, the form of male and female strobili, their gametophyte and development of embryo. These two genera cannot be separated from *Ephedra* because all the three have many common features such as presence of vessels, compound male and female strobili, and the presence of a long micropyle.

a) With Gymnosperms

All these three genera, especially *Ephedra* have got relationships with other gymnosperms. These are as follow:

- (1) Presence of prothallial cell in the male gametophyte.
- (2) Presence of naked ovule.
- (3) Occurrence of free-nuclear divisions in the female gametophyte.
- (4) Presence of archegonia in *Ephedra* and archegonial initial in *Welwitschia*.
- (5) Like *Bennettites*, the fibrous layer at the base of the ovule forms a cup-like structure in *Gnetum africanum*; also occurrence of fibrous and palisade layers in the middle envelope is similar to *Bennettites*.

b) With Angiosperms

According to Arber and Parkin (1907), Gnetales are closely related to angiosperms; both groups derived from common stock, viz. Hemiangiosperms. The characteristics similar to angiosperms are as follow:

- (1) Presence of broad leaf with reticulate venation is strikingly angiospermous.
- (2) Mesoparacytic (Rubiaceous) type of stomatal development.
- (3) All the six main types of sclerieds which are known in angiosperms have been reported in *Gnetum*.
- (4) Presence of vessels; there is a striking similarities between perforation plates of *Gnetum* and angiosperms such as *Paeonia*, *Cydonia* and *Vitis*.
- (5) Though there is absence of companion cells in Gnetales, but the sieve cells are associated with ontogenetically unrelated parenchyma cells (in angiosperms both sieve tube and companion cells are derived from the same cambial initial). Sieve cells associated with ontogenetically unrelated parenchyma cells were also reported in the primitive angiosperm such as *Austrobaileya scandens*. Thus, the phloem of Gnetales also closely approaches the angiospermous taxa.
- (6) The tunica-carpus organization of shoot apex in *Gnetum* is similar to that of angiosperms.
- (7) Small bracts occurred at the base of stamens or ovule of *Gnetum* are considered as perianth of angiospermic flower.
- (8) Presence of stamens with a filament and 1 or 2 anthers.
- (9) Presence of archegonia in *Ephedra* but there is no separation wall between egg and venter canal cell. In *Welwitschia* there is an only one archegonial initial and in *Gnetum* archegonia are completely absent. This character seems to be approaching to angiosperms.
- (10) Inner integument of the Gnetalean ovule can be compared to the ovary that produces the long style in angiosperms. The micropylar tube in Gnetales resembles the style of angiosperms. However, micropylar tube lacks vascular supply in Gnetales.
- (11) Development of female gametophyte (embryo sac) is tetrasporic.
- (12) Occurrence of free nuclear divisions in embryo sac is similar to that of angiosperms.
- (13) Endosperm completes its development after fertilization.

- (14) Absence of free nuclear divisions in Gnetales shows its close approachness towards angiosperms.
- (15) Embryo with two cotyledons.

All these above features show that the group Gnetales is approaching towards angiosperms. But this group is not ancestor of angiosperms. Both Gnetales and angiosperms would have originated from the common ancestor. The Gnetales possessing the angiosperm characters, can be considered as a phylogenetically advanced among the gymnosperms.

7.7 SUMMARY

Gnetales, an important order of Gnetopsida is considered as fascinating group of gymnosperms. The genera of Gnetales approach more nearly to the angiosperms than do any other gymnosperms. The note-worthy features of this order are: 1) presence of vessels in the secondary wood; 2) the arrangement of the flowers in compound strobili; 3) the presence of perianth in male flowers and ovules; 4) the great length of micropyle. The detailed account on the three genera (*Gnetum*, *Welwitschia* and *Ephedra*) with regard to their comparative morphology, anatomy, reproduction and interrelationships, is presented in this lesson.

7.8 KEY TERMS

- i) **Double fertilization:** One of the two male gametes in angiosperm embryo sac merges with egg nucleus to form zygote. The other one undergoes fusion with polar nucleus to form a triploid primary endosperm nucleus is called double fertilization.
- ii) **Epigeal germination:** Seed germinating on the surface of the ground.
- iii) **Liane:** A woody climbing plant.
- iv) **Perforation plate:** The remains of the end walls between two adjacent vessel elements that form an opening.
- v) **Perianth:** The envelop formed in a flower by either calyx or corolla.
- vi) **Polyploidy:** A condition of an individual which possesses more than two sets of chromosomes in its nuclei.
- vii) **Syndetocheilic stomata:** Stomata in which guard cells and subsidiary cells arise from the same initial.

- viii) **Tunica-carpus:** The differentiation of apical meristem into peripheral layer called tunica and inner mass of cells called corpus.
- ix) **Xerophyte:** A plant adapted to physiological drought and desert environment.

7.7 MODEL QUESTIONS

Essay Questions:

1. Write a detailed account on the order Gnetales and its resemblances with angiosperms.
2. Compare the morphological anatomical and reproductive features of the *Gnetum*, *Ephedra* and *Welwitschia*.
3. Describe the male and female gametophyte development in Gnetales.
4. Write an essay on the embryogeny of Gnetales. Comment on its evolutionary significance.

Write short answer to be the following questions:

1. Secondary wood in *Gnetum*.
2. Male inflorescence of *Ephedra*.
3. Ovule in Gnetales

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Prof. Z. VISHNUVARDHAN

ALGAE

LESSON-IV

XANTHOPHYTA
(Yellow-Green Algae)**Objectives**

1. Introduction
2. Thallus Structure
3. Reproduction
 - (i).Vegetative Reproduction
 - (ii).Asexual Reproduction
 - (iii).Sexual Reproduction
4. Life Cycle
5. Phylogeny
6. Summary

1 Introduction

The phylum **Xanthophyta** divided into two classes, viz., **Xanthophyceae** (Tribophyceae) and **Eustigmatophyceae**. Commonly known as yellow-green algae, the members of Xanthophyceae e.g., *Botrydium* and *Vaucheria* are characterized by the following features: (1) Photosynthetic pigments are chlorophyll **a**, chlorophyll **e**, β -Carotene and xanthophylls (antheroxanthin); (2) reserve food materials are lipid, oil and leucosin (chrysolaminarin); (3) the cell walls when present are generally composed of two equal or overlapping halves, e.g., *Tribonema* and made up of pectin substances with smaller amount of cellulose, in some cases, the cell walls may be silicified; (4) the motile cells possess two unequal flagella on their anterior ends; (5) reproduction takes place through vegetative, asexual and sexual methods.

The class **Eustigmatophyceae** includes unicellular, coccoid forms, which were previously classified in the Xanthophyceae. These forms were carved from the Xanthophyceae because of unusual and unique organization of their motile cells, e.g., *Ellipsoidion*, *Polyedriella*, *Vaucheria*.

The members of Xanthophyta are widely distributed in aquatic and terrestrial habitats. Most of them are fresh water forms, e.g., *Vaucheria*. Terrestrial forms, such as *Botrydium*, grow on mud or on tree trunks and on damp walls.

2 Thallus Structure

Thallus is a cylindrical tube, sparingly branched and coenocytic, e.g., *Vaucheria* (Fig.4.1). The thallus of *Botrydium* (Fig. 4.2) which is considered as primitive genus of the siphonaceous Xanthophyta, is a globose, cylindrical vesicle, having rhizoids anchoring the plant body to the substratum.

The cell wall is thin and is composed of cellulose and outer pectin. In *Vaucheria*, a central vacuole runs through out the thallus (Fig. 4.1B). There is a continuous layer of protoplast at the peripheral region containing many discoid chromatophores devoid of pyrenoids.

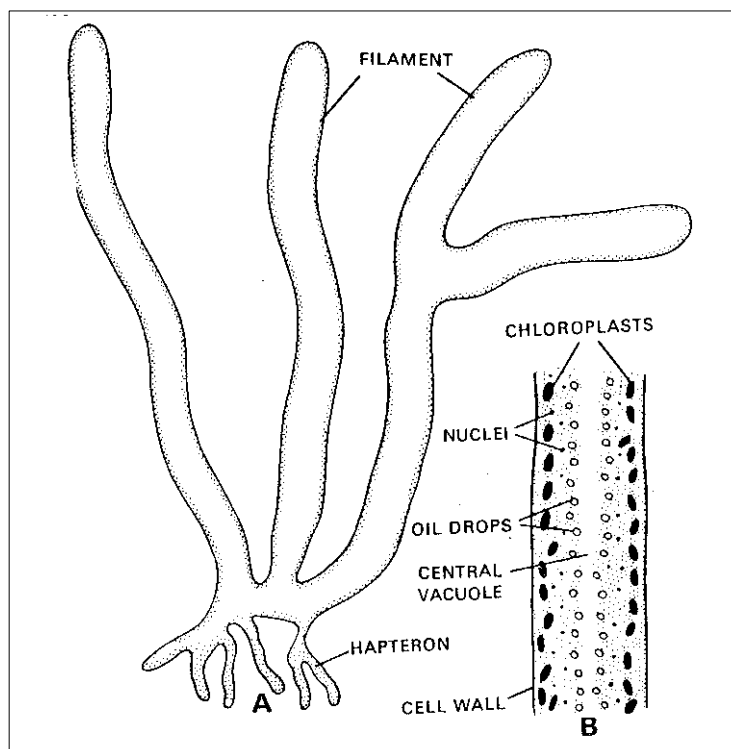


Fig. 4.1 *Vaucheria* sp. Vegetative structure; A, a complete thallus; B, a part of thallus (enlarged).

Numerous minute nuclei lie internal to the chromatophores which exhibit phototactic response, i.e., back and forth movement in response to light. When light intensity is strong, they show lateral movement away from the light source. In other words, the phototactic response is regulated in such a way that it facilitates maximum absorption of photosynthetic light by chromatophores, simultaneously protecting them against excessive photodamage.

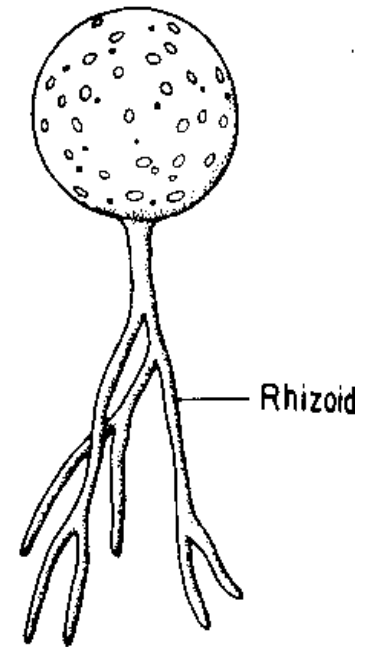


Fig.4.2 *Botrydium granulatum*, habit

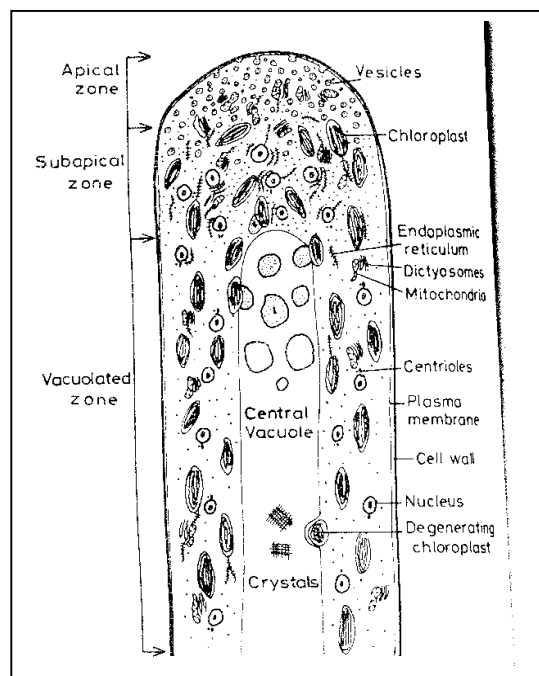


Fig. 4.3 *Vaucheria dillwynii*, showing enlarged part of filament end (adopted from Kumar, 1999).

The thallus grows in length by simple elongation of the terminal portion of the branches.

During mitosis nuclear envelope remains intact and surrounds the spindle, there are no gaps in nuclear envelope of *Vaucheria*. Both *Vaucheria* and certain phycomycetous fungi (*Saprolegnia*) have a closed, centric spindle lacking polar fenestrae, with the centriole situated outside the nuclear envelope at the poles. Also in both cases, each golgi body is characteristically appressed to a mitochondrion with a part of endoplasmic reticulum being sandwiched between the two organelles.

3 Reproduction

Reproduction takes place by vegetative, asexual and sexual methods.

(i) Vegetative Reproduction

It is very rare and may be brought about by the budding of mature vesicles in *Botrydium*.

(ii) Asexual Reproduction

Asexual reproduction takes place by means of zoospores, aplanospores and hydnospores. A variety of environmental factors affect the zoospore formation. High humidity, run-off water, low light intensity or darkness and dilution of growth medium induce the sporulation. It has been further observed that low light intensity enhances sporulation in *Vaucheria*.

A. Compound zoospore or synzoospore – In *Vaucheria*, during zoospore formation apices of branches become delimited from the rest of the thallus by a septum, and each of them develop into a club-shaped sporangium. During this stage, nuclei and chromatophores exchange their position, so that the nuclei which were originally placed internal to the chromatophores, now come to lie external to the chromatophores. Shrinkage of protoplast and a pair of equal flagella (acronematic) develop opposite to each nucleus, are resulted into formation of multiflagellate zoospore from the single zoosporangium (Fig. 4.4A-C, D). This multiflagellate zoospore is regarded as compound zoospore or synzoospore (Fig. 4.5A, B).

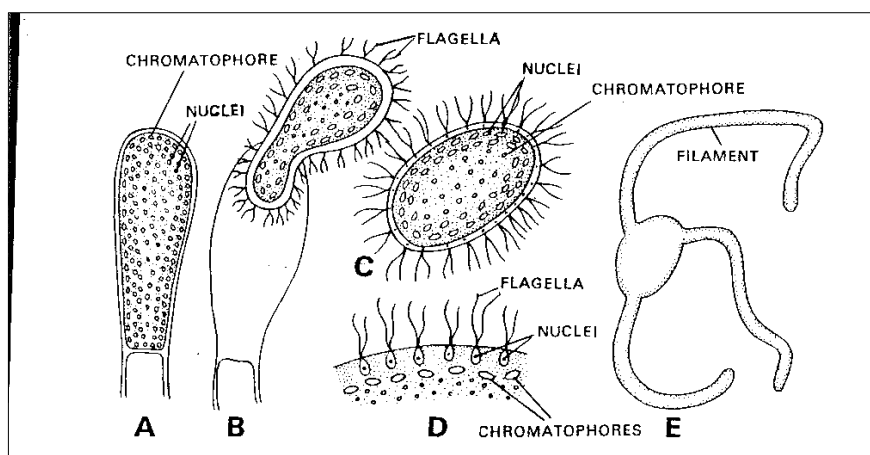


Fig. 4.4. *Vaucheria* sp. Asexual reproduction by zoospore. A, zoosporangium; B, liberation of zoospore from zoosporangium; C, compound zoospore; D, a part of compound zoospore; E, germinating zoospore (adopted from Pandey, 2004).

The terminal portion of zoosporangium softens and small pore develops at its apex. Through this pore synzoospore is liberated, and swims about 20 minutes and then to settle down to some substratum. It withdraws its flagella and secretes a wall around it. Later it germinates and gives rise to adult thallus (Fig. 4.4E).

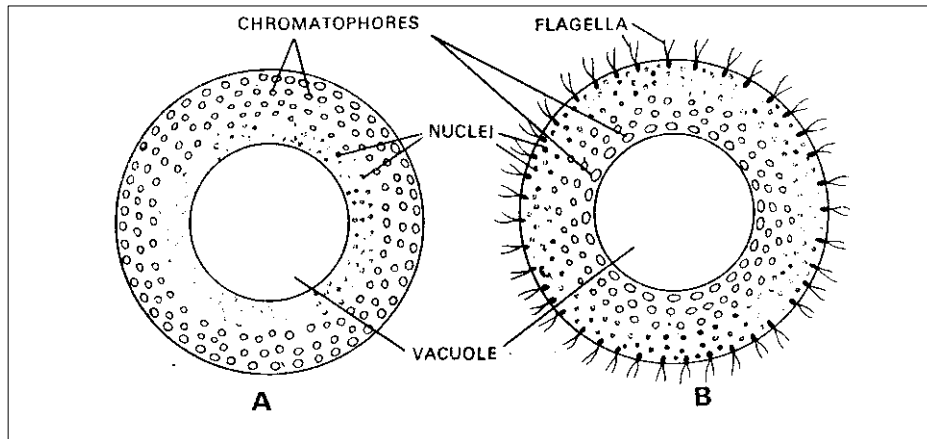


Fig. 4.5 *Vaucheria*. A. transverse section of filament; B, transverse section of synzoospore.

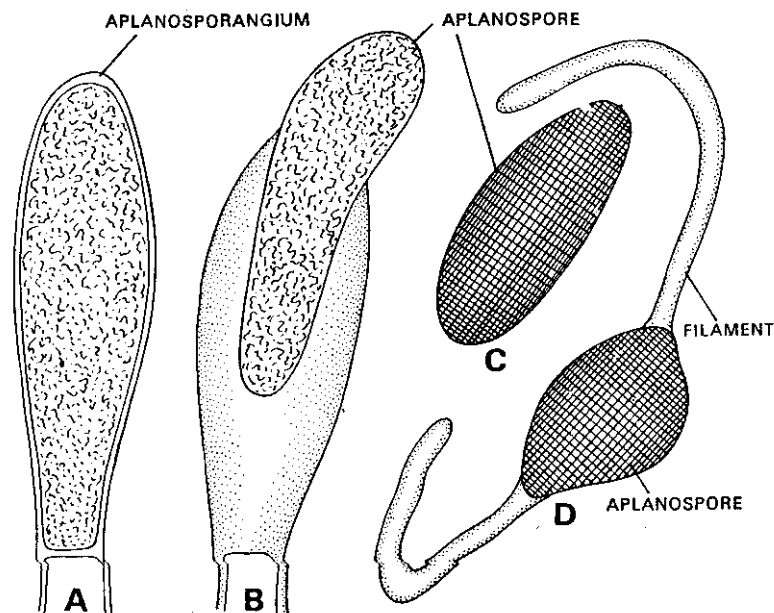


Fig. 4.6. *Vaucheria* sp. Asexual reproduction. A-B, formation of aplanospore in aplanosporangium; C, an aplanospore; D, germination of aplanospore (adopted from Pandey, 2004).

