



**MSCBOT-503**

M.Sc. I Semester  
**PTERIDOPHYTES, GYMNOSPERMS  
AND PALAEOBOTANY**



**DEPARTMENT OF BOTANY  
SCHOOL OF SCIENCES  
UTTARAKHAND OPEN UNIVERSITY**

MSCBOT-503

# PTERIDOPHYTES, GYMNOSPERMS AND PALAEOBOTANY



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## **BLOCK-1- PTERIDOPHYTES**

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## **UNIT-1-GENERAL CHARACTERISTICS, HABITAT, CLASSIFICATION, REPRODUCTION AND ECONOMIC IMPORTANCE OF PTERIDOPHYTES**

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- 1.1 Objectives
- 1.2 Introduction
- 1.3 General Characters of Pteridophytes
- 1.4 Habitat
- 1.5 Classification
- 1.6 Reproduction
- 1.7 Economic Importance
- 1.8 Summary
- 1.9 Glossary
- 1.10 Self Assessment Questions
- 1.11 References
- 1.12 Suggested Readings
- 1.13 Terminal Questions



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## 1.1 OBJECTIVES

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After reading this unit students will be able to-

- Explain and define the meaning of Pteridophyte.
- Describe the characteristic features of Pteridophytes.
- Distinguish and identify the Pteridophytes in your surroundings.
- Classify the Pteridophytes.
- Know the distribution and economic importance of Pteridophytes.

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## 1.2 INTRODUCTION

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The word Pteridophyta is of Greek origin. *Pteron* means “feather” and *Phyton* means plant. The plants of this group have feather like fronds (leaves) (Fig. 1.1). The group pteridophyta included in Cryptogams with Thallophyta (algae & fungi) and Bryophytes. The algae, fungi and bryophytes are called lower cryptogams (non-vascular cryptogams) while the Pteridophytes are called higher cryptogams (vascular cryptogams), because only pteridophytes have well developed conducting system among cryptogams. Due to this reason they are the first true land plants. All cryptogams reproduce by means of spores and do not produce seeds. The Pteridophytes are assemblage of flowerless, seedless, spore bearing vascular plants that have successfully invaded the land.



*Fig.1.1: Feather like fronds of fern*

Pteridophytes have a long fossil history on our planet. They are known from as far back as 380 million years. Fossils of pteridophytes have been obtained from rock strata belonging to Silurian and Devonian periods of the Palaeozoic era. So the Palaeozoic era sometimes also called the “The age of pteridophyta”. The fossil Pteridophytes were herbaceous as well as arborescent. The tree ferns, giant horse tails and arborescent lycopods dominated the swampy landscapes of the ancient age. The present day lycopods are the mere relicts the *Lepidodendron* like fossil arborescent lycopods. Only present day ferns have nearby stature

of their ancestors. *Psilotum* and *Tmesipteris* are two surviving remains of psilopsids, conserve the primitive features of the first land plants.

In the plant kingdom, pteridophytes occupy a position in between bryophytes and gymnosperms, and therefore they have some similarities with the bryophytes on the one hand and with the gymnosperms on the other hand. The similarities with bryophytes are (i) presence of sterile jacket around the antheridium and archegonium, (ii) requirement of water and moisture for the fertilization, (iii) presence of alternation of generations, (iv) formation of spores etc. while with gymnosperms (i) sporophytic plant body and its independent nature, (ii) differentiation of sporophyte into root, shoot and leaves, (iii) presence of vascular tissues for conduction etc.

The presence of vascular elements in pteridophytes makes their grouping with gymnosperms and Angiosperms as Trachaeophyta. The reproduction by spores and similar events of life cycle place them among lower plants. The lower plants algae, fungi, bryophytes and pteridophytes were earlier grouped together as cryptogams. Bryophytes, Pteridophytes and Gymnosperms are also classified as Archegoniatae due to the presence of a common reproductive body archegonium.

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### **1.3 GENERAL CHARACTERISTICS OF PTERIDOPHYTES**

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1. The main independent plant body is sporophyte with vascular system.
2. The pteridophytes grow mostly in cool, moist and shady places, but some are aquatic (*Marsilea*, *Salvinia*, *Azolla* etc.) and few are xerophytic (*Selaginella rupestris*, *S. resplenda*, *Marselia rajasthanensis*, *Marselia condenseta* etc.).
3. Plants are differentiated into true roots, shoots and leaves. Some primitive members lack true roots and well developed leaves (e.g.; in members of order Psilophytales and Psilotales).
4. Except few woody tree ferns all living pteridophytes are herbaceous.
5. They may be dorsiventral or radial in symmetry with branched stems.
6. The leaves of pteridophyte may be Scale like leaf (e.g. *Equisetum*), small sessile leaves (e.g., *Lycopodium* and *Selaginella*) and large, petiolate compound leaves occurs in true ferns.
7. The stem bears leaves which may be microphyllous type in which the leaves are quite small with unbranched midrib (e.g. *Lycopodium*, *Selaginella*, *Equisetum*), or megaphyllous type, in which the leaves are large with branched midrib (e.g. ferns).
8. In fern, the young leaves show circinate vernation (curved inwards).
9. Primary embryonic roots are short lived and replaced by adventitious roots.
10. The pteridophytes reproduce by haploid spores which are produced within a specialized structure called sporangium.
11. Plants may be homosporous (all spores are same in shape and size) and heterosporous (spores are of two different shape and sizes, smaller one called microspore and larger one megaspore).

12. In some pteridophytes the sporangia developed on stems in the axil between leaf and stem, or on leaves (mostly ventral surface of leaves). On the stem sporangia may be terminal e.g. *Rhynia*, lateral in *Lycopodium*, on the surface of leaves in Ferns. The sporangia borne on ventral side of specialized leaf and such leaf is called Sporophyll. In aquatic ferns micro and megasporangia together are covered by a common membrane and this bean shaped structure is called sporocarp.
13. In true ferns the sporangia are located on the lower surface of the leaf as clusters called sori (sorus).
14. The haploid spore is a unit of gametophyte. On germination it develops into gametophytic prothallus.
15. The Gametophytic plant is called prothallus since it more or less looks like the thallus of a primitive bryophytes.
16. Gametophyte bears sex organs archegonia and antheridia. As a result of fertilization the zygote or oospore is formed.
17. The homosporous plants are monoecious (antheridia and archegonia borne on same thallus).
18. Heterosporous plants are mostly dioecious (antheridia and archegonia borne on separate thalli).
19. Microspore gives rise to male prothallus which bears the male sex organs antheridia.
20. Megaspore gives rise to female prothallus which bears the female sex organs archegonia.
21. The sex organs are embedded or projected in the prothallus.
22. The male gametes are called antherozoids and produced inside the antheridium.
23. Antherozoids are unicellular, spirally coiled and flagellate.
24. The archegonia are flask shaped and differentiated into upper neck and lower broader venter.
25. The archegonial neck is projected and the venter is embedded in the prothallus.
26. Water (moisture) is essential for completion of fertilization.
27. The egg and antherozoids fuse to form diploid zygote. The Zygote develops into new sporophytic plant body.
28. Clear alternation of generation takes place in the life cycle of Pteridophytes which is always heteromorphic type.

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## ***1.4 HABITAT***

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Pteridophytes are first land vascular plants, so they are mostly terrestrial in nature, grow in cool, moist and shady places. Some pteridophytes grow in xerophytic, semi-aquatic or aquatic condition also (Fig. 1.2).

**(a) Terrestrial Pteridophyte:** Members of Pteridophyta or ferns grow in terrestrial habitat. Some pteridophytes are Lithophytic on horizontal rocky patches. The fossil pteridophytes were terrestrial in nature. Most species of Lycopods growing in such habitat are *Lycopodium clavatum*, *L.cernuum*, *L. reflexum*, *Selaginella chrysocoulus*, *S. kraussiana*, *I. coramandelina*, etc.

Some pteridophytes are epiphytic. *Psilotum nudum*, *L. phlegmaria*, *S. oragana* and few ferns grow as epiphytes. The tall and well stratified trees in the forests provide a suitable habitat for the growth of epiphytic Pteridophytes. However, a few other ferns prefer open tree trunks and branches. These epiphytes share a common niche along with orchids and ferns.

**(b) Aquatic pteridophyte:** Some pteridophytes grow in aquatic and semi-aquatic habitats. *Isoetes panchananii* and *I. englemanni* are semi-aquatic. Some members of ferns are commonly called water ferns. The examples of water ferns are *Marsilea*, *Salvinia*, *Azolla*, *Regnellidium* etc.

**(c) Xerophytic pteridophytes:** Some species of *Selaginella* and *Marsilea* are xerophytic in nature. The examples are *S. repanda*, *S. lepidophylla*, *M. rajasthanensis*, *M. condensata*.

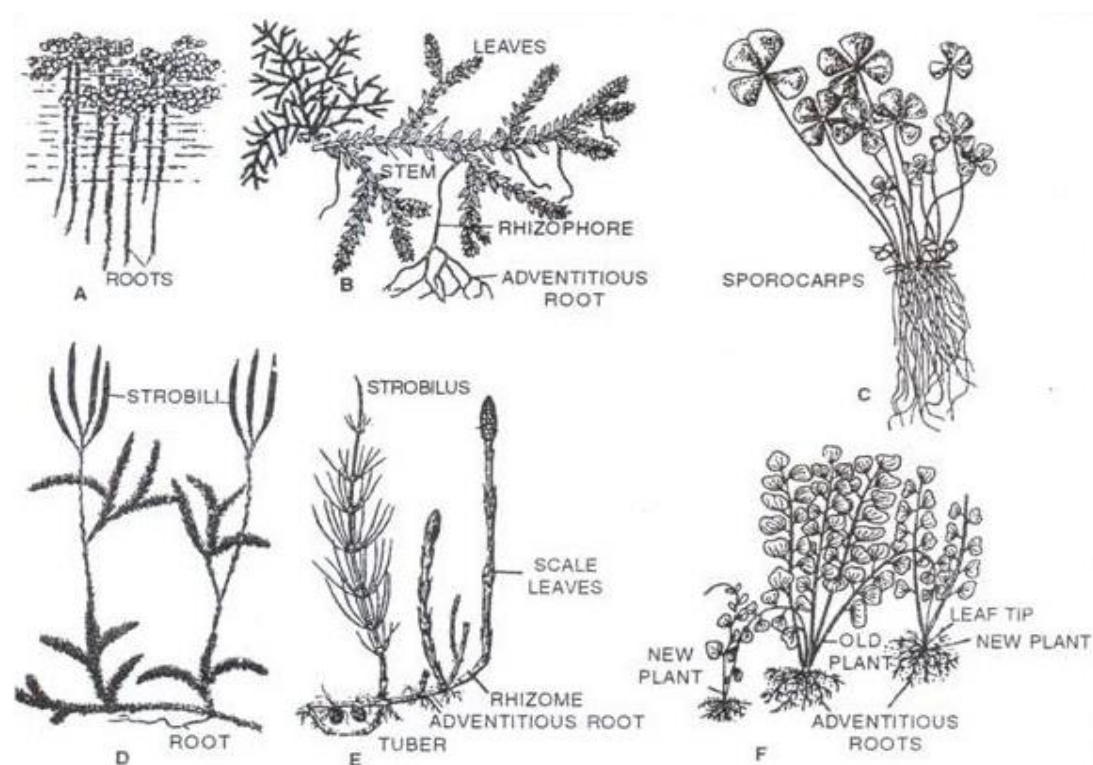


Fig. 1.2 Different types of pteridophytes: A. *Azolla*, B. *Selaginella*, C. *Marsilea*, D. *Lycopodium*, E. *Equisetum*, F. *Adiantum*

## 1.5 CLASSIFICATION

On the basis of presence and absence of seeds the vascular plants were classified by earlier taxonomists into two divisions, **Pteridophyta** and **Spermatophyta**. The division Pteridophyta included primitive vascular plants which bear no seeds. Later some fern like seed bearing fossil plants (Cycadofilicales) were discovered in 1903. The discovery eliminated the distinction between the two divisions **Pteridophyta** and **Spermatophyta**.

Sinnott (1935) therefore introduced a new term “**Tracheophyta**” for a division which includes all the vascular plants. Eames (1936) on the basis of some characters of plants and position of sporangia the division Tracheophyta divided into four groups, Psilopsida, Lycopsida, Sphenopsida and Pteropsida. Zimmermann (1930) and Arnold (1947) considered these groups as divisions and Tippo (1942) considered as subphyla.

### 1.5.1- Classification proposed by Reimers (1954) and Followed by Sporne (1996)

The classification of pteridophytes proposed by Reimers in the 1954 edition of Engler’s Syllabus der pflanzen families.

#### Pteridophytes:

##### 1. PSILOPHYTOPSIDA

Psilophytales e.g. *Rhynia*, \**Asteroxylon*\*

##### 2. PSILOTOPSISIDA

Psilotales e.g. *Psilotum*

##### 3. LYCOPSIDA

a) Protolopododendrales

b) Lycopodiales

e.g. *Lycopodium*, *Phylloglossum*

c) Lepidodendrales

e.g. *Lepidodendron*\*, *Lepidocarpon*\*

d) Selaginellales

e.g. *Selaginella*

e) Isoetales

e.g. *Isoetes*

##### 4. SPHENOPSISIDA

a) Hyeniales

b) Sphenophyllales

e.g. *Sphenophyllum*\*

c) Calamitales

e.g. *Calamites*\*, *Calamostachys*\*

d) Equisetales

e.g. *Equisetum*

##### 5. PTEROPSISIDA

(A) Primofilices

a) Cladoxylales

b) Coenopteridales

e.g. *Botryopteris*\*, *Zygopteris*\*

(B) Eusporangiatae

(a) Ophioglossales,

e.g. *Ophioglossum*

(b) Marattiales,

e.g. *Angiopteris*

(C) Osmundidae

Osmundales

e.g. *Osmunda*

(D) Leptosporangiatae

(a) Filicales

e.g. *Hymenophyllum*, *Adiantum*

(b) Marsileales

e.g. *Marsilea*

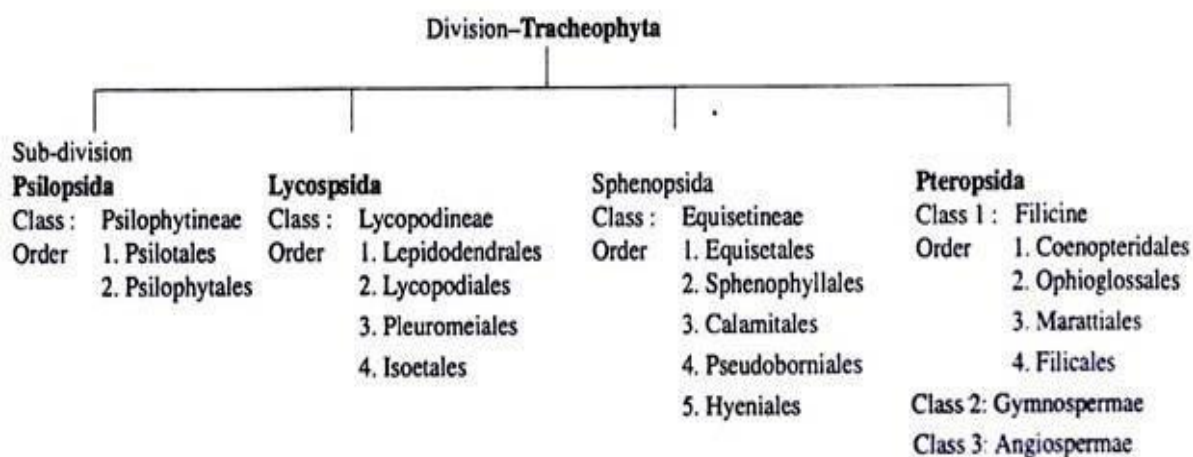
(c) Salviniales

e.g. *Salvinia*, *Azolla*

(Asterisk mark indicates the fossil members).

