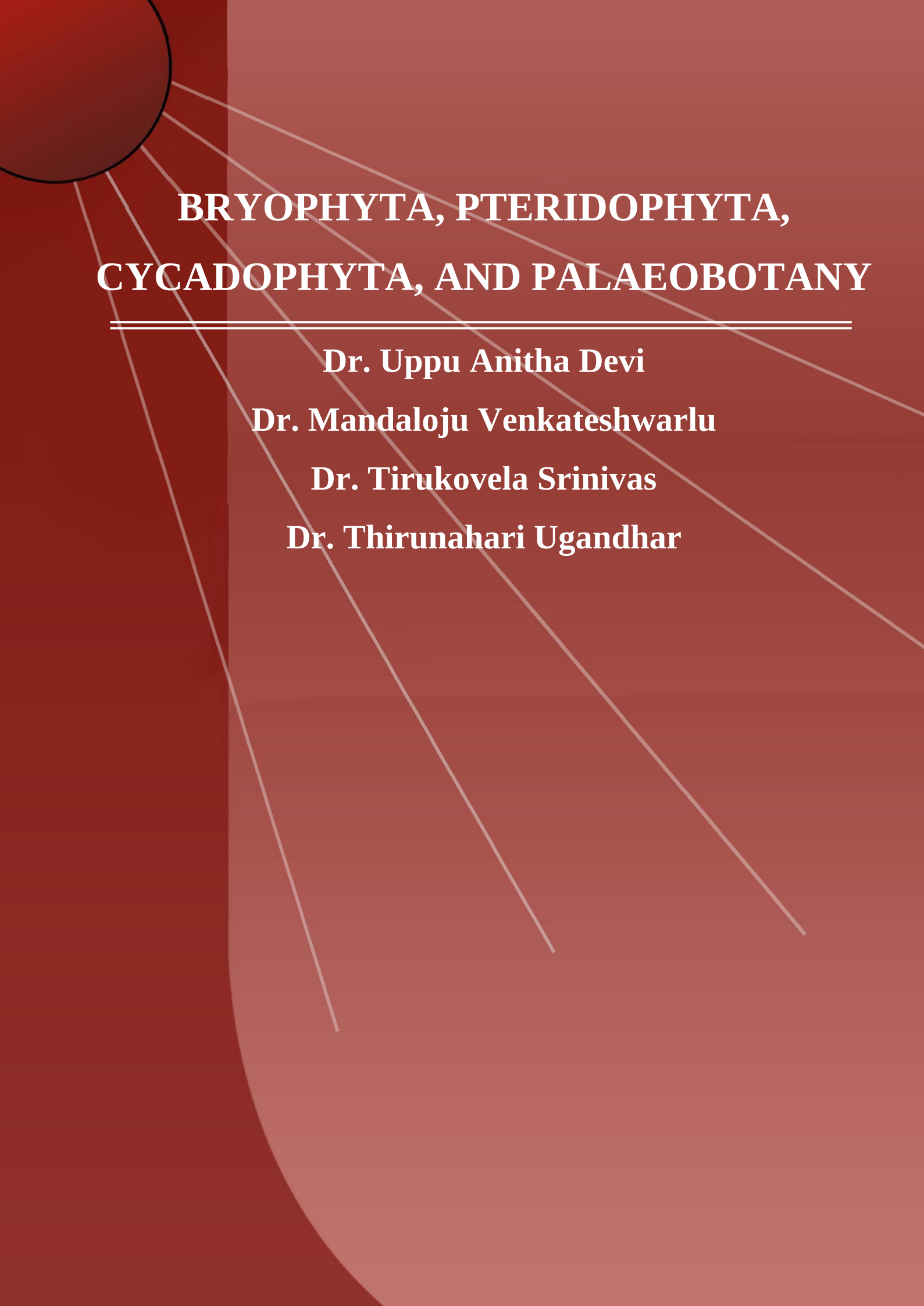




BRYOPHYTA, PTERIDOPHYTA, CYCADOPHYTA, AND PALAEOBOTANY

Dr. Uppu Anitha Devi

Dr. Mandalaju Venkateshwarlu

Dr. Tirukovela Srinivas

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PG & UG Students in Indian Universities.

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PREFACE

This book has been meticulously crafted to serve as a comprehensive guide to the syllabus for the Post Graduate course in M.Sc. Botany, particularly in Indian universities. The content spans across essential topics in Bryophyta, Pteridophyta, Gymnosperms, and Paleobotany, providing students with a thorough understanding of these plant groups, their evolutionary significance, and their ecological roles.

The first unit focuses on Bryophyta, covering their origin, classification, ecological importance, and the morphological, anatomical, and reproductive aspects of key genera like *Marchantia*, *Sphagnum*, *Polytrichum*, and *Anthoceros*. The evolutionary development of sporophytes and gametophytes is also explored in detail, making it an indispensable resource for students in this field.

Unit II delves into Pteridophytes, emphasizing their origin, evolution, morphology, and reproduction. The unit also explores advanced topics such as Telome theory, Stelar evolution, heterospory, and seed habit, providing a solid foundation in understanding the evolution of vascular plants. Detailed discussions on genera such as *Equisetum*, *Selaginella*, *Ophioglossum*, and *Psilotum* are included, along with fossil records to aid in comparative studies.

The third unit focuses on Gymnosperms, their evolution, classification, morphology, and reproduction. Special attention is given to important genera such as *Williamsonia*, *Ginkgo biloba*, and *Ephedra*. The economic significance of Gymnosperms in India is also highlighted, along with a dedicated section on the subclass *Pinidae* and the family *Araucariaceae*.

Unit IV is dedicated to Paleobotany, introducing students to the scope, objectives, and techniques used in this fascinating field. The unit explores fossilization, fossil types, and the geological time scale, with a special focus on fossil Gymnosperms like *Williamsonia* and *Pentaxylon*. The contributions of renowned paleobotanists such as Birbal Sahni are also highlighted, enriching the study of plant evolution through fossil evidence.

Throughout this book, students will find numerous diagrams that enhance their understanding of complex concepts, making it a valuable resource for both academic learning and practical application. It is designed to assist students in mastering the key concepts and developing a deep appreciation for the diversity and evolution of plant life.

This book is intended to be a cornerstone for the M.Sc. The botany curriculum is created to foster a greater understanding of plant biology among students in Indian universities.

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UNIT-1:- BRYOPHYTA**INTRODUCTION****1. Bryophyta: Introduction, Origin, Classification, and Ecology. Economic importance of Bryophyta.**

Bryophytes are a group of non-vascular plants that primarily inhabit moist environments. The term "Bryophyta" was first introduced by Braun in 1864. Bryophytes serve as a connecting link between thallophytes and pteridophytes, and this group includes liverworts, hornworts, and mosses. Due to their ability to live both in water and on land, bryophytes are often called the "amphibians of the plant kingdom."

Bryophytes exhibit a "heteromorphic alternation of generations," consisting of a dominant gametophyte phase and a dependent, reduced sporophyte phase. The gametophyte is the main plant body, which can be dorsiventral and dichotomously branched in primitive forms, or differentiated into stem, leaves, and rhizoids in more advanced forms. Bryophytes lack vascular tissue such as xylem and phloem, and their plant body is composed of parenchymatous tissue.

Reproduction in bryophytes can occur vegetatively through tubers, bulbils, protonemal branches, or fragmentation. Sexual reproduction is oogamous, involving the production of antheridia (male organs) and archegonia (female organs). The antheridium is club-shaped and stalked, while the archegonium is flask-shaped with a swollen venter containing the egg cell. Fertilization occurs in the presence of water, leading to the development of a sporophyte, which is differentiated into the foot, seta, and capsule. The capsule produces haploid spores through reduction division, and in some cases, structures like elaters or pseudo elaters may develop alongside the spores.

Origin of Bryophytes

Bryophytes are believed to have originated from the upper Carboniferous period, although fossil evidence is limited. Two main theories exist regarding their evolution: one suggests that bryophytes arose from an algal ancestor, while the other proposes that they are descendants of pteridophytes.

Algal origin of Bryophytes

The most widely accepted theory is that bryophytes originated from green algae, specifically the Chlorophyceae group. This theory is supported by the similarities in

chlorophyll and xanthophyll pigments between the two groups, as well as the amphibious nature of bryophyte gametophytes and the presence of ciliated antherozoids, which are reminiscent of their aquatic algal ancestors. Fritsch, a prominent phycologist, has suggested that bryophytes may have evolved from members of the order Chaetophorales within the Chlorophyceae.

The idea that green algae contain the essential elements for developing more complex organisms is widely accepted in the context of bryophyte evolution. The heterotrichous habit, including prostrate and erect growth forms, is particularly well-suited to terrestrial life. Parenchymatous terrestrial green algae like *Frittschiella* show the early stages of evolution toward the thallose gametophyte of primitive bryophytes.

Several factors suggest that Chlorophyceae represent the ancestral stock of bryophytes, rather than brown or red algae, despite the latter having differentiated structures like axes and leaves. Many who support the idea that the dorsiventral, prostrate gametophyte thallus of bryophytes is primitive also believe that bryophytes originated from algal stock. However, there are differences between bryophytes and their proposed algal ancestors. Even in simpler bryophytes like *Pellia*, the thallus structure is significantly more advanced than that of algae, being composed of parenchymatous tissue derived from a single apical cell. Moreover, the reproductive organs of bryophytes do not closely resemble the antheridium and oogonium of algae. One key difference is the retention of the female gametophyte within the parent plant, leading to a loss of motility, which is not seen in algae.

Origin of Sex Organs

In the context of an algal origin for bryophytes, it has been suggested that both the antheridium and archegonium originated from gametangia like those found in *Ectocarpus*. The derivation of the archegonium is more complex, but some theories propose that progressive sterilization occurred after the development of a superficial layer to form a wall. This theory suggests that the neck canal cells (NCC) were originally female gametes, with the venter canal cell (VCC) being a sister cell to the oosphere, potentially acting as a gamete. However, there is no evidence of embryos developing from the fertilization of the VCC, leaving the theory of bryophyte derivation from algae still open to question.

Pteridophyte Origin of Bryophytes

The second theory, which suggests a pteridophytic origin of bryophytes, has been proposed by several researchers. This regressive theory posits that bryophytes evolved from more complex forms through a process of reduction. Kashyap (1919) put forward the idea that hepatics, a group of bryophytes, may have arisen from pteridophytes. He suggested that the simplest forms of hepatics are reduced versions of more complex pteridophytes.

According to Kashyap, there are several similarities between pteridophytes and bryophytes in thallus structure, sex organ structure, and spore formation methods. For instance, the gametophyte of *Lycopodium cernuum* is nearly identical to that of *Anthoceros erectus*, leading to the hypothesis that the evolution of the dorsiventral gametophyte in *Marchantia* may have been influenced by similar structures in pteridophytes. Furthermore, the gametophyte of *Equisetum debile* resembles that of *Marchantia*, further supporting the idea of a pteridophytic origin for bryophytes.

Pteridophytic Origin of Bryophytes

Christensen (1954) proposed that bryophytes may have originated from different types of pteridophytes. He suggested three possible sources.

1. **Pteridophytes with leaves on both the gametophyte and sporophyte** - These could have given rise to bryophytes that have a more complex structure with differentiated organs.
2. **Leafless pteridophytes like *Rhynia*** - These could have led to the evolution of simpler bryophytes with a less differentiated structure.
3. **Polyphyletic origins from various pteridophytes** - This theory suggests that different bryophyte groups may have evolved independently from different pteridophyte ancestors.

Proskauer (1960) added to this by suggesting that the Anthocerotean type of bryophytes might have been derived from a pteridophyte known as *Homeophyton*. This suggests a direct lineage from specific types of pteridophytes to groups of bryophytes.

Classification of Bryophytes

Bryophytes have been classified differently by various bryologists over time. Here is an overview of some key classifications.

1. **Eichler (1883)** divided bryophytes into two groups: **Hepaticae** (liverworts), **Musci** (mosses)
2. **Campbell, Smith, and others** divided Bryophyta into three classes: **Hepaticae**, **Anthocerotae**, **Musci**
3. **Rothmaler (1951)** provided a more refined classification, dividing Bryophyta into three classes: Hepaticopsida, Anthocerotopsida and Bryopsida Proskauer (1957) later renamed the second class to Anthocerotopsida.
4. **According to the "International Code of Botanical Nomenclature,"** bryophytes are divided into three classes:

Hepaticopsida, Anthocerotopsida and Bryopsida

Class 1: Hepaticopsida (Liverworts)

The thallus in this class is dorsoventrally flattened and dichotomously branched. The sex organs develop from superficial cells on the dorsal side of the thallus. The sporophyte is differentiated into foot and capsule, or foot, seta, and capsule. Sporogenous cells develop from the endothecium. The capsule wall may be single-layered or multi-layered, and stomata are absent on the capsule wall. This class is further divided into three orders, which organize the diversity within Hepaticopsida based on various structural and reproductive characteristics. Here's a detailed overview of the classification and characteristics of Bryophytes.

Order I: Sphaerocarpales: Example: *Sphaerocarpus*

Characteristics: The plant body is thalloid, lacking air chambers and pores. Sex organs are enclosed singly in flask-shaped involucre. The sporophyte is differentiated into the foot, the seta, and the capsule.

Order II: Marchantiales Characteristics

The plant body is thalloid, with air chambers and pores. The ventral surface has two types of rhizoids (simple and tuberculated) and scales. Sex organs are embedded in the thallus. The sporophyte is differentiated into the foot, seta, and capsule.

Family I: Ricciaceae, Examples: *Riccia*, *Ricciella*, *Ricciocarpus*

Characteristics: The thallus has two distinct regions: assimilatory and storage. The assimilatory zone has air spaces. The capsule is embedded in the archegonial cavity and contains only spores, not elaters.

Family II: Marchantiaceae: Examples: *Conocephalum*, *Cryptometrium*, *Lunularia*, *Marchantia*, *Plagiochasma*.

Characteristics: The thallus has two distinct regions: assimilatory and storage.

The assimilatory zone is divided into several air chambers with branched assimilatory filaments. Pores are barrel-shaped. The sporophyte is differentiated into foot, seta, and capsule, and both spores and elaters are formed.

Order III: Jungermaniales Characteristics

The plant body may be thallus or foliose, with differentiation into axes and leaves. Only smooth-walled rhizoids are present. Antheridia are borne on long stalks. The sporophyte consists of a foot, seta, and capsule with a multilayered jacket. Divided into two sub-orders: Metzgerinae and Jungermanninae.

Sub-order I: Metzgerinae (Jungermanniales Anaerogynae)

Examples: *Pellia*, *Riccardia*, *Pallavicinia*, *Fossombronia*, *Symphyogyna*, *Metzeria*, *Calycularia*, *Blasia*, *Sewardiella*, *Petalophyllum*, *Treubia*.

Characteristics: The plant body is thalloid. Sex organs are scattered on the dorsal surface. The capsule of the sporophyte is spherical or oval with basal melanophores.

Family: Pelliaceae, Examples: *Pellia*, *Noteroclade*, *Calycularia*.

Characteristics: The thallus has irregular lobes. Antheridia and archegonia are scattered on the dorsal surface. The capsule is spherical or oval with basal elatophores.

Sub-order II: Jungermanninae

Examples: *Porella*, *Herberta*, *Frullania*, *Calypogeia*, *Mastigobryum*, *Radula*, *Scapania*, *Plagiochila*, *Cephalozia*, *Lophocolea*, *Nardia*.

Characteristics: The plant body is differentiated into axis and leaves. The axis bears three rows of leaves: two lateral larger leaves and a third smaller ventral leaf. Antheridia develop isolated or in small groups.

Family I: Porellaceae, Example: *Porella*

Characteristics: The thallus is differentiated into axis and leaves arranged in three rows. The perianth is large and inflated. Elaters are free and pointed at both ends.

Family II: Frullaniaceae, Example: *Frullania*

Characteristics: The thallus is pinnately branched and differentiated into axis and leaves. The leaves are arranged in three rows, with ventral leaves bifid and trumpet-shaped. Archegonia develop in groups of 2-12.

Class II: Anthocerotopsida

Characteristics: The thallus is dorsoventrally flattened and attached to the substrate by smooth rhizoids. Internally, the thallus is homogeneous, with each cell containing a chloroplast with a pyrenoid. Sex organs are completely embedded in the thallus. Antheridia develop in groups inside a chamber. The sporophyte is cylindrical and differentiated into foot and capsule, with the basal portion of the capsule being meristematic.

Family I: Anthocerotaceae, Examples: *Anthoceros*, *Phacoceros*, *Megaceros*, *Dendroceros*.

Characteristics: The capsule is linear and vertical, with stomata present on the capsule wall. The archesporium develops from the amphithecium.

Family II: Notothylaceae Example: *Notothylas*

Characteristics: The capsule is cylindrical and horizontal, with no stomata on the capsule wall. The archesporium may originate from either endothecium or amphithecium. Elaters are short and stumpy with irregular thickenings.

Class III: Bryopsida Characteristics: The plants are differentiated into axis, leaves, and multicellular rhizoids. Leaves have no midrib. Sex organs develop on the apical portion of the stem. The sporophyte is differentiated into foot, seta, and capsule, with the

sporogenous tissue and columella developing from the endothecium. The capsule has stomata, and peristomial teeth are present in two rows.

Sub-Class I: Sphagnidae Example: *Sphagnum*

Characteristics: The plant body consists of a protonema that develops into a single gametophore. The leaf has no midrib. Antheridia are lateral, and archegonia are terminal. The archesporium develops from the amphithecium.

Sub-Class II: Andreacidae Example: *Andreaea*

Characteristics: The gametophore is brittle and easily broken. The plant body shows no tissue differentiation. Leaves are often large. The archesporium and columella are formed from endothecium.

Sub-Class III: Bryidae: Divided into 3 cohorts and 15 orders, including 80 families.

Characteristics: The leaves have a midrib, and the sporogenous tissue is derived from the endothecium. The seta is long, and the capsule is more advanced.

Order: Funariales: Characteristics: Leaves are broad, forming a spatulate rosette-like structure. The capsule is wide, without a beak-like operculum. The peristome teeth occur in two rows in the terminal part of the capsule. Includes 5 families.

1. Gigaspermaceae,
2. Funariaceae,
3. Disceliaceae,
4. Oediopodiaceae,
5. Splachnaceae

Order: Polytrichales Characteristics: The leaves are narrow, and the capsule is formed. The calyptra is often hairy, and the peristome teeth are arranged in a simple row. It includes one family, **Polytrichaceae**, with examples like *Polytrichum* and *Pogonatum*.

Economic Importance of Bryophytes: Bryophytes, though small, are of immense ecological and economic significance. Their role in various ecosystems and human activities can be studied under the following headings.

1. Ecological Importance: (a) Pioneers of Land Plants: Bryophytes are considered pioneers in plant evolution as they were among the first plants to colonize barren rocks and lands. They play an essential role in establishing plant communities on new surfaces.

(b) Soil Erosion Prevention: Bryophytes, particularly mosses, grow densely, forming a mat-like structure that acts as a soil binder. This matting protects soil by: **Absorbing the impact of falling rainwater.** Retaining moisture, reducing runoff, and preventing soil erosion.

(c) Soil Formation: Mosses and lichens contribute to soil formation through the secretion of acids that break down rocks. Over time, their progressive decay enriches the soil with organic material.

(d) Bog Succession: Peat mosses (e.g., Sphagnum) play a crucial role in transforming waterlogged areas, such as lake banks, into solid land through the accumulation of dead plant material, enabling the growth of vegetation.

(e) Rock Builders: In streams and lakes with high calcium bicarbonate content, mosses, in association with green algae, help precipitate calcium carbonate. This process leads to the formation of calcareous deposits that harden into rock-like structures.

2. Formation of Peat: Peat is formed from the gradual accumulation and partial decomposition of dead plant matter in bogs, primarily by Sphagnum moss. The acidic environment created by Sphagnum slows down decomposition, leading to the formation of peat.

Uses of Peat include Fuel: In regions like Ireland and Scotland, peat is used as fuel. Production of Industrial Products: Ethyl alcohol, ammonium sulfate, peat tar, ammonia, paraffin, dye, and tannin are extracted from peat.

Horticulture: Peat improves soil texture and water retention.

Surgical Dressings: Due to its absorbent and antiseptic properties.

3. As Packing Material: Dried Bryophytes, especially mosses, have excellent water retention capabilities. This property makes them ideal as packing material for the shipment of perishable goods such as cut flowers, vegetables, fruits, bulbs, and tubers.

4. As Bedding Stock: In nurseries, Bryophytes are used to cover plant beds due to their capacity to retain moisture. This helps in maintaining optimal growing conditions for young plants.

5. Medicinal Uses: Bryophytes have been traditionally used in various medicinal applications: *Marchantia* spp.: Used in treating pulmonary tuberculosis and liver diseases. *Sphagnum* spp.: Decoctions are used for eye diseases and acute hemorrhage. *Polytrichum commune*: Effective in treating kidney and gall bladder stones. Sphagnum leaves and extracts from species like *Conocephalum conicum* and *Dumortiera* spp. exhibit antiseptic properties, aiding wound healing.

6. Experimental Botany: Bryophytes are valuable in scientific research. For instance, in the liverwort *Sphaerocarpos*, the mechanism of sex determination in plants was first discovered, contributing significantly to genetics.

7. As Food: Several Bryophytes, especially mosses, serve as food for animals such as birds, chicks, and reindeer in Alaskan regions, offering a source of nutrition in harsh climates.

Additional Economic Roles of Bryophytes

8. Water Retention in Agriculture: Bryophytes have the potential to be used in agricultural practices for maintaining soil moisture. Their water-retaining capacity helps in reducing irrigation needs, especially in drought-prone areas.

9. Environmental Indicators: Bryophytes are highly sensitive to changes in air and water quality, making them valuable bioindicators. Their presence or absence can help monitor pollution levels in ecosystems.

10. Carbon Sequestration: The ability of peat-forming mosses, such as *Sphagnum*, to sequester carbon in large amounts plays a vital role in mitigating climate change by reducing atmospheric carbon dioxide levels.

Finally, Bryophytes are not only essential for maintaining ecological balance but also contribute to various industries, agriculture, medicine, and environmental conservation. Their economic potential, both direct and indirect, continues to be explored across numerous fields.

2. Morphological distinction of Liverworts, Mosses, and Hornworts. Morphology, Anatomy, and Reproduction: Liverworts are bryophytes with a green, dorsiventral thallus that typically grows close to the ground. They are secured by delicate, simple hair-like processes called rhizoids, which supply water and minerals. Liverworts are among the first plants to complete migration to land, with fossil records showing plants resembling liverworts from about 350 million years ago.

Adaptations for land life include rhizoids, which function as absorbing organs but are less efficient than roots due to their simple structure. The plant body is compact and protected against desiccation, with a reduced surface area compared to aquatic algae. Most cells are protected by an epidermis, reducing water loss through transpiration, and the prostrate habit offers additional protection. However, the thallus is not completely

protected against desiccation, as the epidermal cells lack waterproof thickening, and the epidermal layer has unguarded pores for aeration.

Liverworts must live in very moist habitats and cannot withstand direct sunlight for long periods. They are found on the ground, riverbanks, moist rocks, tree trunks, or floating/submerged in water. High humidity, shade, and abundant soil moisture favor their growth. In terms of reproduction, the sex organs are jacketed and protected against drying air, but the sperm are motile and require external water to swim to the egg, indicating their aquatic ancestry. The quality of water, including factors like temperature, pH, and dissolved substances, affects sperm survival. Spores, however, are non-motile and wind-disseminated, which is an adaptation to a land habitat. Liverworts are still in a transitional stage of becoming fully adapted to land environments, exhibiting features of both aquatic and terrestrial plants.

Distinctive Features of Liverworts: Structure: Almost all liverworts, also known as hepatics, exhibit a dorsiventral structure, meaning they have a distinct top and bottom surface. This feature is consistent across most liverwort species, with very few exceptions.

Size: Liverworts are relatively small plants, typically only reaching a few inches in length. This compact size is a common characteristic of the group.

Plant Body: The liverwort plant body is always a gametophyte, meaning it is the sexual generation of the plant. This gametophyte is an independent organism.

The plant body can either be thallose, which means it is a flattened, undifferentiated structure, or it can be leafy. In leafy liverworts, the plant body is differentiated into a central axis with branches, both of which bear leaf-like structures. These leaf-like structures lack a midrib, a central vein commonly found in the leaves of higher plants.

Attachment: The liverwort gametophyte attaches to the ground using simple, one-celled structures called rhizoids. These rhizoids function primarily as absorptive organs.

Internal Structure: Inside, the gametophyte contains photosynthetic tissue, allowing it to produce food through photosynthesis.

The cells within this tissue have oil bodies, which can be simple or compound in structure. These cells also contain numerous small chloroplasts, which are the sites of photosynthesis. Notably, liverwort chloroplasts lack pyrenoids, which are structures found in the chloroplasts of some other plants and algae that are involved in the storage of starch.

Sex Organs: Liverwort sex organs are exogenous in origin, meaning they develop on the outside of the plant body. These organs can be found in dorsal positions (on the top surface) or at the terminal ends (tips) of the plant. Each sex organ develops from a single initial cell.

Sporogonium: The sporogonium, which is the spore-producing structure, is small and generally does not contain chlorophyll, thus it is not green. It lives almost entirely as a parasite on the parent gametophyte, relying on it for nutrients. The sporogonium lacks stomata, the pores typically used for gas exchange in other plants.

Differentiation of Sporogonium: The sporogonium can be differentiated into three parts: foot, seta, and capsule, or just into foot and capsule. In the genus *Riccia*, the sporogonium is particularly simple, lacking both foot and seta.

Meristematic Tissue: The sporogonium does not contain meristematic tissue, which is the type of tissue responsible for cell division and growth in other plant structures.

Sporogenous Tissue: The tissue that produces spores, known as sporogenous tissue, is endothelial in origin, meaning it develops from the inner tissue layers. A large portion of this tissue forms spores, which is a distinctive feature compared to other classes of Bryophyta. Sterile cells within the sporogonium elongate and develop into elaters, which have spirally thickened walls and help in the dispersal of spores.

Columella: Liverworts do not have a columella, which is a central column of sterile tissue found in the spore capsules of some other bryophytes.

Spore Germination: Upon germination, liverwort spores generally develop directly into new gametophyte plants. In some cases, spores may develop indirectly into gametophytes through an intermediate stage.

Distribution: Liverworts are a well-defined and widely distributed group, comprising more than 420 species across 35 genera. Notable Indian members include *Marchantia*, *Preissia*, *Dumortiera*, *Conocephalum*, *Exormotheca*, *Stephensoniella*, *Aitchisoniella*, *Cyathodium*, *Targionia*, *Cryptomitrium*, *Asterella* (*Fimbraria*), *Grimaldia*, *Reboulia*, *Plagiochasma*, *Athalamia*, and *Riccia*.

These species are predominantly terrestrial and thrive in moist environments, making them strictly hygrophilous. They typically grow on damp soil or rocks, with a few species found in floating water or submerged conditions. Some liverworts with larger thalli can survive in exposed locations that experience dry seasons interspersed with moist periods.

Liverworts are found from arctic to tropical regions, with a significant presence in temperate zones. In India, significant collections of liverworts have been made in the western Himalayas (west of Nepal) and the Punjab plain by Kashyap. Other areas with notable liverwort populations include the eastern Himalayas, the Gangetic Plain, and southern India.

MARCHANTIA (March.) L.

Division: Hepaticophyta

Class: Hepaticopsida

Order: Marchantiales

Family: Marchantiaceae

Genus: *Marchantia*

Habit and distribution. *Marchantia* is the most common, highly differentiated, and in many ways the most interesting genus. It is commonly found in moist, cool, shady situations and areas of burnt ground. The surface of damp soil, the sides of streams, springs, water courses, walls of wells, swamps, damp ravines, and wet rocks are the places suited for the growth of this Liverwort. It grows in large mats (Fig. 1.1). It has about 65 species. They are found all over the world. There are about 11 Indian species as reported by Chopra (1943). They are mostly confined to the Himalayas. The following three species of *Marchantia* have been reported by Kashyap from various parts of India, plains as well as the hills.

1. *M. palmata*. It is found in the plains as well as the hills. It has been reported from Kashmir Kumaon, Punjab India, Lahore, Sialkot, etc. It is distinguished by the presence

of a median, dark streak on the dorsal surface of each lobe of the thallus. The lobes are long, and narrow, the margin entire and the apex emarginate.

2. *M. nepalensis*. The median dark streak is lacking. Lobes d is short and broad and margin is generally crisped. The apex is emarginate. It has been reported from the Outer Himalayas, Punjab Plains, Kashmir, Garhwal, Kumaon, etc.

3. *M. polymorpha* (Fig. 1.2). It has been reported from the hills such as the Outer Himalayas up to 8000 ft., Pangi, Ladakh, Leh, etc. The thallus is relatively large, broad, slightly concave, or flat. The margin of the thallus lobes sinuates too lobed.

GAMETOPHYTE PHASE: It begins, as in Riccia, with the maturation of spores. Each spore on germination, produces a green thallus. Externally it has the same general appearance as that of Riccia. However, it differs in its large size, coarse nature, and more prominent and pronounced elongated lobes. It is somewhat better adapted to grow on land than Riccia. The green thallus is the gametophyte plant.

MARCHANTIALES-MARCHANTIACEAE: MARCHANTIA

External morphology of the thallus (Fig. 1.1). It is a dark, green, somewhat fleshy, flat, once or a few times dichotomously branched with a dorsiventral symmetry (B). Each thallus branch or lobe is traversed by a broad, thick, central midrib. It also has a notch at its apex at the bottom of the notch is located the growing point. The upper surface of the thallus is marked by rhomboidal to polygonal areas called the areolae (B). The boundaries between these areas mark the limit of the underlying air chambers.

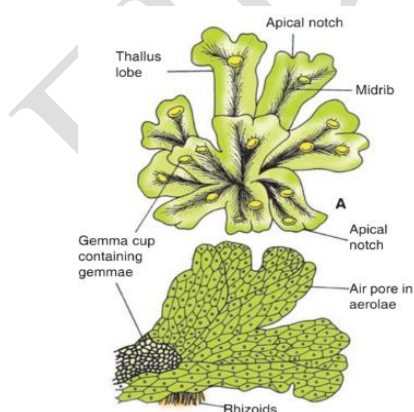


Fig. 1.1

Fig. 1.1. (A-B). *Marchantia* sp. A small patch of plants shows habit; B, part of the thallus, shows air pores, areolae, and gemma cups on the upper surface.

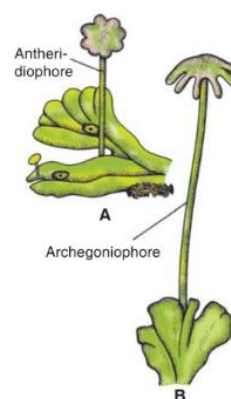


Fig. 1.2

Fig-1.2 *Marchantia*. Male (A) and Female (B) thalli of *M. polymorpha*.

Each area has a tiny conspicuous hole or an air pore in the center. The pore is visible on the surface as a light dot. The air pores permit aeration of the thallus with minimum dehydration. At times little cup-like structures, the gemma cups, are seen on the surface of the thallus. They arise in the midrib region. The margin of the cup is toothed and membranous. From the bottom of the cup arise numerous, green, flat, multicellular bodies called the gemmae. The mature gemmae get detached. The detached gemmae are washed onto the soil where each gives rise to two new gametophyte plants.

When the thallus attains sexual maturity, it bears gametangia bearing upright, stalked umbrella-shaped structures at the apices of certain lobes of the thallus (Fig. 1.2). These are called the gametophores or gametangiophores. They are of two kinds, antheridiophores (A) and archegoniophores (B). The former bear antheridia and the latter archegonia. The two kinds of gametophores are borne on different thalli so that *Marchantia* has male plants distinct from female plants. From the lower or the ventral surface of the thallus arise numerous elongated, single-celled, hair-like outgrowths, the rhizoids (Fig. 1.3A). The latter anchors them to the substratum. In addition, they absorb water and minerals in solution. The rhizoids are of two kinds of smooth-walled (Fig. 1.3 B) and tuberculate (Fig. 1.3 C). The tubercles are pronounced, peg-like invaginations of the wall. They extend across the cavity but do not form complete partitions. The tuberculate or peg rhizoids are thick-walled, narrow, and appressed to the surface of the thallus. They arise from beneath the scales and function as a capillary conducting system that serves to carry water to all the absorptive parts of the thallus. The smooth-walled rhizoids stand out from the thallus and penetrate the substratum to absorb water and to fix the thallus to it. They are broad, thin-walled with colorless contents. They are the first to be formed on germination. Besides the rhizoids the ventral surface bears purplish, flatter scales (Fig. 1.3 D). They are usually arranged in two to four rows on either side of the midrib (A). They are never in a single row as in *Riccia*. Each scale is a plate of cells one cell layer thick. It is attached obliquely and is divided by a narrow constriction into two parts, the body and the appendage (Fig. 1.3 D). In some species the appendage is absent. The scales are separate from the beginning. They are not formed by the splitting of a single lamella as in the case in *Riccia*. Galatis and Apostolakos (1977) reported the development of mucilage papillae from the periphery of the scales in *Marchantia*. These arise as idioblast cells, elongate, and appear club-shaped

the mucilage papillae secrete mucilage which surrounds and thus protects the growing region of the thallus from desiccation.

2. Internal structure (Fig. 1.4). There is greater internal elaboration of the thallus in *Marchantia* as compared with *Riccia*. In a vertical section, the thallus is many cells deep. The cells are arranged in three distinct regions (A) instead of two as in *Riccia*. These are (1) the epidermal region, (ii) the photosynthetic region, and (iii) the storage region.

Upper Photosynthetic zone

The outermost layer is the upper epidermis. Its cells are thin-walled square, compactly arranged, and contain few chloroplasts. Its continuity is broken by the presence of many barrel-shaped air pores. Each pore is surrounded by four to eight superimposed tiers of concentric rings. (Fig. 1.4) with three to four cells in each tier (Fig. 1.4 D).

Air pores are compound in nature. The lower tier consists of four cells that project in the pore, and the pore's opening looks star-like in the surface view (Fig. 1.4 C). The walls of the air pore lie half below and half above the upper epidermis (Fig. 1.4 B). Just below the upper epidermis, photosynthetic chambers are present in a horizontal layer (Fig. 1.4 B). Each air pore opens inside the air chamber and helps in the exchange of gases during photosynthesis. These chambers develop schizogenously (Vocalized separation of cells to form a cavity) and are separated from each other by single-layered partition walls. The partition walls are two to four cells in height. Cells contain chloroplast. Many simple or branched photosynthetic filaments arise from the base of the air chambers (Fig. 1.4 B).

Anatomy of the Gametophyte

A vertical cross-section of the thallus can be differentiated photosynthetic zone and lower storage zone (Fig. 1.4).

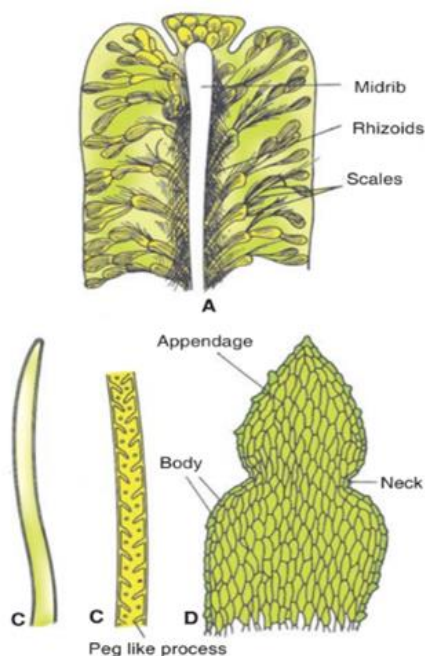


Fig. 1.3.

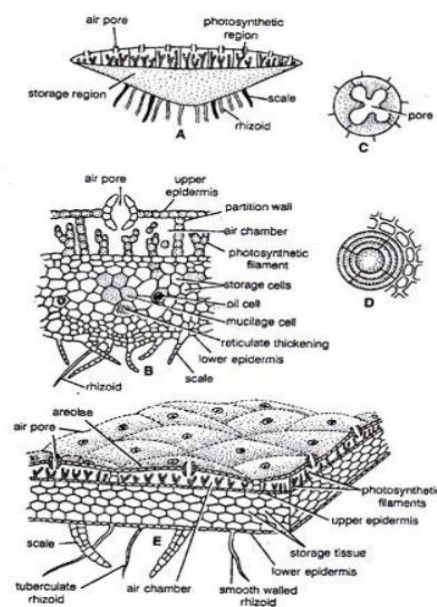


Fig. 1.4.

Fig. 1.3. (A-D). *Marchantia* sp. A thallus lobe bearing scales on the lower surface; B, smooth-walled rhizoid; C, tuberculate rhizoid; D, appendaged scale.

Fig. 1.4. (A-E). *Marchantia*, Internal structure of the thallus. (A) Vertical Transverse Section (V.T.S.) of the thallus (diagrammatic), (B) V.T.S. of the thallus (a part cellular), (C) Air pore as seen in the ventral view, (D) Air pore as seen in the dorsal view, (E) V.T.S. of the thallus in a three-dimensional view.

Storage Zone

It lies below the air chambers. It is thickened in the center and gradually tapers towards the margins. It consists of several layers of compactly arranged, thin-walled parenchymatous isodiametric cells. Intercellular spaces are absent.

Reproduction in *Marchantia*: *Marchantia* reproduces by vegetative and sexual methods.

(i) Vegetative Reproduction: In *Marchantia*, it is quite common and takes place by the following methods.

1. By Gemmae: Gemmae are produced in the gemma cups found on the thallus's dorsal surface (Fig. 1.5 A). Gemma cups are crescent-shaped, 3 m.m. in diameter with smooth, spiny, or fimbriate margins (Fig. 1.5 B). V. S. passing through the gemma cup shows that it is well differentiated into two regions:

The cells of this zone contain starch. Some cells contain a single large oil body or are filled with mucilage. The cells of the midrib region possess reticulate thickenings. The lowermost cell layer of the zone forms the lower epidermis. Some cells of the middle layer of the lower epidermis extend to form both types of scales and rhizoids (Fig. 1.4 B).

Upper photosynthetic region and inner storage region (Fig. 1.5 D).

The structure of both zones is like that of the thallus. Mature gemmae are found to be attached at the base of the gemma cup by a single-celled stalk. Intermingled with gemmae are many mucilage hairs. Each gemma is autotrophic, multicellular, bilaterally symmetrical, thick in the center, and thin at the apex. It consists of parenchymatous cells, oil cells, and rhizoidal cells. It is notched on two sides which lies the growing point (Fig. 1.5 C). All cells of the gemma contain chloroplast except rhizoidal cells and oil cells. Rhizoidal cells are collarless and large. Oil cells are present just within the margins and contain oil bodies instead of chloroplast.

Dissemination of Gemmae: Mucilage hairs secrete mucilage on absorption of water. It swells up and presses the gemmae to get detached from the stalk in the gemma cup. They may also be detached from the stalk due to the pressure exerted by the growth of the young gemmae. The gemmae are dispersed over long distances by water currents.

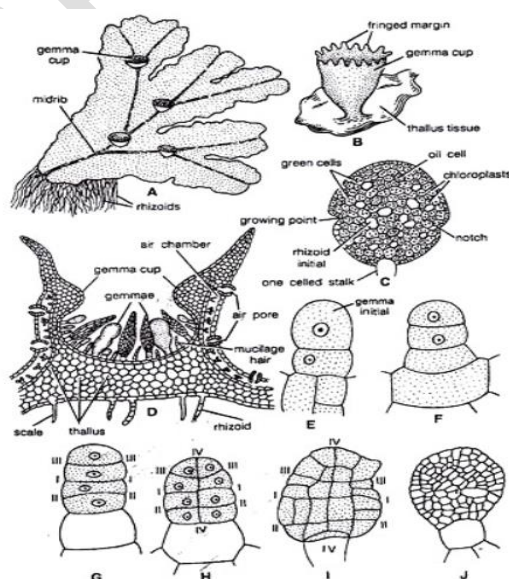


Fig. 1.5. (A-J). Marchantia. Gemma cup. (A) Thallus showing gemma cup on the dorsal surface. (B) A gemma cup, (C) Gemma, (D) Gemma cup in a vertical section, (E-J). Various stages in the development of Gemma.

Germination of Gemmae: After falling on a suitable substratum gemmae germinate. The surface which meets the soil becomes the ventral surface. The rhizoidal cells develop into rhizoids. Meanwhile, the growing points in which the two lateral notches form thalli in opposite directions. Thus, from a single gemma two thalli are formed. Gemmae which develop on the male thalli form the male plants and those on the female thalli form the female plant.

Development of Gemma

The gemma develops from a single superficial cell. It develops on the floor of a gemma cup. It is papillate and called gemma initial (Fig. 1.6 E). It divides by a transverse division to form lower stalk cell and an upper cell (Fig. 1.6 F). The lower cell forms the single-celled stalk.

The upper cell further divides by transverse division to form two cells. Both cells undergo by similar divisions to form four cells (Fig. 1.6 G). These cells divide by vertical and horizontal division to form a plate-like structure with two marginal notches. It is called gemma (Fig. 1.6 H-J).

2. Death and decay of the older portion of the thallus or fragmentation

The thallus is dichotomously branched. The basal part of the thallus rots and disintegrates due to aging. When this process reaches up to the place of dichotomy, the lobes of the thallus get separated. The detached lobes or fragments develop into independent thalli by apical growth (Fig. 1.6A-C).

3. By adventitious branches: The adventitious branches develop from any part of the thallus or the ventral surface of the thallus or rarely from the stalk and disc of the archegoniophore in species like *M. palmata* (Kashyap, 1919). On being detached, these branches develop into new thalli (Fig. 1.6 D).

ii) Sexual Reproduction:

Sexual reproduction in *Marchantia* is oogamous. All species are dioecious. Male reproductive bodies are known as antheridia and female as archegonia. Antheridia and archegonia are produced a special, erect modified lateral branches of thallus called antheridiophore and archegoniophore) respectively (Fig. 1.7 A, B). Further growth of the thallus is checked because the growing point of the thallus is utilized in the formation of

these branches. In some thalli of *M. palmatci* and *L. polymorpha*, abnormal receptacles bearing both antheridia and archegonia have also been reported; such bisexual receptacles are called androgynous receptacles.

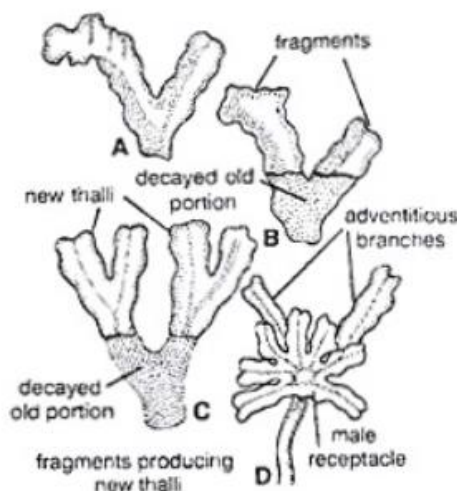


Fig. 1.6. (A-D). Marchantia. Vegetative reproduction. (A-C). Fragmentation, (D) Adventitious branches arising between the lobes from the lower surface of the male disc.

The internal structure of an Antheridiophore or Archegoniophore

Its transverse section shows that it can be differentiated into two sides: ventral and dorsal. The ventral side has two longitudinal rows of scales and rhizoids. These grooves run longitudinally through the entire length of the stalk. The dorsal side shows an internal differentiation of air chambers. (Fig. 1.7 C).

Antheridiophore: It consists of a 1-3-centimeter-long stalk and a lobed disc at the apex. The disc is usually eight-lobed, but in *M. geminata* it is four-lobed. The lobed disc is a result of the created dichotomies.

L.S. through the disc of Antheridiophore

The disc consists of air chambers alternating with heridial cavities. Air chambers are triangular and open on the upper surface by n pores called an ostiole. Antheridia arise in acropetal succession, i.e., the older near the center and the youngest at the margins. (fig. 1.7 A).

Mature Antheridium: A mature antheridium is globular in shape and can be differentiated into two parts stalk and the body. The stalk is short and multicellular and attaches the body to the base of the antheridial chamber. A single-layered sterile jacket encloses the mass of androcyte mother cells, which metamorphose into antherozoids (Fig. 1.9 B, 1.9 G). The antherozoid is a minute rod-like biflagellate structure (Fig. 1.9 H).

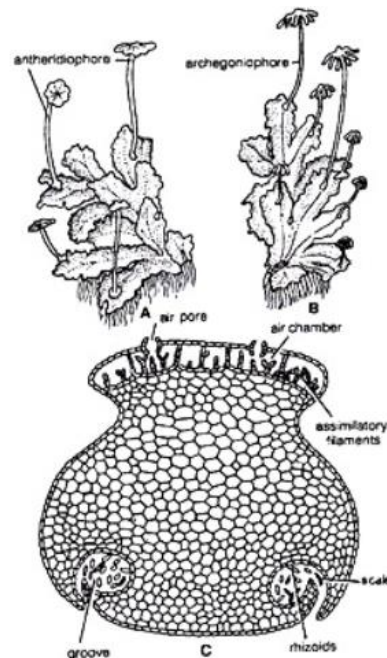


Fig. 1.7. (A-C). Marchantia. Gametophores. (A) Thallus bearing antheridiophores, (B) Female thallus bearing archegoniophores, (C) Transverse section of gametophore.

Development of Antheridium: The development of the antheridium starts with a single superficial cell which is situated on the dorsal surface of the disc, 2-3 cells behind the growing point. This cell is called antheridial initial (Fig. 1.9 A). The antheridial initial increases in size and divides by a transverse division to form an outer upper cell and a lower basal cell (Fig. 1.9 B).

The basal cell remains embedded in the tissue of the thallus, undergoes a little further development, and forms the embedded portion of the antheridial stalk. The outer cell divides to form a filament of four cells. The upper two cells of the four-celled filament are known as primary antheridial cells, and the lower two cells are known as primary stalk cells (Fig. 1.7 C).

Primary stalk cells from the stalk of the antheridium. Primary antheridial cells divide by two successive vertical divisions at a right angle to each other to form two tiers of four cells each (Fig. 1.9 D). A periclinal division is laid down in both the tiers of four cells and there is the formation of eight outer sterile jacket initials and eight inner primary androgonial cells (Fig. 1.9 E).

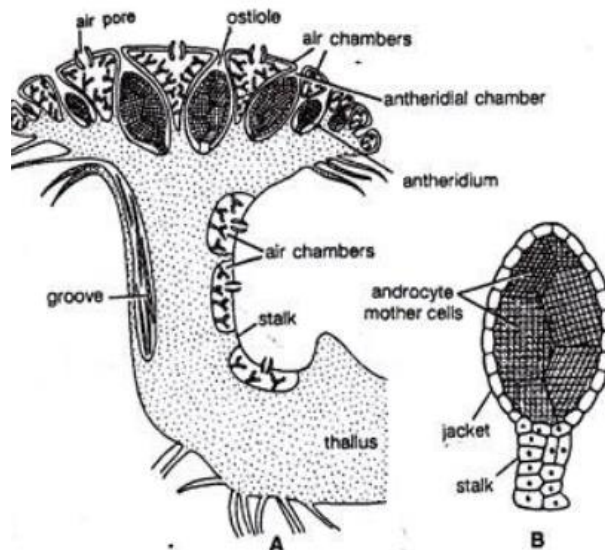


Fig. 1.8 (A-B). Marchantia Antheridia. (A) Vertical or longitudinal section passing through disc of antheridiophore, (B) a mature antheridium antheridium,

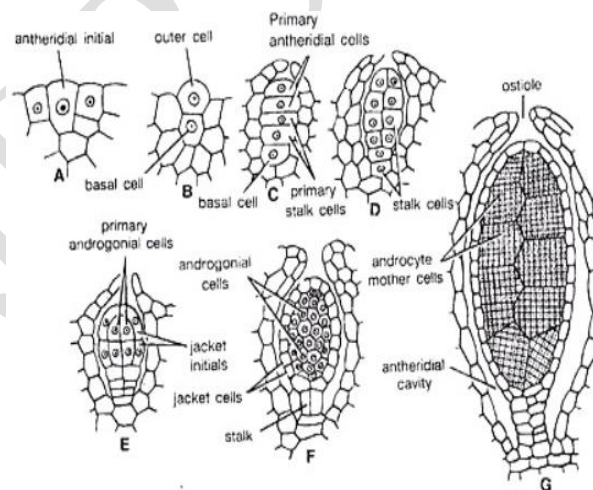


Fig. 1.9 (A-H). Marchantia. Development of antheridium (A-F). Successive stages in the development of (G). A mature.

Jacket initials are divided by several anticlinal divisions to form a single layer of sterile antheridial jacket. Primary androgenic cells divide by several repeated transverse and vertical divisions, forming many small androgonic cells (Fig. 1.9).

The last generation of the androgonial cells is known as androcyte mother cells (Fig. 1.9 G). Each androcyte mother cell divides by a diagonal mitotic division to form two triangular cells called androcytes. Each androcyte cell metamorphoses into an antherozoid (Fig. 1.9 A-G).

Spermatogenesis

The process of metamorphosis of androcyte mother cells into antherozoids is called spermatogenesis. It is completed in two phases.

(1) Development of blepharoplast. (2) Elongation of androcyte nucleus.

1. Development of Blepharoplasty: In the young triangular androcyte (Fig. 1.10 D) blepharoplast appears as a dense granule in one of the acute angles. It elongates to some extent and puts its whole body in close contact with the inner contour of the androcyte. From the elongated blepharoplast emerges the flagella.

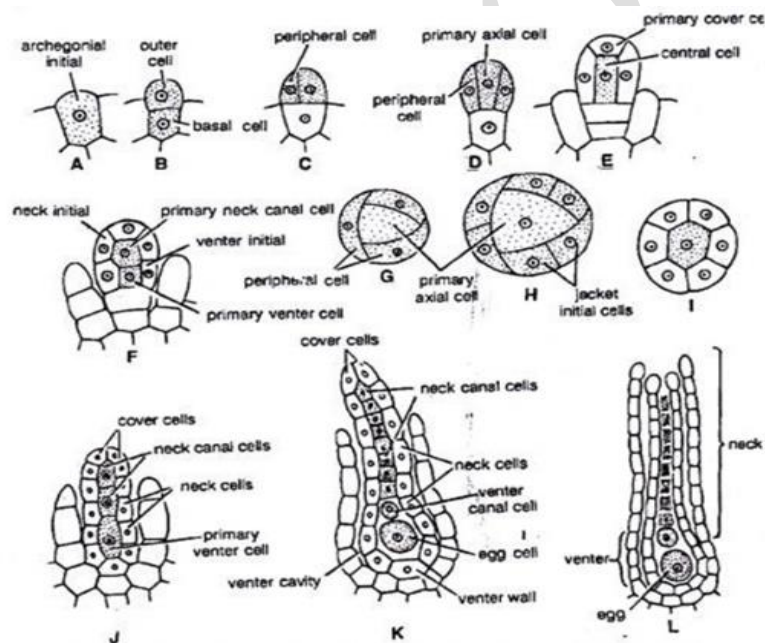


Fig. 1.10. (A-L) Marchantia. Development of archegonium. (A-K) successive stages in the development of archegonium. (L) A mature archegonium.

2 Elongation of Androcyte nucleus: with the elongation of the blepharoplast, the nucleus also elongates. The spline apparatus acts as a cytoskeleton for the elongation of the nucleus. A spline apparatus is a multilayered structure that comprises tubules (Fig. 1.10 E-H).

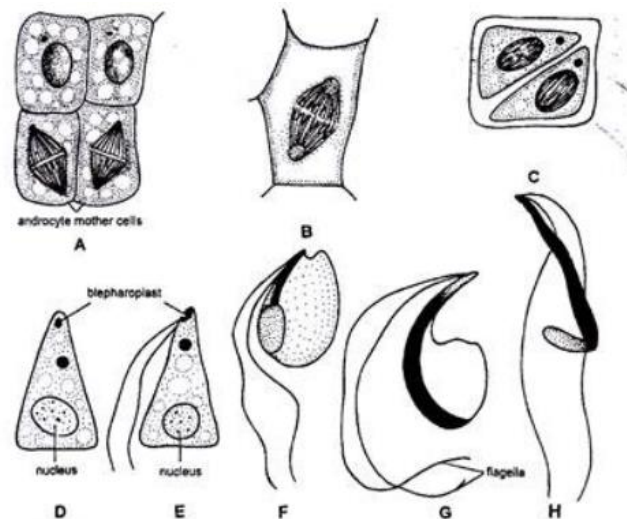


Fig. 1.11. (A-H). Marchantia. Spermatogenesis. (A-C) Formation of androcytes, (D-G). Stages in Spermatogenesis, (H). A single antherozoid.

Archegoniophore or Carpocephalum

It arises at the apical notch and consists of a stalk and terminal disc. It is slightly longer than the antheridiophore. It may be five to seven cm. long. The young apex of the archegoniophore divides by three successive dichotomies to form a lobed rosette-like disc.

Each lobe of the disc contains a growing point. The archegonia begin to develop in each lobe in acropetal succession, i.e., the oldest archegonium near the center and the young archegonium near the apex of the disc. (Fig. 1.11 A). Thus, eight groups of archegonia develop on the upper surface of the disc. There are twelve to fourteen archegonia in a single row in each lobe of the disc.

Development

The development of the archegonium starts on the dorsal surface of the young receptacle in acropetal succession. A single superficial cell that acts as an archegonial initial enlarges and divides by transverse division to form a basal cell or primary stalk cell and an outer cell or primary archegonial cell (Fig. 1.9 A, B).

The primary stalk cell undergoes irregular divisions and forms the stalk of the archegonium. The primary archegonial cell divides by three successive intercalary walls or periclinal vertical walls resulting in the formation of three peripheral initials and a fourth median cells, the primary axial cell (Fig. 1.11 C, D). Each of the three peripheral

initials is divided by an anticlinal vertical division forming two cells (Fig. 1.11 G, H) In this way primary axial cell gets surrounded by six cells. These are called jacket initials (Fig. 1.11H, I). Six jacket initials divide transversely into upper neck initials and lower venter initials (Fig.1.11 F). Neck initial tier divides by repeated transverse divisions, to form a tube-like neck.

Diversity of Algae, Lichens & Bryophytes

The neck of the archegonium consists of six vertical rows. (Fig. 1.11 I). Each row consists of six to nine cells Venter initials tier is also divided by rapid transverse divisions to form a single wall layer of a swollen venter (Fig 1.11 K). Simultaneously, the primary axial cell divides transversely and unequally to form an upper small primary cover cell and a lower large central cell (Fig.1. 9 E).

The central cell divides into a primary neck canal cell and a lower venter cell. Primary neck canal cells divide by a series of transverse divisions to form a row of about eight thin-walled neck canal cells (Fig. 1.11 J, K).

The primary venter cell divides only once and forms a small upper venter canal cell and a lower large egg or ovum (Fig. 1.11 K). The primary cover cell divides by two vertical divisions at the right angle to one another to form four cover cells which form the mouth of the archegonium.

Mature Archegonium

A mature archegonium is a flask-shaped structure. It remains attached to the archegonial disc by a short stalk. It consists upper elongated slender neck and a basal globular portion called a venter. The neck consists of six vertical rows enclosing eight neck canal cells and a large egg. Four cover cells are present at the top of the neck. (Fig. 1.9 L).

Fertilization in Marchantia: Marchantia is dioecious. Fertilization takes place when male and female thalli grow near each other. Water is essential for fertilization. The neck of the archegonium is directed upwards on the dorsal surface of the disc of the archegoniophore (Fig. 1.12 A).

In the mature archegonium, the venter canal cell and neck canal cells disintegrate and form a mucilaginous mass. It absorbs water, swells up, and comes out of the archegonial mouth by pushing the cover cells apart. This mucilaginous mass consists of chemical

substances. The antherozoids are splashed by raindrops. They may fall on the nearby female receptacle or swim the whole way by the female receptacle. It is only possible if both the male and female receptacles are surrounded by water.

Many antherozoids enter the archegonial neck by the chemotactic response and reach up to the egg. This mechanism of fertilization is called the splash cup mechanism. One of the antherozoids penetrates the egg and fertilization is affected. The fusion of both male and female nuclei results in the formation of a diploid zygote or oospore. Fertilization ends the gametophytic phase.

Sporophytic Phase: Post Fertilization Changes

After Fertilization the following changes occur simultaneously.

1. Stalk of the archegoniophore elongates.
2. Remarkable over-growth takes place in the central part of the disc. As a result of this growth, the marginal region of the disc-bearing archegonia is pushed downward and inward. The archegonia are now hanging towards the lower side with their neck pointing downwards (Fig. 1.12 B-D).

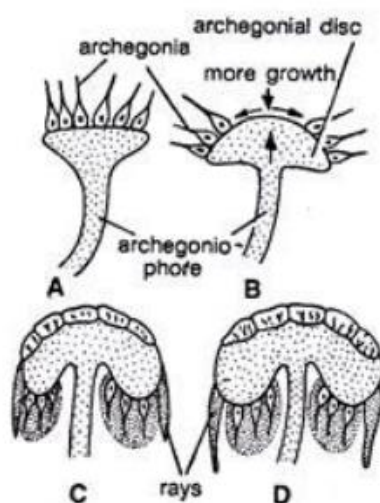


Fig. 1.12. (A-D). Marchantia. (A) Position of the archegonia before fertilization, (B-D). Inversion of the archegonia after fertilization.

3. The wall of the venter divides into two to three layered calyptras.
4. A ring of cells at the base of the venter divides and re-divides to form a one-cell thick collar around the archegonium called perigynium (Pseudoperianth).

5. A one-celled, thick, fringed sheath develops on both sides of the archegonial row. It is called perichaetium or involucre. Thus, the developing sporophyte is surrounded by three protective layers of gametophytic origin, i.e., calyptra, perigynium, and perichaetium (Fig. 1.13). The main function of these layers is to protect against drought to young sporophytes.
6. Between the groups of archegonia, long, cylindrical processes develop from the periphery of the disc. These are called rays. They radiate outward, curve downwards, and give the disc a stellate form. In *M. polymorpha* these are nine in number.
7. Zygote develops into sporogonium.

Development of Sporogonium: After fertilization, the diploid zygote or oospore enlarges and fills the archegonium cavity. It first divides by transverse division (at right angle to the archegonium axis) to form an outer epibasal cell and inner hypobasal cell (Fig. 1.14 A, B).

The second division is at a right angle to the first and results in the formation of four cells. This represents the quadrant stage (Fig. 1.14 C). The epibasal cell forms the capsule and the hypo basal cells form the foot and seta.

Since the capsule is developed from the epibasal cell and forms the sporogonium apex, the embryogeny type is known as exoscopic. The next division is also vertical and results in the formation of eight-celled or octant stages.

Now the divisions are irregular, and a globular embryo is formed (Fig. 1.12 D). The lower cells divide to form a massive and bulbous foot. The cells of the seta divide in one plane to form vertical rows of cells.

In the upper region of the capsule (when the young sporogonium is about a dozen or more cells in circumference) periclinal division occurs and it differentiates it into outer single-layered amphithecium and multilayered endothecium (Fig. 1.14 E, F).

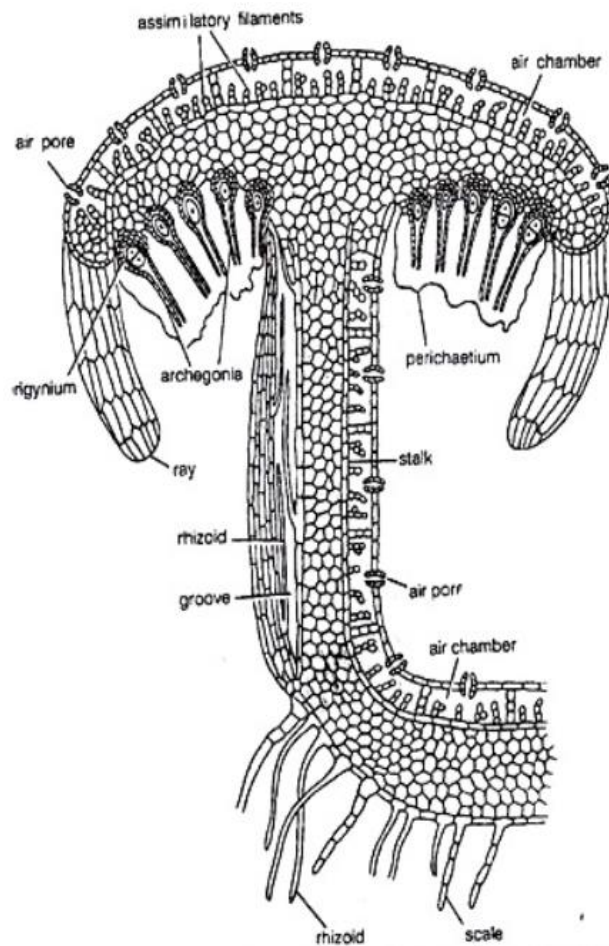


Fig. 1.13: Marchantia. Vertical longitudinal section (V.L.S.) of archegoniophore showing protective layers and rays. (After fertilization)

The cells of the endothecium divide only by anticlinal divisions to form a single-layered sterile jacket or capsule wall. The endothecium forms the archesporium. Its cells divide and re-divide to form a mass of sporogenous cells (sporocytes). Half of the sporogenous cells become narrow and elongate to form the elater mother cells. (Fig. 1.14 G, I).

In *M. polymorpha* sporogenous cells divide by five successive divisions to form thirty-two spore mother cells while in *M. domingensis* sporogenous cells divide only by three to four divisions to form eight or sixteen spore mother cells. The elater mother cells elongate considerably to form long, slender diploid cells called elaters.

Elaters are pointed at both ends and have two spiral bands or thickenings on the surface of the wall. These are hygroscopic in nature and help in dispersal of spores (Fig. 1.14 K). The spore mother cell is diploid and divides meiotically to form four haploid spores

which remain arranged tetrahedrally for quite some time (Fig. 1.14 J). The spores later become free and remain enclosed by the capsule wall along the elaters. (Fig. 1.14 H).

The quadrant type of development of sporogonium is quite common in many species of *Marchantia* (e.g., *M. polymorpha*) but in a few species' zygote divides by two transverse divisions to form the 3-celled filamentous embryo. In it the hypobasal cell forms the foot, the middle seta, and the epibasal cell develops into a capsule. However, it is a rare type of embryo development in *M. chenopoda*.

Mature Sporogonium: A mature sporogonium can be differentiated into three parts, viz., the foot, seta, and capsule (Fig. 1.4 H). **Foot.** It is bulbous and multicellular. It is composed of parenchymatous cells. It acts as an anchoring and absorbing organ. It absorbs the food from the adjoining gametophytic cells for the developing sporophyte.

Seta: It connects the foot and the capsule. At maturity, due to many transverse divisions, it elongates and pushes the capsule through three protective layers viz., calyptra, perigynium, and perichaetium.

Capsule: It is oval and has a single-layered wall that encloses spores and elaters. It has been estimated that as many as 3, 00,000 spores may be produced in a single sporogonium and there are 128 spores about one elater.

Dispersal of Spores: As the sporogonium matures, seta elongates rapidly and pushes the capsule in the air through the protective layers (Fig. 1.15 A). The ripe capsule wall dehisces from apex to middle by four to six irregular teeth or valves. The annular thickening in the cells of the capsule wall causes the valves to roll backward exposing the spores and elaters.

The elaters are hygroscopic. In dry weather, they lose water and become twisted. When the atmosphere is wet, they become untwisted and cause the jerking action. Due to this, the spore mass loosens, and spores are carried out by air currents (Fig. 1.15 B, C).

Structure of Spore

Spores are very small (0.012 to 0.30 mm in diameter). They are haploid, uninucleate, globose and surrounded by only two wall layers. The outer wall layer is thick, smooth, or

reticulate and is known as exospore or exine. The inner wall layer is thin and is called endospore or intine. In *M. torsana* and *M. caneloba* they are tetrahedrally arranged.

Germination of Spores and Development of Gametophyte

Under favorable conditions, the spores germinate immediately. In first year the spore viability is approximately 100%. Before germination, it divides by transverse division to form two unequal cells (Fig. 1.16 A, B). The lower cell is small. It is relatively poor in cell contents, achlorophyllous, and extends to form a germ-rhizoid (Fig. 1.16 C). The large cell is chlorophyllous and undergoes divisions to form a six to eight-cell germ filament or protonema (Fig. 1.16 D). At this stage, the contents of the cells migrate at the apex.

The apex is cut off from the rest of the spore by a division. It behaves as an apical cell. It is wedge-shaped with two cutting faces. The apical cell cuts off five to seven cells alternately to the left and right. These cells by repeated divisions, form a plate-like structure (Fig. 1.16 F).

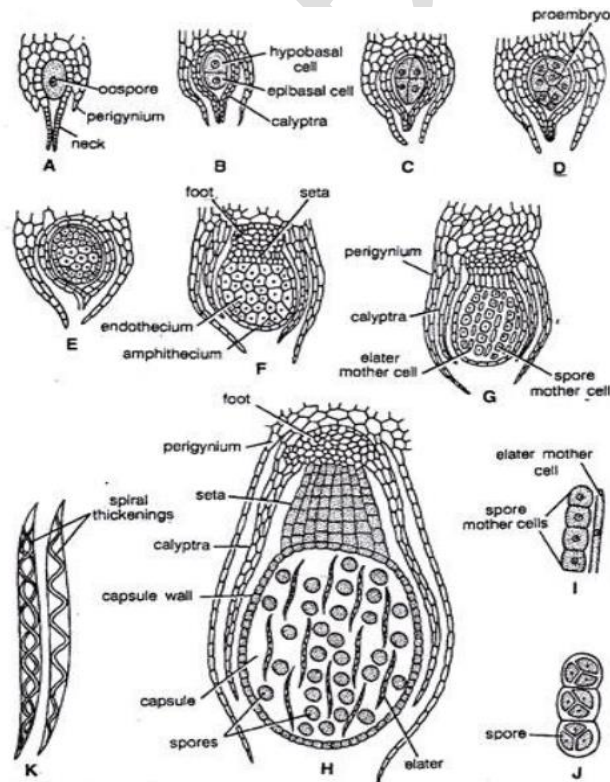


Fig-1.14. (A-J). Marchantia. Development of sporophyte. (A-J). Successive stages in the development of sporogonium, (H). L.S. of mature sporogonium, (J) Spores tetrad, (K) Two elaters.

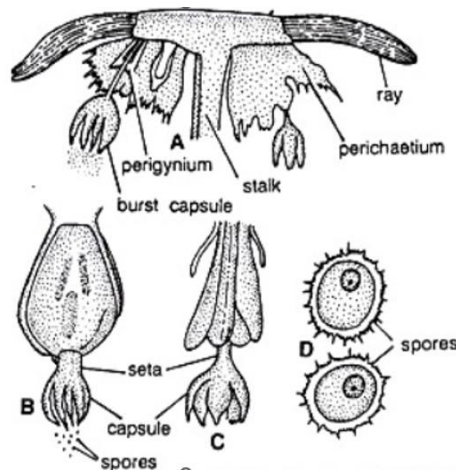


Fig. 1.15. (A-D). Marchantia. Dehiscence of the capsule. (A) V.L.S. of archegoniophore after the formation of the capsule.

According to O'Hanlon (1976), a marginal row of cells appears in the apical region in this plate. By the activity of these marginal cells, the expansion of the plate takes place into the thallus, a characteristic of Marchantia.

Marchantia is dioecious, 50% of the spores develop into male thalli and 50% develop into female thalli (Fig. 1.17).

Alternation of Generation in Marchantia: The life cycle of Marchantia shows regular alternation of two morphologically distinct phases. One of the generations is Haplophase and the other is diplophase.

(i) Haplophase or Gametophytic Phase: In Marchantia, this phase is dominant and produces the sex organs. Sex organs produce gametes to form a diploid zygote.

(ii) Diploid Phase or Sporophytic Phase: Zygote develops into sporophyte. In Marchantia sporophyte is represented by foot, seta and capsule. The sporophyte produces the spores in the capsule. The spores on germination produce the gametophyte. So, in Marchantia two morphologically distinct phases (Haplophase and Diplophase) constitute the life cycle. The life cycle of this type which is characterized by alternation of generations and sporogenic meiosis is known as heteromorphic and diplohaplontic (Fig. 1.18).

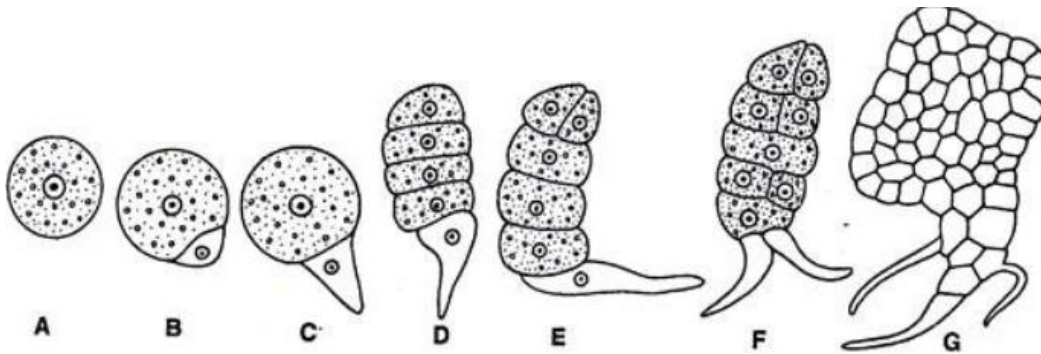


Fig. 1.16. (A-G). *Marchantia*, Successive stages in the germination of spore and development of sporophyte.