B. Aplanospores – Terrestrial forms develop aplanospore during dry conditions. Aplanospores are non-motile and liberated by the irregular rupture of the aplanosporangium (Fig. 4.7A, B). Aplanospore germinates during favourable conditions and gives rise to new thallus (Fig. 4.6 A-D).

C. Hypnospores or Cysts - In terrestrial species, such as *Vaucheria geminata* and *V. hamata*, segmentation takes place by gelatinous transverse walls in the tubular branches forming many small compartments. The segmented thallus looks like an alga '*Gongrosira*' and this stage is known as *Gongrosira* stage (Fig. 4.7C). A thick wall is developed around the protoplast of each segment and they are called hypnospores or cysts (Fig. 4.7D). These cysts either grow directly into new thallus or may give rise to small amoeba like masses. These germinate under favourable conditions and subsequently give rise to new thalli.

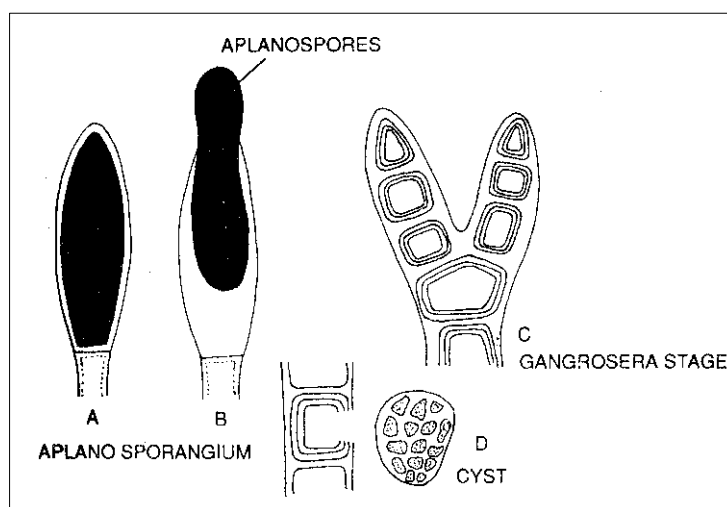


Fig. 4.7 *Vaucheria*. A-D. Aplanospore and cyst development

(iii) Sexual Reproduction

Sexual reproduction is oogamous type in *Vaucheria*. They may be either homothallic or heterothallic and bear well differentiated antheridia and oogonia. Sex organs may be sessile or stalked. Both antheridia and oogonia originate as protuberances which gradually grow in size and accumulate a large number of nuclei and chromatophores.

The antheridia - Most species of *Vaucheria* are protandrous, i.e., antheridium develops first and oogonium afterwards. The antheridia are tubular with their apices slightly curved or coiled (Fig. 4.8A, B). At maturity, the apical, curved portion of antheridium becomes separated from its subtending branch by a transverse septum (Fig. 4.8C). Its coenocytic

protoplast divides into a large number of uninucleate, biflagellate (acro and pantonematic) sperms which usually liberate from the antheridium during the early morning hours.

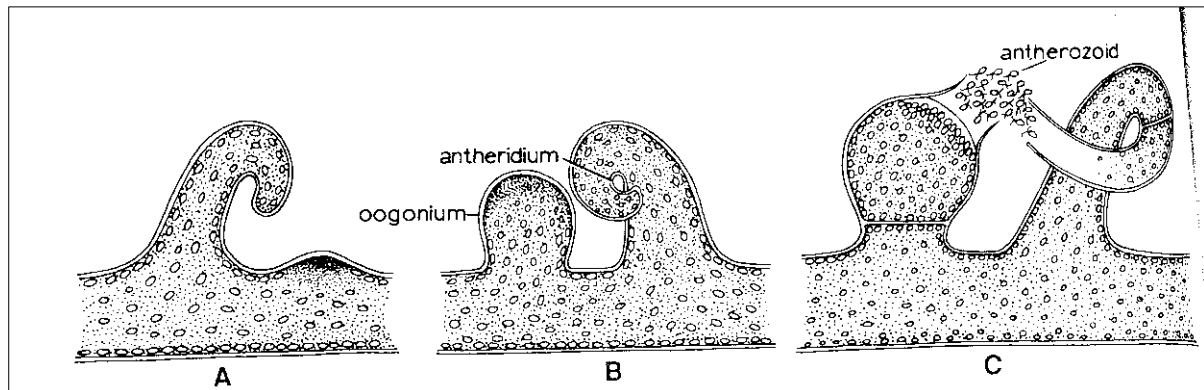


Fig. 4.8. *Voucheria*. A, B, stages in formation of sex organs (after Smith, 1955); C, release of antherozoids.

The Oogonia – These are commonly spherical or subspherical structures. At maturity, all the nuclei except one migrate from the oogonium back to the main filament. Soon a transverse septum is laid down between the oogonium and the filament (Fig. 4.8C). Subsequently, it develops a receptive region with an opening through which a sperm enters the oogonium.

In homothallic species, e.g., *V. geminata*, both kinds of sex organs develop in close proximity but generally do not mature simultaneously, thus self-fertilization is prevented. The zygote with thick wall around it is detached from the parent plant. It is believed that zygotic germination in *Vaucheria* is meiotic and directly gives rise to adult thallus.

4. Life Cycle

In all the members of Xanthophyceae, life cycle is Haplontic, and diploid phase is represented by unicellular zygote only (Fig. 4.9 and 4.10).

5. Phylogeny

The formation of flagellated structures during the life cycle of most of the Xanthophyceae and also the occurrence of predominantly flagellated unicells in the primitive members of the class, suggests a flagellated ancestry for the Xanthophyceae.

The Xanthophyceae resembles the Chrysophyceae in their flagellation, amoeboid habit and food reserves, and the Bacillariophyceae in food reserves and cell wall composition. Bold

(1967) considered the Xanthophyceae, Chrysophyceae and Bacillariophyceae to be closely related and accordingly included them in a single phylum Chrysophycophyta.

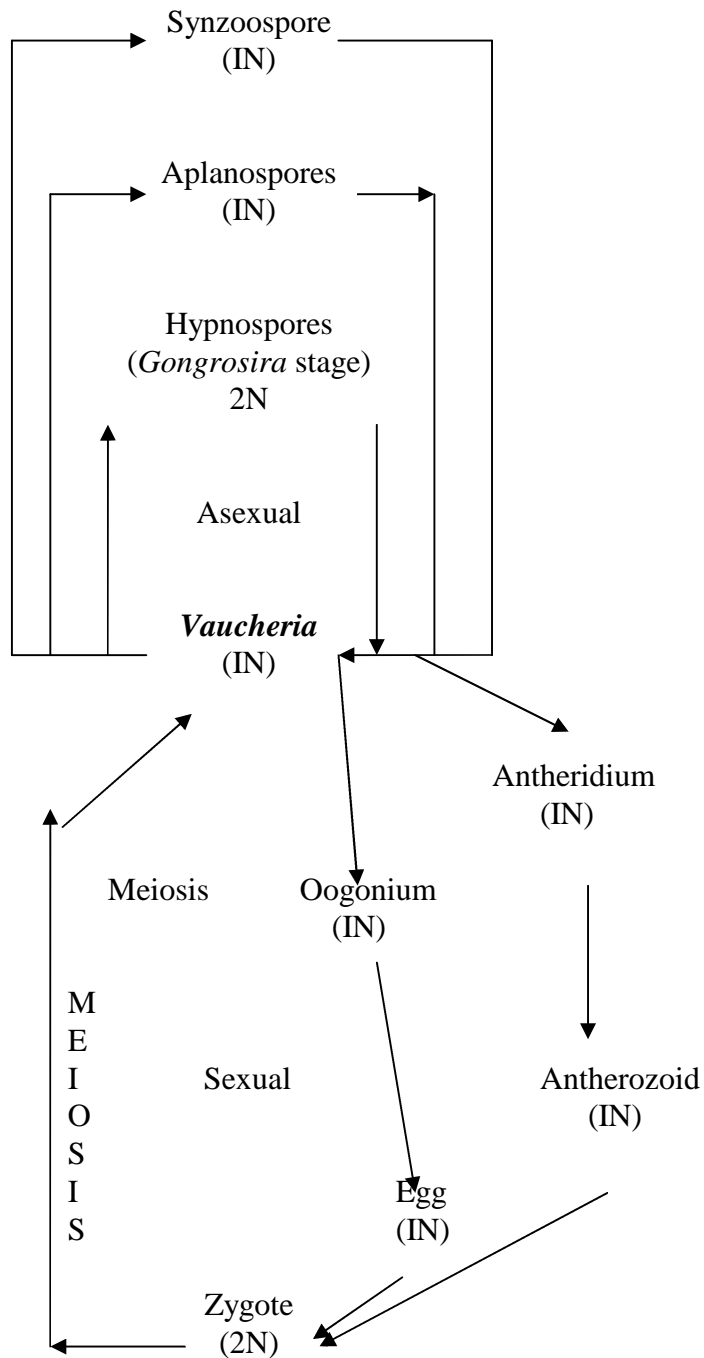


Fig. 4.9 *Vaucheria* – Graphic representation of life cycle

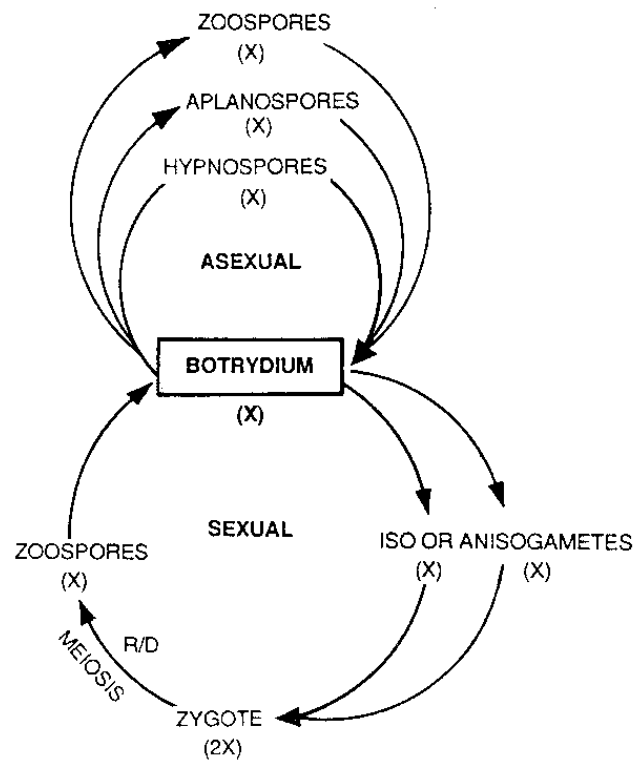


Fig. 4.10. *Botrydium* – Graphic representation of life cycle

4.6 Summary

The phylum Xanthophyta divided into two classes, viz., Xanthophyceae (Tribophyceae) and Eustigmatophyceae; these are all commonly known as yellow-green algae. The class Eustigmatophyceae includes unicellular, coccoid forms; whereas the thallus of Xanthophyceae is coenocytic, e.g., *Vaucheria* and *Botrydium*.

In *Vaucheria*, the cell wall is composed of cellulose and outer pectin, and a central vacuole runs through out the thallus. There is a peripheral protoplasts containing many discoid chromatophores devoid of pyrenoids. Numerous minute nuclei lie internal to the chromatophores which exhibit phototactic response. The thallus grows in length by simple elongation of the terminal portion of the branches.

Reproduction takes place by vegetative, asexual and sexual methods. Formation of multiflagellate compound zoospore (synzoospore) is one of the means of asexual reproduction in

Vaucheria. Sexual reproduction is oogamous type in *Vaucheria*. Well differentiated antheridia and oogonia are found. They may be either homothallic or heterothallic.

The Xanthophyceae resemble the Chrysophyceae in their flagellation, amoeboid habit and food reserves, and the Bacillariophyceae in food reserves and cell wall composition.

Model Questions

(1) Essay questions:

- (i) Give an account on thallus structure and sexual reproduction in Xanthophyta.

(2) Short Questions:

- (i) *Vaucheria* thallus
- (ii) *Botrydium* thallus
- (iii) Synzoospore in *Vaucheria*
- (iv) Reproductive structures in *Vaucheria*.

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Dr. S.M. KHASIM

ALGAE

LESSON-V

BACILLARIOPHYTA (DIATOMS)

Objectives

1. Introduction
2. Occurrence
3. Thallus Organization
 - (i) Valve morphology
 - (ii) Raphe and locomotion
4. Cell Structure
5. Reproduction
6. Phylogeny
7. Economic Importance
8. Summary

1 Introduction

The Phylum Bacillariophyta with a class Bacillariophyceae (diatoms) comprises a homogeneous assemblage of unicellular and colonial forms which differ from other algae in possessing highly sculptured and symmetrically ornamented cell walls. They are also called “Jewels of the plant world”. The unicellular diatoms are of two types namely pennate diatoms (order Pennales) and centric diatoms (order Centrales). The Pennate diatoms are elongated, boat shaped or needle shaped and are radially symmetrical, e.g. *Pinnularia*. The Centrales are isodiametric (circular) with radial symmetry, e.g. *Cyclotella*.

The main characters that differentiate the Bacillariophyta from other phyla are: (1) diploid nature of vegetative cell, (2) presence of chlorophyll **c** and chlorophyll **a** together with fucoxanthin, diatoxanthin, and diadinoxanthin; the usual brown colouration is due to the predominance of carotenoid pigments, (3) silicified nature of cell walls which consist of two highly perforated overlapping pieces, (4) oil and chrysolaminarin as reserved food materials, and (5) the reduction in cell size occurring during vegetative multiplication.

2 Occurrence

Diatoms are cosmopolitan and ubiquitous in distribution. They are the major components of the planktonic vegetation. The most common genera of freshwater habitats are *Asterionella*, *Melosira*, *Navicula*, *Nitzschia* and *Synedra*. Species of *Cocconeis*, *Eunotia* and *Gomphonema* grow epiphytically on other fresh water algae such as *Cladophora* and

Oedogonium. Species of *Triceratium* and *Hyalodiscus* occur in the littoral and sublittoral zones as epiphytes on seaweeds. Some marine diatoms are parasitized by the dinoflagellate *Paulsenella*.

3 Thallus Organization

The thalli of diatoms are unicellular, colonial or filamentous. With respect to their shape and valve morphology, the unicellular diatoms have been classified into two orders, Pennales with isobilateral symmetry, e.g., *Pinnularia* (Fig. 5.1A) and Centrales with radial symmetry, e.g., *Cyclotella* (Fig. 5.1B). *Triceratium* (Fig. 5.1C) has three planes of mirror symmetry.

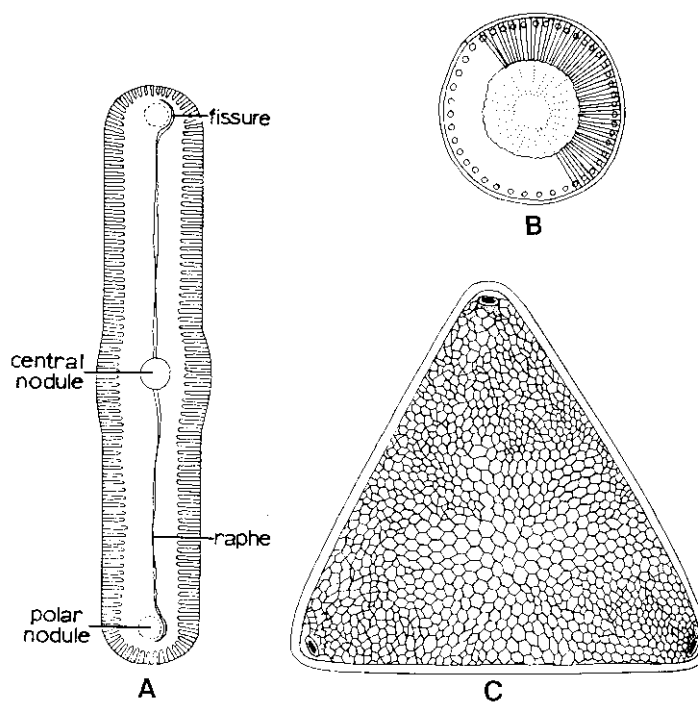


Fig. 5.1 Some common diatoms. A, *Pinnularia*, valve view; B, *Cyclotella*; C, *Triceratium*

Further classification of Centrales is based on the presence or absence of the bristles or horns on the cell structure. Pennales are classified according to the presence or absence of raphes (slits) and number and, morphology of raphes on the valves. These raphes run between the median and the apical pores.

Colonial diatoms are organized into uniseriate filaments, e.g., *Melosira*. The valve-to-valve connections between the cells of *Navicula confervacea* form filaments maintained by organic material adhering to the centres of the valve faces. Stellate colonies result from the union of cells at their basal ends through localized production of mucilage, as in *Asterionella*.