### 1.5.2-Classification proposed by Wardlaw (1955)

According to the International Code of Botanical Nomenclature as amended in 1950, the name of the division should end with the suffix-phyta, and a sub-division should end with-phytina and a class with -opsida. According to recommendations of I.C.B.N, **Wardlaw (1955) divided the Pteridophytes into four divisions:**



On the basis of ICBN recommendations Smith (1955) divided vascular cryptogams into following four divisions:

- 1- Division – **Psilophyta** which was divided into two classes, **Psilophytosida** and **Psilotosida**.
- 2- Division – **Lycophyta** which was divided into two classes, **Eligulopsida** and **Ligulopsida** on the basis of absence and presence of ligule at the axil of leaf.
- 3- Division – **Sphenophyta** or **Calamophyta** which was divided into two classes, **Sphenophyllopsida** and **Calamopsida**.
- 4- Division – **Pterophyta** or **Filicophyta** which was divided into four classes, **Eusporangiopsida**, **Protoleptosporangiopsida**, **Leptosporangiopsida** and **Primopteropsida**.

### 1.5.3-Classification proposed by Cronquist et al. (1966) and followed by Parihar (1977)

Cronquist, Takhtajan and Zimmerman (1966) classified the pteridophytes into five divisions. The classification has also been followed by Parihar (1977). The outline of classification is following:

1. Division :- Rhyniophyta  
Class:- Rhyniatae  
Order:-Rhyniales
2. Division :- Psilotophyta  
Class:- Psilotatae  
Order:-Psilotales
3. Division :- Lycopodiophyta

Class:- Lycopodiatae

Orders:-Asteroxylales, Drepenophycales, Protolepidodendrales and Lycopodiales.

4. Division :- Equisetophyta

Order:-Sphenophyllales and Pseudoborniales

Class: - Equisetatae

Order: - Calamitales and Equisetales

5. Division :-Polypodiophyta

Class:-Polypodiatae (the class divides sub classes.)

Sub-classes:- Prototeridiidae, Archaeteridiidae, Ophioglossiidae, Noeggerothiidae, Marrattidae, Polypodiidae, Marsilleidae, Salviniidae)

These sub-classes are further divided into orders.

Accordingly ICBN amendment the four major groups of pteridophyta are

1. Class Psilopsida
2. Class Lycopsidea
3. Class Sphenopsida
4. Class Pteropsida

However there are no uniformity in nomenclature and accordingly.

**Psilopsida is equivalent to:**

Psilophyta (Zimmermann, 1930; Smith, 1955; Bold, 1957)

**Lycopsidea is equivalent to:**

Lycophyta (Zimmermann, 1930)

Lycopodophyta (Andrew, 1961)

Microphylophyta (Bold,1957)

Lepidophyta (Smith, 1955; Cronquist, 1960)

**Sphenopsida is equivalent to:**

Calamophyta (Smith, 1975)

Sphenophyta (Benson, 1957)

Equisetophyta or Arthrophyta (Bold, 1957; Andrew, 1961)

**Pteropsida is equivalent to:**

Pteridophyta (Benson, 1957)

Pterophyta (Smith, 1955; Bold, 1957)

Filicophyata (Cronquist, 1960)

#### 1.5.4-Latest classification proposed by A. R. Smith (2006) and co-workers

Scientists of three different countries from USA, A.R. Smith, K.M. Preyer and P.G. Wolf (Sweden), E. Schuettpelz and H Schneider (Germany) presented a revised classification of extant ferns. They divided all vascular plants into two groups on the basis of phylogenetic studies.

Recent phylogenetic studies have revealed a basal dichotomy within vascular plants, separating the lycophytes (less than 1% of extant vascular plants) from the euphyllophytes.

Living euphyllophytes, in turn, comprise two major clades: the spermatophytes (seed plants), which are in excess of 260,000 species (Thorne, 2002; Scotland & Wortley, 2003), and the monilophytes (ferns, sensu Pryer & al., 2004b), with about 9,000 species, including horsetails, whisk ferns, and all eusporangiate and leptosporangiate ferns. Plants that are included in the lycophyte and fern clades (Monilophytes) are all spore-bearing or “seed-free”, and because of this common feature their members have been lumped together historically under various terms, such as “pteridophytes” and “ferns and fern allies”—paraphyletic assemblages of plants.

The focus of this reclassification is exclusively on ferns. Within ferns, they recognized four classes (Psilotopsida; Equisetopsida; Marattiopsida; Polypodiopsida), 11 orders, and 37 families.

### **Class 1. Psilotopsida**

A. ORDER Ophioglossales.

1. Family Ophioglossaceae.

B. ORDER Psilotales.

2. Family Psilotaceae

### **Class 2. Equisetopsida**

C. ORDER Equisetales.

3. Family Equisetaceae.

### **Class 3. Marattiopsida**

D. ORDER Marattales.

4. Family Marattiaceae .

### **Class 4. Polypodiopsida**

E. ORDER Osmundales .

5. Family Osmundaceae.

F. ORDER Hymenophyllales.

6. Family Hymenophyllaceae

G. ORDER Gleicheniales.

7. Family Gleicheniaceae.

8. Family Dipteridaceae

9. Family Matoniaceae.

H. ORDER Schizaeales.

10. Family Lygodiaceae.

11. Family Anemiaceae

12. Family Schizaeaceae.

I. ORDER Salviniiales

13. Family Marsileaceae.

14. Family Salviniaceae

J. ORDER Cyatheales.

15. Family Thyrsopteridaceae.

16. Family Loxomataceae.

17. Family Culcitaceae

18. Family Plagiogyriaceae.

19. Family Cibotiaceae

20. Family Cyatheaceae

21. Family Dicksoniaceae

22. Family Metaxyaceae

K. ORDER Polypodiales

23. Family Lindsaeaceae



24. Family Saccolomataceae
25. Family Dennstaedtiaceae
26. Family Pteridaceae
27. Family Aspleniaceae
28. Family Thelypteridaceae
29. Family Woodsiaceae
30. Family Blechnaceae
31. Family Onocleaceae
32. Family Dryopteridaceae
33. Family Lomariopsidaceae
34. Family Tectariaceae
35. Family Oleandraceae
36. Family Davalliaceae
37. Family Polypodiaceae

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## 1.6 REPRODUCTION

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Reproduction through spores is main mode of reproduction in Pteridophytes. Although vegetative reproduction is also common in pteridophytes.

### 1.6.1- Vegetative reproduction

The sporophyte of many pteridophytes reproduce vegetatively by following means:

**(i) By the formation of gemmae or bulbils:** Vegetative reproduction is carried out by bulbils (bulblets) or gemmae. These are leafy side branches with wide base. The gemmae fall on the ground and grow into a new young plant. Ex. *Psilotum*, *Lycopodium phlegmaria*, *L. selago* etc. Certain species of *Selaginella* also propagate by bulbils.

**(ii) Fragmentation:** Death and decay of older parts of stem leads the formation of fragments of stem/rhizomes. The individual fragment possessing roots develops into a new plant. It is common method of vegetative reproduction in species of *Lycopodium*, *Selaginella*, *Dryopteris*, *Pteris*, *Adiantum* etc.

**(iii) Formation of Tubers:** The tubers originate from the paranchymetous regions of shoot and root at the onset of unfavourable conditions. The tubers are formed at surface of the ground, called surface tubers and those developing underground are the underground tubers. They consist of a group of cells with stored food materials and having the capacity to germinate into new plants during favourable season. In some species of *Marsilea* irregular tuberous bodies are formed in the stem. Few species of *Lycopodium*, *Selaginella* and *Equisetum* develop such tubers.

**(iv) Formation of Adventitious Buds:** Such buds have been induced on isolated bulbil leaves. Decapitation of stem near its apex also induces the formation of such buds. Certain species of *Lycopodium*, *Selaginella*, also develop such buds. Few species of *Asplenium*,

*Diplazium* and *Ophioglossum* develop adventitious buds. In *Dryopteris* adventitious buds arise in the axil of leaves and form new plants after getting detached from the plant. In some ferns the root apex develops directly into a leafy bud (*Platynerium* and *Asplenium esculentum*). The leafy bud can grow into a new plant.

### 1.6.2-Asexual Reproduction

Reproduction through spores is main mode of reproduction in Pteridophytes. Pteridophytes reproduce asexually by haploid spores, which are formed in sporangia. The sporangia develop either on the ventral surface or in the axils of the leaves. The Sporangia bearing leaves are called **sporophylls**. However, in Psilophytales the sporangia are **cauline**. The sporangia are **terminal** on the fine aerial branches in *Rhynia*. In *Equisetum* and *Selaginella* these sporophylls present in the form of compact structures called **strobili** or **cones** (Fig.1.4 &1.5). In genera, such as, *Azolla*, *Marsilea* and *Salvinia* the sporangia are present in specialized bodies called **Sporocarps**. The sporangia in higher ferns are present in the form of well organized groups called **sori** (singular sorus) (Fig.1.6). In case of *Psilotum* sporangia are trilobed structures with each lobe containing sporogenous region and this trilobed structure is called synangium (Fig 1.3).



Fig. 1.3 Synangia of *Psilotum*



Fig. 1.4 Cone of *Equisetum*



Fig. 1.5 Strobilus or cone of *Lycopodium*



Fig.1.6 Sori of fern

On the basis of development of sporangia Goebel (1881) classified sporangial development into two types, i.e., **Eusporangiate** and **Leptosporangiate**. The sporangium developing from a group

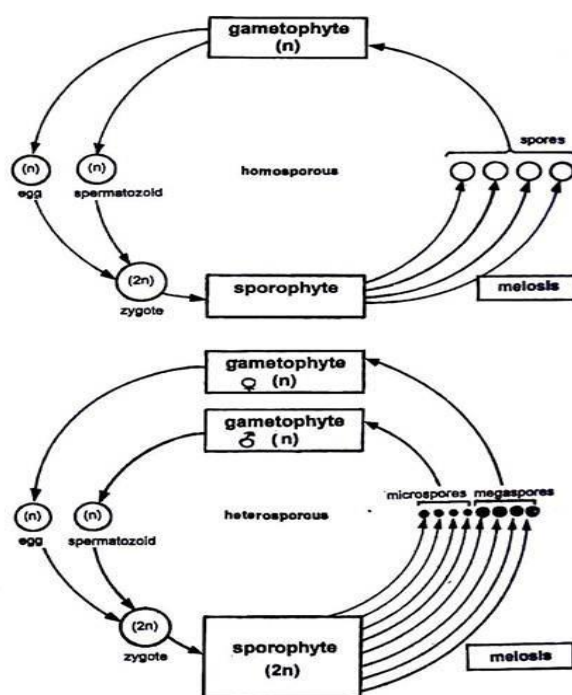
of initial cells is called eusporangiate while the development from a single initial cell is called leptosporangiate development.

### 1.6.2.1-Sporophyte

The spore producing body of Pteridophyta is called **Sporophyte**. The Sporophytic generation is dominant and conspicuous in the life cycle of Pteridophytes. The life cycle of typical Pteridophyte consists of a regular alternation of sporophytic (asexual) and gametophytic (sexual) generations.

In bryophytes the gametophytic phase is dominant in life cycle, and the sporophyte is dependent on gametophyte. By contrast, in Gymnosperms and Angiosperms the gametophytic generation is reduced and is dependent on the sporophyte. Pteridophytes with an **intermediate position** are characterized by free living gametophytic and sporophytic generations. Nevertheless the sporophyte is a dominant generation; it soon becomes independent of the gametophyte and attains a much greater size.

Pteridophytes are characterized by two basic kinds of life-cycles, **homosporous** and **heterosporous** (Fig. 1.7). The heterosporous pteridophytes form two kinds of spores, the larger **megaspores** and smaller **microspores**, from which develop two kinds of gametophytes, female and male gametophytes, respectively.



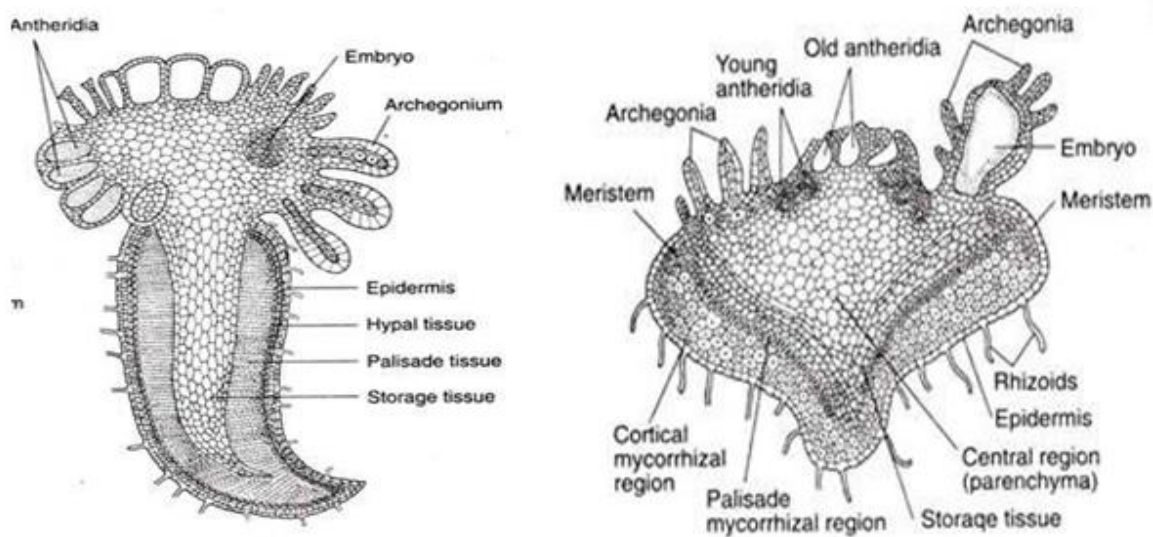
*Fig.1.7 Life cycles of Homosporous and Heterosporous Pteridophytes*

The homosporous pteridophytes form only one kind of spore from which a hermaphroditic (monoecious) gametophyte usually develops. Thus the heterosporous pteridophytes are obligatorily heterothallic, while the homosporous are usually homothallic. Some examples of

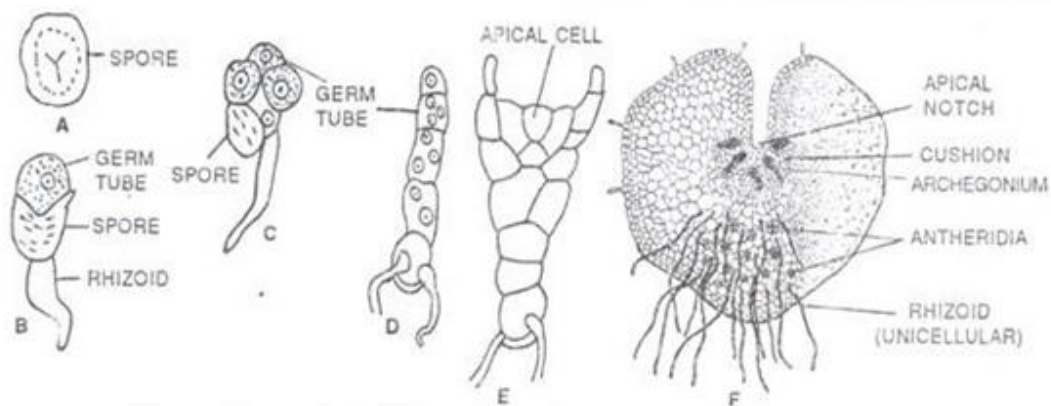
heterosporous pteridophytes are *Selaginella*, *Isoetes*, *Masilea*, *Salvinia*, *Azolla*, *Regnellidium* etc. The homosporous life-cycle is found in the *Psilotum*, *Tmesipteris*, *Lycopodium*, *Equisetum*, and the homosporous Filicopsids.

### 1.6.3- Sexual reproductive phase: Gametophyte

The gametophyte is the **sexual phase** in the life cycle of a plant .**The haploid spore is the first cell of gametophyte**. The spores are haploid and form after reduction division in the sporogenous cells of the sporangium. The spore germinates into a **prothallus** (Fig.1.8, 1.9 & 1.10). Generally the prothalli are green, simple, somewhat branched and aerial structures. But in some genera such as *Lycopodium*, they are subterranean, branched, colourless and saprophytic structure. The two sex organs **antheridia** and **archegonia** develop on the prothallus (Fig. 1.11). Generally the prothalli of homosporous pteridophytes are monoecious. But the prothalli of heterosporous pteridophytes usually are dioecious.