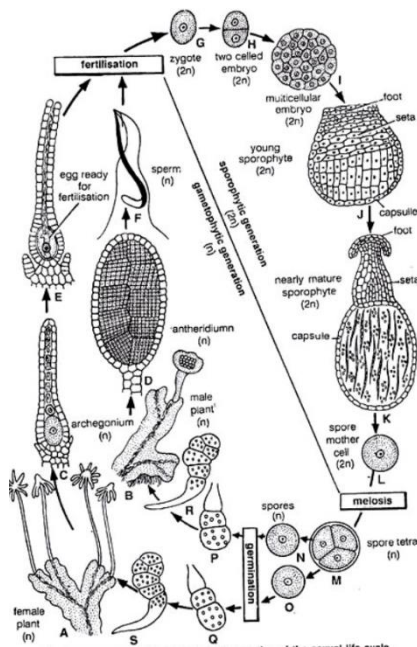


Fig.1.17

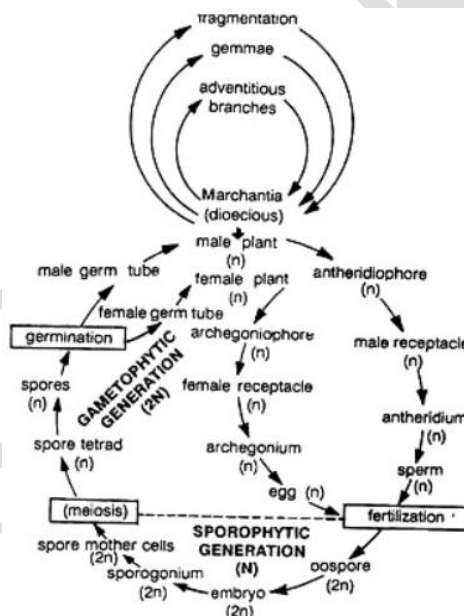


Fig. 1.18

Fig. 1.17. *Marchantia*. Diagrammatic representation of the sexual life cycle.

Fig. 1.18. *Marchantia*. Diagrammatic representation of the life cycle.

Sphagnum

Class: Sphagnopsida

Order: Sphagnales

Family: Sphagnaceae

Genus: *Sphagnum*

Habit and Habitat of Sphagnum

Sphagnum is represented by about 336 species which are cosmopolitan in distribution. In India, it is represented by about 20 species in the Himalayas. These species are aquatic or

semiaquatic and grow in dense masses or cushions in swamps, ponds and lake margins, moist heaths, and wet hillsides.

Gametophytic Phase of Sphagnum: External Features of Sphagnum

The plant body is gametophytic and consists of two stages: Juvenile stage and leafy gametophore. Juvenile stage: It is also called protonema and is formed by the germination of the spores. It is an irregularly lobed thallus-like structure and one cell in thickness. It is attached to the substratum by multicellular rhizoids with oblique septa. From the protonema arises the erect leafy gametophyte called the gametophore (Fig. 2.1).

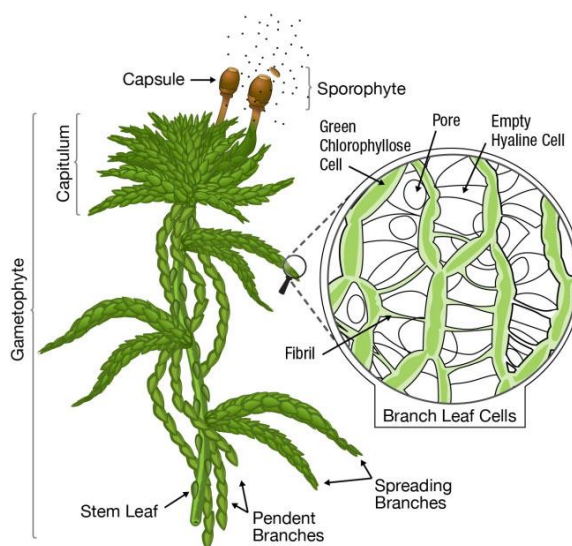


Figure 2.1 Schematic of Sphagnum plants. The Sphagnum plant consists of a stem, leaves, capitulum, and sporophyte during reproduction.

Leafy Gametophore: It represents the adult form. The adult gametophyte (gametophore) is perennial and can be differentiated into axes or ‘stems’ and ‘leaves’.

Stem: It is erect and may be a foot or more in length, with a diameter of up to 1.2 mm. The stem is well-branched, the branching being usually lateral. Near the apex of the stem, the branches are short and of limited growth and are clustered together closely to form a compact head called Comal tuft or coma (Fig. 2 .1). The coma formation occurs due to the presence of very short internodes at the apex of the stem.

Lower down on the stem is borne additional elongated branches. They usually occur in tufts of 3-8 (commonly five) in the axil of every fourth leaf on the main stem. These branches are of two types.

(a) Divergent branches: These branches grow out laterally from the stem and extend outward in a horizontal position.

(b) Drooping or Flagelliform branches: These branches grow out laterally from the stem; droop or hang or run very close to the stem. These pendent or de-current branches act as water conductors.

‘Leaf’: Leaves are borne on the main stem as well as on the branches. On the stem, they are a little apart while on the branches they are overlapping. Leaves are arranged in a spiral manner with a phyllotaxy of 2/5 i.e., the sixth leaf will come above the first leaf. They are thin, small, fleshy, and oblong with a broad base. The margin is entire with an acute apex.

The midrib is lacking. If seen in surface view the leaf consists of meshes composed of two different types of cells: small living photosynthetic cells containing chlorophyll and large, hyaline rhomboidal cells. (Fig. 221). These cells are provided with small pores. These pores are rounded in shape and are concerned with the intake of water.

Spiral thickenings are also present in the cells (Fig. 2.2B). These thickenings compensate for the absence of mechanical issues. The leaves on the branches are smaller in size than the stem. These leaves are compactly arranged in an imbricate fashion.

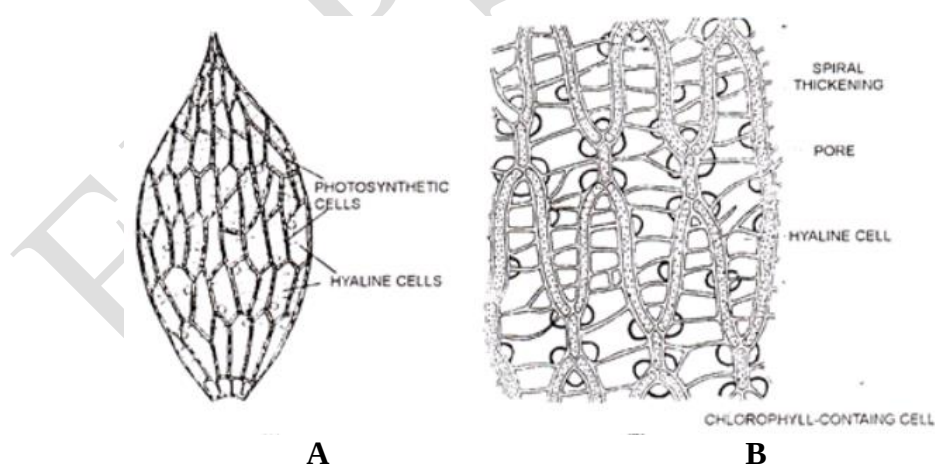


Fig.2.2 (A-B). Sphagnum. (A) A single 'leaf' (B) Enlarged surface view of the 'leaf'.

Internal Structure of Sphagnum

Axis or ‘Stem’: The transverse section of the axis can be differentiated into 3 distinct zones: (i) Cortex or hypoderm, (ii) Prosenchymatous region or hydromel, (iii) Central cylinder or Medulla.

(i) Cortex: It is the outermost region of the axis. Its cells are small and form compact tissue. In the young axis, the cortex is only one cell thick. In *S. subsecundum* it is single layered throughout its life but in most species, it is composed of many layers. In *S. recurvum*, *S. obtusum*, it is composed of two to three layers of hyaline cells.

In *S. acutifolium*, *S. squarrosum* it is composed of two to five layers of cells (Fig. 2.3). In *S. palustre*, these cortical cells develop spiral thickenings and large oval perforations on their walls. In branches, the cortical cells remain one cell thick. Cortical cells store water. These cells absorb water by capillary action and thus compensate for the absence of rhizoids in the adult gametophytic plant.

In some species of Sphagnum e.g., *S. molluscum*, *S. tenellum*, some cortical cells elongate to form a long-curved structure with a curved neck and an opening. These modified cells resemble a retort; hence, these cells are called 'retort cells' (Fig. 2.2A, B). Their cells are inhabited by small, microscopic animals. These cells are absent in those species in which the thickenings and pores are present in the cortical cells.

(ii) Prosenchymatous Region

The cortex is followed by a cylinder of narrow, thick-walled elongated cells. It is 4-6 layered and surrounds the medulla (Fig. 2.3). It gives mechanical support to the axis tissue.

(iii) Medulla or Axial Cylinder

It is composed of thin-walled, colourless, parenchymatous cells (fig 2.3). It is like the pith of the higher plants and functions as a storage region.

The transverse section (T.S.) of the leaf shows that it is one cell thick. In young leaves, the cells are rectangular and are of the same size. However, in mature leaves, the T.S. appears as beaded or moniliform due to the presence of two types of cells large, hyaline, or capillary cells and the small, green assimilatory or Photosynthetic cells., The two kinds of cells regularly alternate with each other. *S. acutifolium* the hyaline cells bulge towards the underside of the leaf and the green cells are triangular. The base of the triangle is directed upwards (Fig. 2.5A).

In *S. tenellum* both types of cells are just reverse to this (Fig. 2.5B). In *S. squarrosum* the green cells are hemmed in, above and below, by the hyaline cells, and may appear

spindle-shaped in transverse-section. Their ends reach neither the upper nor the lower surface of the leaf (Fig. 2.5 C). Hyaline cells are dead and filled with water while assimilatory cells are alive and photosynthetic.

Reproduction in Sphagnum: Sphagnum reproduces by vegetative and sexual methods.

Vegetative Reproduction: It takes place by the following methods.

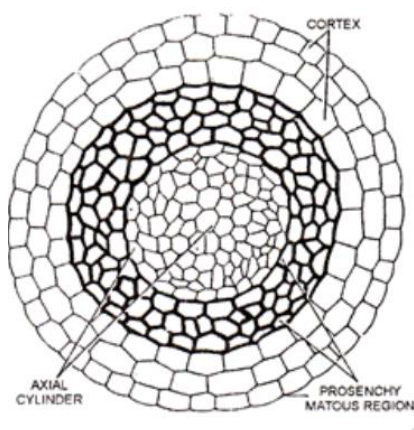


Fig. 2.3.

Fig. 2.3. Sphagnum. T.S. old axis.

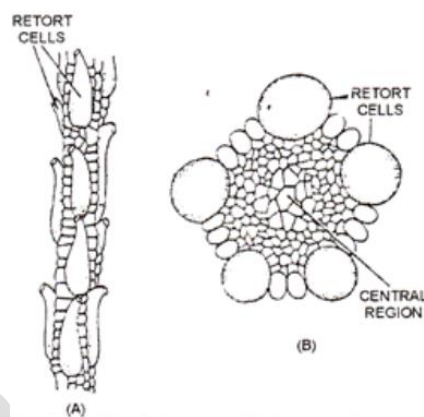


Fig. 2.4

Fig. 2.4. (A, B). Sphagnum (A) Leaves of a portion of the branch are removed to show retort cells. (B) T. S. axis of *S. molluscum* with retort cells.

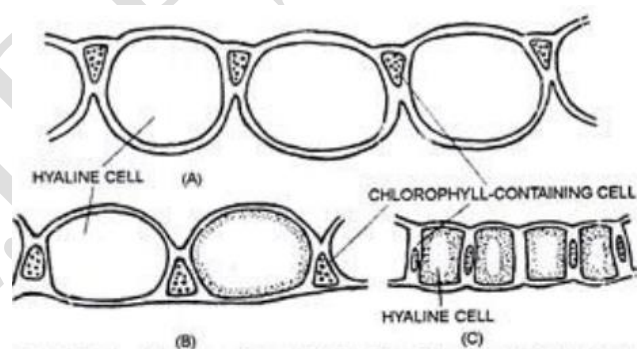


Fig-2.5. (A-C). Sphagnum. Transverse section of leaf. (A) *S. acutifolium*, (B) *S. tenellum*, (C) *S. squarrosum*.

Innovation

It is the common method of reproduction. It takes place through the formation of special vegetative branches known as innovations. Occasionally, one of the branches in the axillary cluster becomes robust and grows upwards. This branch shows all the

characteristics of main axis and is known as innovation. Each innovation develops into a new plant when detached from the parent plant.

Multiplication of Protonemal Branches

Any marginal cell of the primary protonema may become meristematic and forms a green cellular filament. In apical portion grows into flat, thallus-like green secondary protonema. Marginal cells of secondary protonema form the leafy gametophore.

Regeneration: The growth of new tissues or organs to replace those lost or damaged in injury is known as regeneration. Sphagnum has the great power of regeneration. During desiccation, the growth of the Sphagnum is checked because physiological activities like respiration and photosynthesis are suspended, but the cytoplasm shows a high degree of resistance to desiccation. When water is available, these activities are resumed, and normal growth of the plant takes place. Such plants are known as phycophytes (Buch, 1947).

Sexual Reproduction in Sphagnum:

Sexual reproduction is oogamous. It takes place by the formation of male and female reproductive organs, which develop on special branches. Sphagnum may be monoecious or dioecious. Monoecious species are protandrous.

The Antheridium: The antheridia or the male sex organs develop on the catkin-like short lateral branches known as the antheridial or male branches (Fig. 2.7 A). These branches develop near the apex of the main shoot of the plant. These branches bear the leaves which are just like the foliage leaves but in comparison, they are shorter (Fig. 2.6 A).

These leaves are brightly colored (commonly yellow, purple, brown, bright red, or dark green). In the axil of each leaf solitary antheridium develops (antheridia occur alternately arranged with the leaves) (Fig. 2.7). A mature antheridium consists of a long stalk and a globular body. The stalk may be as long as the body of the antheridium. It consists of two to four rows of cells which are 8-10 cells in length. The antheridial body is covered by a single layered sterile jacket which encloses many astrocytes. Each astrocyte metamorphoses into a spirally coiled biflagellate antherozoid.

The Archegonium: One to five archegonia develop at the tip of the short archegonial branches. The leaves of the archegonial branches are green and much larger than the vegetative branches. These leaves are called perichaetium (Fig. 2.8 A). These leaves protect the archegonia, and young sporophytes and provide food to the developing sporophytes.

The archegonia that develop directly from the apical cell of the archegonial branch are known as the primary archegonia while the remaining ones are known as secondary archegonia. A mature archegonium is a long and stalked structure possessing a venter and a long neck enclosing 8 or 9 neck canal cells, a venter canal cell, and an egg cell (Fig. 2.8B).

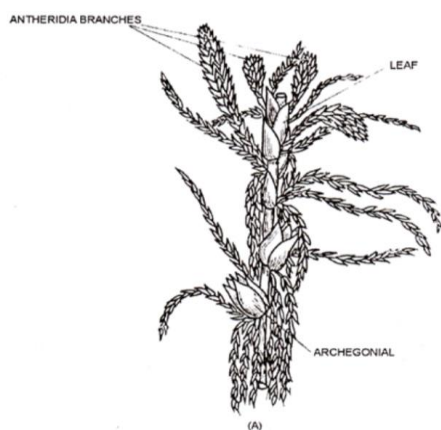


Fig 2.6

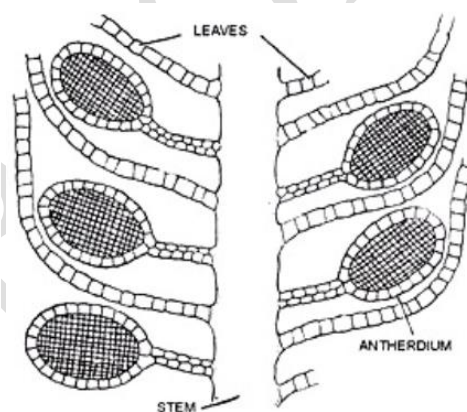


Fig 2.7

Fig 2.6 (A-B). Sphagnum. Sexual Reproduction (A) Monoecious gametophore shows antheridial and archegonial branches; (B) An antheridial branch.

Fig 2.7 Sphagnum. Sexual reproduction. Longitudinal section. (LS.) of antheridial branch. When the antheridium is mature, the apical cells of the jacket absorb water, swell, and undergo irregular separations which turn backward. The antherozoids are liberated and swim in water (Fig. 2.9).

Fertilization in Sphagnum: The process of fertilization is identical with other bryophytes. Water is essential for fertilization. At the time of fertilization, the neck canal cells along with the venter canal cells disintegrate to form a clear passage for the antherozoids. They enter through the cover cells and reach up to the egg, but only one fuse with the egg to form the zygote. In *S. subsecundum* the venter canal cell is persistent and fuses with the egg cell to form a zygote.

The Sporophyte

The sporogonium develops from only one archegonium. The other archegonium, however, may also persist for some time. The mature sporogonium is differentiated into the foot and capsule. Both are connected by a short, narrow neck-like constriction which represents the suppressed seta, sporogonium is elevated on a short cylindrical, leafless stalk, the pseudopodium (Fig. 2.9A).

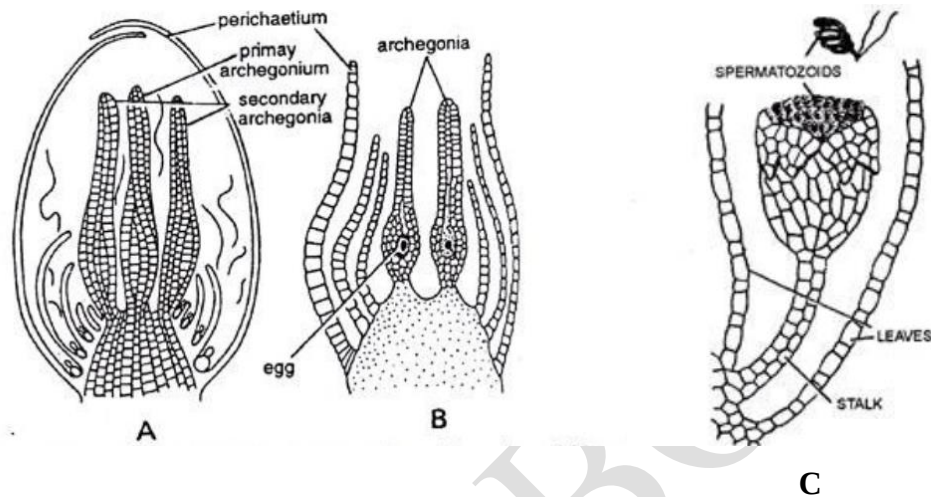


Fig 2.8 AB). Sphagnum. Sexual reproduction (A, B). Longitudinal sections of the archegonial branches showing archegonia (C). Mature archegonium.

The pseudopodium is gametophytic, and it is formed by the post-fertilization intercalary growth of the axis of the archegonial branch.

The pseudopodium, together with the basal portion of the calyptra, forms a sac-like structure, the vaginula, which encloses the foot. The main functions of the pseudopodium are to elevate the capsule above the perichaetial leaves, to compensate for the suppression of the seta, and to help in the dispersal of spores.

Foot: It is bulbous and made up of parenchymatous cells. The main function is to absorb the food material for the developing sporophyte.

Capsule: It is spherical and dark brown. It contains a central columella which is over-arched by a dome-shaped spore sac containing haploid spores (Fig. 2.10A). The wall of the capsule is 4-6 layers thick. The outer layer of the capsule wall is called the epidermis. The cells of the epidermis are compactly arranged and contain chloroplasts. It has many non-functional and rudimentary stomata. In young sporogonium, a circular, convex disc

is present at the top of the capsule. It is called operculum. It is separated from the rest of the capsule region by a circular (ring-like) groove of thin-walled cells called annulus.

Dispersal of spores or Dehiscence of capsule

On sunny days the columella of the mature capsule dries up, breaks down, and forms a large air cavity below the air sac. Air enters this cavity through the rudimentary stomata. The wall of the capsule dries up under the influence of the sun and the spherical form of the capsule gradually becomes cylindrical (Fig. 2.10 A, B). The imprisoned air in the capsule is compressed and held under considerable pressure due to changes in the shape of the capsule.

The operculum also dries and shrinks. Due to this a little difference in the tension is thus set up. It puts a strain on the thin-celled annulus cells which finally rupture under the mounting pressure of imprisoned air. The operculum is blown off with explosive force. The pressure of imprisoned air also ruptures the spore sac and the cloud of yellow or orange-colored spores is blown to a height of several centimeters in the atmosphere (Fig. 2.10 C, D). The method of spore discharge is, therefore, known as the air gun or explosive mechanism.

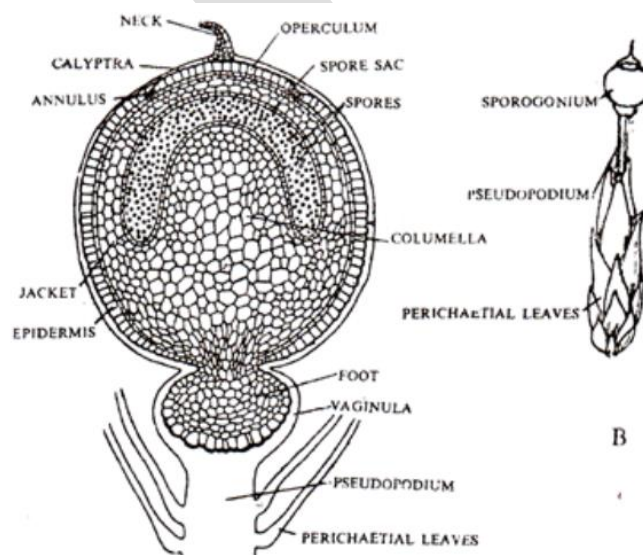


Fig 2.9 (A, B). Sphagnum. (A) L. S. of mature sporogonium, (B) Female branch with sporogonium.

Structure and Germination of Spore

Each spore is uninucleate, triangular to spherical, and has two layered walls with a triradiate mark (Fig. 2.11 B). The outer wall is ornamented and known as exine while the inner wall is smooth and known as intine. The spores remain viable for a few months and germinate under favorable conditions. Spores absorb water and swell up.

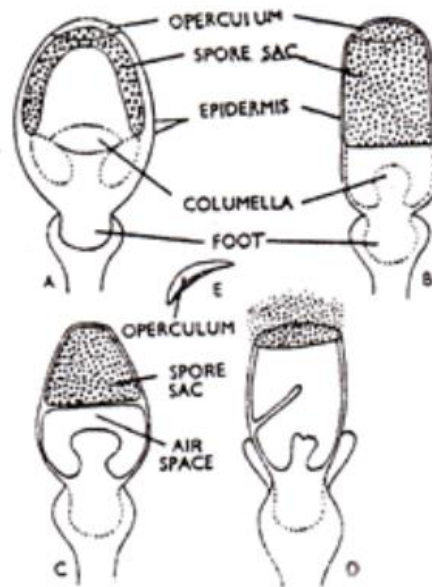
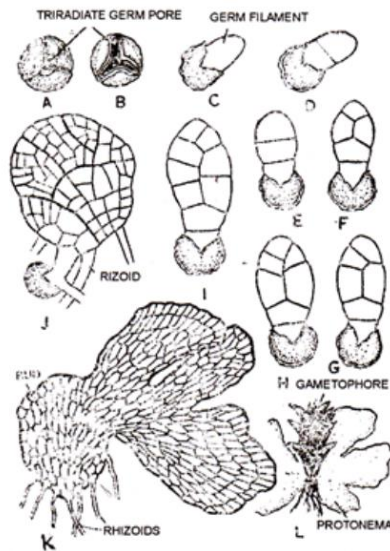


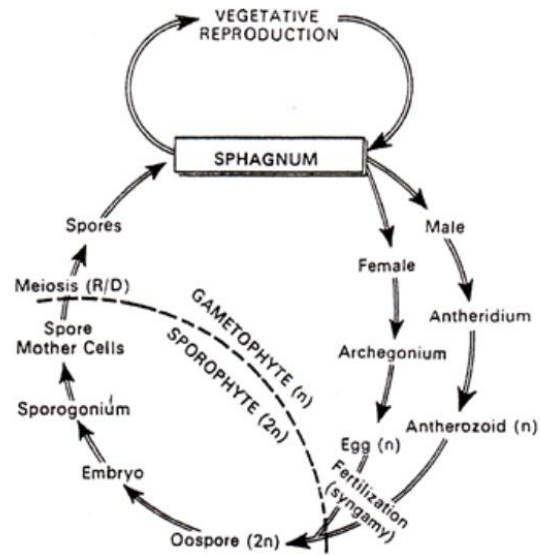
Fig. 2.10 (A-D). Sphagnum: Stages in the dispersal of spores.

Exine ruptures and intine comes out in the form of a germ tube. The germ tube divides transversely to form 2-4 celled green filaments (Fig. 2.11C-E). The terminal cell of the filament develops two cutting faces. It cuts segments alternately on the right and left angles forming a green, single-cell thick plate-like structure.

It is called primary protonema (Fig. 2.11 F-J). The apical cell loses activity and some marginal cells of the plate like protonema become active and form secondary protonema with rhizoids and leaf buds. These buds gradually develop into leafy gametophores (Fig. 2.11 K, L).



2.11



2.12

Fig. 2.11 (A-L) Sphagnum. Gemination of spore and formation of leaf gametophore

Fig. 2.12. Sphagnum. Graphic life cycle.

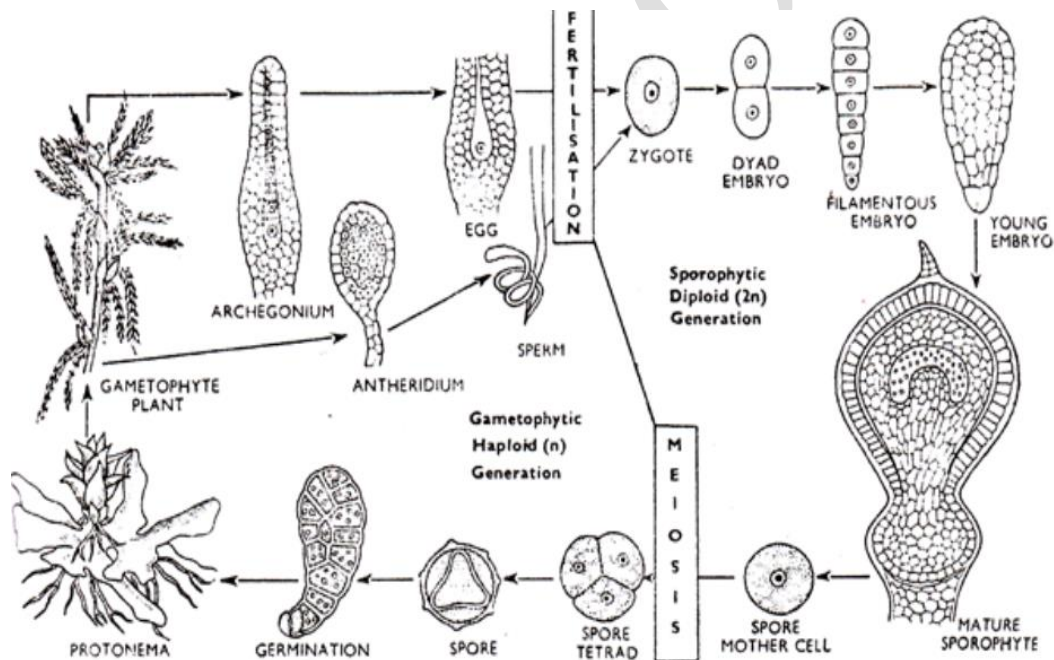


Fig. 2.13: Sphagnum. Diagrammatic life cycle.

Polytrichum

Division: Bryophyta

Subdivision: Musci

Class: Bryopsida

Subclass: Bryidae

Order: Polytrichales

Family: Polytrichaceae

Distribution of Polytrichum

Polytrichum is a prominent genus in the family Polytrichaceae. It is represented by about 111 species and is distributed all over the world, mainly in cool temperate and tropical regions.

Polytrichum mostly prefers to grow in moist and shady places during the rainy season. They are found on wet sandy banks of rivers and ponds, on branches of trees under shade (as epiphytes), on rocks and cliffs, and dry forest bogs.

Polytrichum juniperinum occurs in extremely dry sites, while *P. strictum* grows in peat lands. *P. sexangulare* is found in late-snow areas.

The species of Polytrichum often form a green carpet of vegetation on moist and shaded walls.

Some of the common Polytrichum species are *P. densifolium*, *P. alpinum*, *P. juniperinum*, *P. xanthopilum*, *P. strictum*, *P. formosum*, *P. sexangulare*, etc.

Gametophyte of Polytrichum: The plant body of Polytrichum is gametophytic and consists of an erect leafy shoot.

External Morphology of Polytrichum

External morphology is the external structure of Polytrichum.

The plant body is gametophytic. Like Funaria, the gametophyte of Polytrichum also shows two distinct stages of development: **protonema** and **gametophore**.

The protonema represents the juvenile stage, while the gametophore is the leafy stage of the adult gametophyte.

Protonema: The protonema is a haploid, branched, green filamentous algal-like structure. It is produced by the germination of the spore. Later, the protonema metamorphoses into the leafy gametophore.

Gametophore: The gametophore, i.e., adult gametophyte in Polytrichum, is rhizomatous and is differentiated into two parts: the **rhizome** and the erect **leafy shoot**. **Rhizome**

The rhizome is the horizontally growing underground portion of the gametophore. It bears scale leaves and numerous fluffy rhizoids.

The leaves are small, scale-like, and arranged in three vertical rows (1/3 phyllotaxy). They are usually brown or collarless.

The rhizoids are long, branched, multicellular, thick-walled, and characterised by the presence of oblique septa. They are interwoven to form a dense tangled mass.

Rhizoids are colourless and arise from the base of the rhizome.

Rhizoids attach the leafy shoot to the substratum and help in absorbing water and mineral nutrients from the soil.

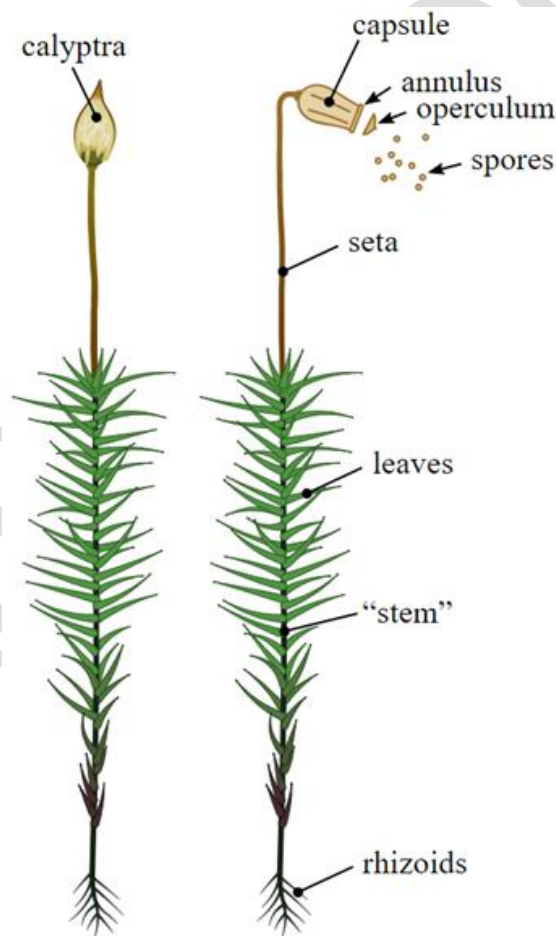


Fig 3.1: Plant body of Polytrichum bearing sporophyte.

Leafy Shoot

The leafy shoot is an erect axis arising from the rhizome. It is the most conspicuous part of the plant and usually grows to a height of about 15-20cm. In *P. commune*, the shoot is maybe 45 cm in height.

Externally, the leafy shoot is differentiated into a stem-like central axis. The central axis bears two types of leaves: scale leaves and foliage leaves.

The scale leaves are small and produced on the lower portion or transition zone of the central axis. The foliage leaves are comparatively large, dark green, and are arranged spirally on the upper portion of the central axis with a divergence of $\frac{3}{8}$. Each foliage leaf is 6–10 mm long. It consists of two parts: the proximal sheathing leaf base and the diverging narrow limb or blade.

The sheathing leaf base is well-developed, broad, colourless, membranous, and unistratose (one cell thick). It is traversed by a relatively narrow midrib.

The limb is green or brown, lanceolate in outline, and has an acuminate apex. It consists of a broad dark green multistratose midrib (nurse of costa) and rudimentary wings. The wings on both sides of the midrib are thin, narrow, and unistratose. The margin of the leaf may be entire (e.g., *P. juniperinum*) or coarsely toothed (e.g., *P. commune*). The erect leafy axis is usually unbranched. Sometimes it is branched, and the branch arises from a primordium below the young leaf. The branch primordia occur at intervals both on the rhizome and the erect axis, roughly at the base of every 12th leaf.

The stem grows using an apical cell with three cutting faces. It cuts off segments in such a way that the position of the apical cell is shifted in a spiral manner.

Internal Morphology of Polytrichum

Internal morphology, or the internal structure of the plant body is the anatomy of Polytrichum.

Internal Structure of Rhizome: In a cross-section, the rhizome is circular in outline in some Polytrichum species (e.g., *P. formosum*, *P. commune*) and triangular with rounded corners in many others (Fig-3.2).

It can be differentiated into the following regions

Epidermis: The epidermis is the outermost layer of the rhizome. It consists of a single layer of thick-walled cells. The rhizoids, which are the direct outgrowth of the epidermal cells, form a dense tangle. In the epidermis, stomata are absent.

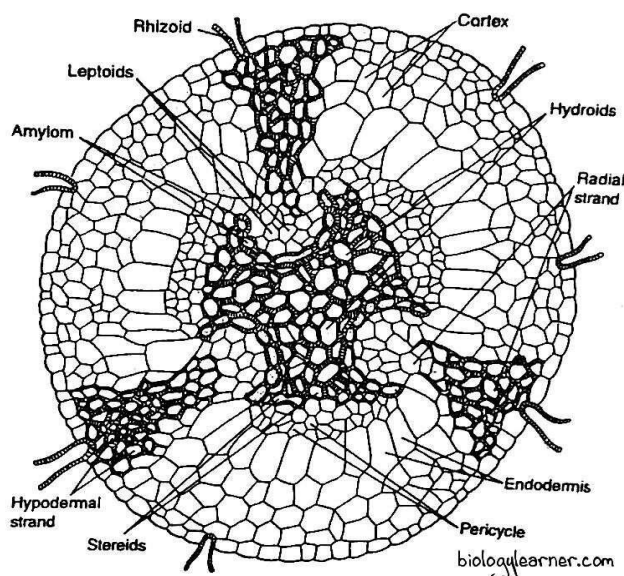


Fig 3.2: T.S. of rhizome showing the detailed structure.

Cortex

The cortex lies between the epidermis and the central strand. It consists of 3–4 layers of thin-walled parenchymatous cells.

The cortex is interrupted by three hypodermal strands, which extend radially from the periphery towards the center. Each hypodermal strand is composed of living parenchymatous cells with a pointed end. Starch grains are present in these parenchymatous cells.

The hypodermal strands gradually narrow down towards the centre of the rhizome and are connected inward by a group of thin-walled cells. These thin-walled cells, together with hypodermal strands, form a wedge-shaped mass of cells, called radial strands.

Inner to the cortex, there is a layer of large radially elongated cells with suberized thickening on the radial and horizontal walls. This layer can be compared with the endodermis of higher plants. The so-called **endodermis** is not continuous but is separated by larger cells of radial strands.

Pericycle: In some species of *Polytrichum*, the pericycle is present between the endodermis and the central cylinder. It is composed of 2-3 layers of thin-walled cells. The pericycle is not continuous and is absent in the region of furrows, where the center of the bay is occupied by the **leptoids**.

Leptoids: In the center of the bay, a group of polygonal proteinaceous cells is present in each furrow of the central cylinder. These cells are large, elongated, sieve tube-like, and are termed the leptoids. The end walls of the leptoids are oblique and, in some cases, the walls are connected to each other through the plasmodesmata.

The leptoids, which resemble the **sieve cells** of vascular plants, collectively form the leptom. The leptom is the food (photoassimilate) conducting system.

Amylom: On the sideway from the radial strand, each group of leptoids is surrounded by a single layer of parenchymatous cells containing starch. This layer is called the amylo or hydrom sheath. The amylo thus separates the leptom from the central 3-lobed hydrom.

Central Cylinder: The central cylinder is the central, compact, 3-lobed mass of tissue forming the core of the rhizome. It is made up of two kinds of cells: **stereids** (or sclereids) and **hydroids**. The central mass consists mainly of the stereids. These are thick-walled, elongated, living cells with oblique end walls. The stereids are collectively called the **stereom**. The stereom functions as the supporting tissue. In addition, it provides an alternative route for water conduction (**Zamski and Trachtenberg, 1979**). Scattered among the stereids are the larger empty cells with very oblique cellulose walls. These are called hydroids. The hydroids collectively constitute the **hydrom**. The hydrom is considered to function as the water-conducting tissue.

The stereom and the hydrom together form the **hydrom cylinder**.

Anatomy of Aerial Stem

A cross-section of the erect aerial stem is circular in outline. Sometimes it is irregular due to the attachment of leaves (Fig-3.3). Internally, the erect stem is differentiated into the outermost **superficial layer (epidermis)**, followed by the wide **cortex**, and the **central cylinder**.

Epidermis: The outermost superficial layer does not form a clearly defined epidermis. It is single layered.

Cortex: Within the epidermis is the wide cortex. It is differentiated into the outer and inner cortex. The outer cortex is thick-walled and composed of compact, elongated parenchymatous cells that gradually merge into the inner cortex. The inner cortex is made up of loosely arranged, thin-walled parenchymatous cells. Leaf traces are also seen in the cortical region. Each leaf trace consists of a central patch of colorless, thin-walled, water-conducting hydroid cells (**Eschrich** and **Steiner**, 1968). It extends across the cortex and joins the central cylinder.

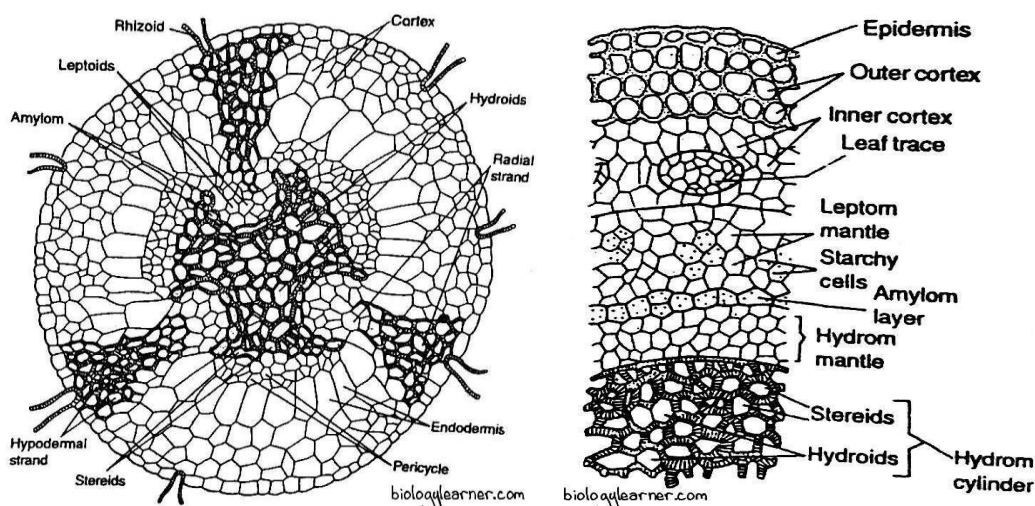


Fig. -3.3: T.S. of the aerial stem in Polytrichum.

Following the cortex is the endodermis (a layer between the cortex and the leptom, **Kawai** and **Ikeda**, 1970). Since the functional aspect of this tissue has not yet been examined, **Tranhtenberg** and **Zamski** (1978) suggested that it would be more appropriate to term this layer as the central strand sheath instead of the endodermis. As the cells of this layer bordering the central cylinder contain starch, the endodermis has also been termed the **starchy sheath**. Within the endodermis is the rudimentary pericycle, which is not differentiated. Inner to pericycle is a broad irregular zone composed of thin walled, sieve tube-like cells. This zone is known as the leptom mantle. It is regarded as equivalent to the phloem of vascular plants. Internal to the leptom mantle is the hydrom sheath or amylo layer. It is a narrow zone consisting of a single layer, sometimes two layers, of cells containing prominent starch. These cells have dark-brown suberized walls.

Central Cylinder: At the centre of the erect stem is a compact mass of thick-walled cells forming the hydrom cylinder. The hydrom cylinder is composed of two kinds of cells: stereids and hydroids. The stereids are thick-walled supporting cells constituting a major part of the hydrom cylinder. Interspersed among the stereids are the thin-walled larger empty cells in groups of 2 or 3. These are the hydroids. The hydroids are considered to function as water conduction.

Surrounding the hydrom cylinder is a zone consisting of two or three layers of thin-walled empty (without content) cells. This layer is called the hydrom mantle.

Anatomy of Leaf: Structurally, the Polytrichum leaf is the most complex of all the mosses. In a cross-section, the leaf shows a broad midrib flanked by a narrow wing or lamina. The lamina is unistratose (one cell thick) and composed of hyaline cells. (Fig-3.4).

The wide midrib makes up most of the width of the leaf. It is several cells thick (multistratose) in the center. Gradually, the midrib merges into the wings.

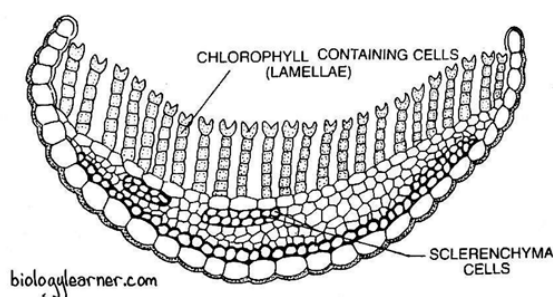


Fig -3.4: T.S. of leaf.

The lower epidermis (epidermis on the abaxial surface) is well-developed and consists of a single layer of regularly arranged large cells. These cells have strongly thickened outer walls. Within the lower epidermis, the midrib generally shows one to two, rarely more, layers of a thick band of small sclereid cells with extremely thickened walls and narrow lumina. On the upper side, a narrow and interrupted band of similar sclereid cells is present. Between these two bands of sclereids, the midrib consists of thin-walled parenchyma cells differentiated into a band of large thin-walled parenchyma cells called the deuters and the much narrow empty central parenchyma cells, the hydroids (Hebant, 1971). The deuters lie just beneath the upper band of sclereids. The hydroids help in

conducting water, and the deuters are involved in the translocation of assimilates out of the leaf. On the upper epidermis, there is a layer of large, thin-walled cells from which arise many parallel plates called lamellae. In a cross-section, the lamellae appear as one-cell thick (uniseriate) rows of green or dark green cells, standing vertically parallel to each other. Each lamella is made up of 4–7 cells containing chloroplasts.

The leaf lamellae, besides functioning as photosynthetic tissue, also hold water due to capillary force. According to Smith (1971), the lamellae function as pseudo mesophyll. The terminal or distal cells of the lamellae, often referred to as the marginal cells, are slightly larger and colorless. They are variously shaped and are ornamented. In *P. juniperinum*, the terminal cells are much wider or papillose, but they are bifid in *P. commune*. The terminal cells of the adjacent lamellae almost touch each other, thus providing a functional equivalent of the upper epidermis. It is, therefore, termed the upper pseudo-epidermis.

Reproduction in Polytrichum: Polytrichum reproduces by both vegetative and sexual methods.

Vegetative Reproduction: Vegetative reproduction in Polytrichum takes place by the following methods.

Bulbils or Vegetative Buds: Sometimes, vegetative buds or bulbils develop on the rhizoids. Under favorable conditions, bulbils may grow into new plants.

Primary Protonema: The spore, on germination, develops a branched, filamentous structure called the primary protonema. It develops multicellular buds which grow into leafy gametophores.

Secondary Protonema: The protonema that develops from any part of the gametophyte is called the secondary protonema. Each secondary protonema forms buds which grow into gametophores.

Fragmentation of Rhizome: The gametophore in Polytrichum is rhizomatous. The horizontally growing rhizome gives rise to erect, leafy stems at intervals.

Death or breakage of the intervening rhizome results in the development of separate, independent *Polytrichum* plants.

Apospory: Development of the gametophyte from the sporophyte without the formation of spores is called **apospory**. The diploid gametophytic protonema may develop from the unspecialized cells of the various parts of the sporophyte.

Sexual Reproduction

Sexual reproduction in *Polytrichum* is of the **oogamous type**. The male gametes (antherozoides) are produced in the antheridium, whereas the female gamete (egg) is developed in the archegonium. *Polytrichum* is **dioecious**, i.e., antheridia and archegonium are borne on different gametophores. Sex organs are developed in groups at the tip of the main axis of the gametophore, which is unbranched.

Antheridial Head: The antheridia are borne in a cluster at the tip of the male. They are surrounded by several bract-like leaves called the perigonal leaves. The perigonal leaves differ from the vegetative leaves in form and color and are modified to form a perianth-like structure. Each perigonal leaf is comparatively shorter and usually consists of a broadly expanded sheathing leaf base terminating in a short bristle point. It may be red brown (*P. juniperinum*) or dull red (*P. piliferum*) in color. (Fig-3.5).

The perigonal leaves lie close together, forming a **rosette (perigonal cup)** around the antheridia, superficially resembling a **small flower**.

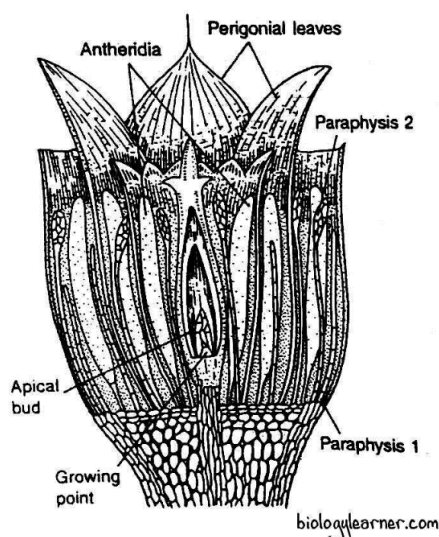


Fig: 3.5 L.S. through the apex of the male gametophore.

The antheridia in the perigonial cup occur in small groups at the base of perigonial leaves in the position of lateral buds. The entire antheridial head in *Polytrichum* is a compound structure, in contrast to that of *Funaria*. The apical cell of the male gametophore is not used in the formation of antheridia. So, the vegetative axis may grow out through the antheridial head and produce antheridia year after year. Such a growth pattern is called “**proliferation.**”

In a longitudinal section, the antheridial head shows a conspicuous apical dome surrounded by many well-developed antheridia. The central dome represents the apical bud containing the growing point (apical cell), which is not used in the formation of antheridia.

Intermingled with the antheridia in the cluster are multicellular hair-like structures called paraphyses. They are simple filamentous structures consisting of a single row of uniform cells. Some may have spatulate tips.

Antheridium: The male reproductive organ of *Polytrichum* is the antheridium.

The antheridia are developed in clusters at the apex of the antheridial branch (male gametophore).

Development of Antheridium: In *Polytrichum*, the development of antheridium is like that of *Funaria*. The antheridium develops from a single embryonic superficial cell at the apex of the male gametophore, called the antheridial initial.

The antheridial initial enlarges in size, becomes papillate, and protrudes above the neighboring cells. It divides transversely to form an upper antheridial mother cell and a lower primary stalk cell. The primary stalk cell (at a very late stage of antheridium development) undergoes a few divisions to form a few-celled antheridial stalk. The antheridial mother cell forms the entire antheridium. It divides by two vertical intersecting walls to form a wedge-shaped apical cell with two cutting faces. The apical cell forms segments in two rows in a regular alternate sequence. In this way, 13 to 15 segments are cut off. Now the apical cell functions as the operculum cell, which develops the operculum (Fig-3.6)

Simultaneously, when the apical cell is dividing, a segment 3–4 cells away from the apical cell starts dividing from the base upward by diagonal vertical walls. The first diagonal wall divides the segment into two cells of unequal size.

The smaller cell is called the first jacket initial. The larger cell further divides periclinal into an outer jacket initial (second) and an inner primary androgonial cell. The jacket initials only divide anticlinally to form a single-layered **jacket** (wall) of the antheridium. The primary androgonial cells undergo further divisions (transversely and vertically) and form the androgonial cells.(Fig-3.7)

The last generation of androgonial cells is called the androcyte mother cells. The androcyte mother cell divides by a diagonal mitotic division and forms two androcytes. Each androcyte ultimately metamorphoses into a biflagellate antherozoid or sperm.

Structure of Antheridium: The mature antheridium of *Polytrichum* is an **elongated structure**. It consists of a club-shaped body with a short, few-celled stalk. The body of the antheridium is encircled by a single-layered jacket. The single-layered sterile jacket surrounds a central mass of androcyte mother cells.

Each androcyte mother cell divides to form two androcytes or spermatids. The androcytes finally metamorphose into antherozoids. At maturity, a thick-walled operculum (cap) can be seen at the tip of the antheridium. It consists of 4-5 distal tiers of small cells.

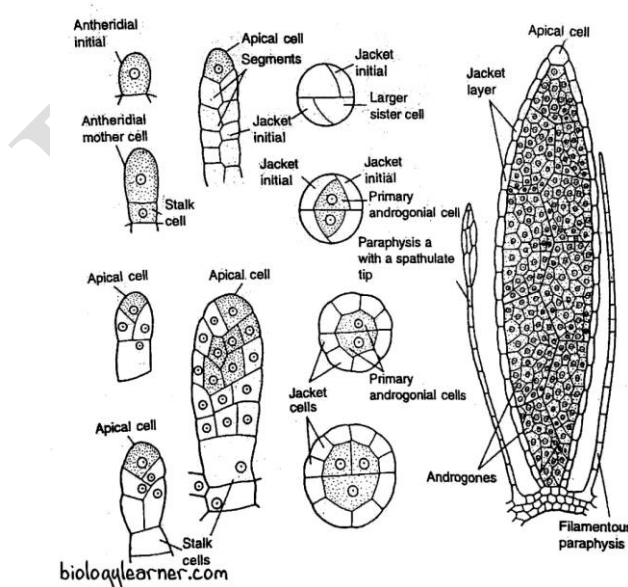


Fig: 3.6

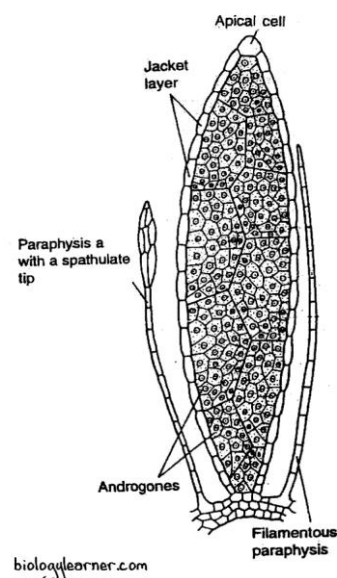


Fig: 3.7

Fig 3.6 Successive stages of development of antheridium in Polytrichum.

Fig. 3.7 A single mature antheridium.

Antherozoids: The antherozoid is a unicellular, uninucleate, biflagellated, spirally coiled, elongated structure. The coiled body remains attached to its posterior end with a cytoplasmic vesicle.

Dehiscence of Antheridium: The mature antheridium dehisces with the help of water. The cells of the operculum swell up by absorbing water. The pressure thus created ruptures the inner wall. Eventually, a narrow pore is formed at the distal end of the antheridium. Many biflagellate antherozoids come out through the pore.

Archegonial Head: The archegonia are also borne at the apex of the female plant, like the antheridia of the male plant. They occur in groups. There are usually 3 to 6 archegonia in a group. (Fig: 3.8).

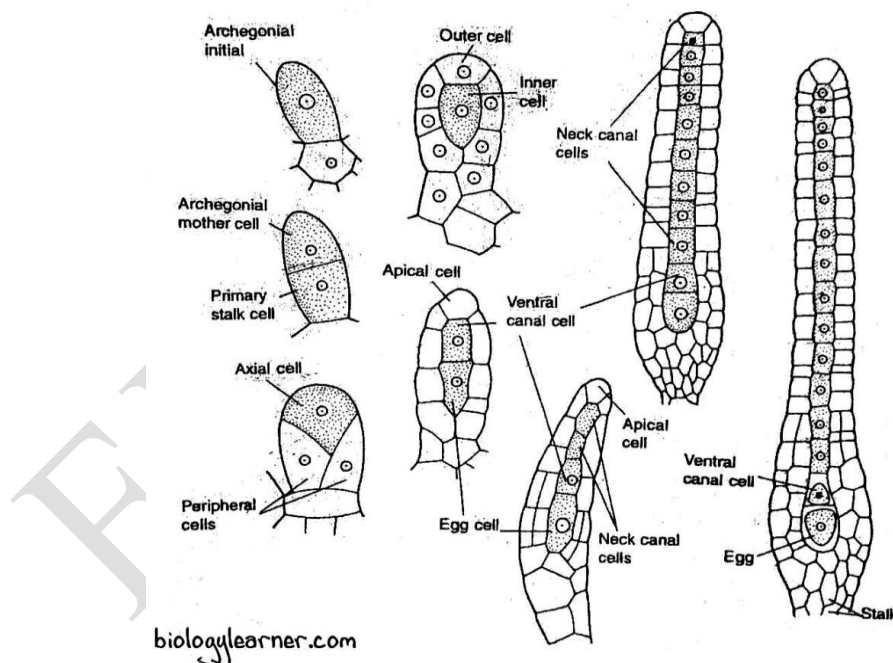


Fig 3.8 Successive stages of development of archegonium in Polytrichum.

The archegonia intermingled with hair-like multicellular paraphyses in the cluster. The paraphyses are simple filamentous structures and consist of a row of uniform cells. The group of archegonia is surrounded by perichaetial leaves (foliage-like). The perichaetial

leaves overlap at the top of the archegonial cluster to form a closed, bud-like structure called the.

Archegonium: The female reproductive organ of *Polytrichum* is the archegonium. The archegonia are developed in clusters at the apex of the archegonial branch (female gametophore).

Development of Archegonium: The archegonium of *Polytrichum* develops from any apical cell at the tip (growing region) of the female gametophore. The apical cell enlarges, slightly projects above the neighboring cells, and functions as the archegonial initial. It divides by a transverse wall to form a basal primary stalk cell and an upper archegonial mother cell.

The primary stalk cell undergoes a few irregular divisions and forms the **massive** stalk of the archegonium. The archegonial mother cell divides by three successive intersecting oblique walls, resulting in the formation of three peripheral cells surrounding a tetrahedral axial cell.

The peripheral cells divide further (transversely, radially, tangentially) to form a 2 or sometimes 3-cell thick jacket or wall of the venter.

Simultaneously, the axial cell divides transversely to form an outer cell and an inner central cell. The central cell divides by an unequal transverse division to form a small venter canal cell and a large egg (oosphere). The outer cell functions as an apical cell with four cutting faces (three lateral and one basal).

The apical cell cuts off successively into three lateral segments and a basal segment.

Each of the lateral segments divides by a vertical wall so that the six vertical rows of cells form the single-layered neck of the archegonium. The fourth basal segment forms neck canal cells.

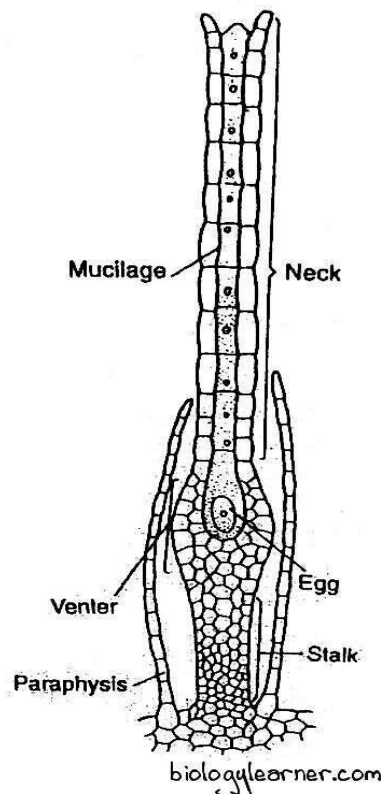


Fig:3.9: A mature archegonium.

Structure of Archegonium: The mature archegonium of *Polytrichum* is typically a flask-shaped structure. It has a massive stalk. Each archegonium consists of an upper, long, twisted neck and a basal, swollen portion, the venter. The neck is one cell thick and consists of six vertical rows of neck cells, which enclose an axial row of 13 or more neck canal cells. The center is composed of a two-cell thick jacket (i.e, wall) of sterile cells. The jacket encircles a small venter canal cell and a large egg. (Fig-3.9)

Fertilization: In *Polytrichum*, water is essential for fertilization. Due to its heterothallic (dioecious) nature, fertilization occurs only when the male and female grow near each other. The neck canal cells and the single venter canal cells in the mature archegonium disintegrate to form a mucilage mass. The mucilage imbibes water, swells, and comes out of the archegonial neck by pushing the cap cells apart, forming an open passage leading to the egg known as the neck canal. The mucilage mass contains some chemical substances, such as sugars, that attract the antherozoids.

The rosette-like perigonial leaves function as a shallow splash cup. Rain drops falling on the perigonial leaves can splash the antherozoids up to two feet (Bridie, 1951). This is

called the splash cup mechanism. Splashing drops bring vesicles containing antherozoids to the archegonial cluster. The vesicles dissolve, and the antherozoids are released to swim into archegonia.

Many antherozoids caught in the mucilage enter the archegonial neck due to the chemotactic response and reach up to the egg. Finally, one of the antherozoids fertilizes the egg to form a diploid zygote.

Fertilization ends the gametophytic phase.

Sporophyte of Polytrichum: The sporophytic phase in Polytrichum starts with the formation of the diploid zygote after fertilization. The zygote is the first cell of the sporophyte.

Development of Sporophyte: After fertilization, the zygote immediately secretes a wall around itself and becomes an oospore. It swells up and gradually enlarges in size. The zygote or oospore divides first by a transverse wall to form an upper epibasal cell and a lower hypobasal cell. Both the hypo basal and epibasal cells divide by two successive intersecting oblique walls to form a young embryo with two growing points at the two opposite ends. The epibasal cell produces a wedge-shaped apical cell with two cutting faces. Similarly, the hypo basal cell also produces an apical cell with two cutting faces. The entire sporophyte is differentiated by the activity of these two apical cells. Hence, the development of the embryo sporophyte in Polytrichum is bi-apical. The apical cell of the epibasal cell develops into the capsule and upper portion of the seta (3/4 portion), while the apical cell of the hypobasal cell forms the slender foot and remaining part of the seta (1/4 portion). Both apical cells cut out alternate segments and form the cylindrical young sporophyte. (Fig-3.10)

The upper region of the young sporophyte divides periclinally to form a four-celled endothecium (a group of central cells), surrounded by eight peripheral cells of the amphithecium. The endothecium forms sporogenous tissue and the columella, while the jacket of the capsule develops from the amphithecium. Along with the development of the sporophyte, the archegonial wall divides to form a fibrous covering (4-6 cells in thickness) known as the calyptra. The calyptra completely encircles the developing embryo (young sporophyte).

Structure of Sporophyte

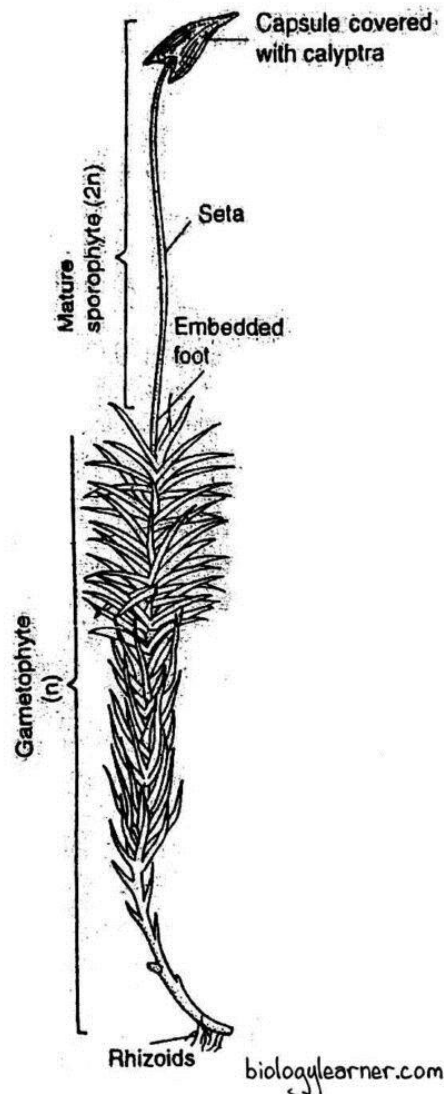


Fig:3,10 Female gametophore bearing sporophyte at its apex

The mature sporophyte of *Polytrichum* is an elongated structure and is relatively complex, like that of *Funaria*. It is developed at the tip of a female gametophore after fertilization. The sporophyte is differentiated into three parts: the foot, the seta, and the capsule. (Fig-3.11)

Foot: The basal portion of the sporophyte is the foot. It is a dagger-like conical structure. The foot is deeply embedded in the apical tissue of the female gametophore and consists of thin-walled parenchymatous cells containing dense cytoplasm. It functions in the anchorage of the sporophyte and in the absorption of water and nutrients from the gametophyte for the developing sporophyte.

Seta: The seta is a long, slender, stalk-like structure that connects the capsule with the foot. It raises the capsule above the apex of the female gametophore. In a transverse section, the seta shows a single layer of thick-walled epidermis with a well-developed central conducting strand of thin-walled hydroid cells surrounded by the cortex. The cortex is composed of loosely arranged, thin-walled, green parenchymatous cells. Within the epidermis, there is the hypodermis, consisting of several layers of very thick-walled brown sclerenchymatous cells. Seta is mechanical in function. It also helps in the conduction of water and nutrients to the developing capsule.

Capsule: The capsule forms the major and most conspicuous part of the sporophyte in *Polytrichum*. It is long, erect, and generally angular-shaped, but shows a polygonal outline in cross-section. The capsule is developed at the apex of the seta and is almost completely covered by the calyptra, with a hairy surface.

The capsule is differentiated internally into three distinct regions: the apophysis (sterile basal region), the theca (central fertile region), and the operculum or lid (apical region).

Apophysis: The apophysis is the lowermost part of the capsule (also called the neck). It is a bulbous, sterile structure that connects the capsule with the seta below. Structurally, the apophysis is composed of a single-layered, thick-walled epidermis, which is interrupted by stomata. The stomata consist of a single ring of guard cells. Usually, two guard cells are present in each stoma. Below the epidermis is the chlorenchyma, consisting of many thin walled, loosely arranged parenchymatous cells. These parenchymatous cells contain chloroplasts. Thus, the sporophyte of *Polytrichum* is actively photosynthetic in function. Therefore, it is not fully dependent on the gametophyte for nutrition.

There is no hypodermis in the apophysis region. The central part of the apophysis is composed of numerous thin-walled cells, forming a conducting strand.

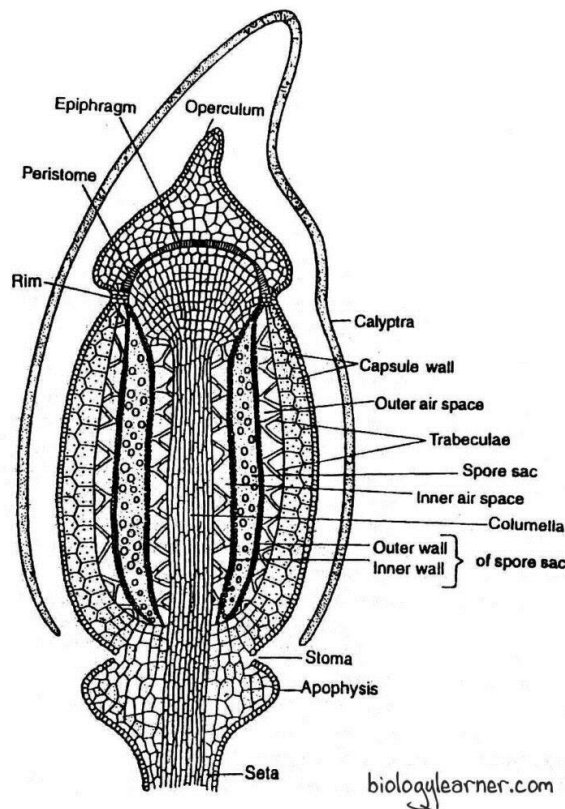


Fig 3.11 L.S. of capsule showing its structure.

Theca: The theca is the middle, fertile region of the capsule. It lies between the apophysis and the operculum.

A longitudinal section of the theca shows the following regions.

Capsule Wall: The capsule wall, or jacket, is several layers thick and composed of parenchymatous cells. The outermost layer of the capsule wall is the single-layered epidermis. It consists of compactly arranged cells with thick outer walls. The epidermis of the wall lacks stomata.

The epidermis is followed by typically two layers of spongy parenchyma. The cells of the spongy parenchyma are thin-walled and achlorophyllous. These cells can manufacture their own food.

Spore Sacs: The spore sacs are situated below the outer air cavities on either side of the columella. Each spore sac has an outer wall and an inner wall. Both walls are made up of two thin-walled cell layers. The spore sacs are derived from the single-layered archesporium (sporogenous tissue).

The archesporium first develops 4-6 layers of sporogenous cells. The sporogenous cells divide to form many spore mother cells, which fill the cavity (a space between the outer wall and the inner wall) of the spore sac. Later, the spore mother cells divide by meiotic divisions and form haploid spores. The spore sac in *Polytrichum* is surrounded by a double air space system, as the air cavities are found on both its outer and inner sides.

Air Cavities: The air cavities (air spaces) are cylindrical and are present on both sides of the spore sacs. The outer air spaces are present just below the spongy parenchyma and outside the spore sacs, while the inner air spaces are found below the spore sacs. These air spaces are traversed radially by delicate strands (short filaments) of elongated green cells called trabeculae. The trabeculae of the outer air spaces connect the innermost layer of the capsule wall with the outer wall of the spore sac, whereas those of the inner air spaces connect the spore sac with the central columella.

Columella: The columella is the central part of the theca region. It is made up of compactly arranged parenchymatous cells. The columella is continuous with the central strand of the apophysis below and extends up to the epiphragm of the operculum above. Columella helps in the conduction of water and mineral nutrients.

Operculum or Lid: The operculum is the apical region of the capsule. It is a conical structure with a beak or rostrum that forms a cap or lid at the apex of the theca. The operculum is differentiated from the theca region by a well-marked, narrow circular constriction. At the base of the constriction, there is a diaphragm or rim composed of two to three layers of radially elongated, thick-walled cells. The annulus is absent in *Polytrichum*.

The columella of the theca is continuous into the operculum. It expands to become a fan-shaped, pale membranous structure known as the epiphragm. The epiphragm stretches like the tympanum of a drum across the mouth of the theca. So, the epiphragm is also called the tympanum. Just within the mouth of the capsule and under the epiphragm, the peristome is present. It is attached below the edge of the diaphragm. The peristome consists of a ring of 64 short, stout, pyramidal teeth known as peristomial teeth.

Each peristomial tooth is solid and made up of several curved, crescent-shaped, fiber-like cells. Hence, the peristome in *Polytrichum* is termed the nematodontous peristome. At

maturity, the teeth are joined to the margin of the epiphragm by their tips. The peristome teeth are not hygroscopic but may control the dispersal of the spores.

Dehiscence of the Capsule and Dispersal of Spores: When the capsule matures, the calyptra falls off. The exposed capsule begins to dry up. Simultaneously, the operculum shrivels and becomes loose. It eventually drops off, exposing the peristome. The central tissue (non-sporogenous tissue) of the theca region, except the spores, degenerates at maturity. The spores come to lie in the center of the capsule. Meanwhile, the thin-walled cells between the peristome teeth also dry up. As a result, small openings are formed in the margin of the epiphragm. The spores are dispersed, a few at a time, through these openings as the capsule sways in the wind (censer mechanism).

Spore: The spores are haploid, uninucleate, and yellow. They are very small, 0.010 to 0.011 μm in diameter. Each spore is surrounded by two wall layers: the outer exosporium (exine) and the inner endosporium (intine). The exine is thick and ornamented, while the intine is thin.

A tiny mass of cytoplasm is present inside the spore wall. It consists of a single nucleus, reserve food materials, and a few plastids (2-4). The reserve food is in the form of lipid droplets.