(i). Valve morphology

The fine markings found on the surface of the valve vary widely. According to Hendey (1959) four types of secondary structures are present on diatom valves:

- (a) The *punctae* are fine perforations arranged in regular rows corresponding to the markings or striae on the valve surface;
- (b) the *Areole*, which are cavity-like depressions, coarser and larger than the punctae;
- (c) the *Canaliculi*, which are tubular canals running through the valve surface; and
- (d) the *Costae*, which are specially thickened regions of the valve, resulting from the heavy accumulation of silica, and represent the valvar ribs. The ribs constitute the backbones of the cell wall.

In Pennate diatoms, the markings are arranged longitudinally, e.g., *Pinnularia*, *Cymbella* etc., whereas in centric diatoms, these are distributed concentrically, e.g., *Arachnoidiscus*.

(ii) Raphe and locomotion

In pennate diatoms, there is a longitudinal slit, known as raphe, which is interrupted in the middle by a central nodule formed by the internal thickenings of the valve. In centric diatoms, raphe is absent, instead, one or more projections, known as labiate processes (merely openings through the valve) are present. The locomotion is brought about by the secretion of mucilage through the labiate processes in Centrales. In Pennales both locomotion and anchorage involve the secretion of mucopolysaccharide material through raphe.

4 Cell Structure

Cell Wall – The cell wall (frustule) of diatoms consists of two overlapping halves, the upper half is known as *epitheca* and lower one *hypotheca* (Fig. 5.2A). Each theca possesses the main surface known as valve and this valve has incurved margins called as connecting band (Cingulum). Overlapping region of epitheca and hypotheca is collectively referred to as girdle. The frustule is enriched with amorphous silica, that may also have small amounts of aluminium, magnesium, iron and titanium.

The epitheca and hypotheca can be compared to a petriplate. The lid is corresponding to the epitheca and the main body is compared to hypotheca. The two connecting bands represent the incurved sides of the lid and the main body, whereas the valve relates to the top or bottom of the petriplate. Accordingly a cell can be seen from two different views, the girdle view (diatom appears rectangular) (Fig. 5.2B) and valve view (shape variable).

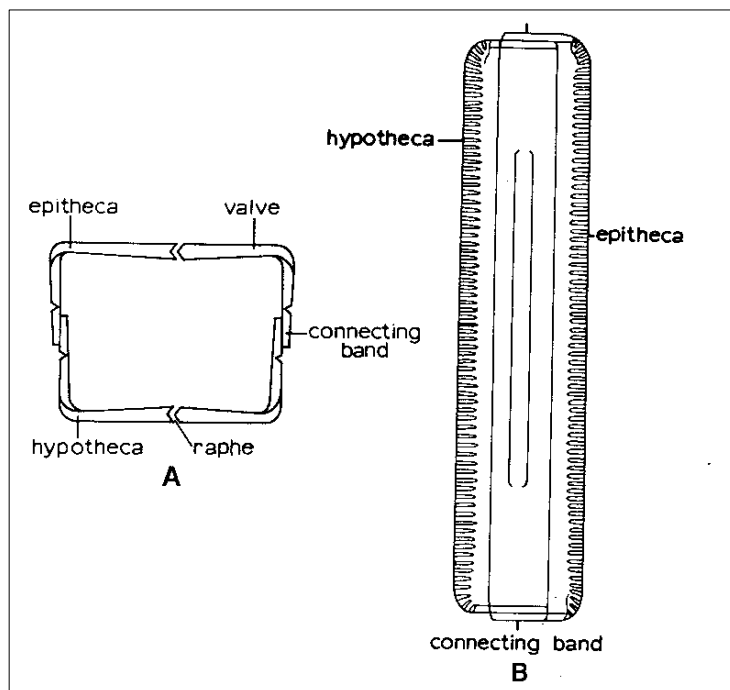


Fig. 5.2 *Pinnularia*. A, transverse section showing relative position of epitheca, hypotheca, connecting band, valve, and raphe; B, girdle view showing relative position of epitheca and hypotheca.

Protoplast – Thin layer of cytoplasm surrounding the large vacuole is bounded by plasmamembrane. The cytoplasm is thicker at the region of poles. The cells are uninucleated. In Pennales, a single large nucleus is located across the middle of the central vacuole and is connected with the lining layer of the cytoplasm next to the cell wall. In Centrales, nucleus occupies the position within the peripheral cytoplasm lining the cell wall.

The cytoplasm also includes other cell organelles such as mitochondria, dictyosomes and endoplasmic reticulum.

The nuclear division is characteristic of this group in possessing intranuclear and cylindrical spindles with flat ends. In resting condition, the nucleus possesses a number of small chromatin granules and one to several nucleoli. Further, the chromosomes do not form an equatorial ring during the metaphase.

Chromatophores – The number and shape of chromatophores varies in this group. In centric diatoms, chromatophores are few and medium sized, and discoidal in shape. In Pennales, one or two large parietal chromatophores with irregular lobes are present. Chromatophore is a double membrane organelle consisting of 4-6 lamellae with or without pyrenoids. Chromatophores are olive green to yellowish green in colour, with chlorophyll **a** and chlorophyll **c**.

5. Reproduction

Both vegetative and sexual reproduction are evidenced in diatoms.

(i) Vegetative multiplication and McDonald-Pfitzer rule

Cell division is the common method of vegetative reproduction. During the process of cell division, the parent cell becomes enlarged and nucleus divides mitotically. Chromatophores also divide longitudinally and daughter chromatophores come to lie on each half. After duplication of cell organelles, the cytoplasm cleaves in the middle along the girdle in a plane parallel to the valve faces. This cleavage proceeds centripetally. This resulted into formation of two daughter protoplasts, each one lying in the each parental theca. The parental hypotheca serves as the epitheca of one of the two daughter cells whereas the parental epitheca remains as the epitheca of the other daughter cell. Accordingly, the newly formed wall pieces always serve as hypotheca.

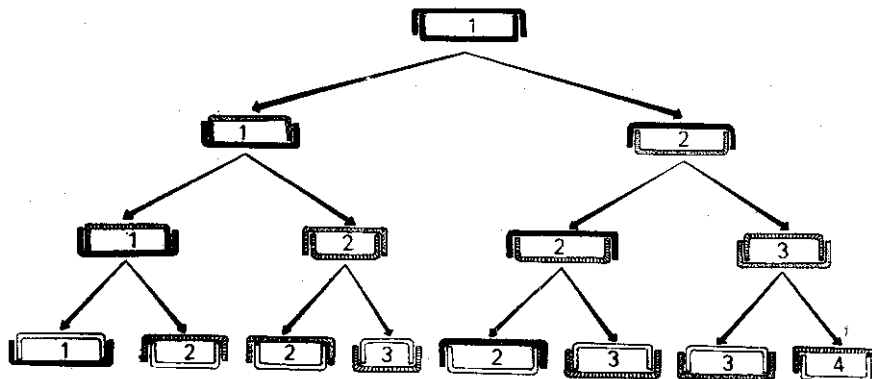


Fig. 5.3 Diminution of cell size in successive generation of a diatom (based on Smith, 1955)

McDonald – Pfitzer rule relates to the phenomenon of gradual size reduction in diatom during vegetative cell division. In the above process, two unequal size of daughter cells are formed. The one daughter cell which retains the parental epitheca, has the same size as of the parental cell; whereas the other daughter cell retaining the parental hypotheca which serves as a epitheca, is smaller in its size than parental cell. Like this, the progenies of a diatoms become progressively smaller during successive cell divisions.

Table 5.1. Differences between Centrales and Pennales

Centrales		Pennales	
1	2,500 species spreading over to 100 genera	1	3,000 species spreading over to 70 genera
2	Widely distributed	2	Mostly freshwater forms
3	Cells circular and radially symmetrical	3	Cells elongated and bilaterally symmetrical
4	Cell walls with coarse markings	4	Fine markings with punctae
5	Chromatophores many and discoid	5	Chromatophores 1 or 2 laminate or lobed
6	Nucleus lies in the peripheral cytoplasm	6	Nucleus in the cytoplasmic bridge connecting the two valves
7	Sexual reproduction – oogamous; flagellated spermatozooids	7	Sexual reproduction – isogamous; amoeboid gametes
8	No movement e.g., <i>Cyclotella</i> , <i>Melosira</i> , <i>Cosinodiscus</i> , <i>Biddulphia</i> .	8	Slow jerky movement e.g., <i>Navicula</i> , <i>Pinnularia</i> , <i>Cocconeis</i> , <i>Synedra</i> , <i>Surirella</i> , <i>Nitzschia</i> .

(ii) Sexual Reproduction

The vegetative phase of diatoms is diploid. Majority of diatoms are homothallic and sexual reproduction takes place within individuals of the same clone. In Pennales, isogamous type of sexual reproduction takes place, through which an enlarged spore, known as auxospore is formed from the union of two amoeboid gametes. In Centrales, on the other hand, the sexual reproduction is oogamous in which flagellated sperm fused with non-motile egg. A secretion of mucilage envelops the conjugating pair. The diploid nucleus of the copulating pair undergoes meiosis and gives rise 4 haploid nuclei. Only two nuclei are involved in the formation of two gametes, and others are degenerated. The gametes of same size and shape move out of the parent cells and fusion takes place within the mucilaginous envelope. As a result, zygote is formed, this inturn is enlarged to become auxospore, e.g., *Cocconeis placentula*.

Physiological anisogamy in which one gamete is mobile and other stationary, has reported in *Navicula seminulum*.

Oogamous type – Oogamy is found in majority of Centrales. The auxospore formation takes place by oogamy, e.g., *Melosira varians*, *Cyclotella tenuistriata* and *Biddulphia mobiliensis*. The diploid diatom cell divides meiotically at the time of gamete formation. About 4 to 128 small uninucleated male gamets bearing single flagellum (spermatozooids) are formed. The diatom cell that produces male gametes is known as spermatogonium.

The female gametes are non-flagellated and are known as eggs. The diploid nucleus of female diatom divides meiotically forming four haploid nuclei. Out of these, three are degenerated. The protoplast with remaining one nucleus becomes functional and acts as an egg (Fig. 5.4).

The male gametes are released out from the spermatogonium and swim to an oogonium. One of the spermatozooids penetrates the egg and fuses with it. The plasmogamy is followed by karyogamy. Zygote ($2x$) escapes from the parent frustule and undergoes enlargement to form the auxospore. Later auxospore secretes a frustule, and gives rise to a new individual.

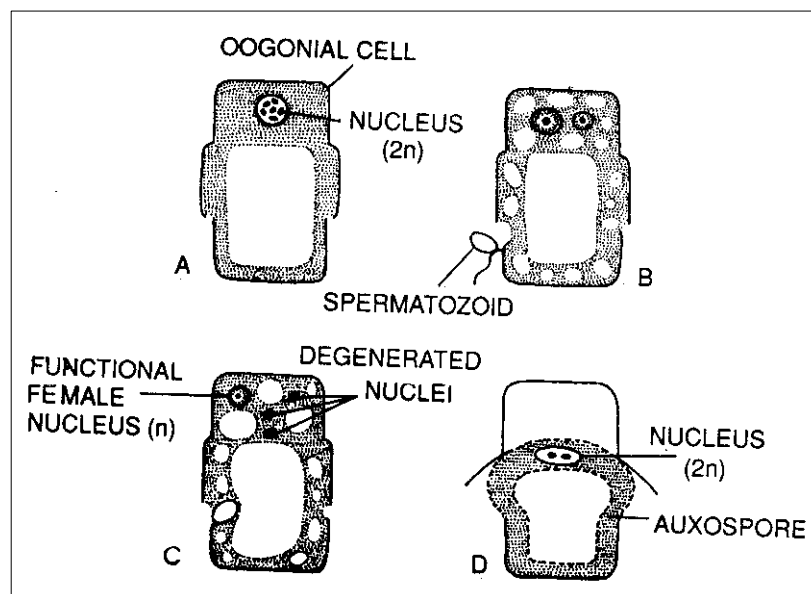


Fig. 5.4 Development of Ovum (egg) and auxospore formation in *Cyclotella* (adopted from Ramakrishna, 1995)

6. Phylogeny

Due to the siliceous nature of cell walls, they are well preserved in the form of fossils. The fossil evidence shows that Centrales are more primitive (reported from jurassic) and Pennales might have originated (early tertiary period) from them. The fact that the most of centric diatoms are marine planktonic forms in contrast to the pennales, which are predominantly freshwater, also indicates a centric ancestry for the pennales.

The presence of fucoxanthin and chlorophyll **a** and chlorophyll **c** links the Bacillariophyta with the Phaeophyta, and the characteristic food reserves (oil and leucosin) relate the diatoms to the Xanthophyta and the Chrysophyta.

7. Economic Importance

The siliceous shells of diatoms are accumulated over a longer period of time at the bottom of the aquatic bodies forming extensive deposits called diatomaceous earth or *Kieselgurh*. Large deposits of diatomaceous earth have been found in California, Germany, France, Japan, Spain, Australia and Nicobar Islands. In Lompoc (California), the largest diatomaceous zone in the world, is present which spread to about 30 sq km area with 425 m thick. It is quarried and used commercially as (1) an abrasive in polishes and tooth pastes, (2) in the filtration of liquids in sugar refineries, (3) used as an inert material filter in paints and plastic industries, (4) as an insulating material for boilers and blast furnaces because it can resist a temperature of 1000°F, and (5) also used as an absorbent for nitroglycerine in the manufacture of dynamite.

8. Summary

The phylum Bacillariophyta with a class Bacillariophyceae (diatoms) comprises a homogeneous assemblage of unicellular and colonial forms which differ from other algae in possessing highly sculptured and symmetrically ornamented cell walls. Unicellular diatoms are of two types, viz., *Pennales* (Pennate diatoms) and *Centrales* (centric diatoms). *Pennales* are with isobilateral symmetry, e.g., *Pinnularia* whereas *Centrales* are with radial symmetry, e.g., *Cyclotella*. Diatoms are the major components of the planktonic vegetation.

The cell wall (frustule) of diatom consists of two overlapping halves, the upper half is known as *epitheca* and lower one *hypotheca*. Each theca possesses the main surface known as valve and this valve has incurved margins called connecting band (Cingulum).

The diatom cells are uninucleated. In *Pennales*, a single large nucleus is located across the middle of the central vacuole and is connected with the lining layer of the cytoplasm next to the cell wall. In *Centrales*, nucleus occupies the position within the peripheral cytoplasm lining the cell wall. Chromatophores are olive green to yellowish green in colour, with chlorophyll *a* and chlorophyll *c*.

The cell division is the common method in vegetative reproduction. As a result of cell division, two daughter protoplasts are formed, each one lying in the each parental theca. The parental hypotheca serves as the epitheca of one of the two daughter cells whereas the parental epitheca remains as the epitheca of the other daughter cell. **McDonald-Pfitzer rule** relates to the phenomenon of gradual size reduction in diatom during vegetative cell division. During successive cell divisions, the progenies of a diatom become progressively smaller, generation after generation.

Sexual reproduction through oogamous type is found in majority of centrales. The auxospore formation takes place by oogamy, e.g., *Melosira varians*, *Cyclotella tenuistriata* and *Biddulphia mobiliensis*.

The siliceous shells of diatoms are accumulated over a longer period of time at the bottom of aquatic bodies, forming extensive deposits called diatomaceous earth or *Kieselgurh*. It has been quarried and used for many industrial purposes.

Model Questions

(1) Essay Questions

- (i) Compare and contrast the Centrales and Pennales and add a note on their reproduction.
- (ii) Give an account on thallus structure and reproduction in Bacillariophyta.

(2) Short answer Questions

- (i) Cell wall of diatom
- (ii) Centrales
- (iii) Pennales
- (iv) Valve morphology
- (v) McDonald-Pfitzer rule
- (vi) *Kieselgurh*.
- (vii) Economic importance of diatoms.

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1. Kumar, H.D. 1999. **Introductory Phycology**. Affiliated East-West Press, New Delhi.
2. Pandey, D.C. 1981. **Algae**, Kitab Mahal, Allahabad.

Dr. S.M. KHASIM

ALGAE

LESSON-VI

PHAEOPHYTA (Brown Algae)

OBJECTIVES

1. Introduction
2. Occurrence
3. Thallus organization
4. Internal structure
5. Cell structure
6. Reproduction
 - (i) Vegetative Reproduction
 - (ii) Asexual Reproduction
 - (iii) Sexual Reproduction
7. Alternation of generations and life cycles
8. Classification
9. Phylogeny
10. Economic Importance
11. Summary

1 Introduction

Brown or yellowish Brown colour of the thallus of Phaeophyta is due to the presence of abundant carotenoids. The pigment fucoxanthin occurs in sufficiently larger quantity and chiefly responsible for brown colouration to the thallus. Other pigments are chlorophyll **a**, chlorophyll **c**, β carotene, violaxanthin, diatoxanthin, neoxanthin, flavoxanthin and other xanthophylls. The plant body is multicellular but motile reproductive structure is unicellular. Photosynthetic reserve food is stored in the form of soluble carbohydrate, called laminarin and also mannitol. Cell wall is made up of cellulose, fusic acid and alginic acid. Zoospores possess laterally inserted two unequal flagella. There are about 1,000 species belonging to 195 genera in the class Phaeophyceae.

2. Occurrence

Except few (e.g., *Bodanella*, *Heribaudiella*, *Pleurocladia*), most of the Phaeophyceae members are marine. They are abundant in tropics (Sargasso sea of the Atlantic) and more prominent in cold waters. They occur in littoral and sublittoral zones of the sea. In sublittoral zone, thick forest of kelps such as *Laminaria* with subflora of *Alaria*, *Cutleria*, *Desmarestia*,

Dictyota and *Himantalia* are present. *Laminaria* and *Macrocystis* are known to contribute to a very high rate of primary production, having annual net production upto 2000 gr/m².