**Fig.1.8: Prothallus of *Lycopodium clavatum* Fig.1.9: Prothallus of *Lycopodium complanatum***



**Fig.1.10 (A-F) Germination of spore and development the of Prothallus in *Dryopteris***

Mostly the antheridia and archegonia remain embedded in the prothallus. The antheridium is always surrounded by a jacket layer. The antheridia produce **antherozoids**. The antherozoids are unicellular, uninucleate and biciliate structure in *Lycopodium*, *Selaginella* etc. but they are multiciliate in *Psilotum*, *Tmesipteris*, *Isoetes*, *Equisetum* and ferns. The **archegonium** consists of a projecting **neck** and the lower embedded portion **venter**. The neck has neck canal cells and the venter has ventral canal cell and egg cell.

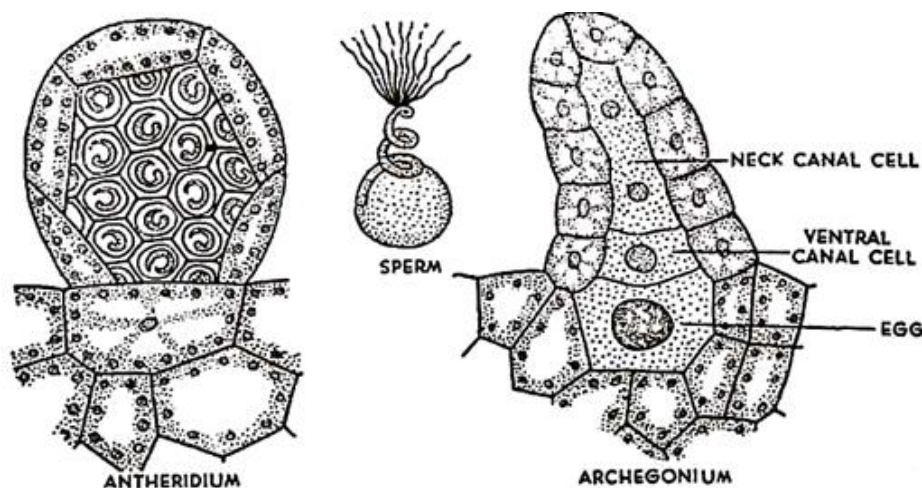


Fig.1.11: Antheridium and archegonium of fern

#### 1.6.4 -Fertilization and zygote formation

The fertilization takes place with the help of water. When a film of water flow between prothallus and substratum, the cap cells of antheridia pushed open to release antherozoids. The neck canal cell and ventral canal cell in the archegonium disorganize, their protoplasm become mucilaginous which absorbs water from the surrounding jacket cells and swell out, due to which pressure is put on the four cover cells at the top of archegonium. Cover cells get apart due to inner pressure and mucilaginous substance having malic acid get accumulated at the opening of archegonium. Antherozoids are attracted chemotactically towards the archegonium, the antherozoids swim towards archegonia in response to malic acid released from mucilaginous mass (chemotactic). Many antherozoids swim down the neck of archegonium, only one of them fuses with egg to form a diploid zygote. Usually, cross-fertilization occurs due to protandrous nature of prothalli (i.e. antheridia mature before archegonia). The fertilization takes place and results into the formation of **diploid zygote**. **The zygote is the first cell of sporophytic generation** and develops into a well-developed sporophyte.

#### 1.6.5-Embryo development

The zygote develops into an embryo. The first division of Zygote is generally (if not always) transverse. After a usual transverse division of zygote, a two celled structure is formed. Transverse division followed by a vertical division and thus developed a quadrant. The successive divisions finally develop a young sporophyte (Fig. 1.12).

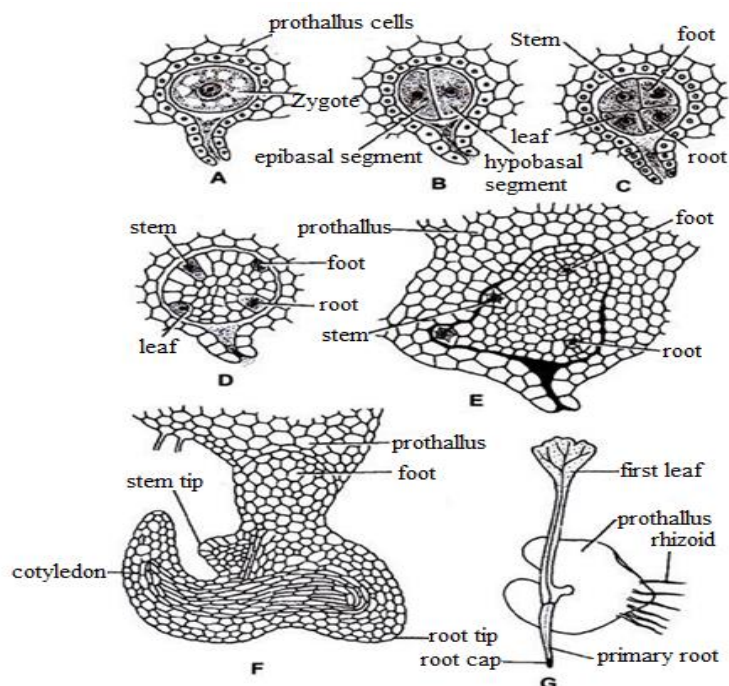


Fig.1.12. (A-G) Successive stages of development of embryo in fern

### 1.6.6 – Alternation of Generation

Pteridophytes show a **true alternation of generations**. Here, the dominant sporophyte produces spores through meiosis. The gametophytic generation forms gametes by mitosis. They have distinct sexual haploid and asexual diploid stages. In these groups, a multicellular gametophyte, which is haploid with  $n$  chromosomes, alternates with a multicellular sporophyte, which is diploid with  $2n$  chromosomes (Fig. 1.13).

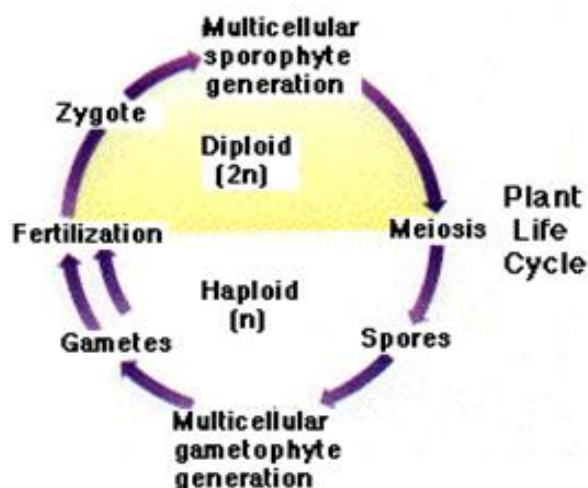


Fig.1.13 Alternation of generation in pteridophytes

A mature sporophyte produces spores by meiosis, a process which reduces the number of chromosomes to half, from  $2n$  to  $n$ . The haploid spores germinate and grow into a haploid gametophyte. At maturity, the gametophyte produces gametes by mitosis. Two gametes (originating from different organisms of the same species or from the same organism) fuse to

produce a zygote, which develops into a diploid sporophyte. The sporophyte and gametophyte alternate one by one in life cycle. This is called alternation of generation. This alternation of generations is a **survival strategy** in which a plant alternates between different reproductive techniques.

### 1.6.7- Abnormalities in the Life cycle

The normal life cycle of the vascular plant has two alternating generations. Both haploid and diploid generations alternate regularly in the life cycle of the Pteridophytes. The regular alternation of chromosome numbers is sometimes impaired by the occurrence of two common phenomena called apospory and apogamy.

**(a) Apogamy:** Development of sporophyte directly from the gametophyte without producing gametes or any sexual fusion (syngamy). The sporophyte has same haploid chromosome numbers as in gametophyte. It was first discovered by Farlow (1874) in *Pteris cretica*. It is a common and widespread phenomenon in ferns. The natural apogamy reported in a number of ferns including *Pteris*, *Pteridim*, *Dryopteris*, *Adiantum*, *Osmunda*, *Todea*, *Athyrium*, *Asplenium* etc.

**(b) Apospory:** The development of gametophytes from the vegetative parts or cells of the sporophyte without of any meiotic division and formation of spores. Such types of gametophytes are diploid and this phenomenon of their formation is called apospory. The phenomenon of apospory was first discovered by Druery (1884) in *Athyrium filix-foemina*. Since then apospory has been reported in many pteridophytes including *Pteridium aquilinum*, *Asplenium dimorphum*, *Osmunda regalis*, *Todea* etc.

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## 1.7 ECONOMIC IMPORTANCE OF PTERIDOPHYTES

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Besides being a lower plant, pteridophytes are economically very important. About 170 species of Pteridophytes have been found to be used as food, flavor, dyes, medicines, biofertilisers, oil, fibers and biogas production (Manickam and Irudayraj 1992).

**(1) Food:** Like other plants, pteridophytes constitute a good source of food and fodder. Sporocarps of *Marsilea*, a water fern, yield starch that is cooked and eaten by certain tribal communities. Young circinately coiled leaf tips of *Diplazium esculentum*, *Diplazium maximum* and some other ferns are eaten as vegetable. *Marselia* is used as a substitute for clover to feed animals. In Canada the crozires of *Matteuccia struphiopteris* are served as common spring vegetables. They are also stored and frozen for later use.

**(2) Biological fertilizer:** *Azolla* (a water fern) has a symbiotic association with nitrogen fixing cyanobacterium *Anabaena azollae*. *Azolla* is a very small pteridophyte and has small microscopic leaves. Each leaf has a small cavity at its base. Inside this cavity the filaments of nitrogen fixing blue green alga *Anabaena azollae*. Due to this, *Azolla* has the ability f to fix

atmospheric nitrogen and thus increases the fertility of the soil. It is inoculated to paddy fields to function as biofertilizer.

**(3) Medicines:** Many plants are used for treating several human diseases. An anthelmintic drug is obtained from rhizomes of *Dryopteris* (Male Shield Fern). Fronds and rhizome of *Adiantum caudatum* used for wound healing. The leaf and root decoction of commonly occurring *Adiantum lunulatum* syn. *Adiantum philippense* has been found to be very effective in the treatment of chest complaints. Leaves of *Marsilea minuta* and leaves of *Pteris quadrifolia* used for cough and bronchitis and fresh leaves of *Ophioglossum reticulatum* are used in menstrual disorders. Tender leaves of *Tectaria cicularia* used for wound healings, eczema and scabies.

**(4) Ornamentals:** Some species of *Lycopodium* and *Selaginella* are used as ornamentals in big gardens and green houses because of their variously coloured, feathery moss like leaves. Ferns are grown as ornamental plants for their delicate and graceful leaves. Some such examples are *Adiantum*, *Marattia*, *Pteris*, *Salvinia*, *Osmunda regalis*, *Lycopodium obscurum*ect.

**(5) Soil Binding:** By their growth pteridophytes bind the soil even along hill slopes. The soil is protected from erosion.

**(6) Scouring:** *Equisetum* stems have been used in scouring (cleaning of utensils) and polishing of metals. *Equisetum* species are therefore, also called scouring rushes.

**(7) Ecological Indicators:** Pteridophytes are also used as a indicator plants. *Equisetum* accumulates minerals, especially gold, in their stem, so it is the ecological indicator of gold in the soil. Similarly, *Asplenium adulterinum* is an indicator of nickel and *Actinopteris australis* is a cobalt indicator plant.

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## 1.8 SUMMARY

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In this unit we have discussed meaning of pteridophytes, their general characters and classification. The division Pteridophyta includes primitive vascular plants. So also called vascular cryptogams (cryptogams with vascular system). We also learnt the economic importance of Pteridophytes. It can be summarized as follows:

1. The main plant body of pteridophytes is sporophyte (diploid).
2. The gametophytic and sporophytic generations are two independent plants in the life cycle.
3. The pteridophyte shows much variation in shape, size and habitat.
4. The pteridophytes grow mostly in cool, moist and shady places.
5. Some pteridophytes are aquatic (*Marsilea*, *Salvinia*, *Azolla*) and few are xerophytic (*Selaginella rupestris*, *M. rajasthanensis*,) as well.



6. The sporophyte plant body differentiated into true roots, shoots and leaves. Some primitive members (members of Psilotopsida) lack true roots and well developed leaves.
7. The stem bears leaves which may be microphyllous or megaphyllous.
8. The sporophytes reproduce by haploid spores which are produced within sporangia. Plants may be homosporous or heterosporous.
9. The sporangia bearing leaf is called sporophyll. In *Equisetum* and *Selaginella* these sporophylls present in the form of compact structures called strobili or cones. In water ferns sporangia are present in specialized bodies called Sporocarps. The sporangia in some higher ferns are present in the form of sori.
10. The haploid spore germinates in gametophytic prothallus. Prothallus bears sex organs archegonia and antheridia. As a result of fertilization the zygote or oospore is formed.
11. The zygote is the first cell of sporophytic generation.
12. Water medium is essential for fertilization.
14. The Zygote develops into new sporophytic plant body.
15. The clear alternation of generation takes place in the life cycle of Pteridophytes.
16. The division Pteridophyta divided into four classes- Psilopsida, Lycopsida, Sphenopsida and Pteropsida.
17. Pteridophytes are economically very important. They are used as food, flavor, dyes, medicines, biofertilisers, oil, fibers and biogas production etc.

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## 1.9 GLOSSARY

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**Asexual:** Having no sexual organs.

**Bio-fertilizer:** the fertilizer obtained from living microbes or plants e.g., *Azolla*

**Cauline:** Arising from upper part of the stem.

**Dioecious:** Having male and female sexes on different prothalli.

**Embryo:** A young organism in early stages of development.

**Fertilization:** The union of male and female nuclei.

**Fossil:** Petrified plant parts found in rocks.

**Gametes:** Sexual cells.

**Gametophyte:** The haploid phase meant for the production of gametes.

**Habitat:** The locality or external environment in which a plant lives.

**Haploid:** Having x number of chromosome (n).

**Heterosporus:** Producing two kinds of spores, i.e. Microspores and Megaspores.

**Lithophyte:** Plants that grow on rocks.

**Megasporophyll:** A fertile leaf attached with megasporangium.

**Microsporophyll:** A fertile leaf attached with microsporangium.

**Monoecious:** Having male and female sexes on same prothallus.

**Pinnate:** A compound leaf having leaf lets on each side of an axis or mid rib.

**Prothallus:** Gametophytic plant body.

**Rachis:** The axis bearing leaf-lets.

**Sporophyte:** The diploid phase producing spores.

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## 1.10 SELF ASSESSMENT QUESTIONS

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### 1.10.1 Short answer type questions:

- Q.1. What are vascular cryptogams?
- Q.2. Which is the most important character of pteridophytes?
- Q.3. Which generation is dominant in pteridophytes?
- Q.4. What is the example of aquatic pteridophyte?
- Q.5. What is the name of sporangium bearing leaf?
- Q.6. Which pteridophyte have sori?
- Q.7. Name some pteridophytes having sporocarps.
- Q.8. Which era is called the age of pteridophytes?
- Q.9. Which pteridophyte is used as biofertilizer?
- Q.10. Which pteridophyte has cone/strobillus?

### 1.10.2-Multiple choice questions:

1. Vascular cryptogams are:  
(a) Bryophytes (b) Pteridophytes  
(c) Algae (d) fungi
2. Bio-fertilizer obtained from:  
(a) *Rhynia* (b) *Equisetum*  
(c) *Psilophyton* (d) *Azolla*
3. Spores of pteridophytes are:  
(a) Haploid (b) Diploid  
(c) Triploid (d) Tetraploid
4. Sporophytic generation is dominant in-  
(a) Bryophytes (b) Pteridophytes  
(c) Algae (d) Fungi
5. Prothallus occurs in:  
(a) Pyrophyta (b) Pteridophyta  
(c) Gymnosperm (d) Angiosperm

### 1.10.3-Fill up the following blanks:

1. Pteridophyte is also known as .....
2. The two categories in which the pteridophyte may be grouped on the basis of size of leaves are.....and.....
3. Many sporangia grouped together to form a .....in higher fern.
4. The aquatic pteridophyte which used for biofertilizer is.....
5. The main stage of Pteridophyta is.....
6. *Lycopodium*, *Equisetum* and *Adiantum* are .....ferns.

7. The production of two different sizes, structures and functions of spores by the same species of a plant is known as.....
8. The haploid spore is a unit of .....
9. The sporangia of *Equisetum* organized in the form of.....
10. The sporocarp is found in.....