Germination of Spores and Formation of the Young Gametophyte: The spore is the first cell of the gametophytic generation. Each spore of *Polytrichum* germinates upon falling on a suitable, moist substratum. It absorbs moisture from the substratum and increases in size considerably. The exosporium ruptures at the centre of the aperture region, and the endosporium comes out in the form of a small germ tube. The germ tube elongates, becomes septate, and produces a green, algal filament-like protonema. The protonema forms two types of branches: the rhizoidal branches and the chloronemal branches. The rhizoidal branches are comparatively narrow, have no chloroplasts, and develop below the substratum. They are colorless and possess oblique septa between the cells. Rhizoidal branches anchor the protonema in the substratum.

The chloronemal branches are spread over the surface of the substratum. They are green and contain chloroplasts in their cells. The cells of chloronemal branches have partition walls at right angles to the lateral walls (transverse septa) between them. The

chloronemal branches develop many green buds. Each bud grows into a leafy gametophore.

Anthoceros

Class: Anthocerotopsida

Order: Anthoceratales

Family: Anthecerataceae

Genus: Anthoceros

Distribution and Habitat of Anthoceros

Anthoceros is represented by about 200 species. All species are terrestrial and cosmopolitan in distribution. The species grow in very moist and shady places like slopes, rocks or sides of the ditches. Some species are found growing on decaying wood (Cavers, 1911). Unlike other bryophytes, Anthoceros is usually not well adapted to resist dry conditions.

In India, the Anthoceros is represented by about 25 species. Out of these three species of Anthoceros viz., *A. himalayensis*, *A. erectus* and *A. chambensis* are commonly found growing in the Western Himalayan region at an altitude of 5000-8000 feet (Kashyap, 1915). These species are also found growing in Mussoorie, Kulu, Manali, Kumaon, Chamba Valley, Punjab, Madras and in the plains of South India. Mehra and Handoo (1953) reported *A. himalayensis* and *A. erectus* from Simla, Nainital and Dalhousie. Some other species of Anthoceros and their places of occurrence are *A. dixitii*, *A. sahyadrensis* (Poona and neighbouring hills), *A. crispulus* (Lucknow), *A. assamicus* (Assam), *A. shvianandani* (Kerala), etc. The species of Anthoceros may be perennial (*A. himalayensis*) or annual (*A. erectus*).

Gametophytic Phase of Anthoceros:

External Features: The gametophytic plant body is thalloid, dorsiventral, prostrate, and dark green with a tendency towards dichotomous branching. Such branching results in an orbicular or semi-orbicular rosette-like appearance of the thallus. The thallus is bilobed (*A. himalayensis*,

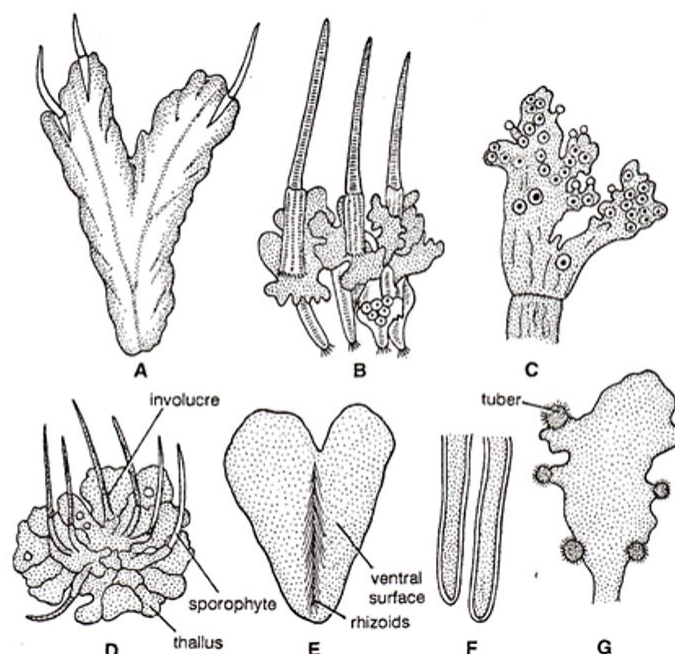


Fig. 4.1 A) or pinnately branched (*A. hallii*) or spongy with many sub-spherical spongy bodies like a gemma (*A. gemmulosus*, Fig. 4.1 C) or raised on a thick vertical stalk-like structure (*A. erectus*, Fig. 4.1B).

4.1 (A-F). *Anthoceros*. External features (A) *A. himalayensis*, (B) *A. erectus*, (C) *A. gemmulosus*, (D) *A. crispulus* (dorsal surface), (E) Ventral surface, (F) Smooth-walled rhizoids, (G) Thallus with tubers.

Dorsal Surface: The dorsal surface of the thallus may be smooth (*A. laevis*) or velvety because of the presence of several lobed lamellae (*A. crispulus*) or rough with spines and ridges (*A. fusiformis*). It is shining, thick in the middle, and without a distinct midrib (Fig. 4.1 D).

Ventral Surface: The ventral surface bears many unicellular, smooth-walled rhizoids (Fig. 4.1 E, F). Their main function is to anchor the thallus on the substratum and to absorb water and mineral nutrients from the soil. Tuberculated rhizoids, scales, or mucilaginous hairs are absent. Many small, opaque, rounded, thickened dark bluish green spots can be seen on the ventral surface. These are the mucilage cavities filled with *Nostoc* colonies. In September and October, the mature thalli have erected, elongated, and cylindrical sporogonia. These are horn-like and arise in clusters. Each sporogonium is surrounded by a sheath-like structure on its base. It is called involucre (Fig. 4.1 D).

Internal Structure: The vertical transverse section (V. T. S.) of the thallus shows a very simple structure. It lacks any zonation (Fig. 4.2 A, B). It is uniformly composed of thin-walled parenchymatous cells. The thickness of the middle region varies in different species.

It is 6-8 cells thick in *A. laevis*, 8-10 cells thick in *A. punctatus*, and 30-40 cells thick in *A. crispulus*. The outermost layer is the upper epidermis. The epidermal cells are regularly arranged, smaller in size, and have large lens-shaped chloroplasts. In *A. hallii* the epidermal layer is not distinguishable.

Each cell of the thallus contains a single large discoid or oval-shaped chloroplast. Each chloroplast encloses a single, large, conspicuous body called pyrenoid, a characteristic feature of class Anthocerotopsida (Fig. 4.2 C, D). 25-300 disc to spindle-shaped bodies aggregate to form pyrenoid. The number of chloroplasts per cell also varies in different species. In *A. personi* each cell has two chloroplasts and in *A. hallii* the number may be even four. The nucleus lies in the close vicinity of the chloroplast near the pyrenoid (Fig. 4.2 D). Sometimes the chloroplast enfolds. The air chambers and air pores are absent in Anthoceros. However, in a few species, intercellular cavities are present on the lower surface of the thallus. These cavities are formed due to the breakdown of the cells (schizogenous).

The cavities are filled with mucilage and are called mucilage cavities. These cavities open on the ventral surface through stoma-like slits or pores called slime pores (Fig. 4.2 B). Each slime pore has two guard cells with thin walls (Fig. 4.2 F). The guard cells are non-functional and do not control the size of the pore.

The pore remains completely open. These pores are formed by the partial separation of two adjacent cells. The slime pores represent the vestigial remnants of a previously existing aerating system. With the maturity of the thallus the mucilage in the cavities dries out. It results in the formation of air-filled cavities. The blue-green algae *Nostoc* invades these air cavities through slime pores and forms a colony in these cavities. The presence of *Nostoc* colonies in the thallus of *Anthoceros* is beneficial for the growth of gametophyte is not known. Pierce (1906) assumed that the thalli without *Nostoc* grow better than the ones containing the endophytic algae. However, according to Rodgers and Stewart (1977), it is a symbiotic association.

The thallus supplies carbohydrates to the Nostoc and the latter, in turn, adds to nitrate nutrients by fixing atmospheric nitrogen. The lowermost cell layer is lower epidermis. Some cells of the lower epidermis extend to form the smooth-walled rhizoids (Fig.4. 2 B).

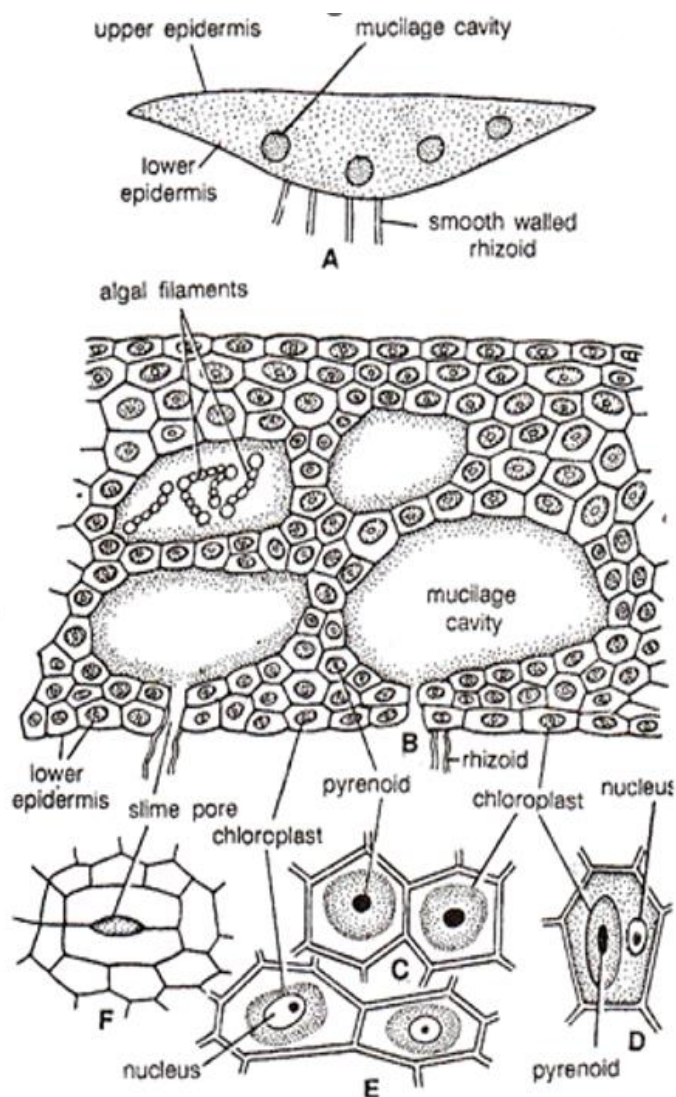


Fig 4.2 (A-F). Anthoceros. Internal structure of the thallus. (A) Vertical transverse section (V.T.S.) of thallus (diagrammatic), (B) V.T.S. of thallus (a part cellular), (C) Cells showing chloroplast and pyrenoid, (D) cells showing chloroplast, pyrenoid and nucleus, (E) Parenchymatous cells with chloroplast and nucleus, (F) Surface view of slime pore.

Reproduction in Anthoceros: Anthoceros reproduce by vegetative and sexual methods.

Vegetative Reproduction: It takes place by the following methods.

1. By death and decay of the older portion of the thallus or fragmentation:

The older portion of the thallus starts rotting or disintegrating due to aging or drought. As it reaches up to the place of dichotomy, the lobes of the thallus get separated. Thus, detached lobes develop into independent plants by apical growth. This method is not so common in *Anthoceros* as in liverworts.

2. By tubers

Under unfavourable conditions or prolonged drought, the marginal tissues of the thallus get thickened and form the perennating tubers. (Fig. 4.1 G). Their position varies in different species. They may develop behind the growing points (*A. laevis*) or along the margins of the thallus (*A. hallii*, *A. pearsoni*). In *A. himalayensis* the tubers are stalked and develop along the margins on the ventral surface of the thallus.

The tubers have outer two to three layers of corky hyaline cells which enclose the tissue containing oil globules, starch grains and aleurone granules. They are capable to pass on the unfavorable conditions. On resumption of favourable conditions tubers produce new thalli.

3. By Gemmae: In some species of *Anthoceros* like *A. glandulosus*, *A. propaguliferus*, *A. formosae* many multicellular stalked structures develop along the margins of the dorsal surface of the thallus. These structures are called gemmae. When detached from the parent thallus, each gemma develops into a new plant.

4. By persistent growing apices: Due to prolonged dry summer or towards the end of the growing season, the whole thallus in some species of *Anthoceros* (*A. pearsoni*, *A. fusiformis*) dries and gets destroyed except the growing point. Later it grows deep into the soil and becomes thick under unfavorable conditions. It develops into a new thallus. It is more a method of perennation than multiplication.

5. By apospory: In *Anthoceros*, unspecialized cells of the many parts of the sporogonium (e.g., intercalary meristematic zone, subepidermal and sporogenous region of the capsule) form the gametophytic thallus. This phenomenon is called apospory (Schwarzenbach, 1926, Lang, 1901). The thalli are diploid but normal in appearance e.g., *A. laevis*.

Sexual reproduction

Sexual reproduction is oogamous. Male reproductive bodies are known as antheridia and female as archegonia. Some species of *Anthoceros* like *A. longii*, *A. gollani*, *A. fusiformis*, *A. punctatus*, *A. crispulus* and *A. himalayensis* are monoecious while some species like *A. erectus*, *A. chambensis*, *A. hallii*, *A. pearsoni* and *A. laevis* are dioecious. The monoecious species are protandrous i.e., antheridia mature before archegonia.

Structure of Antheridium: A mature antheridium has a stalk and club or pouch-like body. The stalk attaches the antheridium to the base of the antheridial chamber. Stalk may be slender and composed of four rows of cells (e.g., *A. punctatus*, *A. erectus*, Fig. 4.3) or more massive (e.g. *A. laevis* Fig. 4.3 J). A single or a group of two to four or more antheridia are present in the same antheridial chamber (Fig. 4.3 H). A single layered sterile jacket encloses the mass of androcytes which metamorphosis into antherozoids.

In some species e.g., *A. punctatus* and *A. erectus* jacket layer is formed of four tiers of cells. Each tier appears to be composed of elongated rectangular cells (Fig 4.3 I). In *A. laevis* and *A. himalayensis* jacket is composed of many relatively smaller and less regularly arranged cells (Fig. 4.3 1).

The cells of the uppermost tiers are triangular with a narrow end towards the apex (Fig. 4.3 J). Each cell of the jacket consists of plastids. At maturity, these plastids change their color from green to red to bright orange. Young antheridia are, therefore, green, and mature ones turn bright orange or reddish.

The Antherozoid: A mature antherozoid is unicellular, uninucleate, bi-flagellated, and has a linear body. The flagella are of almost the same length as the body (Fig. 4.3 K, L). Proskauer (1948) observed that the body of antherozoids shows some degree of residual curvature (Fig. 4.3 M, N).

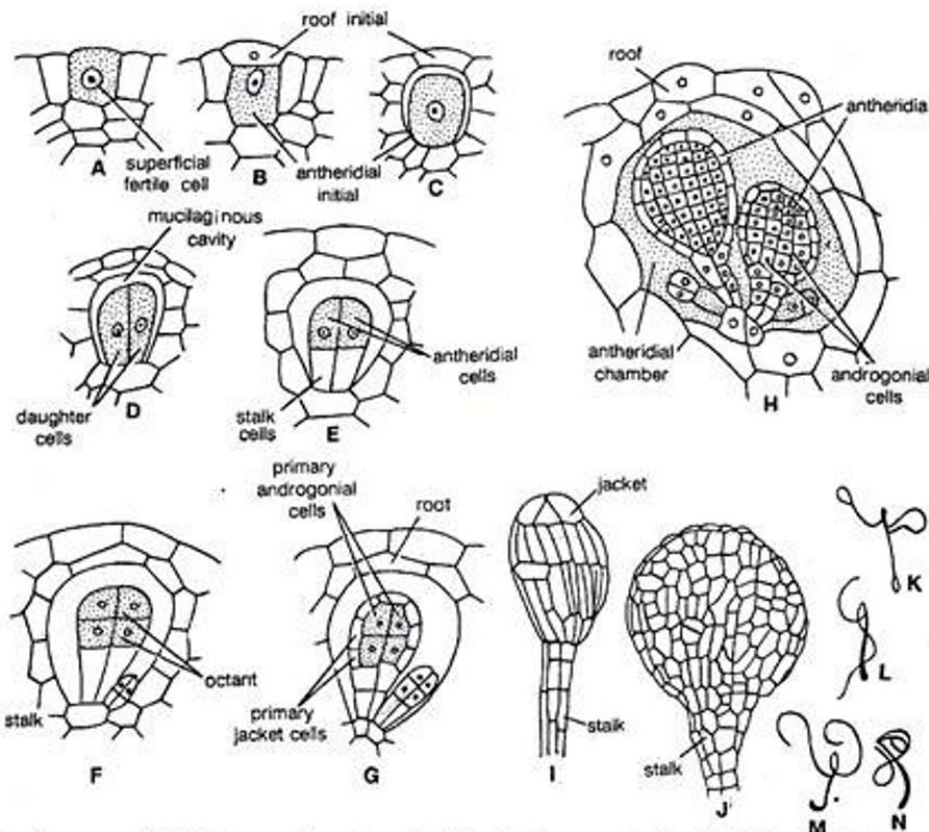


Fig 4.3 (A-N) Anthoceros. (A-H) Successive stages in the development of antheridium, (I) Mature antheridium of *A. punctatus* (J) Mature antheridium of *A. laevis*, (K, L) Antherozoids of *A. laevis*, (M, N) Antherozoids of *A. punctatus*.

Development: The development of the antheridium starts from a superficial dorsal cell. This cell never becomes papillate. It divides by periclinal division into an outer roof initial and an inner antheridial initial (Fig. 4.3 A, B). Unlike the class Hepaticopsida (e.g., *Marchantia*), the antheridium develops from the inner cell. Therefore, the antheridium is endogenous in origin. Soon after the division a mucilaginous filled space develops between the antheridial initial and roof initial. (Fig. 4.3 C).

The roof initial divides by periclinal divisions followed by many anticlinal divisions to form two-layered roof of the antheridial chamber. The antheridial initial either directly develops into a single antheridium (e.g., *A. pearsoni*) or it may divide vertically into two, four or sometimes more daughter cells (e.g., *A. erectus*).

Each of the daughter cells functions as an antheridial initial. The antheridial initially divides by two vertical divisions at a right angle to each other to form four cells (Fig. 4.3D). At this stage, the young antheridium consists of four cells.

All four cells divide by transverse division to form eight cells, arranged in two tiers of four cells each (Fig. 4.3 E). The cells of the lower tier are called stalk cells. These cells divide and re-divide by transverse divisions to form a multicellular stalk of the antheridium.

The four cells of the upper tier form the body of the antheridium. These cells divide by transverse division to form eight cells (Fig. 4.3 F).

Each cell of the octant divides by a curved periclinal division to form the eight outer primary jacket cells and eight inner primary androgonial cells (Fig. 4.3 G). Primary androgonial cells divide by several repeated transverse and vertical division resulting in the formation of large number of small cubical androgonial cells. The last generation of androgonial cells is known as androcyte mother cells. Each androcyte mother cell divides by a diagonal mitotic division to form the two triangular cells called androcytes.

The protoplast of each androcyte metamorphosis into bi-flagellated antherozoid. In some species secondary antheridia develop later from the stalk of the older one. Therefore, in more advanced stages the antheridial group inside a single antheridial chamber consists varying numbers of antheridia in different stages of development (Fig. 4.3 H).

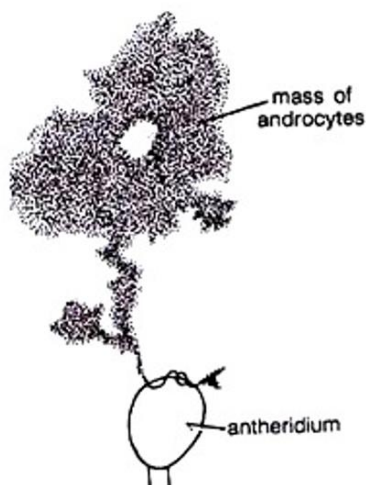


Fig. 4.4

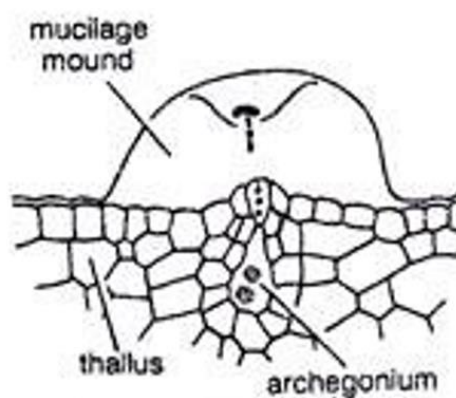


Fig. 4.5

Fig. 4.4. Anthoceros. Dehiscence of antheridium. Fig 4.5 Anthoceros. Mature archegonium with mucilage mound.

Dehiscence of Antheridium: Water helps in the dehiscence of the antheridium. As the antheridia mature the roof of the antheridial chamber breaks down irregular, exposing the

antheridia in a cup-like chamber. The antheridia absorb water, and the uppermost tier of triangular cells fall apart releasing a mass of antherozoids. After dehiscence, the antheridium loses turgor and collapses. It is followed by other antheridia to converge towards the opening in the roof and in this way a continuous stream of antherozoids is possible. It explains the formation of many sporophytes of Hornworts. (fig 4.4)

Archegonium: Archegonia develop in the flesh of the thallus on dorsal surface. The place of an archegonium on a thallus can be identified by the presence of a mucilage mound (Fig. 4.5).

Structure: A mature archegonium consists of two to four cover cells, an axial row of four to six neck canal cells, a venter canal cell, and an egg. The jacket layer is not distinct from the other vegetative cells like other Bryophytes (Fig. 6 G, H).

Development: The development of the archegonium starts on the dorsal surface of the thallus from a single superficial cell which acts as an archegonial initial (Fig.4.6 A). It can be differentiated from other cells by its dense protoplasm.

The archegonial initial may divide by transverse division to form an upper primary archegonial cell and lower primary stalk cell (e.g., *A. crispulus*, *A. gemmulosus*) or it may directly function as a primary archegonial cell (e.g., *A. erectus*).

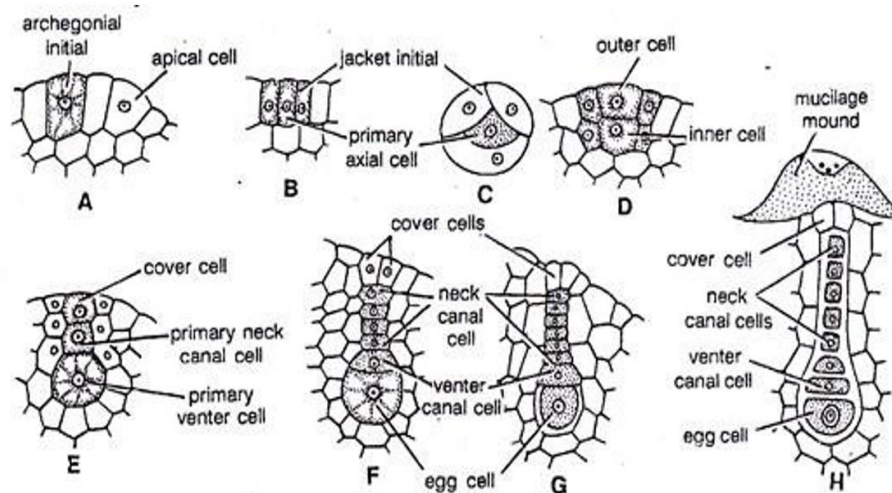


Fig. 4.6. (A-H). Anthoceros. Development of archegonium. (A-H). Successive stages in the development of archegonium.

The primary archegonial cell divides by three successive intersecting walls or periclinal vertical walls to form the three peripheral initials or jacket initials and a fourth median cell, the primary axial cell (Fig. 4.6 B, C). Jacket initials divide by transverse divisions to form into two tiers of three cells each. The cells of the upper tier divide by anticlinal division to form six cells. These cells divide transversely to form a jacket of six rows of sterile neck cells. The three cells of the lower tier divide by transverse and vertical divisions to form a venter wall. Since the archegonium is embedded in the thallus, it is difficult to trace the development of the cells and to distinguish them from the vegetative cells (Fig. 4.6).

The primary axial cells divide by a transverse division to form an outer cell and an inner (central) cell (Fig. 4.6 D). The outer cell divides by a transverse division to form a terminal cover initial and inner primary neck canal cell (Fig. 4.6 E). The inner cell directly functions as the primary venter cell and divides only once to form an upper small venter canal cell and a lower large egg. The primary neck canal cell divides by a series of transverse divisions to form four to six neck canal cells. Cover is initially divided by one-two vertical division to form two to four rosette-like cover cells at the tip of the neck (Fig 4.6 G, H).

Fertilization: Water is essential for fertilization. In the mature archegonium, the venter canal cell, and neck canal cells disintegrate and form a mucilaginous mass. It absorbs water, swells up, and becomes out of the archegonial neck by pushing the cover cells apart. This mucilaginous mass becomes continuous with the mucilage mound and in this way, an open passage down to the egg is formed.

The mucilaginous mass consists of chemical substances. Many antherozoids caught in the mucilage enter the archegonial neck because of the chemotactic response, reach up to the egg, and fertilization is affected. Before fertilization, the egg enlarges and fills the cavity of the venter. Fusion of both male and female nuclei results in the formation of a diploid zygote or oospore. Fertilization ends the gametophytic phase.

Sporophytic Phase: After fertilization the diploid zygote or oospore still enlarges in size and fills the cavity of the venter of the archegonium. It secretes an outer cellulose wall.

Development of Sporophyte: The first division of the zygote (Fig. 4.7 A, B) is vertical. In other Bryophytes the first division of the zygote is transverse. This is the important difference in the development of the sporophyte of Hornworts and the rest of the Bryophytes.

The second division is transverse (Fig. 4.7 C) and is so oriented that the upper two cells are usually longer than the lower two (quadrant stage). All four cells divide by vertical walls to produce eight cells (octant stage). The eight cells are arranged in two tiers of four cells each. Further development of the sporophyte varies in different species. In *A. erectus* the lower tier of four cells of the octant stage forms the foot while the seta and capsule are formed from the upper tier of four cells.

In most of the species like *A. fusiformis*, *A. pearsoni* and *A. himalayensis* upper tier of four cells divide by transverse division to form three tiers of four cells each (Fig. 4.7 D). The lowermost tier forms the foot, the middle tier forms the meristematic zone or intermediate zone, and the uppermost tier develops into the capsule. The four cells of the lower tier divide by irregular divisions to form broad, bulbous foot, made up of parenchymatous cells. In some species (e.g., *A. punctatus*) the superficial cells of the foot form a palisade layer of cells while in some species (e.g., *A. laevis*, *A. himalayensis*) the superficial layer grows into haustoria-like projections. The uppermost tier of four cells which forms the capsule divided by one to two transverse divisions to form two to three tiers of cells.

It is followed by periclinal division to form an outer layer of amphithecium and the central mass of cells called endothecium (Fig. 4.7 F). The entire endothecium develops into the sterile columella. In young sporophyte it is made of four cells but in mature sporophyte, it is made of sixteen vertical rows (Fig. 4.8 D, E) of cells (4 x 4).

The amphithecium divides by a periclinal division to differentiate into an outer sterile layer of jacket initials and an inner fertile layer (Fig. 4.7 A).

The cells of the jacket initials divide by anticlinal and periclinal divisions to form a four to six-layered capsule wall. The outermost layer of the capsule wall is called the epidermis (Fig. 8 A). It is characterized by the presence of stomata (Fig. 4.8 F). The cells of the inner layers of capsule wall have chloroplast.

In young sporophytes the archesporium over arches the columella (Fig. 4.7 G). The archesporium may single layered in thickness throughout its further development (e.g., *A. erectus*) or become two-layered (e.g., *A. pearsoni*) or two to four-layered (e.g., *A. hallii*).

On maturity, the archesporium gives rise to two types of cells: spore mother cells and elater mother cells. These cells are arranged alternately one above the another (Fig. 4.8 A). Spore mother cells are spherical or oval with dense cytoplasm and large nuclei. These cells divide by meiotic divisions to form spore tetrads (Fig. 4.8 A). Elater mother cells are elliptical with small nuclei. These cells divide mitotically to form four-celled elaters.

The four cells of the elaters may remain attached or may break into 1-celled, 2-celled, or 3-celled units. The broken units are called pseudo-elaters. (The elaters are without thickening bands and therefore, called pseudo elaters, (Fig. 4.8 A). By the activity of the meristematic zone various tissues of the capsule are continuously produced so that it becomes elongated.

The young sporophyte of the *Anthoceros* is surrounded by a fleshy covering or sheath. It is called involucre (Fig. 4.8 A). It is developed partly from the tissue of the archegonium and partly from the tissue of the gametophytic thallus. In young stages, the sporophyte is surrounded by an involucre.

Structure of Mature Sporogonium

The mature sporophyte consists of a bulbous foot and a smooth, slender, erect, cylindrical structure called a capsule. Capsule varies in length from two to fifteen centimeters in different species. The sporogonium appears like a 'bristle' or 'horn', hence, the species are called 'hornworts' (Fig. 4.1 A, 4.8 A).

Internal structure: A mature sporogonium can be differentiated into three parts viz., the foot, seta and the capsule.

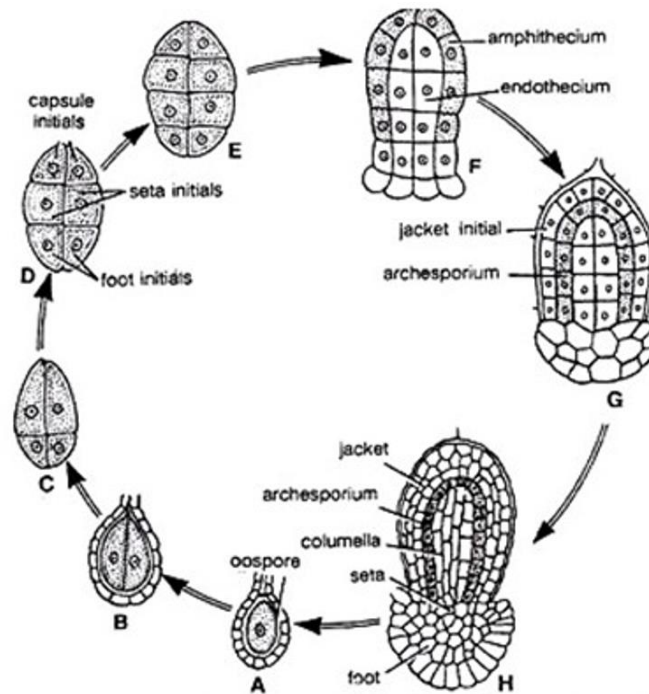


Fig. 4.7. (A-H). Anthoceros. Successive stages in the development of the sporophyte.

Foot: It is bulbous, multicellular, and made up of a mass of parenchymatous cells. It acts as a haustorium and absorbs food and water from the adjoining gametophytic cells for the developing sporophyte (Fig. 4.8 A).

Seta is represented by the meristematic zone. This is present at the base of the capsule and consists of meristematic cells. These cells constantly add new cells to the capsule at its base.

The presence of the meristem at the base enables the capsule to grow for a long period and form spores. It is a unique feature of *Anthoceros* and is not found in any other bryophyte. We can see different stages of development from base upwards in the sporogonium of *Anthoceros* (Fig.4. 8 A).

Capsule: Its internal structure can be differentiated into the following parts

Columella: It is central sterile pan, extending nearly to its tip. It is endothecial in origin. In young sporophyte, it consists of four vertical rows of cells but in mature sporophyte, it is made up of 16 vertical rows of cells (4 x 4). In a transverse section these cells appear as a solid square (Fig.4. 8 D, E). It provides mechanical support, functions as water-conducting tissue, and helps in the dispersal of spores.

Archivesporium: It is present between the capsule wall and the columella. It extends from the base to the top of the capsule. It originates from the inner layer of amphithecium. In young sporophyte it over arches the columella (a feature in contrast to liverworts). In a few species of *Anthoceros* e.g., *A. crenatifrons*, *A. hawaiiensis* and *A. erectus*, the archivesporium may remain one cell in thickness throughout its further development.

However, in *A. pearsoni* and *A. himalayensis* it may become two layered thick a little above the base. In *A. hallii* it may even become two to four cells in thickness (Fig. 4.8 A). In the upper part of the capsule, it is differentiated into sporogenous tissue which produces spores and pseudo-elaters.

Pseudo elaters may be unicellular or multicellular, branched or un-branched, and may consist of elongated cells (Fig. 9 A-D). The spiral thickenings are absent (characteristic of *Anthoceros*) but in *A. physocladus* the cells have long and thick walls with extremely reduced lumen (Pande, 1960). In some species of *Anthoceros*, their secondary walls possess helical thickenings (Proskauer, 1960).

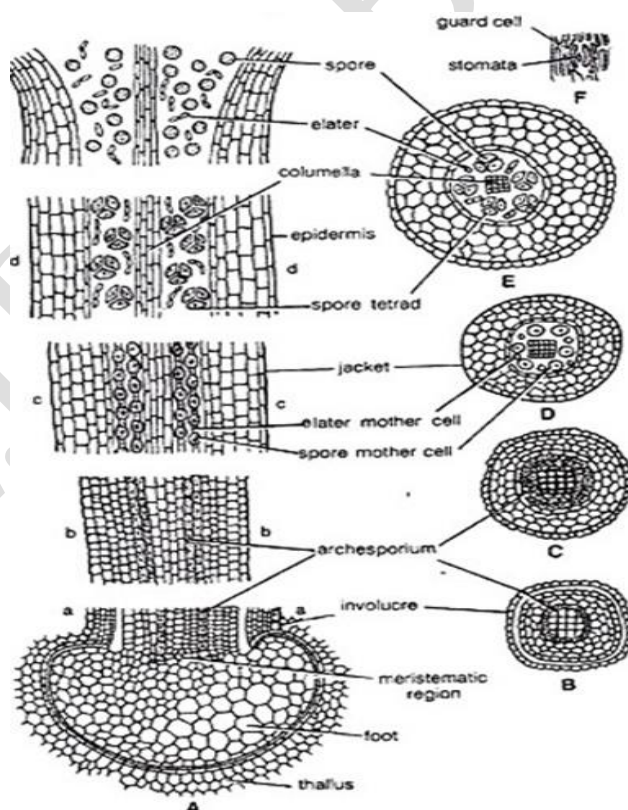


Fig. 4.8. (A-F). *Anthoceros*, Internal structure of the sporogonium (A) Longitudinal Section (LS.) through the mature sporogonium. (B) Cross section of the sporogonium at s-a level, (C) cross-section of the sporogonium at b-b level, (D)

cross-section of the sporogonium at o-c level, (E) Cross section of the sporogonium at d-d level, (F) Structure of stomata from the epidermis of sporogonium wall.

Capsule wall: It consists of four to six layers of cells, of which the outermost layer is epidermis (Fig. 4.8 A, d-d). The cells of the epidermis are vertically elongated and have deposits of cutin on their walls. The continuity of the epidermis is broken by the presence of stomata. The stomata are oriented vertically with the axis of the sporogonium and are widely separated from each other.

Each stoma consists of a pore surrounded by two guard cells (Fig. 4.8 F). The cells of the inner layers have intercellular spaces and contain chloroplast. Thus, the sporogonium is partially self-sufficient to synthesize its organic food but partially it depends on the gametophyte for the supply of water and mineral nutrients.

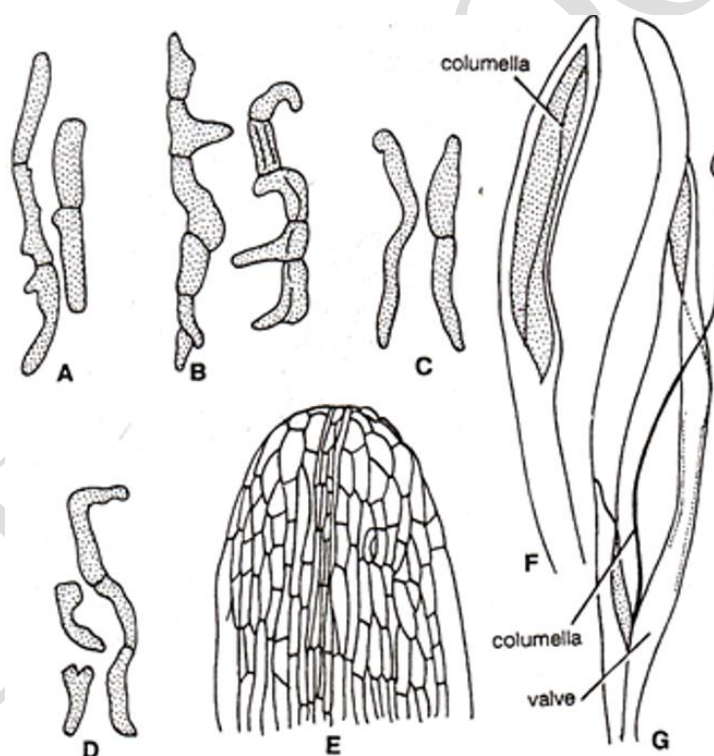


Fig. 4.9. (A-G). Anthoceros (A-D). Pseudo elaters of different species, (E). The apex of the capsule with line of dehiscence, (F) Single line of dehiscence, (G) Bivalved dehiscence.

Dehiscence of the capsule: Capsule dehisces basipetally i.e., from apex to base. As the capsule matures, its tip becomes brownish or black. Vertical lines of dehiscence appear in the jacket layer (Fig. 4.9 E). The dehiscence of the capsule is usually by two

longitudinal lines, occasionally it is by a single line (Fig. 4.9 F) or rarely by four lines. The capsule wall dries and shrinks at maturity. Consequently, narrow slits appear in the capsule wall all along the shallow grooves (line of dehiscence), which gradually widen and extend, towards the base. (In *A. crispulus* capsule splits first along one line of dehiscence and it is followed by splitting along another line of dehiscence).

It results in the formation of two valves of the capsule wall (Fig. 4.9 G). till attached at the tip and exposing the columella is the mass of spores and pseudo elaters. The two valves thus separated, diverged and twist hygroscopically. The pseudo elaters also dry out, twist and help to loosen the spores. Thus, the twisting of the valves and the movement of the pseudo elaters in the exposed spore mass helps in the shedding of the spores. Air currents also help in the dispersal of spores.

Structure of Spore: The spores are haploid, uninucleate, semicircular with a conspicuous triradiate mark (Fig. 4.10 A). Each spore remains surrounded by two wall layers. The outermost layer is thick ornamented and is known as exospore. It varies in color from dark brown to black (e.g., *A. punctatus*) or yellowish (e.g., *A. laevis*). The inner layer is thin and is known as an endospore. Wall layers enclose colorless plastids, oil globules, and food material.

Germination of spore and formation of young gametophyte: Under favorable conditions, the spores germinate immediately in *A. erectus* and *A. punctatus* (Mehra and Kachroo, 1962). However, in *A. fusiformis* the spores undergo a resting period of a few weeks or months before germination (Campbell, 1928). At the time of germination spore absorbs water and swells up Exospore ruptures at the triradiate mark and the endospore comes out in the form of a tube. It is called a germ tube (Fig.4.10 B). Contents migrate into the germinal tube where the colorless plastids turn green. Two successive transverse walls are laid down at the tip of a germinal tube, resulting in the formation of a three-celled filament (Fig. 4.10 C, D). The upper cell divides by a vertical division (Fig. 4.10 E) followed by a similar vertical division in the lower cell (quadrant stage Fig. 4.10 F). These four cells again divide by a vertical division at a right angle to first form eight cells (octant stage). This octant stage is known as sparkling. The total tier of four cells functions as apical cells and forms the new gametophyte. First rhizoid develops as an elongation of any cell of the young thallus (Fig- 4.10 G, H). As the growth proceeds, the mucilage slits appear on the lower surface and these slits are infected by Nostoc.

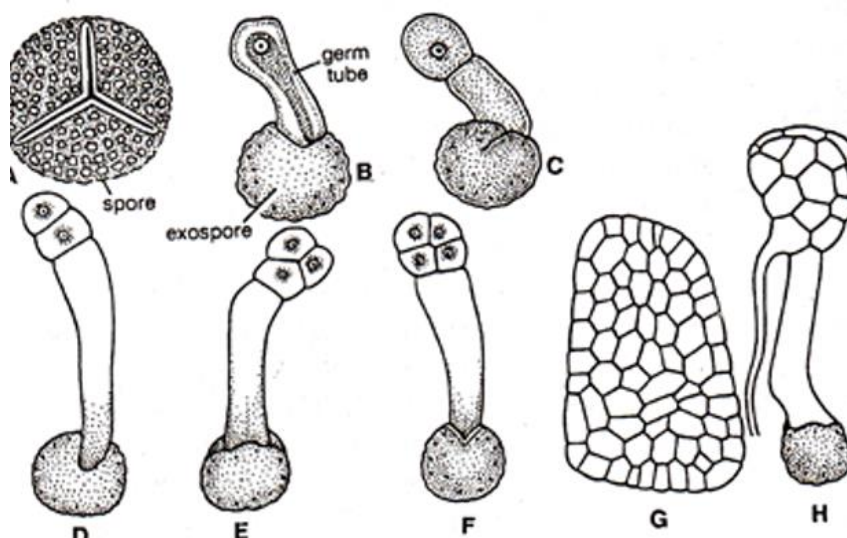


Fig. 4.10. (A-H). Anthoceros. Successive stages in the germination of spore and formation of gametophyte.

Alternation of Generation: The life cycle of *Anthoceros* show regular alternation of two morphologically distinct phases. One of these generations is haplophase and the other is diplophase.

Haplophase or gametophytic phase: In *Anthoceros* this phase is dominant and produces the sex organs. Sex organs produce gametes to form a diploid zygote.

Diploid phase of sporophytic phase: Zygote develops into sporophyte. In *Anthoceros* sporophyte is represented by foot, meristematic zone and capsule. The sporophyte produces the spores in the capsule. The spores on germination produce the gametophyte. So, in *Anthoceros*, two morphologically distinct phases (haplophase and diplophase) constitute the life cycle. The life cycle of this type which is characterised by alternation of generation and sporogenic meiosis is known as heteromorphic and diplohaplontic. (Fig. 4.11,4.12).

Affinities of Anthoceros or Primitive and Advanced Characters of Anthoceros

The thallus of the *Anthoceros* shows both primitive and advanced characters. *Anthoceros* on the one hand forms a connecting link with the Chlorophyceae (green algae), liverworts, and mosses and on the other hand it is linked with primitive Pteridophytes.

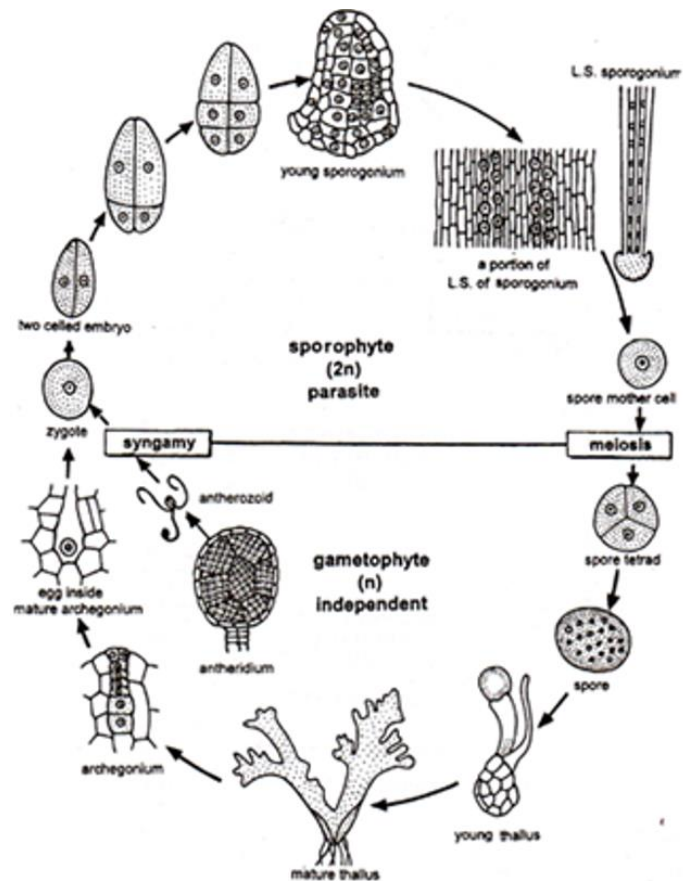


Fig. 4.11. *Anthoceros*. Diagrammatic life cycle.

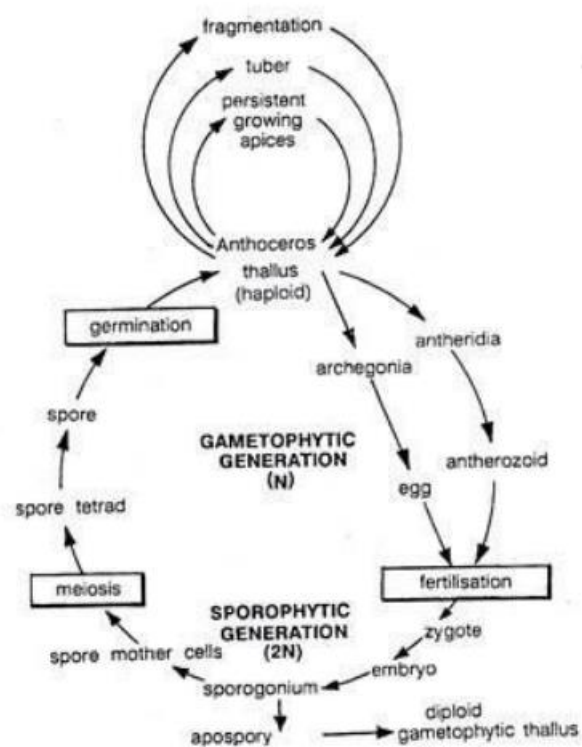


Fig. 4.12. *Anthoceros*. Schematic life cycle.

1. Evolution of Gametophytes and Sporophytes in Bryophytes.

Evolution of Sporophyte in Bryophytes

The sporophyte of bryophytes is called sporogonium which generally consists of a single, terminal sporangium (monosporangiate) with a bulbous foot and with or without an unbranched stalk or seta. The sporogonium is very delicate, short-lived and nutritionally dependent on its gametophyte.

The sporophytic phase begins with the formation of a diploid zygote within the venter of the archegonium. In the simplest form of sporophyte (e.g., *Riccia*) the entire zygote is taking part in the formation of sterile capsule wall and the central sporogenous cells. In complex forms, zygote differentiates and sporogenous cells form more sterile tissues.

There are two opposing theories regarding the evolution of sporophytes in bryophytes.

(i) Theory of Progressive evolution i.e., Evolution of sporophytes by the progressive sterilisation of potentially sporogenous tissue,

This theory was advocated by Bower (1908- 35) and supported by Cavers (1910) and Campbell (1940). According to this theory, the primitive sporophyte of bryophytes was simple and most of the sporogenous tissue was fertile (e.g., *Riccia*) and from such a sporophyte, the more complex sporophytes (e.g., mosses) have been evolved by the progressive sterilisation of potential sporogenous tissue. This theory is also known as “theory of sterilisation”.

The increasing sterilisation of sporogenous tissue from simple sporophyte of *Riccia* to the most complex type of *Funaria* can be arranged through the following stages.

First stage: The simple sporophyte of *Riccia* consists of a single-layered sterile jacket enclosing sporogenous cells with very few absorptive nutritive cells (nurse cells). The zygote divides by a transverse wall, followed* by a vertical wall to form a four-celled embryo. Subsequently, a 20-30-celled embryo is formed by further divisions, in which periclinal divisions differentiate a single-layered outer amphithecium and the inner multicellular mass, the endothecium.

Here the zygote has no polarity. The amphithecium forms the sterile jacket while the whole sporogenous cells (endothecium) differentiate into spores with a very few sterile nurse cells, possibly the forerunners of elaters.

Second stage: In this stage, the zygote divides transversely to form hypobasal and epibasal cells. A small foot is formed from the hypobasal cell. The epibasal cells differentiate into an outer apothecium and an inner endothecium.

The apothecium forms a single-layered sterile jacket of the capsule, while the endothecium differentiates into fertile sporocytes and long sterile elater-like nurse cells without the thickening bands. Thus, the zygote has polarity showing more sterilisation of sporogenous cells like nurse cells and sterile foot. This stage has been noted in *Corsinia*.

Third stage: The development of sporophyte is like that of *Corsinia*, but there is more sterilisation of sporogenous tissue. This condition is noted in *Sphaerocarpus* sporophyte which consists of a sterile bulbous foot, a narrow sterile seta developed from hypobasal cell, and a fertile capsule developed from endothecium containing sporocytes and sterile nurse cells.

Fourth stage: This stage is represented by *Targionia*, where the sporophyte consists of a sterile bulbous foot, a sterile narrow seta and a fertile capsule. Here about half of the endothelial cells produce fertile sporogenous tissue, while the remaining half gives rise to sterile elaters with 2-3 spiral thickening. Hence, in *Targionia*, more sterilisation of sporogenous tissue has been observed.

Fifth stage: This stage is illustrated by *Marchantia*, where further sterilisation of sporogenous tissue has been noted in comparison with *Targionia*. In *Marchantia*, the sterile tissue consists of a broad foot, a massive seta, a single-layered jacket of capsule, sterile apical cap at the apex of capsule and many long elaters with spiral thickening.

Sixth stage: This stage is represented by some members of *Jungermanniales* like *Pellia*, *Riccardia*, etc. Here more sterilization of sporogenous tissue has been observed. Sporophyte is differentiated into foot, seta and capsule having a multilayered jacket. The sporogenous tissues produce mass of sterile elatophores and diffuse elaters.

Seventh stage: This stage is illustrated by members of *Anthocerotophyta* like *Anthoceros*. Here marked reduction in the sporogenous tissue has been noted. The multilayered capsule differentiates into epidermis with stomata and chlorophyllous cells. The central columella derived from endothecium is composed of 16 vertical rows of sterile cells. The further sterilisation of sporogenous tissue has been observed in the

formation of pseudoelaters which are elongated 3-4 celled, simple or branched structure without thickening bands.

Eighth stage (Final stage)

The members of Bryopsida, like *Funaria*, *Polytrichum*, *Pogonatum*, etc., show the highest degree of sterilization. The sporophyte is differentiated into a foot, a long seta, and a capsule. The sterile tissue of the capsule consists of the apophysis, operculum, many-layered jacket, the columella, trabeculae, the wall of the spore sac, and the peristome. The sporogenous tissue is restricted to the spore sacs only, hence, it forms a negligible portion of the sporophyte.

(ii) Theory of Regressive evolution, i.e., evolution of sporophytes due to the progressive reduction or simplification.

This theory is known as regressive or retrogressive theory, and is supported by several scientists like Church (1919), Kashyap (1919), Goebel (1930) and Evans- (1939). According to this theory, the most simple sporophyte of *Riccia* (comprised of a simple capsule) is the most advanced type which has been evolved by the simplification or progressive reduction of the complex sporophytes (foliose with complex assimilatory tissue and functional stomata) of mosses (e.g. *Funaria*, *Pogonatum*, *Polytrichum* etc.).

The stages of progressive reduction of the foliose sporophyte (primitive type) to the simpler sporophyte (advanced type) have been enumerated.

- (a) The semiparasitic foliose sporophyte gradually lost its leaves and became embedded within the gametophyte.
- (b) There is a gradual reduction of the assimilatory (photosynthetic) tissue in the sporophytes, and subsequently this tissue is confined only to the jacket of the capsule (e.g., *Funaria*, *Anthoceros*).
- (c) Stomata are restricted in the apophysis region (e.g., *Funaria*, *Polytrichum*) that communicate with the intercellular spaces. In *Sphagnum*, the stomata of apophysis are non-functional and become rudimentary. In all liverwort members, stomata are completely absent in sporophytes.
- (d) The capsules of most mosses (*Funaria*, *Polytrichum*, *Sphagnum*, etc.), hornwort (*Anthoceros*), and some Jungermanniales (*Pellia*, *Porella*) are multilayered, which subsequently became single-layered (*Marchantia*, *Plagiochasma*, *Riccia*) by reduction.

(e) The foot and seta are well-developed in mosses (*Pogonatum*, *Funaria*, etc.) and some liverworts (*Pellia*, *Marchantia*, etc.). The seta became much reduced and forms a narrow sterile part of the sporophyte (*Corsinia*, *Targionia*).

In hornworts, the sporophyte is made up of a foot and an elongated capsule only, the seta is absent. Finally, in *Riccia* foot and seta are absent, and the sporophyte is represented by a single capsule only, which is supposed to be the simplest as well as advanced sporophyte among bryophytes.

(f) The sporophytes of mosses show the highest degree of sterilisation with a negligible amount of sporogenous tissue. There has been a gradual reduction in the sterile tissue of the capsule, with a simultaneous increase in the amount of sporogenous tissue.

In hornworts, a good amount of sporogenous tissue is formed from the inner layer of amphithecium. In liverworts (*Riccia*, *Marchantia*) the entire endothecium gives rise to sporogenous cells.

Evolution of Gametophytes in Bryophytes: The evolution of thalli in bryophytes is a much-disputed problem. There is no substantial fossil evidence of bryophytes that supports to the sequential evolution theory of gametophytes among bryophytes.

There are two opposing theories regarding the nature of the vegetative structure of the primitive bryophytic gametophyte and its subsequent evolution:

1. The upgrade or the progressive evolution theory, and
2. The downgrade or the regressive evolution theory.

1. The upgrade or the progressive evolution theory

According to this theory, the primitive gametophyte was a simple, dorsiventral, prostrate thallus, both in external as well as in internal forms. Cavers (1910) and Campbell (1891-1940) were the main proponents of this theory. The evolution of gametophytes took place from liverworts to mosses in an ascending series of gradually increasing complexity about the organization of internal tissue and sex organs.

According to Cavers the ancestor gametophyte resembles the present-day *Sphaerocarpus* and *Marchantiales* has been considered as a blind line of evolution from the hypothetical *Sphaero- Riccia*. While Campbell suggested that thalli of the present-day *Riccardia* and

Metzgeria resemble the simplest ancestral gametophyte. From the simple thallus, the evolution of complex gametophytes took place in two different lines.

In the first line, the gametophyte retained its external simple, thallose form as found in Marchantiales. Simultaneously, there was a gradual increase in complexity in cellular organisations. This has been evidenced by the nature of pores, air chambers and the aggregation of sex organs in a definite receptacle (e.g. Marchantia). The sexual receptacles show a wide range of organization. In Riccia, the individual sex organs are scattered over the median portion of the thallus. In Marchantia, the sex organs are borne on a complex stalked receptacle called a gametophore.

An intermediate condition between Riccia and Marchantia has also been observed, where sex organs are aggregated into a cushion-like or ridge-like receptacle. These receptacles are borne on the thallus dorsally or terminally.

In the second line, the gametophytes retained their simple internal structure (lack of airpores and air chambers). But there was a gradual elaboration of the external part of the gametophyte, leading to the formation of the appendicular organs. Further, the thalloid forms were replaced by the leafy forms. This has been observed in the members of Jungermanniales and Calobryales. These leafy forms finally led to the establishment of a higher degree of internal differentiation of the tissue in Bryopsida. The schematic representation of the progressive evolution of gametophytes in liverworts has been depicted in Fig 4.12 a. b

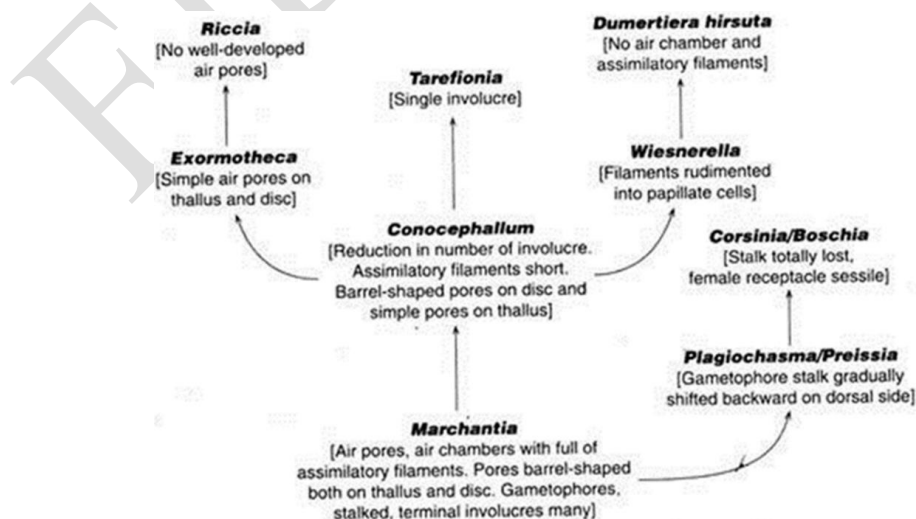


Fig. 4.12 a: Regressive evolution of gametophytes in liverworts.

2. The downgrade or the regressive evolution theory

According to the downgrade theory, the primitive gametophyte was an erect leafy shoot having radial symmetry (members of Calobryales and true mosses). From such ancestral forms, the dorsiventral thalli of liverworts and hornworts evolved in reverse direction i.e., regression of increasing simplicity.

Among the proponents of the downgrade theory, Wettstein (1903-1908), Church (1919), Evans (1939), Goebel (1930) and Kashyap (1919) are the most prominent scientists. Kashyap (1919) advocated regressive evolution from the results of his extensive studies of Indian Marchantiales. The principal points in the reduction series from *Marchantia* as the basic type along the various phyletic lines have been summarised below.

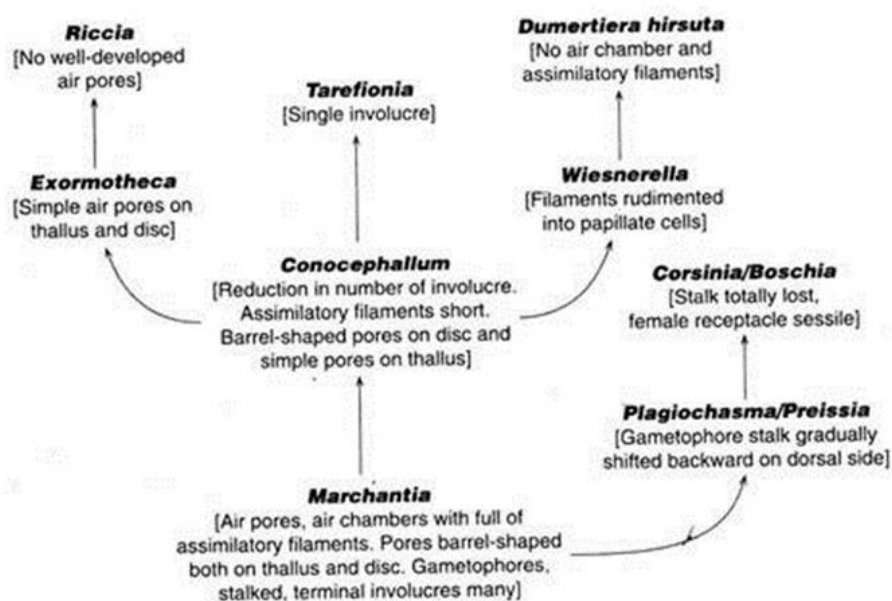


Fig. 4.12 b: Regressive evolution of gametophytes in liverworts.

(a) Reduction in the number of involucre: In *Marchantia*, sex organs are well-protected by many involucre. A gradual reduction in the number of the involucre has been observed in *Conocephallum*, *Aitchinsoniella* and *Exormotheca*, which has finally culminated in *Tarefionia* with a single involucre.

(b) The loss of assimilatory filaments in the air chamber: A gradual reduction series has been noted in many members (Fig. 4.12). In *Marchantia* and *Preissia*, the thallia show complexity in having air pores and air chambers full of assimilatory filaments. There is a gradual reduction in the assimilatory filaments in *Conocephallum conicum*

(the filaments are short in the air chambers), *Wiesnerella decundata* (the filaments rudiments into papillate cells). The assimilatory filaments ultimately disappear in the aquatic *Dumortiera hirsute*.

(c) Simplification of Pores: In complex forms like *Marchantia* and *Preissia*, the pores are complex, barrel-shaped, and present both on the thallus and the discs of the gametophores. In *Conocephallum* and *Reboulia*, discs bear only barrel-shaped pores, while thalli bear only simple pores. In *Exormotheca* and *Stephansoniella*, the pores are simple both on the thallus and in the discs. The well-defined pores are absent in *Riccia* (Fig. 4.13).

(d) The gradual shifting of the stalks of antheridiophores and archegoniophores from the terminal to the dorsal position: Mehra (1969) proposed the above hypothesis. In *Marchantia*, the antheridia and archegonia are borne terminally on the stalked gametophores. In *Preissia quadrata* and *Plagiochasma articulatum*, the stalk is initially terminal but becomes dorsal by the further growth of the thallus. A further downward shifting of the stalk is observed in *Corsinia* and *Boschia*, where the female receptacle almost becomes sessile by the elimination of the stalk. The schematic representation of the regressive evolution of gametophytes in liverworts has been depicted in (Fig- 4.13).

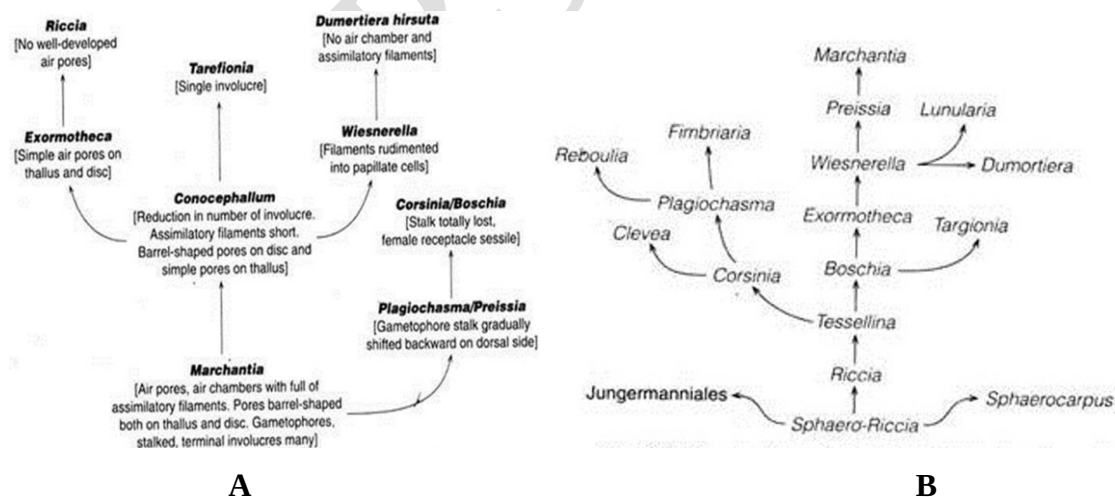


Fig. 4.13 a, b: Regressive evolution of gametophytes in liverworts.

UNIT-11: PTERIDOPHYTA

Origin and Evolution of Vascular Plants

The origin of vascular plants has been a subject of significant debate, with various theories proposed to explain the development of an independent sporophyte. These theories are based on two main assumptions.

1. Origin from Bryophytes

Some botanists believe that vascular cryptogams (spore-producing vascular plants like ferns and their allies) evolved from bryophytes. This view was supported by researchers like Bower (1935), Lignier (1903), and Zimmermann (1930, 1938), who suggested that bryophytes and pteridophytes evolved from a common group of hypothetical archegoniate (female reproductive organ-bearing) land plants. Notably, Campbell (1895) and Smith (1958) proposed that vascular cryptogams originated from an anthocerotean (hornwort-like) type of bryophyte.

2. Origin from Algae

The second theory posits that algae are the ancestors of vascular cryptogams. This theory has been supported by several researchers, including Scott (1900), Lotsy (1909), Church (1919), Fritsch (1916), Eames (1936), Arnold (1947), Andrews (1956), Gregus (1955), Axelrod (1959), and Mehra (1968). According to this view, pteridophytes evolved from various groups of algae, drawing evolutionary connections between aquatic and terrestrial plants.

Anthocerotean Theory

The Anthocerotean theory, proposed by Campbell in 1895 and later supported by Smith in 1938, suggests that vascular cryptogams evolved from ancestors resembling *Anthoceros*, a genus of hornworts. Key features of this theory include:

- 1. Intercalary Meristem and Independent Sporophyte:** The presence of intercalary meristem (a region of active cell division) and photosynthetic tissue in the sporophyte of *Anthoceros* is believed to have contributed to the development of an independent sporophyte in vascular cryptogams.
- 2. Shifting of Meristem to Dichotomous Branching:** In the evolution of vascular cryptogams, it is proposed that the intercalary meristem in *Anthoceros* gradually shifted to support dichotomous branching. This process likely played a role in the

evolution of early vascular plants, such as *Rhynia* and *Psilophyton*, which exhibit this type of branching.

3. **Development of Terminal Sporangia:** The dichotomous branching led to the formation of terminal sporangia, which are characteristic of primitive vascular plants like *Psilophytales*.
4. **Transformation of Columella into Conductive Strand:** The central column (columella) found in *Anthoceros* may have evolved into a conductive strand, similar to the vascular tissue in vascular plants.
5. **Conducting Tissue in the Sporophyte:** Conducting tissue (precursor to vascular tissue) is observed in the lower portion of the sporophyte of *Anthoceros*, hinting at the early stages of vascular tissue evolution.

Smith's Contributions

Smith highlighted several resemblances between the structures of *Anthoceros* and eusporangiate vascular cryptogams (pteridophytes with thick-walled sporangia). Notably,

- Both groups have embedded sex organs (archegonia and antheridia) that lack a stalk.
- The main difference between *Anthoceros* and pteridophytes is the presence of a protective jacket layer around the archegonium in *Anthoceros*, which is absent in pteridophytes. This is attributed to the division of the archegonial initial cell in *Anthoceros* into jacket initials and an axial cell.
- The entire antheridium of *Anthoceros* is equivalent to the fertile region of the antheridium in eusporangiate pteridophytes.

Smith also compared the embryos of primitive plants like *Psilotum* and *Tmesipteris* with those of *Anthoceros*, pointing out superficial similarities in their development.

Strobilus Theory

The **Strobilus Theory**, proposed by Bower in 1894, suggests that the sporophytes of vascular cryptogams originated from liverworts. According to this theory, the simple sporophyte of liverworts evolved into more complex structures along the following lines:

1. **Progressive Sterilization of Sporogenous Tissue:** Initially, the sporogenous (spore-producing) tissue in the liverwort sporophyte underwent sterilization, resulting in the formation of alternating sterile and fertile regions.
2. **Sporangia Became Superficial:** The fertile regions or sporangia (spore-producing organs) shifted to a more superficial position.

3. **Formation of Enations:** The sterile regions produced lateral projections known as enations. These enations were located either beneath or alongside the sporangia. At this stage, the sporophyte resembled a strobilus (cone-like structure), where the sporangia were located at the base or axils of the enations. This is like structures observed in plants like *Phylloglossum*, *Isoetes*, and *Lycopodium*, where all leaves function as sporophylls (sporangium-bearing leaves).
4. **Sterilization of Sporophylls:** Further sterilization resulted in the disappearance of sporangia on some sporophylls.
5. **Formation of Central Axis:** The central part of the sporophyte, which resembled a columella (a central sterile column), increased in size and developed into an axis or stem bearing leaves and sporophylls.
6. **Development of Roots:** Roots emerged from the base of the stem, leading to the evolution of an independent sporophyte capable of surviving on its own.

Historical Relevance: This theory is of historical importance only, as it has been largely discarded. Extinct plants from the Psilophytales group do not support the existence of such a simple sporophyte as proposed by Bower. Although the **Enation Theory** explains the origin of microphyllous leaves, the Strobilus Theory suggests that these microphylls later evolved into larger megaphylls. This idea was further developed into Zimmermann's **Telome Concept**, which explains the evolution of complex plant structures.

Protocorm Theory

The **Protocorm Theory** was introduced by Treb in 1884. According to this theory, the protocorm (a structure found in the embryos of some *Lycopodium* species) is considered a primitive organ that has been retained in certain species, such as *Phylloglossum* and *Lycopodium*. Treb believed this to be an ancestral feature.

However, the theory has been largely rejected by morphologists and is now of historical significance. Brown (1930) argued that the protocorm is a modified and reduced stem. The main criticisms of this theory are.

1. The protocorm is absent in many primitive lycopods.
2. It likely represents a resting stage with ecological importance rather than a primitive structure.
3. *Phylloglossum* is not primitive but a reduced plant.

4. Protocorms are also found in other groups like *Ophioglossum* and certain monocotyledons.

Phyton Theory

The **Phyton Theory** was proposed by Celakovsky in 1901 and is closely related to the Strobilus Theory. Celakovsky postulated that early land plants had a strobilus-like organization, with repeated units (phytons) consisting of leaf and stem segments. This theory suggested that plant organs like leaves and stems evolved from repeated, modular units of these early plants.

However, this idea was heavily criticized. Schoute (1931), in his paper "On Phytonism," argued that Celakovsky's theory lacked sufficient evidence and was overly speculative. Earlier, Wolff (1759) had already pointed out that plants consist mainly of leaves and stems, without the need for a complex theory of phytonism.

Thus, while the Phyton Theory introduced interesting concepts about plant organ development, it did not gain significant support in the scientific community.