3. Thallus organization

The structure of thallus of the brown algae ranges from heterotrichous filamentous types through pseudoparenchymatous uniaxial forms to true parenchymatous forms. Phenotypic plasticity is wide spread in this class. Unicellular, colonial and unbranched forms are absent. The simplest thallus organization in this phylum is the branched, heterotrichous habit, e.g. *Ectocarpus*. The large sized brown algae are called kelps (*Laminaria*, *Nereocystis*). Some are called rock weeds (*Fucus*). *Postelsia* resembles a palm. *Macrocystis* reaches upto 100 meters. In general, the vegetative organization of Phaeophyceae is of three following types.

(i) **Ectocarpoid type** – In *Ectocarpus*, heterotrichous type of organization is found. The thallus is profusely branched and cells are joined end to end in a single series.

(ii) **Pseudoparenchymatous (corticated) type** – *Arthrocladia*, *Desmarestia* and *Myronema*, the lateral branches at the lower region of the plant body become rhizoidal and coil around the main axis to form a compact pseudoparenchymatous cortex around the main axis. They are also called **haplostichous** forms.

(iii) **Truly parenchymatous type** – These are also called **Polystichous** forms. In these forms, thallus is leaf-like and true parenchymatous, e.g., *Punctaria*. Members of Laminariales and Fucales possess improved type of parenchyma. The other examples for true parenchymatous thallus organization are *Fucus*, *Sargassum*, *Postelsia* etc.

The plant body of *Nereocystis* is 20-25 meters long. It consists of a haptera, a stipe and terminal large gas bladder having many blades on it.

In *Laminaria*, the thallus is morphologically distinguishable into holdfast, stipe and blade (Fig. 6.1). The blade which is primarily photosynthetic and spore producing portion, is highly dissected. Intercalary meristem is located at the junction of the stipe and the blade (Fig. 6.1). Intercalary growth takes place in Laminariales and leads to formation of gigantic plant body (giant kelp).

4. Internal structure

In *Dictyota*, the strap-like thallus undergoes dichotomous branching repeatedly (Fig. 6.3A). The basal portion of the thallus forms a disc-like branched holdfast by which the thallus remains attached to the solid substratum. In transverse section, the thallus is seen to be composed of three layers (Fig. 6.3B, C), the central one with large cells and, an upper and lower epidermis with assimilatory cells from which tufts of mucilage hairs arise. Growth is restricted to the apical region of the branches (apical growth).

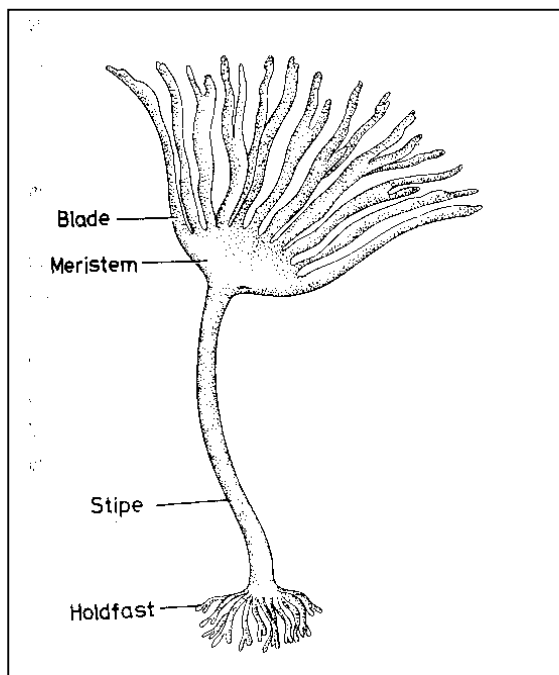


Fig. 6.1 *Laminaria hyperborea*, sporophyte structure showing differentiation into holdfast, stipe, and blade.

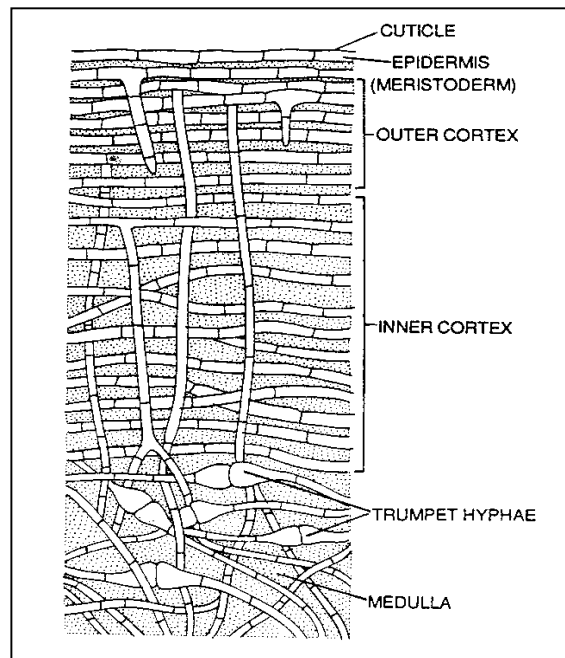


Fig. 6.2 *Laminaria* sp. Longitudinal section through medulla of stipe. (adopted from Pandey, 2004).

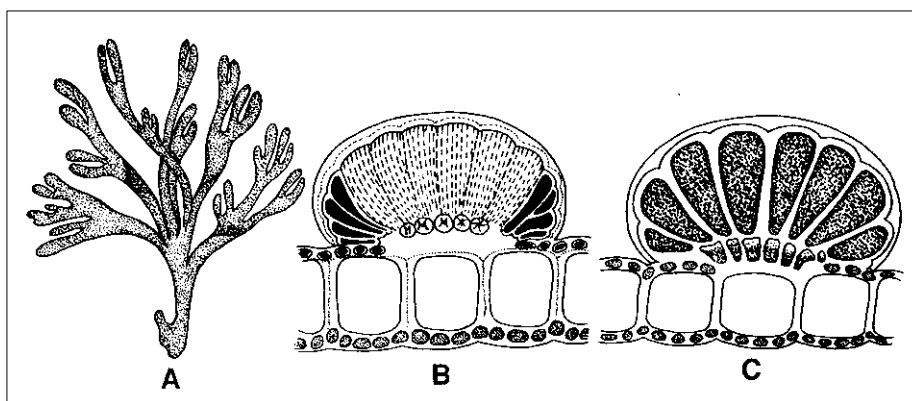


Fig. 6.3. *Dictyota dichotoma*. A, habit; B, cross-section through antheridial sorus; C, cross-section through oogonial sorus.

In *Laminaria*, the stipe consists of epidermis, cortex and medulla. Some of the medullary cells produce vertically elongated hyphae, known as trumpet hyphae (Fig. 6.2), lacking chloroplast and, involve in water and nutrient conduction.

5. Cell structure

The cell wall is two layered. The outer layer is mucilaginous. The mucilage contains gum-like substances such as algin, fucoidin etc. In Laminariales, special mucilage ducts are found, secreting mucilage. Callose is found in the cell membranes of *Laminaria digitata*. The inner layer is made up of cellulose.

In cytoplasm, mitochondria which are closely connected with chromatophores and numerous vacuoles are present. In *Dictyota* and *Fucus* each cell contains a large vacuole. The special bodies called fucosan vesicles are abundantly found in meristematic, photosynthetic and reproductive cells.

Generally, the chromatophores are discoidal and parietal in position. In each cell, there may be one or more chloroplasts (Fig. 66D). Double membraned chloroplast has got many bands of photosynthetic lamellae. There are 3 or more photosynthetic lamellae (discs) stacked into bands. Generally chromatophores lack pyrenoids. When present, usually protrudes from the chromatophores (Fig. 6.4). These chromatophores contain chlorophyll **a**, chlorophyll **b**, xanthophyll and carotenoids as pigments. Fucoxanthin over masks the other pigments, giving a tinge of brown colouration to the plant body. The characteristic reserve food materials of this group are the laminarin, mannitol, fats, hydrolases etc. Iodine is also stored in many algae. In *Laminaria*, iodine concentration is 0.08 – 0.35%.

Majority of Phaeophyceae have uninucleate cells. Large nucleus with one or two nucleoli is present in the cell. In Fucales the nucleoli are vacuolated. In Phaeophyceae the basic chromosome number is 8.

6 Reproduction

The reproduction takes place by (i) Vegetative, (ii) Asexual, and (iii) Sexual methods.

(i) Vegetative Reproduction

Vegetative propagation takes place by fragmentation of thallus, e.g., *Sargassum*. In some cases, specialized reproductive branches are formed. They are called Propagules, e.g., *Sphacelaria*. Adventitious buds develop in *Fucus*. They develop by the activity of meristematic cells in young plants. These buds detach from parent plant and develop into a new plant.

(ii) Asexual Reproduction

Asexual reproduction takes place by means of zoospores and also aplanospores formed inside the sporangia.

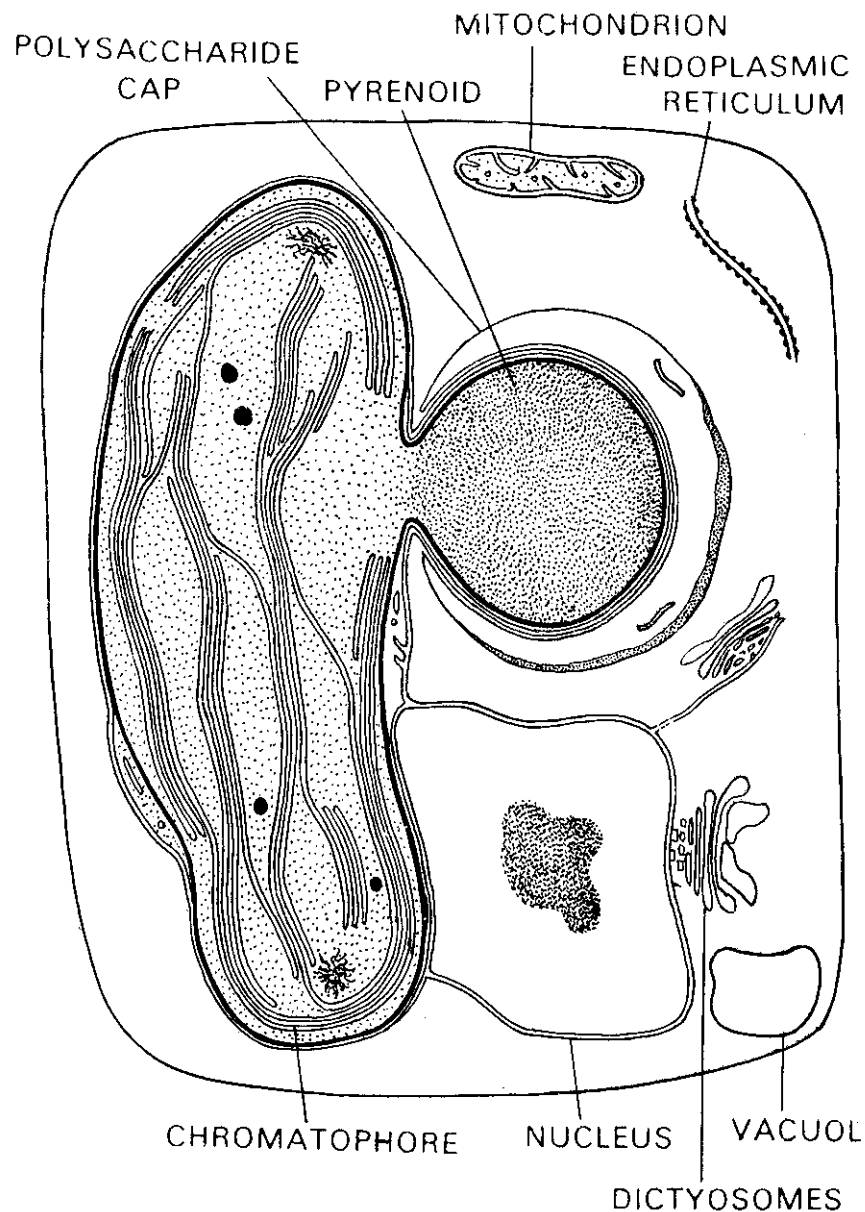


Fig. 6.4 Phaeophyceae, diagrammatic representation of a vegetative cell (Based on Bouck, 1965)

Zoospores – The formation of zoospores is most common in all the members of Phaeophyceae except *Dictyota* and *Fucus*. The zoospores are pyriform and biflagellate. The anterior flagellum is larger than the posterior one (Fig. 6.5) except in Fucales. In Dictyotales single flagellum is found on the zoospore. These zoospores are produced in the zoosporangia, which are of two types, unilocular sporangia and multilocular sporangia (or Plurilocular sporangia) (Fig. 6.6A, B).

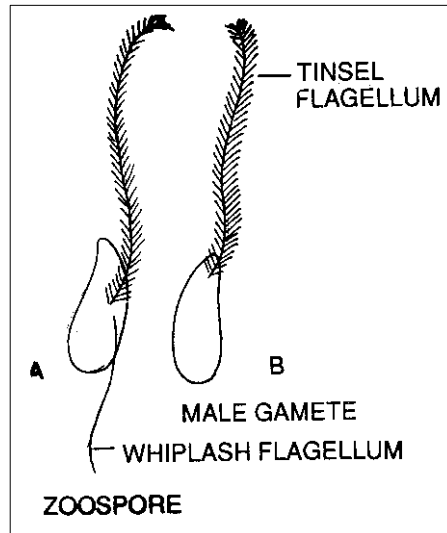


Fig. 6.5 Zoospores of Phaeophyceae

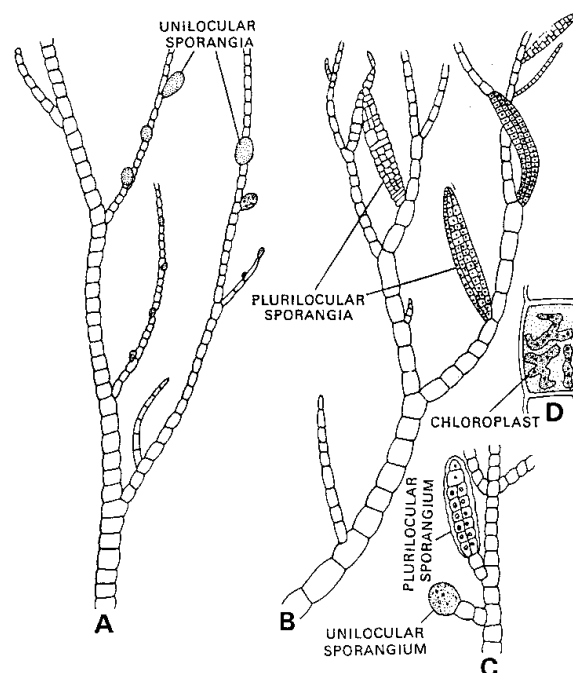


Fig. 6.6 *Ectocarpus siliculosus*. A, a part of the plant with unilocular sporangia; B, a part of the plant with plurilocular sporangia; C, a part of the plant of *E. cylindricus* with both uni- and plurilocular sporangia; D, a cell.

The unilocular sporangium may be terminal or intercalary in position. The nucleus in the unilocular sporangium undergoes reduction division and gives rise haploid zoospores. They germinate and gives rise gametophytic thalli, e.g. *Ectocarpus*.

The plurilocular sporangia are always terminal in position. Zoospores formed from the plurilocular sporangium are diploid in nature and, they germinate and give rise to sporophytes, e.g., *Ectocarpus*. The plurilocular sporangia are not known in Fucales and Laminariales.

Aplanospores – In some cases, instead of zoospores unilocular sporangia also produce aplanospores. They are non-motile, e.g., Dictyotales (Fig. 6.8A). The first division is always reductional. The aplanospores are always less in number. In *Dictyota*, and *Zonaria* each sporangium produces 4 aplanospores and 8 aplanospores respectively.

(iii) Sexual Reproduction

Isogamous to oogamous types of sexual reproduction are found in Phaeophyta. Sexual reproduction takes place only in haploid plant (gametophyte).

(A) Isogamous type – In this type, two similar gametes are fused together. Isogamy is common in Ectocarpales, Sphacelariales, Dictyosiphonales etc. In *Ectocarpus siliculosus*, physiological anisogamy is found. In this, isogametes are formed from plurilocular gametangium (Fig. 6.7A, B) but some gametes are more active. Several active male gametes cluster around a single passive female gamete with their forwardly directed flagellum. It is called **clump formation** (Fig. 6.7C).

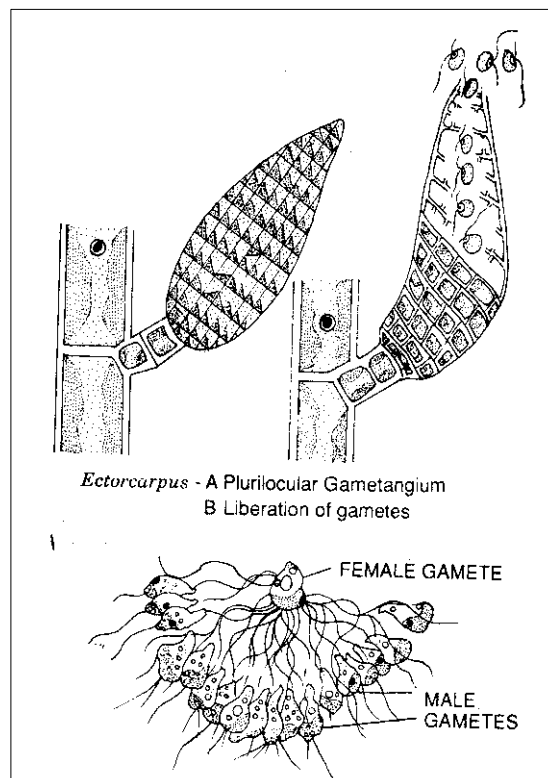


Fig. 6.7 *Ectocarpus* – A. Plurilocular Gametangium, B. Liberation of gametes, C. *Ectocarpus* showing clump formation

(B) Anisogamous type – The fusion of two dissimilar gametes takes place, e.g., *Cutleria*, *Soranthera* and members of Ectocarpales.