**1.10.1 Answer key:** 1. Pteridophytes; 2. Seedless and Vascular system; 3. Sporophytic; 4. Marsilea; 5. Sporophyll; 6. Rynia; 7. Prothallus; 8. Palaeozoic; 9. Azolla; 10. Equisetum.

**1.10.2 Answer key:** 1.(b); 2.(d); 3.(a); 4.(b); 5.(b).

**1.10.3 Answer key:** 1. Vascular cryptogams; 2. Megasporophylls and Microsporophylls; 3. Sori; 4. Biofertilizer; 5. Sporophytic; 6. Homosporous; 7. Heterospory; 8. Gametophyte; 9. Cone; 10. Water fern.

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## 1.12 SUGGESTED READINGS

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- A Text Book of Botany: V. Singh, P.C. Pande and D.K. Jain (2008).
- Botany for Degree Students –Pteridophyta (vascular cryptogams) : P.C. Vashishta, A.K. Sinha and A. Kumar (2006).
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## 1.13 TERMINAL QUESTIONS

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- Q.1. Describe the characteristic features of pteridophytes.
- Q.2. Discuss the classification of pteridophyte.
- Q.3. Describe about habit and habitat of pteridophytes in detail.
- Q.4. Write an essay on Alternation of generation of pteridophytes.
- Q.5. Explain the economic importance of pteridophytes giving suitable examples.

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## **UNIT-2- STELE, SORI EVOLUTION, HETEROSPORY AND SEED HABIT**

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- 2.1 Objectives
- 2.2 Introduction
- 2.3 Stele
  - 2.3.1 Types of Steles
- 2.4 Sorus (pl. Sori)
- 2.5 Heterospory and Seed habit
  - 2.5.1 Origin of heterospory
  - 2.5.2 Significance of Heterospory
- 2.6 General account of Fossil Pteridophytes
  - 2.6.1 Fossil Psilopsids
  - 2.6.2 Fossil Lycopsids
  - 2.6.3 Fossil Sphenopsids
  - 2.6.4 Fossil Pteropsids
- 2.7 Summary
- 2.8 Glossary
- 2.9 Self Assessment Question
- 2.10 References
- 2.11 Suggested Readings
- 2.12 Terminal Questions

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## 2.1 OBJECTIVES

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After reading this unit learners will be able to:

- Definition and types of Steles.
- What is sorus, structure and types of sori and their evolution?
- What is heterospory? Heterospory in pteridophyta.
- Heterospory and seed habit.
- General description of Fossil Pteridophytes.

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## 2.2 INTRODUCTION

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The land plants have complex internal organization. The pteridophytes are first land plants on the earth, who have well developed vascular system. They have central vascular cylinder. The central vascular cylinder of plants is called stele.

Pteridophytes resemble higher land plants (Gymnosperms and Angiosperms) in having complex internal organization with vascular elements but differ from them lacking seed habit. Some of the pteridophytes are heterosporous, they approach closely to seed habit.

The phenomenon of development of two types of spores (differing in size, structure and function) by the same species is known as heterospory. Of the two different sizes the smaller (microspores) are produced in large number and larger (megaspores) are produced in comparatively much smaller number.

Heterospory has been a well debated and intereit is the pre-requisite for the origin of seed. In homosporous genera the sex determination is observed in the gametophytic stage but in heterosporous genera it is observed in sporophytic stage. So it is clear that the heterospory ultimately leads to seed development.

The *Selaginella* is common heterosporous genus, but complete and well developed seeds are not found in *Selaginella* and other heterosporous genera. Absence of integuments, permanent retention of megaspores within megasporangia and histological union between the megasporangial wall and mega spore are the short comings in the formation of complete and true seeds.

Heterospory was present in many fossil genera of Lycopsidea, Sphenopsida and Pteropsida. They were very common in late Devonian and early Carboniferous periods. During this period the important heterosporous Lycopsidea genera were *Lepidocarpon*, *Lepidodendron*, *Lipidostrobus*, *Pleuromea*, *Sigilariostrobus* etc.

The members of Sphenopsida were *Calamocarpon*, *Calamostachys* and *Palaeostachya*. Among them certain members had an advance stage of heterospory. Some carboniferous Lycopsidea and Sphenopsids were arborescent (tree like). Their contribution in present day economy in the form of coal cannot be ignored.

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## 2.3 STELE

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The term stele has been derived from a Greek word meaning pillar. The stele is defined as a central vascular cylinder, with or without pith. Endodermis is the boundary between cortex and stele. The central cylinder or core of vascular tissue, consisting of xylem, phloem, pericycle and sometimes mudullary rays and pith, is technically called the stele.

Van Tieghem and Douliot (1886) interpreted the plant body of vascular plant in the different way. They developed stelar theory. According to them, the fundamental parts of a shoot are the cortex and a central cylinder (known as stele).

Foster and Gifford (1959) have mentioned that the most debated and controversial aspect of the stelar theory on the basis of the anatomical boundaries, which separate the cortex from stele. According to Van Tieghem and Douliot (1886), the endodermis represents the inner boundary of the cortex. But in the stem of many seed plants, the characteristic endodermal layer is not present. Some have mentioned that in such cases, the pericycle serves as the separating layer between the stele and the cortex. But the pericycle is itself the layer of stele. However, stele word is applicable to Pteridophytes while vascular bundle word is used in case of seed plants.

### 2.3.1 Types of Steles

Jeffrey (1898), for the first time pointed out the stelar theory from the point of view of the phylogeny. On the basis of stelar theory, various types of vascular cylinder can be recognised in shoot and root. Most researchers (Jeffrey 1898 and 1917, Esau, 1953; Smith, 1955; Foster and Gifford, 1959) recognise two main types of stelar organisations: **Protostele and Siphonostele**.

#### 1- Protostele

The stele was named protostele by Jeffery (1898). There is no pith in protostele. In protostele, the vascular tissue is a solid mass and the central core of the xylem is completely surrounded by the strand of phloem. This is the most primitive and simplest type of stele. There are several forms of protostele. Researchers such as Brebner (1902), Wordsdell (1902) and Zimmerman (1930) categorized protostele into following types:

**(a) Haplostele:** It was named haplostele by Brebner (1902). This is the most primitive type of protostele. Here the central solid smooth core of xylem remains surrounded by phloem (Fig 2.1.A & 2.2.A). It is found in several fossil genera like *Rhynia*, *Horneophyton* and many living genera *Selaginella crysocaulos*, *S. Kraussiana*, *Selaginella selaginoids*, *Lygodium* etc.

**(b) Actinostele:** This is the modification of the haplostele and somewhat more advanced in having the central xylem core with radiating ribs (Fig.2.2.B). In this type the xylem core is star shaped or stellate. (e.g., in *Psilotum*, *Astroxylon*, *Lycopodium serratum* etc).

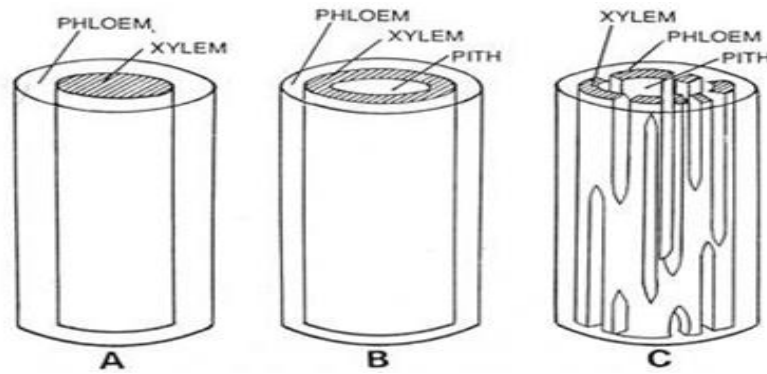


Fig.2.1 Types of arrangement of vascular tissues in stele, A. Protostele, B. Siphonostele, c. Dictyostele

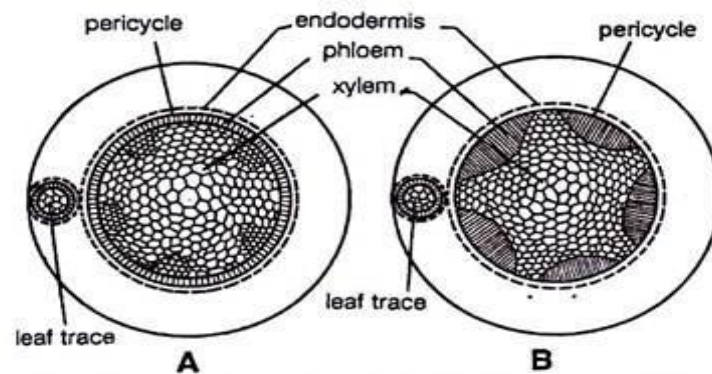


Fig.2.2, A. Haplostele, B. Actinostele

(c) **Plectostele:** This is the most advanced type of protostele. Here the central core of xylem is divided into number of plates arranged parallel to each other (Fig.2.3A). The phloem alternates with the xylem (e.g., in *Lycopodium clavatum* and *L. volubile*).

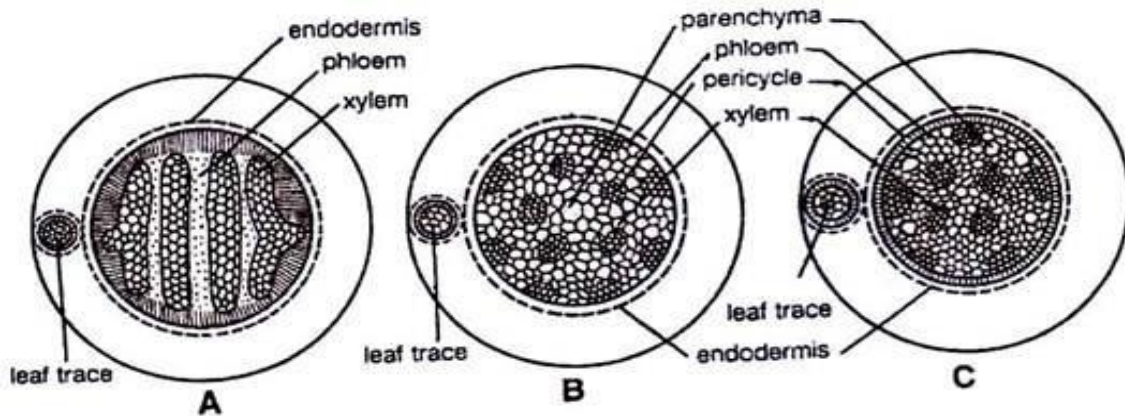


Fig. 2.1, (A-C) Stellar System: A. Plectostele B. Mixed protostele C. Mixed protostele with pith

(d) **Mixed protostele:** Here xylem groups are uniformly scattered in the ground mass of the phloem, called mixed protostele (Fig.2.3 B). e.g., *Lycopodium cernuum*.

(e) **Mixed-pith protostele:** Here the xylem elements (i.e., tracheids) are mixed with the parenchymatous cells of the pith (Fig.2.3-C). 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.*, *Hymenophyllum dilatatum*; *Lepidodendron spp.*; *Osmunda spp.*).

## 2- Siphonostele

Medullated protostele is called siphonostele. It is characteristic of Filicophyta. This is the modification of protostele. During the development of siphonostele, the central core of xylem is replaced by paranchymatous cells hence definite pith surrounded by xylem appears in the centre. Such stele contains a tubular vascular region and a paranchymatous central region.

On the basis of branch and leaf gaps Jeffrey (1910), distinguished two types of siphonosteles, **cladosiphonic siphonosteles** and **phyllosiphonic siphonosteles**. In one type, the leaf gaps are not found and are known as cladosiphonic siphonosteles while in the other type both leaf and branch gaps are present and are known as phyllosiphonic siphonosteles.

Jeffrey (1898) classified Siphonostele into following two types, on the basis of position of phloem.

(a) **Ectophloic siphonostele**: In this type of siphonostele, the pith is surrounded by concentric xylem cylinder and next to xylem the concentric phloem cylinder. It means the phloem is restricted only on the external sides of the xylem. (e.g., *Osmunda* and *Schizea*). The phloem is externally surrounded by pericycle and endodermis (Fig.2.4A).

(b) **Amphiphloic siphonostele**: 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 outer phloem cylinder. It means phloem is present both sides of xylem. (e.g., *Marsilea* rhizome) (Fig.2.4B).

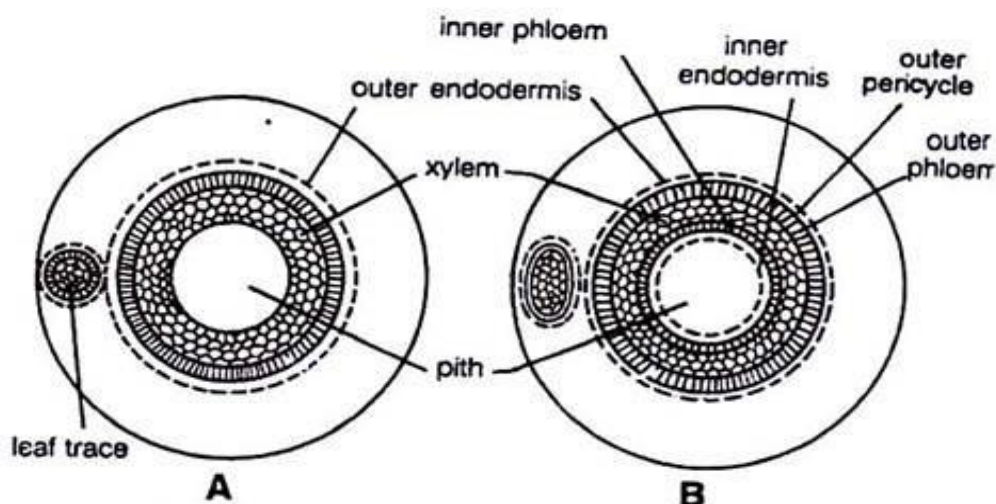


Fig.2.2 (A-B): A. Ectophloic siphonostele, B. Amphiphloic siphonostele



## Other modifications of Siphonostele

### 3-Solenostele

If the siphonostele is perforated at any place due to the origin of the leaf trace, such a condition is known as Solenostele. It is of following two types-

(a) **Ectophloic solenostele:** This type of solenostele derived from the ectophloic siphonostele. So, here the phloem is present on the outer side of xylem.

(b) **Amphiphloic solenostele:** This type of solenostele derived from the amphiphloic siphonostele. In this case the phloem is present on either the sides of the xylem.