Algal Origin of Vascular Cryptogams: A Detailed Explanation

The idea that early land plants, including **vascular cryptogams** (like ferns, clubmosses, and horsetails), evolved from **algae** is supported by many scientists. Vascular cryptogams are non-seed-bearing plants that reproduce through spores, and they are considered among the earliest plants to colonize land. To understand this theory better, we can look at the evidence and theories presented by different researchers.

Key Evidence Supporting the Algal Origin of Land Plants

Several similarities between **green algae** and **vascular cryptogams** point to a shared ancestry.

1. **Chloroplasts:** Both green algae and vascular cryptogams have chloroplasts that contain **chlorophyll a** and **chlorophyll b**, which are essential for photosynthesis. This similarity in pigments suggests a common photosynthetic mechanism inherited from a shared ancestor.
2. **Carotenoid Pigments:** Carotenoids are pigments that protect plants from damage by light and play a role in photosynthesis. The types of carotenoids found in both algae and vascular cryptogams are very similar, further suggesting a connection.

3. **Food Storage:** Both groups store energy as **starch**, which is made of two types of glucose molecules called **amylose** and **amylopectin**. This common storage method is another clue that they share a common ancestor.
4. **Cell Wall Composition:** Both algae and vascular cryptogams have **cell walls** made primarily of **cellulose**. They also contain layers of **pectin**, a complex carbohydrate made of galacturonic acid, which strengthens the plant's cell walls. These structural similarities suggest that they inherited these traits from a common ancestor.
5. **Male Gametes (Sperm Cells):** In both algae and vascular cryptogams, the male gametes (sperm cells) are flagellated and have a similar type of whip-like tail. This is important because it shows a shared method of reproduction that could have been passed down from ancient algae.

Theories Explaining the Algal Origin of Vascular Cryptogams: Several scientists have proposed theories over time to explain how land plants evolved from algae. Below are some of the most important theories, along with their strengths and weaknesses.

1. **Church's Hypothesis (1919):** Church proposed that land plants originated from a group of **marine algae** he called **Thalassiophyta**. According to him, the evolution of plants happened in two stages.

Plankton Stage: Small, free-swimming algae in the ocean.

Benthic Stage: Some of these algae settled on the ocean floor, evolving into larger, rooted seaweeds.

These seaweeds eventually moved to land and adapted to life outside water, forming the first land plants. He believed this transition happened as the land rose above sea level, exposing the seaweeds to air, which forced them to adapt to a dry, terrestrial environment.

Criticism: Church's theory has been criticized because: Geologists have found that land existed before oceans, contradicting his idea that land plants evolved from seaweed that "migrated" to land. Marine seaweeds are highly specialized for ocean life and would not easily adapt to land.

2. Greguss's Hypothesis (1953)

Greguss suggested that vascular plants evolved from three different groups of algae.

Chlorophyta (green algae), **Phaeophyta** (brown algae), **Rhodophyta** (red algae)

He based this on the way these algae branched, focusing on whether they had dichotomous (forked), monopodial (main stem with side branches), or verticillate (circular arrangement) branching.

Criticism: His theory was criticized because it ignored other important traits, like pigment composition or reproductive structures. Also, closely related plant groups (like **Psilophytales** and **Psilotales**) were traced to entirely different algal groups, which seemed unlikely.

3. Andrew's Hypothesis (1956): Andrew supported the idea that vascular plants had a **polyphyletic origin**, meaning that they evolved from several different types of algae, not just one group. He identified several ancient marine algae that he thought could have given rise to vascular plants.

Nematothallus: Algae with a cuticle (waxy layer to prevent water loss).

Crocophyton: Algae with tracheid-like structures (primitive vascular tissue).

Protosalvia: Algae with a spherical or bilobed head.

Andrew believed these different types of algae gave rise to different groups of vascular plants independently.

4. Leclercq's Hypothesis (1954, 1956): Leclercq studied fossilized spores (pollen) and the remains of early land plants and concluded that land plants originated from algae during the **Pre-Cambrian period** (over 540 million years ago). She studied extinct plants from the **Cambrian** (about 540-485 million years ago), **Silurian**, and **Devonian** periods, connecting these fossils to their algal ancestors. Her work focused on plants like **Rhynia** and **Horneophyton**, which were among the earliest land plants.

5. Axelrod's Hypothesis (1959): Axelrod built on the work of Leclercq and Andrew, proposing that vascular plants evolved along **five different lines** from a common algal ancestor: **Psilophyta**: Simple plants like **Rhynia** and **Psilotum**. **Lepidophyta**: Clubmoss-like plants.

ArthropHYTA (Sphenophyta): Horsetail-like plants. **Pterophyta**: Fern-like plants.

Pteridospermophyta: Plants that eventually gave rise to gymnosperms and angiosperms (flowering plants). He believed that these lines evolved independently but shared a common ancestor in the Pre-Cambrian algal stock.

6. Merker's Hypothesis (1961): Merker believed that land plants, including bryophytes (mosses and liverworts), evolved independently from different types of algal ancestors during the Pre-Cambrian period. He proposed five major evolutionary lines.

1. **Rhyniaceae, Psilotales, and Ophioglossaceae:** Early vascular plants.
2. **Bryopsida:** Mosses and liverworts.
3. **Sphenopsida:** Horsetails.
4. **Lycopsida:** Clubmosses.
5. **Pteropsida:** Ferns, gymnosperms, and angiosperms.

7. Lam's Hypothesis (1955)

Lam proposed that vascular plants evolved from **thallophytes** (a large group of simple algae) and that two main lines emerged: One line gave rise to Sphenopsida (horsetails) and Pteropsida (ferns). Another line gave rise to Cycadopsida, which later evolved into seed plants like gymnosperms.

Criticism: Lam's idea that conifers evolved from lycopods (clubmosses) has been criticized as unlikely.

8. Mehra's Hypothesis: Professor P.N. Mehra believed that land plants likely evolved from **green algae** because of their similar pigments, photosynthetic activity, and flagellated reproductive cells. He suggested that plants with **Frittschiella-like** (chaetophoraceous) green algae ancestors developed several key features that allowed them to survive on land, such as.

1. **Radial Symmetry:** A circular arrangement of body parts.
2. **Cortication:** Development of a protective outer layer (cortex).
3. **Sterile Jacket:** A layer of cells around reproductive organs to protect them.

He also proposed that early land plants followed two evolutionary paths: the Psilophytaceous line (early vascular plants) and the Lycopodiaceous line (clubmoss-like plants).

The content you've shared outlines the evolutionary development of vascular cryptogams (early land plants that reproduce by spores) from algae. It explores different lines of development and key hypotheses from scientists like Professor P.N. Mehra and Professor B.K. Nayer. Let's break it down for clarity and understanding.

Evolutionary Development of Vascular Cryptogams: Early land plants evolved from algal ancestors through complex processes involving changes in both their sporophyte (the diploid, spore-producing phase) and gametophyte (the haploid, sex-cell-producing phase).

The plants developed crucial structures to survive on land, such as.

1. **Cuticle:** A waxy outer layer that prevents water loss.
2. **Jacketed Sex Organs:** Protects the reproductive organs from desiccation (drying out).
3. **Sporophyte Independence:** The sporophyte phase of these plants became **independent** of the gametophyte phase, with the ability to produce spores and reproduce on its own.

Two Lines of Sporophyte Development

1. Line 1: Sporophyte from Oospore (Enclosed in Archegonia)

The sporophyte develops from the oospore (fertilized egg) inside the archegonium (female sex organ), remaining attached to the gametophyte for some time. These plants had **biciliate spermatozoids**, meaning their sperm cells had two flagella for movement. Over time, the sporophyte became independent of the gametophyte.

2. Sporophyte with Vascular Tissue

This line led to the appearance of vascular tissues (xylem and phloem) in the sporophyte, which allowed the plant to transport water and nutrients more efficiently and grow larger. The gametophyte had embedded sex organs and produced multiflagellate spermatozoids (sperm cells with many flagella).

These plants, often branching dichotomously (forking in two), bore sporangia (spore-producing structures) at the tips of their branches. This development is linked to the Rhyniaceous stock, a group of early land plants, leading to four major evolutionary lines.

Four Evolutionary Lines from the Rhyniaceus Stock

1. **Prospheopsid Line:** Gave rise to plants like Hygenia and Calamophyton. These plants were linked to the early Rhyniaceus stock, with a resemblance to protohygenia.
2. **Pro-pteropsid Line:** Gave rise to the Filicales (ferns) and Filicophyta. These plants had terminal sporangia (spore-producing structures at the tips) and short sterile branches, leading to modern ferns.
3. **Pro-gymnospermous Line:** Represented by plants like Archaeopteris and Callixylon, which showed secondary growth (thickening of stems and roots). This line led to Pteridosperms (seed ferns), which in turn gave rise to Bennettitales, Cycadales, and modern groups like Gnetophyta, Coniferales, and Ginkgoales.
4. **Psilophytaceous Line:** This line bifurcated (split into two), with one path leading to Rhyniaceae and the other to Psilotales, represented by plants like Psilotum and Tmesipteris.

Lycopodiaceous Line of Evolution: This line evolved from a group of proto-plants called proto-archegoniate, with embedded sex organs and biciliate spermatozoids. These early plants formed what was termed a lateral sporangiate plexus, a sporangium-producing system. Two notable genera in this line were **Baragwianathia** and **Drepanophycus**.

Mehra's Hypothesis: Professor P.N. Mehra, a notable figure in botany, suggested that early vascular plants evolved along two main lines:

1. **Psilophytaceous Line:** Gave rise to early plants like **Psilotum** and **Rhyniaceae**.
2. **Lycopodiaceous Line:** Led to clubmoss-like plants, represented by genera like **Baragwianathia**.

Mehra emphasized the evolutionary importance of **biciliated spermatozoids** and **lateral sporangiate structures** in these early plants. However, he did not include angiosperms (flowering plants) in his evolutionary scheme, considering their origin is still a mystery.

Nayer's Hypothesis (1976): Professor B.K. Nayer proposed a **monophyletic origin** for pteridophytes (ferns and their relatives), meaning they all descended from a single common ancestor. Key points of his hypothesis include.

1. **Algal Ancestors:** Pteridophytes evolved from algae with isomorphic alternation of generations (where both sporophyte and gametophyte phases looked similar).

2. **Aerial Branches:** Early pteridophytes developed **special aerial branches** that bore simple **sporangia** at their tips.
3. **Protostelic Vascular Cylinder:** These plants developed a **protostele** (a simple type of vascular system) for efficient transport of nutrients and water.
4. **Photosynthetic Organs:** Early sporophytes developed **aerial photosynthetic organs** (leaves or leaf-like structures).
5. **Rhizome-like Sporophytes:** The ancestral land plants had tuberous rhizomes with unbranched aerial organs. Nayer also proposed that the gametophyte of pteridophytes evolved underground with a symbiotic association with fungi (mycorrhizae), and sex organs developed around the prothallus (the gametophyte body). Over time, the sporophyte and gametophyte became distinctly different in form. In a later work (1982), Nayer suggested that the Fritschella algae could be the "missing link" between early algae and land plants. He believed this alga had a structure like the Equisetum prothallus (the gametophyte of horsetails), providing clues about the evolution of land plants.

2. Morphology, Anatomy and Reproduction in five representatives Pteridophytes as per the Pteridophyte Phylogeny Group (2016).

(1) Class Lycopodiopsida (Lycophytes) Club mosses, quill worts and spike mosses- Equisetum): Selaginellaceae, Selaginella.

Equisetum

Division: Polypodiophyta

Class: Polypodiopsida

Subclass: Equisetidae

Order: Equisetales

Family: Equisetaceae

Genus: *Equisetum*. L.

Habit and Habitat of Equisetum:

The plant body of Equisetum has an aerial part and an underground rhizome part (Fig. 5.1). The rhizome is perennial, horizontal, branched, and creeping in nature. The aerial part is herbaceous and usually annual. Most of the species are small with a size range between 15 and 60 cm in height and 2.0 cm in diameter.

However, some species grow up at higher heights (e.g., *E. giganteum* (13 m), *E. telmateia* (2 m); *E. ramosissimum* (4 m), though their stem are relatively thin (0.5-2.0 cm in diameter) showing vine-like habits and climbing over adjacent forest trees. Equisetums generally grow in wet habitats and are particularly common along the banks of streams or irrigation canals (*E. debile*, *E. palustre*). However, some species are adapted to xeric conditions (e.g., *Equisetum arvense*). Some common Indian species are *E. arvense*, *E. debile*, *E. diffusum*, *E. ramosissimum*. Some species of Equisetum are indicators of the mineral content of the soil in which they grow. Some species accumulate gold (about 4.5 ounces per ton of dry wt.), thus they are considered ‘gold indicator plants. Hence these plants help in the prospection/exploration of new ore deposits. In Equisetum, silica is deposited on the outer wall of.

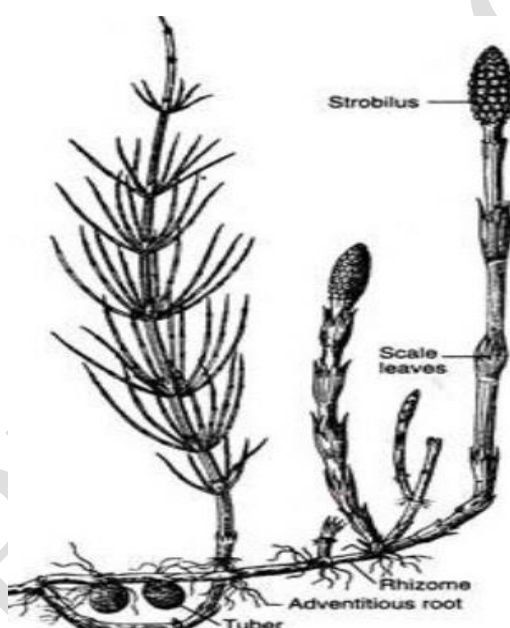


Fig 5.1 Sporophyte of *E. arvense*.

the epidermal cells giving the characteristic rough feeling; thus, it provides a protective covering against predators and pathogens.

Structure of Equisetum: The Sporophyte: The sporophytic plant body of Equisetum is differentiated into stem, roots, and leaves (Fig. 5.1).

Stem: The stem of Equisetum has two parts: perennial, underground, much-branched rhizome, and an erect, usually annual aerial shoot. The branching is monopodial, shoots are differentiated into nodes and internodes. In majority of the species, all the shoots are

alike and chlorophyllous and some of them bear strobili at their apices (e.g., *E. ramosissimum*, *E. debile*). Sometimes shoot shows dimorphism (two types of shoots i.e., vegetative and fertile) e.g., *E. arvense*. Some shoots are profusely branched, green (chlorophyllous) and purely vegetative. The others are fertile, unbranched, brownish (achlorophyllous), and have terminal strobili. The underground rhizome and the aerial axis appear to be articulated or jointed due to the presence of distinct nodes and internodes. Externally, the internodes have longitudinal ridges and furrows and, internally, they are hollow, tube-like structures. The ridges of the successive internodes alternate with each other and the leaves are normally of the same number as the ridges on the stem.

Internal Features of Stem: In T.S., the stem of *Equisetum* appears wavy in outline with ridges and furrows (Fig. 5.2). The epidermal cell walls are thick, cuticularized and have a deposition of siliceous material.

Stomata are distributed only in the furrows between the ridges. A hypodermal sclerenchymatous zone is present below each ridge which may extend up to stele in *E. giganteum*. The cortex is differentiated into outer and inner regions.

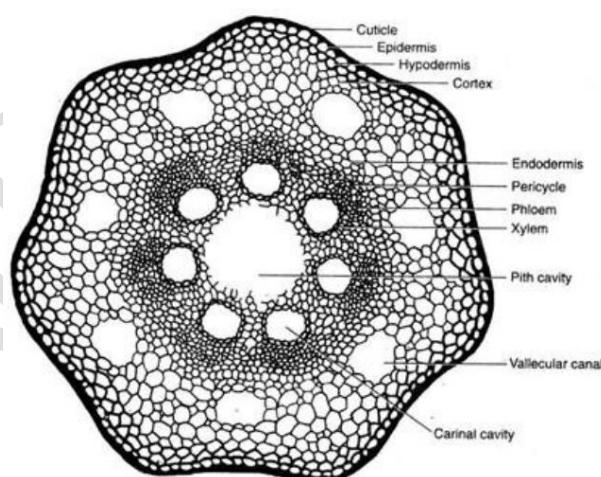


Fig 5.2 Equisetum T.S of Stem (Rhizome).

The outer cortex is chlorenchymatous, while the inner cortex is made up of thin-walled parenchymatous cells. There is a large air cavity in the inner cortex corresponding to each furrow and alternating with the ridges, known as vallicular canal. These are schizolysigenous canals extending the entire length of internodes and form a distinct aerating system.

New leaves and branches of *Equisetum* are produced by the apical meristem, however, most of the length of the stem are due to the activity of the intercalary meristem located just above each node. The activity of intercalary meristem causes rapid elongation of the inter-nodal region.

The stele is ectophloic siphonostele which is surrounded by an outer endodermal layer. An inner endodermis is also present in some species of *Equisetum* (e.g., *E. sylvaticum*). The endodermis is followed by a single-layered pericycle.

The vascular bundles are arranged in a ring that lies opposite to the ridges in position and alternate with the vallecular canals of the cortex. Vascular bundles are conjoint, collateral, and closed. In the mature vascular bundle, protoxylum is disorganised to form a carinal cavity which lies opposite to the ridges.

The metaxylem tracheid (scalariform or reticulate) are present on both sides of the phloem. In some species vessels with reticulate perforations are reported. The central part of the internode of the aerial shoot is occupied by a large pith cavity which is formed due to rapid elongation of the internodal region.

The vascular bundles remain unbranched until they reach the level of the node. At the nodal region, each vascular bundle trifurcates (divided into three parts). The middle branch of the trifurcation enters the leaf. Each lateral branch of the trifurcate bundle joins a lateral strand of an adjacent trifurcate bundle to form a vascular bundle of internode (Fig. 5.3). Thus, the vascular bundles of internode alternate with those of inter nodes above and below.

In the nodal region, the xylem is extensively developed as a conspicuous circular ring. There are no vallecular or carinal canals at this level. In addition, a plate of pith tissue occurs at the node which separates one internode from another.

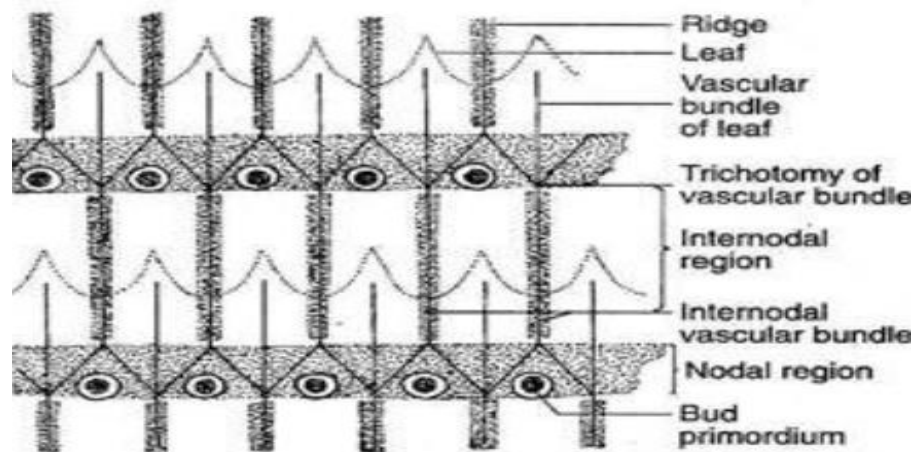


Fig 5.3. Equisetum: Schematic representation of a portion of the vascular system in nodal and internodal regions.

The xerophytic features are

- (i) Ridges and furrows in the stem,
- (ii) Deposition of silica in the epidermal cells,
- (iii) Sunken stomata,
- (iv) Sclerenchymatous hypodermis,
- (v) Reduced and scaly leaves, and
- (vi) Photosynthetic tissue in the stem.

The hydrophytic characteristics, on the other hand, are.

- (i) A well-developed aerating system like a carinal canal, vallecular canal, and central pith cavity, and
- (ii) Reduced vascular elements.

Root: The primary root is ephemeral. The slender adventitious roots arise endogenously at the nodes of the stems. In T.S., the root shows the epidermis, cortex, and stele from the periphery to the center. The epidermis consists of elongated cells, with or without root hairs.

The cortex is extensive; cells of the outer cortex often have thick walls (sclerenchymatous), and those of the inner cortex are thinner, parenchymatous. The stele is protostelic, where the xylem is triarch or tetrarch, or, in smaller roots, may be diarch. A large metaxylem element is present in the centre of the stele, and the protoxylem

strands lie around it. The space between the protoxylem groups is filled with phloem. There is no pith.

Leaves: The leaves of *Equisetum* are small, simple, scale-like and isophyllous; they are attached at each node, united at least for a part of the length and thus form a sheath around the stem. The sheath has free and pointed teeth-like tips.

The number of leaves per node varies according to the species. The species with narrow stems have few leaves (e.g., 2-3 leaves in *E. scirpoides*) and those with thick stem have many leaves (e.g., up to 40 leaves in *E. schaffneri*). The number of leaves at a node corresponds to the number of ridges on the internode below. The leaves do not perform any photosynthetic function, and their main function is to protect young buds at the node.

Reproduction in Equisetum: *Equisetum* reproduces vegetatively and using spores.

i. Vegetative Reproduction: The subterranean rhizomes of some species (e.g., *E. telmateia*, *E. arvense*) form tubers which, on separation from the parent plant, germinate to produce new sporophytic plants. The tubers develop due to irregular growth of some buds at the nodes of the rhizomes.

ii. Reproduction by Spores

Spores are produced within the sporangia. The sporangia are borne on the sporangiophores which are aggregated into a compact structure termed strobilus cone or sporangiophores spike.

Strobilus: The strobilus is terminal in position and generally is borne terminally on the chlorophyllous vegetative shoot (Fig. 5.4). However, they may be borne terminally on a strictly non-chlorophyllous axis (e.g., *E. arvense*).

The strobilus is composed of an axis with whorls of sporangiophores. Each sporangiophore is a stalked structure bearing a hexagonal peltate disc at its distal end. On the undersurface of the sporangiophore disc 5-10 elongate, cylindrical hanging sporangia are borne near the periphery in a ring.

The flattened tips of the sporangiophores fit closely together which protects the developing sporangia. The axis bears a ring-like outgrowth, the so-called annulus immediately below the whorls of sporangiophores which provide additional protection

during early development. The annulus has been interpreted as a rudimentary leaf sheath by some botanists, whereas others consider it to be sporangiophoric in nature as occasionally it bears small sporangia.

Development of Sporangium: The mode of development of sporangium is eusporangiate, as it is not entirely formed from a single initial. Superficial cells adjacent to the original initial may also take part in the development of sporangium. Sporangia are initiated in a single superficial cell around the rim of the young sporangiophore. The periclinal division of the sporangium initially forms an inner and an outer cell. The inner cell, by further divisions in various planes, gives rise to sporogenous tissue.

The outer cell, by periclinal and anticlinal divisions, gives rise to irregular tiers of cells, the inner tiers of which may transform into sporogenous tissue and the outer tiers become the future sporangial wall cells. The innermost layer of the sporangial wall differentiates from the tapetum. The sporogenous cells separate from each other, round off, and eventually transform into spore mother cell. All but the two outermost wall layers disorganize to form periplasmodial fluid.

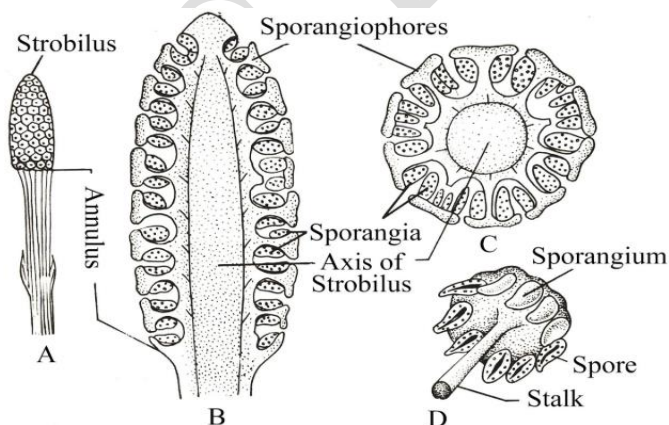


Fig. 5.4. Equisetum spp. (A) A part of a fertile shoot bearing strobilus; (B) LS of strobilus; (C) TS of strobilus; (D) Single sporangiophore.

However, not all sporogenous cells function as spore mother cells. Many of them degenerate to form a multinucleate nourishing substance for the spore mother cells. Each spore mother cell undergoes meiotic division (reductional division) and produces a spore tetrad. All spores in a sporangium are of the same size and shape, i.e., homosporous.

Structure of Mature Sporangium: The mature sporangium is an elongated sac-like structure, attached to the inner side of the peltate disc of the sporangiophore (Fig. 5.4). It is surrounded by a jacket layer which is composed of two layers of cells. The inner layer is generally compressed, and the cells of the outer layer have helical thickenings which are involved in sporangial dehiscence.

Dehiscence of Sporangium: At maturity, the strobilar axis elongates, as a result, the sporangiophores become separated and exposed. Then the sporangium splits open by a longitudinal line due to the differential hygroscopic response of the wall cells.

Spores: The spores are spherical and filled with densely packed chloroplasts. The spore wall is laminated and shows four concentric layers. The innermost is the delicate intine, followed by thick exine, the middle cuticular layer and the outermost episporium or perispore. The intine (endospore) and exine (exospore) are the true walls of the spore.

The outer two layers i.e., cuticular layer and episporium are derived due to the disintegration of the nonfunctional spore mother cells and tapetal cells. At maturity, the episporium (the outermost layer) splits to produce four ribbon-like bands or strips with flat spoon-like tips. These bands are free from the spore wall except for a common point of attachment and remain tightly coiled around the spore wall until the sporangium is fully matured.

These are called elaters. The elaters are hygroscopic in nature. The spores remain moist at the early stages of development; thus, the elaters are spirally coiled around the spore. The spores dry out at maturity and consequently the elaters become uncoiled. These uncoiled elaters become entangled with the elaters of other spores. Through these actions, the elaters help in the dehiscence process and the dispersal of spores in large groups from the sporangium. The elaters of *Equisetum* are different from those of the bryophytes.

Gametophyte Generation: *Equisetum* is a homosporous pteridophyte. The haploid spores germinate to form gametophytes. The germination takes place immediately if the spores land on a suitable substratum. If the spores do not germinate immediately, their viability decreases significantly.

The spores swell up by absorbing water and shed their exine. The first division of the spore results in two unequal cells: a small and a large cell. The smaller cell elongates and forms the first rhizoid. The larger cell divides irregularly to produce the prothallus. The prevailing environmental conditions determine the size and shape of the prothallus.

If many spores are developed together within a limited space, then the prothalli formed are of thin filamentous type. But relatively thick and cushion-shaped prothalli are formed from sparsely germinating spores. Mature gametophytic plants may range in size from a few millimeters up to 3 centimeters e.g., *E. debile*) in diameter. They are dorsiventral and consist of a basal non-chlorophyllous cushion-like portion from which several erect chlorophyllous multicellular lobes develop upwards. Unicellular rhizoids are formed from the basal cells of the cushion (Fig. 5.4).

The prothallus bears sex organs and reproduces using sexual methods.

Sexuality in Equisetum.

The gametophytic plant body bears sex organs i.e., antheridium (male) and archegonium (female). The gametophyte is bisexual (homothallic) i.e., they bear both male and female sex organs (Fig. 5.5D). Although, some unisexual (dioecious) members are also reported (Fig. 5.5 E, F). Some are initially unisexual and then become bisexual.

This early sex determination appears to be related to the environmental conditions viz., temperature, light, humidity, and the supply of nutrients as well. Duckett (1977), to explore the sexuality in *Equisetum*, observed that some of the fragments of male gametophyte remained male throughout the successive subcultures under laboratory conditions. Some other fragments produced archegonia, which subsequently bore antheridia in increasing numbers. This phenomenon supports the contention that *Equisetum* gametophytes are potentially bisexual. However, Hanke (1969) observed that gametophyte of *Equisetum bogotense* were unisexual (bearing antheridia) and never changed to bisexual type. However, the initial male gametophyte of *E. ramosissimum*, *E. variegatum* and *E. bogotense* never became bisexual.

Schratz (1928) observed that 50% of spores germinate to produce male gametophytes, while the remaining 50% of spores produce female gametophytes though they do not lose their male potentiality (i.e., antheridia develop later if fertilization fails). He termed

this as ‘incipient heterospory’. A study of sexuality based on enzymatic analysis revealed the intra gametophytic self-fertilisation in *E. arvense*.

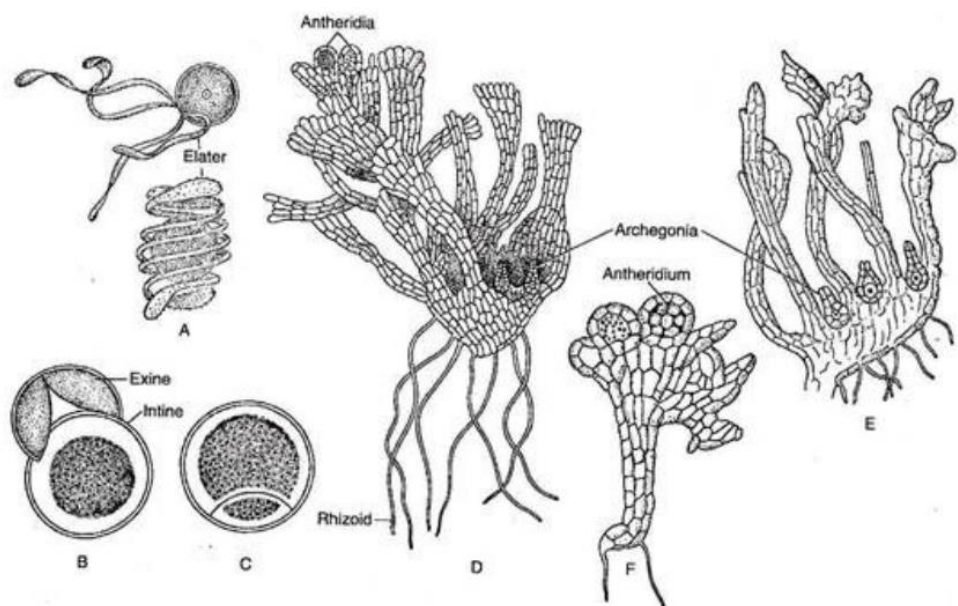


Fig. 5.5: Equisetum: A. Spores with elaters, B-C. The stages of germination of spore, D. Monoecious gametophyte, E. Female gametophyte, F. Male gametophyte.

Equisetum is homosporous and, therefore, the definite sex-determining mechanism is absent. However, the sexuality demonstrated by some of the members appears to be related to environmental factors. Therefore, it is termed environmental sex determination.

Sex Organs of Equisetum

Antheridium: In monoecious species, antheridia develop later than archegonia. They are of two types: projecting type and embedded type. Antheridia first appear on the lobes of the gametophyte (Fig. 5.5 D). The periclinal division of the superficial antheridial initial gives rise to a jacket initial and an androgenic cell (Fig. 5.6 A, B). The jacket initially divides anticlinal to form a single-layered jacket. The repeated divisions of androgenic cells form numerous cells which, on metamorphosis, produce spermatids/antherozoids. The antherozoids escape through a pore created by the separation of the apical jacket cell. The apical part of the antherozoid is spirally coiled, whereas the lower part is, to some extent, expanded. Each antherozoid has about 120 flagella attached to the anterior end.

ii. Archegonium: Any superficial cell in the marginal meristem acts as an archegonial initial which undergoes periclinal division to form a primary cover cell and an inner central cell (Fig. 5.7 B). The cover cell, by two vertical divisions at right angle to each other, forms a neck (Fig. 5.7 C). The central cell divides transversely to form a primary neck canal cell and a venter cell (Fig. 5.7 D).

Two neck canal cells are produced from the primary neck canal cell. While, the venter cell, by a transverse division, forms the ventral canal cell and an egg (Fig. 5.7 E). At maturity, an archegonium has a projecting neck comprising of three to four tiers of neck cells arranged in four rows, two neck canal cells of unequal size, a ventral canal cell, and an egg at the base of the embedded venter (Fig. 5.7F-G). The archegonia are confined to the cushion region in between the aerial lobes.

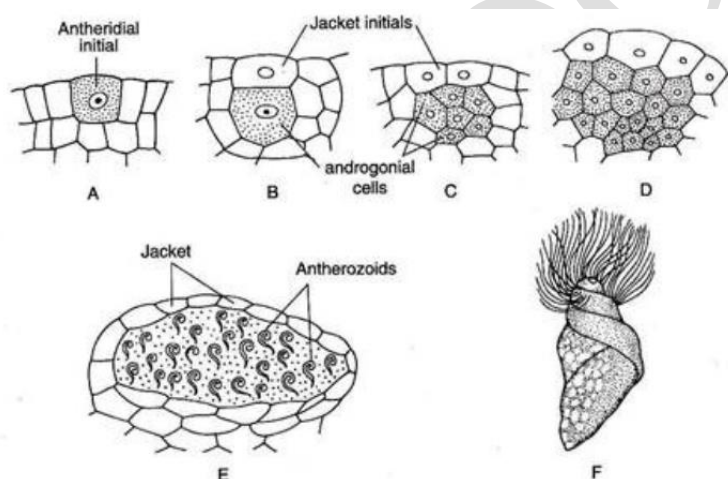


Fig. 5.6: Equisetum Development of antheridium. A-D, Successive stages in the development of antheridium, E. A mature antheridium, F. An antherozoid.

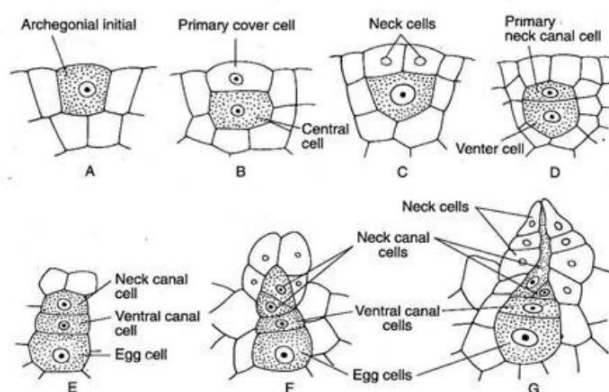


Fig. 5.7: Equisetum. Development of archegonium: A-E. Successive stages in the development of archegonium, G. A mature archegonium.

Fertilization

Water is essential for fertilization. The gametophyte must be covered with a thin layer of water in which the motile antherozoids swim to the archegonia. The neck canal cells, and ventral canal cells of the archegonia disintegrate to form a passage for the entry of antherozoids. Many antherozoids pass through the canal of the archegonium but only one of them fuses with the egg. Thus, diploid zygote is formed. Generally, more than one archegonia is fertilised in a prothallus.

Embryo (The New Sporophyte): The embryo is the mother cell of the next sporophytic generation. Unlike most pteridophytes, several sporophytes develop on the same prothallus. The first division of the zygote is transverse. This results in an upper epibasal cell and a lower hypobasal cell. The embryo is therefore exoscopic (where the apical cell is ducted outward i.e., towards the neck of the archegonium) in polarity. No suspensor is formed in *Equisetum*. The epibasal and hypobasal cells then divide at right angles to the oogonial wall, and as a result, a four-celled quadrant stage is established (Fig. 5.8A). All the four cells of the quadrant are of different size and shape. The four-celled embryo undergoes subsequent divisions and the future shoot apex originates from the largest cell and leaf initials from the remaining cells of one quadrant of the epibasal hemisphere.

One cell of the epibasal quadrant and a portion of the adjacent quadrant of the hypobasal region contribute to the development of the root. The first root develops from one of the epibasal quadrants and a portion of the adjacent hypobasal quadrant. The shoot grows rapidly.

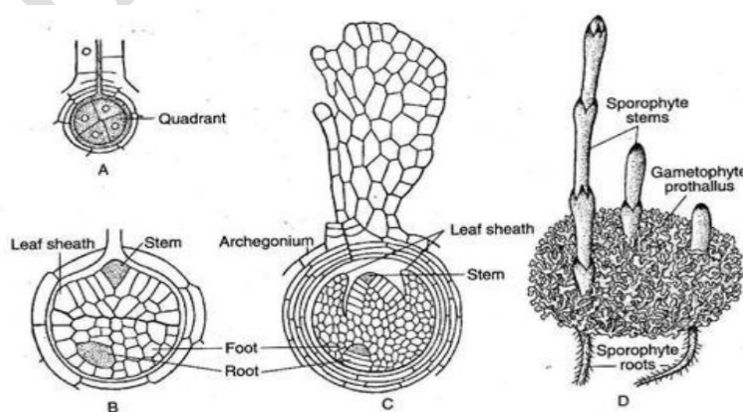


Fig. 5.8: Equisetum: A-C. The stages in the development of the embryo within the ventral region, D. Young sporophytes developing from a gametophyte.

Later, the root grows directly downward and penetrates the gametophytic tissue to reach the soil or substratum. Many such sporophytes may develop from a large mature gametophyte if more than one egg is fertilized (Fig. 5.9D).

Life Cycle of Equisetum

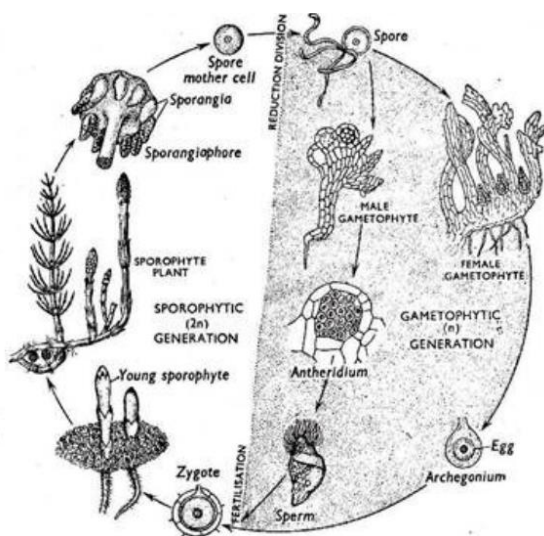


Fig. 5.9 depicts the life cycle of *Equisetum*.

5.9: Life cycle of *Equisetum arvense* (dioecious)

Selaginella

Division Lycopodiophyta

Class Lycopodiopsida

Order Selaginellales

Family Selaginellaceae

Genus Selaginella

Habit and Habitat of Selaginella

Selaginella is the only living genus of the order Selaginellales and is commonly known as 'spike moss' or 'small club moss'. It is a large genus comprising of about 700 species distributed all over the world. Abundantly it is found growing in tropical rain forests.

Mostly the species prefer moist and shady places to grow but a few species are also found growing in xerophytic conditions i.e., on dry sandy soil or rocks e.g., *S. lepidophylla*, *S. rupestris* etc. A very few species are epiphytes e.g., *S. oregana*. It is found growing on tree trunks.

A few xerophytic species of Selaginella e.g., *S. lepidophylla* and *S. pilifera* show cespitose habit and are sold as curiosities under the name of resurrection plants. They curl and become ball like when dry and again become green and fresh when moisture is available. About 70 species have been reported from India.

They are mainly found growing in the eastern as well as Western Himalayas and the hills of South India. Some of the common Indian species are *S. repanda*, *S. biformis*, *S. denticulata*, *S. monospora*, *S. semicordata*, *S. adunca* etc. *S. kraussiana* is cultivated in greenhouse.

External Morphology of Selaginella

The sporophyte is an evergreen, delicate herb. Its size varies greatly from species to species i.e., from a few cm. to 20 meters. Plants may be erect or prostrate depending upon the sub-genus. In the sub-genus homoeophyllum the plants are erect e.g., *S. rupestris*, *S. spinulosa* etc. and in the sub-genus heterophyllum the plants are prostrate e.g., *S. kraussiana*, *S. lepidophylla* etc.

The plant body is distinctly differentiated into the following structures (Fig. 6.1A, C):

- i) Stem.
- ii) Leaves.
- iii) Ligules.
- iv) Rhizophore.
- v) Roots.

i) Stem

It is usually profusely branched, delicate, and evergreen. The branching is of monopodial type. The growing apex of the stem consists of either meristematic tissue or a single apical cell. In the sub-genus homoeophyllum the stem is erect and somewhat cylindrical and in the sub-genus heterophyllum it is prostrate with stout erect branches and is somewhat dorsiventral.

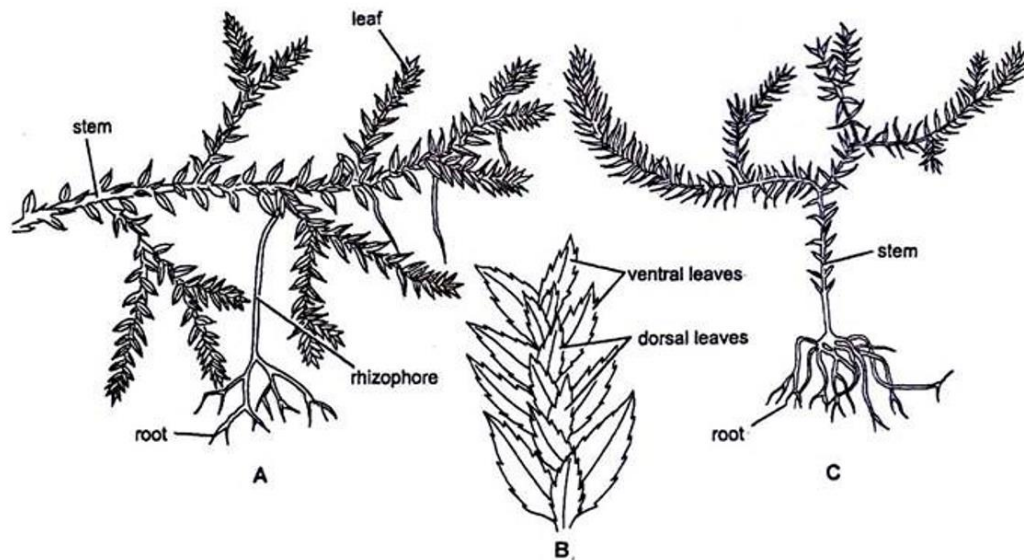


Fig. 6.1: (A-C). Selaginella. External features: A. *S. kraussiana*, B. Leaf arrangement in a branch of *S. kraussiana*, C. *S. spinulosa*.

ii) Leaves: They are usually small, simple, and lanceolate with a pointed apex. Each leaf is provided with a single unbranched midrib. In the sub-genus homoeophyllum, all the leaves are of the same size and are spirally arranged, forming a dense covering.

In the sub-genus heterophyllum, the leaves are dimorphic, i.e., of two sizes (small and big), and are arranged in pairs. Small leaves are present on the dorsal side of the stem and bigger ones on the ventral side of the stem (Fig. 6.1 B). The bigger leaves alternate with bigger ones, and smaller leaves alternate with smaller ones.

Usually, the leaves near the apical portion of the branch bear sporangia (micro- or mega) and are called sporophylls (micro- or mega) respectively. The sporophylls are usually aggregated into a condensed structure, which is known as a strobilus.

(iii) Ligules: On the adaxial side of the leaf, near the base, is a small membranous outgrowth known as a ligule. It is embedded at the base of a leaf in a pit-like structure known as the ligule pit.

It may be tongue-shaped (e.g., *S. vogelii*), fan-shaped (e.g., *S. martensii*), fringed (e.g., *S. cuspidata*), or lobed (e.g., *S. caulescens*). It is more than one cell in thickness except at the apex. The structure of the ligule can be differentiated into two parts, glossopodium and the body of the ligule (Fig. 6.2 A, B).

Glossopodium: It is the basal hemispherical part made up of large thin-walled cells. It is surrounded by a glossopodial sheath.

Body of the ligule: Above the glossopodium is the body of the ligule. It is made up of many large and small cells. The function of the ligule is not well known. It may be a water-secreting water-absorbing or protective organ. According to Earner (1936), the ligule is perhaps a vestigial organ.

(iv) Rhizophore: This structure arises from the prostrate axis at the point of dichotomy and elongates downward. It is a colourless, leafless, unbranched and cylindrical structure.

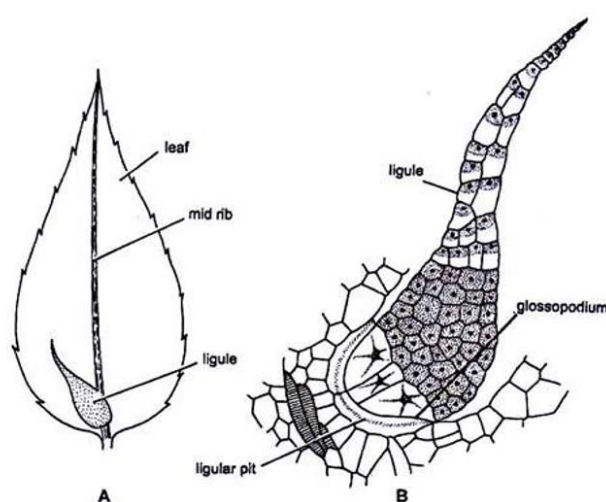


Fig. 6.2 (A, B). Selaginella. Structure of ligule: A. Leaf with ligule, B. Longitudinal section of ligule.

As soon as the free end of rhizophore touches the soil it develops a tuft of adventitious roots at its free end. In few species the rhizophore is present e.g., *S. krciussiana* while in others it is absent e.g., *S. cuspidata*. It differs from the root in having no root cap and from the stem in having no leaves.

The following views regarding the morphological nature of the rhizosphere have been proposed.

1. Capless root hypothesis

According to Harvey Gibson (1902), Uphof (1920), Wochok and Sussex (1974), the rhizophore is a capless root because.

- (i) It is positively geotropic.
- (ii) It is a leafless structure.
- (iii) It is almost similar in the anatomy of the root.
- (iv) It has a monostelic stele.

2. Leafless shoot hypothesis: According to Worsdell (1910), Williams (1937), Cusic (1954) etc. The rhizophore is a leaf-less shoot because.

- (i) Root cap is absent. (ii) Root hairs are absent. (iii) It is exogenous in origin.
- (iv) It arises from the angle meristem present at branching. (v) It can develop into leafy shoot under experimental conditions.

3. Sui-generis hypothesis: According to Goebel (1905), Bower (1908), the rhizophore is an organ “Suigeneris” i.e., having no parallel structure anywhere in the plant kingdom. Thus, it is altogether a new structure.

Schoutt (1938) regarded rhizophore as specialized stem modified in the direction of root because of the root bearing nature.

(v) Roots: They originate either from the tips of rhizophores or directly from the stem or from the swollen base of hypocotyl (Fig. 6.1 A, B). Their origin is endogenous. They are usually dichotomously branched structures. The roots are provided with root caps and root hairs.

Internal Structure of Selaginella: Stem: A Transverse section (T.S.) of the stem of Selaginella is somewhat circular in outline and shows the following structures.

(i) Epidermis: It is the outermost covering layer comprising a single cell in thickness. The cells of the epidermis are without hairs and stomata. The epidermis is surrounded by a thick coating of cuticle.

ii) Cortex: Inner to the epidermis is presents a well-defined zone of cortex. The cortex may or may not be differentiated into inner and outer cortex. In the case of *S. selaginoides*, the whole of the cortex is made up of parenchymatous cells while in *S. kraussiana*, it is differentiated into sclerenchymatous outer cortex and parenchymatous inner cortex.

The parenchymatous cortex is usually made up of angular cells i.e., without intercellular spaces but in some cases, the cells are rounded and provided with a few inter-cellular spaces.

(iii) Stele: The central portion of the stem is occupied by a well-developed stele. The stele is of protostelic type i.e., xylem is present in the centre and surrounded by phloem on all sides. Phloem, in turn, is surrounded by a single layered pericycle. Pith is absent. The stele remains suspended in the centre by radially elongated tubular, unicellular structures known as trabeculae. These are formed by the radial elongation of the endodermal cells. Trabeculae are provided with conspicuous casparian strips. In between the trabeculae are present large spaces known as air spaces.

The number of stele is variable in different species of Selaginella. It is 1 (monostelic e.g., *S. spinulosa*), 2 (distelic e.g., *S. kraussiana*) or 12-16 (polystelic e.g., *S. laevigata*). The organization of the stele is also variable in different species. It may be protostele (e.g., *S. spinulosa*) to siphonostele (e.g., *S. laevigata*, var. *lyalli*).

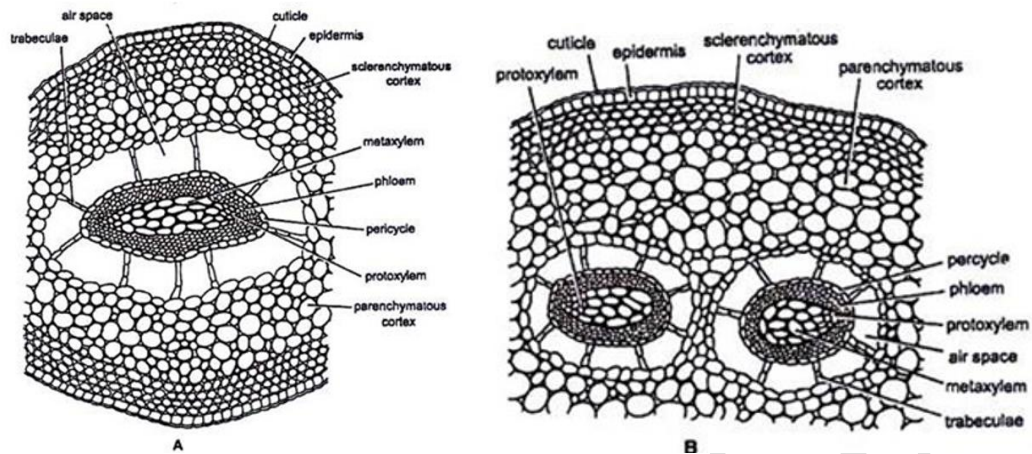
The stele is surrounded by a single-layered pericycle made of parenchymatous cells. The xylem is usually monarch (e.g., *S. kraussiana*), or diarch (e.g., *S. oregana*) or multiarch (e.g., *S. spinulosa*).

It is usually exarch but sometimes it may be mesarch (e.g., *S. selaginoides*). Xylem is usually made of tracheids. Vessels are completely absent. Xylem is surrounded by phloem, which consists of sieve cells and phloem parenchyma. Companion cells are absent in the phloem.

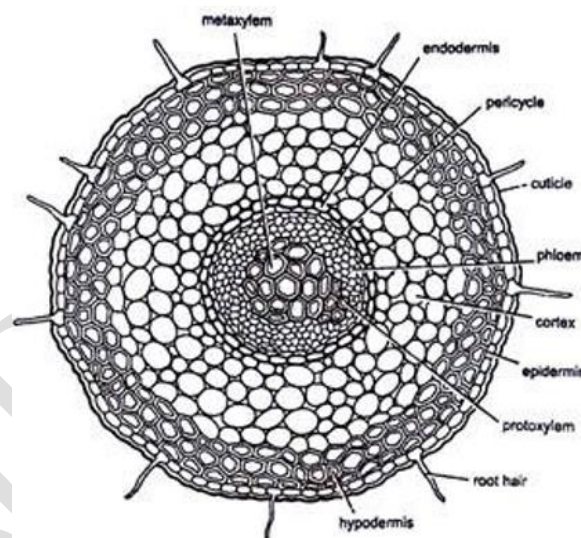
2. Root: A T.S. of the root is somewhat circular in outline and shows the following internal structures:

- (i) Epidermis: It is the outermost covering layer and is only one cell in thickness. The cells are large, and the unicellular root hairs arise from them.
- (ii) Cortex: Just below the epidermis is a wide zone of cortex. The cortex may be either wholly made up of thin-walled parenchymatous cells or there may be sclerenchymatous outer cortex (hypodermis), 3 to 5-celled in thickness, and parenchymatous inner cortex. In mature roots of *S. densa* the entire cortex may consist of thick-walled sclerotic cells.

Air spaces have also been reported in the inner cortex (e.g., *S. willdenovii*). It is traversed by trabeculae.



6. 3 (A-B). *Selaginella*. T. S. Stem. (A) *S. monostelic* stem, (B) *S. distelic* stem (a part cellular).



6. 4. *Selaginella*. T. S. Root.

Fig 6.4: T.S. of rhizome showing the detailed structure.

- (i) **Epidermis:** It is single-layered, and the outer wall of epidermal cells is covered with a thick cuticle. Root hairs and stomata are absent.
- (ii) **Cortex:** Inner to the epidermis is a wide zone of cortex differentiated into outer sclerenchymatous and inner parenchymatous zones.
- (iii) **Endodermis:** It is the innermost layer of the cortex. It is an ill-defined single-layered structure.

(iv) Pericycle: Inside the endodermis is a single layered parenchymatous pericycle.

(v) Stele: It is typically a protostele. The xylem is surrounded by phloem. Xylem shows distinct protoxylem and metaxylem elements. The position of protoxylem is different in different species. In *S. martensii* xylem is exarch and monarch. In *S. atroviridis* the metaxylem is crescentric with several protoxylem strands situated on the concave adaxial side. In *S. kraussiana*, *S. poulteri* etc. protoxylem is mesarch (centroxylic).

4. Leaf: T.S. of the leaf shows epidermis, mesophyll, and a single median vascular bundle which has been discussed below in detail.

(i) Epidermis: It is the outermost surrounding layer and is only one cell in thickness. In most of the species, the stomata are present only on the lower epidermis near the midrib. The stomata may be present on both the outer and inner epidermis. The cells of the epidermis are provided with chloroplasts.

(ii) Mesophyll: It occupies a wide zone between upper and lower epidermis. The mesophyll is usually made up of parenchymatous cells which have conspicuous intercellular spaces. Each mesophyll cell has one (e.g., *S. martensii*), two (e.g., *S. kraussiana*), or eight (e.g., *S. willdenovii*) chloroplasts.

Each chloroplast has several pyrenoid-like bodies like order Anthocerotales (Bryophyta). In some species (e.g., *S. concinna*) the mesophyll is distinguished into upper palisade and lower spongy parenchyma.

(iii) Vascular bundle: Only one vascular bundle is present in the center. It is concentric and amphicribal (ectophloic). It is made up of a few xylem tracheids (annular or spiral) surrounded by phloem elements (a few sieve elements). A single-layered bundle sheath encircles the phloem on all sides.

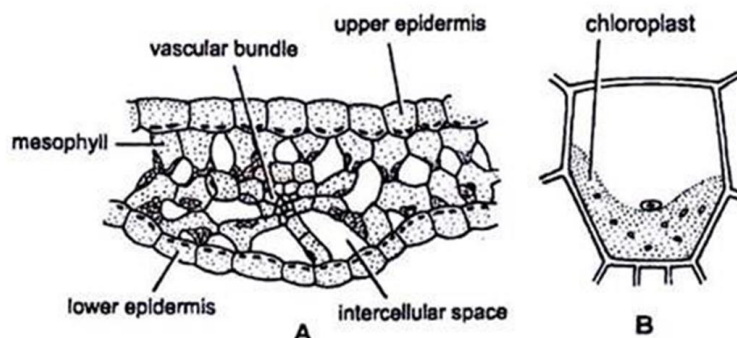


Fig. 6.5. (A-B). Selaginella: Internal Structure of leaf. A. T. S. of a part leaf of *S. kraussiana*, B. A mesophyll cell.

Reproduction in Selaginella: Selaginella reproduces by two methods: Vegetatively and by formation of spores.

1. Vegetative reproduction: It takes place by following methods.

(i) Fragmentation: Under humid conditions in *S. rupestris*, trailing branches of the stem develop adventitious branches. These branches later disjoin from the parent plant and develop into separate individual plants.

(ii) Tubers: These appear towards the end of the growing season. The tubers may be aerial, developing at the apical end of aerial branches (e.g., *S. chrysocaulos*) or subterranean (e.g., *S. chrysorrhizos*). Under favorable conditions, tubers germinate into a new plant (Fig. 6.6A).

(iii) Resting buds: These are the compact structures that develop at the apical end of some aerial branches. The leaves in this region are closely arranged and overlap the growing points. These resting buds can pass on the unfavourable conditions. Under favorable conditions, these buds give off rhizophore that bears roots at their tips (Fig. 6.6B).

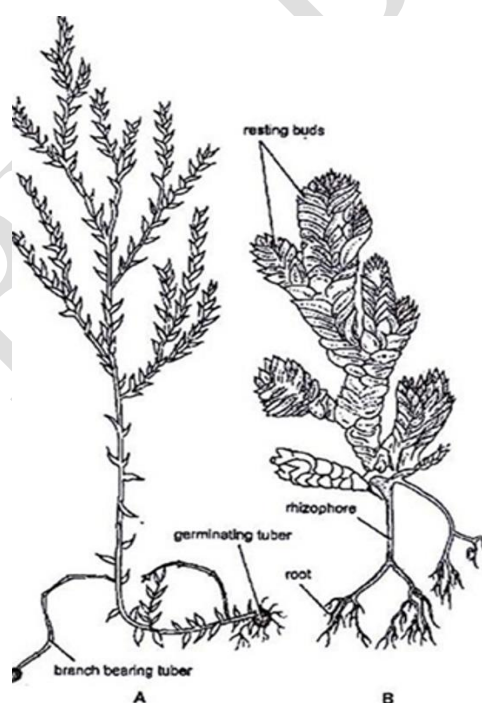


Fig. 6.6 (A-B). Selaginella. Vegetative reproduction, A. Tubers, B. Resting buds.

2. Sexual Reproduction: Spore-producing organs

Selaginella is a sporophytic plant (2x) and reproduces sexually. The plants are heterosporous, i.e., produce two different types of spores, megaspores and microspores.

These spores are produced in megasporangia and microsporangia, respectively, which, in turn, are produced on fertile leaves known as megasporophylls and microsporophylls, respectively. Usually, both these structures are grouped to form a compact structure known as strobilus, which is usually a terminal structure (Fig.6.7 A).

Strobilus: It is a reproductive structure formed by the aggregation of ligulate sporophylls at the apex of the branches of the stem. The length of the strobilus varies from 1/4 inch to 2-3 inches in different species. In some species, e.g., *S. cuspidata*, *S. patula*, etc., the growth of the stem continues beyond the strobilus, and such a condition is called the selago condition (fertile part is alternated by vegetative parts) (Fig.6.7 B).

The Longitudinal section (L.S.) of the strobilus shows that it is a very simple structure. It consists of a central axis covered with spirally and densely arranged ligulate sporophylls. Each sporophyll adaxially bears a single stalked sporangium in its axis (Fig. 6.7).

The positions of the sporangia differ in different species. It may be in axil (axillary) or a little upward on in position (cauline). *Selaginella* produces two types of spores' megaspores and microspores. The dimorphic condition of the spores is known as heterospory. In between the sporophyll and sporangium is present a small membranous structure known as ligule i.e., the sporophyll is like a vegetative leaf. The microsporangium produces a large number of microspores whereas megasporangium usually produces 4 megaspores.

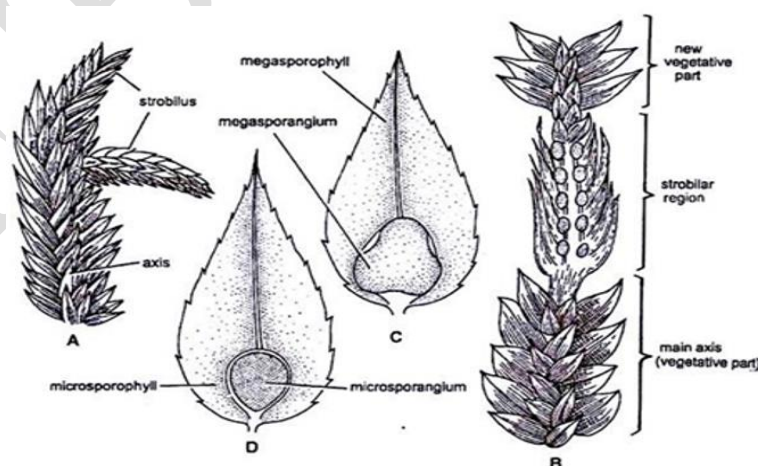
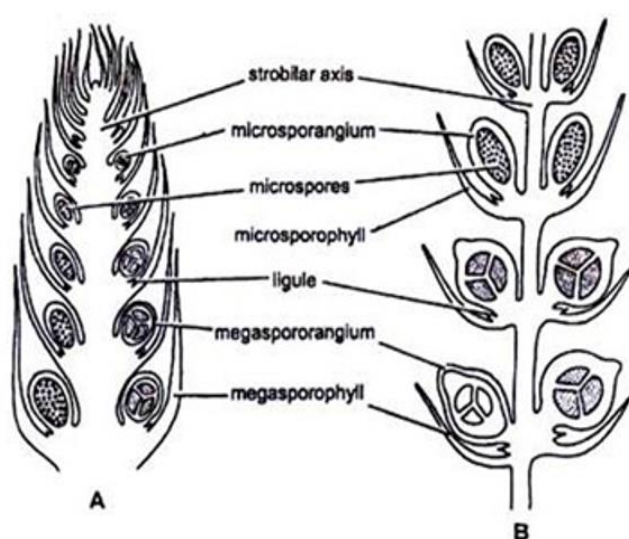


Fig. 6.7 (A-D). *Selaginella*: Structure of strobilus. A. A branch bearing strobilus, B. A branch, after the formation of the strobilus region, again changes into a vegetative region, C. A megasporophyll, D. A microsporophyll.

Strobili are usually bisporangiate, but the arrangement of microsporophylls and megasporophylls differs in different species. In *S. inaequalifolia* (Fig. 6.8 A) the microsporophylls are present on one side and megasporophylls on the other side.

In *S. rupestris* megasporophylls are present on the lower side and microsporophylls on the upper side of the strobilus (Fig. 6.8 A). In the case of *S. martensii*, the microsporophylls are mixed irregularly with megasporophylls (Fig. 6.8). In *S. kraussiana*, only one megasporophyll is present while all the rest are microsporophylls (Fig. 6.8). In the case of *S. gracilis*, the strobilus is eusporangiate, i.e., either it bears microsporophylls or megasporophylls alone.

Microsporangium: Each microsporangium is a stalked, globular, or elongated structure (Fig. 6.8D). Its color varies from red and yellow to brown in different species. The wall is 2-layered, which is followed by a conspicuous tapetum (Fig. 6.9 F). In the young sporangium inside the wall is present a mass of sporogenous cells which in due course of development separate into microspore mother cells and later, by meiotic divisions, produce numerous haploid tetrads of microspores. The microspores at maturity separate from each other. At maturity the tapetal cells as well as the inner wall of the microsporangium disorganizes i.e., wall of the sporangium is usually one layered at maturity. Microspores are smaller in size.



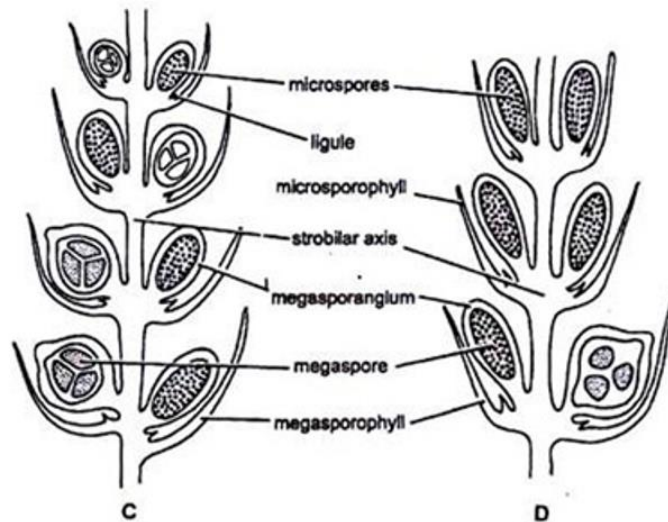


Fig. 6.8. (A-D). Selaginella. Longitudinal sections of strobilus of different species showing position of microsporangia and megasporangia: A. *S. inaequalifolia*, B. *S. rupestris*, C. *S. martenall*, D. *S. kraussiana*.

Megasporangium: Each megasporangium is also a stalked but lobed structure and somewhat bigger than the microsporangium. Its color varies from whitish yellow to red. Its wall is also 2-layered thick and followed by a single-layered tapetum (Fig. 6.9 G). In the young sporangium inside the wall is present a mass of sporogenous cells which in due course of development separate into megaspore mother cells. All the megaspore mother cells except one degenerate.

The remaining one later by meiotic division produces only 4 haploid megaspores. Sometimes less than 4 megaspores are produced inside each megasporangium. As, *S. rupestris* produces only one megaspore per megasporangium. At maturity, the tapetal cells usually along with an inner wall of the sporangium disorganize. Megaspores are larger than microspores (Fig. 6.9 G). The sporangia usually dehisce by a vertical slit formed in the apical region of the sporangia and the spores are disseminated in the air.

Development of sporangium and formation of spores: As the position of sporangium is either cauline or foliar, the initials are either situated on the axis or the leaf respectively. The development of sporangium and formation of spores (micro-and mega) is like the formation of spore mother cells and is as follows.

The development is of eusporangiate type i.e., it takes place with the help of a row of initials which are known as sporangial initials e.g., *S. kraussiana* (in some cases from a

single sporangial initial cell e.g., *S. spinulosa*). These cells are superficial in position (Fig. 6.9 A).

These cells divide periclinally forming outer jacket initials and inner archesporial initials (Fig. 6.9 B). The jacket initials by further periclinal and anticlinal divisions form the jacket which is 2-celled thick (Fig 6.9 E). The archesporial initials divide in all directions forming a group of cells known as sporogenous tissue.

The cells of the outermost layer of sporogenous tissue divide periclinal forming a single-layered tapetum just inner to wall of the sporangium. It is a nourishing layer (Fig 6.9 C-E). The tissue at the base of the sporangium divides to form the sporangial stalk. The cell of sporogenous tissue in the case of microsporangium finally gives rise to microspore mother cells and in the case of megasporangium gives rise to megaspore mother cells.

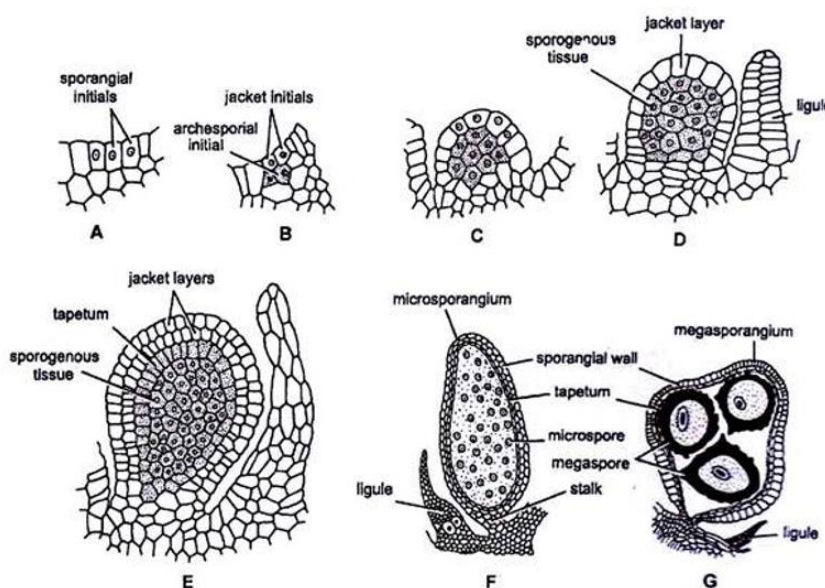


Fig. 6.9. (A-G). *Selaginella*. Development of sporangium. (A-E). Successive stages in the development of microsporangium in *S. kraussiana*, F. Mature microsporangium, G. Mature megasporangium.

In microsporangium all the microspore mother cells are functional and each one divides reductionally forming a tetrad of 4 haploid microspores, because of which many tetrads of microspores are formed inside microsporangium. Later on, these microspores separate from each other. The mature microsporangium dehisces by a vertical slit in the apical region. By the drying of unsplitted portion, the spores are forced out and then they are dispersed away by wind.

In megasporangium all the megaspore mother cells degenerate except one which divides reductionally forming a tetrad (Fig. 6.10 D) of 4 haploid megaspores. The dehiscence of megasporangium is like that of microsporangium.

Gametophytic Generation: The development of male and female gametophytes (prothalli) takes place from the haploid microspores and megaspores respectively i.e., microspores and megaspores are the unit of male and female gametophytes, respectively.

Spore: The microspores are small, 0.015 to 0.05 millimeters in diameter, spherical or round and double-layered structures. The outer wall is thick and known as exospore (exine). While the inner wall is thin and is called an endospore (intine, Fig 6.10 A-C).

The megaspores are much larger than microspores, 1.5 to 5 millimeter in diameter, tetrahedral in shape, and show triradiate ridge. The megaspore has three wall layers namely exospore, mesospore, and endospore (Fig. 6.10 D, E). The microspores on germination give rise to male prothalli and megaspores to the female prothalli.

Development of male gametophyte

The microspore is the initial stage in the development of male gametophyte. The development of the microgametophyte is in situ or precocious i.e., it starts within the microsporangium. Generally, a 13-celled microgametophyte is formed before the microsporangium dehisces.