(C) Oogamous type – Oogamy is quite common in majority of Phaeophyceae. The species may be homothallic or heterothallic. In Dictyotales the oogonial sorus (Fig. 6.8B) and antheridial sorus (Fig. 6.8C, D) occur on different plants whereas in *Fucus* they may occur in the same conceptacles or in separate conceptacles as in *Sargassum*.

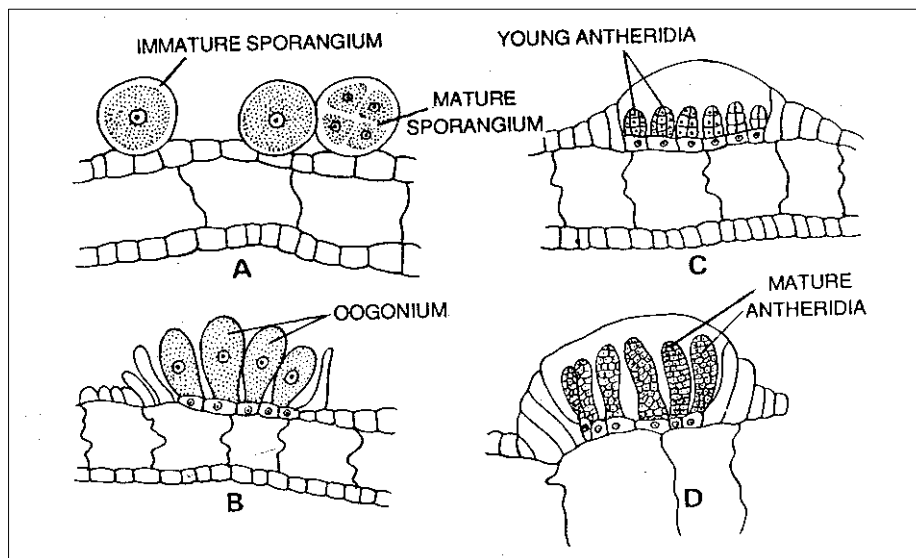


Fig. 6.8 *Dictyota dichotoma*. A, transverse section through a portion of sporangial sorus showing immature and mature sporangia; B, transverse section through an oogonial sorus showing oogonia; C, transverse section through antheridial sorus showing young antheridia; D, transverse section through antheridial sorus showing mature antheridia (adopted from Pandey, 2004).

In Dictyotales, the antheridia are multilocular structures (Fig. 6.8C, D). Each cell of antheridium gives rise to spermatozoid. In Desmarestiales and Laminariales, the antheridia are unilocular and each antheridium produces a single spermatozoid. Usually each oogonium produces a single ovum or oosphere (Fig. 6.8B).

In Fucales, the special reproductive branches bearing receptacles at their tips, are found, e.g., *Sargassum* and *Fucus* (Fig. 6.9). Several fertile conceptacles are scattered over these receptacles.

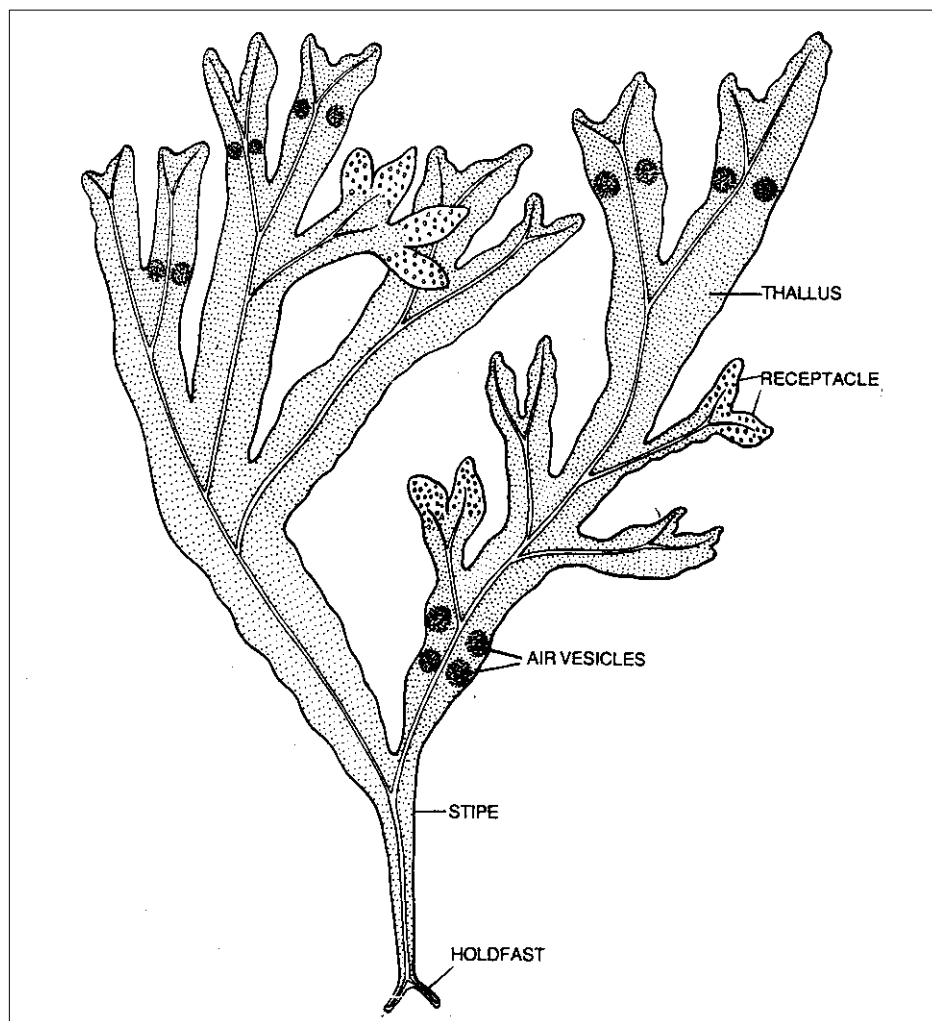


Fig. 6.9 *Fucus* sp. A, complete plant--thallus

The development of conceptacle – The conceptacle develops from any superficial cell of the meristoderm usually situated near the apical region of the receptacle. The cell of the meristoderm becomes prominent. The other surrounding cells of the meristoderm undergo divisions comparatively at a higher rate and bring down the conceptacle initial in the bottom of the flask-like cavity (Fig. 6.10A-E). This initial divides transversely into the tongue cell and basal cell. The tongue cell degenerates but basal cell divides and redivides anticlinally and gives rise to a fertile layer of cell sheet. This fertile sheet develops the antheridia or oogonia, as the case may be.

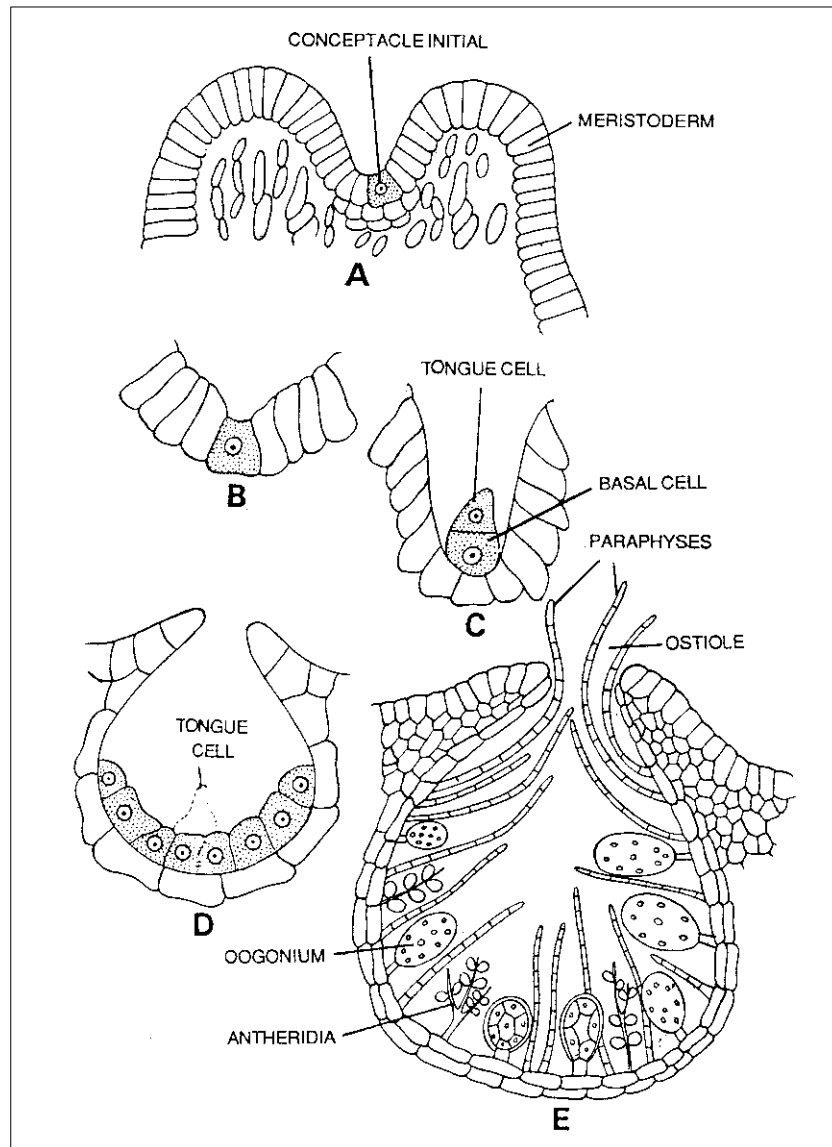


Fig. 6.10 *Fucus* sp. Sexual reproduction, development of conceptacle. A-D. successive stages in the development of conceptacle; E. a conceptacle, with antheridia, oogonia and paraphyses (Adopted from Pandey, 2004)

In *Fucus*, eight eggs are produced in the oogonium. The eggs liberate in the water and fertilization takes place externally.

7 Alternation of Generations and Life Cycles

There are three general types of life cycle found in the class Phaeophyceae.

(i) **Isomorphic life cycle** – Isomorphic alternation of generations is found in this cycle. Both sporophyte and gametophytes are morphologically similar, as seen in the members of Ectocarpales, Spacelariales, Dictyotales, Cutleriales and Tilopteridales.

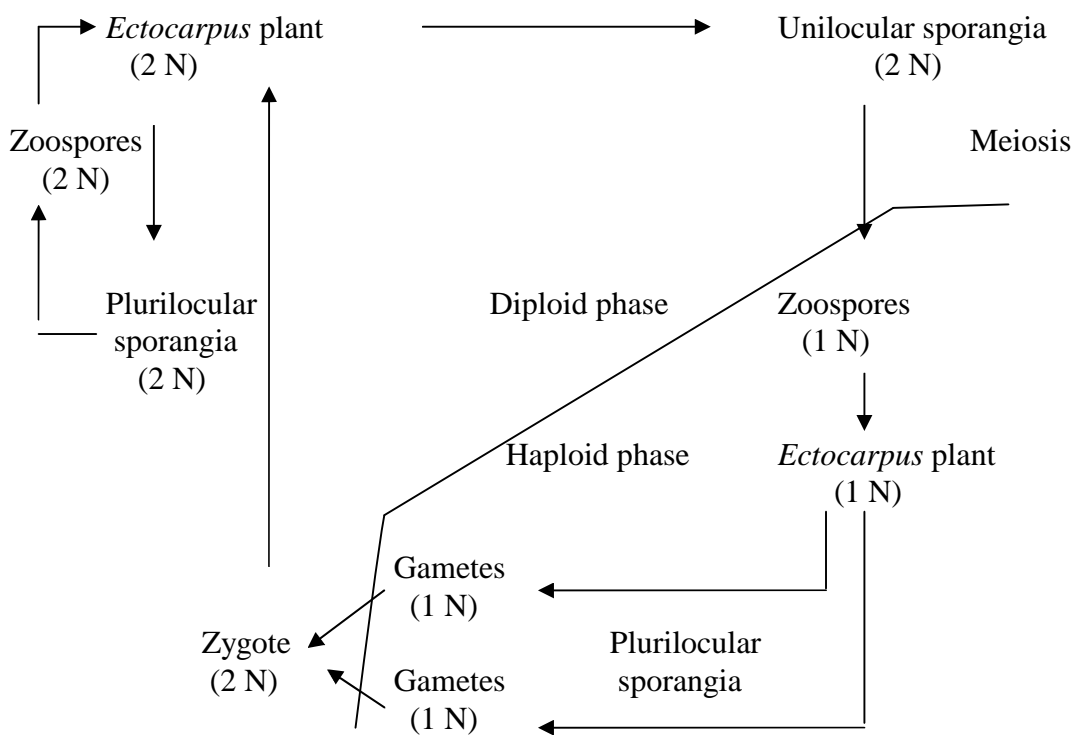


Fig. 6.11 *Ectocarpus* – Graphic representation of Isomorphic alternation of generations

(ii) **Heteromorphic life cycle** – An alternation of morphologically dissimilar (heteromorphic) diploid and haploid generations is found, e.g., *Laminaria*, *Nereocystis* (Laminariales).

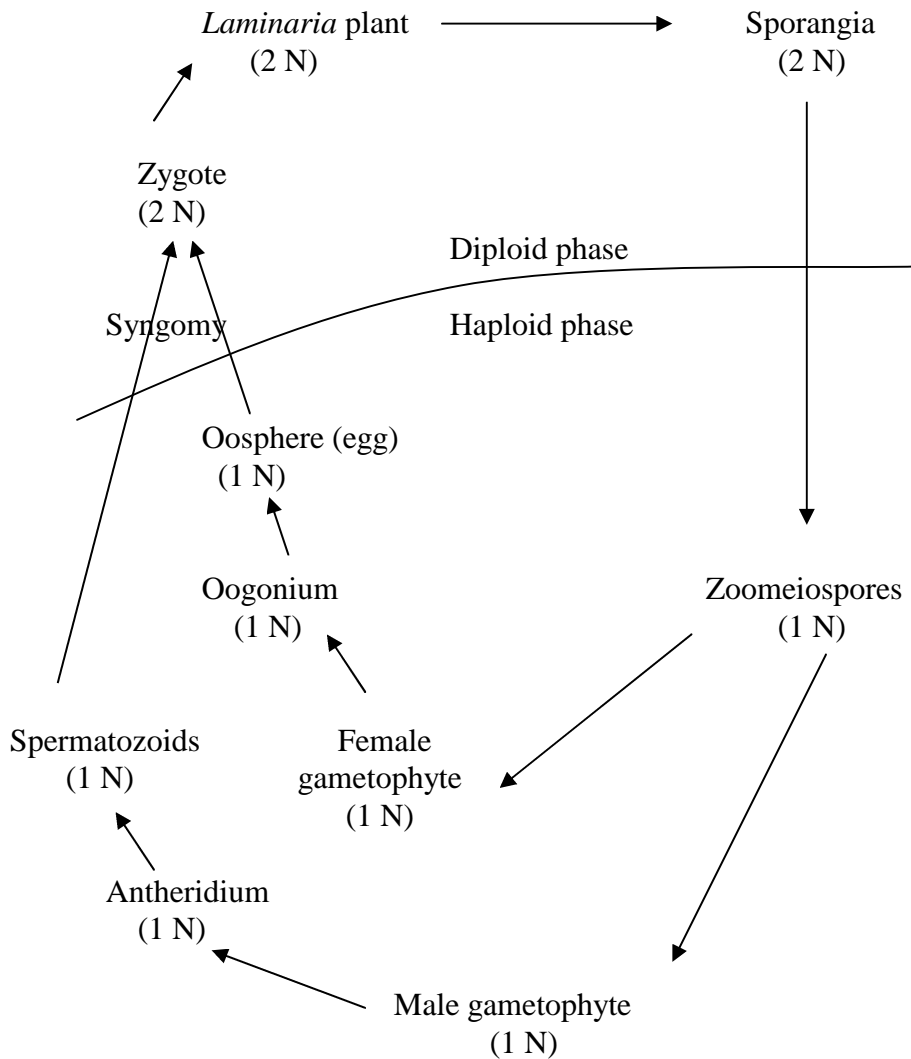


Fig. 6.12. *Laminaria* – Heteromorphic alternation of generations

(iii) Diplontic life cycle – In this, there is no alternation of generations and complete suppression of the haploid generation, as seen in *Fucus*. In this genus, gametophytic phase is represented by egg and antherozoids.