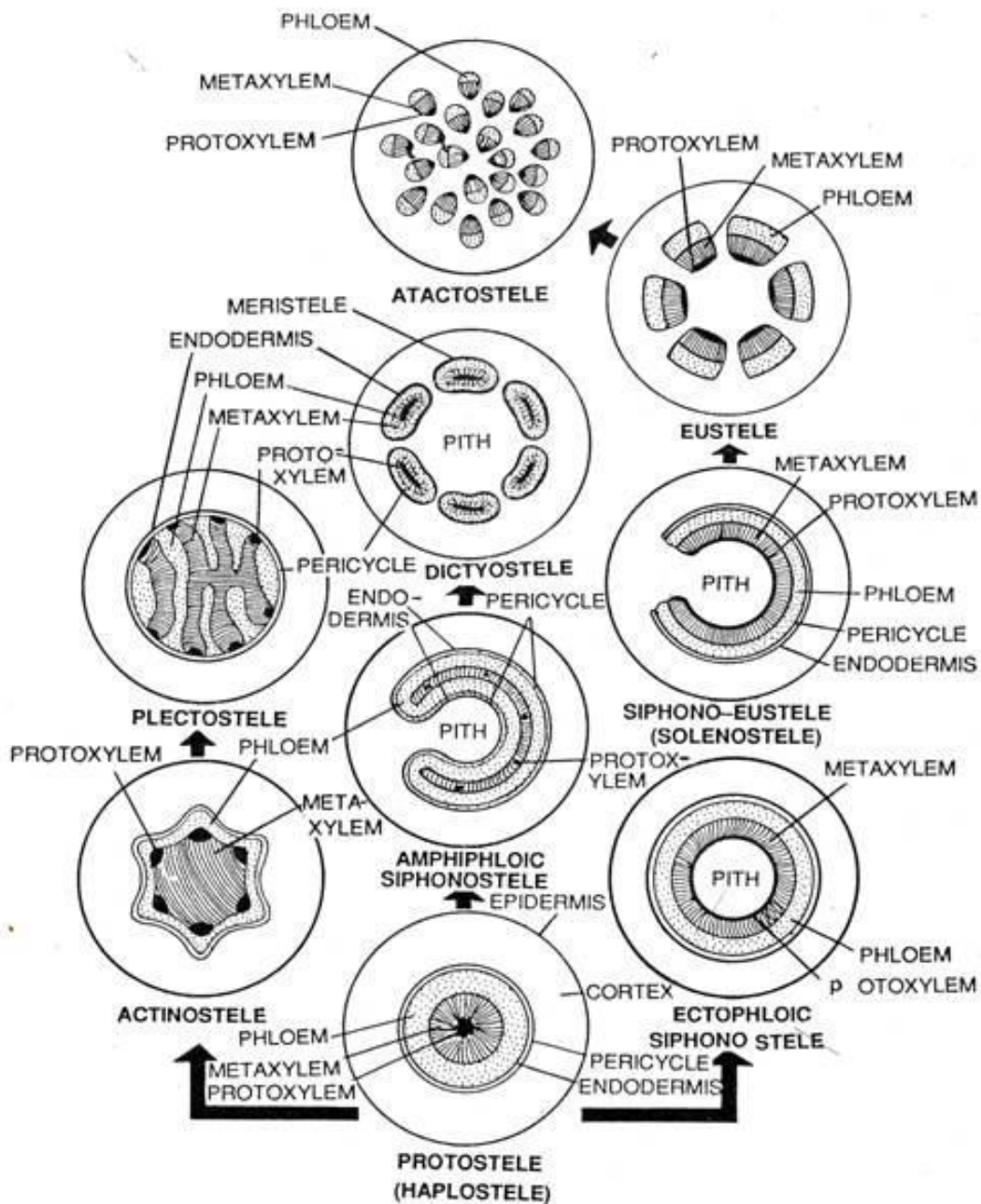


Fig.2.3- Different types of steles arranged in evolutionary sequence

#### 4. Dictyostele

In case of Pteropsida, the successive leaf gaps may overlap each other. Brebner (1902) called the siphonosteles with overlapping leaf gaps as dictyostele. So, in this case the solenostele is broken into a network of separate vascular strands due to crowded leaf gaps. In such cases each separate vascular strand is known as meristele. Each meristele is of protostelic type. Hence the dictyostele is a ring of many meristeles.

#### 5. Eustele

According to Brebner (1902), there is one more modification of the siphonostele known as eustele (Fig.2.6). Here the stele splits into distinct collateral vascular bundles. So 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. The example of this type is *Equisetum*.

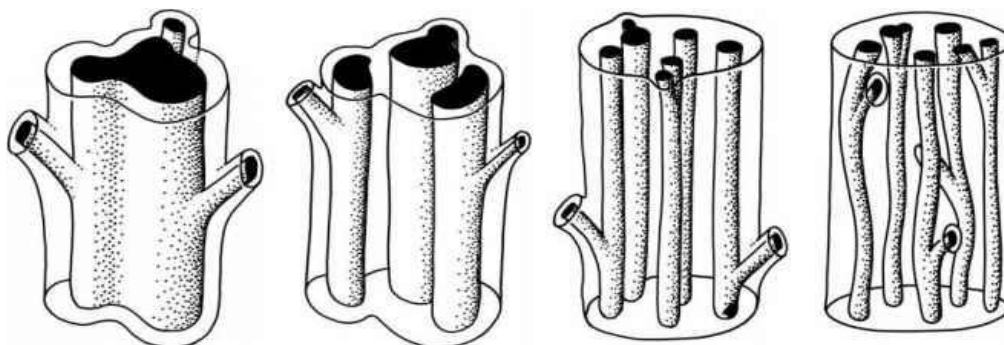


Fig.2.4- Suggested stages in the evolution of the eustele (Taylor and Taylor,1993)

#### 6. Atactostele

In atactostele the vascular strands are scattered. It occurs in monocotyledons (Fig.2.7). George Brebner (1902) coined the term atactostele (Greek *atact*—without order) for vein arrangement seen in transverse view which has been described later as “scattered” by Berg (1997).

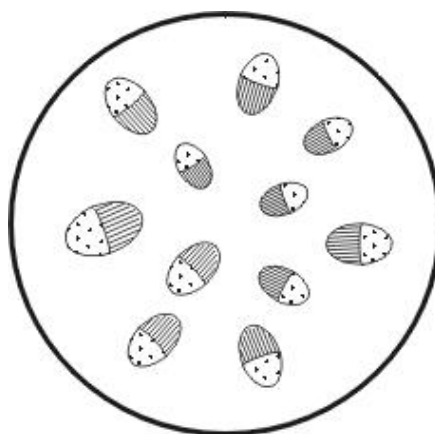


Fig.2.5- Atactostele in Monocots

## 7. Polycyclic Stele

When the vascular tissue present in the form of two or more concentric rings, such a stele is called polycyclic stele. 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*.

## 8- Polystele

When more than one stele is present in the axis of some pteridophytes. Such a condition is called Polystelic condition. Certain species of *Selaginella* have polystelic condition (Fig. 2.8).

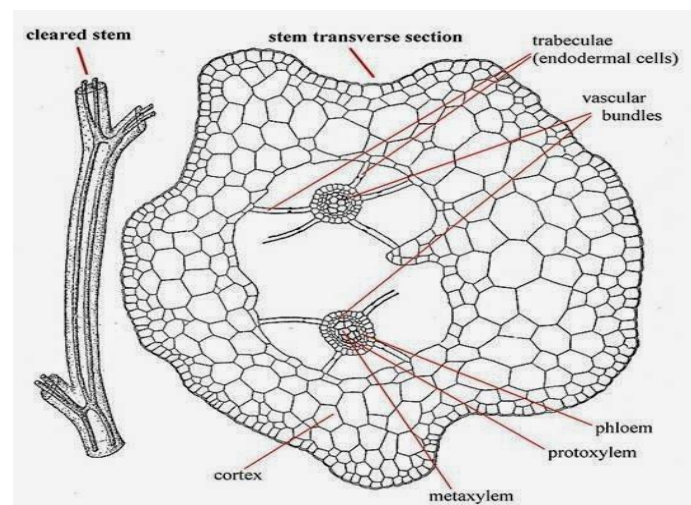


Fig.2.8: Polystelic (distelic) condition in *Selaginella* Stem

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## 2.4 SORUS (pl. Sori)

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A **sorus** (pl. **sori**) is a group of sporangia (Fig. 2.9). Sorus is a Greek word that means 'stack, pile, or heap'. In ferns, these form a yellowish or brownish mass on the edge or underside of a fertile frond. In some species, they are protected during development by a scale or film of tissue called the **indusium**, which forms an umbrella-like cover.

The sporangia within produce haploid spores. As the sporangia mature, the indusium shrivels so that spore release is unimpeded. The sporangia then burst and release the spores.

Protection of the sporangial cluster from exposure, drying, and other hazards is accomplished in various ways, such as by the formation of the sori in grooves or pockets or by the production of various forms of covers. One is the so-called false indusium which is a rolled-over leaf margin under which sporangia form and mature. The true indusium is a separate and unique formation, in some ferns the sori are naked and do not form sori. Their sporangia scatter on veinlets of leaves. The sori have variation in shape, size and arrangement. They are mostly linear, circular and reniform. Sometimes the sori may be large in size due to the fusion, they are called coenosori.



Fig.2.9: Arrangement of sori in different ferns

The shape, arrangement, and location of the sori are often valuable clues in the identification of fern taxa. They may be arranged in rows, either parallel or oblique to the veins or randomly arranged. Their location may be marginal or away from the margin on the frond lamina. The presence or absence of indusium is also used to identify fern taxa.

A widespread type of indusium among members of the family Cyatheaceae is one shaped like a cup, which arises around the base of the sorus, often enclosing the sorus until the sporangia are mature (e.g., *Cyathea*). In some genera, marginal sori are protected by a two-lipped, or valvate, indusium (e.g., *Dennstaedtia*, *Dicksonia*, and *Hymenophyllum*). When sori fuse laterally to form continuous lines, or coenosori, indusia also tend to fuse.

The sorus is classified on the basis of origin as marginal sorus (origin on margin of pinnae), intramarginal and abaxial (superficial) sorus. While on the basis of development of sporangia, they may be simple, gradate and mixed sorus.

**(a) Simple sorus:** A sorus in which all the sporangia appear, grow and mature at the same time is called simple sorus.

**(b) Gradate sorus:** A sorus in which centre or apex is occupied by oldest sporangium and the successive youngest sporangia are present towards the base is called a gradate sorus. Such sorus is also called basipetal sorus.

**(c) Mixed Sorus:** When sporangia of different ages are present in a sorus, without any definite arrangement such sorus is called mixed sorus.

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## 2.5 HETEROSPORY AND SEED HABIT

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Heterospory is a phenomenon in which two kinds of spores are borne on the same plant. The spores are differing in size, structure and function. The smaller one is known as microspore and larger one as megaspore. Such Pteridophytes are known as heterosporous. Most of the

Pteridophytes produce one kind of similar spores, Such Pteridophytes are known as homosporous and this phenomenon is known as homosporous. The sporangia show greater specialization. They are differentiated into micro and megasporangia. The microsporangia contain large number of microspores whereas megasporangia contain few megaspores.

The production of two types of spores with different sexuality was first evolved in pteridophytes. Even though, the condition of heterospory is now represented by only eight living species of pteridophytes, they are *Selaginella*, *Isoetes*, *Marsilea*, *Salvinia*, *Azolla*, *Regnellidium*, *Pilularia* and *Stylites*.

### 2.5.1 Origin of Heterospory

The fossil and developmental studies explain about the origin of heterospory. A number of fossil records proved that heterospory existed in many genera of Lycopsidea, Sphenopsida and Pteropsida. They are very common in late Devonian and early Carboniferous periods. During this period the important heterosporous Lycopsidea genera were *Lepidocarpon*, *Lepidodendron*, *Lipidostrobus*, *Pleuromea*, *Sigilarios robus* etc. The members of Sphenopsida were *Calamocarpon*, *Calamostachys* and *Palaeostachya*. Among them certain members had an advance stage of heterospory.

Williamson and Scott (1894) discovered and described two species of *Calamostachys*. These species are *C. binniana* and *C. casheana*. Former *C. binniana* showed homosporous while later *C. casheana* showed heterospory. The megasporangia contained small and aborted spores. This shows that abortion of spores leads to the differences in the size and number. Chaloner (1958), reported that in *Stauropteris bruntis landica* the megasporangia contained tetrad of megaspores in which two spores were large and two small. Only one megaspore was functional and rest aborted in case of *Lepidocarpon*. All these evidences from fossil records indicate that heterospory occurred quite early in plants and originated by the degeneration of spores in the sporangia.

In living representative of heterosporous pteridophytes the sex determinant exert their influence during the differentiation of spore mother cells (Sporocytes). In *Selaginella* the development up to sporocyte formation is same in micro and megasporangia. After this stage they follow the different course. In the microsporangia all the microspore mother cells are functional and undergo meiosis to form tetrahedral tetrads of microspores while in megasporangia few or mostly one megaspore mother cell remains functional and other start degenerating.

In *Marselia* there is no difference between the microsporangial and megasporangial development before the stage of meiosis. In case of microsporangia, all the 64 spores survive but in megasporangium only one out of 64 spores survives. In case of *Salvinia* only one out of 32 megaspores survives but no degeneration takes place in microsporangium. Here it is clear that in some cases the heterospory originate at the pre-meiotic stage but in others the heterospory originates at the post meiotic stage. So there is no generalisation of the origin of

heterospory. The experimental studies also proved that the nutritional environment of sporangia may alter the pattern of spore formation.

### 2.5.2 Significance of heterospory

Heterospory is an expression of sex determination in plant. Because the microspore gives rise to male gametophyte bearing male sex organs and megaspore develops into female gametophyte bearing female sex organs. So differentiation in the size of spore is directly related to the differentiation of sex of the gametophyte. In homosporous genera the sex determination is observed at gametophytic stage during the formation of antheridia and archegonia. In heterosporous genera the differentiation observed during sporogenesis at sporophytic stage.

The differentiation of microspores and megaspores and their dependence upon the sporophyte has certain advantages. The gametophytes of the ferns are however, dependent for their nutrition upon soil and environmental conditions, whereas in case of *Selaginella*, as far as the nutrition of gametophytes is concerned they derive it from the sporophyte and therefore they are more independent to the external condition than those of ferns.

The phenomenon of Heterospory is of great biological advantage because of the fact that a large megaspore which contains female gametophyte derives its food from the sporophyte, and is independent of the external conditions which might interfere with the growth of a free living gametophyte. Thus it forms a better starting point for the new embryo than an independent green prothallus which has to manufacture its own food.

Heterospory has the considerable importance in the development of seed. Heterospory is rather a pre-requisite for seed habit. The Gametophyte depends upon sporophyte, reduction of gametophytic tissue, reduction in the number of megaspores, retention of megaspore in the megasporangium, all these lead to the seed habit.

In brief, the origin of seed habit is associated with the following important prerequisites:

1. The production of two kinds of spores (i.e., heterospory).
2. Development of only one megaspore in the megasporangium.
3. The retention and germination of the megaspore within the megasporangium.
4. Retention of megaspore inside megasporangium till the formation of female gametophyte and after fertilization.
5. The female gametophyte absorbs nourishment from sporophyte.

In *Selaginella*, there is remarkable approach to the seed habit on account of the following important features:

1. *Selaginella* shows heterospory.
2. The megaspore usually germinates within the megasporangium and their times of release from the megasporangia vary from species to species.
3. There is reduction to one megaspore in some species, e.g., *S. rupestris* and *S. monospora* and a confirmed tendency of reduction in others.

4. In *Selaginella rupestris* the megaspore is never shed and germinates as a gametophyte. Fertilization, embryo development and finally young sporophyte develops on parent plant (Fig. 2.10 & 2.11). The development of young sporophyte on parent plant of *Selaginella* can be linked to viviparous habit of angiosperms.

It becomes quite evident that *Selaginella* has considerably advanced towards the seed habit in a few species, but its approach to the true seed is not complete due to the following features:

1. The megasporangium lacks an integument or covering.
2. The permanent retention of the megaspore within the megasporangium has not become established.
3. After the development of the embryo, the resting period is not there.
4. No histological union between megaspore and megasporangium.