Each microspore is a unicellular, uninucleate, rounded or spherical, haploid structure with outer spiny thick exosporium and inner thin endosporium. The first division is in such a way that 2 unequal cells are formed, smaller prothallial cell and a larger antheridial cell (Fig. 6.12 A).

The prothallial cell does not divide further and takes no part in further development of male gametophyte. The antheridial cell divides to form a group of 12 cells. The antheridial cell divides vertically (2-2) to the prothallial cell to form the two primary cells of the antheridium (Fig. 13B). At this stage the young gametophyte consists of 3 cells (2+1 cell, Figs. 6.11 A, B; 6.12 B).

The wall that separates the two primary cells is called a first primordial wall. Two primary cells thus formed divide transversely (3-3 Figs. 6.11 C). This division is at right

angle to the first and can be seen only if we cut a vertical section of the spores. This stage of gametophyte consists of 5 cells (2 + 2+1 cells).

Out of these four cells formed by the division of primary cells, the basal cells divide no further and become the cells of the jacket layer of the antheridium. The upper two cells divide further by curving or arching wall (4-4, Fig. 6.11 D). In this way, 6 cells are formed and microgametophyte has seven cells at this stage (4+ 2+1 cells). Out of the four cells formed by the last division, two bigger cells divide again by curved wall (5-5, Fig. 6.11 E) and thus a 9-celled microgametophyte is formed (6 + 2+1 cells, 8 antheridial cells and one prothallial cell). These antheridial cells are arranged in such a manner that four cells are present in the middle and two cells are present on either side i.e., above and below.

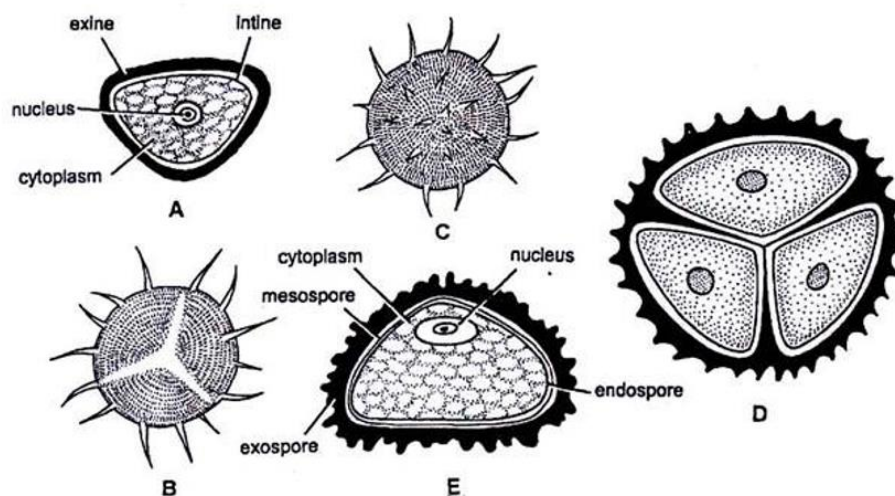


Fig. 6.10 (A-E). Selaginella. Structure of spores: A. A single microspore showing detailed structure, B. Apical view of spore, C. Basal view, D. Megaspore in tetrad, E. A single megaspore.

The middle four cells divide by periclinal walls (Fig 6-6, Fig. 6.11 F; 6.12 D) to form 4 primary androgonial cells and 8 jacket cells. The gametophyte now consists of 13 cells (1 prothallial cell + 4 androgonial cells + 8 jacket cells). In *S. kraussiana* the gametophyte is shed at this stage. Further development takes place after shedding.

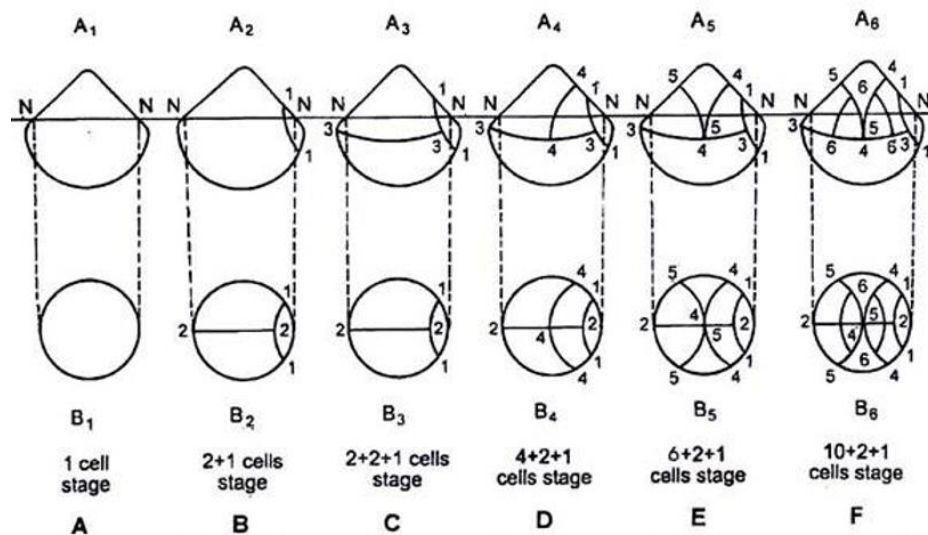


Fig. 6.11 (A-F). *Selaginella*. Diagrammatic representation of the development of microgametophyte.

At this stage the spores are liberated and their exosporium ruptures. Primary androgonial cells divide and redivide to form 128 or 256 androcytes or antherozoid mother cells. Each antherozoid mother cell finally metamorphoses into a single antherozoid (Fig. 6.12 F, G) which is a spirally coiled, uninucleate, and biflagellate structure. The two flagella are unequal in size. The antherozoids are liberated by the rupturing of endosporium and swim in water till they reach the neck of archegonium.

Development of female gametophyte: The megaspore is the initial stage in the development of female gametophyte. The development of female gametophyte starts while the megaspore is still inside megasporangium. The megaspores are liberated from the megasporangium either at the time of first archegonium formation or just after fertilization. First, the exospore or outer wall grows faster than the mesospore which result in the formation of space between exospore and mesospore. The whole structure increases in size because of which a big central vacuole appears (Fig. 6.13 A).

Now nucleus divides by free nuclear divisions, forming many nuclei. First the nuclei are equally distributed in the cytoplasm, but later more nuclei collect in the apical region.

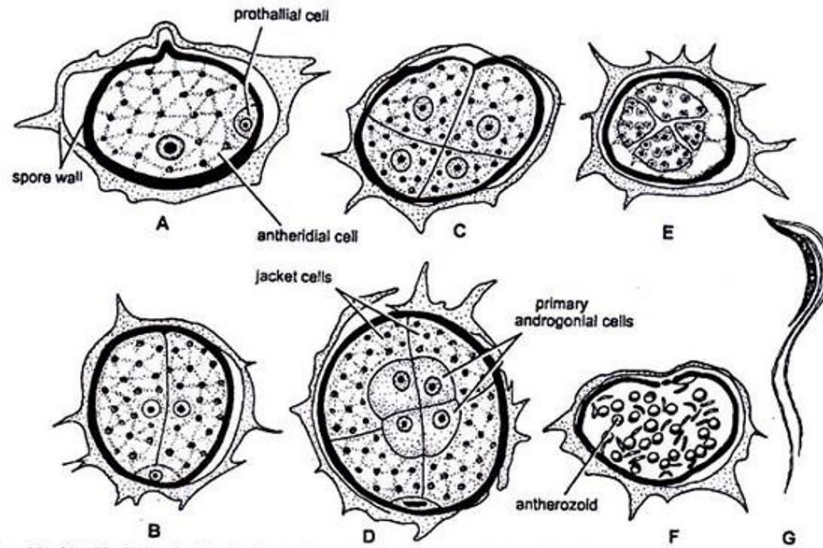


Fig. 6.12. (A-G) Selaginella. Schematic representation of the development of male gametophyte.

At this stage wall formation starts from the apical region downwardly thus forming an upper cellular region known as the female prothallus and a lower non-cellular region known as the storage region. The wall of the lower cells becomes thick, forming a diaphragm (Fig. 6.13 B-E). Later, the vacuole also disappears as the cytoplasm increases in amount.

This may be absent in a few species e.g., *S. martensii*. At this stage usually, the female gametophyte is liberated from the gametangium. If it falls on a suitable substratum, it germinates. The exine and mesine ruptures. The cellular tissue protrudes out and a few rhizoids develop which fixes the gametophyte to the substratum and absorbs water (Fig. 6.14).

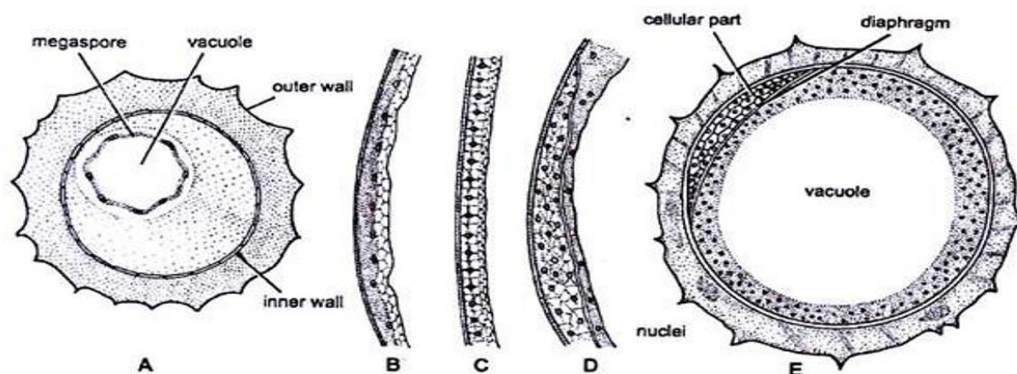


Fig. 6.13 (A-E). Selaginella. Stages in the development of the female gametophyte.

Development of archegonium

A few cells near the apex of the female prothallus behave as archegonial initials which by further divisions, give rise to archegonia (Fig. 6.15H). Each archegonium develops from a single superficial cell of the female prothallus situated near the apical region and is termed an archegonial initial (Fig. 6.15 A).

It divides transversely forming an upper primary cover cell and a lower central cell (Fig. 6.15 B). The primary cover cell, by two vertical divisions at right angle to each other, forms 4 cells which by a transverse division forms a neck of 2 tiers of 4 cells each (Fig. 6.15 C, D).

The central cell again divides to form an upper primary neck canal cell and a lower primary venter cell (Fig. 6.15 D). The former forms a single neck canal cell while the latter divides to form a ventral canal cell and egg (Fig. 6.15 E).

Structure of Mature Archegonium

The archegonium is a short flask-shaped structure embedded in female gametophytic tissue (Fig. 6.15 H). Only the upper tier of neck cells projects out. Each archegonium consists of a short neck of 2 tiers of 4 cells each and a broad venter. The four cells of the upper tier of the neck function as cover cells.

The neck encloses a single neck canal cell, and the venter consists of a ventral canal cell and an egg (Fig. 6.15 G). There is no definite wall of venter. At maturity, the neck canal cell and the ventral canal cell disorganize and absorb water which creates pressure to separate apart the cover cells (Fig. 6.15 F) through which the antherozoids enter the archegonium and reach the egg.

Fertilization: Water is necessary to carry out the process of fertilization. The swimming antherozoids reach the egg through the neck of the archegonium and the nucleus of the antherozoid fuses with the egg nucleus thus forming a zygotic nucleus. The fertilized egg secretes a wall around it forming a diploid structure known as zygote or oospore (2x). Thus the gametophytic generation ends and the initial stage of sporophytic generation is formed. In some species e.g. *S. intermedia* the egg develops into an embryo without fertilization. This phenomenon is known as parthenogenesis.

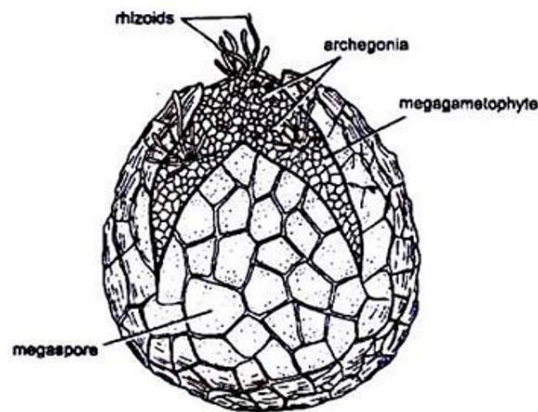
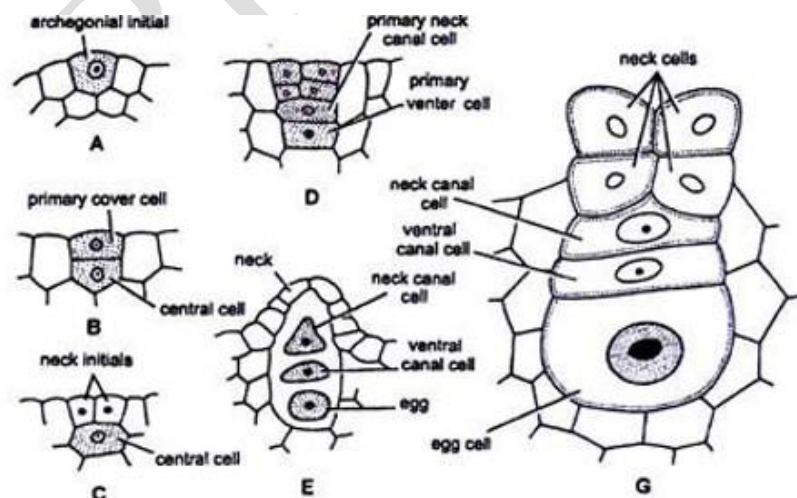


Fig. 6.14. *Selaginella*. Female gametophyte. A. Dehiscent megaspore and rhizoids In *S. kraussiana*.

Embryo Development (Young Sporophyte): Development of embryo: Oospore is the initial stage of sporophytic generation. During the development of the embryo, the oospore first divides by a transverse division into an upper suspensor initial (epibasal) and a lower embryo initial (hypobasal) (Fig. 6.16 A, B).

The suspensor initially further divides in all directions forming a multicellular suspensor that thrusts the developing embryo deep into the female gametophytic tissue to absorb food for further development of the embryo. The embryo initially divides into 2 vertical divisions at a right angle to each other thus forming 4 cells (quadrant. Fig. 6.16 C).



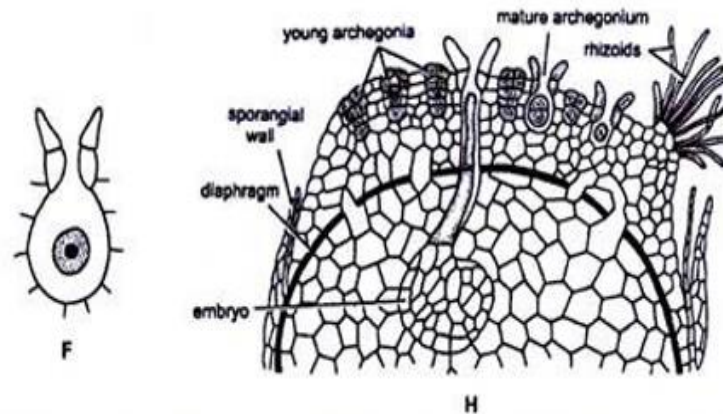


Fig. 6.15 (A-G). Selaginella: Development of archegonium. A-F. Various stages in the development, G. A mature archegonium before fertilization, H. A nearly median section of a mature prothallus.

One of these 4 cells divides by an oblique wall forming a shoot initial (Fig 6.16 D). Now the cells except the shoot initially divide sporophyte transversely forming 2 tiers of 4 cells each. Later, by further divisions, it forms a multicellular structure that gets differentiated into foot, rhizophore, stem, and cotyledons (Fig. 6.16 E-J).

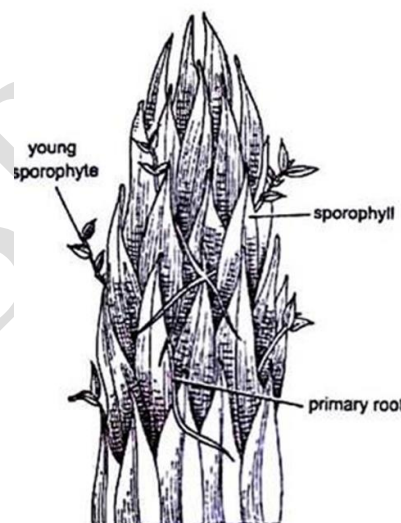


Fig 6.16. (A-J). Selaginella: Development of embryo. A-I various stages in the development J. Longitudinal section of female gametophyte bearing embryo.

In some species of Selaginella (e.g., *S. apus* and *S. rupestris* the megagametophytes are never shield from the megasporangium and remain on the strobilus. The oospore completes its development within the megasporangium, and the young embryo grows into a seedling, develops a primary root, and then falls on the ground (Fig. 6.17).

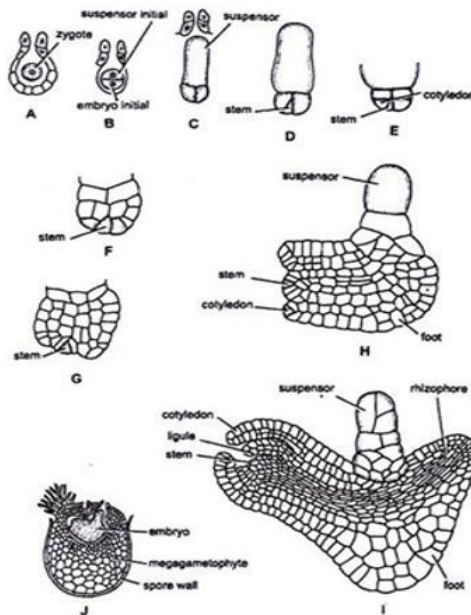


Fig. 6.17. Selaginella. Young sporophytes develop upon the strobilus of parent plant In Selaginella rupestris.

Life Cycle Patterns of Selaginella: Selaginella is a sporophytic plant ($2x$) and produces two different types of spores i.e., microspores and megaspores. In other words, we may call it a heterosporous plant. These spores on germination produce male and female gametophytes (x) respectively which in turn develop upon the strobilus of parent to produce antherozoids and eggs in antheridia and archegonia respectively.^[6.18]

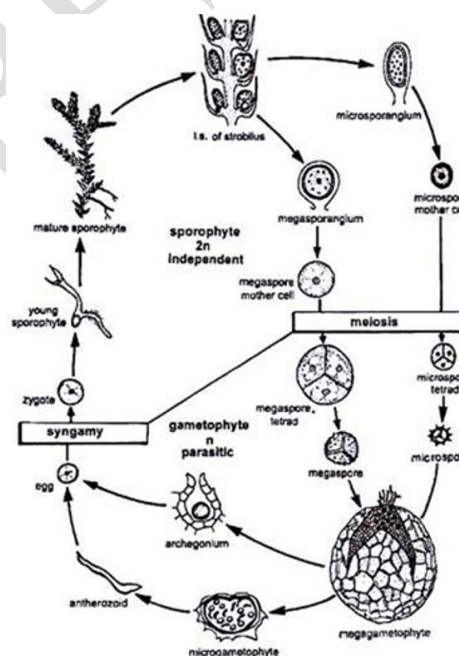


Fig. 6.18. The diagrammatic life cycle of Selaginella.

These reproductive structures after fertilization produce a zygote (2x) which again on germination gives rise to a sporophytic plant (2x). In this way, the saprophytic and gametophytic generations alternate with each other although the sporophytic phase is dominant over the gametophytic phase (Figs. 6.18).

iii) Class Polypodiopsida; Pteridaceae: Polypodium; Ophioglossidae; Ophioglossaceae: Ophioglossum. Psilotaceae: Psilotum.

Ophioglossum

Division: Pteridophyta

Class: Polypodiopsida

Order: Ophioglossales

Family: Ophioglossaceae

Genus: Ophioglossum

Occurrence and Distribution of Ophioglossum

Ophioglossum is the most widely distributed genus in the family Ophioglossaceae, found across almost all parts of the globe. This genus is particularly known for its unique and ancient characteristics among ferns, often referred to as "adder's-tongue ferns." It is divided into three sub-genera.

1. **Euophioglossum** – Examples include *O. moluccanum* and *O. vulgatum*.
2. **Ophioderma** – Examples include *O. pendulum*.
3. **Cheiroglossa** – An example is *O. palmatum*.

Global Distribution: Ophioglossum species are spread worldwide, thriving in a wide range of environments. These plants are primarily terrestrial, although some species have adapted to epiphytic or even saprophytic lifestyles.

Number of Species: The exact number of species in the genus Ophioglossum varies according to different taxonomic opinions. However, most pteridologists recognize around 28 species globally.

Occurrence in India: In India, approximately 12 species of Ophioglossum are found. Some of the most common Indian species include *Ophioglossum vulgatum* Found in areas like the Nandi Hills (Bangalore District). *Ophioglossum pendulum*, *Ophioglossum*

aitchisoni in addition: **Khandelwal and Goswami (1984)** reported a new species from India, *Ophioglossum eliminatum*.

Bir and Bhusri (1985) reported the presence of Ophioglossaceae (genera *Ophioglossum* and *Botrychium*) in the Shimla Hills.

Sharma and Singh (1985) described the morphology and anatomy of seven species found in India, including *O. reticulatum*, *O. petiolatum*, and *O. nudicaule*.

Habitat and Growth

Ophioglossum species typically prefer **humus-rich, moist, and shady soils**, often found in forests and grasslands. Some species exhibit more specialized habits: *O. pendulum* is epiphytic, growing on humus-filled pockets of trees. *O. palmatum* is found on decaying tree trunks, indicating a possible saprophytic nature.

Additional Points: Ecological Importance: The unique adaptation of *Ophioglossum* to different environments, including epiphytic and saprophytic conditions, makes it an interesting subject for ecological studies.

Chromosome Count: *Ophioglossum* species are also known for having the highest chromosome count of any plant, with some species possessing over 1,260 chromosomes.

Conservation Status: While *Ophioglossum* species are widely distributed, habitat loss and environmental changes potentially threaten some populations, making their conservation important.

Sporophyte of Ophioglossum

Morphology of the plant: In most of the species, the plant body possesses a short, erect, tuberous rhizome exhibiting radial symmetry. In *O. pendulum*, *O. intermedium* the rhizome is dorsiventral. The branching of the rhizome is infrequent and may be dichotomous or lateral. The upper surface of the rhizome produces leaves in an irregular species, the number of leaves produced per season varies. In temperate species, only one leaf is formed per growing season.

In tropical species, however, the number may be 4-5 per year. The growth of the leaf is extremely slow. A leaf primordium is underground for the first three years and only in

the fourth year, it comes above the ground. The leaves may be erect or pendant as in *O. pendulum*.

A great amount of diversity is exhibited in the nature of the leaves. Generally, a leaf has two parts viz., petiole and lamina. The petiole is erect and long. It bears an expanded, simple, and entire lamina. At the junction of the lamina and the petiole arises the fertile spike the reproductive structure of the plant.

In *O. pendulum* the distinction between the lamina and the petiole is lost. Here the leaf is long (1-1.5 meters) and dichotomously branched. In *O. palmatum* the petiole bears at its tip several palmate lobes of the lamina. Below the lamina, there are two rows of fertile spikes. The lamina has a reticulate venation, but it is not closed. Bhambie and Prakash (1982) have reported that the reticulate venation of *Ophioglossum* is in contrast with the open dichotomous venation seen in *Botrychium* and *Helminthia achys*. The veinlets end blindly in the mesophyll (Fig.7.1). This is very characteristic of *Ophioglossum*. There is no distinct midrib. At the base of the petiole are found two stipules (forming a sheath) enclosing the young leaf of the next season.

The leaves of *Ophioglossum* do not exhibit circinate vernation that is so typical to ferns. The rhizome is anchored to the soil with the help of numerous adventitious roots that are produced from its (rhizome) under the surface. There are no root hairs. The roots may be unbranched (*Euophioglossum*), infrequently branched (*Cheiroglossa*), or frequently branched (*Ophioderma*). Usually, only one root is formed at the base of the leaf of the current season. Unlike leaves, the roots are perennial. The roots have a mycorrhizal association which compensates for the absence of root hairs.

Internal Structure

1. Rhizome: A transverse section of the rhizome shows an epidermis, cortex and the central stele. The outline of the section is irregular and discontinuous due to the presence of roots and leaf bases. The epidermis is single layered. The cortex is wholly parenchymatous. The cells are loosely arranged with many intercellular spaces. In older rhizomes, epidermis is replaced by a periderm layer, but there is no cork cambium. According to Campbell (1939), the periderm belongs to the old leaf bases. The presence of endodermis is doubtful in older rhizomes. In younger rhizomes an endodermis has

been identified (*O. pendulum*). According to Lang (1922), there may be an internal as well as an external endodermis. Pericycle may be present.

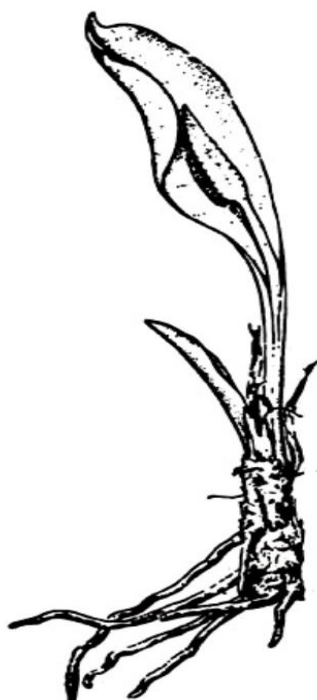


Fig.7.2. *Ophioglossum*: T.S. of Rhizome (ground plan).

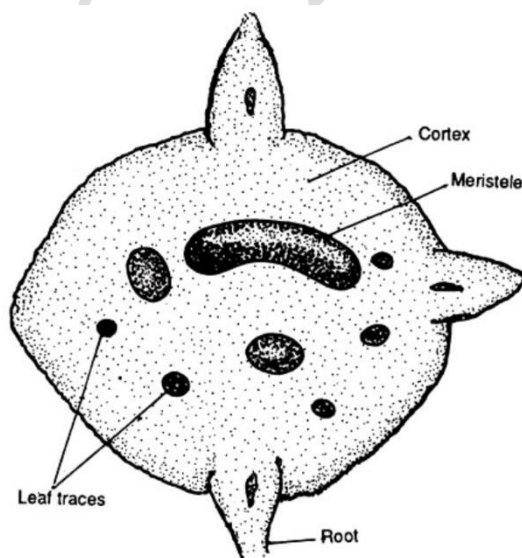


Fig. 7.1. *Ophioglossum*: Plant Body of *O. lusitanicum*.

The stelar organization is variable. In *O. reticulatum* the basal region of the rhizome is protostelic which becomes solenostelic as it travels up. In most of the species the stele is an ectophloic solenostele. Occasionally leaf gaps may overlap resulting in a dictyostelic

condition (Fig. 7.2). Sometimes in the same rhizome at different regions, the stele ranges from protosteles to a dictyostele.

Each meristele is semi-lunar in shape with the concave side directed towards the center. Xylem is endarch. In *O. palmatum* the protoxylem elements are not well defined. Phloem is collaterally arranged about xylem. Generally, phloem consists of four to five layers of cells. But in *O. pendulum* phloem is single-layered and is separated from xylem by a layer of parenchyma cells.

Boodle (1899) recorded a small amount of secondary thickening in the rhizome of *O. vulgatum*. The pith is composed of thin-walled parenchyma. Mixed pith has been reported in *O. pendulum* and *O. aitchisoni* where tracheids are intermixed with parenchyma cells. Anatomical studies in the family ophioglossaceae by Prakash and Bhambie (1980) have shown that true vessels are absent in *Ophioglossum*.

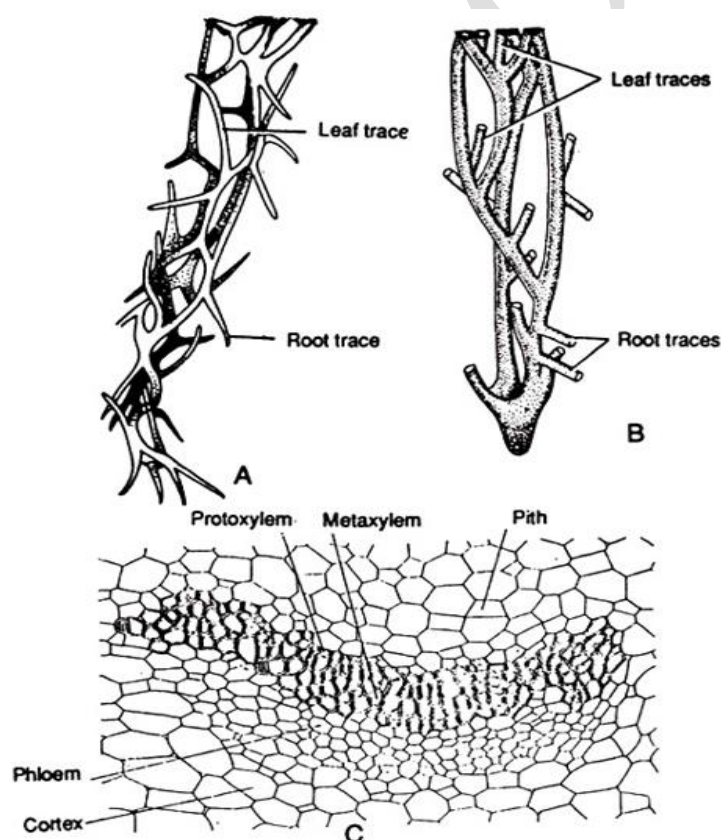


Fig. 7.3. Ophioglossum: Details of Vasculature of Rhizome A. Vascular Skeleton of *O. lusitanicum*, B. Vascular Skeleton of *O. vulgatum*, C. Transverse Section of Meristele.

2. Leaf: From the rhizome a single leaf trace is given off; but at the base of the petiole, it divides into two strands and enters the leaf. But in *O. palmatum* and several other species, each leaf gap is associated with two leaf traces. The leaf traces, further up in the petiole divide into several vascular bundles and are arranged in a 'C' shaped outline with the opening directed towards the adaxial surface.

The bundles are collateral with endarch xylem. The phloem is on the outer surface of the xylem and is separated from the latter by a layer of parenchyma. There is no bundle sheath. Surrounding the vascular bundles is a ground tissue composed of parenchyma, a few outer layers of which have chloroplasts. The ground tissue is protected by a single-layered thick-walled epidermis. The lamina on either side is bounded by a single-layered epidermis. Leaves are amphistomatic, but the number of stomata in the upper and lower epidermis varies. In *O. vulgatum* they are equal in number on both surfaces; in others (*O. reticulatum*) stomata are more in number towards the lower epidermis.

Stomatal studies in the leaves of *Ophioglossum reticulatum* have shown that they are amphistomatic with anomocytic and diacytic types of stomata. The mesophyll is undifferentiated (Fig. 7.4) and is composed of thin-walled isodiametric chlorophyllous cells. The mesophyll consists of a few veins (bundles) whose structure is like those of the petiole.

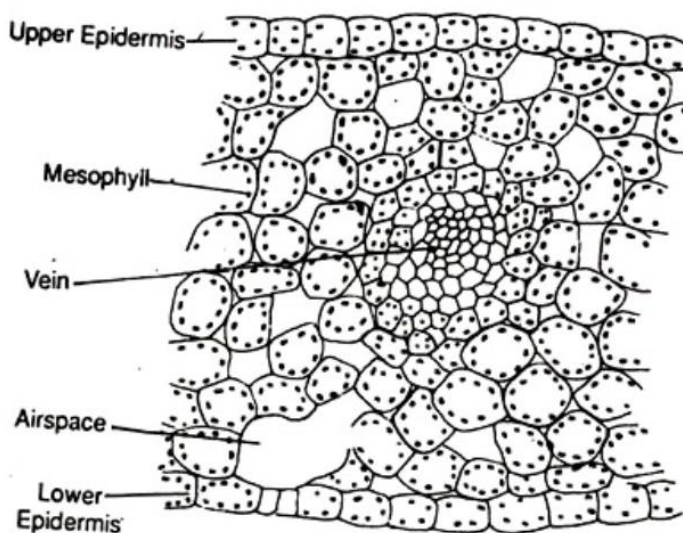


Fig. 7.4. Ophioglossum; Venation and Anatomy of Leaf A. Lamina showing Venation, B. T.S. of Leaf.

3. Root: A root in a transection shows a single-layered epidermis, a massive parenchymatous cortex, and a central stele (Fig. 7.5). The epidermis is short-lived and is replaced by exodermis (*O.fibrosum*), or it may persist with suberization. The cortex though wholly parenchymatous is divisible into two zones.

In the outer zone, the cells are angular and closely packed without any intercellular spaces. It is in this zone that the fungal hyphae are present. The hyphae are aseptate. The inner zone of the cortex has loosely arranged parenchyma cells with no mycorrhizal fungus.

The stele of the root may be mono, di- tri tetra, or even pentarch. But the first two conditions are more frequent. In diarch roots (Fig. 7.5), the xylem is plate-like with a protoxylem point at each end of the plate. In triarch stele, the xylem groups are separated by parenchyma.

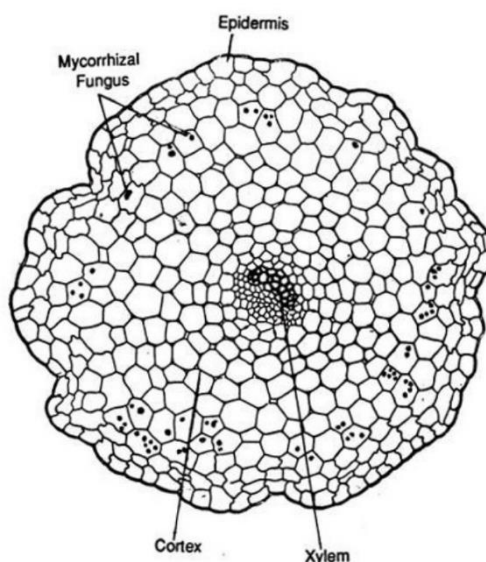


Fig. 7.5. Ophioglossum: T.S. of Rhizome of *O. lusitanicum*.

Reproduction in Ophioglossum: The majority of Ophioglossum species reproduce using spores. Spores are of same size and shape i.e., Ophioglossum is a homosporous pteridophyte. However, some species e.g., *O. pendulum*, *O. vulgatum*, *O. reticulatum*, *O. nudicaule* and *O. aitchisonii* reproduce vegetatively through adventitious buds formed on roots.

Spore-Producing Organ: The spores are present in sporangia. The sporangia are produced in two rows on a fertile segment that arises at the junction of the petiole and the sterile lamina (Fig. 7.6A). This sporangia-bearing fertile segment is known as a sporangiferous spike. Generally, a single spike is associated with a leaf but in *O. palmatum* several spikes are present on a single leaf (Fig. 7.6C).

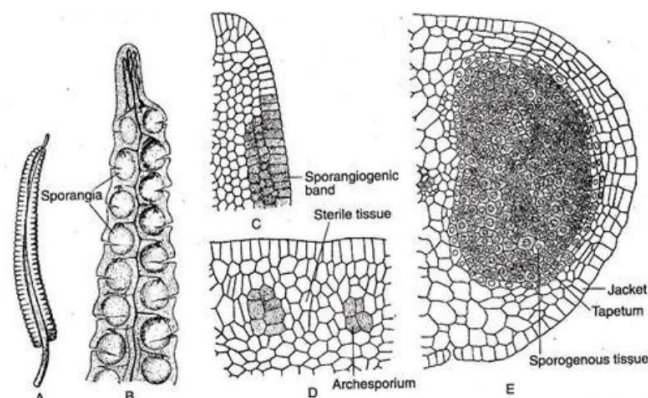


Fig- 7.6: Ophioglossum: A. Sporangiferous spike, B. A mature spike showing dehiscence, C-D. The stages in the development of sporangium, E. A nearly mature sporangium.

Structure of the Sporangiferous Spike: The spike is a simple, somewhat cylindrical, and stalked structure (Fig. 7.6A). It bears two rows of embedded sporangia on either side, except at the apical region. The length of the spike and the number of sporangia in each spike varies according to the species. Several vascular strands run longitudinally along the axis and from these strands, many lateral branches develop which lead to sporangia (Fig. 7.6B).

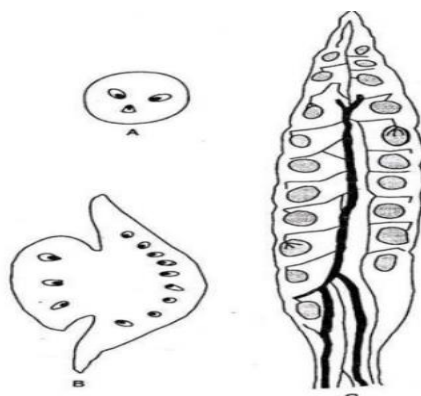


Fig. 7.7: Ophioglossum vulgatum: A. T.S. of the base of aerial complex stalk showing 3 vascular bundles, B. T.S. at the junction of fertile and sterile lobes showing 3+ 9 bundles, C.

The fertile spike has been considered as an aerial complex by many scientists. Convincing evidence for this interpretation has been provided by the vascular traces. According to U. Sen (1968), the single leaf trace at the base of each aerial complex splits into three before entering the base of the stalk (Fig. 7.7A).

Then the three traces again split up into 12 traces at levels where the stalk divides into fertile and sterile lobes. Out of the 12 traces, 9 enter the sterile lobe (lamina) and do not anastomose, 'whereas the rest 3 pass on to the base of the fertile spike where they divide and anastomose in the axial region (Fig. 7.7B).

From this axial system, small traces extend horizontally into the sterile tissue in between the sporangia. Then the tips of each of these traces bend sharply towards the respective sporangia and frequently branch into two or more strands (Fig. 7.7C). Only one of these ultimate strands enters the sporangial wall, the others end blindly. Thus, the aerial complex is represented by a condensed dichotomous branch system where fertile spike and lamina are the two limbs of the dichotomy.

Structure of the Sporangium: The development of a sporangium in *Ophioglossum* is of the eusporangiate type. At the very young stage, the primordium of spike differentiates on the lateral side into two vertical strips of cells in the epidermal layer.

Each strip is known as a sporangiogenic band (Fig. 7.6C); the hypodermal cells of each band now differentiate into alternate groups of fertile (archesporial) and sterile cells (Fig. 7.6D). The archesporial cells mature into sporogenous cells, thus representing a future sporangium. Each mature sporangium is spherical or oval and remains embedded in the tissue of the fertile spike. L.S. of sporangiferous spike showing courses of vascular bundles (after U. Sen, 1968). The size ranges between 0.5 to 3 mm in diameter. It remains surrounded by a multi-layered wall of which the innermost wall layer functions as a tapetum (Fig. 7.6E). The sporangial cavity is filled with many spore mother cells. Usually, all the spore mother cells are functional and eventually develop into spore tetrads. The number of spores per sporangium varies from 1500 to 15,000.

Dehiscence of the Sporangium: The sporangia have no specialized dehiscence mechanism. The annulus, a characteristic structure of other fern sporangia is absent in

Ophioglossum. The dehiscence takes place using a transverse slit or simply by drying out and shrinking the sterile tissue within the spike.

Gametophyte Generation

Spores: Ophioglossum is homosporous and the haploid spores are the mother cells of the gametophytic generation. The spores are small, and round, with an outer sculptured exine and inner thin intine which germinate shortly after dispersal.

Development of Gametophyte: The spores, on germination, produce a subterranean gametophyte (Fig. 7.8A, B). Ophioglossales is the only order under ferns showing subterranean gametophytes. The spore absorbs water and enlarges considerably. The first division is transverse to form a lower and an upper cell. The lower cell divides vertically, resulting in a 3-celled stage. Further development only proceeds if it gets infected with mycorrhizal fungi.

The gametophytes are non-green and contain an endophytic fungus that enters gametophytic cells soon after germination and is necessary for sustained growth (Fig. 7.8A, B). The mature gametophytes may be irregularly cylindrical to conical and unbranched (e.g., *O. nudicaule*, *O. vulgatum*) or branched (e.g., *O. palmatum*, *O. pendulum*).

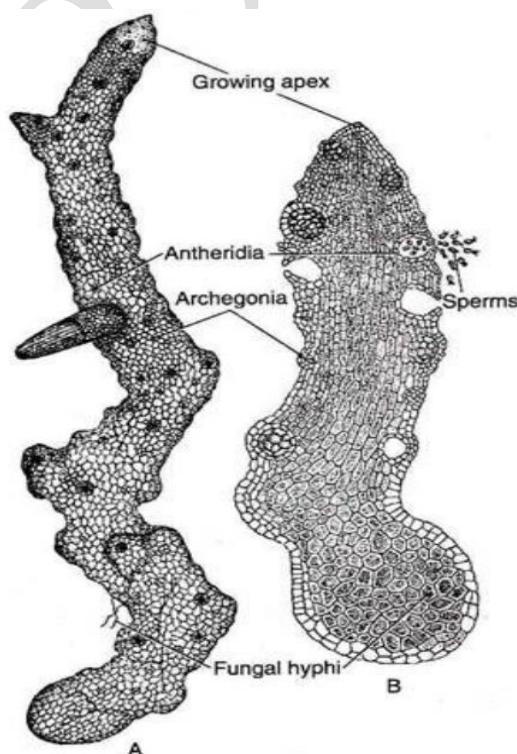


Fig. 7.8: *Ophioglossum vulgatum*: A. Gametophyte, B. L.S. of gametophyte.

There is considerable size variation in the gametophytes. The gametophyte of *O. crotalophoroides* is globose or approximately hemispherical. The size ranges from 2 mm to 6 cm in length and less than 1 mm to 3 mm in diameter.

Sex Organs of Ophioglossum: The gametophytic prothallus of *Ophioglossum* is homothallic (monoecious) i.e., the prothallus bears both male (antheridia) and female (archegonia) sex organs. The antheridia and archegonia in most species are scattered and intermingled over the entire surface of the gametophyte.

i. Antheridia: The antheridia are embedded in the tissue of the prothallus. The antheridium develops from a single superficial cell of the derivatives of apical meristem called antheridial initial (Fig. 7.9A-F). The antheridial initial divides periclinal (transverse) to form an outer jacket initial and an inner primary androgenic cell. The derivatives of the jacket initial form a jacket with a triangular opercular cell which, on disintegration, forms an opening. The primary androgenic cell (spermatogenous initial) divides repeatedly to form androcyte mother cells. An androcyte mother cell divides to form two androcytes, each of which ultimately metamorphoses into an antherozoid or sperm. Each antherozoid has a large basal vesicle and the terminal part bears numerous flagella (Fig. 7.9G).

ii. Archegonia: The archegonium is also initiated in the derivatives of apical meristem (Fig. 7.10A-E). One of the superficial cells functions as an archegonial initial which, on periclinal division, forms an outer primary cover cell and an inner cell. The primary cover cell, by two vertical divisions at right angles to each other, forms a quadrant of neck initials.

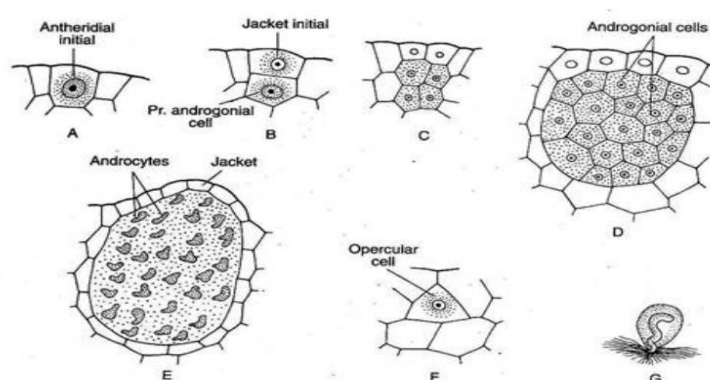


Fig. 7.9: *Ophioglossum vulgatum*: A-F. The stages in the development of antheridium, G. An antherozoid.

Further anticlinal divisions of neck initials form the neck of the archegonium. The neck barely protrudes out of the thallus. The inner cell, on the other hand, divides periclinally (transverse) to form a basal cell and a central cell. The central cell divides transversely into a primary canal cell and a primary venter cell. The primary canal cell directly functions as neck canal cell. The primary venter cell, however, divides transversely and forms a ventral canal cell and a large egg.

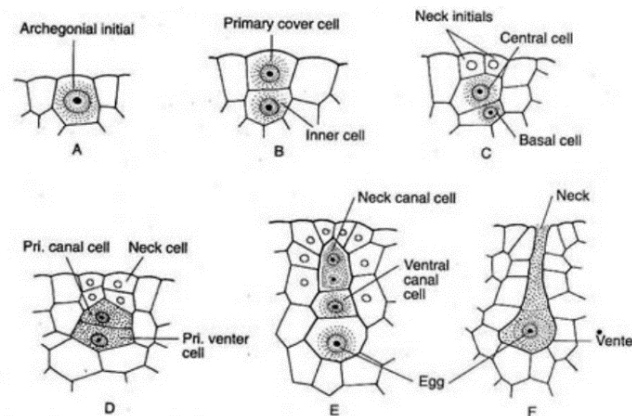


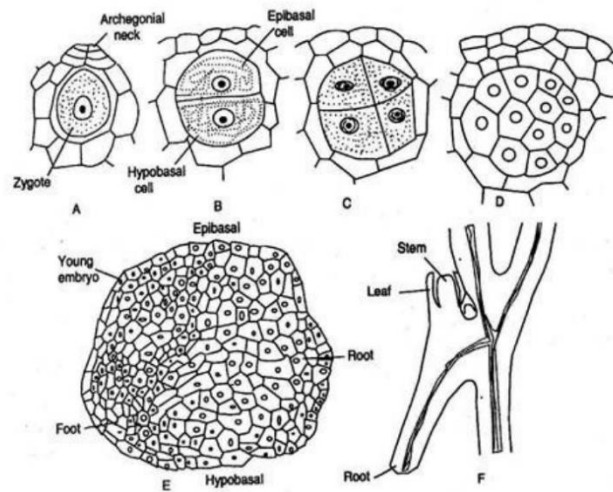
Fig: 7.10: *Ophioglossum vulgatum*: A-D. The stages in the development of archegonium, E. Mature archegonia.

At maturity, the ventral canal cell, the neck canal cell, and the neck cells at the top are well-disorganized; they thus form an open passage for the antherozoids to come towards the egg (Fig. 7.10F).

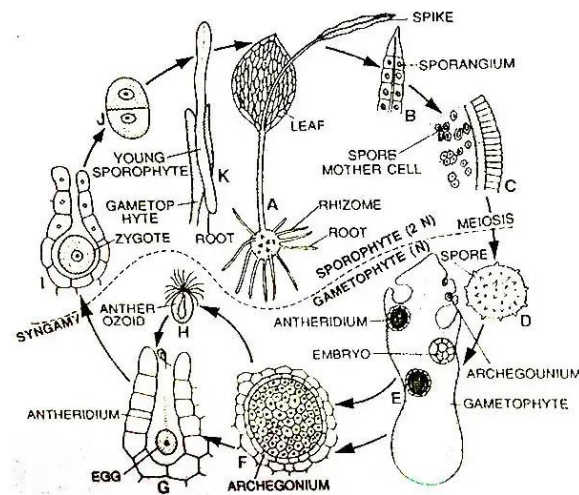
New Sporophyte: As usual, the zygote is the mother cell of the next sporophytic generation. The first division of the zygote is transverse, i.e., perpendicular to the long axis of the archegonium, giving rise to an epibasal and a hypobasal cell (Fig. 7.10 A, B). The embryo is exoscopic in polarity, i.e., the apical cell projects towards the neck of the archegonium. Both cells are embryonic. A cell division (vertical) of the apical and the basal cells results in the formation of four cells in the quadrant stage of embryogeny (Fig. 7.11C). Subsequent cell divisions are irregular and indefinite. There is no suspensor in the embryo, and it takes a long time for further differentiation of organs. The root is the first and the prominent organ which arises near the middle of the embryo (from derivatives of epibasai cell) and enlarges rapidly. The first leaf and future shoot apex derive from the epibasai region of the embryo, and the foot derives from the hypobasal region (Fig. 7.10 D-F).

Chromosome Number of Ophioglossum

The chromosome number of Ophioglossum is generally high, although there is no uniformity in the basic number. *O. pusitanicum* has $n = 125-130$, while in *O. vulgatum* $n = 250-260$. The highest chromosome number has been recorded in *O. reticulatum*, where $n = 631 + 10$ fragments. Life cycle of Ophioglossum Fig 7.12.



7.11: Ophioglossum: A-E. The stages in the development of the embryo, F. A young sporophyte.



7.12: Life cycle of Ophioglossum

Psilotum

Division: Polypodiophyta

Class: Polypodiopsida

Order: Psilotales

Family: Psilotaceae

Genus: Psilotum

Distribution of Psilotum

Though several species have been reported in *Psilotum*, all of them usually fall into two well-defined species, viz., *P. nudum* (*P. triquertum*) and *P. flaccidum* (*P. complanatum*). The earlier reports of the existence of several species is probably due to the polymorphic nature of the sporophyte. As has already been pointed out, *Psilotum* is distributed both in the tropics and the subtropics. Of the two species, *P. nudum* seems to enjoy a wider distribution being found in all the warmer regions of the world, including India.

In India, it is found in Bengal, Assam, and the hilly districts of Madhya Pradesh, Himachal Pradesh, and Karnataka. *P. nudum* is also cultivated as a curiosity in botanical gardens. *P. flaccidum* is somewhat uncommon and is reported from tropical islands like Jamaica, Java, etc., besides the Malayan peninsula and Mexico. In their habitat, they are either terrestrial or epiphytic. While *P. nudum* is predominantly terrestrial, *P. flaccidum* is mainly epiphytic growing in the humus packets of trees.



Fig. 8.1. Psilotum: Habit of *Psilotum nudum* (A) and a Part of the Shoot Bearing Synangia (B): Habit of *Psilotum flaccidum* (C) and a part of the Shoot bearing Synangia (D).

Sporophyte of Psilotum: Morphology: The plant body of *Psilotum* is differentiated into two parts viz., a horizontal underground rhizome and an erect aerial shoot. The rhizome is brownish in color and dichotomously branched. There are no roots. The rhizome is studded with several long, fine, thread like rhizoids. According to Bierhorst (1954 or 1958), the branching of the rhizome is irregular. Some of the branches of the rhizome grow up and constitute the erect (*P. nudum*) or pendulous (*P. flaccidum*) shoot system. The aerial shoots are 20-75 cm long and are usually ribbed and multi-angular. The ultimate branches however are triquertous. While the above description holds good for *P. nudum*, in *P. flaccidum* the base of the aerial shoot is triquertous while the tips are flattened. Unlike the rhizome, the aerial shoots are regularly dichotomously branched and are deep green indicating their photosynthetic activity. Here and there on the aerial shoot are found several scales or appendages which are often called leaves. These are of two types viz., sterile and fertile.

The sterile ones are found all along the length of the aerial shoot while the fertile ones are generally restricted to the upper portions and bear in their axils a trilobed spore-bearing structure which is often called a Synangium. The leaves whether fertile or sterile are devoid of any vasculature and could be regarded as only emergences.

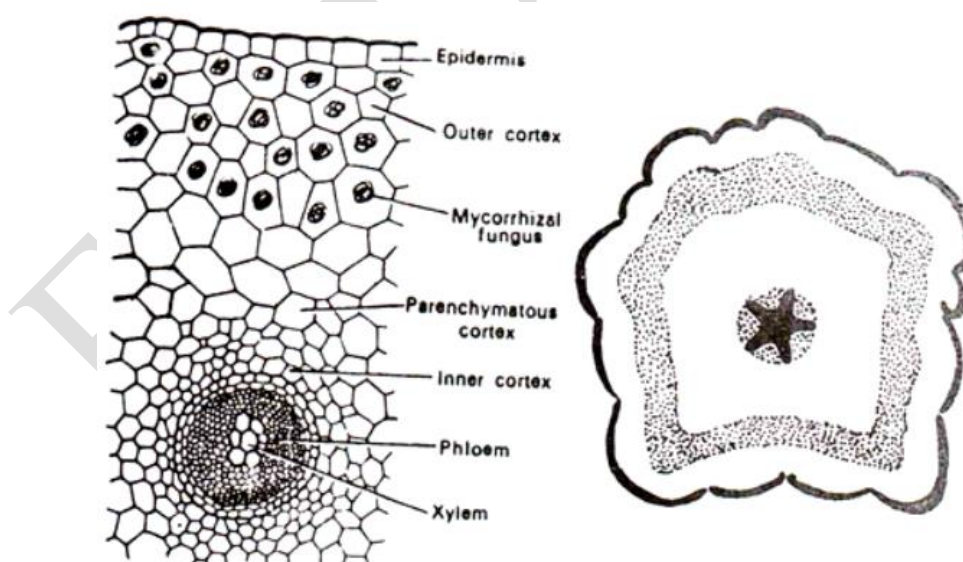


Fig 8.2. *Psilotum*: T.S. of Rhizome. A. Sector Enlarged, B. Ground Plan.

Internal Structure

1. Aerial shoot: A transverse section of the stem shows three regions, viz., epidermis, cortex, and stele (Fig.8.3). Epidermis is single-layered and has closely packed cells. The

xylem is exarch with the protoxylem points located at the lips of the rays. The xylem consists of scalariform pitted or annular tracheids. Sometimes spiral tracheids are also found. Surrounding the xylem is the phloem. According to Parihar (1965), the nature of phloem is difficult to determine because the distribution of sieve areas in these cells is imperfectly known.

In the ultimate branches, the xylem may be smooth instead of the usual stellate nature.

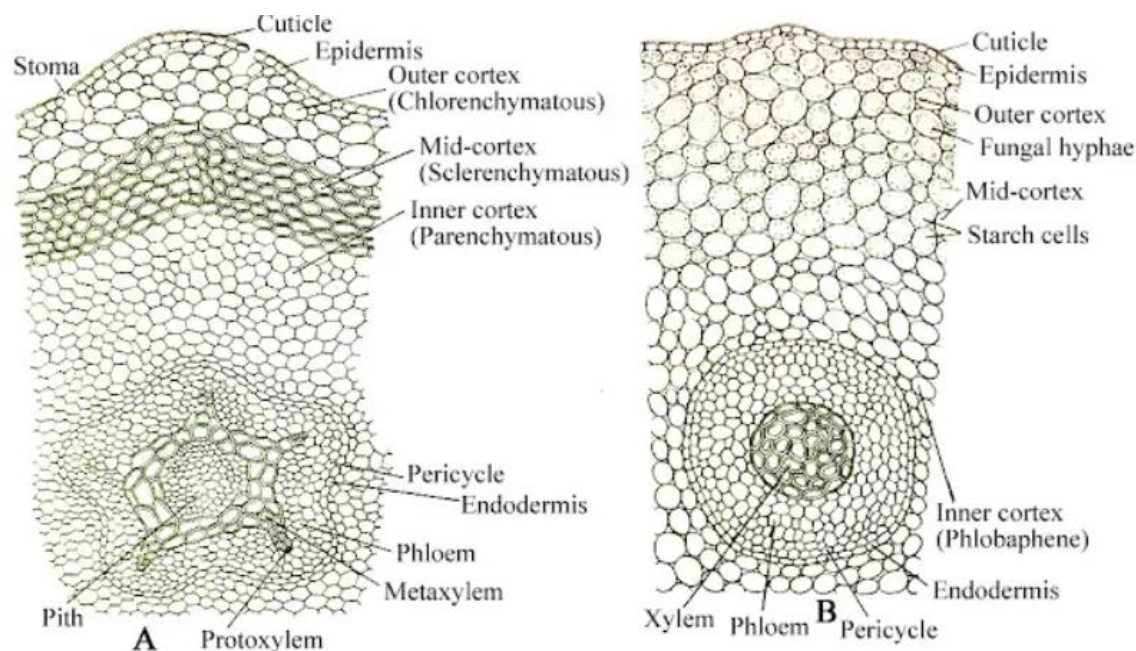


Fig. 8.3. Psilotum: T.S. of Aerial Shoot (a sector enlarged) and TS of Rhizome.

At the extreme base of the aerial stem between the xylem and phloem some, scattered xylem elements are found. Boodle (1904), Ford (1904) and others regard it as secondary xylem. According to Schoute (1938) however, these are primary xylem elements that differentiating a little later in ontogeny. His opinion is, based on the absence of a definite cambium.

2. Rhizome: This also shows an epidermis, a cortex, and a stele. The epidermis is ill-defined. The cortex is divided into three zones. The outer cortex is parenchymatous, and the cells have mycorrhizal fungus. The middle cortex has parenchyma cells rich in starch grains. The innermost region of the cortex also consists of parenchyma that is usually dark brown due to the deposition of a substance called phlobaphene. This is believed to be an oxidation product of tannins. The stele is protostelic and is surrounded by a typical endodermis which is followed by a layer of pericycle. The shape of the xylem varies

with the diameter of the axis. Usually, it is circular in outline. The xylem is exarch and is surrounded by phloem.

3. Leaf: Anatomically, the leaves show the epidermis and the mesophyll. The epidermal cells are cutinized. The mesophyll has chlorophyllous cells which may be loosely or closely packed. The stomata are absent in the epidermis as such the chlorophyllous cells have no means of gaseous exchange. There is no vascular supply to the leaf. But in *P. flaccidum* a leaf trace that starts from the stem terminates at the leaf base. The absence of stomata and the lack of vascular supply make the chlorophyllous cells of the leaf ineffective in photosynthesis.

Apical growth: A single wedge-shaped apical cell contributes to the growth of the stem.

Reproduction: The sporophyte reproduces by vegetative propagation as well as by spore production.

1. Vegetative Propagation: The sporophyte increases its number by the production of gemmae or brood bodies. These are formed on the rhizome and are usually restricted to the tips or the axils between the branches. Each gemma is an oval body, one cell in thickness having an apical cell with two cutting faces. The cells are rich in reserve food especially starch. The gemmae detach from the plant body germinate and give rise to a new plant of *Psilotum*.

2. Spore Production: The sporophyte reproduces asexually by the formation of spores. Spores are produced in special trilobed structures called synangia which are generally restricted to the upper portions of the aerial shoots where they are borne in the axils of minute bifid scales. Rouffa (1971) has reported that appendages are absent in the shoots of *Psilotum* plants growing in Japan. Here synangia are borne at the tips of branches.

Development of the Synangium: Our knowledge of the development of synangium is mainly due to the work of Bower (1935). The development is apparently of the eusporangiate type, even though each sporogenous mass appears to originate from a single cell. According to Bower (1935), the synangium arises as an outgrowth on the adaxial face of the appendage.

According to Bierhorst (1934) however, the synangium arises earlier than the appendage. In many cases the first division of the synangial initial produces an outer jacket initial

and an inner archesporial cell (Fig.8.4). The jacket initial undergoes several anticlinal and periclinal divisions to produce the multilayered wall of the synangium.

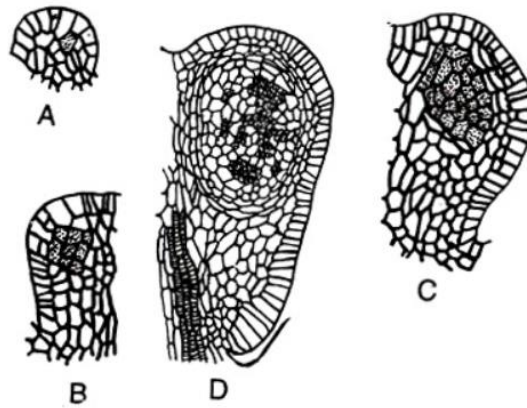


Fig. 8.4. Psilotum, Stages in the Development of Sporangium.

Meanwhile, the archesporial cell divides into all the planes to form many sporogenous cells (Fig.8.5). There is no well-defined tapetum. In the sporogenous tissue, some cells here and there distinguish themselves by their dense granular cytoplasm from the remainder. These are the spore mother cells. The rest of the sporogenous cells gradually degenerate.

The spore mother cells undergo reduction division to produce tetrads of haploid spores.

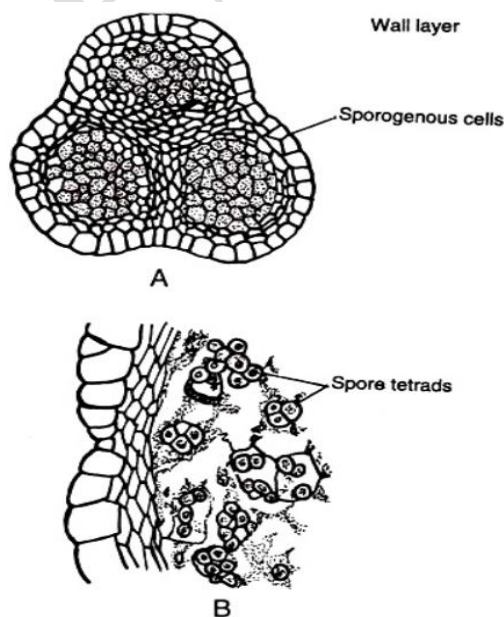


Fig. 8.5. Psilotum A. T.S. of Young Synangium, B. Sectional View (a portion) of Synangium with Spore Tetrads.

Structure of the Mature Synangium: The wall of the trilobed synangium is made up of 4-5 layers of cells. The outermost layer of the wall is prismatic. Within the synangium, there are three chambers of spore cavities containing spores. All the spores are of the same type. (Fig. 8.6).

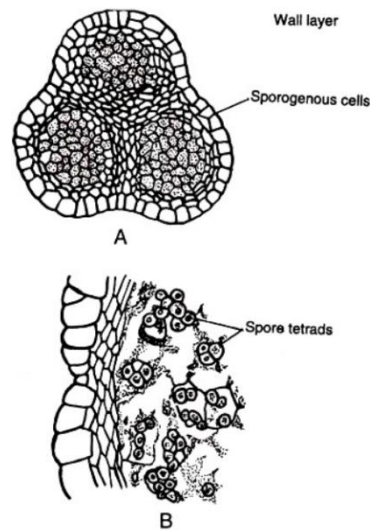


Fig. 8.6. Psilotum, T.S., of Mature Synangium with Spores.

Dehiscence of the Synangium: When the spore mother cells are undergoing reduction division, some of the wall cells thicken except in a small vertical row marking the future line of dehiscence. The synangium splits open along this line, liberating the spores.

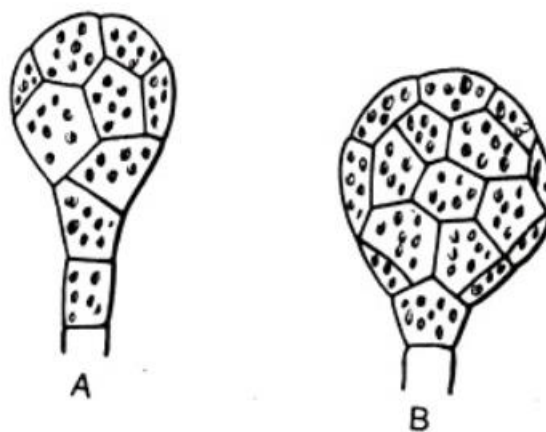


Fig. 8.7. Psilotum: Sporophytic Gemmae (Note the starch grains in cells).

Structure of the spore: Spores vary in shape from bilateral to tetrahedral type. Their average size is 0.065 x 0.032 mm.

Gametophyte of Psilotum

Germination of the Spore and Development of Gametophyte: The spores were germinated, and the development of the gametophyte was studied for the first time in 1947 by Darnell-Smith. Germination starts after four months when the spores are placed on a suitable substratum. The first sign of germination is the splitting of the outer spore wall and the projection of a small tubular outgrowth.

Later a cross wall cuts off the outgrowth from the remainder of the spore. In this way two cells are formed. Of the two cells, the upper by further divisions establishes an apical cell which produces a mass of tissue. Early in the development, the gametophyte gets infected by the fungus.

Structure of the Mature Gametophyte: The gametophyte is partly or totally subterranean. It is usually cylindrical in shape with dichotomous branches. The branching however need not be always dichotomous. In size, the gametophyte ranges from 0.5 to 2 mm. The color of the gametophyte is usually dark brown. This is due to the presence of endophytic fungus. The gametophyte is wholly parenchymatous with strongly cutinized cell walls. The outermost layer of the cells gives rise to several rhizoids. In the hypodermal region, the cells have the endophytic fungus. According to Beirhorst (1953) the fungus is probably *Cladochytrium tmesepteridis*. The cells are achlorophyllous, and the nutrition of the gametophyte is saprophytic. (Fig. 8.7).

Internal Structure of the Gametophyte: A transverse section of the mature gametophyte shows that it is wholly parenchymatous. Some of the superficial cells give rise to rhizoids. The outer walls, radial walls, and even the inner corner of the walls of the peripheral cells are highly cutinised. Mycorrhizal association is found in some of the cells. The central region of the gametophyte also consists of parenchyma with no trace of any vasculature.

In some of the abnormal gametophytes of *P. nudum* found in the volcanic island of Ranjitoto near New Zealand, Holloway (1939) described certain unusual features. These gametophytes were much bigger than the normal ones and had a diameter of 1 mm. The interesting feature in these gametophytes was the presence of a central vascular strand. The vascular strand consisted of a few annular and scalariform or scalariform reticulate tracheids. The tracheids were surrounded by phloem. There was even a clearly

recognizable endodermis. In these prothalli there was a cortex of parenchyma cells between the vascular strand and the superficial layer.

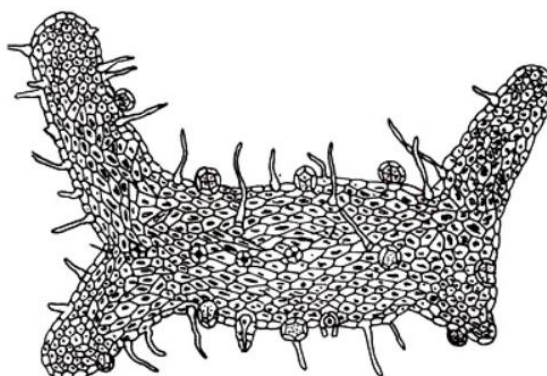


Fig. 8.8. Psilotum, Gametophyte of *P. nudum*.

Reproduction

The gametophyte reproduces by two methods

(1) Vegetative propagation and (2) Sexual reproduction.

(1) Vegetative Propagation: Holloway (1939) and Bierhorst (1953) have described the production of gemmae on the surface of the gametophyte. The gemmae arise as proliferations from a rhizoid-like structure and are like those produced on the rhizome. A mature gemmae has 8-12 cells., usually spheroidal or occasionally flattened and on germination gives rise to a new gametophyte. Holloway (1939) has also described the formation of special vegetative buds on the gametophyte. These function like gemmae but arise directly from the surface cells of the gametophyte.

(2) Sexual Reproduction: This is brought by the formation of antheridia (male) and archegonia (female). The gametophytes are monoecious.

Development and Structure of the Antheridium: The antheridium develops from a superficial cell called an antheridial initial. This undergoes a periclinal division to form two superposed cells (Fig.8.8a). Of the two cells the outer cell is called the jacket initial, and the inner cell is called the primary androgonial cell. The primary androgonial cell divides in all the planes to form many cells (Fig.8.8d). Meanwhile, the jacket initial divides anticlinally to form a jacket layer, one cell in thickness. The androgonial cells divide further to form the androcytes. These androcytes metamorphose themselves into spirally coiled multi-ciliate antherozoids. When the antheridium is reaching maturity, it bulges out from the surface of the gametophyte.

A mature antheridium is somewhat spherical in shape and projects out of the gametophyte as a hemispherical protruberance. The jacket is made up of about 12 cells and has a special cell called the opercular cell which degenerates at maturity allowing for the liberation of the antherozoids. Approximately about 250 antherozoids are found inside the antheridium.

Development and Structure of the Archegonium: The archegonia are also produced from the superficial cells of the gametophyte. A superficial cell that is destined to form an archegonium is called an archegonial initial. This undergoes periclinal division to form an outer primary cover cell and an inner central cell.

The primary cover divides twice vertically, where the second division is at right angles to the first one to form four quadratically arranged cells called the neck initials. A long sectional view at this stage, however, reveals two neck initials and a central cell (Fig. 8.10). The central cell subsequently extends in between the neck initials to form an elongated structure. The neck initials divide several times transversely to form an archegonial neck 4-7 cells in height.

As the archegonial neck is elongating, the central cell keeps pace with it by extending into the neck. After some time, the central cell divides transversely to form an upper primary neck canal and a lower primary venter cell (Fig.8.9g). The primary canal cell divides once to form two neck canal cells, whereas the primary venter cell divides once transversely to form an upper short-lived venter canal cell and a lower egg cell with a prominent nucleus.