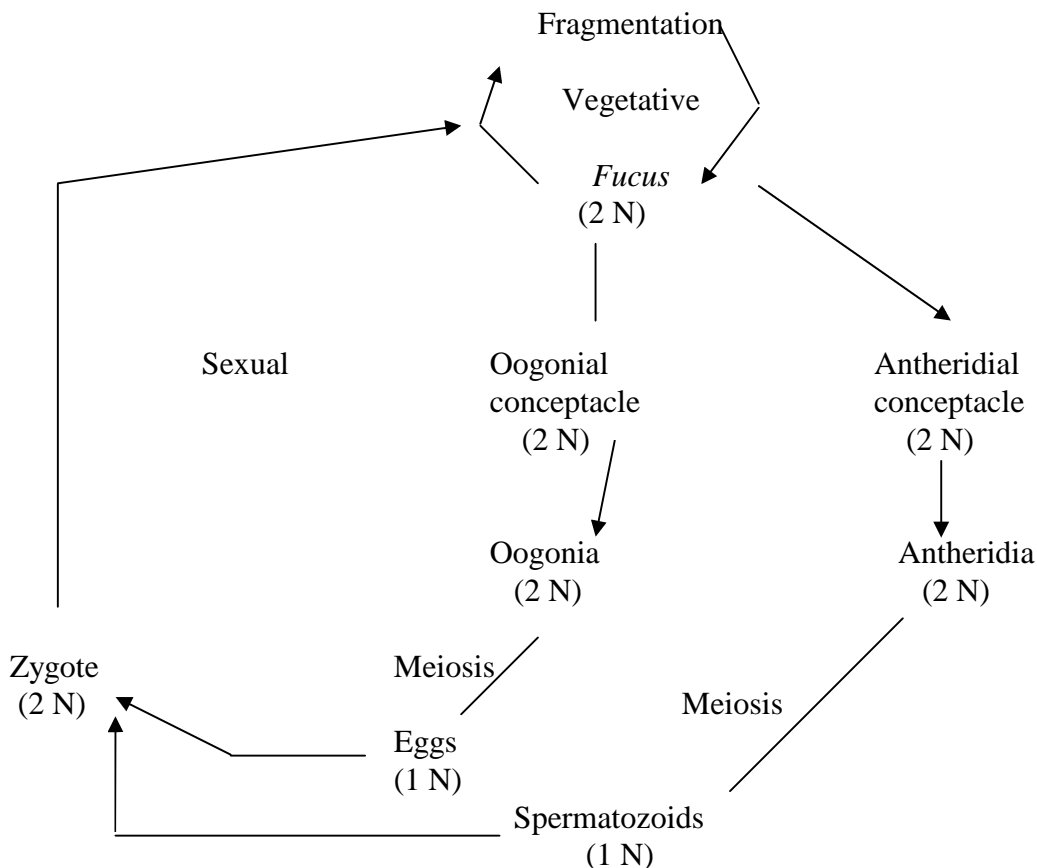


Fig. 6.13 *Fucus* - diplontic life cycle

8. Classification

Fritsch classified the class Phaeophyceae into nine orders: (i) Ectocarpales, (ii) Tilopteridales, (iii) Cutleriales, (iv) Sporachnales, (v) Desmarestiales, (vi) Laminariales, (vii) Spacelariales, (viii) Dictyotales, (ix) Fucales.

Taylor divided the class Phaeophyceae into 3 subclasses: (I) Isogeneratae, (II) Heterogeneratae, and (III) Cyclosporaes.

(i) Subclass Isogeneratae: Those species showing isomorphic alternation of generations are classified under this subclass. This includes 8 orders.

- (A) **Ectocarpales** – Branched heterotrichomes plant body; trichothallic growth; reproductive structures terminal or intercalary; the sporophyte produces zoospores; isogamy.
- (B) **Spacelariales** – Growth by a single large apical cell divides lengthwise in a regular polysiphonous manner; sporophyte may produce haploid or diploid zoospores; iso or anisogamy.
- (C) **Tilopteridales** – Thallus freely branched showing trichothallic growth; upper portion of thallus monosiphonous and lower portion polysiphonous. Sporophytes produce unilocular sporangia, each sporangium gives rise a single quadrinucleate aplanospore; gametangia intercalary.
- (D) **Cutleriales** – Thallus flattened, blade-like or disc-like, dichotomously branched; the sporophyte produces unilocular sporangia only; anisogamy.
- (E) **Dictyotales** – Flattened, erect, dichotomously branched parenchymatous thallus; growth by a single apical cell; sporophyte produces unilocular sporangia, each sporangium contains 4 or 8 aplanospores; Oogamy.

(ii). **Subclass : Heterogeneratae:** This includes two series, Haplostichineae and Polystichineae.

Series Haplostichineae: Thallus consists of one or more filaments; trichothallic growth. Three orders included in this series.

- (A) **Chordariales** – Branched filamentous sporophyte; isogamy.
- (B) **Sporochnales** – Each branch of the sporophyte terminates in a tuft of hairs; trichothallic growth; only unilocular sporangia borne terminally in dense clusters; oogamy.
- (C) **Desmarestiales** – Macroscopic thallus, pseudoparenchymatous cortication; gametophyte microscopic; oogamy.

Series Polystichineae: Longitudinal and transverse intercalary cells form a parenchyma.

- (A) **Punctariales** – Parenchymatous, sporophyte of medium size; sporophyte produces by zoospores; gametophyte microscopic; isogamy or anisogamy.
- (B) **Dictyosiphonales** – Profusely branched cylindrical thallus, growth by single apical cell; unilocular sporangia on sporophyte; gametophyte microscopic, isogamy.
- (C) **Laminariales** – Sporophyte differentiated into holdfast, stipe and blade, growth by intercalary meristem; internal differentiation of thallus into epidermis, cortex and medulla; sporophyte bears only unilocular sporangia in sori; gametophyte microscopic; oogamy.

(iii) Subclass: Cyclospora

Order Fucales: Life cycle is diplontic; parenchymatous thallus; growth by a single apical cell; antheridia and oogonia develop in the conceptacles situated on the receptacles; gametophytic phase represented by eggs and antherozoids; oogamy.

9. Phylogeny & Interrelationships

Members of Phaeophyceae show parallel evolution with Chlorophyta and Rhodophyta in having the heterotrichous, uniaxial or multiaxial plant bodies. They also resemble Cryptophyta, Pyrrophyta and Bacillariophyta in possessing chlorophyll *c*. Further, presence of oil and saturated fats is a common feature of the brown algae as of the Xanthophyceae, Chrysophyceae and Bacillariophyceae. The swimmers (swimming cells) of the Phaeophyta are also very similar to those of Xanthophyceae and Chrysophyceae with reference to the morphology of flagella.

Two divergent lines have been established in the evolution of Phaeophyceae. One of these lines has given rise to the groups possess isomorphic alternation of generations, and the other to the groups of heteromorphic alternation of generations. In both the series, there has been a progressive evolution towards the complexity of the thallus and from isogamous to oogamous type of reproduction. The order Fucales may be considered as an advanced one in heteromorphic series.

10 Economic importance

In Japan, people use more than 20 species of brown algae as food. They begin to collect the kelps in July and continue upto October. The acetic acid is extracted from seaweed by means of fermentation. In many places, *Nereocystis* is used in the preparation of medicines, poultry feed, and for the extraction of potash salts. About 30 per cent of the dry weight is potassium chloride.

Macrocystis and *Laminaria* are the chief source for the extraction of algin. Algin is used in the preparation of paints and varnishes, and also in the preparation of ice creams. *Egregia* (kelp) is used as fertilizer. Seaweeds also contain iodine and other salts.

11. Summary

The members of Phaeophyta are brown or yellowish brown in colour due to the presence of sufficiently larger quantity of fucoxanthin. The plant body is multicellular but motile reproductive structure is unicellular. They are abundant in tropics (Sargasso sea of the Atlantic) and more prominent in cold waters.

The thallus structure of the brown algae ranges from heterotrichous filamentous types through pseudoparenchymatous uniaxial forms to true parenchymatous forms. The simplest thallus organization in this phylum is the branched, heterotrichous habit, e.g., *Ectocarpus*. The large sized brown algae are called kelps (*Laminaria*, *Nereocystis*).

In *Laminaria*, the thallus is morphologically distinguishable into holdfast, stipe and blade. The blade which is primarily photosynthetic and spore producing portion, is highly dissected. Intercalary growth takes place in Laminariales and leads to formation of gigantic plant body.

In *Dictyota*, the thallus is repeatedly branched dichotomously. In transverse section, the thallus is seen to be composed of three layers, the central one with large cells and, an upper and lower epidermis.

The cells are uninucleated and one or more discoidal chromatophores which are parietal in position. The characteristic reserve food materials are the laminarin, mannitol, fats, hydrolases etc.

The reproduction takes place by vegetative, asexual and sexual methods. Asexual reproduction takes place by zoospores produced in the unilocular and plurilocular sporangia, e.g., *Ectocarpus*. Isogamous to oogamous types of sexual reproduction are found in Phaeophyta. Oogamy is quite common in majority of Phaeophyceae. In Dictyotales the oogonial sorus and antheridial sorus occur on different plants; whereas in *Fucus* they may occur in the same conceptacles or in separate conceptacles as in *Sargassum*.

Two divergent lines have been established in the evolution of Phaeophyceae. One of these lines has given rise to the groups possess isomorphic alternation of generations, and the other to the groups of heteromorphic alternation of generations. In both the series, there has been a progressive evolution towards the complexity of the thallus and from isogamous to oogamous type of reproduction.

Model Questions

(1) Essays Questions

- (i) Describe the thallus organization and ultrastructure of cell in Phaeophyceae.
- (ii) Give an account on reproduction and alternation of generations in Phaeophyceae.

(2) Short answer questions

- (i) Cell ultrastructure in Phaeophyceae
- (ii) Conceptacles in *Fucus*.

- (iii) Life cycle of *Laminaria*.
- (iv) Asexual reproduction in *Ectocarpus*.
- (v) Classification of Phaeophyta.
- (vi) Economic importance of Phaeophyceae.

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Dr. S.M. KHASIM

ALGAE

LESSON-VII

RHODOPHYTA (Red Algae)

Objectives

1. Introduction
2. Occurrence and Ecological Importance
3. Range of Thallus Organization
4. Cell Structure
5. Reproduction
 - (i) Vegetative Reproduction
 - (ii) Asexual Reproduction
 - (iii) Sexual Reproduction
6. Life Cycles
7. Classification
8. Phylogeny and Interrelationships
9. Economic Importance
10. Summary

1 Introduction

The phylum Rhodophyta with a single class Rhodophyceae divided into two subclasses, viz., Bangioideae (or Bangiophycidae) and Florideae (or Florideophycidae).

Due to the presence of excess of γ -phycoerythrin in their chromatophores, the thalli of various species of Rhodophyta are appeared red in colour. This red pigment masks the colour of other photosynthetic pigments. The Rhodophyta are characterized by the following features:

- (i) Flagellated motile stages are completely absent.
- (ii) The sexuality is highly specialized in this group. The non-motile, male gamete, known as spermatium is passively transported to and lodged on the trichogyne of female carpogonium. Besides, distinct post-fertilization developments are found in this group.
- (iii) Cell wall is made up of polysulphate esters of carbohydrates, in addition to cellulose and pectin.
- (iv) In multicellular forms, cytoplasmic connections (pit connections) are found between adjacent cells.

- (v) Characteristic pigments in this group are biliproteins (γ -phycoerythrin, γ -phycocyanin), taraxanthin and chlorophyll **d**, in addition to chlorophyll **a**, α - and β -carotene, lutein, zeaxanthin and neoxanthin.
- (vi) The reserve food materials are floridean starch and galactoside floridosides.
- (vii) Majority of red algae show the triphasic life cycle, and others biphasic life cycle.

2. Occurrence and Ecological importance

Majority of red algae are marine growing in littoral and sublittoral zones. They grow in almost all marine habitats but their greatest concentration occur in warmer seas. Red algae prefer to grow in deeper waters where they receive only blue-green wavelengths of light. This spectral region is sufficient for the generation of γ -phycoerythrin, the dominant red pigment for photosynthesis found in the thalli of this group of algae. They also exhibit complementary chromatic adaptation, so that the colour of the incident light induces the development of a particular photosynthetic pigment which has maximum absorption of the incident light.

Unicellular red alga *Porphyridium* grows in damp soil. Some are fresh water forms, e.g., *Batrachospermum*, *Lemanea* etc. Some of the calcareous algae, e.g., *Corallina* and *Lithothamnion* are responsible for the formation of coral reefs.

Certain parasitic red algae, e.g., *Gardneriella tuberifera*, *Ceratocolax hartzii*, *Choreonema thuretii* etc., lack pigments and penetrate host tissues.

3. Range of thallus organization

There is a great diversity in the vegetative structure of red algae. The subclass Bangioideae, with a single order Bangiales, comprises unicellular (*Porphyridium*), filamentous (*Goniotrichum*), and parenchymatous (*Porphyra*) forms.

The subclass Florideae show more elaborative thalli with two main types of organization, **uniaxial** and **multiaxial**. In both the cases pseudoparenchymatous thallus results from the coalescence of filament branches.

The **uniaxial thalli** have a single central or axial filament, which may be corticated, with a number of richly branched laterals organized to form a pseudoparenchymatous structure, e.g., *Batrachospermum* and *Dumontia*.

In *Batrachospermum*, the thallus is uniaxial (monosiphonous). There is a central filament of unlimited growth with a single dome shaped apical cell. This apical cell divides transversely to produce an axial row of large and cylindrical cells. At a short distance, below the apical cell, there are four lateral projections, which grow out as lateral branches, limited in their growth. These lateral branches form a spherical or globose cluster (Fig. 7.1A, B). This globose cluster of laterals is called glomerule which gives the whole thallus a beaded appearance to the naked eye. As the axis (central filament) becomes elongate, the whorls of lateral branches get separated. The basal cells of the lateral branches give rise to rhizoid like branches (unlimited growth) which grow out and cover the axial cell downwards and form a multicellular axis with cortication.

In the **multiaxial forms**, such as *Polysiphonia* (Fig. 7.2), the axial cell divides vertically to form a central and a number of pericentral siphons. The pericentral cells undergo division periclinally and anticlinally to produce a multicellular cortex giving rise to a pseudo-parenchymatous thallus or may serve as the initials of lateral branches. Thus the multiaxial cylindrical thallus (Fig. 7.2A, B) is differentiated into a central medulla, a cortex for the storage of food and an outer layer of cells with chromatophores as in *Gelidium*. The inner cells do not divide any more and become stretched and elongated while the cells from the centre to periphery become progressively smaller (Fig. 7.2C, D, E, F).

4. Cell structure

The red algae are truly eukaryotic. They have microtubules but lack centrioles and flagella.

Cell Wall – It is distinguished into two layers, the outer layer is made up of pectic substances and inner layer with cellulose. In some forms, e.g., *Porphyridium*, mucilaginous envelope is found around the cell and they show gliding motility. The pit connections are lenticular plugs and they are occupied a central position in the septa between adjacent cells (Fig. 7.1D). The rhodophycean pit connections are very similar to septal plugs of fungi.

The protoplasm – It is highly viscous. Many scattered grains of floridean starch occur in the cytoplasm. In Bangiales there is no central vacuole, but in all Florideae the cytoplasm possess a conspicuous central vacuole (tonoplast bound).

The nucleus – The cells are uninucleate in lower Rhodophyceae orders such as Cryptonemiales, Bangiales etc. In higher orders, Ceramiales, Rhodymeniales etc., cell are multinucleate. In some rhodophycean forms, e.g., *Griffithsia*, each cell possesses 3,000-4,000 nuclei. The nuclei are with one or more prominent nucleoli. The nuclei may migrate from one cell to another through a pit connection. There is a well-developed chromatin net work.

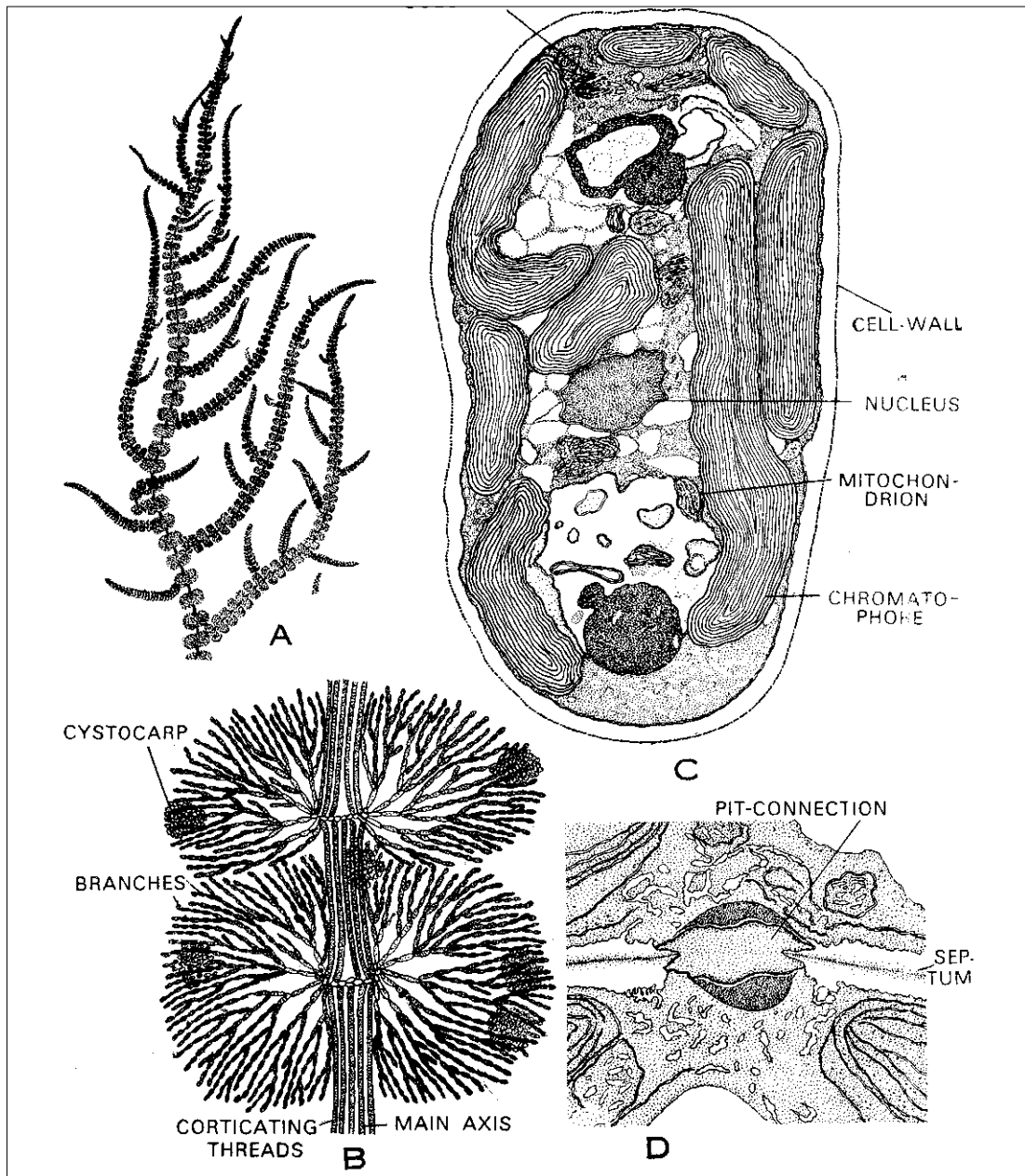


Fig. 7.1 *Batrachospermum*, A. Thallus showing habit; B. Part of thallus with glomerules and cystocarps; C. Electron micrograph (diagrammatic) of a vegetative cell, D. Electron micrograph (diagrammatic) at the region of a septum showing pit connection. (C and D – after Brown and Weier, 1970).