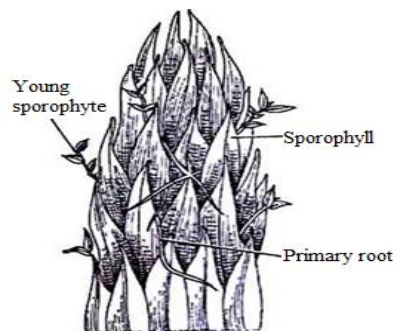


Fig. 2.10, Young sporophyte developing upon the strobilus of parent plant in *Selaginella rupestris*

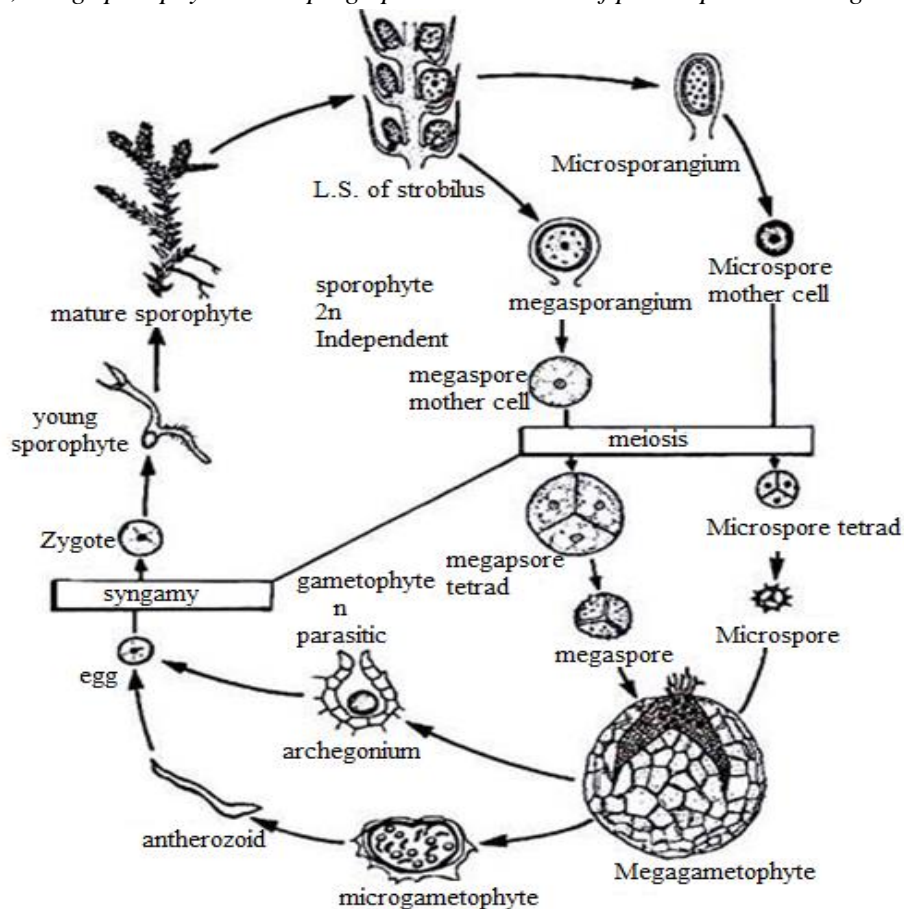


Fig. 2.11- Diagrammatic life cycle of *Selaginella*

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## 2.6 GENERAL ACCOUNT OF FOSSIL PTERIDOPHYTES

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Pteridophytes have a long fossil history. They have been recognized in the late Silurian period of the Paleozoic era. These plants have the dominance in whole of the Palaeozoic era. The middle and the late Palaeozoic era can be regarded as the age of ferns or ages of pteridophytes. The giant lycopsids, the horse tails and the arborescent tree ferns dominated the whole biota at that time. The main fossil groups of pteridophytes are discussed as follows:

### 2.6.1 Fossil Psilopsids

They are the simplest extinct vascular plants that were discovered among the rocks of the early Devonian period of the Palaeozoic era. In this class few genera was included like *Rhynia*, *Horneophyton*, *Cooksonia*, *Zosterophyllum*, *Psilophyton*, *Asteroxylon* etc. These plants were distributed during the late Silurian, Devonian and the Upper Carboniferous periods. These plants lack true roots, leaves and the other structures. However, developed vascular system can be seen in these groups.

Among these plants, the first to be recorded in 1858 was Sir William Dawson's *Psilophyton princeps* that was discovered from the Gaps sandstone. It is the first plant with which our knowledge of the division Psilophyta started.

#### 1-Cooksonia

*Cooksonia* is an extinct & oldest known land plant. The *Cooksonia* dates from the middle of the Silurian to the early Devonian with a total time span of 433 to 393 million years ago. *Cooksonia* includes primitive known land plant to have a stem with vascular tissue. *Cooksonia* is a transitional form between the primitive non-vascular bryophytes and the vascular plants.

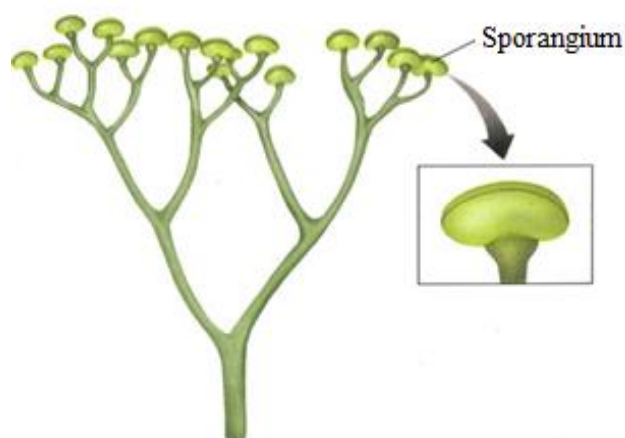


Fig.2.12: Reconstruction of *Cooksonia*

The sporophytes of *Cooksonia* were small, a few centimeters tall, and had a simple structure. The stem width varies from about 0.03 mm to 3 mm. They lacked leaves and roots, although rhizome was present. Plant had a simple stalk that branched dichotomously a few times. Each branch ended in a sporangium (Fig.2.12).



## 2-*Rhynia*

In 1917 the genus *Rhynia* was discovered by Kidston and Lang from Rhynie chert bed in Aberdeenshire district of Northern Scotland. The plant was found in different stems, leaves and the isolated sporangia. Typical dichotomous division can be seen in the stems of the *Rhynia* plants. The aerial shoots of *Rhynia*, were photosynthetic in nature and had stomata all over. The surface of the axis of smaller species bears numerous conspicuous emergences or hemispherical projections. *Rhynia* possesses two species *R. gwynne-vaughani* and *R. major* (Fig. 2.13 A & B).

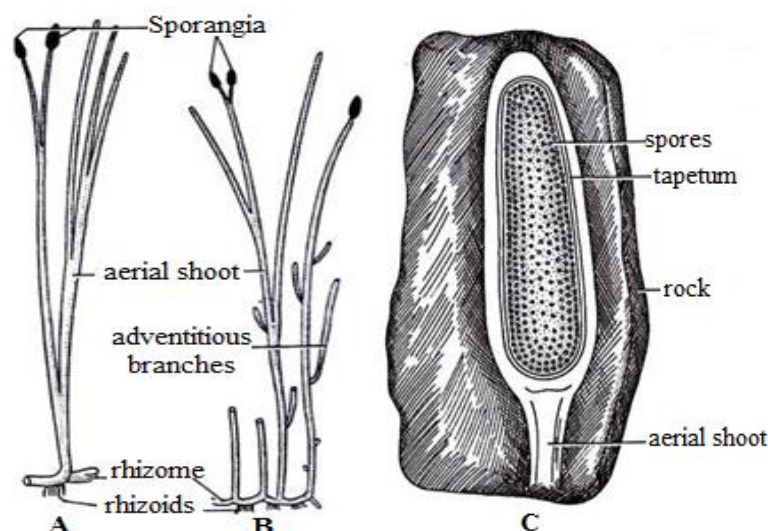


Fig.2.13: *Rhynia*, External features, A- *R. major*, B- *R. gwynne-vaughani* and C-sporangium

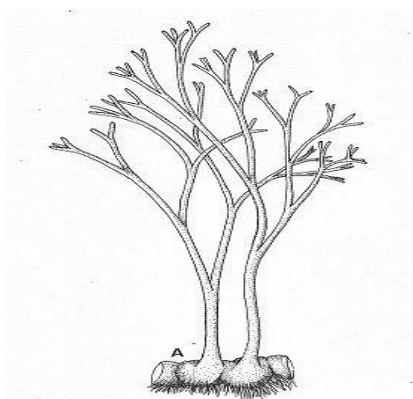
*R. major* was larger and attained a height of 50 cm. with a diameter of 1.5 to 6 mm., while *R. gwynne-vaughani* had a height of 20 cm. and a diameter of 1 to 3 mm. The larger size, absence of hemispherical outgrowths and the absence of adventitious branches are characters that differentiate *R. major* from the smaller *R. gwynne-vaughani*.

The transverse section of aerial stem reveals distinct epidermal layer, an outer and inner cortex and vascular strands. The pericycle and endodermal layers were lacking. Stele is a typical protostele. There are no roots but rhizoids present. The rhizoids are unicellular and grow in tufts from the ventral surface of rhizome.

The aerial shoots have typically terminal sporangia. The sporangia were about 12 mm. in length and about 4 mm. in diameter. The wall of sporangia is three layered. The sporangium contained numerous spores in the form of spore tetrads. *Rhynia* was homosporous.

## 3. *Horneophyton*

*Horneophyton*, is the fossil pteridophytes and it is the linkage between the fossil psilotales and the other living members of the Sphenopsida. These members were also reported from the *Rhynie* chert bed of the Scotland in 1920.

Fig. 2.14: Reconstruction of *Horneophyton*Fig.2.15: *Psilophyton*

The plant body is dichotomous (Fig.2.14) and the sporangium having the central columella. The presence of the columella in the *Horneophyton* shows its affinity and link with the bryophytes whereas the presence of the tracheids in the vascular tissues shows the resemblance with the higher plants. Internal structure of stem resemble with the *Rhynia*.

#### 4. *Psilophyton*

*Psilophyton* is an important extinct genus of order Psilophytales. Specimens of *Psilophyton* collected from Lower Devonian rocks of Gaspé Canada, named by J. W. Dawson. The name *Psilophyton princeps* was given to the reconstruction. This included examples of the markedly spiny stems, and relatively smooth upper branch system that bears sporangia. *Psilophyton princeps* was having creeping rhizome, dichotomously forked aerial branches, spiny lower part of stem, young branch tips circinate curled and terminally paired sporangia on the fertile aerial shoots. More than 20 species of *Psilophyton* have been discovered (Fig.2.15).

#### 2.6.2-Fossil Lycopoids

The Lycopoids has a very long evolutionary history. All the modern living Lycopods are herbaceous plants but their Palaeozoic relatives were herbaceous as well as large trees. The large tree-like lycopods were the major part of forest at that time and they contributed in our present day economy in the form of coal and other biofuel. *Lepidodendron* and *Sigillaria* are the best examples of arborescent lycopods. They were heterosporous. The herbaceous lycopods were *Protolpidodendron* and *Baragwanathia* and these were homosporous. The both types of fossil Lycopods described here in brief.

##### (i) Herbaceous homosporous fossil Lycopods

##### Protolpidodendrales

The Protolpidodendrales comprising the fossil homosporous herbaceous plants (Fig.2.16). Protolpidodendrales consists of Palaeozoic fossils extending from the Silurian to the Devonian. They are usually placed within a single family Protolpidodendraceae which may be rather artificial as the details of most of the genera are not known.

The sporophytes were herbaceous with the branches densely covered by microphyllous, eligulate leaves. Sporophylls were dispersed and not localised on definite strobili. The sporangia, where known, were homosporous. The Protolepidodendrales include genera: *Baragwanathia*, *Archaeosigillaria*, *Leclercqia* and *Protolepidodendron*. Many were short, herbaceous plants, but some reached heights of at least 50 cm. They had rhizomatous rooting structures, dichotomous branching and were probably homosporous.

*Baragwanathia longifolia* from the Silurian of Australia is better known. Even this is older than the Psilophytes. The plant was probably larger than the present day *Lycopodium*. Microphyllous narrow leaves with single median vein up to 4 cm long and 1 mm wide are laxly borne on the stout, dichotomous stems 1 to 5 cm in diameter. The tips of the aerial shoots and the prostrate system are closely covered with small, spinous, eligulate leaves which bifurcate at the tips. On the middle part of the stem sporophylls are laxly borne intermixed with vegetative leaves.

Reniform sporangia, about 2 mm in diameter, are present in certain areas of the stem in axillary position of leaves (sporophylls) intermixed with vegetative leaves. Although it is not definite whether the sporangia were adaxial on the leaves, the general pattern seems to be Lycopodiaceous. The stele, though not well preserved, seems to be actinostelic with annular tracheides in the 12 or more xylem rays.

The sporophylls resemble the vegetative leaves with bifurcate tips and bear single sporangium on the adaxial face and little above the base. The stems are protostelic with triradiate exarch xylems. The metaxylem contains scalariform tracheides. Leaf traces depart from the angles of the xylem and median veins are present in the leaves but it is not clear if the two were continuous. Leaf scars were not formed on the stem when the leaves were shed.

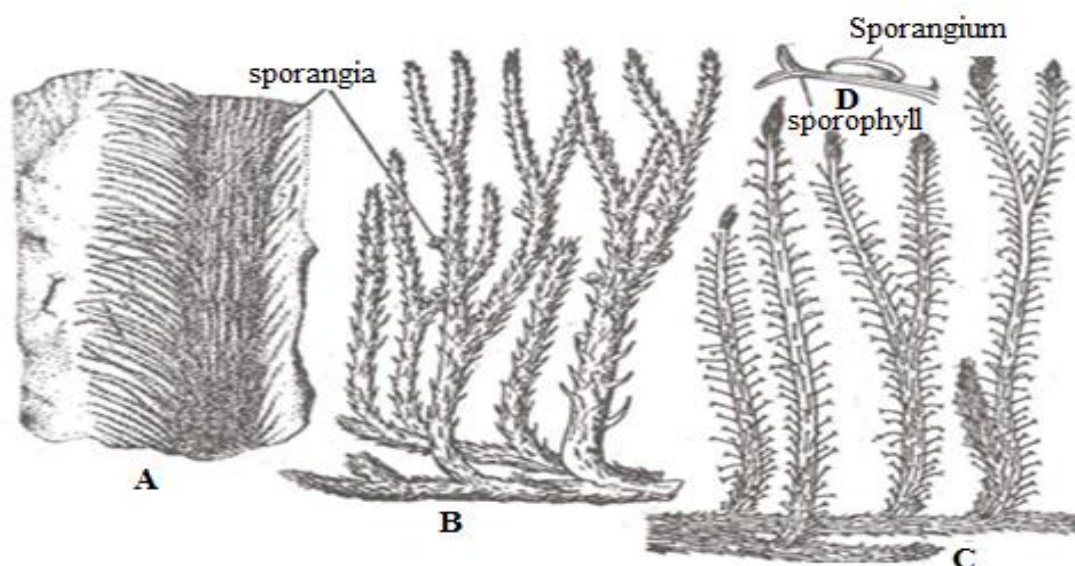


Fig.2.16, Members of Protolepidodendrales, A. *Baragwanathia longifolia*, B. *Drepanophycusspinae formis*, C. *Protolepidodendron scheryanum*, D. Sporophyll of *Protolepidodendron* (after Lang & Cookson)

Protolopodendron is a type genus of this group. It was 30 cm. in height and 1 cm. in diameter. The branches were prostrate as well as erect. The plant body covered with small bifurcated leaves. The sporangia are arranged on upper surface of some leaves (Fig.2.16 C&D). The Stem had a triangular protosteles with lobed xylem.

## (ii) Arborescent (Tree like), Heterosporous fossil Lycopods Lepidodendrales

Lepidodendrales were big trees attaining a height of 30 m or more and a diameter of about 2 m at the base (Fig.2.17). The plants belonging to Lepidodendrales appeared on the Earth during the upper Devonian period i.e. about 359 to 345 million years ago. They were in extreme abundance during carboniferous period (345 to 280 millions years ago). They started declining on the earth during early Permian and became extinct by the end of Permian period. The two most common genera of lepidodendrales found in Pennsylvanian rocks are *Lepidodendron* and *Sigillaria*. *Lepidodendron* stems have diamond shaped leaf scars that are inspiral rows around the tree trunk. *Sigillaria* stems have somewhat rounded leaf scars that are arranged spirally, but vertical ridges between the scars give the appearance that the scars are in vertical rows. The long grass like leaves and reproductive cones of these lycopods are known from fossils. Lycopods were trees of moist, swampy areas and many species became reduced in abundance or extinct as the climate became drier in the Late Pennsylvanian and Permian.

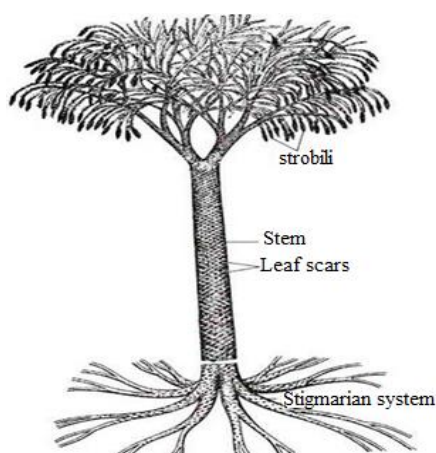


Fig. 2.17: Reconstruction of *Lepidodendron*

*Lepidodendron* is the form-genus for impressions of the outer bark of large arborescent lycophytes. *Lepidodendron* is also the name that paleobotanists use to refer to the biological genus for entire plant, including all of its individual parts. *Lepidodendron* grew to over 100 feet (30 meters) tall and preferred the wetter, areas in swamps. *Lepidodendron* is recognized by the diamond-shaped pattern of leaf scars, each scar being generally longer than wide. *Lepidodendron* also called 'scale tree' (Fig.2.18).

Rooting pattern of the plant indicates presence of humid environment. In all the members of Lepidodendrales, the root-bearing underground axes are called rhizomorph and the detached

rhizomorph and their roots are called *Stigmaria* which are mostly found as siliceous casts or molds (Fig. 2.19).