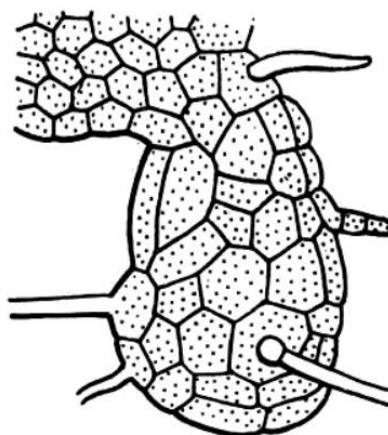


Fig. 8.10. Psilotum: Gametophytic

Gemma of *P. nudum*

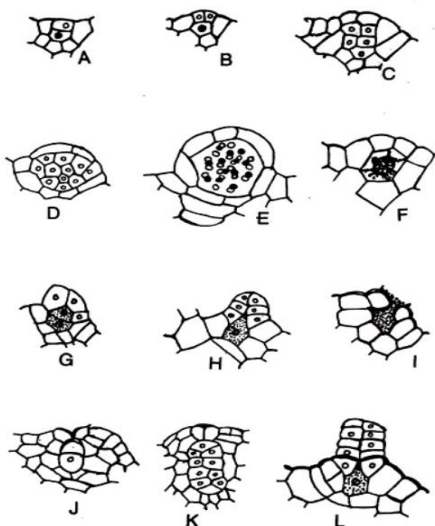
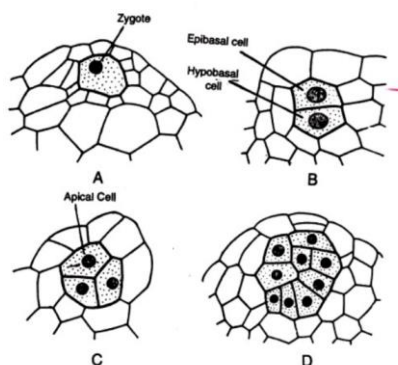


Fig. 8.9. Psilotum: Development of Sex Organs in the Gametophyte of *P. nudum*; A-E. Antheridium, F-J Archegonium, K-L. Archegonium and embryo, respectively

As the archegonium reaches maturity, the neck canal cells degenerate. In some cases, they degenerate as soon as they are formed. In a mature archegonium, some of the terminal tiers of the neck slough off (Fig.8. j), leaving only the basal one or two tiers. At this stage, except for egg, all other cells in the archegonium disintegrate.

Fertilization: The antherozoids come out of the antheridium through the passage formed by disintegration of the opercular cells. They swim in a thin film of moisture, approach the archegonium, enter it and fertilize the egg.



8.11. Psilotum: Stages in early Embryogeny of *P. nudum*.

Embryogeny: Soon after fertilization, the zygote enlarges in the cavity of the venter. The first division of the zygote is transverse, and it results in forming an upper epibasal

cell (cell nearer to the archegonial neck) and a lower hypobasal cell (cell away from the archegonial neck) (Fig.8.9 k). The hypobasal cell gives rise to the foot, and the epibasal cell gives rise to the shoot.

This type of embryogeny, where the shoot apex is pointed towards the archegonial neck is called exoscopic. There is no formation of roots or cotyledons. The hypobasal cell divides in all the planes to form a bulbous foot which gives rise to haustorial outgrowths into the gametophyte. Meanwhile, the divisions in the epibasal cell result in the formation of a three-sided apical cell. By the activity of this apical cell the shoot apex projects out of the gametophyte. At this stage, it gets infected with the mycorrhizal fungus. This assures independent nutrition to the young sporophyte. When the young sporophyte is about 8-10 mm long, it detaches from the gametophyte and leads an independent life. In the beginning it is subterranean, later some of the branches grow Apo geotropically and form aerial shoots.

Morphology of the Spore-Bearing Organs: The morphological nature of the trilobed spore-bearing organ has been a subject matter of debate for a long time.

Phylogeny of Psilotum: Psilotopsida represents perhaps the most primitive of the extant pteridophytes. Among the living pteridophytes, they possess the simplest plant body that could be imagined for a vascular plant. There is no trace of leaf or root. Photosynthesis is carried out chiefly by the main axis. Psilotaes show a close resemblance to the Psilophytales than to any other group of pteridophytes. This close relationship has been advocated by Kidston and Lang, Holloway, Bower, and others. Arber (1921) suggested that the group psilotaes might have originated from algae.

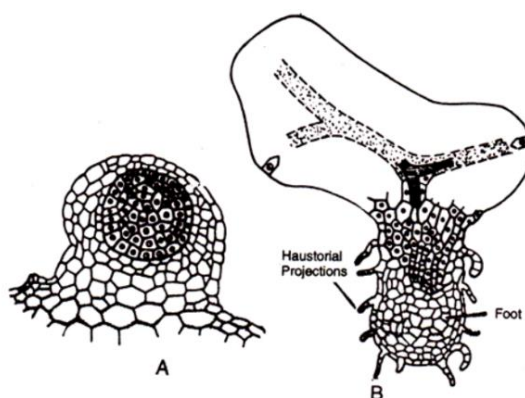


Fig. 8.12. Psilotum: Stages in Late Embryogeny of *P. nudum*.

Introduction to Telome Theory

It is now widely accepted (based on the overwhelming amount of evidence) that land-dwelling plants evolved from aquatic ancestors. All organisms known in the Precambrian, Cambrian, and Ordovician periods of the Paleozoic Era lived in aquatic environments. The evolution-ary conquest of land probably occurred some-times between the late Cambrian and early Silurian. The concrete evidence of early vascular land plants came from the Silurian in the form of the fossil plant *Cooksonia* of the *Rhynia* group of plants.

Several theories on land-plant evolu-tion exist of which the Telome theory of Walter Zimmermann (1930, 1952) is the most compre-hensive. This theory is based on the fossil record and synthesizes the major steps in the evolution of vascular plants. According to this theory, all vas-cular plants evolved either directly or indirectly from a simple leafless *Rhynia*-type ancestral form made up of sterile and fertile axes (the telomes). Evolutionary modification of its parts produces more advanced vascular plants with roots, stems, leaves, more complex vascular systems, and protected sporangia.

Meaning of Telome Theory: A telomere is defined as “the single-nerved ultimate terminal portion (at base or apex) of a dichotomizing axis” i.e., it is the point of the most distal dichotomy to the tip of a branch. The connecting axes between dichotomies are called mesomes (Fig. 9.1). Functionally, telomes are of two types viz., fertile telome and sterile telome.

If the ultimate branch is terminated by a sporangium, then it is a fertile telome (Fig. 9.1), whereas those terminal branches without sporangia are called sterile (vegetative) telomes (Fig. 9.1). Several telomes, either fertile or ste-rile, becomes grouped by connecting mesomes to form a more complex structure, called syntelome or telome truss (Fig. 9.1).

A syndrome is designated as a phylloid truss if com-posed of only sterile or vegetative telomeres, or as a fertile truss when composed of only fertile telomeres, or a mixed welcome truss when com-posed of both sterile and fertile telomeres Telcome and the evolution of the independent sporophyte among pteridophytes.

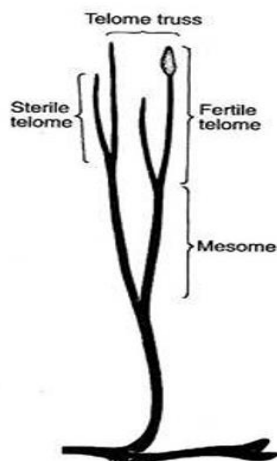


Fig 9.1A primitive Rhynia plant showing telome and mesome.

Processes of Telome Theory: According to Zimmermann, these telomes or telome trusses of primitive Rhynia type of vascular plants have been subjected to certain evolutionary processes in varying degrees among the various taxonomic groups.

These evolutionary processes are

- (i) Overtopping
- (ii) Reduction,
- (iii) Plantation,
- (iv) Syngeneses or webbing, and
- (v) Curvation.

(a) Overtopping: In this process, one of the two dichotomising branches of the primitive axis produced by the apical meristem outgrows or overgrows the other. The larger axis thus produced becomes the stem, while the shorter or overtopped branches represent the beginnings of lateral branches or leaves (Fig. 9.2-C). Now, the earlier dichotomy will be transformed into a pseudomonopodial branch.

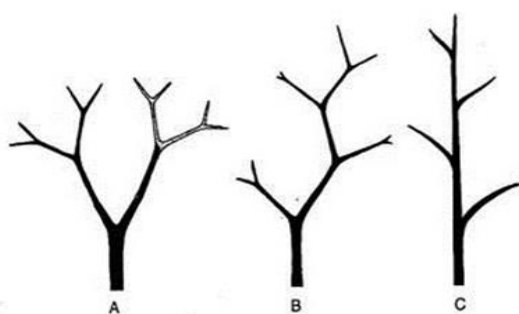


Fig. 9.2: Telome concept: A-C. Evolutionary process of overtopping and reduction.

(b) Reduction: In this process, the activity of the terminal meristem of each telome of the truss becomes suppressed, resulting in much shorter branches by decreasing the length of telomes and mesomes (Fig. 9.2B, C). This process is responsible for the formation of microphyllous leaves of the Lycopsidea and Sphenopsida as well as the needle-like leaves of conifers.

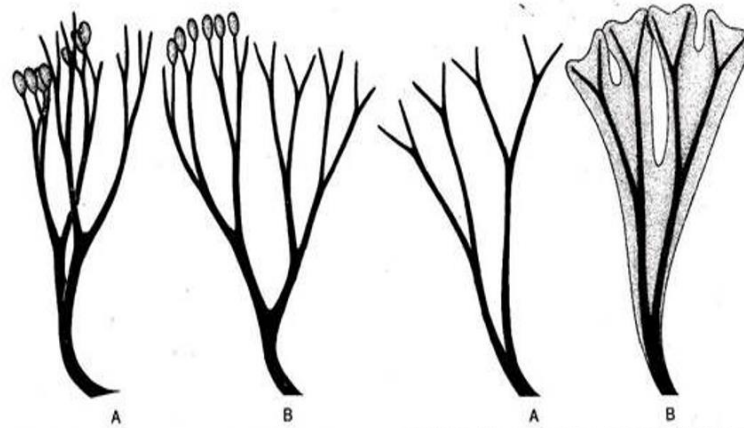


Fig. 9.3

Fig. 9.4

Fig. 9.3: Telome concept: A-B. Evolutionary process of plantation.

Fig. 9.4: Telome concept: A-B. Evolutionary process of webbing.

c) Plantation: The process of plantation caused the telomes and mesomes of the truss to shift from a three-dimensional pattern (cruciate dichotomy) to a single plane (fan-shaped dichotomy) (Fig. 9.3A, B). The process of infilling with photosynthetic and other tissues between the planted branches is called webbing, which has led to the evolution of a flattened leaf-like structure with a dichotomously veined lamina.

(d) Syngensis: This is an evolutionary process where a tangential fusion of mesomes and telomes takes place (Fig. 9.4 B). The lateral fusion of sterile vegetative telomes and mesomes resulted in complex anastomosing vascular systems in the stem (e.g., polystelic condition in *Selaginella*). The fusion of fertile trusses with their terminal sporangia resulted in the formation of synangia of *Psilotum*. The closed or reticulate venation pattern of some ferns, gymnosperm, and many flowering plants is the result of syngensis of the dichotomizing veins of the primitive leaf.

(e) Curvation: This evolutionary process is caused due to the unequal growth of the tissues on two opposite flanks of the telome. It has two sub-processes.

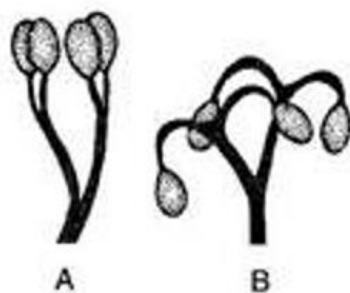


Fig. 9.5: Telome concept: A-B. Evolutionary process of recurvation.

(i) Recurvation: In this sub-process, the telome bends inward toward an axis (Fig. 9.3 A, B). The inward-projecting sporangia on a sporangiophore of *Equisetum* (Sphenopsida) are the result of this sub-process.

(ii) Incurvation: In this sub-process, the fertile telome bends downward, resulting in the downward shifting of the sporangia from terminal to the ventral surface of the leaf. This sub-process is responsible for the formation of the ventral position of the sporangia in the fern (Pteropsida) leaf.

Concept of Telome Theory: The telome concept has been used in understanding the origin and evolution of the following major groups of plants.

1. Psilopsida: The telome theory can be applied to interpret the evolution of a synangium of *Psilotum*. The overtopping, reduction, and syn-gensis have combined to produce a synangium of *Psilotum* (Fig. 9.6 A-D).

Initially, the over-topping occurred in the aerial branch of the *Rhynia* type plant to form a pseudomonopodial branching system with laterals having 3-dimensional dichotomously branched fertile and sterile telomere trusses.

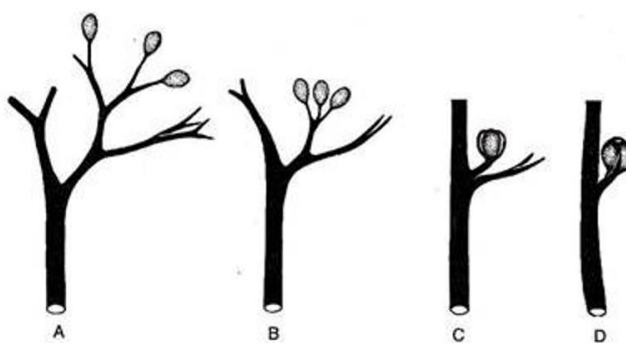


Fig. 9.6: Telome concept: A-D. Evolutionary process of overtopping, reduction, and syngenesis to depict the origin of synangium in *Psilotum*.

Then, due to the continuous reduction in both the telomere trusses, the sporangia were placed in a condensed cluster and became proximal to the main axis. Then the further reduction had occurred in the fertile telome which allowed sporangia to come in close contact with each other and, again, allowed syngensis to occur resulting in the formation of a synangium.

The bifid appendage which subtends a synangium in *Psilotum* is a product of the reduction of vegetative telome truss associated with fertile telomes.

2. Pteropsida: A megaphyllous leaf of Pteropsida originates following the three steps overtopping, planation and webbing (Fig. 9.6 A-D). By overtopping, the original dichotomous branching system changed to a pseudomonopodial branch with a main stem and lateral branches.

Now, the lateral telomes and mesomes of the truss, which were originally 3-dimensional (cruciate) type, became planted (one-dimensional). The planted telomes which have come closer became a flattened leaf-like structure with several tree-ending veins by webbing through the infilling with photosynthetic and other tissues between the planted telomes and mesomes. Further, a reticulate venation pattern was obtained in some Pteropsida due to the syngensis of the dichotomising veins.

4. Sphenopsida: The chief trends in the origin of sporangiophore in Sphenopsida were recurvation and syngensis resulting in a pellate structure with reflexed sporangia (Fig. 9.7 A-C). Here the fertile telome truss followed recurvation which has been evidenced in many fossil members of Sphenopsida like *Hyeria*, *Calamophyton*, etc.

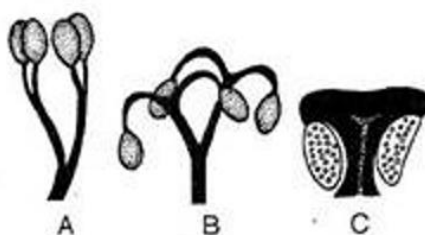


Fig 9.7: Telome concept: Stages in the evolution of the sporangiophore in Sphenopsida from the primitive dichotomous fertile axis (A) following recurvation (B) and syngensis (C)

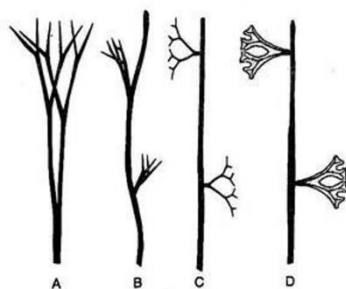


Fig. 9.8: Telome concept: Stages in the evolution of the megaphyll of Pteropsida from the primitive dichotomous axis (A) following overtopping (B), planation of axis (C) and syngensis (D).

Subsequently, a pellate sporangiospore with reflexed sporangia had evolved due to syngensis. The nature of the sporangiophore of *Calamites* and *Equisetum* provides examples of such process. However, the leaf of sphenopsida had evolved following planation and reduction.

5. **Lycopsida:** The origin of microphyllous leaf of Lycopsida can also be demonstrated in the light of telome concept following overtopping and reduction (Fig. 7.142A-C). Here the lateral branch of pseudomonopodial branch system followed successive reduction to form a linear, unbranched microphyll.



Fig. 9.9: Telome concept: Stages in the origin of micro-phyll following overtopping and reduction. A. Dichotomising lateral branch, B. Bifurcated microphyll of Protolopodendroides, C. Microphyll of Lycopsids, D. Asteroxylon enation.

Thus, the pentafid (*Leclercquia*), trifid (*Colpodoxylon*) and bifid (*Protolopodendron*) leaves and sporophylls are the intermediate forms. However, the stages of successive reduction of leaves do not coincide with the ages of the fossil plants. Say, for example, the microphylls of Upper Devonian lycopods are reported later despite their primitiveness than the much-reduced enation (advanced) of Lower Devonian

Zosterophyllopsida. Hence, the Telome theory is ‘misfit’ for interpreting the origin and evolution of micro-phylls in Lycopsidea.

Enation Theory: This theory was propounded by F. O. Bower (1935). The enation theory seems to be more convincing than the telome theory in explaining the origin of microphyllous leaves (Fig. 9.10 A-D). According to Enation theory, the microphylls were initiated as non-vascularised spine-like outgrowths (enations) on the shoot of primitive vascular plants (e.g., Zosterophyllopsida).

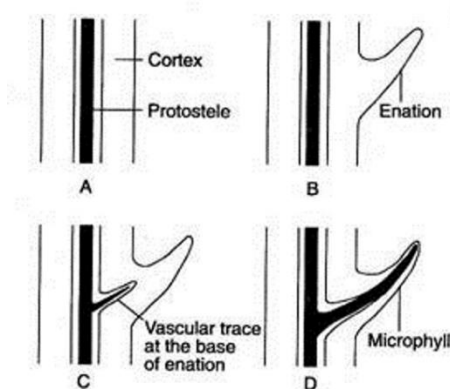


Fig-9.10: Enation theory: A-C. Stages in the origin of microphyll. A. Axis of Rhyniopsida, B. Axis of Zosterophyllopsida, C. Axis of Asteroxylon, D. Axis of Lycopsidea showing a microphyll.

These spine-like enations were not arranged in a definable pattern. Initially, tooth-like formations were arranged in vertical rows on opposite sides of the axes (e.g., *Crenatacaulis*, *Serrulacaulis*).

However, in *Sawdonia*, irregularly disposed tapered and pointed spine-like enations are reported on the axes. In zosterophylls, enations are devoid of any vasculature (first step). However, in the next step (second step) as exemplified by *Asteroxylon*, a trace of vascular tissue arises directly from the protostele of the axis and enters the base of the enation. Here, elements are spirally arranged on the axes. In the final step, the enations become elongated, flattened, and leaf-like and the vascular trace grew up to the tip of the leaf. In this way, a microphyllous leaf (a single unbranched leaf trace arises directly from the protostele) evolved in the **Lower Devonian**. The further elaboration of the micro-phyll (with branched tips) in early herbaceous lycopods (*Leclercquia*, *Protolpidodendron*, *Estinnophyton*) can only be explained by telome theory.

Significance of Telome Theory

- (i) The telome theory portrays the origin and evolution of the sporophytes in the earliest known land plants.
- (ii) The theory is based mostly on account of the comparative study of the fossil as well as living genera of the vascular plants. It explains the phylogenetic relation-ship between the fossil and the living plants.
- (iii) The five elementary processes like over-topping, reduction, planation, recurvation and syngensis give a unified concept of the way evolution might have proceeded in the land plants. These pro-cesses explain simply and lucidly as to how the primitive land plants led to the evolution of both the simple and the com-plex land plants of today.

Moreover, these processes provide a basis of interpretation in solving the morphological controversies of different organs in the vascular plants, such as.

- (a) The nature of the aerial portion of the plant body of the Ophioglossaceae,
- (b) Anatomy of some species of the Medullosaceae,
- (c) Nature of the plant body in the Coenopterid forms,
- (d) Evolution of the vegetative and repro-ductive structure of Cordaitales and early conifers,
- (e) Phylogeny and origin of stamens and carpels.

The theory explains in a satisfactory manner that the entire sporophyte is an axis that has an underground portion called the root and an aerial part called the shoot. The appendages of the shoot that is the sporophylls, sporangia and sterile leaves are nothing but modified parts of the shoot.

Stelar evolution

Definition of Stelar System: According to older botanists, the vascular bundle is the fundamental unit in the vascular system of pteridophytes and higher plants. Van Tieghem and Douliot (1886) interpreted the plant body of vascular plant differently.

According to them, the fundamental parts of a shoot are the cortex and a central cylinder, is known as a stele. Thus, the stele is defined as a central vascular cylinder, with or without a pith and delimited the cortex by endodermis.

The term stele has been derived from a Greek word meaning pillar. Van Tieghem and Douliot (1886) recognized only three types of steles. They also thought that the monostelic shoot were rare in comparison of polystelic shoots.

It is a fact that all shoots are monostelic and polystelic condition rarely occurs. The stele of the stem remains connected with that of leaf by a vascular connection known as the leaf supply.

Types of Steles

1. Protostele: Jeffrey (1898), for the first time pointed out the stelar theory from the point of view of the phylogeny. According to him, the primitive type of stele is protostele. In protostele, the vascular tissue is a solid mass, and the central core of the xylem is surrounded by the strand of phloem. This is the most primitive and simplest type of stele.

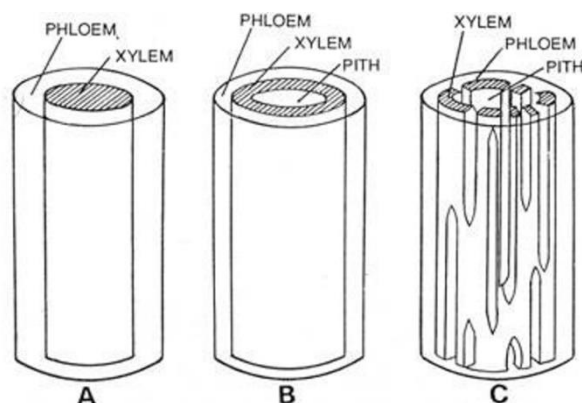


Fig. 10.1 Types of arrangements of vascular tissues in steles. A, protostele; B, siphonostele; C, dictyostele.

here are several forms of protostele

(a) Haplostele: This is the most primitive type of protostele. Here the central solid smooth core of xylem remains surrounded by phloem (e.g., in *Selaginella* spp.).

(b) Actinostele: This is the modification of the haplostele and is somewhat more advanced in having the central xylem core with radiating ribs (e.g., in *Psilotum* spp.).

(c) Plectostele: This is the most advanced type of protostele. Here the central core of the xylem is divided into several plates arranged parallel to each other. The phloem alternates the xylem (e.g., in *Lycopodium*).

(d) Mixed-pith stele: Here the xylem elements (i.e., tracheids) are mixed with the parenchymatous cells of the pith. This type is found in primitive fossils and living ferns. They are treated to be the transitional types in between true protosteles on the one hand and siphonosteles on the other (e.g., in *Gleichenia* spp. and *Osmunda* spp.).

2. Siphonostele: This is the modification of the protostele. A stele in which the protostele is medullated is known as siphonostele. Such stele contains a tubular vascular region and a parenchymatous central region. Jeffrey (1898) interpreted that the vascular portion of siphonostele possesses a parenchymatous area known as a gap immediately above the branch traces only or immediately above the leaf and branch traces. Based on these branch and leaf gaps Jeffrey (1910), distinguished two types of siphonosteles. In one type, however, the leaf gaps are not found, and they are known as cladosiphonic siphonosteles. In the other type both leaf and branch gaps are present, and they are known as phyllosiphonic siphonosteles.

Jeffrey (1902, 1910, and 1917) interpreted the evolution of the siphonostele from the protostele as follows. He supported that the parenchyma found internal to the phloem and xylem has originated from the cortex.

The supporters of this theory believe that the inner endodermis found to the inner face of the vascular tissue and the parenchyma encircled by this endodermis have originated from the cortex. According to Jeffrey and other supporters of this theory, the siphonosteles with internal endodermis are more primitive than those without an internal endodermis.

The siphonosteles which do not possess the inner endodermis are believed to have originated by the disintegration of the inner endodermis during evolution.

According to the theory proposed by Boodle (1901), and Gwynne Vaughan, the siphonostele has evolved from the protostele by a transformation of the inner vascular tissue into parenchyma.

A siphonostele may be of the following types.

(a) Ectophloic: In this type of siphonostele, the pith is surrounded by a concentric xylem cylinder, and next to the xylem the concentric phloem cylinder.

(b) Amphiphloic: In this type of siphonostele, the pith is surrounded by the vascular tissue. The concentric inner phloem cylinder surrounds the central pith. Next to the inner phloem is the concentric xylem cylinder which is immediately surrounded by the outer phloem cylinder (e.g., in *Marsilea*).

3. Solenostele: The vascular plants have been divided into two groups since the presence or absence of the leaf gaps. These groups are Pteropsida and Lycopsidea. The ferns, gymnosperms and angiosperms are included in Pteropsida, whereas the lycopods, horsetails, etc., are included in Lycopsidea.

The simplest form of siphonostele has no gaps, such as some species of *Selaginella*. However, among the simplest siphonostelic Pteropsida and siphonostelic Lycopsidea, the successive leaf gaps in the stele do not overlap each other and are considerably apart from each other.

According to Brebner (1902), Gwynne-Vaughan (1901) such siphonosteles which lack overlapping of gaps are known as solenosteles. They may be ectophloic or amphiphloic. Some authors (Bower, 1947; Wardlaw, 1952; Esau, 1953) however, interpret the solenostele as an amphiphloic siphonostele.

4. Dictyostele: In the more advanced siphonosteles of Pteropsida, the successive gaps may overlap each other. Brebner (1902) called the siphonosteles with overlapping gaps as dictyosteles. In such cases the intervening portion of the vascular tissue between lateral to such leaf gaps is known as meristele. Each meristele is of protostelic type. The dictyostele with many meristeles looks like a cylindrical meshwork.

5. Polycyclic Stele: This type of stellar organization is the most complex one amongst all vascular cryptogams (pteridophytes). Such type of steles are siphonostelic in structure. Each such stele possesses an internal vascular system connected with an outer siphonostele. Such connections are always found at the node.

A typical polycyclic stele possesses two or more concentric rings of vascular tissue. This may be a solenostele or a dictyostele. Two concentric rings of vascular tissue are found in *Pteridium aquilinum* and three in *Matonia pectinata*.

6. Eustele: According to Brebner (1902), there is one more modification of the siphonostele known as eustele. Here the vascular system consists of a ring of collateral or bicollateral vascular bundles situated on the periphery of the pith. In such steles, the inter-fascicular areas and the leaf gaps are not distinguished from each other very clearly. An example of this type is Equisetum.

Heterospory and Seed habit

Most of the Pteridophytes produce one kind of similar spore. Such Pteridophytes are known as homosporous, and this phenomenon is known as homospory. However, there are some Pteridophytes which produce two different types of spores (differing in size, structure and function).

Such Pteridophytes are known as heterosporous and the phenomenon is known as heterospory. The two types of spores are microspores and megaspores. Microspores are smaller in size and develop into the male gametophyte while the megaspores are large and develop into female gametophyte.

According to Rashid (1976) only 9 genera of Pteridophytes are heterosporous. These are Selaginella, Isoetes, Stylites, Marsilea, Pilularia, Regnellidium, Salvinia, Azolla and Platyzoa.

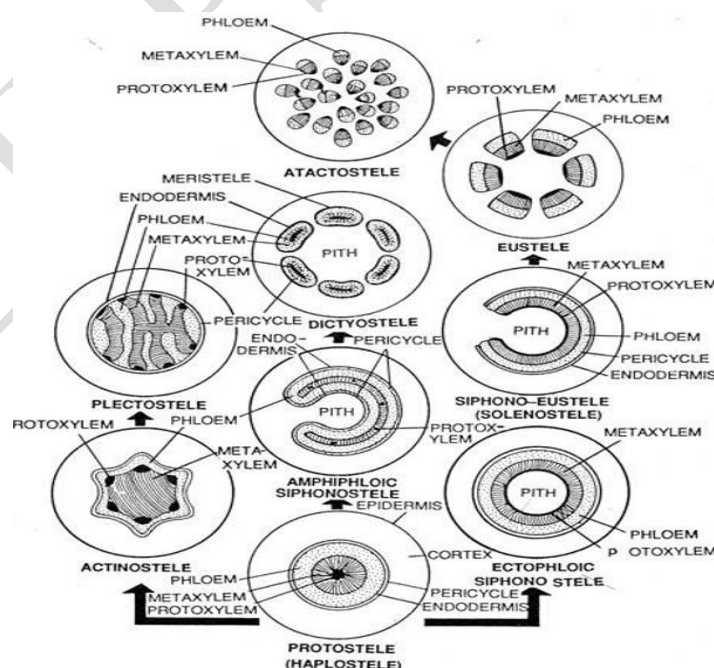


Fig. 9.11. The stellar system. Different types of steles are arranged in evolutionary sequence.

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Origin of Heterospory: The origin of heterospory can be better discussed based on evidence from paleobotany, and developmental and experimental studies.

1. Palaeobotanical evidence: It has been suggested that heterospory arose due to degeneration of some spores in a few sporangia. As more nutrition becomes available to a smaller number of spores, the surviving spore grows better, hence increasing their size. Palaeobotanical evidence shows that the earlier vascular plants were all homosporous and the heterosporous condition appeared subsequently in the lowermost upper Devonian. A number of heterosporous genera belonging to the Lycopsiida, Sphenopsida and Pteropsida were known in the late Devonian and early Carboniferous periods.

During this period important heterosporous genera were Lepidocarpon, Lepidostrobus, Mazocarpon, Plaeuromeia, Sigillariostrobus (members of Lycopsiid) Calamocarpon, Calamostachys, Palaeostachys (members of Sphenopsida). Some of these forms even arrived at the seed stage.

According to Williamson and Scot (1894), two species of Calamostachys form the initial stage that might lead to the heterospory. These species were *C. binneyana* and *C. casheana*. In *C. binneyana* most of the sporangia had with large number of small spores in tetrads but in some sporangia spores were large.

However, in *C. casheana* two different types of spores-microspores and megaspores were present in different sporangia. A similar type of abortion of spores was also observed in Stauropteris (Chaloner, 1958 Lepidocarpon and Calamocarpon).

2. Evidence from Developmental Studies: In heterosporous Pteridophytes, the development of micro and megasporangia follow the same pattern. They have identical

organization but for their size. While in megasporangia most of the spore mother cells degenerate but in microsporangia only a few mother cells are disorganized.

The phenomenon of heterospory becomes distinct either before or after meiosis. In *Selaginella* *Isoetes* it is distinct before meiosis. In the microsporangium all the sporocytes undergo meiosis and form many microspores. However, in megasporangium, a part of the sporogenous tissue degenerates they provide nutrition to growing sporocytes (megaspores).

In *Isoetes*, there are only 50-300 megaspores in megasporangium. In *Selaginella erythropus* megasporangium contains only one functional megaspore.

In *Marsilea*, *Salvinia*, and *Azolla* the phenomenon of heterospory becomes distinct after meiosis. In *Marsilea* 64 microspores and 64 megaspores are formed after meiosis in microsporangium and megasporangium respectively. In microsporangium all the microspores are functional while in megasporangium one megaspore is functional and rest degenerate.

3. Evidence from Experimental Studies: Experimental studies on *Selaginella* (Goebel, 1905) and *Marsilea* (Shattuck, 1910) suggest that nutritional factors mainly govern the heterospory. Under conditions of low light intensity, the photosynthetic activity of *Selaginella* was retarded and it produced microsporangia. By sudden lowering of the temperature, the size of the microspores in the sporocarp of *Marsilea* increases by six times.

Biological Significance of Heterospory: The phenomenon of heterospory is of great biological significance on account of the following facts.

(i) The development of the female gametophyte starts while the megaspore is still inside the megasporangium. (ii) The same is true of microspores i.e., they also start germinating into male gametophytes while they are still inside the microsporangium. (iii) The female gametophyte derives its nourishment from the sporophyte i.e., the female gametophyte is dependent on the sporophyte for its nourishment. (iv) The dependence of female gametophytes on sporophytes for its nourishment provides a better starting point for the development of a new embryo than an independent green prothallus which must manufacture its food.

Seed Habit in Pteridophytes: Adopting heterospory and the retention and germination of a single megaspore within megasporangium to form a female gametophyte, led to the phenomenon of “seed habit”, a characteristic feature of the spermatophytes. A seed is an ovule that contains an embryo developed because of fertilization.

The origin of seed habit is associated with the following

(i) Production of two types of spores (heterospory). (ii) Reduction in the number of megaspores finally to one per megasporangium. (iii) Retention and germination of the megaspores and fertilization of the egg. (iv) Continued development of the fertilized egg into the embryo while still in situ. From the above observations it is concluded that the life history of *Selaginella* approaches seed habit because of the following features.

1. The occurrence of the phenomenon of heterospory.
2. Germination of megaspore inside megasporangium.
3. Retention of megaspore inside megasporangium either till the formation of female gametophyte or even after fertilization.
4. Development of only one megaspore per megasporangium for example, in *Selaginella monospora*, *S. rupestris*, *S. erythropus* etc.

Though *Selaginella* as well as lower Spermatophytes shows homologies in their structure as follows: *Selaginella*: 1. Megasporangium. 2. Megaspore. 3. Female gametophyte. 4. Archegonium. 5. Egg. Lower Spermatophytes (Gymnosperms): 1. Nucellus of ovule. 2. Megaspore (Embryosac). 3. Endosperm. 4. Archegonium. 5. Egg. Even then the seeds are not formed in *Selaginella* because: 1. Megasporangium is not surrounded by integument, 2. The retention of megaspore permanently inside the megasporangium has not been well established. 3. The embryo immediately gives rise to the sporophyte without undergoing a resting period.

General Account of Fossil Pteridophytes Pteridophytes are a group of vascular plants that reproduce through spores rather than seeds. This group includes ferns, horsetails, and club mosses. They are considered some of the earliest vascular plants, having evolved during the late Silurian and Devonian periods (about 400 million years ago). Pteridophytes played a significant role in the development of the earth's plant diversity and are believed to be one of the key groups that helped transform the landscape from non-vascular plants like algae and bryophytes.

Fossil records of pteridophytes provide important clues about plant evolution and the environmental conditions that existed during ancient times. Fossilized pteridophytes are crucial for understanding the transition from simple, early land plants to more complex vascular plants.

Key Features of Fossil Pteridophytes: Vascular Tissue: Fossil pteridophytes show evidence of vascular tissues like the xylem and phloem, which help in the conduction of water, nutrients, and food. This vascular system allowed these plants to grow larger and colonize drier land habitats.

Spores: Like their modern counterparts, fossil pteridophytes reproduced through spores. Fossils often contain evidence of sporangia (spore-producing structures), which play a key role in their life cycle. These sporangia were typically found on the underside of the leaves or on specialized structures called strobili.

Leaves: Many fossilized pteridophytes have preserved their leaves, known as fronds in ferns. These leaves were often compound and divided into smaller leaflets, making them easier to identify in fossil form. Early pteridophytes, however, may have had simple, needle-like leaves.

Major Fossil Pteridophyte Groups: Rhyniophytes: One of the earliest groups of vascular plants, Rhyniophytes existed in the Devonian period. These plants were relatively simple, with no true roots or leaves, and had naked sporangia at the tips of their stems. Fossils like Rhynia are famous for being some of the earliest vascular plants discovered.

Zosterophylls: Another early group, the Zosterophylls, had small, scale-like leaves and sporangia arranged laterally along the stems. These plants are also from the Devonian period and are thought to be precursors to modern lycophytes (clubmosses).

Lycophytes: Fossil lycophytes were large, tree-like plants during the Carboniferous period, often referred to as Lepidodendrids. These plants had scale-like leaves and produced spores in cone-like structures (strobili). Their fossils, such as Lepidodendron, indicate that they were major contributors to the vast coal deposits that formed during this era.

Sphenophytes: Also prominent during the Carboniferous period, fossil sphenophytes were relatives of the modern horsetails. One of the well-known fossil genera from this group is *Calamites*, which were tall, tree-like plants with jointed, ribbed stems. They also had cone-like spore-producing structures.

Ferns: Ferns have an extensive fossil record dating back to the Devonian period. Some fossilized ferns show striking similarities to modern ferns. The fossil fern genus *Pecopteris* is commonly found in Carboniferous deposits, often with beautifully preserved fronds that resemble the large, divided leaves of modern ferns.

Fossil Record and Environmental Importance: Pteridophyte fossils are often found in coal deposits from the Carboniferous period, which spanned about 360 to 300 million years ago. During this time, the earth had vast swampy forests that were dominated by giant pteridophytes. As these plants died, their remains were buried and eventually compressed into coal, making fossil pteridophytes important contributors to fossil fuel formation. These fossils also provide evidence of the shift in climate and atmospheric conditions over geological time. For instance, fossil records show that the large lycophyte forests disappeared as the climate became drier during the Permian period.

Significance of Fossil Pteridophytes in Evolution: Fossil pteridophytes are significant for understanding the evolution of land plants. They represent a key stage in the transition from non-vascular to vascular plants, with innovations such as vascular tissue, true roots, and complex leaves. The evolution of these features allowed plants to grow taller and inhabit new environments, which paved the way for the later dominance of seed plants (gymnosperms and angiosperms).

Additionally, fossil pteridophytes provide insights into early ecosystems and plant-animal interactions. For example, they were likely one of the primary food sources for early herbivorous insects.

Fossil pteridophytes are a window into the past, offering crucial evidence of the early evolution of vascular plants and the ecosystems they shaped. Their fossils, often preserved in coal deposits, not only tell us about the ancient plants themselves but also provide valuable information about the environmental and climatic conditions of Earth's

distant past. Studying these fossils helps scientists better understand the evolution of modern plants and the history of life on land.

EJBPS BOOK

UNIT-111: GYMNOSPERMS

Definition of Gymnosperms

The term gymnosperm was given by Theophrastus in his book *“Enquiry into Plants”* (300 BC). It is derived from two Greek words, **Gymnos** which means naked, and **“Sperma”** which means seeds. Gymnosperms and angiosperms are two groups of seed plants (Spermophyta). The former are naked seeded plants in which ovules are not enclosed by the ovary wall, born freely on **open megasporophylls**, whereas later, ovules are born in the **closed megasporophylls** and are completely enclosed within the ovary. Due to this reason (protected seed), angiosperms are more advanced than gymnosperms. As **gymnosperms** do not possess an ovary, hence. they don't produce fruits, whereas angiosperms possess ovaries and produce fruits.

In gymnosperms, ovules are either borne naked or on the surface of megasporophylls, often arranged in cones. These plants evolved approximately 300 million years ago from non-seed-producing ancestors of the extinct division Progymnospermophyta, which had a fern-like appearance and acted as a bridge between pteridophytes and angiosperms. During the Jurassic and Cretaceous periods of the Mesozoic era, gymnosperms were the dominant plants on Earth's surface. Today, approximately 83 genera and around 790 species of living gymnosperms are distributed across temperate, tropical, and arctic regions worldwide.

GENERAL CHARACTERS OF GYMNOSPERMS

1. They are slow growers and lack vegetative means of propagation such as by cuttings, layering, etc.
2. They are unable to grow under varied habitats as they can grow in some specific habitats and conditions.
3. They have limited means of dispersal of seeds and can be dispersed only by wind, animals or human beings.
4. Most of the gymnosperms are terrestrial and unable to grow in aquatic habitats, except a few.
5. They lack vessels in the xylem (with few exceptions) and companion cells in the phloem.
6. Most of the gymnosperms are unisexual; thus due to the absence of bisexuality, the chances of Self-pollination are reduced.

7. As wind is the main source of pollination, hence large number of pollen grains are wasted.

Morphology: The living gymnosperms with approximately 70 genera and 725 species, include trees (tall and medium sizes) and shrubs. There is complete absence of herbs and climbers. Vegetative propagation is not reported in this group but reproduction by bulbils is known in *Cycas*. Generally, the plant possesses tap roots but sometimes mycorrhizal (*Pinus*) and coralloid (*Cycas*) roots are also present.

Stem: The stem may be aerial, erect, unbranched (e.g. *Cycas*, *Zamia*), or branched (e.g. *Pinus*, *Cedrus* etc.). In gymnosperms the branches may be of two types- i) the long shoots and ii) the dwarf shoots based on their branching system. Leaves are present at their apices of dwarf shoot. Dwarf shoot with leaves collectively known as a spur.

Leaf: Gymnosperms bears both microphyllous and megaphyllous leaves. The megaphyllous leaves are large and well-developed with their vascular supply leaving a leaf gap in the stem. The leaves may be simple or compound and vary in shape, size, and form, as a minute scale leaf to several feet long megaphylls (e.g. in *Cycas*). Gymnosperms show diversity in leaf venation, it may be parallel (*Welwitschia*), reticulate (*Gnetum*), or even dichotomous (*Ginkgo*). The leaves are always evergreen and mostly possess resin canals as in *Pinus*, *Cedrus*, and *Abies*. The leaves of members of Gnetales lack resin passages but *Gnetum* possesses latex tubes. The arrangement of leaves may be whorled (*Cedrus*), opposite, and decussate (*Gnetum*, *Ephedra*, etc.) or spiral (*Taxus*, *Podocarpus*, etc.). Conifers usually have sunken stomata. The shape of leaves may also vary from triangular (*Pinus roxburghii*), semi-circular (*Pinus sylvestris*), bifid or circular (*Pinus microphylla*), and bifacial leaflet of *Cycas*, *Zamia*, and *Gnetum*. The arrangement of vascular bundles also shows great variations. The leaf base remains permanently meristematic while the tip starts drying off.

Due to secondary growth gymnosperms possess primary and secondary wood. The manoxylic secondary wood is the characteristic feature of Cycadophyta. This wood is porous, soft and more parenchymatous, while pycnoxylic wood is the characteristic feature of Coniferophyte as this wood is compact and hard with narrow medullary rays. Xylem lacks wood vessels except in *Ephedra*, *Gnetum*, etc. The xylem is usually endarch

or mesarch in stem while it is exarch in roots. The vascular bundles in the stem are conjoint, collateral, endarch, and open.

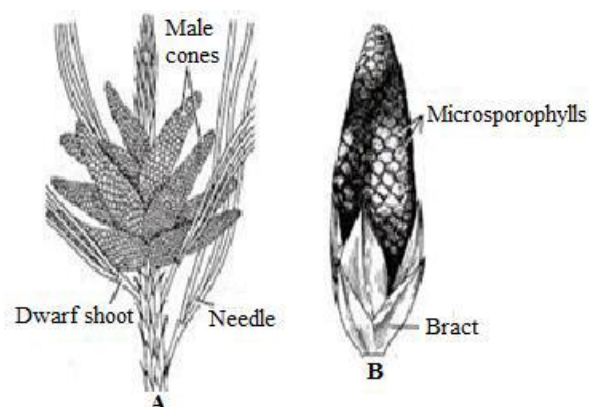


Fig.11.1 *Pinus wallichiana*, A- Cluster of male cones, B- A single male cone.



Fig.11.2: Habit sketch of some Gymnosperms.

Reproduction: (life cycle)

Gymnosperms possess two different types of spores and are hence referred as heterosporous. The microspores are smaller and there may not be any difference in the size of the spore while another spore larger in size called a megaspore. These two kinds of spores on germination produce two different types of gametophytes. The microspore or pollen grain produces male gametophyte, while the larger megaspore produces female gametophyte, which bears two or more archegonia or female sex organs. These spores are produced within the sporangia that are borne on sporophylls. These sporophylls are spirally arranged along an axis to form compact strobili or cones. The male or microsporangiate strobili bear microsporophylls and microsporangia while the female or megasporangiate strobili bear megasporophylls with megasporangia (ovules). The two types of cones or strobili may be borne on the same tree as in *Pinus* or on different trees like *Cycas* and *Ginkgo*. The microsporangium contains numerous small microspores whereas the megasporangium contains only one large megaspore. Both micro and megaspores are haploid and develop due to meiosis in the respective spore mother cells. They are the pioneers or primary structures of the male and female gametophytes respectively. In gymnosperms the gametophytes are endosporic i.e. they develop within the spore wall. In general, the strobili or cones are of varying shapes and sizes in different species. Their position also varies from plant to plant.

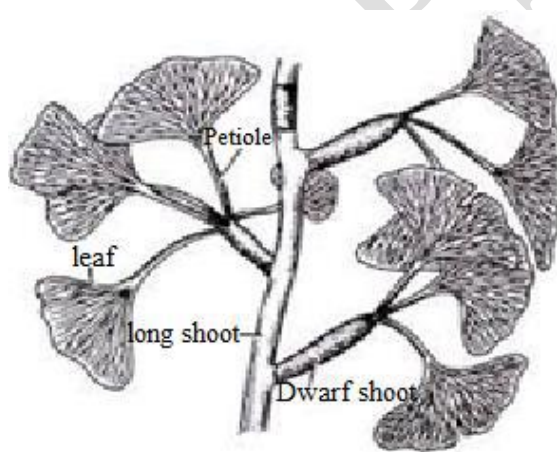
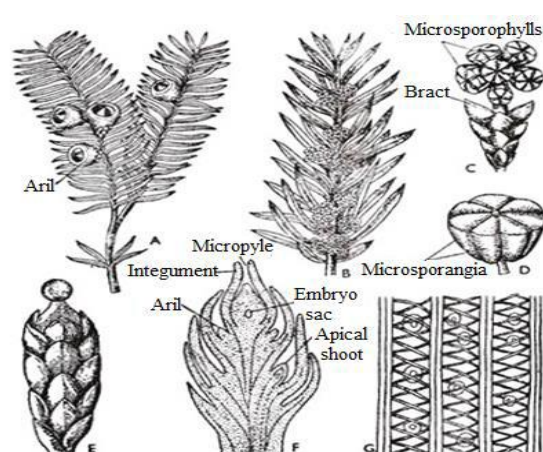
**Fig.11.3****Fig.11.4**

Fig.11.3: *Ginkgo biloba* along a shoot bearing dwarf shoots.

Fig.11.4 *Taxus baccata*: A. Shoot bearing seeds, B. Male shoot, C. A male strobilus, D. A microsporophyll, E. A female flowering shoot, F. Median L.S. female flowering shoot, and G.

L.S. of *Taxus* wood showing tracheids with tertiary spiral thickening in addition to bordered pits.

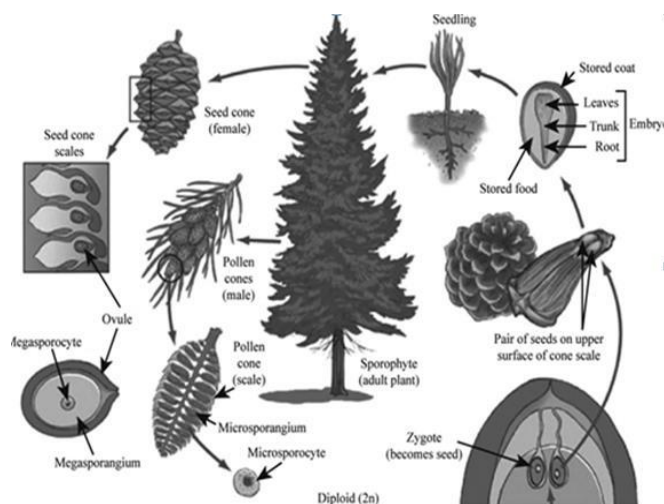


Fig.11.5 Life cycle of a Gymnosperm plant.

Ovule and female gametophyte: The ovules of gymnosperms are without any covering or naked and are borne on usually spirally arranged megasporophylls around a central axis. The ovules are generally sessile. Among gymnosperms, ovules of *Cycas* are the largest in the plant kingdom. Inside an ovule, there is a parenchymatous mass of cells known as nucellus surrounded by an integument. The integument grows all around except the apical part leaving a small pore i.e. micropyle and this end is known as the micropylar end. The nucellus has a single megaspore mother cell at a later stage which undergoes meiosis and forms 4 haploid cells (megaspores) arranged linearly. Out of the four megaspores only one, usually the lower one remains functional, and the rest degenerates. The functional megaspore enlarges and undergoes free nuclear divisions resulting in many free nuclei. This transforms into a young gametophyte that has developed within the megaspore. Now centripetal wall formation starts, and it continues till the whole female gametophyte becomes cellular.

The single integument of the ovule of gymnosperms consists of three layers namely).

- i) The outer fleshy layer or outer sarcotesta,
- ii) The middle stony layer or sclerotesta,
- iii) The inner fleshy layer or inner sarcotesta. Thus, the integument of the ovule consists of one middle stony layer covered by inner and outer fleshy layers.

The apical region of the nucellus forms a pollen chamber by degeneration of cells of the nucellar beak. Semi-germinated pollen grains or microspores are seen in the pollen chamber. These microspores remain in the chamber till further growth of female prothallus which develops two or more archegonia towards the apical end. Depending upon the species the archegonia have a short or long neck of 2, 4, or 8 cells as in *Cycas*, *Taxus*, and *Biota* respectively.

After free nuclear divisions the cell wall formation starts because of which the female gametophyte becomes a cellular structure. The female gametophyte or prothallus gets differentiated into an upper reproductive region, middle storage region, and lower basal haustorial region. Generally, in gymnosperms, the female gametophyte has cellular tissue at its lower end while few free nuclei remain at its upper end. a. After fertilization the apical end, however, becomes cellular (the exception is *Welwitschia*).

Microspores: The pollen grains or microspores are unicellular and haploid structures developed within specific structures, the microsporangia. They differ in shape and size in different groups of gymnosperms. They may be uniaperturate, tetrahedral with a definite polarity due to the thicker exine towards the base (e.g. *Cycas*) and may be almost spherical. (*Ginkgo*), maybe winged (saccate), and may have reticulate exine (*Abies* *pin-drow*, *Cedrus deodara*, *Pinus roxburghii*, *P. wallichiana*, *Picea smithiana* etc.) whereas in *Ephedra* the pollen grains are inaperturate, elongated with palcate exine surface. *E. foliata* pollen grains show parallel ridges along their long axis and possess two tiny sac-like structures. These sacs are almost absent in other species.

Based on studies it is suggested that there is a gradual reduction in the wings or sacs and ultimately resulting in non-winged pollen grains as found in *Ephedra*. There is also an indication of the relationship of *E. foliata* with Coniferales and Cordaitales as there is a minute.

Male Gametophyte: The male gametophytes in gymnosperms are endosporic in nature and show variations regarding their release from sporangia, the number of prothallial cells (they complete their development partly in the microsporangium and partly in the pollen chamber in the ovule), size and motility of male gametes and their time of formation and discharge. In lower gymnosperms- Cycadophytes male gametophyte is with one male prothallial cell and a large sterile cell or stalk cell. Stalk cell divides to

form a body cell or a spermatogenous cell and a tube nucleus. They are arranged in a linear row. The body cell again divides into two multiciliate male gametes. In all Cycads, the pollen tube is formed and is more haustoria in nature than a sperm carrier. In *Microcycas*, the stalk cell divides into 10 or 11 body cells or spermatogenous cells. These cells divide to produce 20 or 22 spermatozoa. Contrary to this in *Ceratozamia* there are 4 spermatozoids. Generally, in Gymnosperms, the generative cell divides transversely into stalk cell and body cell except in *Cycas revoluta*, where it divides anticlinal.

In case of *Ginkgo biloba*, the male gametophyte contains two male prothallial cells, a stalk cell, a body cell and a tube nucleus. Here the generative cell divides anticlinally into stalk and body cell. Later the stalk cell surrounds the second male prothallial cell. The male gametes are multiflagellate.

In case of different families of Coniferales, slight variations are noticed in the sequence of development of male gametophyte, although major events show similarities. In Pinaceae the nucleus of microspore divides twice by periclinal walls and cuts off three cells- two male prothallus cells and one antheridial cell. The latter divides periclinally and forms a tube cell and a generative cell. The grains are liberated at this four-celled stage (two prothallus cells, one tube cell, and one generative cell). The generative cell then undergoes periclinal division forming a stalk cell and a body cell. All these cells lie in an axial row. The semi-germinated pollen grains may germinate immediately or after a month. The pollen tube may start branching on entering the nucellus, then the tube nucleus migrates into one of the branches of pollen grain and moves to the tip while the generative cell remains within the spore wall and divides into stalk cell and body cell between the pollination period of the year or in the following spring these two moves into the pollen tube. Simultaneously about a week before fertilization, the body cell divides into two non-motile, unequal-sized male gametes. There is a difference of opinion regarding the male gamete. According to some workers, the two male gametes are two nuclei of binucleate sperm cells, whereas others regard them as two sperm cells. Sometimes the generative cell divides before pollination in some genera e.g. *Abies*, *Cedrus*, *Picea*, and *Larix* etc. In *Abies*, the cell sometimes divides into two male gametes before pollination or shortly after pollination. However, Chowdhury (1960) reported equal male gametes in *Cedrus*. The period between pollination and fertilization varies in

different members of Pinaceae. It is longest in *Pinus* ranging up to one year, up to nine months in *Cedrus*, 4-5 weeks in *Abies* and a few days in *Picea*. Similarly, the number of prothallial cells also varies in different plants of gymnosperms.

In *Abies balsamea* formation of 3 or 4 prothallial cells have been reported by Hitchinson (1915). While in Taxodiaceae the male gametophyte lacks prothallial cell and divides into a generative cell and a tube cell before pollination. Further, the generative cell divides into stalk cell and body cell after pollination. The male gametes are non-motile and equal in size. In family Cupressaceae also prothallial cells are absent, here the pollen grains directly act as an antheridial cell and may divide into generative cells and tube cells before pollination. Based on studies, in *Cupressus semipervirens* the body cells divide into 4- 20 male gametes, contrary to this in *C. fusiberus* only two male gametes are produced. Gymnosperms show variations in the production of prothallial cells. Among them the Araucariaceae are unique in producing many prothallial cells, the two non-motile male gametes are equal in size. In the members of Podocarpaceae the number of male prothallial cells may be 1-8 in *Podocarpus*, 3-6 in *Dacrydium* and 1-3 in *Phyllocladus* while in *Pherosphaera* the male prothallial cell is absent.

The male gametes also vary in size they may be equal (*Phyllocladus*) or unequal (*Podocarpus*) in size. In Cephalotaxaceae there is no prothallial cell in any species of *Cephalotaxus*, whereas in *Taxus* there is no male prothallial cell. The male gametes are unequal in size. In *Ephedra* the cells of male gametophyte are arranged in a single axial row including two prothallial cells, a stalk cell, a body cell, and a tube cell. Out of the two prothallial cells one is without a cell wall and is thus called prothallial nucleus. After pollination the body cell divides into two male gametes. Contrary to this in *Gnetum* there is only one prothallial cell, a tube nucleus and a generative nucleus. Further division takes place after pollination while at that time the pollen grain contains only three nuclei. The generative nucleus divides into two male gametes. In *Welwitschia* there is no prothallial cell and the released pollen grain contains a tube nucleus and a generative nucleus. Based on above the general characteristics of male gametophyte in gymnosperms following points emerges.

1. The Cycadales, Ginkgoales, Coniferales, and *Ephedra*(Gnetales) all have the same cellular organization of the male gametophytes including the tube cell, the stalk cell, and the male gamete except one difference in the formation of prothallial cell.

2. In case of Araucariaceae and Podocarpaceae formation of a very large number of prothallial cells which develop secondarily at the base of the microspore may be considered as a later evolutionary development. This condition is neither reported in any living or fossil gymnosperms or nor among lower heterosporous tracheophytes.
3. Another specific ontogenic feature is the orientation of the division of spermatogenous cell which produces the stalk cell and the body cell, (e. g. Ginkgo, Auricuriaceae, Podocapeceae and Cycas revolute and in some species of Ephedra) the division is anticlinal while in Cycads and Pinaceae the division is periclinal and the two cells are superimposed.
4. Beside this in Microcycas the stalk cell which is sterile divides and gives rise to additional spermatogenous cells or body cells.
5. While in some other gymnosperms i.e. Cupressus and sometimes in Juniperus more than two male gametes are produced. It is assumed that this condition may have arrived as the gametes are formed from the sub- division of a single spermatogenous cell. This feature may be related with the presence of large number of archegonial complexes.

Pollination and Fertilization: In gymnosperms the medium of pollination is wind; it results in the transfer of semi-germinated pollen grains on the micropyle of the ovule. In most gymnosperms, the pollen grains are caught in a pollination drop secreted at the micropylar end of the ovule. After drying of the pollination drop, the microspores in the semigerminated stage are drawn into the ovule. Just after the drawing of the microspores in the micro gametophyte, the micropyle closes. A distinct pollen chamber is formed at the apex of the nucellus which receives the micro-gametophytes as in some gymnosperms (Cycas, Ginkgo, Ephedra, etc.) In Conifers and other gymnosperms, the semi-germinated pollen grains come in direct contact with the nucellar beak. Contrary to this in the paleozoic gymnosperms (now extinct), the pollen chamber contained liquid-filled cavities in which the motile sperms were liberated due to the dehiscence of the microspore wall. In general, in all the living gymnosperms, the microspores produce a pollen tube as a tubular outgrowth that grows through the nucellar tissue. In Cycads and Ginkgo, the pollen tubes mainly act as the haustorial organ and grow for a long time (several months) into the nucellar tissue absorb food and supply it to the micro gametophyte.

The pollen tube bursts during fertilization and liberates of multiciliate male gametes along with some liquid in the cavity above the megagametophyte. At that time the sperms swim to the archegonial neck and enter the archegonia and only one of them fuses with the egg or oosphere and form the diploid zygote or oospore.

In the conifers, the pollen tube plays an important role of a sperm carrier. The male gamete along with the stalk and tube nucleus migrates to the tip of the pollen tube. The tube grows through the nucellar tissue, reaches the archegonial neck, enters through it, and after bursting liberates the male gametes. Among them, one fuse with the egg to form a diploid zygote. This specific process of fertilization is termed as Siphonogamy. However, in Cycadofilicales, Bennettitales, and Cordaitales, the orders with extinct members of gymnosperms did not produce pollen tubes and sperms were liberated directly into the pollen chamber. This process is known as Zoodiogamy. In the case of *Welwitschia* the female gametophyte gives out tubular prolongations that meet the pollen tips and fertilization takes place after the intervening wall dissolves. In *Welwitschia* and *Gnetum* there are no archegonia.

Embryology: In different groups of gymnosperms embryogeny differs at different stages. It also differs in living and fossil forms. In living or present-day gymnosperms, the first phase in embryo development is the free nuclear divisions (except in *Gnetum*, *Welwitschia*, and *Sequoia semipervirens*). While it is completely absent in angiosperms and other tracheophytes. In *Pinus* and *Cycas* formation of free nuclei is present. In *Pinus*, there are only four free nuclei whereas in *Cycas* as many as 1,000 free nuclei. Just after free nuclear division, wall formation begins, and the embryo transforms into cellular form. Later it is differentiated into a suspensor, radicle, hypocotyl, plumule and cotyledons. When the shoot end of the embryo is directed away from the micropylar end of the ovule, that type of embryo development or embryogeny is called “Endoscopic”.

Polyembryony is the characteristic and significant feature of gymnosperms. This is possible as more than one archegonia are fertilized and so more than one zygote are formed. These zygotes later develop into embryos, but one of them succeeded in developing into a complete embryo. Comparative to Cycads, in Conifers there is a “Cleavage Polyembryony”. As reported earlier in conifers only four nuclei formed, so in this case all four cells of the young embryo separate after wall formation and develop into 4 embryos, but only one completes further development while others abort.

In Thuja, no cleavage Polyembryony was reported and only one embryonal initial develops into an embryo. No free nuclear division is reported in Sequoia semipervirens and the zygote divides first by a transverse wall and forms two cells which divide further by longitudinal walls to form four cells. All these cells may function as embryo initial and give rise to filamentous embryos. Generally, the embryo initially divides by a longitudinal wall but in rare cases, there is an indication of formation of an apical cell, and cleavage polyembryony is present. The embryo has two cotyledons.

In most conifers, the zygote develops four free nuclei and later because of further divisions and wall formation results in forming a “Proembryo” with a four-celled distal embryonal tier, middle suspensor tier, and upper rosette tier (Pinus, Cycas, Tsuga, etc.) While in other gymnosperms as in Abies, Picea, and Larix the rosette tier disappears at a later stage. In further developmental stages, the lower embryo tier develops into all the organs at a later stage. The suspensor tier develops into additional embryos. While the uppermost tier ends are in open contact with the egg cytoplasm. This end is active in transmission of nutrients to the growing embryos.

The number of cotyledons varies in different species and even in the same species. It is 10 in *Pinus roxburghii*, 3-6 in *P. banksiana*, 2-8 in *P. contorta*, 7-8 in *P. sabiniana*. Cleavage Polyembryony is not reported in *Araucaria angustifolia*, a member of Araucariaceae. In this species, 32-45 free nuclei are formed. Later after polar elongation, wall formation takes place. The cells at the distal end develop into enlarged cap cells. The central cells develop into embryo and those situated towards the micropylar end give rise to suspensor. There is complete absence of “**Cleavage Polyembryony**”.

In the case of Cupressaceae, the genus *Actinostrobus* shows Cleavage Polyembryony and shows a somewhat different pattern of development. Here 4 free nuclei are formed. Wall formation results in the forming of 4 cells among which two vertically placed cells below the archegonial neck and two transversally placed cells below. The lower cells divide once to form four embryonic initials while the upper cells do not divide further. The lower ones are polarized in a transverse plane and each of them forms a small distal initial cell and a large suspensor cell and forms four small embryonal cells and four large suspensor cells that elongate considerably. Hence shows cleavage polyembryony. The rosette tier and upper tier are not formed in this case. The embryo has two cotyledons. The embryonal cells are binucleate in Podocarpaceae. While the number of binucleate

cells and the pro- suspensor cells varies with species and genera. The maximum and minimum number of the embryonal cell are 9-12 in *Podocarpus spicatus* and 1-2 in *P. totterra*, *P. nivalis* and *P. macrophyllus*. *Podocarpus spicatus* has 9-12 and *P. macrophyllus* has 14-15 prosuspensor cells. The embryo has two cotyledons.

Development of embryos in the members of Gnetales is different than in the above-mentioned cases. In *Ephedra trifurcata* the zygote nucleus divides into eight free nuclei of unequal sizes distributed unevenly in the protoplasm. Three to five of these nuclei become enclosed individually by irregular walls which become globular later. All these globular cells are proembryos, an example of polyembryony. Later the globular pro-embryo develops into an embryo with a massive embryonal mass at the distal end and several suspensors. In *Ephedra foliata* exceptionally there is only one suspensor tube.

In *Welwitschia* embryo develops differently. In this case, the zygote elongates and divides into different parts- an upper elongated primary suspensor and a distal embryonal cell, later it divides to form an apical wall. The outer mass of this apical mass is called the inner cortical ring and is situated adjacent to the primary suspensor. The outer cortical ring is formed later which elongate around the suspensor. Thus, the primary suspensor cell is now surrounded by two layers of 8- 16 cells. Later by division of these cells, more layers are added around these. At the distal end, the cells form cap cells while those in the middle develop into embryos. Comparatively to this embryo development in *Gnetum* is quite different. In this case, free nuclear division is not found and the zygote divides and develops into a two-celled body that gives out elongated and tube-like suspensors. These suspensor cells may branch, and all have a distal, densely granulose embryonal cell. Further these terminal cells develop into an embryo out of which only one reaches maturity. In *Gnetum* embryo development is completed after the detachment of the seed. Based on comparative studies of embryonal development in gymnosperm, it is concluded that there is no close relationship or resemblances between the embryogenic of pteridophytes, gymnosperms, and angiosperms. This suggests parallel evolution among these groups rather than evolution from a common ancestor. However, the gymnosperms embryo Share some common features with other embryos-

1. Axial development of embryo.
2. Early determination of polarity.
3. A conspicuous meristematic distal pole.

These similarities point out the possibility of a common ancestry of gymnosperms with other vascular plants.

Seed formation: After fertilization, the structure developing from a fertilized ovule and its consequent enlargement is known as a seed. The zygote develops into an embryo while the endosperm persists as a nutritive tissue, whereas the nucellus disorganizes (or serves as nurse cells for developing embryo) or it may remain in the form of dry tissue at the micropylar end of the seed known as a nucellar cap. In gymnosperms, the inner fleshy layer called the tegmen, may persist as a thin layer of seed coat. The middle stony layer later changes into a hard layer called the testa, which mechanically protects the female gametophyte and the embryo. Development of seed may vary in different species of gymnosperms. In *Cycas* and *Taxus* the outer fleshy layer develops into scarlet red and fleshy outermost seed coat.

In *Gnetum* the seed develops before the embryo completes its development. In *Taxus* a fleshy aril develops from the basal cup-shaped structure. Except for *Cycas* and *Ginkgo*, the seeds of all gymnosperms remain dormant for some time. While in these two genera, the seeds germinate immediately, they lose their viability when fall on moist substratum. In gymnosperms, the seed represents two sporophytic and one gametophytic generation. Different parts of a seed of gymnosperms represent different generations. 1) The young embryo represents the new sporophytic generation. 2) The seed coat represents the old sporophytic generation and 3) The endosperm represents the gametophytic generation. In most of the genera of gymnosperm, the germination of seed is epigeal means the cotyledons come above ground except in *Ginkgo* where the cotyledons remain embedded in the endosperms. While in *Ephedra trifurcata* Vivipary has been reported. All the gymnosperms represent heterologous alternation of generation.

Evolutionary trends: Geological history revealed that the gymnosperms are the most ancient seed plants that evolved during the Upper Devonian and Lower Carboniferous periods in the Palaeozoic era around 350 million years ago. They flourished well during the period of the Mesozoic era. Most of the primitive members may have flourished well but gradually became extinct and now available only in the fossil forms. Hence gymnosperms have a long fossil history which gives the idea of diverse line of evolution. The studies of fossil records show that gymnosperms originated from the oldest and most primitive group of Psilophytes which flourished during the Devonian period of Palaeozoic era. Based on the studies, scientists put forward three lines of evolution of gymnosperms- one of three lines of evolution included Cycadofilicales

or Pteridospermales generally known as “Seed Ferns”, and included plants like *Neuropteris decipiens*, *Medullosa noel*, *Lyginopteris oldhamia* etc. These appeared during the Carboniferous period and are evidence of the origin of gymnosperms from fern or an ancient fern-like ancestor. These plants had a fern-like general appearance and foliage but also had primitive types of seed. The gymnosperms morphologically also resemble so much with the ferns or pteridophytes so this period is generally known as the “Age of ferns”. The second line of evolution of gymnosperms is represented by the Cycadeoidales or Bennettitales, which includes extinct forms that flourished well during the Mesozoic and showed striking resemblances with modern Cycads.

The third line of evolution, which is also a group of extinct members, is Cordaitales which emerged during Upper Devonian and reached its full development in the Upper Carboniferous period and disappeared by the end of the Permian period. Thus Cycadofilicales, Bennettitales and Cordaitales are now extinct, whereas Cycadales, Ginkgoales and Coniferales represent both fossil and living forms and the Gnetales is a recent group. Hence four groups of gymnosperms viz. Bennettitales, Cycadales, Ginkgoales and Coniferales which evolved independently from the two Palaeozoic extinct groups, formed the dominant vegetation of the earth during the mid- Mesozoic era. They, however, began to disappear towards the late Mesozoic age. One group i.e. Bennettitales became quite extinct while a few descendants of the other three groups continued till the Cenozoic age as the present-day living forms of the four groups of Mesozoic gymnosperms contemporaneous and widely distributed. The Bennettitales originated from the Cycadofilicales, flourished and disappeared during the same age. The Cycadales which originated from the Cycadofilicales but independently from the Bennettitales have left some living representatives. Ginkgoales and Coniferales originated independently of one another, from the Cordaitales. The former has left only one living representative, *Ginkgo biloba*- a large tree in western China now cultivated, while the latter has left over 500 living representatives, the biggest group of living gymnosperms. The Gnetales is regarded as the most recent and advanced group which comes close to the angiosperms. It has 3 genera and about 71 spp. Fossil records of the Gnetales are rare and fragmentary and not formed earlier than the Tertiary period. This group is of recent origin and possibly an offshoot of some Coniferales.

Classification

The Gymnosperm is a very large group that includes both living and fossil forms. Due to ample records of fossil forms, the classification has become somewhat complicated. Several workers have classified Gymnosperms differently from time to time. Some important ones are as follows.

The pioneer workers in this field were Coulter and Chamberlain (1917) who divided gymnosperms directly into seven orders viz.

1. Cycadofilicales 2. Bennettitales, 3. Cycadales, 4. Cordaitales, 5. Ginkgoales, 6. Coniferales 7. Gnetales Jefferey (1917) recognized two classes among gymnosperms as:

A. Class-Arachigymnospermae: It includes all those gymnosperms that resemble ferns from their general appearance and anatomy. They possess motile spermatozoids and divided this class into five orders-

1. Order Pteridospermae-It includes all extinct forms, primitive and that lived in Paleozoic period.
2. Order Cycadeoidae- It includes all extinct forms.
3. Order Cycadales- Includes extinct and living forms.
4. Order Cordaitales- Includes all extinct forms.
5. Order Ginkgoales- Includes extinct and single living genera.