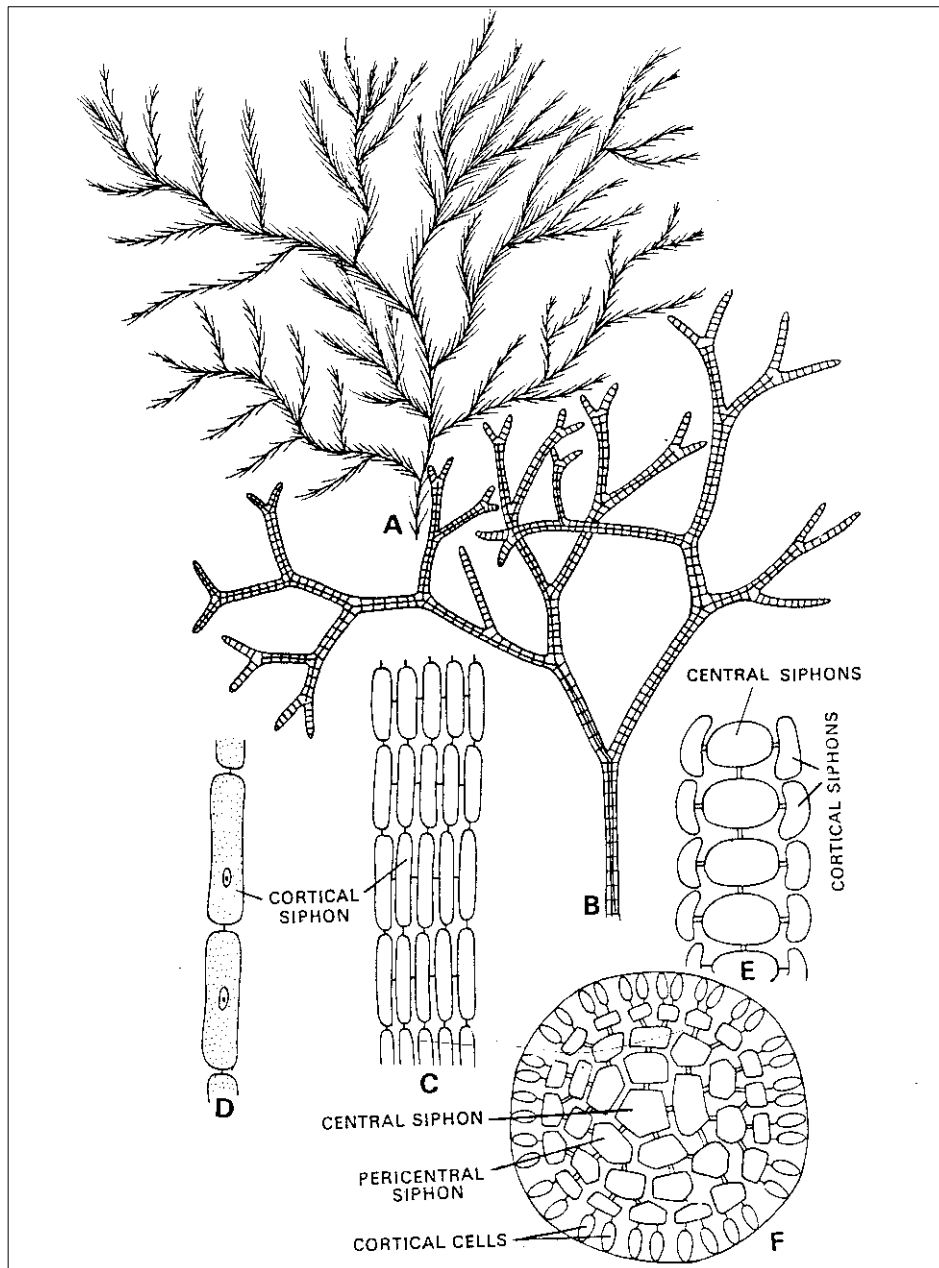


Fig. 7.2 *Polysiphonia* sp. A.habit of the plant; B. a portion of the plant (somewhat enlarged); C-D. cortical siphons; E. filament showing central siphons; F. T.S. of siphonous filament (Adopted from Pandey, 2004).

The Chromatophores and Pigments – In majority of Rhodophyceae, the number of chromatophores is more than one per cell (Fig. 7.1C). They may be band-like in Ceramiales, and irregularly lobed or discoidal in *Polysiphonia*. In lower Rhodophyceae (order Bangiales), there is a single stellate chromatophore in each cell.

Chromatophore possesses a centrally placed naked (without starch sheath) pyrenoid. The pigments which are abundantly occurred in red algae are γ -phycoerythrin (red water soluble pigments) and γ -phycocyanin (blue water soluble pigments). Besides, chlorophyll **a**, chlorophyll **b**, xanthophylls and carotenes (β -carotene) are present.

Reserve food products – The most important food product is floridean starch. In the form of small grains, it is distributed throughout the cytoplasm. The floridean starch differs from the chlorophycean starch in being devoid of amylose. In some respects, the floridean starch resembles the amylopectin of higher plants. In many Rhodophyceae a soluble sugar, **floridoside**, is found; Floridoside is a galactoside of glycerol.

Endoplasmic reticulum – In red algae the functions of endoplasmic reticulum are diverse and manifold including (a) septal plug formation, (b) fibrous vacuole formation, (c) spermatial vacuole formation, (d) vesicle formation in spores, (e) mucilage production by fusion cells, and (f) cleavage channel formation and wall secretion during cytokinesis.

Golgi bodies – The golgi-derived vesicles play an important role in cell wall formation and in the production storage food materials. Golgi bodies consist of vesicles of fibrillar, cored or striated.

5. Reproduction

The reproduction takes place by vegetative, asexual and sexual methods.

(i) Vegetative Reproduction

Rarely fragmentation of thallus has been reported in fresh water Bangioideae, e.g., *Asterocystis*. The Red Sea alga *Centroceros clavatum* produces missile-shaped vegetative propagules, carried away by ocean currents and settle on leaves of seagrasses where they develop into new individual plants.

(ii) Asexual Reproduction

Motile reproductive structures are completely absent in Rhodophyceae. Asexual reproduction of the gametophyte takes place by monospores, neutral spores, tetraspores and carpospores. Production of monospores in monosporangia (a single monospore in a single monosporangium) is the chief method of propagation in the *Chantransia*-stage of *Batrachospermum*. Asexual reproduction takes place by neutral spores in *Porphyra* and *Bangia*. These spores are produced directly by transformation of vegetative cells into spores. *Tetraspores* are produced in the tetrasporangium after meiotic division. Tetraspore germinates and gives rise gametophyte, e.g. *Polysiphonia*. Production of carpospores is a common feature in Florideae. In the order Nemalionales, the carpospores are haploid and on germination give

rise to sexual gametophytic plant; in the order Florideae, the carpospores are diploid and germinate into a sporophytic plant.

(iii) Sexual Reproduction

In majority of Rhodophyta, the sexual reproduction is *oogamous* which is highly elaborative and specialized type. The entire reproductive process in Rhodophyta is unlike that of any other group of the plant-kingdom. Sexual reproduction has not reported in Bangioideae except *Bangia* and *Porphyra*. In oogamy female sex organ known as *Carpogonium* and male sex organ, *spermatangium* (antheridium) are involved.

Male reproductive structure – Non-motile male gametes termed as spermatia are brought about by water currents and lodged on the tip of the female reproductive structure. The spermatia are borne singly within an spermatangium. The spermatangia may be disposed in clusters on certain special branches as in *Polysiphonia* (Fig. 7.3 A, B, C) or in others they may lie in sori as in *Apoglossum*.

Female reproductive structure – The female organ, carpogonium may be sessile in Bangioideae (the most primitive group); but in Florideae, they are borne on a special branch, carpogonial branch or procarp (Fig. 7.3D, E). The procarps are present on greatly reduced fertile trichoblasts of the female gametophyte. The initial of the fertile female trichoblast arises 3-4 cells away from the apex of the thallus. This initial grows into 5-7 cells in length. The three basal cells undergo divisions to give rise pericentral cells. One of the pericentral cells on the adaxial side (facing axis side) functions as the supporting cell of the future carpogonial filament (Fig. 7.3E). This supporting cell by undergoing successive transverse divisions, forms 4-celled, curved carpogonial filament. The terminal cell of the carpogonial filament metamorphoses into a carpogonium with a swollen base and a long, erect trichogyne (Fig. 7.3F). The trichogyne is demarcated by a median constriction from the basal, swollen portion of the carpogonium in which egg nucleus is located. Egg cell is rich with protoplasm and reserve food materials.

Fertilization – Spermatia are lodged on the trichogyne (Fig.74A, B). The tip of the trichogyne becomes mucilaginous and the wall between spermatium and the trichogyne dissolves. The male nucleus enters through the opening, moves down the trichogyne and finally fuses with the egg nucleus. After fertilization trichogyne shrivels away.

Post-fertilization changes – Immediately after the fertilization, the zygote divides meiotically to form four haploid nuclei in *Batrachospermum* and other members of the order Nematiales. At this time, the fertilized carpogonium develops several small protuberances. Haploid nuclei divide mitotically and migrate into the protuberances. Each protuberance consisting of a single nucleus starts functioning as a initial of a gonimoblast filament. Thus, several branched gonimoblast filaments (Fig. 7.4C) arise from the base of the carpogonium. The terminal cells of the gonimoblast filaments later differentiate into carposporangia within which the haploid carpospores are formed singly.

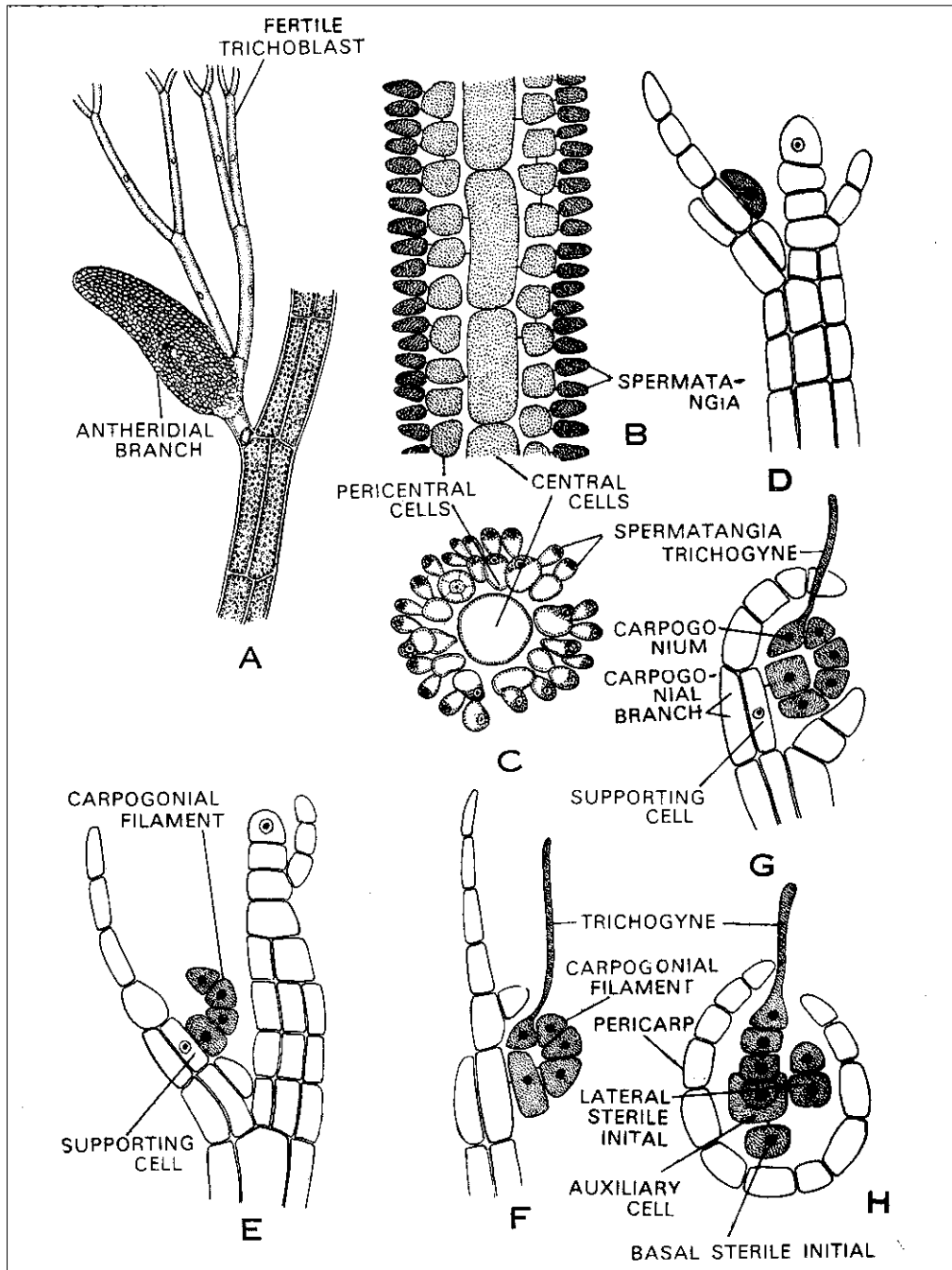


Fig. 7.3 *Polysiphonia*, A. part of a thallus with an antheridial branch; B. antheridial branch in longitudinal section, C. transverse section of antheridial branch; D-G. showing stages in development of carpogonium.

(adopted from Pandey, 1981).

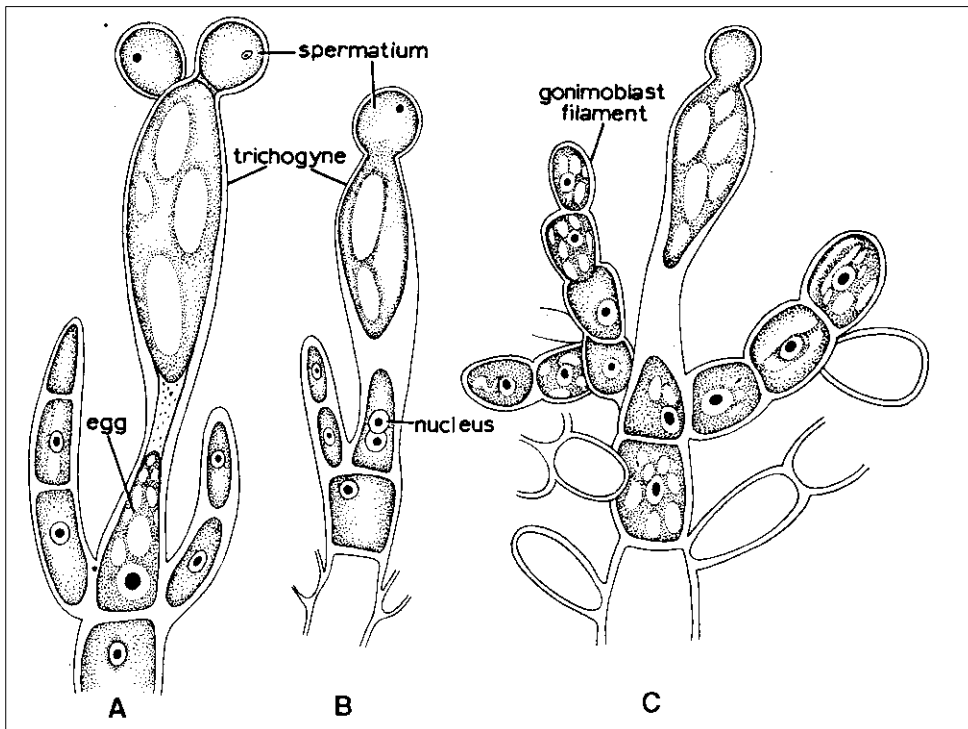


Fig. 7.4 *Batrachospermum moniliforme*. A-C, fertilization and post-fertilization stages.

In *Polysiphonia*, zygote divides mitotically and gives rise diploid carpospores. After fertilization in *Polysiphonia*, the supporting cell divides and produces an auxiliary cell just near the base of the carpogonium (Fig. 7.5A, B). A tubular connection is established in between the base of the carpogonium and auxiliary cell, and the diploid zygotic nucleus lying in the carpogonium now passes down into the auxiliary cell. Later the diploid nucleus divides mitotically produces gonimoblast filaments on the upper side (Fig. 7.5B). Carposporangia and carpospores are diploid in this genus. After the formation of carposporangia, there is a gradual fusion of the supporting cell, the auxiliary cell and the cells of sterile filaments. This leads to a formation of large irregularly-shaped cell, termed as placental cell (Fig. 7.4C). In the meantime, fleshy pericarp around the carposporangia is formed by the divisions of pericentral cells near the supporting cell of the female trichoblast. As a result, an urn-shaped fruit body known as cystocarp with a ostiole (opening) is formed (Fig. 7.4D). This is carposporophyte stage with cystocarp in which carposporangia are present.