Fig.2.18: Bark pattern of *Lepidodendron*

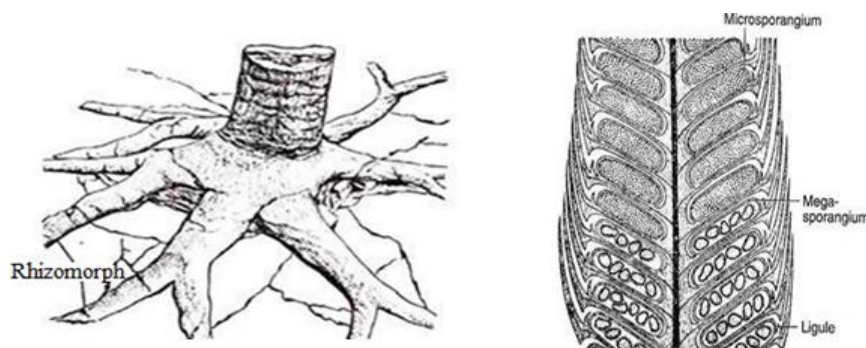


Fig.2.19: Stump cast of *Stigmaria*      Fig. 2.20 L.S. of *Flemingites* cone

The roots of lycopod trees are commonly preserved as casts in clay beds (under clays) beneath coal beds. These structures bear a series of circular pits that represent the attachment points of rootlets. *Stigmaria ficoides*, the commonest species of *Stigmaria*, was a large trunk base that divided dichotomously into four large massive descending axes. The *Stigmaria* spread over an area of about 20 ft (6 m) across.

The *Lepidodendron* was a large tree with a prominent trunk. The ultimate dichotomies bear leaves. The branches and the foliage formed a spreading crown bearing cones at their tips. The plant had bipolar growth, thus the main axis developed branches at both ends. The aerial branches formed three-dimensional dichotomies bearing branches and foliages, similarly the basal branches formed three-dimensional dichotomies bearing stigmarian root system. The leaf cushions are rhomboidal in shape and broader in their vertical dimension than their transverse length. A leaf scar is situated just above the middle line of the cushion. In most species, secondary growth is characteristic of the genus, which was initiated by the unifacial activity of the cambium. Thus, only secondary xylem was produced externally and the cambium did not produce secondary phloem. There was massive extrastellar secondary growth by the meristematic activity of cortical parenchyma. Bisporangiate cones called *Flemingites* (*Lepidostrobus*) were borne terminally (Fig.2.20). The sporophylls were helically attached to the central cone axis. The microsporophylls bearing microsporangia usually borne in the apical portion, while megasporophylls bearing megasporangia occupied

the basal portion of the cones. Hence lepidodendron was heterosporous and the strobili were described as *Lepidostrobus* and *Lepidocarpon*. *Lepidocarpon* is the generic name given to megasporangiate cones in which a single megaspore was present. It developed into megagametophyte. The development was *in situ* because gametophyte was seen retained in the megasporangium. According to Phillips (1979) the entire structure was shed like a seed from the plant. Ovules and seed had not been reported. Due to this it cannot be considered as a true seed rather it is a false seed or seed like structure.

### 2.6.3- Fossil Sphenopsids

**Sphenopsids (horsetails)** first appeared in the Devonian and reached the peak of its development and diversity during the Carboniferous forming a major component of the coal-swamp vegetation. They grew into stout trees that produce a small amount of secondary xylem. Sphenopsids are characterized by jointed stems with whorls of leaves and branches borne at the joints (or nodes). The internodal part of the stem is vertically ridged and spores are produced in rings of sporangia arranged in cones, usually at the tips of the fertile shoots. One of the best-known fossil genus, *Calamites* included tree-like forms that grew up to 30m in height. Another common fossil Sphenopsid, *Sphenophyllum*, was a slender plant with a ribbed stem only 1–7 mm in diameter but up to several metres in length, that probably succeeded in competition over other vegetation. They are type members of two major groups among sphenophytes the Calamitales and Sphenophyllales.

#### 1-Calamitales

The order Calamitales was at its peak of development during the upper carboniferous and become extinct at the end of Permian. Although *Neocalamites* and *Equisetites* were recovered from Mesozoic strata.

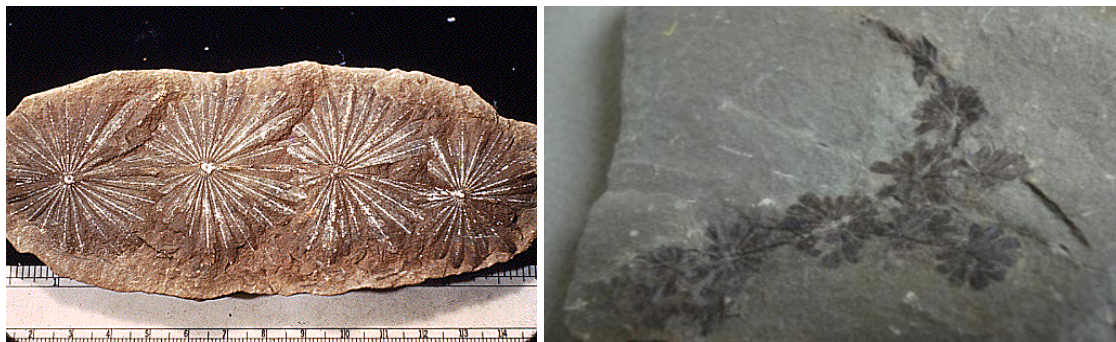


Fig.2.21: Foliage (Annularia) of *Calamites*

*Calamites* is a genus of extinct arborescent (tree-like) horsetails to which the modern horsetails (genus *Equisetum*) are closely related. Its upright stems were woody and connected by an underground runner; however, the central part of the stem was hollow, and fossils of *Calamites* are commonly preserved as casts of this hollow central portion (Fig.2.21). The name *Calamites* was originally given to the pith casts of the hollow stems, but now also used for the whole plant. The organ genera belonging to *Calamites* include following:

<b>Stem</b>	:	<i>Calamites</i>
<b>Leaves</b>	:	<i>Annularia</i> or <i>Asterophyllites</i>
<b>Root</b>	:	<i>Asteromyelon</i>
<b>Fructification</b>	:	<i>Calamostachys</i>

*Calamites* grew to 20 metres tall standing mostly along the sandy banks of rivers. They had upward slender branches, arranged around a bamboo-like trunk in rows spaced several meters apart and had conifer-like needles arranged around the ends of the branches. The leaves were needle-shaped and grew in whorls around the trunk. There were up to 25 leaves per whorl. The trunk was hollow but woody and was very slim so it was not very strong. *Calamites* could either reproduce by spores, which were stored in small sacs and organized into cones, or they could have reproduced by massive underground rhizomes. These underground rhizomes allowed the plant to produce clones of itself. So they had the ability to sprout vigorously from underground rhizomes (Fig.2.22).

*Annularia* is a genus of Calamitalean foliage. The leaves were found at the node in the form of rosette. *Asterophyllites* is another type of foliage of Calamitalean plants. They are needle shaped, in the form of rosette at the node, but all leaves were directed towards the apex of the shoot. *Asteromyelon* given to calamitalean roots.

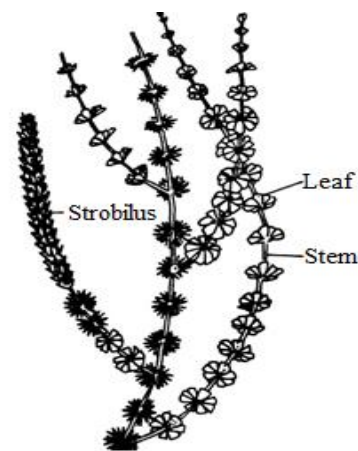
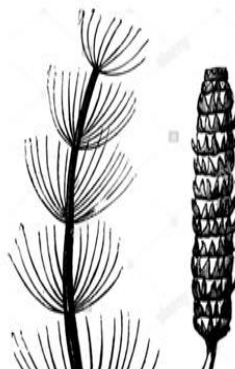


Fig.2.22: Reconstruction of *Calamites* Fig.2.23: *Calamostachys* Fig.2.24: Plant body of *Sphenophyllum* (Reconstruction)

### *Asterophyllites* and *Calamostachys*

***Calamostachys* is the generic name of calamitalean fructification.** The sporophyll holding sporangia are inserted in between on the internodes (Fig.2.23). *Calamostachys binneyana* is a homosporous plant and *Calostachys casheana* is heterosporous.

**Sphenophyllales:** Sphenophyllales represent a small and compact group of sphenopsids. They have left no surviving representative. The geological history of Sphenophyllales dates back to a time earlier than carboniferous period. Some of the genera like *Sphenophyllum*

appeared during Devonian, reaching maximum development during carboniferous period. A few of these Sphenophyllales survived upto Triassic.

They are typified by *Sphenophyllum*, a small, branching plant, probably of trailing habit. The plant body consisted of a main stem, which was slender with jointed stems rarely exceeded 1 cm in diameter and had superposed, longitudinal, superficial ribs between nodes. The vascular system contained a solid xylem core with triangular primary xylem. The leaves were wedge-shaped, usually shorter than 2 cm, and had toothed, notched, or rounded distal margins. They were attached at the nodes by their narrow ends and were in whorls of usually 6 or 9 and rarely 18. Anatomically the stem showed the occurrence of secondary growth. The central pith was completely absent. Instead, the central region was occupied by a triradiate exarch xylem mass. Secondary xylem formed a thick sheath surrounding the primary xylem.

Long, terminal cones, usually called Sphenophyllostachys (*Bowmanites*) when found detached, contained sporangia and spores. The sporangia terminated to slender stalks, forming concentric whorls that alternated with whorls of sterile bracts. Most species were homosporous. Some species could have been heterosporous.

#### 2.6.4-Fossil Pteropsids

Fern-like plants appear in the late Devonian, specialized to colonize disturbed sites such as volcanic landscapes. By the middle Carboniferous, all major fern growth forms were present: trees, vines, and ground cover, mostly specialized to exploit disturbances. Among these plants, however, were tree ferns up to 10 meters tall that lived in swampy wetlands, and whose remains fossilized into coal. Surange (1966) had described *Gondwanidium*, *Pecoteris*, *Merianopteris*, *Belamnopteris*, *Alethopteris* and *Cyclopteris*.

Under the Mesozoic ferns he described many species of Marrattiaceae, Osmundaceae, Glecheniaceae, Cyatheaceae, Dicksoniaceae, Dipteridaceae, Matoniaceae etc. Under the Coenozoic pteropsids the fossil genera of Azollaceae, Salviniaceae and Marsileaceae have been discussed.

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## 2.7 SUMMARY

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Pteridophytes also called vascular cryptogams, they have central vascular cylinder and reproduce by means of spores. Van Tieghem and Douliot (1886) proposed stelar theory. Jeffrey (1898), for the first time pointed out the stelar theory from the point of view of the phylogeny. The most primitive and simplest type of stele is protostele. There is no pith in protostele. It is found in several fossil genera like *Rhynia*, *Horneophyton* etc. If the central xylem core is star shaped (e.g., in *Psilotum*), the protostele is called actinostele. If xylem is divided into number of plates arranged parallel to each other and the phloem alternates the xylem (e.g., *Lycopodium clavatum*), the stele named plectostele. when xylem groups are uniformly scattered in the ground mass of the phloem then it is called mixed protostele (e.g. *Lycopodium cernuum*)



Medullated protostele is called siphonostele. It is characteristic of Filicophyta. It is of two types Ectophloic siphonostele and Amphiphloic siphonostele. If the siphonostele perforated at any place due to the origin of the leaf trace, the stele is Solenostele. Siphonosteles with overlapping leaf gaps develops in dictyosteles. When the vascular strands are scattered, the stele is atactostele, It occurs in monocotyledons.

The phenomenon of development of two types of spores (differing in size, structure and function) by the same species is known as heterospory. The smaller is called microspore and larger is called megaspore. Heterospory impacts on the origin of seed. In homosporous genera the sex determination is observed in the gametophytic stage but in heterosporous genera it is observed in sporophytic stage. So it is cleared that the heterospory is rather a pre-requisite for seed habit and ultimately leads to the seed development.

Heterospory was present in many fossil genera of Lycopsidea, Sphenopsida and Pteropsida. They were very common in late Devonian and early Carboniferous periods. Some carboniferous Lycopsidea and Sphenopsida were arborescent (tree like).

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## 2.8 GLOSSORY

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**Arborescent:** Approaching the size and habit of the tree.

**Basal:** Situated or attached at the base.

**Clone:** A plant derived from the vegetative reproduction of a parent plant,

**Dimorphic:** Occurring in 2 different forms

**Heterospory:** Producing two kinds of spores, i.e. Microspores and Megaspores.

**Indusium:** Outer covering of sorus

**Megaspore:** The larger of two kinds of spores produced by a heterosporous plant.

**Microspore:** The smaller of two kinds of spores produced by a heterosporous plant.

**Pericycle:** A layer of parenchyma or sclerenchyma cells that lies just inside the endodermis.

**Pith:** The central parenchymatous (generally) region of a stem.

**Prostrate:** Lying parallel with the ground.

**Revolute:** Rolled downwards or backwards,

**Stele:** Central vascular cylinder.

**Viviparous:** Referring to seeds which germinate when still attached to the parent plant.

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## 2.9 SELF ASSESSMENT QUESTION

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### 2.9.1-Multiple choice questions:

1. Heterospory is found in:

(a) *Lycopodium*

(b) *Selaginella*

(c) *Rhynia*

(d) *Psilotum*

2. Which of the following was tree?

(a) *Rhynia*

(b) *Lepidodendron*

(c) *Psilophyton*

(d) *Azolla*

3. Lepidodendron is a fossil of
  - (a) Root
  - (b) Fruit
  - (c) Stem
  - (d) Ovule
4. Medullated protostele is called
  - (a) Haplostele
  - (b) Atactostele
  - (c) Siphonostele
  - (d) Actinostele
5. In dictyostele each component is called
  - (a) Meristele
  - (b) Plectostele
  - (c) Protostel
  - (d) Actinostele
6. *Psilophyton* was discovered by
  - (a) Kidston and Lang
  - (b) Birbal Sahni
  - (c) J.W. Dawson
  - (d) C.A. Arnold
7. *Rhynia* lacks
  - (a) Root
  - (b) Sporangia
  - (c) Rhizoids
  - (d) Spore

### 2.9.2-Fill up the following blanks:

1. *Rhynia* is a .....pteridophyte.
2. Stele in *Marsilea* rhizome is.....
3. *Rhynia* was discovered from.....by Kidston and Lang
4. Stellar theory was proposed by.....
5. In actinostele the xylem core is .....shaped.
6. *Lepidodendron* is .....fossil pteridophyte.
7. Fossils of tree Lycopods have been assigned to .....period.
8. ....is medullated protostele.
9. *Calamites* is a fossil of.....
10. Heterospory means presence of .....types of spores

**2.9.1- Answer key:** 1-(b), 2-(b), 3-(c), 4-(c), 5-(a), 6-(c),7-(a)

**2.9.2 Answer keys:** 1. Fossil, 2. Amphiphloic siphonostele, 3.Devonian rocks of rhynie of Scotland, 4.Van Teigham and Douliot, 5. Star, 6. Arborescent, 7.Carboniferous, 8. Siphonostele, 9.Sphenopsids, 10.two.

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## 2.10 REFERENCES

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## 2.11 SUGGESTED READINGS

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### Books

- A Text Book of Botany: V. Singh, P.C. Pande and D.K. Jain (2008).
- Botany for Degree Students –Pteridophyta (vascular cryptogams) : P.C. Vashishta, A.K. Sinha and A. Kumar (2006).
- College Botany, Vol. 2: H.C. Ganguly and A.K. Kar (1999).
- Pteridophyta, Sharma, O P (2012).
- Pteridophyta: Rashid, A (1999).

### Important websites and links

- <http://www.biologydiscussion.com/pteridophytes>
- <https://species.wikimedia.org/wiki/Pteridophyta> assessed in 2018

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## 2.12 TERMINAL QUESTIONS

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### 2.12.1 Short answer type Questions:

- Q.1. What is the stele?
- Q.2. Who proposed the stelartheroy?
- Q.3. Which age regarded as 'age of pteridophytes' comment?
- Q.4. What is a solenostele?
- Q.5. What are different types of protosteles?
- Q.6. What is heterospory?
- Q.7. Name any five heterosporous living pteridophytes.
- Q.8. Write the names of any three form genera of Lepidodendrales.
- Q.9. Give an account of Calamitales.
- Q.10. Comment on Sphenophyllales.