B. Class-Metagymnospermae: Plants of this class possess simple leaves and have no resemblance with the ferns. Plants possess non-motile male gametes; the pollen grains grow in the pollen tube. It included two orders-

1. Order Coniferales- It included living genera e.g. Pinus, Cedrus, Taxus, Podocarpus, Taxodium etc., and included fossil genera.
 2. Order Gnetales- Included Ephedra, Gnetum Welwitschia and many fossil genera.
- Based on composition of wood the gymnosperms were divided into two classes)
- Manoxylic- when possesses porous wood with loose texture.

ii) Pycnoxylic- When the wood was compact. The former included Cycadales, Cycadeoidales and Cycadofilicales while the latter included Cordaitales, Ginkgoales, Coniferales and Gnetales. This classification was given by Seward (1919). However, Chamberlain in 1934 divided the gymnosperms into two classes which were further divided into orders with their respective characters such as A. Class Cycadophyta. i) Most of the plants of this group are unbranched, and stems are stumpy. ii) Male cones

large and compact with simple sporophylls bearing large ovules. iii) Anatomically the stems have wide cortex and manoxylic wood. This class included three orders)

a) Cycadofilicales- Includes extinct forms. b) Cycadeoidales-Included both living and fossil forms. c) Cycadales- Included in both living and fossil forms.

B. Class- Coniferophyta- i) profusely branched stem is the characteristic feature of this group.

ii) Leaves simple and the foliage gives cone like appearance.

iii) Both male and female strobili are compact and bear complex sporophylls.

iv) Wood is pycnoxylic. It included four orders.

a. Cordaitales- It included extinct forms. b. Ginkgoales- It included extinct and only one living representative i.e. Ginkgo biloba. c. Coniferales- It included both extinct and living forms. d. Gnetales- Included both living and extinct forms.

D. D. Pant (1957) proposed a classification in which the Gymnosperm is divided into three divisions.

i) Cycadophyta, ii) Clamydospermatophyta, iii) Coniferophyta

Coniferophyta, Clamydospermatophyta and Coniferophyta were further divided into classes and orders. Raizada and Sahn (1958-61) have classified Gymnosperms after the discovery of a new and unique group of Jurassic periods- Pentoxylae- Gymnosperm- Sub-division-1. Cycadophyta-Order - a. Pteridospermales, b. Cycadeoidales, c. Cycadales

Sub- division-2- Pentoxylae

Sub- division-3-Coniferophyta- order- a. Cordaitales, b. Ginkgoales, c. Coniferales,d. Gnetales. After that Andrew (1961) another renowned scientist classified Gymnosperms and divided it into six divisions i) Pteridospermatophyta ii) Cycadophyta. iii) Ginkgophyta iv) Coniferophyta. v) Gnetophyta vi) Gymnosperms of uncertain affinities. K.R. Sporne (1965) in his book “The Morphology of Gymnosperms” classified.

Gymnosperms based on Pilger and Melchior (1954) classification- Gymnosperms- divided into three divisions.

1. Cycadopsida 2. Coniferopsida and 3. Gnetopsida

These divisions were further divided into orders- 1.Cycadopsida-

Order1. Pteridospermales- Families- (7)-1. Lyginopteridaceae -(Lyginopteris),

2- Medullosaceae (Medullosa), 3. Calamopityaceae (Calamopitys), 4- Glossopteridaceae (Glossopteris), 5- Peltospermaceae (Xylopteris), 6- Corystospermaceae (Xylopteris), 7- Caytoniaceae (Caytonia)

Order- 2. Bennettitales - Families (3) 1- Williamsoniaceae (Williamsonia)

2. Wielandiellaceae (Wielandiella), 3. Cycadeoideaceae (Cycadeoidea)

Order 3. Pentoxylales -Family(1) 1. Pentoxylaceae (Pentoxylon)

Order 4. Cycadales-Family (2) 1. Cycadaceae (Cycas, Zamia etc.),

2. Nilssoniaceae (Nilssonia)

2. Division Coniferopsida: Order1. Cordaitales-Families (3) 1. Eristophytaceae(Eristophyton). 2. Cordaitaceae(Cordaites), 3. Poroxylaceae (Poroxylon).

Order 2. Coniferales -Families (9) 1. Lebachiaceae(Lebachia)

2. Voltziaceae(Voltziopsis), 3. Palissyaceae (Palissya), 4. Pinaceae (Pinus, Abies, Picea),

5. Taxodiaceae (Taxodium), 6. Cupressaceae (Cupressus), 7. Podocarpaceae (Podocarpus), 8. Cephalotaxaceae (Cephalotaxus), 9. Araucariaceae (Araucaria, Agathis).

Order 3. Taxales-Family (1) 1. Taxaceae (Taxus, Torreya), Order

4.Ginkgoales.-Families(2) 1.Trichopityaceae (Trichopitys), 2. Ginkgoaceae (Ginkgo), 3.

Division Gnetopsida, Order 1.Gnetales- Families (3) 1. Gnetaceae (Gnetum), 2. Welwitschiaceae (Welwitschia), 3. Ephedraceae (Ephedra).

Recently Taylor (1980) classified Gymnosperms into six divisions as.

1. Progymnospermophyta, 2. Pteridospermophyta Cycadeoidophyta., 4. Cycadophyta. 5. Ginkgophyta., 6. Coniferophyta.

Thus, after reviewing the different classifications of Gymnosperms adopted by different workers from time to time, it is evident that there are great variations regarding the classification of Gymnosperms. But even then the last and the most important classification may be taken as correct one for studies.

Stewart (1983) placed Progymnospermopsida, Gymnospermopsida and Gnetopsida as distinct classes under the division Tracheophyta, the vascular plants of kingdom Plantae.

These three classes were further divided as.

Kingdom Plantae- Division Tracheophyta, Class-1. Progymnospermopsida, Order- 1.

Aneunophytales, 2. Aracheopteridales, 3. Protopityales, Class-2. Gymnospermopsida,

Order- 1. Pteridospermales, 2. Cycadales, 3. Cytoniales, 4. Glossopteridales, 5.

Pentoxylales, 6. Czekanowskiales 7. Ginkgoales, 8. Cordaitales, 9. Voltziales, 10. Coniferales, 11. Taxales, Class-3. Gnetopsida

Order- 1.Gnetales, 2. Ephedrales, 3. Welwitschiales. Birbal Sahni (1920), based on morphological nature of ovule bearing organs and axial or foliar, nature of ovules divided gymnosperms into two major groups as.

1-Stachyospermae (ovules arise in the axil of stem) spread over orders- Cordaitales, Ginkgoales, Coniferales, Taxales and 2-Phyllospermae (ovules borne on leaves) divided into three orders-Cycadofilicales, Bennettitales and Cycadales, Christenhusz *et al.*, (2011) proposed a new classification and linear sequence of the living or existing gymnosperms based on molecular and morphological phylogenetic studies. They divided all existing gymnosperms into 4 sub-classes, 8 orders, and 12 families as follows.

Sub Class I. Cycadidae, Order A. Cycadales, Family 1. Cycadaceae Family 2. Zamiaceae, Sub Class II Ginkgoidae, Order B. Ginkgoales, Family 3. Ginkgoaceae, Sub Class III Gnetidae, Order C. Welwitschiales, Family 4. Welwitschiaceae, Order D. Gnetales, Family 5. Gnetaceae, Order E. Ephedrales.

Family 6. Ephedraceae, Sub class IV Pinidae, Order F. Pinales, Family 7. Pinaceae, Order G. Araucariales, Family 8. Araucariaceae, Family 9. Podocarpaceae, Order H. Cupressales.

Family 10. Sciadopityaceae, Family 11. Cupressaceae, Family 12. Taxaceae

Subclass 1 Cycadidae Cycadales W Williamsonia (Williamsonia)

Class. Cycadopsida Order. Cycadeoideales Family. Williamoniaceae Genus. Williamsonia.

Williamsonia

Kingdom: Plantae

Clade: Tracheophytes

Order: Bennettitales

Family: Williamoniaceae

External Features of Williamsonia

Williamsonia (Fig. 12.1) resembled *Cycas* in appearance, and its best-known species is *W.ewardiana*. A reconstruction of this species was published by Sahni (1932). The leaves of *W.ewardiana* were like that of *Ptilophyllum*. The plant had an upright, branched, stout stem covered by persistent leaf bases.

A terminal crown of pinnately compound leaves was present. For the stem genus *Bucklandia*, Sharma (1991) opined that features of leaf bases such as their shape, size, and arrangement pattern are of taxonomic significance. He observed that leaves in *Williamsoniaceae* show syndetocheilic stomata with rachis possessing collateral endarch vascular bundles arranged in a double U-manner. A distinct constriction was present at the base of lateral shoots as shown in Fig. 12.1.

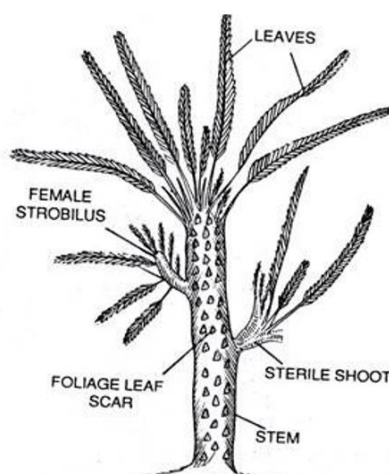


Fig. 12.1. *Williamsonia seawardiana* Sahni. Reconstruction shows a female strobilus and a sterile shoot.

Reproduction in *Williamsonia*: The fructifications of *Williamsonia* were large and attained a diameter of about 12 cm. They were borne on a peduncle. Many spirally arranged bracts were present around the base of the floral axis. In *W. gigas* the cones were present among the crown of leaf bases while in *W. seawardiana* they were present on the short lateral branches. *Williamsonia* plants were unisexual.

Female Flower: Genus. *Williamsoniella* (*Williamsoniella angustifolia*)

In another genus *Williamsoniella*, the strobilus was bisexual but round and there were no basal bracts, so it differed from *Cycadeoidea* only in the absence of bracts.

Affinities: In many respects the *Cycadeoideales* resemble the ferns on one hand and the cycads on the other. They resemble the ferns in the presence of a crown of leaves, persistent leaf bases, mesarch nature of vascular bundles direct course of leaf traces through the cortical region. In *Cycadeoidea* the presence of synangium is much like that of ferns in which we know the sporangia are fused to form synangia. The *Cycadeoideales* are closely related to *Pteridosperinales* on one hand and to cycads on the other, but they

have their characteristic features which distinguish them from all other gymnosperms except the Gnetales; this important feature that separates the Cycadeoideales from other Gymnosperms is the presence of eusporangiate strobili.

Some types of this group had short columnar stems like most of the living cycads. The short columnar stem was usually un-branched and at the apex of the plant there was a terminal crown of leaves. In present-day cycads the young leaves and megasporophylls remain covered up by unicellular ramenta whereas in Cycadeoideales these ramenta were scale-like. Like cycads the plants had well-organized strobili or cones.

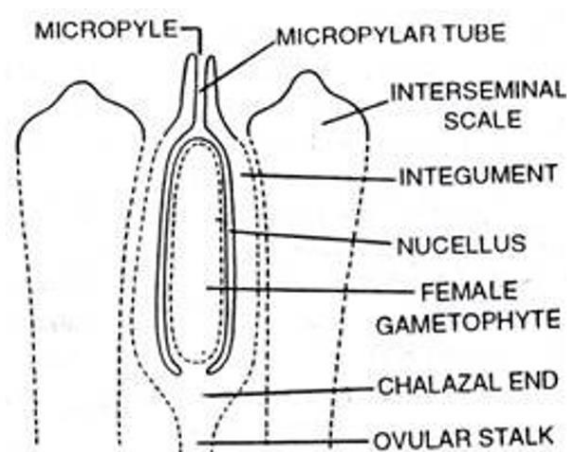


Fig. 12.2 Williamsoniella angustifolia. L.S. of ovule with inter-seminal scales.

A Majority of Cycadeoideales seems to have flowered only once in their life and after flowering the plant died out as we find in some of present angiosperms.

The female ‘cones’ of *Williamsonia gigas* and *W.ewardiana* have been investigated in detail. Instead of ‘strobili’ or ‘cones’, Sporne (1965) has proposed to use the term “flower” in *Williamsonia*. The structure of the female flower of *W. gigas* is illustrated in Figs. 12.3, 12.4. The conical receptacle was surrounded by many perianth-like bracts. The ovules were stalked.

The apex of the receptacle was naked and sterile. The nucellus was surrounded by a single vascularized integument, which was fused with the nucellus. The nucellus had a well-marked beak and a pollen chamber. In young ovules the micropylar canal was long and narrow. In mature ovules, the canal widened because of the formation of nucellar plug and the disappearance of interlocking cells. In the apical part of endosperm, Sharma (1979) observed 2 or more archegonia.

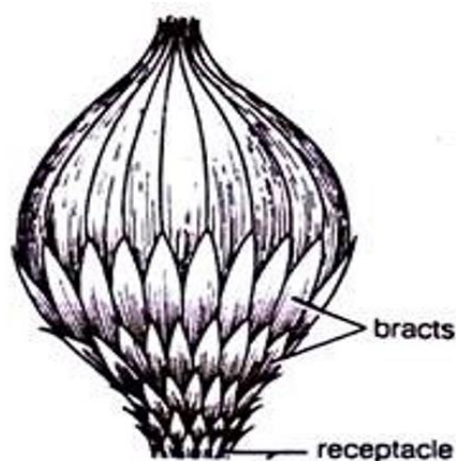


Fig. 12.3

Fig. 12.3. *Williamsonia gigas*. A female flower bud. (after Williamson).

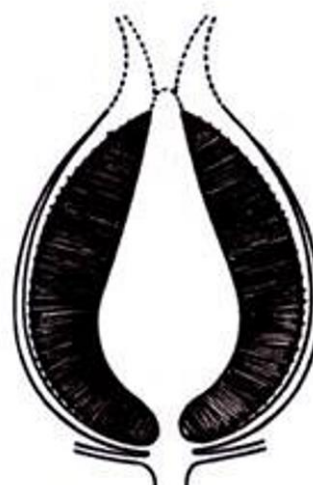


Fig. 12.4

Fig. 12.4. *Williamsonia gigas*. L.S. female flower. (after Williamson).

Male Flower

The male strobilus rather which has been described in some other species of *Williamsonia* had several stamens that fused to form a cup or disc-shaped structure. The free parts of the stamens had two rows of slender leaflets that were absent and only stalks were present. Out of several known male flowers of Bennettitales some have been described to belong to *Williamsonia*. Male fructifications have never been found in actual connection with the plant and are sometimes referred to as the genus *Weltrichia*. So, either on leaflets or on stalks there were two rows of pollen sacs. This way, the male portion of *Williamsonia* was like that of Cycadeoidea. Many male strobili have been described, but no trace of a female portion in them has been found, so these male strobili were unisexual while the female ones might have been bisexual.

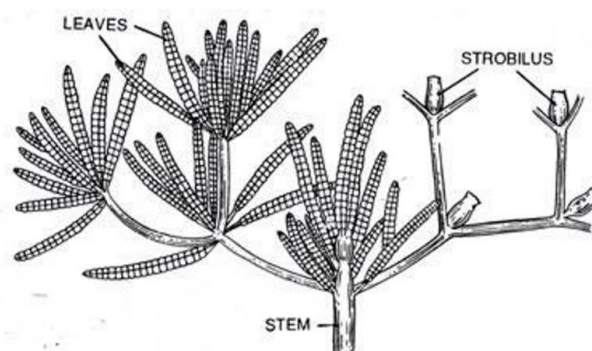


Fig. 12.5. *Williamsoniella angustifolia*. Reconstruction of a portion of a plant showing branched stem, simple leaves, and strobili.

Male flowers consisted of a whorl of microsporophylls, which were united to form a cup-like structure. In the majority of the investigated species (e.g. *Williamsonia whitbiensis*) the sporophylls were un-branched (Fig. 12.9) but in some species (e.g. *W.spectabilis*) they were also pinnately branched (Figs. 12.8, 12.7).

Sitholey and Bose (1953) discovered *Williamsonia santalensis* from Upper Gondwana (India), and observed that microsporophyll's in the species were bifid. One of the branches of microsporophyll was fertile while the other was sterile. The fertile part had finger-like structures called synangia. Each synangium had two rows of chambers enclosing microsporangia. Sharma (1977,1983, 1991) has confirmed the synangiate nature.

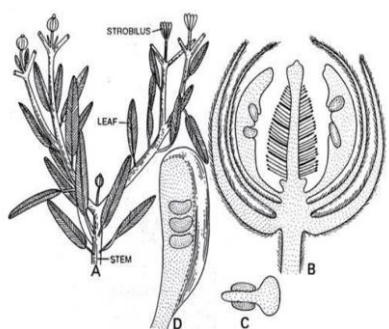


Fig. 12.6

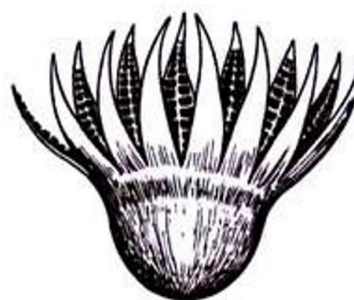


Fig. 12.7

Fig. 12.6. *Williamsoniella coronata*. A reconstruction of a portion of the plant showing branched stem, simple leaves, and strobili; B, V.S. of bisexual flower, C-D, microsporophylls.

12.7. *Williamsonia whitbiensis*. Pollen-bearing organs. (after Nathorst).

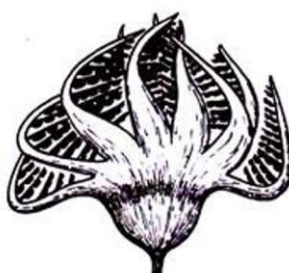


Fig. 12.8.



Fig. 12.9.

Fig. 12.8. *Williamsonia spectabilis*. Pollen-bearing organs. (after Thomas).

Fig. 12.9. *Williamsonia spectabilis*, showing the upper side of one lobe of pollen-bearing organs. (after Nathorst).

The entire male flower attained a length of about 20 cm, while a single microsporophyll was about 10 cm long. The fertile branch of the bifid sporophyll possessed many purse-like capsules, in which many monocolpate pollen grains.

GINKGO BILOBA

Division: Ginkgophyta

Class: Ginkgoopsida

Order: Ginkgoales

Family: Ginkgoaceae

Genera: Ginkgo

Ginkgoales is represented by only one living member, i.e. *Ginkgo biloba*. Ginkgoales were abundantly present during the Triassic period of Mesozoic era and were represented by 16 genera. All other genera, except *Ginkgo biloba* are now extinct. Dallimore and Jackson (1948) reported *G. biloba* to be represented by five different varieties which are *Ginkgo biloba* var. *aurea* (Nelson) Beisson, *G. biloba* var. *fastigata* Henry, *G. biloba* var. *paciniata* Carriere, *G. biloba* var. *pendula* Carriere and *G. biloba* var. *variegata* Carriere. Kaempfer.

(European botanist) first introduced the name “Ginkgo” in 1690. The same name was adopted by Linnaeus (1771). Due to the presence of several primitive characters, and because of its long geological records, Ginkgo is regarded as a living fossil. The name Ginkgo was first proposed in 1690 by, and the same name was adopted by Linnaeus (1771). Linnaeus proposed the name of species ‘biloba’ owing to presence of notch in leaves of the plant. Details of the geological history of Ginkgoales indicate that its members started appearing on the earth during Permian period and achieved worldwide distribution during Triassic and Jurassic periods of Mesozoic era and then started declining during Cretaceous period and now is represented only in some parts of Southern and Eastern China by one living member i.e. *Ginkgo biloba*. Ramanujam (1976) had reported some records of this order from Late Palaeozoic of India which includes Ginkgophyton, Psymophyllum and Rhipidopsis. Seward (1938) has considered Ginkgo to be one of the wonders of the world as the plant has survived and persisted with little changes till the present through a long succession of ages.

Characteristic features of *Ginkgo biloba*

1. Tall trees with excurrent habit
2. Deep penetrating roots with tap root system.
3. Deciduous nature of leaves.
4. Leaves are fan-shaped and possess open dichotomous venation.
5. Leaves arise singly along terminal branches.
6. Buds present in axil of leaves give rise to dwarf shoots. These shoots also bear cluster of leaves at their apex.
7. Growth of plant is comparatively slow.
8. Plant are dioecious in nature.
9. Wood is pycnoxylic.
10. Inflorescence is catkin like, contains microsporangiophores having 2-12 microsporangia that arise in axil of leaves on dwarf shoots.
11. Ovules arise in groups from apices of axillary branches.
12. Presence of tent pole in ovule is a characteristic feature.
13. Seeds are large and fleshy and produced in large numbers.
14. Integument comprises of outer fleshy orange colored portion and hard inner stony layer. fleshy coat is rich in butyric acid and produces an unpleasant smell on crushing. Seeds hang out for a period of 1-2 months after leaves are shed. This gives a beautiful look to the female tree. *Ginkgo biloba* is also known as the maidenhair tree.
15. Spermatozoids are motile.

Anatomy

Root: The transverse section of roots shows them to be circular in outline. Mature roots are surrounded by suberized cells of cortex. Young roots possess extensive cortex which is made up thin-walled cells. Tannin filled cells, mucilage cavities and cells with crystals of calcium oxalate are present in cortex. Young roots clearly depict the presence of a layer of endodermis and pericycle (Fig. 13.1). Such distinction is not visible in mature roots. Diarch or triarch condition is found in young roots, it means that two or three xylem strands alternate with same number of phloem strands. Xylem is exarch. Indistinct annual rings develop due to secondary growth.

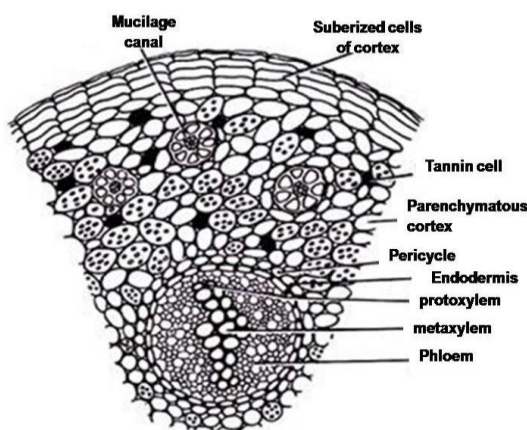


Fig.13.1: *G. biloba*: T.S. of young root.

Stem: The young stem is circular in outline. The outermost layer is the epidermis is single-layered made of brick-shaped cells and covered by thick cuticles (Fig.13.2 A). In older stem epidermis is replaced by periderm which originates from the cortex. The cortex layer next to the epidermis is extensive in dwarf shoots and comparatively narrow in long shoots. It contains mucilaginous canals, sphaeraphides and many tannin-filled cells. No distinct endodermis and pericycle are present. Stem of young stem contains several vascular bundles arranged in a ring. These are conjoint, collateral, open and endarch. These vascular bundles run longitudinally through the stem and branch to give rise to leaf traces. Once the secondary growth starts the vascular cylinder of the stem becomes an endarch siphonostele with no parenchyma in the wood except that of uniseriate medullary rays (Fig. 13.2 B). Uniseriate medullary rays are present which are 1-5 cells high in dwarf shoots and 1-15 cells high in long shoots. The stellar system in Ginkgo is eustele type. Protoxylem possess spiral thickenings while bordered pits are present on the radial walls of the metaxylem tracheids. Phloem consists of sieve tubes and phloem parenchyma. The centrally located pith is extensive in dwarf shoots and narrow in long shoots. Pith contains mucilage canals and calcium oxalate crystals.

Secondary stem growth: Secondary growth takes place through the activity of a single ring of cambium which remains active throughout the plant life. The wood is characterized to be pycnoxylic as well as manoxylic. Cambium after developing a complete ring cuts off secondary phloem elements towards outer side and secondary xylem towards the pith.

Cambium is made up of fusiform initials (which give rise to vascular elements) and ray initials (which give rise to uniseriate rays). The secondary phloem is made up of sieve elements, parenchyma, and phloem fibers. Companion cells are, however, absent. The secondary xylem is made up of tracheids and possesses weakly developed annual rings. Tracheids have moderately thick walls and most tracheids end at the same level. This makes the wood brittle having no economic value, tracheids contain circular bordered pits which may be present alternately or in opposite position. Cork cambium is present in the outer cortex and forms the periderm which replaces the epidermis. Cambium also forms a secondary cortex towards the inner side (Fig. 13,2 B).

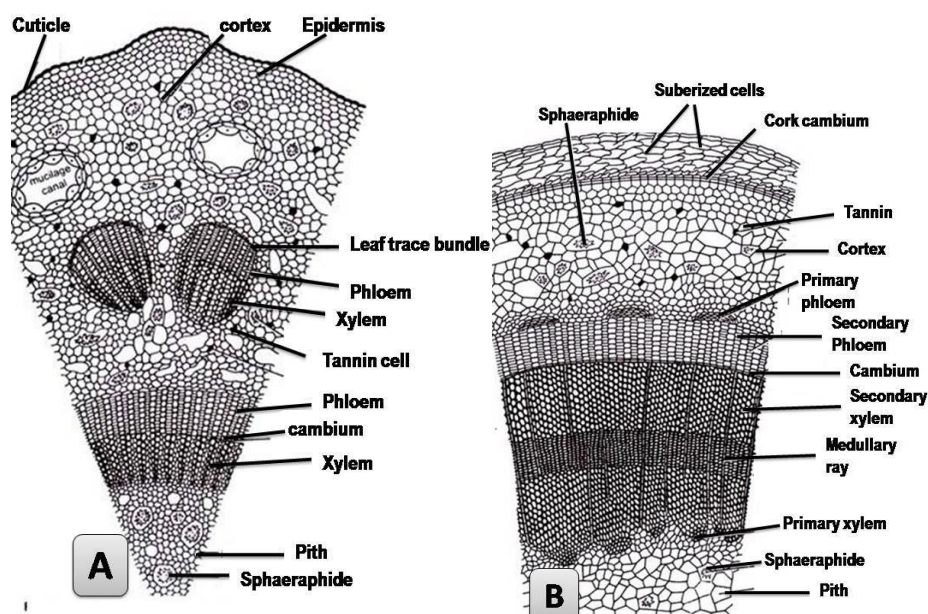


Fig. 13.2: *G. biloba*: (A)-T.S. of young and (B) mature stem.

Leaf: The upper as well as lower surfaces of the leaf are lined by a layer of epidermis covered by a cuticle. Epidermal cells are polygonal between the veins and rectangular over the vein. Stomata are haplocheilic type and present only on the lower epidermis. Kanis and Karstens (1963) have, however, reported some stomata to be present on the upper epidermis of the leaves on long shoots of male plants. Stomata guard cells are surrounded by accessory cells, which may be 4-6 or 7 in number. The mesophyll present between two epidermal layers is not well-differentiated into palisade and spongy parenchyma except in the old and mature leaves of long shoot. Many mucilage canals or secretory canals and a few tannin-filled cells are also present in the mesophyll region. Many loosely arranged chloroplasts are present in the mesophyll cells. The loose arrangement of chloroplast allows air spaces to be enclosed between them (Fig 13.3A).

Petiole: Petioles are covered with thickly cuticularized epidermis, whose continuity is broken by stomata. Inner to the epidermis are present a few hypodermal layers. Few mucilage canals, tannin-filled cells, and sphaeraphides are irregularly distributed in the cortex. The petiole has a pair of endarch vascular bundles (Fig.12.3 B). The vascular bundle is surrounded by a sclerenchymatous bundle sheath. Protoxylem contains spiral thickenings. The xylem is traversed by uniseriate rays. The medullary rays of the xylem are continuous with those of the phloem.

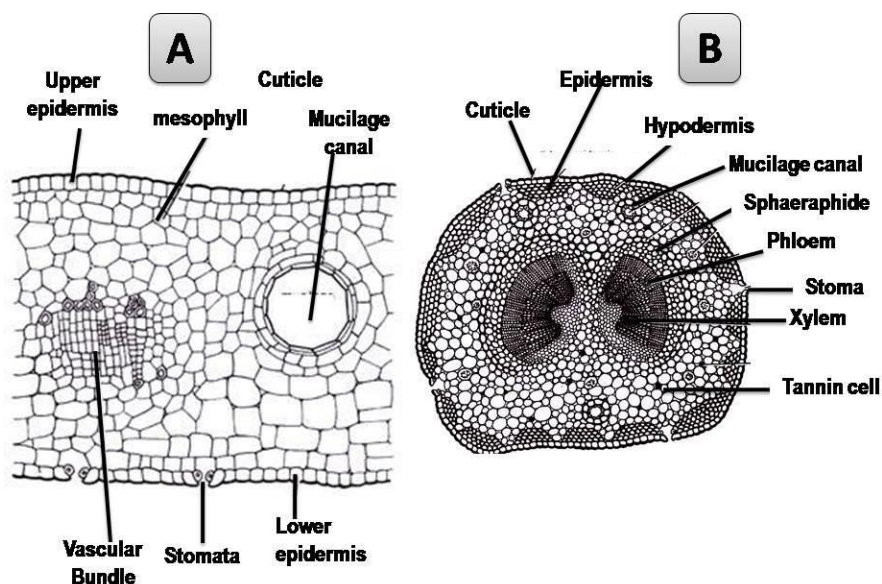


Fig. 13.3: A- T.S. of leaf of *G. biloba*, B- T.S of petiole of *G. biloba*.

Structures: *Ginkgo biloba* is dioecious. Male and female plants are, however, difficult to be differentiated when young. According to Lee (1954), sex in *Ginkgo* is determined by sex chromosomes (XY in males and XX in females).

Reproductive bodies of *Ginkgo* are the most primitive among living seed plants except for some Cycads.

(i) Male Strobilus: Microsporangiate strobilus arises in terminal and pendulous clusters from tips of spur shoots of male trees. They exhibit superficial resemblance with catkin inflorescence (Fig.13.4A). Each male strobilus contains several microsporophylls arranged loosely on a central axis. Each microsporophyll has a long stalk terminating into a hump or knob. It contains two pendant microsporangia (Fig.13.4 B). According to some workers, this terminal knob represents an abortive sporangium. A mucilage duct is present in the knob. Rarely more than two sporangia are present in a microsporophyll. Sporangia are tubular in structure having multilayered sporangial walls. The outermost layer is specifically differentiated into single-layered tapetum. Sporogenous cells form many tetrads of haploid microspores (through meiosis) which later separate into spherical microspores. Development of microsporangium is eusporangiate i.e., the single archesporial cell divides by a periclinal wall forming a primary wall cell and a primary sporogenous cell. The former develops into the wall of microsporangium while the latter develops into sporogenous tissue. Sporangium dehisces through a longitudinal slit.

Female Strobilus: Megasporangiate organs are borne on dwarf shoots of female trees. They arise in axils of foliage or scaly leaves at apices of dwarf shoots (Fig.13.4A). These are much-reduced structures, each having a long stalk or peduncle. Ovules are borne on long stalks or peduncle. Each long stalk possesses 2 or 3 (rarely more) ovules at the tip (Fig.13.4B). Peduncle bifurcates at tip to give rise to two branches each of which bears sessile ovules, from these only one exhibits maturation, and others get aborted. Each ovule is encircled at the base by a collar (which was regarded as megasporophyll by Chamberlain), four vascular traces supply to peduncle having two ovules, and with an increase in several ovules' vascular traces double. For example, if 3 ovules are present then many vascular traces will be six. The leaves surrounding the ovules do not show their bilobed character.

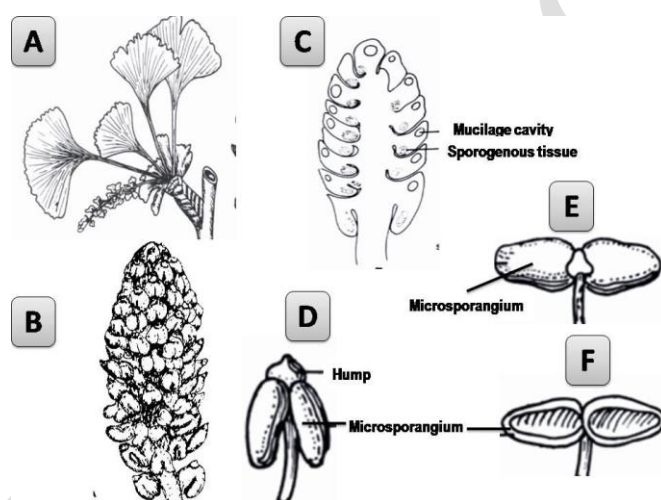


Fig. 13.4 *G. biloba*: A- Part of long shoot bearing short shoot and male strobilus, B- Male strobilus showing arrangement of sporophylls, C-L.S. of male strobilus, D- Microsporophyll with two pendant sporangia, E-Mature sporangia pulled apart due to dehydration, F- Condition after sporangia has dehisced.

The development of ovule, mega-sporogenesis and structure of the mature ovule is like that of *Cycas*. There is a thick integument consisting of three layers, i.e., outer fleshy, middle stony and inner fleshy layers. Each ovule is characterized by the presence of large and prominent nucellus. Free apex of the nucellus (nucellar beak) breaks down into a pollen chamber. A functional spore mother cell is present deep inside nucellar tissue. The spore mother cell undergoes meiosis and develops a tetrad, of which only the innermost megaspore remains functional developing into a female gametophyte. Ovule possesses well developed vascular supply. However, two vascular strands enter the inner fleshy

layer which reaches up to a free part of the nucellus without branching and the outer fleshy layer lacks vascular supply. Phylogeny of Ginkgoales: Ginkgo biloba exhibits several peculiar characteristic features such as bilobed and fan-shaped leaves having dichotomous open venation, presence of collar at the base of the ovule, a hump-like outgrowth at the apex of microsporophyll, presence of tent pole at the tip of the female gametophyte and absence of suspensor in its embryo. Besides these unique characteristics, Ginkgoales also exhibits similarity with different plant groups including Cordaitales, Pteridospermales, Filicales, Cycadales, and Coniferales.

Similarities between Ginkgoales and Cordaitales

(i) Presence of double leaf trace, (ii) Presence of endospermic beak in mature ovule, (iii) Motility of the spermatozoids.

between Ginkgoales and Pteridospermales

- (i). The presence of leaf gap in the stem,
- (ii). Wedged-shaped leaves with dichotomous open venation in Ginkgoales can be compared to pinnules of some seed ferns.,
- (iii). A distinct pollen chamber,
- (iv). A massive fleshy layer in the ovules,
- (v). The collar at the base of the ovules in Ginkgo can also be compared to cupule.

The ovules of some members of Pteridospermales.

Similarities between Ginkgoales and Filicales

- (i). Structure of the primary xylem, secondary xylem, and periderm of Ginkgo exhibit similarity with some ferns.,
- (ii). Leaves of both groups possess dichotomous open venation.,
- (iii). Spermatozoids are multilayered and motile.
- (iv). Distinct ventral canal cell in the archegonium.

Similarities between Ginkgoales and Cycadales

- (i). Large and multi-flagellated spermatozoids,
- (ii). Haustorial nature of pollen tube,
- (iii). Both the groups possess well-developed nucellar beak and pollen chamber, (iv). Presence of large egg, massive female gametophyte and well-developed venter of archegonia,

- (v). Endoscopic embryo development and embryo contains two cotyledons,
 - (vi). Seed with thick and well-developed integument,
 - (vii). Hypogeal seed germination.
 - (viii). Long period of free nuclear division in proembryo. Beside these similarities, there exist several differences between Ginkgoales and Cycadales which are:
 - (i). Difference between reproductive organ,
 - (ii). Difference in vascular supply of their ovules,
 - (iii). Branched stem in Ginkgoales and generally un-branched stem in Cycadales, (iv). Simple leaves in Ginkgoales and compound leaves in Cycadales.
 - (v). Presence of circinate venation in leaves of Cycadales which is absent in Ginkgoales.
- Resemblances with Coniferales: Ginkgo exhibits similarity with several members of Coniferales, due to which Ginkgoales are also viewed and kept under Coniferophyta. According to Florin Ginkgoales, Coniferales, Cordaitales, and Taxales belong to the same class "Coniferopsida".

Similarities between Ginkgoales and Coniferales are

- (i). Tree with cone like appearance.
- (ii). Monopodial and extensively branched stem.
- (iii). Leaves are of two types, green leaves and scales leaves,
- (iv). Leaves possess sunken stomata,
- (v). Wood pycnoxylic, with narrow cortex and pith.
- (vi). Secondary wood is well-developed,
- (vii). Medullary rays are uniseriate,
- (viii). Circular bordered pits are arranged uniseriately along the radial walls of the tracheids.
- (ix). Microsporangia show longitudinal dehiscence,
- (x). Sessile nature of ovule.

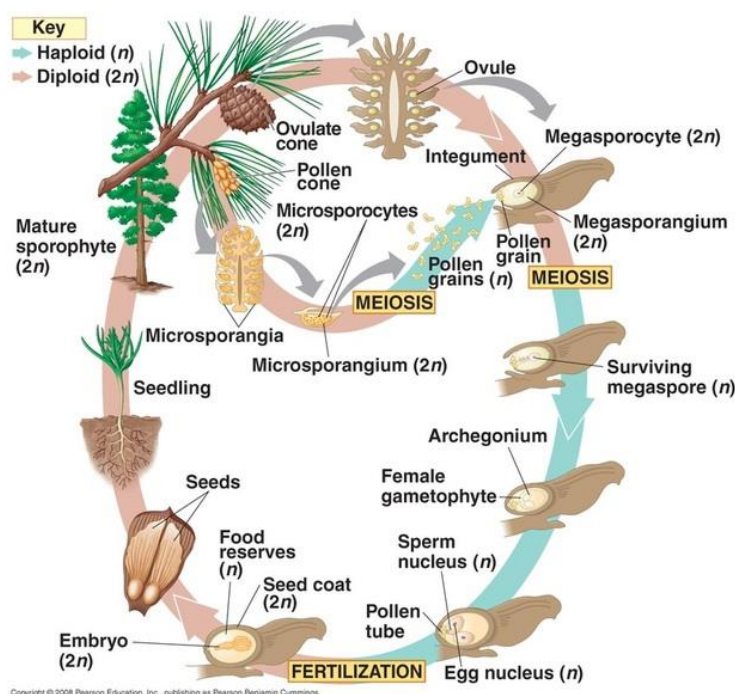


Fig. 13.5 Life cycle of *G. biloba*.

EPHEDRA

Division: Gnetophyta

Class: Gnetopsida

Order: Ephedrales

Family: Ephedraceae

Genus: Ephedra

Ephedrales with one family Ephedraceae is represented by a single genus Ephedra. Ephedra is uniformly distributed in regions of Western as well as Southern hemispheres including North and South America, France, Arabia, China, and northern parts of India. Out of about 40 reported species, 18 species have been reported from the Old World (France, Canary Islands, India, China) and about 22 species belong to the New World (North and South America). In India, it is represented by 6 species namely *Ephedra foliata*, *E. gerardiana*, *E. intermedia*, *E. nebrodensis*, *E. regeliana* and *E. saxatilis*. They are distributed in dry parts of Punjab, Haryana, Rajasthan, Kashmir and Sikkim.

1. The vegetative plant body is represented by roots, stem and leaves and exhibit xerophytic characteristics.
2. The Shrub plant body usually remains less than two meters in height in most of the species.

Ephedra compacta attain a height of about 30 cm and *E. triandra* reaches up to several meters.

3. The stem is green, ribbed, hard, profusely branched and glabrous.
4. Stem is distinctly jointed and bears long internodes (Fig.14.1).
5. Branches are green and photosynthetic.
6. The leaves are small, scaly, and rudimentary. They are present in opposite and decussate manner, or whorls of three or rarely four
7. Scaly leaves fuse at the base to form a basal sheath. Each leaf contains two unbranched, parallel veins. A bud, which forms the branch, is present in the axil of each leaf. True foliage leaves are absent in *Ephedra*.
8. Internodes grow through basal or intercalary meristem which is present at base of each internode.
9. A prominent underground tap root system is present having long, branched and deep roots. Roots lack mycorrhiza.
10. Plants are generally dioecious and rarely monoecious

Anatomy of Leaf: T.S. of the leaf shows presence of reduced and membranous scaly leaves which are oval in outline. The epidermis is cuticularized and contains elongated or oval cells. Stomata when present are sunken. Two to three (or even more) layers of chlorophyll-containing cells of palisade tissues are present. The major remaining part of the scaly leaf is filled with cells of spongy parenchyma (Fig.14.2). Several air spaces are present in the parenchymatous and palisade regions. The vascular bundles are small, two in number and remain embedded in the parenchymatous tissue (Fig.14.2).

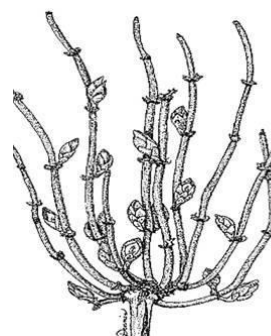


Fig. 14.1 Images of *Ephedra viridis* and *E. coryi*.

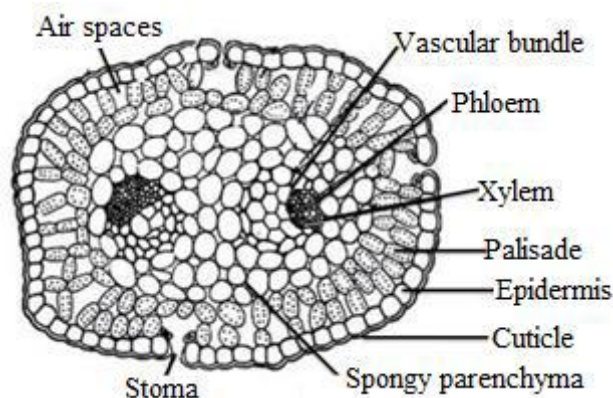


Fig.14.2. L. S. of a leaf of Ephedra.

Stem: Young stem contains thick-walled epidermis with thick cuticle. Several sunken stomata are present either in the grooves or along the sides of the grooves. Between thick-walled sclerenchyma and the vascular cylinder are present thin walled, chlorophyll containing cells. In some species green region is differentiated into palisade and spongy parenchyma. In very young stems endodermis is demarcated. However, clear demarcation of pericycle is not seen. The vascular cylinder is an endarch siphonostele formed by an interrupted ring of 8- 12 conjoint, collateral, open and endarch vascular bundles. Generally, the number of the primary vascular strands is eight, out of which four are foliar traces while the other four are stem-bundles. In each vascular bundle the xylem is present towards inner side while the phloem towards outer side. Xylem is made up of tracheids (annular or spiral), vessels, and xylem parenchyma. The vessels are characterized by bordered pitted thickenings. The phloem is made up of sieve cells, phloem parenchyma and albuminous cells. The albuminous cells in appearance resemble companion cells. Parenchymatous pith is well developed and centrally located which gradually becomes thick and sclerenchymatous in older stems (Fig.14.3A).

Secondary growth occurs due to vascular cambium present in between primary xylem and phloem. When a complete ring of cambium is formed, it cuts the secondary phloem towards the outer side and the secondary xylem towards the inner side. The formation of distinct annual rings occurs due to the varied activity of the cambium in different seasons. The secondary xylem is made of vessels, tracheid, and small amount of xylem parenchyma. Fibers are however, absent. The secondary phloem consists of sieve tubes and companion cells along with some albuminous cells. Vessels are modified tracheids. The largest vessels are formed in spring, but the size eventually decreases in the later part

of the season. The bordered pits sometimes become simple perforations as they may lose the torus and border of the pits (Fig.14.3 B).

Medullary rays are long, wide and clearly demarcated and consist of isodiametric, elongated or curved cells of varying sizes. They are uniseriate but can become multi-seriate through longitudinal divisions. Their walls are thick, lignified and pitted. The pits are simple and small. The wood of *Ephedra* is hard because of presence of thick-walled cells. The tracheids contain bordered pits which are uniseriate and more on the radial walls. Due to secondary growth in stems pith gets narrower and becomes very scanty in old stems.

Reproduction: *Ephedra* is dioecious as the male and female reproductive organs are present in different plants. However, in *E. foliata*, monoecious individuals are also known. Occasionally, an ovulate flower may be replaced by a staminate flower due to which strobilus becomes bisporangiate (*E. campylopoda*). *Ephedra* exhibits heterosporous condition i.e., two types of spores are found microspores in male flowers and megaspores in female flowers. Both male as well as female flowers are present in the form of cone-like, compact strobili. Since male and female plants of *Ephedra* do not show any specific morphological difference hence male and female plants can be identified or differentiated only at the stage of flowering.

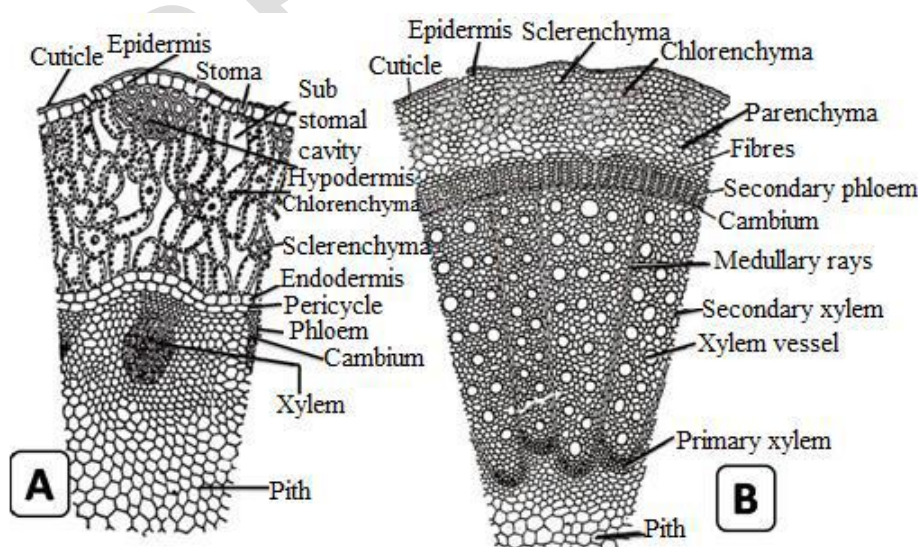


Fig.14.3 Stem of *Ephedra*, A- T S of the young stem, B- T S of the old stem.

Male strobilus: Male strobilus is a round or ovoid compound structure that arises in clusters at the node of the branches (Fig.14.4A). The strobili develop in the axil of a scaly leaf. Two to eight pairs of bracts remain arranged in opposite and decussate manner on the strobilus axis. All the bracts are fertile except a few on the lower side. A single male or staminate flower arises in the axil of each bract. Each male flower consists of two bracteoles and a stalked stamen. Bracteoles are thin opposite scales united at the base. They have been interpreted as perianth (Fig.14.4B). The stalk continues into a short axis or micro sporangiophore which bears terminally located about two to eight or even more microsporangia. Microsporangia are sessile and are bilocular or trilocular (Fig.14.4C).

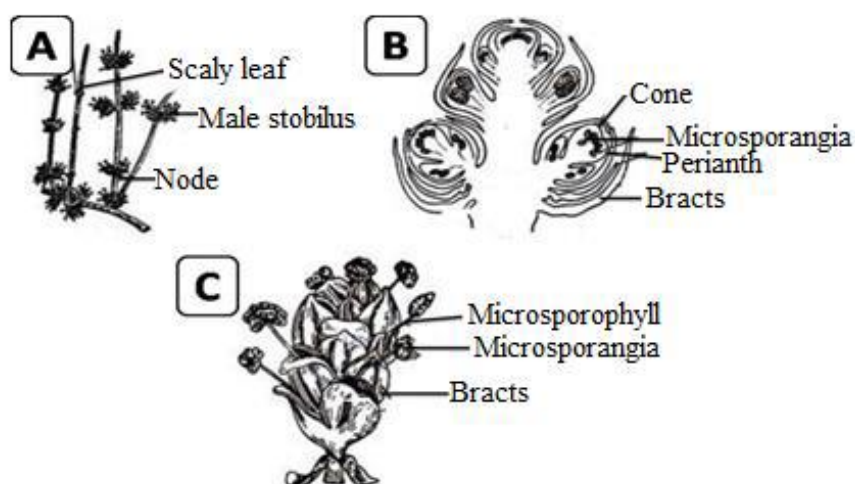


Fig.14.4 A-Shoot of Ephedra with male strobili, B- L.S. of Male strobilus, C- Complete male strobilus.

Development of Microsporangium: The development of microsporangium occurs from group of hypodermal cells which function as archesporium. Cells of archesporium are large with dense cytoplasm and a prominent nucleus. These cells divide periclinally to form outer primary parietal cells and inner primary sporogenous cells. Parietal cells further divide to form a tapetum (one cell thick). However, Singh and Maheshwari (1962) have reported primary wall layer functions directly as an outermost wall of the sporangium while the primary sporogenous cells form a middle wall layer, an inner tapetal layer, and sporogenous cells. The sporogenous cells divide to form many microspore mother cells (Fig.14.5). The latter divide meiotically to form spore tetrads. The haploid microspores later get separated. Rarely, the spores are arranged isobilaterally.

Male Gametophyte: The microspore is the first cell of the male gametophyte. Microspores are wingless, inaperturate and contain a thick exine. Germination of the microspore begins within the microsporangium, the microspore elongates and divides to form a prothallial cell. The second division results in the formation of a second prothallial cell. In *E. trifurcata* and *E. foliata* this second prothallial cell is not separated from the antheridial initial by a wall. However, Mehra (1938) reported the presence of a wall around the second prothallial nucleus in case of *E. gerardiana* and *E. saxatilis* however, it soon breaks down. The antheridial initial divides to form a tube cell and a generative cell. The generative cell further divides into the nuclei of stalk cell and body cell. The nuclei of stalk cell and body cell are surrounded by a mass of cytoplasm and these two are never separated by cell wall. Wind acts as pollinating agent, pollens shed at 5-celled stage are transferred up to the micropyle of ovule by wind. When the pollens reach ovule, the exine of the pollen grain gets ruptured and the intine comes out in the form of a tube. The generative cell divides and forms two male nuclei.

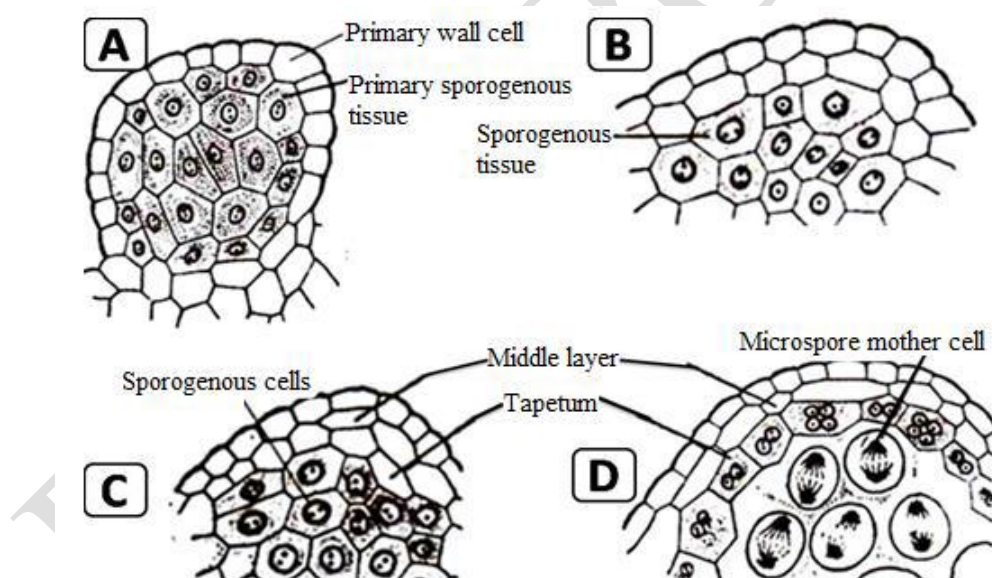


Fig.14.5 Different stages during microsporogenesis in Ephedra.

Female or megasporangiate strobilus: Female strobili arise in pairs at nodes, in the axil of leaves. Sometimes 3-4 strobili are found at each node. Female cone appears as an elliptical structure with a pointed apex. Each cone has a short axis to which 3 or 4 pairs of decussate bracts are attached (Fig.14.6A). Lower bracts are sterile while upper two bracts bear an ovule in the axil of each bract. The ovule has a short stalk, and this stalk ovule is known as a female flower (Fig.14.6 B).

Ovule or Megasporangium: Young ovule has a nucellus of parenchymatous cells. Nucellus is surrounded by outer and inner integuments (bitegmic). Inner integument grows at its tip into a long cylindrical tube (micropyle) that projects through the apical opening of the outer integument. This is called micropylar tube (Fig. 14.6 C). The archesporial cell (a hypodermal cell in nucellus at micropylar end) divides forming several outer cells (parietal cells) and one inner cell (megaspore mother cell). Megaspore mother cell divides meiotically forming linear or 'T' shaped megaspore tetrads. Usually lowest (chalazal) megaspore is functional and rest degenerate. Female Gametophyte: The functional megaspore is the first cell of the female gametophyte which enlarges, and its nucleus divides many times through free-nuclear divisions for about 20 days and about 256 nuclei in *Ephedra trifurcata* and 500 nuclei in *E. foliate* are formed. Nuclei are arranged around the central vacuole on the periphery of the megaspore. These nuclei are evenly distributed throughout. Formation of wall begins from outside which rapidly proceeds towards the center and makes the complete structure cellular. In female gametophyte cells in the upper part (reproductive region) are larger and elongated than the cells of the lower part (nutritive region). The nutritive region is differentiated into upper storage region and lower haustorium. The haustorial region is present near the chalazal end and bears some haustorial processes. A small pollen chamber develops near the micropyle in the nucellus.

Archegonium: Generally, *Ephedra* contains two archegonia, but the number varies from 1-3. An archegonial initial is differentiated in the upper reproductive region of the female gametophyte. Archegonial initial divides periclinal to form an upper primary neck cell and an inner central cell. The primary neck cell divides several times to form 4-5 or more tiers and followed by anticlinal divisions which result in the formation of more than 32 cells. Due to certain irregular divisions in neck cells, its tissue sometimes becomes indistinguishable from the other cells of the female gametophyte. The central cell enlarges, and its nucleus divides into ventral canal nucleus and egg nucleus. There is no wall formation between these two nuclei. The ventral canal nucleus may or may not move down towards the egg nucleus. The cells adjacent to the cytoplasm. A cell wall gets organized around each of these nuclei, and functions as a potential proembryo. Since more than one embryo is formed, hence it represents polyembryony without any cleavage. This is a unique feature of *Ephedra*. Some of the proembryos show initial development but ultimately only one matures. A tubular outgrowth, called suspensor

tube, develops from the proembryo. Its nucleus also divides simultaneously to form two nuclei i.e., embryo nucleus and suspensor nucleus separated by a wall. The embryo nucleus passes into the tube and develops continuously and carries the lower embryonal cell deep into the female prothallus. While the embryonal cell divides and develops into the embryo-proper containing two cotyledons. Organelles of proembryo are reported to be derived from the egg only i.e., they are maternal in origin. The seed contains a dicotyledonous embryo and is embedded within the tissue of female gametophyte. Seed germination occurs without any resting period and is of epigeal type central cell may divide transversely to form a clear 2-3 layered jacket. A mature archegonium thus consists of a long multilayered neck and a central cell containing a ventral canal nucleus and an egg nucleus.

Fertilization and embryogeny: During the process of fertilization, the pollen tube penetrates the archegonium and releases its contents into the egg cytoplasm. One out of two male nuclei fuse with the egg nucleus and form an oospore or zygote. The remaining male nucleus may fuse with the ventral canal nucleus, which results in double fertilization. However, no embryo formation occurs due to this second fusion. The zygotic nucleus divides by free-nuclear divisions to form eight free nuclei which are uniformly distributed throughout.

Economic importance of Ephedra: Some of the species are ornamental; an antibiotic ‘ephedrine’ is synthesized by many species including *E. gerardiana*, *E. intermedia* and *E. nebrodensis*. A decoction prepared from the roots and stems of several species is utilized in the treatment of syphilis and rheumatism.

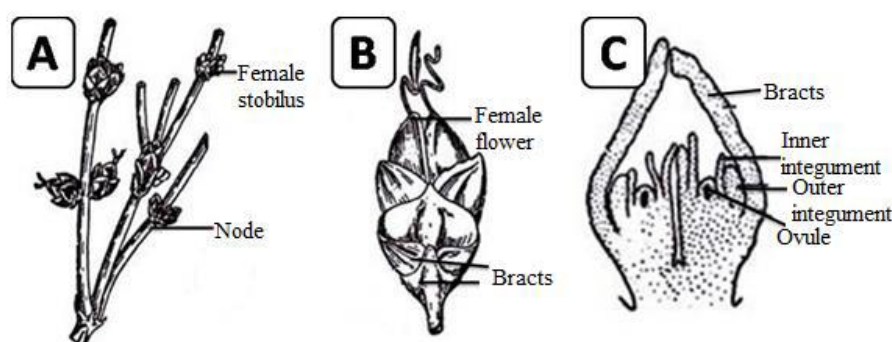


Fig.14.6 Ephedra female strobilus, A- Ovulate shoots, B- Female strobilus, C- L S of ovule.

ECONOMIC IMPORTANCE OF GYMNOSPERMS

Gymnosperms are of great economic importance in nature and have large economic importance for human beings. It gives valuable wood, resin, essential oils, gums, paper, turpentine, medicines, food, ornamentals, and miscellaneous items. Gymnosperms are frequently used as ornamentals in parks and gardens for their evergreen habit and symmetrical appearance. The trees are used for timber, building construction, resin, paper manufacturing, etc. They are also used in medicines, perfumes, varnishes, paints, and essential oils. While roasted seeds of *Ginkgo* are eaten at the feasts in China and Japan, to promote digestion and lower the effects of drinking wine. Seeds of *Pinus gerardiana* (Chilgoza) are used as dry fruit. Seed kernels of *Gnetum ula* yield oil for illumination and massage in rheumatism. The bark of *Taxus baccata* is used as the main ingredient of the famous 'Bhatia tea'.

1. **Food:** In some parts of India, Malaya, Philippines, and Indonesia, young succulent leaves of various species of *Cycas* are cooked and eaten as vegetables. The famous "Sago" starch is obtained from the stem/seeds of *Cycas* and used as food. This stem starch is obtained from *Macrozamia spiratis* is an important source of food for poultry, dairy animals, and pigs. The seeds of *Cycas* are used as a paste and eaten as cakes in the Nicobar Islands.
2. **Green Manure:** Leaves of *Cycas* are rich in nitrogen and used as green manure for rice, sweet potato, and sugarcane.
3. **Medicine:** Leaf extract of *Ginkgo biloba* is useful in the treatment of cerebral insufficiency and vertigo.
4. **Ornamental:** *Ginkgo biloba* and *Cycas* species are grown as an avenue tree and in gardens for beautification. These trees are preferred especially due to their slow growth, evergreen nature, and beautiful symmetry.
5. **Timber:** Conifers and Taxales are the most important genera to produce high-quality, straight-grained, light-colored, high-weight and strong wood in comparison to their weight. They take a fine finish with sharp tools, polish, and paint well. They are suitable for making cabinets and furniture due to their strength and durability. The wood of *Abies* is light and termite-free. It also has a pleasant smell and is used for packing cases, match wood, wood wool, aircraft work, plywood, light camp furniture, and as household materials. Juniper wood is fragrant, reddish brown, and rarely damaged by insects. *Cedrus* wood is also durable, oily, fragrant, insect repellent, and rot resistant. The wood of *Taxus* is strong, oily, elastic, close-grained,

fragrant, and very durable with a smooth, glossy surface. Besides this, the wood of *Araucaria cunninghamii* is used for plywood manufacture.

6. **Resin:** Conifers exudate resins, which makes the wood resistant to decay. Conifers are the major resin yielders of the world. These resins evaporate their oil and become harder which makes them invaluable in paints, varnishes, paper sizing, medicines, and liquor industries.
7. **Canada balsam:** A resin obtained from *Abies balsamea* which has a very high refractory index approximately that of glass. Due to this property, it is extremely suitable as an mounting medium for microscopic objects and as a cement for uses in optical work.
8. **Essential oils:** Steam distillation of young branches and leaves of conifers provide essential oils. Himalayan Cedar oil (*Cedrus deodara*) and Red Cedar Wood (*Juniperus virginiana*) are used for cleaning tissues in histological works and with the oil immersion lenses of the microscope. The oil obtained from *Cedrus atlantica* possesses medicinal properties and is used against bronchitis, tuberculosis, skin diseases, and gonorrhea. The essential oils are used extensively in the preparation of deodorants, room sprays, disinfectants, perfumery, medicine etc.
9. **Fatty Oils:** Many conifer seeds are rich in fatty oils. The oil from the seeds of *Pinus cembra* and *Torreya nucifera* is edible and used for paints. The Tail Oil obtained as a byproduct from sulphate process of cooking conifer wood for making Kraft paper is used in paints, soaps, linoleum, emulsifiers, etc.
10. **Pharmaceuticals:** The leaves of *Taxus baccata* are used in asthma, bronchitis, hiccoughs, epilepsy, and indigestion. Taxol (from *Taxus brevifolia*) is found effective against ovarian cancer, breast cancer, melanoma, and colon cancer. Ephedra is the source of a valuable drug, Ephedrine, obtained from *E. equisetina*, *E. gerardiana*, *E. major*, *E. sinica*, *E. intermedia*, and *E. nebrodensis*. It is used against colds, respiratory disorders, and hay fever. An aromatic beverage, known as Mormon tea, is also brewed from the species of Ephedra in the southwestern United States.
11. **Amber:** It is a fossil, water-insoluble tree resin that was secreted by the now extinct pine (*P. succinifera*). It is yellow, brown to black, hard, and brittle with an aromatic odor. *Araucaria* is a genus of evergreen coniferous trees in the family *Araucariaceae*. While today they are largely confined to the Southern Hemisphere, during the Jurassic and Cretaceous, they were distributed globally. There are 20 extant species in New Caledonia (where 14 species are endemic, see New Caledonian *Araucaria*),

Norfolk Island, eastern Australia, New Guinea, Argentina, Brazil, Chile, and Uruguay.

Araucaria

Class Pinopsida

Order Pinales

Family Araucariaceae

Genus *Araucaria* Juss. *araucaria*

Araucaria are mainly large trees with a massive erect stem, reaching a height of 5–80 meters (16–262 ft). The horizontal, spreading branches grow in whorls and are covered with leathery or needle-like leaves. In some species, the leaves are narrow, awl-shaped, and lanceolate, barely overlapping each other; in others, they are broad and flat and overlap broadly.

The trees are mostly dioecious, with male and female cones found on separate trees, though occasional individuals are monoecious or change sex with time. The female cones, usually high on the top of the tree, are globose and vary in size among species from 7 to 25 centimetres (2.8 to 9.8 in) in diameter. They contain 80–200 large edible seeds, like pine nuts, though larger. The male cones are smaller, 4–10 cm (1.6–3.9 in) long, and narrow to broad cylindrical, 1.5–5.0 cm (0.6–2.0 in) broad.

The genus is familiar to many people as the genus of the distinctive Chilean pine or monkey-puzzle tree (*Araucaria araucana*). The genus is named after the Spanish exonym Araucano ("from Arauco") applied to the Mapuche of south-central Chile and south-west Argentina, whose territory incorporates natural stands of this genus. The Mapuche people call it pehuén and consider it sacred. Some Mapuche living in the Andes name themselves Pehuenche ("people of the pehuén") as they traditionally harvested the seeds extensively for food.

No distinct vernacular name exists for the genus. Many are called "pine", although they are only distantly related to true pines, in the genus *Pinus*.

Distribution and paleoecology: Three members of the genus growing together left to right, *A. columnaris*, *A. cunninghamii* and *A. bidwillii* Members of *Araucaria* are found in Argentina, Brazil, New Caledonia, Norfolk Island, Australia, New Guinea, Chile, and

Papua (Indonesia). Many if not all current populations are relicts and of restricted distribution. They are found in forest and maquis shrubland, with an affinity for exposed sites. The earliest records of the genus date to the Middle Jurassic, represented by *Araucaria mirabilis* of Argentina and *Araucaria sphaerocarpa* from England. Fossil records show that the genus also formerly occurred in the northern hemisphere until the end of the Cretaceous period. By far, the greatest diversity exists in New Caledonia, likely due to a relatively recent adaptive radiation, as all New Caledonian species are more closely related to each other than they are to other *Araucaria*. Much of New Caledonia is composed of ultramafic rock with serpentine soils, with low levels of nutrients, but high levels of metals such as nickel. Consequently, its endemic *Araucaria* species are adapted to these conditions, and many species have been severely affected by nickel mining in New Caledonia and are now considered threatened or endangered, due to their habitat lying in prime areas for nickel mining activities.

Some evidence suggests that the long necks of sauropod dinosaurs may have evolved specifically to browse the foliage of tall trees, including those of *Araucaria*. An analysis of modern *Araucaria* leaves found that they have a high energy content but are slow fermenting, making their ancestors a likely attractive target.

General Architecture: Both genera have symmetrical growth. *Araucaria* branches form regular whorls at each node. The bottom branches are deciduous leaving a bare trunk with an umbrella-like crown at the apex. *Agathis* also has early deciduous branches that leave smooth scars and a smooth cylindrical trunk. The trees generally have large dividing branches near the top that form an immense spreading crown. Much research must still be done on *Wollemia*, but it is generally a larger tree with similar architecture to *Araucaria* and *Agathis*. However, it does not have a smooth trunk, but instead a bumpy or warty bark.

Leaves: *Araucaria* has broad sessile leaves that completely cover the shoot. They can be lanceolate, flat, leathery, sharp-pointed, or awl-shaped, with several parallel veins or smaller with a single vein. The leaves are spirally arranged, and they are clasping the stem while overlapping. The leaves can vary in size and shape on different parts of the same tree. *Agathis* leaves are also broad, but they are less crowded and are generally bigger than *Araucaria*. The leaves can also be lanceolate to ovate. They have a distinct petiole and tapering apices and are oppositely arranged on branches. *Agathis* leaves also

have an obvious palisade level. The leaves of *Wollemia* are very distinct; with parallel longitudinal veins, trimorphic leaves, and no conspicuous midrib.

Reproductive Structures: *Araucaria* can be monoecious or dioecious, in some species the male and female cones are found on different branches of the same tree. The pollen cones are dense and cylindrical occurring solitarily or clustered at the points of branches. The female cones can be round or ovoid. They are woody with closely overlapping scales that fall when the seeds are mature. The cones ripen for 2-3 years. There is one seed on each scale, and they adhere to the scale. The seeds are winged on each edge allowing easier dispersal. *Agathis* is monoecious. The male and female cones are usually found on the same tree. The seed of *Agathis* is free from the scale, usually having only one well-developed wing. The pollen cone is stiff, dense, cylindrical, and solitary; usually being found in the leaf axils. The female cones are also round and ovoid, but they are compact and symmetrical. The scale is usually fan-shaped with a thickened margin and usually overlap the scale above it. The cone usually falls after the seeds are away.

Agathis is monoecious. The male and female cones are usually found on the same tree. The seed of *Agathis* is free from the scale, usually having only one well-developed wing. The pollen cone is stiff, dense, cylindrical, and solitary; usually being found in the leaf axils. The female cones are also round and ovoid, but they are compact and symmetrical. The scale is usually fan-shaped with a thickened margin and usually overlaps the scale above it. The cone usually falls after the seeds are away.

Significant differences in *Wollemia* cones are still being cataloged, but some details are known. For instance, both female and male cones are fused completely to the spiny bracts, which are helically arranged. The seed has a single circumferential wing which is free from the bract-scale complex.

Wood: The wood of *Araucaria* is resinous, yellowish-white, and straight-grained. It is easily worked with and is useful for many purposes, especially for paper pulp. The bark of *Araucaria* is resinous and very thick on old trees. It is ridged with the bases of old leaves; or, in some species, it is rough and peeling off in papery scales. *Agathis* wood is of good quality and is also easily worked. It is very useful for various building purposes. The bark of *Agathis* is thick, scaly, and resinous. It emits a thick milky liquid when punctured, this liquid eventually solidifies and forms an incrustation on the bark.

Wollemi has a thin, spongy, nodular bark that sheds its outer surface in thin papery scales.

EJBPS BOOK

UNIT-IV: PALEOBOTANY

1. Palaeobotany: Scope and Objectives, Geological time scale.

The study of fossils across geological time, how they were formed, and the evolutionary relationships between taxa (phylogeny) are some of the most important functions of the science of paleontology. Such a preserved specimen is called a "fossil" if it is older than some minimum age, most often the arbitrary date of 10,000 years. The word fossil was derived from the Latin word fodere, which means to dig. The observation that certain fossils were associated with certain rock strata led early geologists to recognize a geological timescale in the 19th century. The development of radiometric dating techniques in the early 20th century allowed geologists to determine the numerical or "absolute" age of the various strata and thereby the included fossils.

The geological time scale (GTS) is a system of chronological measurement that relates stratigraphy to time and is used by geologists, paleontologists, and other Earth scientists to describe the timing and relationships between events that have occurred throughout Earth's history. The first serious attempts to formulate a geological time scale that could be applied anywhere on Earth were made in the late 18th century. The most influential of those early attempts divided the rocks of Earth's crust into four types: Primary, Secondary, Tertiary, and Quaternary. Each type of rock, according to the theory, formed during a specific period in Earth's history.