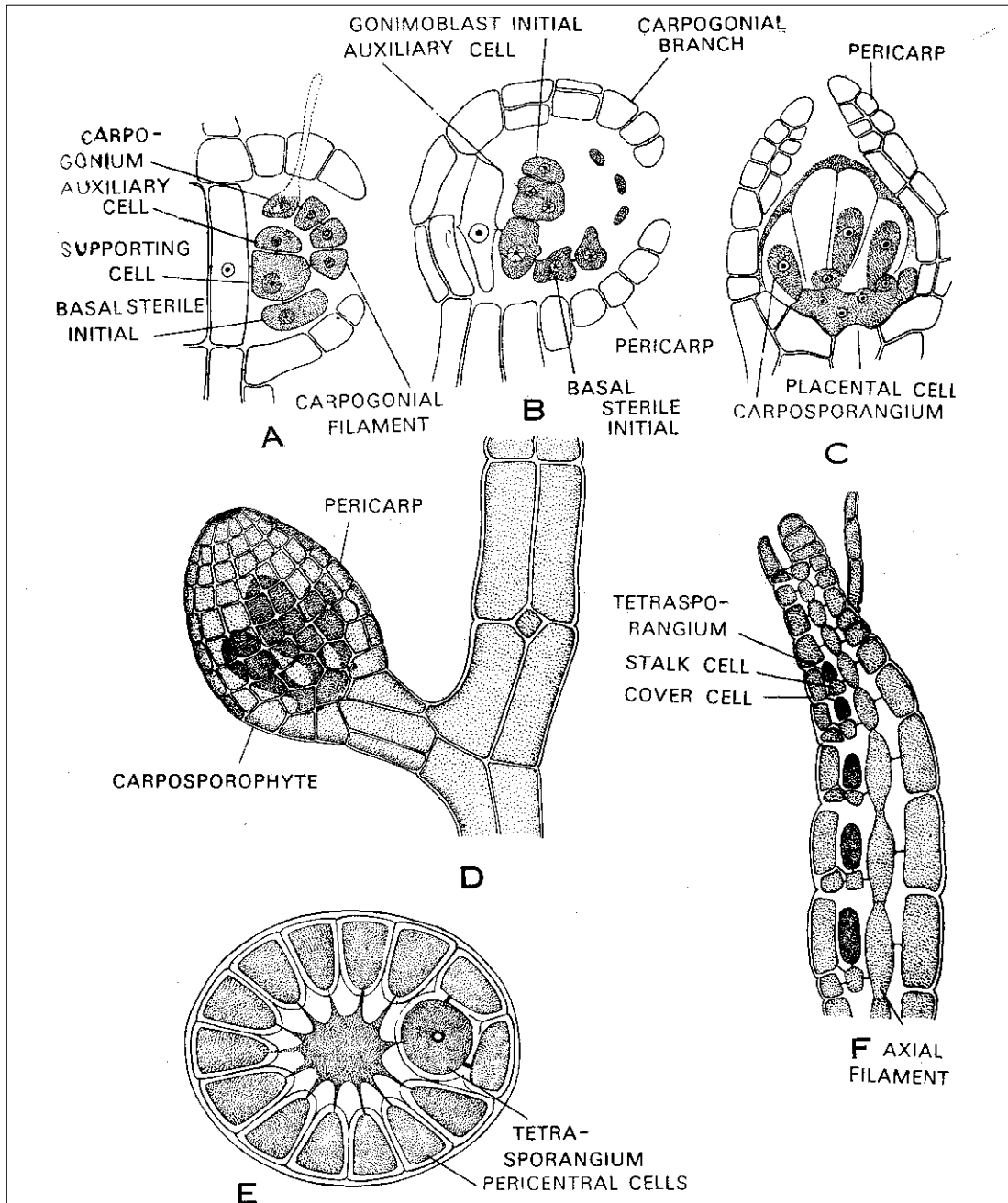


Fig. 7.5 *Polysiphonia*. A. a fertilized carpo-gonium with auxiliary cell; B & C. stages of development of a carposporophyte; D. a mature cystocarp; E & F. showing development of a tetrasporophyte in transverse and longitudinal section respectively (Based on Smith, 1955).

Germination of carospores – In *Batrachospermum*, haploid carospore germinates and gives rise heterotrichous habit of *Chantransia* stage which later differentiates into adult plant of *Batrachospermum*.

In *Polysiphonia*, the diploid carpospore is germinated to give rise diploid tetrasporophyte which bears tetrasporangia. This tetrasporophyte is morphologically similar to the haploid gametophyte bearing sex organs. Now the nucleus of tetrasporangium undergoes meiotic divisions and gives rise 4 haploid tetraspores. On germination, these tetraspores develop into gametophytic plants bearing sex organs.

6. Life Cycles

Red algae exhibits two types of life cycles:

(i) *Haplobiontic* – Two well developed haploid phases alternate with diploid zygote, e.g., *Batrachospermum* (Fig. 7.6).

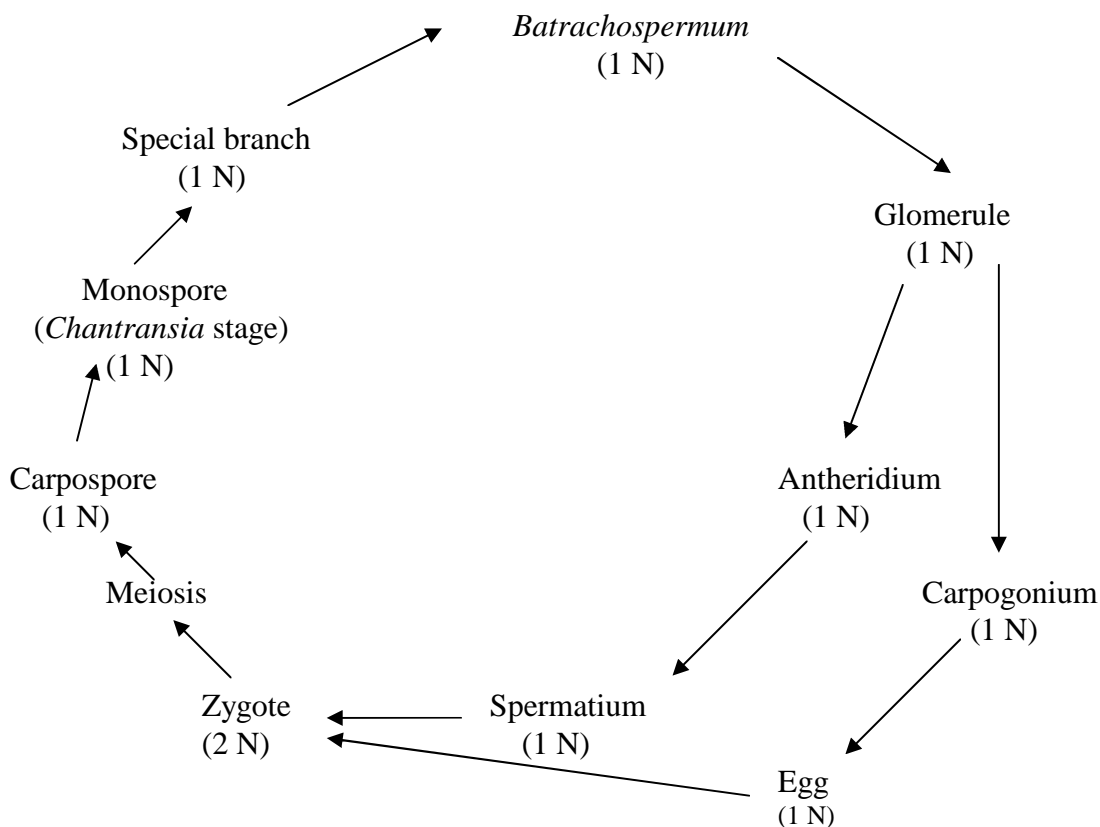


Fig. 7.6 Life cycle of *Batrachospermum*.

Morphologically, *Batrachospermum* is *triphasic* (or *trigenic*) as it involves alternation of three successive, dissimilar haploid somatic generations. So it is also known as Haplohaplohaplontic life cycle. Cytologically, it is haplobiontic life cycle.

(ii) **Diplobiontic** – Two diploid phases and one haploid phase occur, e.g., *Polysiphonia* (Fig. 7.7).

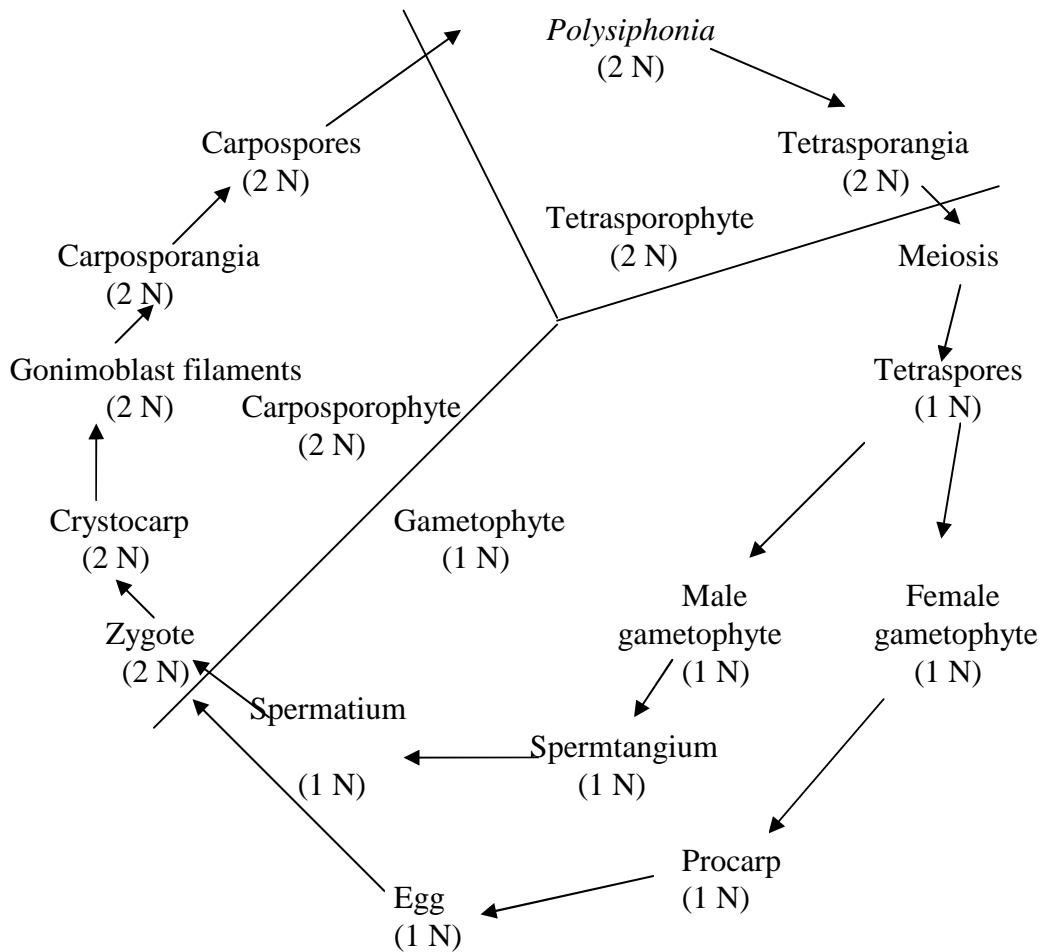


Fig. 7.7 Life cycle of *Polysiphonia*

7. Classification

The class, Rhodophyceae divided into two subclasses, (i) Bangioideae and (ii) Florideae.

(A) Bangioideae

The subclass *Bangioideae* is characterized by having the intercalary growth of thallus and diploid carpospores derived directly from the zygote.

There is a single order Bangiales in this subclass.

(B) Florideae

In the subclass Florideae, the growth of the thallus is strictly apical and plasmodesmatal strands are very conspicuous. The carpospores are formed indirectly from the zygote.

There are six orders in this subclass, viz., (A) Nemalionales, (B) Gelidiales, (C) Cryptonemiales, (D) Gigartinales, (E) Rhodymeniales, and (F) Ceramiales.

(a) Nemalionales – The members of this order are non-tetrasporic, and carposporophytes are derived from zygote which undergoes meiosis, e.g., *Batrachospermum*.

(b) Gelidiales – This order possesses only the tetrasporic plants of Florideae where the carposporophyte develops directly from the carpogonium. There is absence of auxiliary cells. The thallus is compact and all the members are uniaxial in construction, e.g., *Gelidium*.

(c) Cryptonemiales – They are the only tetrasporic Florideae which bear an auxiliary cell borne in a special filament of the gametophyte. Auxiliary cell filaments are supposed to be modified carpogonial filaments. These plants show diplobiontic type of life cycle and possess the most elaborative carposporophytes in the Rhodophyceae. The members of Cryptonemiales have their cell walls impregnated with lime. Some of these calcareous algae develop coral reefs, e.g. *Corallia*.

(d) Gigartinales – They are the tetrasporophytic Florideae. The auxiliary cell is developed before the fertilization and it is a vegetative cell of the gametophyte.

(e) Rhodymeniales – They are also tetrasporic Florideae. Auxiliary cell is formed before fertilization. Closed cystocarp (without an ostiole) is present in this order.

(f) Ceramiales – They are tetrasporic Florideae. The auxiliary cell is formed after fertilization. Diploid carpospores give rise the diploid sporophyte, e.g., *Polysiphonia*.

8. Phylogeny and Interrelationships

Fossil evidences show that the Rhodophyta must have evolved after Cyanophyta during the precambrian era. Both groups resemble each other in many morphological and biochemical features (Table 7.1). Although the members of Bangioideae are less elaborative than the Florideae but they resemble the Cyanophyta in lacking the sexual reproduction and also in cell structure.

The most important resemblances these two groups show are: (1) Presence of biliprotein pigments, (2) total lack of flagellated stages, (3) similarity of rhodophycean and cyanophycean

starch, (4) thylakoids arranged singly and widely separated, (5) xylans as chief component in cell wall, (6) sulphated galactose, uronic acid, glucose and xylose as main components in the mucilage of Cyanophyta and, Bangiales and Nematinales of Rhodophyta, and (7) presence of pit connections in many Florideae and Stigonematales of Cyanophyta.

In spite of these similarities, there are some fundamental differences in the cell structure, pigmentation and reproduction in between these two groups (Table 7.1).

Table 7.1. Differences between Rhodophyta and Cyanophyta

Sl.No.	Character	Rhodophyta	Cyanophyta
1	Cell structure	Eukaryotic	Prokaryotic
2	Pigments	Chlorophyll a , and chlorophyll d , zeaxanthin, neoxanthin	Chlorophyll a , myxoxanthin, myxoanthophyll, oscillaxanthin
3	Cell wall	Cellulose and other carbohydrates	Mucopolymers are main components in some forms
4	Motile stages	Completely absent	Non-flagellate multicellular motile stages, i.e., hormogonia formed in many forms
5	True sexuality	Present	Absent; a primitive type of parasexuality, i.e., genetic recombination, occurs in some members
6	Heterocyst and nitrogen fixation	Absent	Many species have heterocysts and can fix atmospheric nitrogen
7	Chromosomes	Typically eukaryotic	True chromosomes not known, DNA fibrils not associated with histones but present in nucleoplasm
8	Endoplasmic reticulum	Present	Absent
9	Golgi bodies	Present	Absent

On account of the above similarities and differences, it is widely believed that the Rhodophyta and Cyanophyta might have evolved from the common ancestor. Modern phycologists believe that the Rhodophyta is a distinct group of having primitive eukaryotic algae with many similarities with Cyanophyta.

9. Economic importance

The gelling agent, *agar* used in microbiological media is extracted from red algae. The *Porphyra* is used as an important ingredient in soups and also cooked as a flavouring agent with

meat in China and Japan. The alga *Rhodymenia palmata* is used as a food and also in the preparation of medicines. Another important edible alga, *Chondrus crispus*, commonly known as Irish moss, is utilized in the preparation of various pharmaceuticals including laxatives and cosmetics.

10. Summary

The phylum Rhodophyta is characterized by the pigment, γ -phycoerythrin which gives red colour to the thallus. There is a great diversity in the vegetative structure of red algae. The subclass Bangioideae, with a single order Bangiales, comprises unicellular (*Porphyridium*), filamentous (*Goniotrichum*) and Parenchymatous (*Porphyra*) forms.

The red algae are truly eukaryotic. They have microtubules but lack centrioles and flagella. The cells are uninucleate in lower Rhodophyceae orders such as Cryptomonales and Bangiales. In higher orders, ceramiales, Rhodymeniales etc., cells are multinucleate. The most important food product is floridean starch.

The reproduction takes place by vegetative, asexual and sexual methods. The sexual reproduction is oogamous, which is highly elaborate and specialized type. The female sex organ is known as carpogonium and the male sex organ is spermatangium. During post-fertilization, an urn-shaped fruit body, known as cystocarp with a ostiole (opening) is formed. This is a carposporophyte stage with cystocarp in which carposporangia are present. In *Batrachospermum*, haploid carpospore (present in carposporangia) germinates and gives rise *Chantransia* stage which in turn differentiates into adult plant of *Batrachospermum*. In *Polysiphonia*, the diploid carpospore germinates to give rise to the diploid tetrasporophyte that bears tetrasporangia. Now the nucleus of tetrasporangium undergoes meiotic divisions and gives rise 4 haploid tetrasproes. On germination, these tetraspores develop into gametophytic plants bearing sex organs.

Model Questions

(1) Essay Questions

- (i) Give an account on characteristic features and reproduction in Rhodophyta.
- (ii) Discuss characteristic features and post-fertilization changes in *Polysiphonia*.

(2) Short Answer Questions

- (i) Post-fertilization changes in Rhodophyceae
- (ii) Phylogeny and interrelationships of Rhodophyceae
- (iii) Thallus organization in Rhodophyceae
- (iv) Classification of Rhodophyceae.
- (v) Cystocarp in *Polysiphonia*.

- (vi) Thallus organization in *Batrachospermum*.
(vii) Differences and similarities between Rhodophyceae and Cyanophyceae.

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