Geologists and paleontologists constructed the geologic table based on the relative positions of different strata and fossils and estimated the time scales based on studying rates of various kinds of weathering, erosion, sedimentation, and lithification. Until the discovery of radioactivity in 1896 and the development of its geological applications through radiometric dating during the first half of the 20th century which allowed for more precise absolute dating of rocks, the ages of various rock strata and the age of Earth were the subject of considerable debate. The first geologic time scale that included absolute dates was published in 1913 by the British geologist Arthur Holmes. He greatly furthered the newly created discipline of geochronology and published the world-renowned book *The Age of the Earth* in which he estimated Earth's age to be at least 1.6 billion years.

Evidence from radiometric dating indicates that Earth is about 4.54 billion years old. The geology or deep time of Earth 's past has been organized into various units according to events that took place in each period. Different spans of time on the Geological Time Scale are usually delimited by changes in the composition of strata that correspond to them, indicating major geological or paleontological events, such as mass extinctions. Based on time the geological time history of the earth has been divided into many categories named differently by the workers. The largest defined unit of time is the supereon, composed of eons. Eons are divided into eras, which are in turn divided into periods, epochs, and ages. Geologic units from the same time but in different parts of the world often look different and contain different fossils, so the same period was historically given different names in different locales.

Scope of Palaeobotany: Paleobotany research assists in solving the difficulties connected with the formation of the earth and the evolutionary connection among plants. It assists in observing the initial occurrence of various kinds of plants in the geological record. Paleobotany is significant in the reconstruction of ancient ecological procedures and climate, realized as paleobotany and paleoclimatology respectively; and is important to the survey of green plant improvement and evolution. Paleobotany, the study of fossilized plants and plant materials, offers valuable insights into the history of plant life on Earth. By examining the remains of ancient flora, palaeobotanists can reconstruct past environments, understand evolutionary processes, and elucidate the interactions between plants and their surroundings over geological time. This field intersects with various scientific disciplines, including geology, biology, and climate science, making it an essential area of research for understanding the Earth's history and the development of its biosphere.

Evolutionary Connections Among Plants: One of the primary objectives of paleobotany is to trace the evolutionary history of plants. By studying plant fossils, paleobotanists can identify the first appearance of different plant groups and trace their evolutionary trajectories. This research helps to.

- **Identify Ancestral Lineages:** Fossil evidence can reveal the characteristics of early plants and their relationships to modern species. This is crucial for constructing phylogenetic trees that illustrate the evolutionary pathways of plant lineages.

- **Understand Diversification Events:** Paleobotanical data can pinpoint periods of significant diversification, such as the explosion of angiosperms (flowering plants) during the Cretaceous period. These events often correlate with major ecological shifts and can provide insights into the factors driving plant evolution.
- **Study Extinct Species:** Fossils allow scientists to study species that have no living counterparts, offering a more comprehensive view of plant diversity and evolution through time.

Geological Record and Plant Occurrence: Paleobotany plays a critical role in documenting the first occurrences and subsequent evolution of plant types in the geological record. This involves:

- **Dating Plant Origins:** By examining the stratigraphic layers in which plant fossils are found, paleobotanists can date the emergence of different plant groups. This helps to establish a timeline for the evolution of major plant lineages.
- **Tracking Environmental Changes:** Plant fossils serve as indicators of past environmental conditions. Changes in plant assemblages over time can reflect shifts in climate, atmospheric composition, and other environmental factors.
- **Biogeography:** Fossil plants provide evidence of the historical distribution of plant species, offering clues about past continental configurations and the movement of plant lineages across the globe.

Reconstruction of Ancient Ecological Processes: Paleobotany is instrumental in reconstructing ancient ecosystems and understanding how plants interacted with their environment. This includes.

- **Paleoecology:** By studying plant fossils within their geological context, paleobotanists can infer the structure and composition of ancient ecosystems. This involves analyzing plant communities, their spatial distribution, and their interactions with other organisms, such as herbivores and pollinators.
- **Paleoclimatology:** Plant fossils are valuable indicators of past climate conditions. For example, the presence of certain leaf types or growth rings in fossilized wood can provide information about temperature and precipitation patterns during different geological periods.
- **Sedimentology:** Fossil plants can also aid in the interpretation of sedimentary environments. The types of plants found in a particular sediment layer can reveal

whether the area was a swamp, river delta, coastal plain, or another type of environment.

Contributions to Modern Science: Research in paleobotany extends beyond historical reconstructions, offering valuable contributions to modern science, including.

- **Climate Change Studies:** Understanding past climate conditions through plant fossils helps scientists predict future climate trends. This historical perspective is crucial for developing accurate models of climate change and its potential impacts.
- **Biodiversity Conservation:** Insights into past biodiversity and extinction events can inform current conservation efforts. By understanding how plants responded to past environmental changes, conservationists can better predict how modern ecosystems might react to ongoing climate change and habitat destruction.
- **Agricultural Development:** Studying the evolution of crop plants and their wild relatives can provide information about plant domestication processes and genetic diversity. This knowledge is essential for developing resilient agricultural systems in the face of climate change and other challenges.

Methodological Approaches in Paleobotany

Paleobotany employs a range of methods to study plant fossils, including:

- **Fieldwork:** Collecting fossils from various geological formations is a fundamental aspect of paleobotanical research. Fieldwork involves mapping fossil localities, excavating specimens, and recording their stratigraphic context.
- **Laboratory Analysis:** Fossils are often analysed using microscopy, chemical assays, and imaging techniques such as CT scanning. These methods allow scientists to examine the fine details of plant structures and identify microscopic features that are not visible to the naked eye.
- **Comparative Studies:** Comparing fossil plants with modern relatives helps to interpret their morphology and ecological roles. This comparative approach can involve both morphological and molecular analyses, including DNA studies from well-preserved fossils.

Interdisciplinary Connections

Paleobotany intersects with several other scientific disciplines, enhancing its scope and impact.

- **Geology:** Understanding the geological context of plant fossils is crucial for interpreting their age and environmental setting. Paleobotany often collaborates with stratigraphy, sedimentology, and paleogeography to reconstruct past landscapes.
- **Biology:** Evolutionary biology, ecology, and taxonomy are integral to paleobotanical research. Insights from modern plant biology help to interpret fossil data, and paleobotanical findings, in turn, contribute to broader biological theories.
- **Archaeology:** Fossil plants can provide information about ancient human environments and agricultural practices. Paleobotanical evidence from archaeological sites helps to reconstruct the diets and subsistence strategies of past human populations.

The scope of paleobotany is vast and multifaceted, encompassing the study of plant evolution, geological history, ancient ecosystems, and climate change. By integrating data from diverse sources and employing a range of methodologies, paleobotanists contribute to our understanding of the Earth's history and the development of life. Their research not only unravels the mysteries of ancient plant life but also provides valuable insights for addressing contemporary scientific challenges.

Significance of Palaeobotany

1. Palaeobotany research is helpful in solving the problems connected with the formation of earth and evolutionary (gradual development) relationship among plants.
2. It helps to discover the earliest occurrence of different kinds of plants in the geological record. This knowledge of sequential occurrence of taxa is then used to develop an understanding of environmental relationship among groups of plants.
3. Palaeobotany research may be helpful in determining what fossil plants were like, and the kinds of animals that utilised then as food and habitat. This information may be helpful to infer the characteristics of the ancient environment including the type of climate in which plants grow (reconstruction of ancient ecological system and climate is known as palaeoecology and paleoclimatology respectively.)
4. It is said that long ago continents moved. Palaeobotany helps in the study of problem.
5. The knowledge of Palaeobotany is also helpful in solving certain problems connected with the search of petroleum and coal.
6. Palaeobotany has also become important to the field of archaeology (the analysis and interpretation of plant tissues found at archaeological sites) primarily for the phytoliths (a

minute particle formed of mineral matter by a living plant and fossilized in rock) in relative dating and relative Paleoethnobotany.

(It is also called earth science, the study of fossil seeds and grains to farther archaeological knowledge, especially of the domestication of cereals. The proper chronological placement of a feature, object or happening in the geological time scale without reference to its absolute age is called relative dating).

Geological time scale: The geologic time scale is an essential tool for understanding the history of Earth and the evolution of life. In this lesson, explore the principal eons, eras, periods, and epochs that help us track major events in geologic history. How do we know when the dinosaurs died out? How do we know when birds first appeared on Earth or when humans evolved? What about the beginning of life itself? How was our planet formed and populated by living things over time?

To answer these questions, geologists use a special timeline called the Geologic Time Scale. It's a record of the earth's geologic history as scientists have come to understand it by studying the layers in rock. The geologic time scale is broken up into larger and smaller subdivisions, which help us, get a better sense of how historical events fit together.

The largest defined unit of time is the supereon, composed of eons. The first shows the entire time from the formation of the Earth to the present, but this compresses the most recent eon. Therefore, the second scale shows the most recent eon with an expanded scale. The second scale compresses the most recent era, so the most recent era is expanded in the third scale. Since the Quaternary is a very short period with short epochs, it is further expanded in the fourth scale.

Age: An age is a unit of geological time which is distinguished by some feature (like an Ice Age). An age is shorter than epoch, usually lasting from a few million years to about a hundred million years.

Epoch: An epoch is a division of a geologic period; it is the smallest division of geologic time, lasting several million years.

Period: Period is the basic unit of geological time in which a single type of rock system is formed, lasting tens of millions of years.

Era: Two or more geological periods comprise an era, which is hundreds of millions of years in duration.

Eon: Two or more geological eras form an Eon, which is the largest division of geologic time, lasting many hundreds of millions of years.

Geologic units from the same time but different parts of the world often look different and contain different fossils, so the same period was historically given different names in different locales. A key aspect of the work of the International Commission on Stratigraphy is to reconcile this conflicting terminology and define universal horizons that can be used around the world. The term "Anthropocene" is used informally by popular culture and a growing number of scientists to describe the current epoch in which we are living. In which humans have had an enormous impact on the environment--polluting its oceans, killing its species, etc. It has evolved to describe an "epoch" starting sometime in the past and overall defined by our carbon emissions and the plastic that is left in the ground. Geological time scale is a record of Earth's history based on the organisms that lived at different times.

P A L E O Z O I C	Late Paleozoic	PERMIAN 290	LYCOPODS, SEED FORMS AND AMPHIBIANS	Rise of conifers and cycads
		UPPER CARBONIFEROUS 323		Dominance of ferns, Calamitales, Lepidodendrales and Gymnosperms
		LOWER CARBONIFEROUS 323		Development of Lycopsidea, Calamitales, seed ferns
	middle paleozoic	DEVONIAN 417	FISHES AND EARLY PLANTS	Psilotopsida, Lycopsidea, Sphenopsida, ferns, Bryophytes and some algae
		SILVRURIAN 443		First known land plants, Dominance of algae
	Early Paleozoic	ORDOVICIAN 490		Marine and green algae, The time of rising of land plants
		CAMBRIAN 540		Evidence of algal origin
	P R O T E R O Z O I C			ALGAE AND BACTERIA
A R C H A E O I C			UNICELLULAR ALGAE	Probably very simple unicellular organisms

The geological time scale is a system of chronological measurement that relates stratigraphy (the study of rock strata, especially the distribution, deposition, and age of sedimentary rocks) to time, and is used by the geologists, paleontologists, and other earth scientists to describe the time and relationship between the events that have occurred throughout earth's history.

The first geological time scale was proposed in 1913 by the British geologist Arthur Holmes (1890-1965). This was soon after the discovery of the radioactivity and using it Holmes estimated that the earth was about 4 billion years old (evidence from radioactive dating indicates that the earth is about 4.5 billion years old). This was much greater than previously believed.

ERA	Major Divisions	Periods	Epochs	Dominant Organisms	Advances in Plant Life
C O E N O Z O I C	Quaternary		Holocene .01	Age of herbs Age of Angiosperms, Birds and Mammals	Increasing dominance of herbs
			Pleistocene 1.8		Specialization of herbaceous plants
	Tertiary	Late Tertiary	Pliocene 5.3		Increasing restriction of plants distribution and forests rise in herbs
			Miocene 23.8		Restriction distribution in plants
		Early Tertiary	Oligocene 33.7		Dispersal of woody angiosperms
			Eocene 54.8		Development flowering plants
			Paleocene 65.0		Modernization of angiosperms.
M E S O Z O I C	Late mesozoic	Upper Cretaceous		Higher Gymnosperms and Reptiles	Dominance of angiosperms, Dwindling of Gymnosperms
		Middle Cretaceous			Rapid development of angiosperms
		Lower Cretaceous 144			Origin of angiosperms, Dominance of cycads and conifers
	Early mesozoic	JURASSIC 206			Origin of angiosperms Dominance of cycads and conifers.
		TRIASSIC 248			Disappearance of seed ferns, cycads, conifers and Ginkgoales increasing

The geological time scale is divided into five main eras: Coenozoic, Mesozoic, paleozoic, Proterozoic, and Archezoic. Each era is divided into periods and each period is divided into epochs. It as follows.

There is another kind of time division used – the eon. The entire interval of the existence of visible life is called the Phanerozoic eon. The great Precambrian expanse of time is divided into the Proterozoic, Archean and Hadean eons in order of increasing age. The

names of the eras in the Phanerozoic eon (the eon of visible life) are the Cenozoic (recent life), Mesozoic (middle life), and Paleozoic (ancient life). The further subdivision of the eras into 12 periods is based on in identifiable but less profound changes in life forms.

2. Fossilization, Fossil types, Techniques in Palaeobotany.

Fossilization The formation of a fossil is an exceptional event, one that requires a special combination of favorable environmental conditions. In the most common fossilization process, the plant becomes covered by soft sediment that then hardens to form a sedimentary rock. This type of rock forms gradually, over long periods, as particles produced by erosion are compacted on the bottom of the body of water. The large-scale process by which plant parts become impregnated with minerals produces what has traditionally been called petrified wood. The modern term for this process is permineralization. Soluble carbonates, silicates, and other compounds infiltrate plant cells and the spaces between them.

Proterozoic and Archaean era together are known as Precambrian and comprises about 88% of the geological time (4500).		
P R E C A M B R I A N	COMPRISES ABOUT 88% OF THE GEOLOGICAL TIME 4500	First multicellular organisms
		First one celled organism
		Origin of earth

Eventually, the mineral deposits may completely replace the naturally occurring organic matter, preserving the details of the plant 's microscopic architecture. Being trapped in a sedimentary rock does not automatically guarantee that the organism will be preserved. The environment must be an anaerobic one that is, one in which oxygen is excluded thus preventing the decay that would otherwise result. The process may be interrupted by the action of waves or other erosive forces which re-expose the developing fossil before the process of fossilization is completed. Even after the process is completed, the well-preserved specimen may become distorted or altered in appearance because of the

combined effects of time, pressure, and high temperatures that convert sedimentary rocks into metamorphic rocks.

As one would expect, the harder cells and tissues of plants are more likely to be preserved as fossils than are softer ones. For example, the thick-walled cells of wood and bark (called xylem) are more often preserved than are those of the pith (centre of a stem) or cortex (found in stems and roots beneath the bark or outer covering). Other cells that are often fossilized are pollen grains and spores, both of which have outer shells that are highly resistant to decay. Limestone and dolomite are among the most common types of rocks that form in such a way that they trap plants and form fossils. Coal, a combustible sedimentary rock, is formed in much the same way as other rocks but is distinctive because the sediment involved is of plant, rather than mineral, origin. Within this matrix of plant-derived material is often embedded a variety of plant parts.

Preservation methods for fossils vary. Plants are fragile and often cook so that the carbon only remains. Animal bones and hard-shelled animals are harder, and often have minerals leaching into them replacing the original bone. Sometimes volcanic ash layers cover the plants or animals and preserve them. The most common method of fossilization is called permineralization or petrification. After an organism's soft tissues decay in sediment, the hard parts particularly the bones are left behind. Water seeps into the remains, and minerals dissolved in the water seep into the spaces within the remains, where they form crystals. These crystallized minerals cause the remains to harden along with the encasing sedimentary rock.

In another fossilization process, called replacement, the minerals in groundwater replace the minerals that make up the bodily remains after the water completely dissolves the original hard parts of the organism. Fossils also form from molds and casts. If an organism completely dissolves in sedimentary rock, it can leave an impression of its exterior in the rock, called an external mold. If that mold gets filled with other minerals, it becomes a cast. An internal mold forms when sediments or minerals fill the internal cavity, such as a shell or skull, of an organism, and the remains dissolve.

Organic Remnants: In recent years, researchers have discovered that some fossils aren't just made of minerals. Fossil analyses have shown, for instance, that some retain organic material dated to the Cretaceous, a period that lasted from 65.5 million to 145.5 million

years ago, and the Jurassic period, which lasted from 145.5 million to 199.6 million years ago. Tests suggest that these organic materials belong to dinosaurs because they match certain proteins from birds, which evolved from dinosaurs.

It's unclear how the organic material is preserved, but iron might help the proteins become cross-linked and unrecognizable, or unavailable to the bacteria that would otherwise consume them. Another idea is "microbial masonry, the bacteria that initially chomped through the tissue may be secreting minerals as a waste product that then hermetically [airtight] seal a little bit of what remains behind," almost like a stone mason sealing off a structure.

Moreover, sandstone rock made of sand-size grains of minerals, sediments or inorganic material seems to be the best type of environment for preserving organic material in fossils. The study of dead remains of the organism, or their imprints preserved in the geological rocks is called fossil. Fossils are used to study organisms present in the past. Word Fossil is derived from a Latin word for meaning to dig. Fossils are impressions or cast of the organelles (organism) living sometime back but now extinct,. They are present in rocks. Now they are required to be dug out. Normally the plant dies, and its degeneration starts immediately. This degeneration continues till the entire body is broken into chemical compounds. Thus, no evidence of its former remains in existence. But sometimes under certain circumstances, the degeneration of the plant body stops. Thus, parts of the body remain in visible form. These remains are known as fossils. These fossils are lifeless.

Plant fossils are normally present in rocks composed of sediments deposited in waters. These stratified rocks are superimposed upon one another in series. These rocks are built of sediments. These accumulate in the bottoms of seas, lakes, swamps, flooded valleys, subsiding beaches etc. The rock formation is correlated with the geological approach in the subject paleobotany. Fossil are the makers of geologic time. The study of botany as well as geology is essential for the study of fossil plants. The classification of fossil plants is very difficult as there are many chances for error.

A plant fossil is any preserved part of a plant that has long since died. Such fossils may be prehistoric impressions that are many millions of years old, or bits of charcoal that are

only a few hundred years old. Prehistoric plants are various groups of plants that lived before recorded history (before about 3500 BC).



Fig:15.1 *Ginkgo iteshuttonii*, Leaves preserved as compressions.

Plant fossils can be preserved in a variety of ways, each of which can give different types of information about the original parent plant. These modes of preservation are discussed in the general pages on fossils but may be summarized in a palaeobotanical context as follows. Six broad categories of plant fossils are commonly recognized. Although these categories seem well-defined, a given fossil may fall into several categories or may elude them all. Consequently, these categories should be thought of as broad modes of preservation rather than shoe boxes into which all fossils must go. When thinking about types of fossils and modes of preservation, it is more important to consider what types of biologically interesting information are or is not present than to fret over strict classifications. With that caveat, the basic types of plant fossils include.

1. Compressions
2. 2-dimensional, with organic material. Impressions imprints, 2-dimensional, devoid of organic matter. Casts and Molds.
- 3-dimensional may have a surface layer of organic material. Permineralization or Petrification 3-dimensional, tissue infiltrated by minerals, allowing internal preservation.
- Compactions 3-dimensional, reduced volume, flattened, wholly organic.

Molecular Fossils are non-structural preserves of organic compounds.

Each type of plant fossil carries different types of anatomical and biological information. Consequently, to piece together the most complete picture of an ancient plant, paleobotanists hope that the same type of plant or plant part will be preserved in several different styles.

Compressions are plant parts that have suffered physical deformation such that the three-dimensional plant part is compressed to two dimensions. Compressions retain organic matter, usually more or less coalified. Compressions of leaves, for example, differ from impressions in that some organic substance, often cuticle, is preserved. Peat, lignite, and coal are essentially compressions of thick accumulations of plant debris relatively free of encasing mineral sediment.

Compressions are excellent records of external form, especially for planar structures like leaves. They often preserve cuticle that can be recovered by dissolving the mineral matter in hydrofluoric acid (HF) or disaggregating in mild peroxide. The cuticle retains the imprint of epidermal cells, but other than this, cellular information can seldom be recovered from compressions. Consequently, compressions generally preserve plants at the organ, organism, and/or environment level. In addition, because compressions preserve organic material, carbon isotopic studies can be performed on compressions. From these studies, paleobotanists can sometimes recognize the biochemical signature of C3, C4, and CAM photosynthetic physiology in extinct species. Study the assortment of compressions available. Note color, texture, and type of deformation (usually flattening) experienced by each specimen. Notice distortion in original morphology is introduced by flattening.

Examine samples of coal, noting their weight, texture and surface features (dull vs. shiny). Identify discrete plant parts in the different ranks (essentially grades of metamorphism) of coal. Coal geologists recognize a continuum of degree of metamorphism in coal: peat - lignite bituminous coal (A-C) - anthracite. Peat is an accumulation of virtually unaltered plant material, while anthracite is nearly pure carbon with little trace of the original plant material. All materials can be burned for fuel, but the energy content per weight increases with degree of metamorphism and the proportion of impurities generally decreases. Study thin sections of coal at the microscope. Can you identify specific plant parts in the thin sections? Study samples of fusain (fossil charcoal).

Impressions: Impressions are two-dimensional imprints of plants, or their parts found, most commonly, in fine-grained sediment such as silt or clay. Impressions are essentially compressions sans organic material. If the sediment is very fine-grained, impressions may faithfully replicate remarkable details of original external form, regardless of

subsequent consolidation of the sediment. Study the specimens of impressions, noting the several categories of plant parts represented. Because of their shape, texture, and abundance, leaves are among the most common organ preserved in impression. Impressions may also occur if, when layers of rock are split apart, the organic material adheres to only one side of the rock. In this case, the side with organic material is the compression, known as the "part", while the corresponding impression known as the "counterpart".

One particularly interesting type of impression forms in "dirty" sand. In this type of sediment, relatively coarse sand grains are mixed with silt and clay. This type of sediment is common in river and flood plain environments so is important for terrestrial plant preservation. When a leaf falls into this type of sediment and begins to decay, the first organic bonds to break leave charged molecular tails hanging off the leaf surface. This charged tail attracts clay particles with opposite charge that linger within the sediment. The clay migrates to the leaf surface, coating the organic structure. This has two remarkable consequences: First, further decay is retarded because clay is occupying sites of organic reaction. Second, the fine clay allows remarkable detail to be preserved. Because most of the sediment is relatively coarse (sand), the organic material is lost later, but an exquisitely detailed impression is retained in the clay film. This mode of preservation is important in the Dakota Sandstone flora of Cretaceous age. It is also important in the preservation of remarkable animal fossils such as the Jurassic bird *Archaeopteryx* and the strange Cambrian invertebrates of the Burgess Shale.

Impressions, like compressions, record information about external shape and morphology of plant organs. However, because they lack organic material, cuticle and organic carbon cannot be recovered from them. In cases of impressions in very fine-grained sediment, some cellular detail can be recovered by making latex or silicone rubber cast of the impression.

Cast and molds: When sediment is deposited into cavities left by the decay of plant parts, a cast results. A mold is essentially a cavity left in the sediment by the decayed plant tissue. Molds are generally unfilled or may be partially filled with sediment. Casts and molds commonly lack organic matter, but a resistant structure like periderm may be preserved as a compression on the outside of the cast or the inside of a mold. Casts and molds may be found together, with the cast filling the mold.

Molds are formed when soft sediment surrounding the structure lithifies or hardens before the structure decays. When the mold fills in with sediment that subsequently hardens, a cast is formed. Casts of an internal hollow structure, like a pith cavity, are also common. Pith casts can be confusing because you are looking at the inside of the fossil-what in life would have been empty space. Like compressions and impressions, casts and molds record external (or sometimes internal) organ features well but provide no cellular or tissue information. Unlike compressions/impressions, molds, and casts often are truer records of the original three-dimensional shape of the structure. Casts of ancient trees are among the most impressive plant fossils.

Permineralizations or petrification: Permineralization occurs when the plant tissues are infiltrated with mineral-rich fluid. Minerals (commonly silica, carbonate, phosphate or pyrite, or rarely other minerals) precipitate in cell lumens and intercellular spaces, thus preserving internal structures of plant parts in three dimensions. This type of preservation is known as "structural preservation". Because organic material (commonly cell walls but in some cases finer detail) is preserved, permineralizations can yield detailed information about the internal structure of the once living plant. When mineral matter replaces the cell-wall and other internal structures, the preservation may be called petrification.

In petrified specimens, cellular details are lost with the organic material of the cell wall. Silica permineralization (silification) commonly occurs in areas where silica-rich volcanoclastic sediments are weathering. Silification is also an important preservation mode for Precambrian microbial remains deposited in near-shore marine environments.

Permineralization with calcium carbonate (calcite or dolomite) is particularly common in Carboniferous coal seams, where whole regions of peat were permineralized. Called coal balls (because of their sometimes round or ellipsoidal shape) or widow makers (because of their tendency to drop out of mine roofs onto the heads of unsuspecting miners), these fossils commonly preserve a hodge-podge of plants and plant organs. Permineralization with phosphate is uncommon for land plants, but can be important in some types of marine settings.

5. Compactions In this type of plant fossil, the plants or their parts get compressed by vertical pressure against one another. Mostly plant rudiments found in peat and coal as compactions. Coal or coal balls are the important sources of plant fossils. Coals are

irregular or sub spherical mass of calcium or magnesium carbonates (or some other mineral matter).

In peat, brown coals (lignite), middens and soft sediments, plant remains may retain their external form with only slight volume reduction due to compaction. Such tissues are not mineralized, retain resistant organic material, and may show unidirectional compression (flattening). Internal structure, especially of thick-walled, hard fruits is sometimes well preserved. These fossils may be sectioned by microtome or embedded and treated much like living tissues. Compactions are most common in the youngest plant fossils. Examine specimens of Tertiary fruits and seeds, and thin sections made from them. Pollen and spores are also preserved as compactions. The material making up their outer shells (sporopollenin) is extremely resistant to decay and can remain for hundreds of millions of year practically unaltered in the rock record. However, the pollen and spore shells, once spherical, are flattened by the compressive forces of lithification.

6. Molecular fossils: As more becomes known about the chemistry of modern plants, paleobotanists have begun to examine the fossil record for corresponding chemical data. For example, characteristic breakdown products of chlorophylls and lignin have been found in well preserved fossil leaves. Lipids and their derivatives have also been recovered from sediments. Some carbohydrate break-down products may also survive in sediment. An increase in abundance of these molecules in sediments of mid to Late Cretaceous age is used to document the increasing abundance of flowering plants.

Molecular fossils are recovered and studied using chromatographic techniques, mass spectrometry, and spectrophotometry. The preservation of these chemical products is highly variable, and depends on oxygen levels during deposition, temperatures experienced by the rocks since preservation, and many other physical and chemical factors. Fossil DNA and RNA have also been making headlines in the scientific press. In some exceptional cases, genetic material or proteins have been sufficiently well-preserved to permit their use in the reconstruction of evolutionary relationships, in much the same way as one might sequence living organisms. However, much of this work is controversial due to the difficulty of preserving and isolating these fragile molecules. Also, contamination by other materials is a common and difficult-to-recognize problem.

Amber: Coniferous plants exude resinous substance. It drops on the floor of forests. It accumulates and hardened over ages. Insects, fragments of plants and other animals get preserved in it and become fossilized. It is called ambers. Coal Balls: Plant organs of spherical shape and petrified are known as coal balls. These are formed by infiltration of calcium carbonate, magnesium carbonate, iron sulphide etc. in buried plant parts. These substances prevent the conversion of plant organs into coal and result in petrification. Hence these fossils occur in the form of coal balls. Majority of coal balls occur in localized region and may be congregated in definite bands or in scattered pockets. Coal balls are specifically significant in elucidating palaeobotanical information regarding the plant communities of geological past.

Coal Balls: Many millions of years ago (about 300 million to be more accurate) much of the earth's surface was covered by a swamp forest made up of plants quite different from anything living today. Some of the trees bore conspicuous markings on their bark which resembled fish scales. Another group of plants looked very much like ferns but reproduced by seeds rather than spores. These strange looking plants lived in a continuously mild, moist climate which made conditions for coal formation very favourable. Because of the large amount of coal formed from the remains of these plants, an appropriate name for this geologic time span is the Carboniferous. Coal balls are limestone nodules which are usually found in the upper layers of the coal seam, and which contain petrified plant fragments. Nobody knows for sure just how coal balls were formed, but the presence of limestone strongly suggests an oceanic or marine environment either close by or covering the organic litter. Coal miners do not like coal balls because they obviously do not burn and frequently are so hard and in such large masses as to make mining coal very difficult. Consequently, coal balls are discarded (Figure 1) along with other mine wastes. However, to a palaeobotanist (a person who studies fossil plants), such discarded coal balls are almost like Christmas presents. By studying these fragments, we can gain a large amount of information concerning their anatomy and very often their morphology.

Fossil-taxa Plant fossils almost always represent disarticulated parts of plants; even small herbaceous plants are rarely preserved whole. Those few examples of plant fossils that appear to be the remains of whole plants in fact are incomplete as the internal cellular tissue and fine micromorphological detail is normally lost during fossilization.

An added complication is that, as explained above, plant remains can be preserved in a variety of ways, each revealing different features of the original parent plant. Because of these difficulties, paleobotanists usually assign different taxonomic names to different parts of the plant in different modes of preservation. For instance, in the Sub arborescent Paleozoic Sphenophytes, an impression of a leaf might be assigned to the genus *Annularia*, a compression of a cone assigned to *Palaeostachya*, and the stem assigned to either *Calamites* or *Arthroxyton*, depending on whether it is preserved as a cast or a petrification. All these fossils may have originated from the same parent plant, but they are each given their own taxonomic name. This approach to naming plant fossils originated with the work of Brongniart (1822) and has stood the test of time; although non-palaeobotanists may find it a confusing system, it is generally regarded as the most practical way to overcome the special taphonomic difficulties encountered with plant fossils. For many years this approach to naming plant fossils was tacitly accepted by Palaeobotanists but not formalized within the International Rules of Botanical Nomenclature. Eventually, Thomas (1935) and Jongmans, Halle & Gothan (1935) proposed a set of formal provisions, the essence of which was introduced into the first International Code of Botanical Nomenclature (Lanjouw *et al.* 1952). These early provisions allowed fossils representing parts of plants in a particular state of preservation to be referred to as organ-genera.

The situation in the Vienna Code (McNeill 2006) was that any plant taxon except Diatoms whose type is a fossil is referred to as a fossil-taxon. Such taxa can refer to a morphotaxon, a particular part of a plant preserved in a particular way, as defined in the diagnosis of that taxon. Otherwise, the names of fossil-taxa are subject to essentially the same regulations as control the nomenclature of living plants, notably that the names are fixed to a type specimen, and that competing names are chosen mainly since chronological priority of first publication. Although the name is always fixed to the type specimen, the circumscription (i.e. range of specimens that may be included within the taxon) is defined by the diagnosis and can be changed by formal emendation. Such emendation could result in an expansion of the range of plant parts and/or preservation states that can be incorporated within the taxon. For instance, a fossil-genus originally based on compressions of ovules could be emended so that it also included the multi-ovulate cupules within which the ovules were originally borne. A complication can arise if, in this case, there was an already named fossil-genus for these cupules. If

paleobotanists were confident that the type of the ovule fossil-genus and of the cupule fossil-genus could be included within the newly emended genus, then the two names would compete as to being the correct one for the newly emended genus. However, this only happens if the actual type specimens (and not just specimens that are like the types) can be included within the newly revised taxon.

Clues from Fossils: Fossils are our best form of evidence about the history of life on Earth. In addition, fossils can give us clues about past climates, the motions of plates, and other major geological events. The first clue that fossils can give is whether an environment was marine (underwater) or terrestrial (on land). Along with the rock characteristics, fossils can indicate whether the water was shallow or deep, and whether the rate of sedimentation was slow or rapid. The amount of wear and fragmentation of a fossil can allow scientists to estimate the amount of wave action or the frequency of storms. Often fossils of marine organisms are found on or near tall mountains. For example, the Himalayas, the tallest mountains in the world, contain trilobites, brachiopods, and other marine fossils. This indicates that rocks on the seabed have been uplifted to form huge mountains. In the case of the Himalayas, this happened when the Indian Subcontinent began to ram into Asia about 40 million years ago. Fossils can also reveal clues about past climate. For example, fossils of plants and coal beds have been found in Antarctica. Although Antarctica is frozen today, in the past it must have been much warmer. This happened both because Earth's climate has changed and because Antarctica has not always been located at the South Pole. One of the most fascinating patterns revealed by the fossil record is several mass extinctions, times when many species died off. Although the mass extinction that killed the dinosaurs is most famous, the largest mass extinction in Earth history occurred at the end of the Permian period, about 250 million years ago. In this catastrophe, it is estimated that over 95% of species on Earth went extinct! The cause of these mass extinctions is not known, but most scientists believe that collisions with comets or asteroids were the cause of at least a few of these disasters.

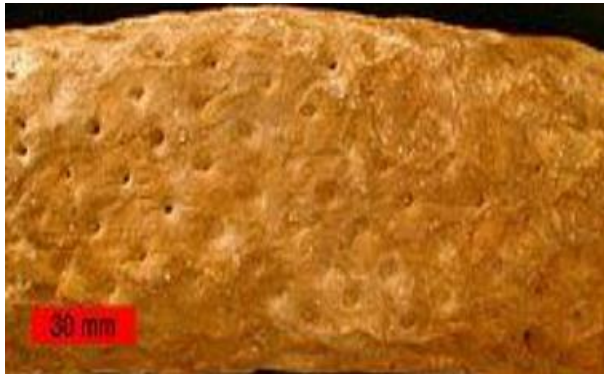


Fig.15.2 Stigmaria, a common fossil tree root

Fig.15.3 External mold of *Lepidodendron*

Process of Fossilization

Fossilization is the process that preserves evidence of life in earth's rock record. Understanding the process of fossilization, and the different means through which it can occur is used by taphonomists, paleontologists, and geologists to understand the lives of past organisms and the ancient environment in which they lived. The fossil record, however, is not a representative sample of past life, because certain organisms, and particular elements of those organisms, are more likely to be preserved than others. In addition, certain environments are more suitable for fossilization than others, and some environment will yield no fossil remains through time. Plants become fossilized in a variety of ways. Each type of preservation carries different information about the once-living organism. Thus, an appreciation of plant fossils requires that one understand the processes of fossilization and how each type of preservation may influence our view of once-living organisms. The study of how organisms or their parts become fossils is called taphonomy. Taphonomy is literally everything that happens to an organism or part of an organism, as is often the case with plants from the moment that it dies until it is collected and curated for scientific study.

Fossils include body fossils, left behind when the soft parts have decayed away, as well as trace fossils, such as burrows, tracks, or fossilized waste (faeces). The process of a once living organism becoming a fossil is called fossilization. Fossilization is a very rare process: of all the organisms that have lived on earth, only a tiny percentage of them ever become fossils. To see why, imagine an antelope that dies on the land, most of its body is quickly eaten by scavengers, and the remaining flesh is soon eaten by insects and bacteria, leaving behind only scattered bones. As the years go by, the bones are scattered and fragmented into small pieces, eventually turning into dust and returning their

nutrients to the soil. It would be rare for any of the antelope 's remains to be preserved as a fossil.

On the ocean floor, a similar process occurs when clams, oysters, and other shellfish die. The soft parts quickly decay, and the shells are scattered over the sea floor. If the shells are in shallow water, wave action soon grinds them into sand-sized pieces. Even if they are not in shallow water, the shells are attacked by worms, sponges, and other animals. Fossils are found in different types of rock like sedimentary and volcanic. Fossils are preserved in rocks and especially in sedimentary rocks. Igneous and metamorphic rocks do not contain fossils due to the high temperature and pressure involved in their formation. Igneous rocks form when magma cools, and metamorphic rocks form in the extremely high temperature and pressure under Earth's crust. For animals that lack hard shells or bones, fossilization is even rarer. As a result, the fossil record contains many animals with shells, bones, or other hard parts, and few soft bodied organisms.

There is virtually no fossil record of jellyfish, worms, or slugs. Insects, which are by far the most common land animals, are rarely found as fossils. Because mammal 's teeth are much more resistant than other bones, a large portion of the mammal fossil record consists of teeth. This means the fossil record will show many organisms that had shells, bones or other hard parts and will almost always miss the many soft-bodied organisms that lived at the same time. Because most decay and fragmentation occur at the surface, the main factor that contributes to fossilization is quick burial. Marine animals that die near a river delta may be buried by sediment carried by the river. A storm at sea may shift sediment on the ocean floor, covering and helping to preserve skeletal remains.

On land, burial is rare, so consequently fossils of land animals and plants are less common than marine fossils. Land organisms can be buried by mudslides or ash from a volcanic eruption or covered by sand in a sandstorm. Skeletons can be covered by mud in lakes, swamps, or bogs as well. Some of the best-preserved skeletons of land animals are found in the La Brea Tar Pits of Los Angeles, California. Despite the difficulties of preservation, billions of fossils have been discovered, examined, and identified by thousands of scientists. The fossil record is our best clue to the history of life on Earth, and an important indicator of past climates and geological conditions as well. The fossil record also plays a key role in our lives. Fossil fuels such as coal, gas, and oil formed

from the decayed remains of plants and animals that lived millions of years ago. The fossil record has its limitations, and its representation is more important.

- (i) The fossil records just present a snapshot of life in the past.
- (ii) Recognition of this limitation is critical in interpreting the fossil record.
- (iii) The Fayum in Egypt has a rich record of early primate evolution ending at about 31 mya, later fossilization conditions may not have been as ideal as in previous millennia.
- (iv) The same is true of the human fossil record: the best preservation is in eastern and southern parts of Africa after 4 mya.

There are two major types of fossils - body fossils and trace fossils. Both are the remains of living organisms. Body fossils reveal the body structure of the organism while trace fossils reveal the activities of these organisms. The process of fossilization is called taphonomy. There are three main components. First, there is the death of the organism. Then, there are certain processes that can happen to the organism before it is buried. These processes can include body decay due to natural elements such as wind, water or attack from predators. Finally, certain processes occur after the organism's body is buried. These processes result in the different categories of fossils.

How do fossils form?

There are many ways fossils can be formed including permineralization, recrystallization, replacement, and entrapment by amber. Methods of fossilization often involve rapid burial in such a way that predators and erosional effects are eliminated. This allows for the preservation of the body parts or trace evidence. Below are some examples.

Permineralization: Permineralization is a major method that involves the hardening of minerals that have entered the small pores and cavities of dead organisms. As hard water (water containing minerals) enters these pores, minerals are deposited and, under high pressures, become solid. Many biological tissues are full of pores and canals. After the soft parts decay, these hard parts are buried and then permeated with flowing groundwater. Calcium carbonate and silica precipitate out of groundwater and fill up the pores. New material comes in but none of the original material is removed. Example: "Petrified wood" completely permineralized with silica. Natural molds and casts form when the hard parts (such as shells) are buried in sediment leaving behind an impression

of its shape. If the interior of the shell were to be filled with sediment that hardened, an internal mold would be created. However, if the shell should dissolve away over the years, it will leave behind a mold of the shell (external mold).

Recrystallization: Some shells are made of unstable minerals (e.g. aragonite) that may revert to calcite after burial. Also, shells made from small calcite crystals may recrystallize into larger crystals.

The original shape is preserved, and the chemical composition remains the same, but the difference in texture is apparent.

Replacement: The original shell material may be dissolved due to water circulation. Original bone or shell material is then replaced without leaving a void; the original mineral is dissolved, and another mineral precipitates.

Carbonization: Fossils preserved as thin films of carbon on the bedding planes of sandstones and shales preserve the outline and details of the organisms.

How is fossilization dependent upon the environment? The environment plays a crucial role in an organism's ability to fossilize. The best scenario would be in which an organism is buried at the bottom of a lake where it is then covered by a lot of sediment. In this type of environment, the organism is protected from other animals and natural elements that would cause the body's breakdown. It is crucial that the body be in an environment that allows for rapid burial. An area in which there is a high rate of sediment deposition is ideal because of the presence of minerals and the increase of pressure. The environment can also affect where the fossil is found. For example, river currents can carry a body away from the site of death before it is buried. Drier environments, such as land, are more susceptible to the effects of erosion and so it is more difficult to preserve the organism before it decays.

Levels of preservation. The preservation of plant fossils can take place at several levels. Each level contains a different type of information. The fate of most organic material produced by living systems is to be decomposed to carbon dioxide and water and recycled into the biosphere. The circulation of elements through biogeochemical cycles indicates that decomposition is, indeed, efficient; however, the presence of organic material in sedimentary rocks (e.g., coal, petroleum, dispersed organic matter, and

fossils) shows that some organic matter - or its traces - escapes these cycles to be preserved in the rock record. The study of paleobotany relies on this preserved material fossils as evidence of past life. In the early history of modern paleontology, fossils were thought of mostly as static parts of the rock record ("sticks in mud"). Plants become fossilized in a variety of ways. Each type of preservation carries different information about the once living organism.

(i) Cellular Level: Not all organic compounds are equally resistant to chemical degradation and decay. Plant cell walls (composed primarily of the polysaccharide polymer cellulose) are far more likely to escape decomposition than internal membranes and organelles, which are rich in proteins, lipids and sugars. Preservation of cytological details has been reported in fossil plants, but occurrences are rare, and most reports of fossilized nuclei and organelles should be read with caution. Secondary compounds, such as those impregnating or covering cell walls, can also be resistant to decomposition; examples include lignin, waxes, cutin (which comprises plant cuticle), and sporopollenin, which forms the external shell of spores, pollen, and the resting cysts of some marine algae.

(ii) Tissue Level: Decay-resistant materials are distributed differentially throughout the plant. Consequently, some tissues are more amenable to preservation in the fossil record than others. Concerning vascular tissue, xylem is often preserved, while phloem is commonly not. This is because the cell walls of xylem are impregnated with decay-resistant lignin, while phloem cell walls are cellulose. Cuticle, composed of the resistant material cutin and various waxes, is more likely to be preserved than actual epidermal cells, however, the shape and distribution of epidermal cells, including guard cells, is faithfully preserved in cuticle. Spores and pollen, because of their resistant spore coats, are the most abundant and ubiquitous structural remains of vascular plants preserved in the rock record. Because they are easily preserved and found in great numbers, pollen and spores (palynomorphs) provide important quantitative data for vegetation reconstruction and a variety of paleoecological questions.

(iii) Organ Level: Plants break apart, both in life and after death, dispersed parts may be transported before settling into the sediment to be buried and become fossils. Assemblages of plant fossils that are preserved close to where their parent-plants originally grew are called autochthonous; assemblages that have been transported are

referred to as allochthonous. Whether an assemblage is autochthonous or transported has obvious implications for what sorts of ecological interpretations we can make from it. Therefore, as you study each type of plant fossil preservation, think about whether fossils produced in these ways are autochthonous or not.

Some deposits contain only palynomorphs (e.g., pollen, spores, and a few other dinoflagellates), while others may contain only large chunks of wood or scattered leaves. Reproductive organs, especially flowers, are relatively rare in the fossil record because they are delicate and full of energy-rich, easily broken-down compounds. Other reproductive structures are sometimes preserved, however, constitute a valuable source of taxonomic and evolutionary information. Fruits and seeds often contain resistant tissues (e.g., sclerenchyma) that yield clues to the reproductive morphology and biology of ancient plants.

When organs are found isolated (not in organic connection), each type of leaf and seed is given its own binomial name (genus and species name according to the International Code of Botanical Nomenclature), without making any assumption about what belongs to what. To use the example discussed by Oliver and Scott (1904), leaves were described as *Lyginopteris* (genus only for brevity), seeds as *Lagenostoma*, and stems as *Lyginodendron*.

The last syllable of each name gives a hint to the organ type such as "dendron" is used for stem, "pteris" is often used for frond-like foliage, and "stoma" for seed. However, after Oliver and Scott's recognition of the unique glands on *Lagenostoma* and species in the other organ form genera, they were able to make the whole-plant link with greater confidence. The whole plant then takes the name of the organ first described, in this case of *Lyginopteris*.

(iv) Organism Level: Not all plants in each community are equally likely to find their way into the fossil record. Processes of fossilization often favor large or woody plants with resistant tissues over small herbs. Likewise, wind dispersed pollen is much more common in the fossil record than pollen dispersed by animals. Also, plants growing in or near an area of preservation (e.g., riverbank or swamp) are more commonly preserved than their counterparts growing far from water or anoxic sedimentary environments. Plant preservation depends on removing the organic material from the zone of aerobic

decomposition. This is most easily accomplished by burying the plant. Consequently, swamps, deltas, lakes, lowland flood plains, and volcanic areas are good spots for fossilization.

Conditions required for plant fossil preservation Three conditions are required for the preservation of plant fossils.

1. Removing the material from oxygen-rich environment of aerobic decay.
2. "Fixing" the organic material to retard anaerobic decay.
3. Introducing the fossil to the sedimentary rock record (burial).

Consequently, plant fossils are generally preserved in environments very low in oxygen (e.g., anaerobic sediment) because most decomposers (e.g., fungi, most decomposing bacteria and invertebrates) require oxygen for metabolism. Such sediments are commonly Gray, green or black rather than red, a sedimentary signal of oxygen-rich conditions. The "fixing" requirements means that plant material must fall into an environment rich in humic acids or clay minerals, which can retard decay by blocking the chemical sites onto which decomposers fasten their degrading enzymes. Plant material can also be "fixed" by removing degradable organic compounds during the process of charring by wildfire. This is a common and spectacular mode of preservation for flowers. Plant material can then be incorporated into the rock record in areas where sediment is being deposited, which usually, but not always, requires the presence of water. Consequently, streams, flood plains, lakes, swamps, and the ocean are good candidates for fossil-forming systems. Plant fossils are commonly preserved in fine-grained sediment such as sand, silt, or clay, or in association with organic deposits such as peat (coal).

3. General account of Fossil Gymnosperms with special reference to *Williamsonia* and *Pentoxylon*.

Systematic Position of Pentoxylales.

Sporne (1965) has rightly stated that "the correct phylogenetic placing of the Pentoxylales is a most fascinating problem". Birbal Sahni (1948) had already expressed almost similar views.

We are faced with a real difficulty when we try to ascertain the place of the Pentoxyleae" While in their seed attachment they are clearly stachyosperms (Coniferophytes), and they also have a coniferous type of secondary wood, their stomatal structure is fundamentally

bennettitalean, the vascular anatomy of their leaves is truly cycadean, and the general anatomy of the stem is unique” (Sahni, 1948).

According to him, Pentoxyleae “occupy a unique and rather isolated position”. Vishnu-Mittre (1957) opined that if characters of stems, leaves, and male and female reproductive organs are compared, Pentoxyleae exhibits close affinities with Cycadales. The group (Pentoxylales) “should thus be given an equal rank amongst the Bennettitales and the Cycadales”.

Rao (1974) has also expressed almost similarly. Because definite organic connections between the discovered organ genera of Pentoxylales has not so far been established or completely proved, this fascinating topic should be kept pending “till more structural data about them and their mutual organic connections are discovered”.

Discovery of Pentoxylales

This group has been discovered and named “**Pentoxyleae**” by well-known Indian Palaeobotanist Professor Birbal Sahni (1948). This is a group of some fossil plants described from Rajmahal Hills in Amrapara District (Santhal Parganas) of Eastern Bihar (India) revealing their existence in Jurassic Period.

Sahni (1948), while introducing this group, remarked: “Some discoveries in size help or appear to help in the solution of the old standing problems, others and these are perhaps the most interesting, seems to create new difficulties in our path.”

True to his words, Professor Sahni’s discovery of Pentoxyleae has created many new problems to the taxonomy of gymnosperms, as well as has become a threat to our understanding of the evolution of gymnosperms.

While Pentoxyleae exhibits certain characteristics, not shown by members of any other group of gymnosperms, this also shows a combination of features characteristic of the Bennettitales, Cycadales and Coniferales.

Lam (1952) suggested that Pentoxylae should be given a rank equivalent to Bennettitales and Cycadales in the Gymnospermous classifications. Sporne (1965) has treated this group as an order under the name “Pentoxylales”.

Harris (1962) also discovered some members (*Carnoconites cranwelli*) of this group from New Zealand. B P. Srivastava (1946) and Vishnu-Mittre (1953, 1957) are some of the major Indian contributors on Pentoxylales.

Stems, leaves and male and female reproductive organs of this group have been described under following names

Stems: *Pentoxylon* and *Nipanioxylon* Leaves: *Nipaniophyllum*.

Distinguishing Features of Pentoxylales:

1. Extinct Mesozoic plants found in the Jurassic period.
2. Although the exact habitat of these plants is not established, these were probably shrubs or very small trees.
3. Long and short shoots were present on these plants.
4. Short shoots had spirally arranged leaves and terminally located reproductive organs.
5. Leaves were thick, simple, lanceolate, and had diploxylic leaf trace.
6. Stomata were formerly thought to be syndetocheilic, but now they are haplocheilic.
7. Leaves possessed open venation.
8. Stems were polystelic. Basinger et al. (1974) opined that “it may be more appropriate to call each stele as vascular segment or sympodium”.
9. Wood of *Pentoxylon* was pycnoxylic and resembled *Araucaria*.
10. Ovules were sessile.
11. Female reproductive organs were like stalked mulberry, consisting of about 20 sessile seeds attached to central receptacle and surrounded by stony layer and then fleshy outer layer of integument uniting them.
12. Male reproductive organs or microsporophyll's form whorl of branched micro-sporangiophores.
13. The micro-sporangiophores were fused basally into a disc-like structure.

Stem Genera of Pentoxyleae

(i) *Pentoxylon Sahnii*

Pentoxylon sahnii and *Nipanioxylon guptai* are the stem genera of “Pentoxyleae”. The stems of *Pentoxylon sahnii* attained a diameter from 3mm to 2 cm. The stem has always been reported in association with the leaves called *Nipaniophyllum*.

Presence of five steles in a cross-section of the stem has been the main reason for giving the name *Pentoxylon* to the genus. Many short lateral shoots or dwarf shoots were also present on the stem. Five steles (Fig.15.4) occupied the greater part of the stem in a cross-section. Each stele had its own cambium. The cambium was uniformly active in the young stems, but at maturity, more secondary tissue developed towards the center, and thus the secondary wood appeared eccentric.

Primary phloem and primary xylem were present towards outer and inner sides of the cambium, respectively. Six steles have also been observed by Sahni (1948), although rarely. According to Vishnu-Mittre (1953) the number of steles varied along the length of the stem.

There were present five much smaller bundles just alternating with the main bundles of the stem i.e. five steles. Each such bundle had a large amount of secondary wood. These were probably the leaf trace bundles.

Medullary rays of the main steles were uniseriate, and they lacked ray tracheids, wood parenchyma and resin canals. The secondary wood resembled greatly with that of *Araucaria*. Uniseriate or bi-seriate bordered pits were present on the radial wall of tracheids.

(ii) *Nipanioxylon*: This stem genus of *Pentoxyleae* was discovered from the village Nipania and hence named *Nipanioxylon*. Village Nipania is in Rajmahal Hills, near Dumarchir in the Amrapara district (Santhal Parganas) in Bihar (India). *Nipanioxylon* differed from *Pentoxylon* in possessing larger number of bundles (steles) and less developed secondary growth in the stem. *Nipanioxylon* resembled *Pentoxylon* in other details.

5. Leaves of *Pentoxyleae*

***Nipaniophyllum*:** The leaves have been described under the name *Nipaniophyllum raoi*. They were found attached with the shoots or *Pentoxylon sahnii*. They were originally described under the name *Taeniopteris*. They were present on the short lateral shoots (Fig. 15.5). Each leaf was simple, petiolate, strap-shaped, and possessed a well-developed mid rib with many parallel lateral veins. Branching has not been observed in lateral veins

6. Seed-Bearing Organ of Pentoxyleae

(i) **Carnoconites:** The female cones or seed-bearing organs have been described under the name Carnoconites. Two species (*C. compactum* and *C. laxum*) have been described. Both these species have, however, not been reported in organic connection with the stem genus *Pentoxylon* but from the same rocks.

Seed-bearing organs (Fig. 15.6) were forked and found attached terminally on the lateral dwarf shoots. They were mulberry-like and attained a length of about 1.8 cm in *Carnoconites compactum* and 3 cm in *C. laxum*. They were, however, narrower in *C. laxum*. About 20 sessile ovules were seen attached on the receptacle, and there were no inter-seminal scales. Any sporophyll-like structure was also not reported. In spite of these facts Sahni (1948) used the word 'cone' for these structures. The ovules were covered by a single integument. The nucellus was free from the integument.



Fig. 15.4 *Pentoxylon sahnii*. T.S. stele. (after Sahni).

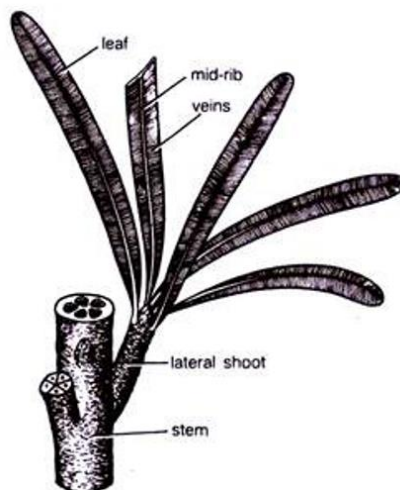


Fig. 15.5. *Pentoxylon sahnii*. Reconstruction of stem and leaves (*Nipaniophyllum raoi*). (after Sahni).

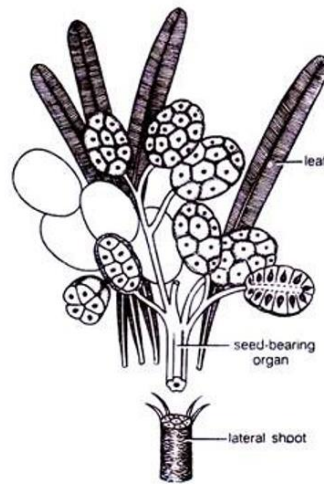


Fig. 15.6. *Carnoconites compactum*. Female cones. (after Sahni).

(ii) *Sahnia Nipaniensis*: The probable microsporangiate or male organs of Pentoxyleae were named as *Sahnia nipaniensis* by Vishnu-Mittre (1953). They were present terminally on the shoot and fused basally in a shallow dish (Fig. 15.4). Vishnu-Mittre (1953) reported as many as 24 such pollen-bearing organs.

Each microsporophyll possessed many pear-shaped, unilocular sporangia. The terminal position of the sporophyll was also occupied by a sporangium (Fig. 15.7). Several monocolpate and boat-shaped pollen grains were present in each microsporangium.

The sexine of the pollen wall is homogeneous while its nexine is present in the form of thin dark zone. In the region of aperture, the sporoderm is highly folded. Taylor & Taylor (1987) observed a few lamellae in the region of aperture. Other details of the male flowers are not yet fully known.



Fig. 15.7

Fig. 15.7. *Sahnia nipaniensis*. Reconstruction of the male "flower". (after Vishnu-Mittre).



Fig. 15.8

Fig. 15.8. *Sahnia nipaniensis*. A detached microsporophyll. (after Vishnu-Mittre).

7. Affinities of Pentoxylales

Some of their possible affinities are discussed below.

Affinities with Cycadales: The two groups (Pentoxyleae and Cycadophytes) resemble each other in:

- (i) Possession of direct leaf trace in Pentoxyleae and seedlings of some cycads,
- (ii) Leaf traces anatomy in showing diplomantic nature of their vascular bundles,
- (iii) Haplocheilic stomata,
- (iv) Vestigial politely in the seedling stages of some modern cycads,
- (v) Nature of wood and pittings,
- (vi) possessing similar kind of pollen grains, and
- (vii) structure of their seeds and peduncles.

However, vascular bundles in Pentoxylon are not arranged in the Cycadean manner. There is also no similarity between the polystelic condition of Pentoxylon and mature modern cycads.

Affinities with Conifers

Some of the characteristics, which Pentoxylales resemble with conifers, include the presence of:

- (i) Pycnoxylic wood,
- (ii) Tracheids with circular bordered pits arranged in uniseriate or bi-seriate manner,
- (iii) Uniseriate wood rays, and
- (iv) Dimorphism in the stems of *Pentoxylon sahnii* and several conifers. However, the general anatomy of the stem of Pentoxylales is not at all coniferous as mentioned also by Sahni (1948). Pentoxylales are stachyospermous (i.e., both the male and female organs were borne on stems, rather than on leaves) while conifer ales are partly phyllospermous and party stachyospermous.

Affinities with Medullosaceae: Pentoxylales also resemble members of family Medullosaceae of Palaeozoic Pteridospermales (e.g. Medullosa) in possessing a polystelic primary vasculature in their stems. The secondary wood of Pentoxylon was pyroxylin, character also encountered in some species of Medullosa.

The two groups also resemble each other in their mode of branching as well as the nature of their steles. Coniferous type of pittings were present in the stems of Pentoxylon and some species of Medullosa.

Affinities with Bennettitales

Undermentioned are some of the resemblances between Pentoxylales and Bennettitales:

1. Presence of syndetocheilic stomata, in addition to haplocheilic ones.
2. Diploxylic nature of the vascular bundles.
3. Whorled micro-sporangiophores.
4. Superficial resemblances between male flowers of both groups.
5. The way the ovules were born in Pentoxylales was like that of Bennettitales. However, the inter-seminal scales, found in members of Bennettitales, were absent in Pentoxylales.
6. Stachysporous nature of their male and female organs, i.e., instead of leaves, these organs were borne on the stems.
7. Both the groups share several common characters in their dwarf shoots.
8. Presence of direct leaf trace also brings the two groups quite close to each other.

However, the polystelic condition of the stems of *Pentoxylon* and *Nipanioxylon* has no similarity with that found in Bennettitales. In Pentoxyleae, the sporangiophores were erect, radial structures without any sterile part.

They were spirally branched and possessed sac-like unilocular microsporangia. On the other hand, in Bennettitales these structures were completely different. They had circinate dorsiventral pinnate sporophyll with a sterile and synangium-bearing portion.

Affinities with Some Other Groups:

While the stem dimorphism of *Pentoxylon sahnii* is a Ginkgoalean feature as well as a coniferous one, the diploxylic vascular bundles of Pentoxylales are seen in Cordaitales as in Bennettitales. Meeuse (1961) observed several resemblances between Pentoxylales and *Pandanus* (a member of the family Pandanaceae of Monocotyledons) and opined that “Pandanaceae and some related monocotyledons” have descended directly from Pentoxylales.

Features Unique to Pentoxylales: The mulberry-like female cones or infructescences of Pentoxylales (*Carnoconites compactum*) with over twenty sessile ovules attached to a central receptacle is a unique feature of this group.

Furthermore, these infructescences had neither any inter-seminal scales, nor anything that could be called a sporophyll, a unique feature again. The sporangiophores of Pentoxylales had spirally arranged branches and the sporangia were unilocular as well as terminal.

Williamsonia: Occurrence, External Features and Reproduction

Occurrence of Williamsonia: Williamsonia belongs to the family Williamsoniaceae of Bennettitales. It has been reported from the Upper Triassic period but was more abundant in Jurassic. This was earlier discovered under the name *Zamia gigas* by Williamson (1870) but has now been named as Williamsonia.

Professor Birbal Sahni (1932) described *W. sewardiana* from Rajmahal Hills of Bihar (India). Professor AC. Seward, a well-known palaeobotanist, described *W.scotti*. Gupta (1943) discovered *Williamsonia sahnii* from Rajmahal Hills and named it after Professor Birbal Sahni.

Other reported species from Rajmahal Hills are *Williamsonia indica*, *W. microps* and *W. santalensis*. *Bucklandia indica*, described from Rajmahal Hills, is now considered to be the stem of *Williamsonia seawardiana*.

External Features of *Williamsonia*

Williamsonia resembled *Cycas* in appearance, and its best-known species is *W. seawardiana*. A reconstruction of this species was published by Sahni (1932). The leaves of *W. seawardiana* were like that of *Ptilophyllum*. The plant had an upright, branched and stout stem covered by persistent leaf bases. A terminal crown of pinnately compound leaves was present. For the stem genus *Bucklandia*, Sharma (1991) opined that features of leaf bases such as their shape, size, and arrangement pattern are of taxonomic significance.

He observed that leaves in *Williamsoniaceae* show syndetocheilic stomata with rachis possessing collateral endarch vascular bundles arranged in a double U-manner.

Reproduction in *Williamsonia*

The fructifications of *Williamsonia* were large and attained a diameter of about 12 cm. They were borne on a peduncle. Many spirally arranged bracts were present around the base of the floral axis. In *W. gigas* the cones were present among the crown of leaf bases while in *W. seawardiana* they were present on the short lateral branches. *Williamsonia* plants were unisexual.

Female Flower: The female ‘cones’ of *Williamsonia gigas* and *W. seawardiana* have been investigated in detail. Instead of ‘strobili’ or ‘cones’, Sporne (1965) has proposed to use the term “flower” in *Williamsonia*. The conical receptacle was surrounded by many perianth-like bracts. The ovules were stalked.

The apex of the receptacle was naked and sterile. The nucellus was surrounded by a single vascularized integument, which was fused with the nucellus. The nucellus had a well-marked beak and a pollen chamber. In young ovules the micropylar canal was long and narrow.

In mature ovules, the canal widened because of the formation of nucellar plugs and the disappearance of interlocking cells. In the apical part of the endosperm, Sharma (1979) observed 2 or more archegonia.

Male Flower

Out of several known male flowers of Bennettitales, some have been described to belong to *Williamsonia*. Male fructifications have never been found in actual connection with the plant, and are sometimes referred to the genus *Weltrichia*. Sitholey and Bose (1953) discovered *Williamsonia santalensis* from Upper Gondwana (India) and observed that microsporophylls in the species were bifid. One of the branches of microsporophyll was fertile while the other was sterile. The fertile part had finger-like structures called synangia. Each synangium had two rows of chambers enclosing microsporangia. Sharma (1977, 1983, 1991) has confirmed the synangiate nature.

The entire male flower attained a length of about 20 cm., while a single microsporophyll was about 10 cm long. The fertile branch of the bifid sporophyll possessed many purse-like capsules, in each of which there were present many monocolpate pollen grains.

Birbal Sahni Institute of Paleobotany: Contributions of Birbal Sahni

The Birbal Sahani Institute of Palaeobotany (acronym BSIP) is an autonomous institute constituted under the Department of Science and Technology, Government of India. The Institute is located at Lucknow, Uttar Pradesh, India and is a seat of higher learning in the field of plant fossil research. The Institute of Palaeobotany was established in the year 1946 by the Palaeobotanical society formed by a group of botanists led by the renowned Indian botanist, Professor Birbal Sahani. Professor Birbal Sahni was appointed as first Director of the Institute who is called as the father of Denrology. The initial office of the Institute was at the Department of Botany, Lucknow University. The then government of the United Provinces gifted a bungalow sitting on 3.50 acres of land to the Institute in 1948, which till today remains its campus.

Savitri Sahani took over the reins of the Institute on her husband's death in 1949, and the Institute moved into a new purpose-built building in 1953. The Institute, by that time, had already started to be known and, in 1951, UNESCO included it in its Technical Assistance Program. On 9th July 1969, the research activities were alienated from the society and Birbal Sahni Institute of Palaeobotany was formed, in honor of the scientist, as an independent, autonomous research organization funded by the Government of India.

BSIP works in close coordination with various organizations such as Geological Survey of India, Physical Research Laboratory, Oil and Natural Gas Commission, Oil India Limited, Coal India Limited, Coal Mine Planning and Design Institute, Council of Scientific and Industrial Research Laboratory, Neyveli Lignite Corporation, Mineral Exploration Corporation Limited, Indian Institutes of Technology, Institute Francais de Pondicherry, Botanical Survey of India, Forest Research Institute, Dehradun, Bhabha Atomic Research Center, Laboratories under Department of Science and Technology, Archaeological Survey of India, Wadia Institute of Himalayan Geology, different State Departments of Archaeology and Geology Departments of several Universities. The Institute has signed specific MOUs with Oil and Natural Gas Corporation, Geological Survey of India (Coal Wing), Delta Studies Institute, Vishakhapattanam (for delta/basin modeling with parametia and hydrocarbon exploration), and National Institute of Oceanography, Goa (for Quaternary palaeoclimate of marine and coastal areas).

Objectives: The main objectives of the Institute are set as

1. To develop paleobotany in all its botanical and geological aspects.
2. To constantly update data for interaction with allied disciplines.
3. To coordinate with other palaeobotanical and geological research centers in the areas of mutual interest, such as diversification of early life, exploration of fossil fuels, vegetational dynamics, climatic modeling, and conservation of forests.
4. To disseminate palaeobotanical knowledge in universities, educational institutions, and other organizations.

Museum basis: nurses a museum, originally housing the fossil collections of Professor Sahni, but now holds later collections made by the scientists over the years. The collection includes holotype specimens, slides, and figured specimens.

Figured specimens: 6679 Figured slides: 12740

Slide negatives: 17504 The museum, with its foundation stone laid by Prof. Birbal Sahni, composed of fossils of various geological ages embedded in a marble-cement block, displays the specimens based on their general and geological relevance. The museum also maintains a Geological Time Clock.

Herbarium: The Herbarium functions with four different sections

General collection of dried plants mounted on herbarium sheets

Xylarium - a collection of woods and their thin sections

Sporothek - a collection of pollen and spore slides and polleniferous material

Carpothek - collection of fruits, seeds.

The fossil specimens such as leaves, cuticle, pollen, spores, fruits, seed and wood, numbering 51,472, are preserved according to their variation, local names, uses, distribution, ecology and include contributions from J. F. Duthie, R. R. Stewart, K. N. Kaul, Birbal Sahni, O. A. Hoeg and A. L. Takhtajan. Birbal Sahni Institute of Paleobotany (BSIP) will now be able to date fossils as old as a million years. Till now, fossils dating back to 50,000 years can be studied. With seven ultramodern instruments that the institute inaugurated on its 60th foundation day on Saturday, BSIP claims to be the first institute in the country to have the rare combination of all machines for palaeobotanical studies under one roof.

Radiocarbon dating has its limitations with a bracket of age. The sample should also have organic carbon in its composition to be assessed with it. Luminescence dating will provide us with specific ages of sediment samples ranging between 10 years and a million years of even carbon-less minerals," said Dr Chandra Mohan Nautiyal, scientist in charge of the radiocarbon lab. Another instrument, the X-ray diffraction, procured by BSIP, will help in the identification of a mineral extracted from a particular area. Based on that, details about the climatic conditions of the area can be known since different minerals are found in different climatic conditions. Three of the imaging machines now at BSIP will be able to photograph even the minutest of samples. "The seven instruments will give us a multipronged approach, addressing samples from various angles. We will be able to know elements and minerals, their size and shape, the nature of minerals (biotic or abiotic), their age and the type of vegetation (terrestrial, aquatic or desert) present on the earth over a million years ago," explained Dr. Nautiyal.



Dr. Uppu Anitha Devi Head & Assistant Professor, Indira Priya Darshini Government Degree & P.G. College for Women (Autonomous), Nampally, Hyderabad. Dr. Uppu Anitha Devi holds an M.Sc. and Ph.D. from Kakatiya University with over 22 years of teaching experience. She has published 50+ research papers, authored seven books, completed a Minor Research Project sponsored by SERO-UGC, and holds four patents. An active member and Executive Member of various academic societies, she has attended over 60 conferences and served as a Resource Person at more than five national seminars.



Dr. Mandalaju Venkateshwarlu, Assistant Professor of Botany, University College, Kakatiya University, Warangal. Dr. Venkateshwarlu holds an M.Sc., Ph.D., and B.Ed. from Kakatiya University with over 27 years of teaching experience. He has published 135 research papers in national and international journals, authored 12 books, and filed 5 patents. He served as Chief Editor and Senior Scientist for the Asian Journal of Biosciences (2010–2022). He has attended over 100 national and international seminars and is a lifetime member of several academic societies. Dr. Venkateshwarlu has received more than 10 awards for his contributions to teaching and research.



Dr. Tirukovel Srinivas CoE, Associate Professor & HOD, Department of Botany, SRR Government Arts & Science College (Autonomous), Karimnagar, Telangana. Dr. Tirukovel Srinivas holds an M.Sc., Ph.D., and M.Ed. from Osmania University and has over 25 years of teaching experience. He has published more than 43 research papers, authored and edited five patents, and serves as a Fellow, Executive Member, and reviewer for over 50 national and international journals. He has received more than six awards, including the prestigious **State Best Teacher Award from Telangana in 2022**.



Dr. Thirunahari Ugandhar, Associate Professor, Department of Botany, Kakatiya Govt. College (A) Hanumakonda, Telangana. Dr. Thirunahari Ugandhar holds an M.Sc. and Ph.D. from Kakatiya University and has over 20 years of teaching experience. He has published 143+ research papers, edited and authored over six books, and guided ten M.Phil theses. He completed a Minor Research Project sponsored by SERO-UGC, Hyderabad. Dr. Ugandhar serves as a Fellow, Executive Member, and reviewer for over 30 national and international journals. He has received more than ten awards, including the prestigious **State Best Teacher Award from Telangana in 2022**.

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