### 2.12.2 Long answer type Questions:

- Q.1. Describe the characteristic features of fossil pteridophytes.
- Q.2. Give an illustrated but brief discussion of various types of steles.
- Q.3. What is heterospory? Describe Seed habit in *Selaginella*.
- Q.4. Write an essay on Heterospory and seed habit.
- Q.5. What is protostele? Describe its various types.

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## UNIT-3-PSILOPHYTOPSIDA, PSILOTOPSISIDA AND LYCOPSISIDA

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- 3.1 Objectives
- 3.2 Introduction
- 3.3 Salient features of important groups and life cycle of some genera
  - 3.3.1 Psilophytopsida
    - 3.3.1.1 *Rhynia*
  - 3.3.2 Psilotopsida
    - 3.3.2.1 *Psilotum*
  - 3.3.3 Lycopsidea
    - 3.3.3.1 *Lycopodium*
    - 3.3.3.2 *Lepidodendron*
    - 3.3.3.3 *Selaginella*
    - 3.3.3.4 *Isoetes*
- 3.4 Summary
- 3.5 Glossary
- 3.6 Self Assessment questions
- 3.7 References
- 3.8 Suggested readings
- 3.9 Terminal questions

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### 3.1 OBJECTIVES

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This unit describes salient features of class Psilophytopsida, Psilotopsida and Lycopsidea and salient features of *Rhynia*, *Psilotum*, *Lycopodium*, *Lepidodendron*, *Selaginella* and *Isoetes*. After reading this unit student will be able:

- To discuss about the external, internal and reproductive structures of *Rhynia*
- To explain the external, internal and reproductive structures of *Lepidodendron*
- To understand habit and habitat of *Psilotum*, *Lycopodium*, *Selaginella* and *Isoetes*
- To discuss morphology and Internal Structure of *Psilotum*, *Lycopodium*, *Selaginella* and *Isoetes*
- To explain Reproduction in *Psilotum*, *Lycopodium*, *Selaginella* and *Isoetes*
- To understand life cycle patterns in *Psilotum*, *Lycopodium*, *Selaginella* and *Isoetes*

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### 3.2 INTRODUCTION

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In previous units you have learn about the classification, general characteristics, habitat, reproduction and economic importance, stele and sori structures in Pteridophytes. This unit describes salient features of class Psilophytopsida, Psilotopsida and Lycopsidea and some of their representative genera. The Psilophytopsida comprises of the fossilized ancient Silurian-Devonian order Psilophytales. This class is often regarded as the most primitive group of the vascular plants and is represented solely by Silurian-Devonian fossil remains. The fossil remains are mostly fragmentary and incomplete so that much of the details of these plants are still unknown. The gametophyte has never been discovered though there are some hypotheses about them. The Psilotopsida comprise of present day living plants which like Psilophytopsida are rootless, dichotomously branched sporophytes differentiated into a rhizomatous horizontal part and aerial shoots. The aerial shoots are with rudimentary leaves with simple (protostele) vascular supply. Because of the similarities of sporophytes they are often combined with the Psilophytopsida to form a class Psilopsida. But the absence of fossil history connection with the Silurian-Devonian Psilophytopsida and the presence of complex sporangial structure lead to treat it as separate class. This class is represented by a single order Psilotales.

The class Lycopsidea which referred to all lycopods has had a long and varied history. It comprises of plants which are rather small in size today although in ancient time they were prevalent trees. The stelar structure is protostelic, siphonostelic or polystelic but never showing leaf gaps. The most important characteristic is the sporophyll with a single sporangium apparently on the adaxial surface near its base. The Lycopsidea are the oldest known vascular plants though not the simplest. From the earliest time the Lycopsidea seem to have been evolved along two different lines. In one group each leaf shows a tongue-like ligule (Ligulatae) developing from the base of each leaf on the adaxial surface. In the ligulate lycopsidea which shows great variation in size as well as evolution of heterospory. Against these, there are other Lycopsidea which are without ligule (Eligulatae) and never became heterosporous.

### 3.3.1 Distinguishing Features of Class Psilophytopsida

1. It includes only extinct plants.
2. The fossil remains are fragmentary and incomplete so that much of the details are still unknown.
3. Only sporophyte is known. The gametophytes have never been discovered though there are some views expressed about gametophytes.
4. The sporophytic plant body is rootless, simple dichotomously branched showing a horizontal, rhizomatous portion bearing rhizoids and aerial shoots arising at different intervals.
5. Aerial shoots are devoid of leaves or bearing simple spinous or leaf like appendages.
6. The vascular system is protostelic while the sporangia are homosporous and terminal on the aerial shoots.

It comprises of the fossilized ancient Silurian-Devonian order Psilophytales. The order is further divided into families. There are five well recognized families out of nine families. These are Rhyniaceae, Psilophytaceae, Asteroxylaceae, Zosterophyllaceae and Pseudosporochneaceae. Family Rhyniaceae includes the genus *Rhynia* which is being described here.

#### 3.3.1.1 *Rhynia*

**External Structure:** The plants of *Rhynia* were herbaceous. *R. major* was 50 cm. in height and 1.5 to 6 mm in diameter whereas *R. gwynne-vaughani* was only about 20 cm. in height and 1 to 3 mm in diameter. The plant body was differentiated into a subterranean rhizome with an abruptly turned upright photosynthetic aerial shoots. Roots were absent but at places rhizome was provided with tufts of unicellular rhizoids (Fig.3.1 A, B). The aerial shoots were cylindrical and leafless with a tapering dichotomously branched system. In *R. major* the aerial shoots were smooth (Fig.3.1 A) but in case of *R. gwynne-vaughani* many adventitious branches were present on the aerial shoots (Fig.3.1 B).

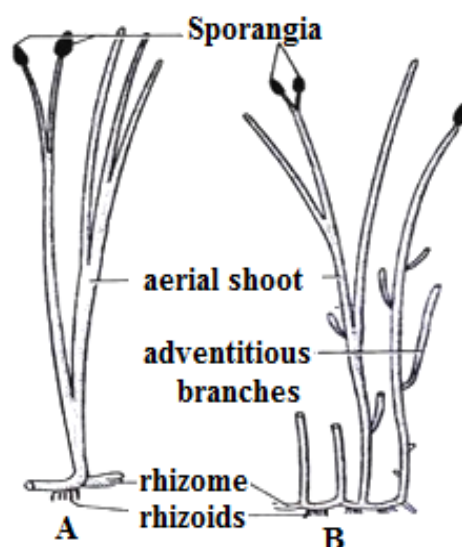


Fig.3.1: External feature of *Rhynia*, A: *R. major*, B: *R. gwynne-vaughani*

These branches perhaps help in vegetative propagation. Some hemi-spherical outgrowths were also reported to be present at the basal portion of the aerial shoots of this smaller species. The tip of the aerial branch usually bears a solitary terminal sporangium which was about 12 mm in length and about 4 mm in diameter.

### Internal Structure

**Transverse section (T.S.) of Aerial shoot and Rhizome:** Anatomically, the aerial shoots and rhizome are almost similar. T. S. of aerial shoot is differentiated into three parts: epidermis, cortex and stele (Fig.3.2A). Epidermis was the outer-most surrounding layer. It was one cell thick and covered by thin cuticle. In aerial shoots it was interrupted at certain places by stomata (Fig.3.2B) but stomata were absent in rhizome. Epidermis was followed by cortex. It is differentiated into outer and inner cortex. The outer cortex was only 1-4 cells thick, thin walled and without intercellular spaces. The inner cortex had large intercellular spaces and its cells had chloroplast. It is thought that this was the chief photosynthetic region of the plant. The endodermis and pericycle layers were absent. The centre of the aerial shoot/rhizome was occupied by stele. The stele was a protostele (haplostele). The xylem was made up of annular tracheids and there were no sieve plates in phloem.

### Reproductive Structures

The sporangia were borne singly on the apices of some aerial branches, each sporangium being oval or slightly cylindrical structure with a little greater diameter than that of aerial branch on which it is developed. They were 12 mm long and 4 mm in breadth in *R. major* and 4 mm long and 1 to 1.5 mm broad in *R. gwynne-vaughani*.

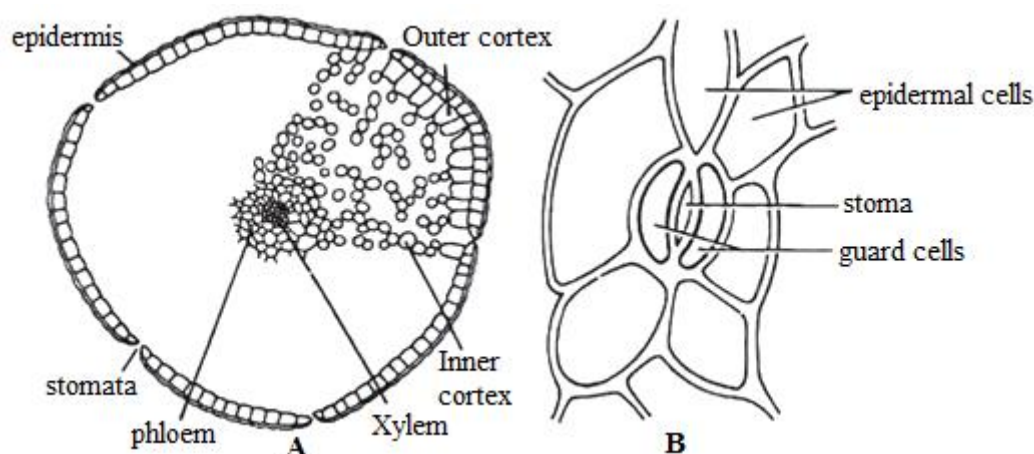


Fig.3.2: Internal structure of *Rhynia*: A. T.S. Stem. B. Stomata in surface view

A longitudinal section (L.S.) of sporangium shows that it had a five cells thick wall. The outermost layer was 1 cell thick cuticularized epidermis. It was followed by 3 cells thick middle layers of thin walled cells. The inner-most layer was 1 cell thick tapetum. The wall was surrounding a spacious sporangial cavity which was without columella and contained large number of spores. The spores were of same size and measured upto 60  $\mu$  in diameter. It means that *Rhynia* was homosporous. In many specimens the sporangium contained

tetrahedral tetrads of spores (Fig.3.3B&C) which suggest that they were formed by reduction division and the plant bearing them represented the sporophytic generation. There was no special mechanism of sporangium dehiscence. The liberation of spores seems to have taken place by disintegration of the sporangial wall. Nothing definite about the gametophyte of *Rhynia* is known.

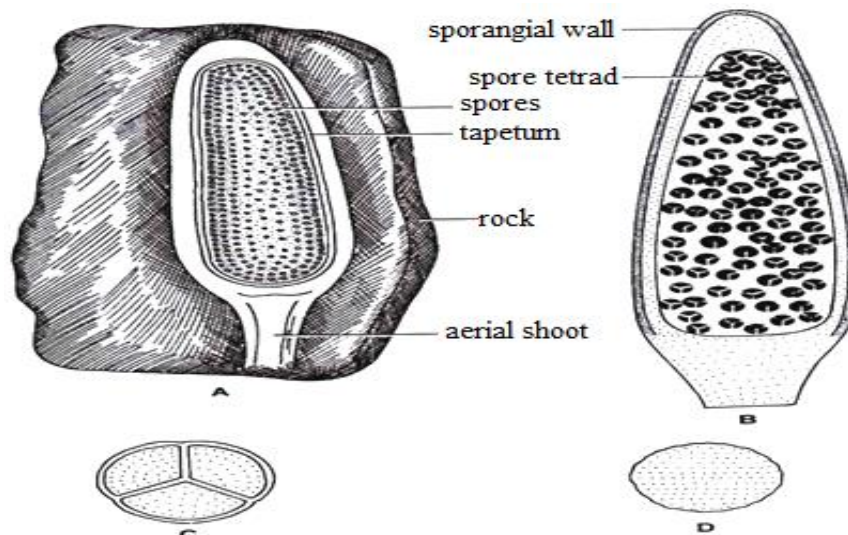


Fig.3.3: *Rhynia* sporangia and spore. A- *R. major*, B- *R. gwynne-vaughani*

### *Aglaophyton major*

*Aglaophyton major* was first described as *Rhynia major* by Kidston and Lang in 1920. In 1986 D.S. Edwards re-examined fossil specimens and reported that they did not contain true vascular tissue, but rather conducting tissue more similar to that of bryophytes. As the diagnosis of *Rhynia* was that it was a vascular plant, he created a new genus, *Aglaophyton*, for this species.<sup>1</sup> (The other species of *Rhynia*, *R. gwynne-vaughanii*, was not affected.) As *Rhynia major* the species had been placed in the *rhyniophytes*, but no alternative higher level classification was proposed for the new genus. Kidston and Lang (1920) interpreted the plant as growing upright to about 50 cm in height, but Edwards (1986) has re-interpreted it as having prostrate habit, with shorter aerial axes of about 15 cm height. The axes branched dichotomously, the aerial axes branching at a comparatively wide angle of up to 90°, and were terminated with elliptical, thick-walled sporangia, which when mature, opened by spiral slits, so that the sporangia appear to be spiral in form (Remy and Hass 1996). Sporangia contained many identical spores (isospores) bearing trilete marks. The spores may therefore be interpreted as meiospores, the product of meiotic divisions, and thus the plants described by Edwards and by Kidston and Lang were diploid, sporophytes. The plant was originally interpreted as a tracheophyte, because the stem has a simple central vascular cylinder or protostele (Kidston and Lang 1920), but more recent interpretations in the light of additional data indicated that *Rhynia major* had water-conducting tissue lacking the secondary thickening bars seen in the xylem of *Rhynia gwynne-vaughanii*, more like the water-conducting system (hydrome) of moss sporophytes. Edwards (1986) reinterpreted the species as non-vascular plant and renamed it *Aglaophyton major*.



### 3.3.2 *Psilotopsida*

#### General characteristics

1. The plant body is a rootless sporophyte that differentiated into a subterranean rhizome and an aerial erect shoot.
2. Branching is dichotomous in both subterranean rhizome and aerial shoot.
3. The large rhizoids borne on the rhizome absorb water and nutrient from the soil.
4. On the aerial shoots, spirally arranged scale like (e.g. *Psilotum*) or leaf-like appendages (e.g. *Tmesipteris*) are borne.
5. Stele is protostelic or siphonostelic with sclenchymatous pith.
6. Secondary growth is absent.
7. Bi or tri-locular sporangia are borne on the axils of leaf like appendages.
8. Mode of sporangial development is of eusporangiate type.
9. Spores are of equal sizes and shapes i.e. homosporous.
10. The gametophytes are green, cylindrical, branched and subterranean. They grow as sporophytes with an associated endophytic fungus.
11. Antherozoids are spirally coiled and multi-flagellated.

This class has a single order Psilotales and family Psilotaceae which includes two living genera *Psilotum* and *Tmesipteris*.

#### 3.3.2.1 *Psilotum*

##### Distribution and habitat

The genus has two well defined but polymorphic species- *Psilotum nudum* (Syn. *P. triquetrum*) and *P. flaccidum* (Syn. *P. complanatum*). This genus is frequently found in tropical and sub-tropical regions of both eastern and western hemispheres. *Psilotum nudum* is the common species while *P. flaccidum* is a rare species and is found in the tropical islands.

##### The Sporophyte

**External features:** The plant is slender and shrubby, rarely as much as a meter in height. It possesses green, ridged and dichotomously branched stems. The stems are perennial and somewhat xerophytic in structure. The stems merge below the surface into slender dichotomous rhizomes which branch freely and may be one meter or more long. There are no roots. The rhizomes remain covered with hair-like absorbing structures or rhizoids (Fig. 3.4). The green aerial shoots of epiphytic plants are commonly pendant and those of terrestrial plants are usually erect. The aerial shoots bear small, scale-like leaves which remain more or less irregular in distribution.

##### Anatomy

**Aerial stem:** In transverse section the aerial stem shows the well-marked epidermis, one cell in thickness. The stomata are found in the grooves of the surface. The cortex consists of three

zones. The outermost zone consists of cells which are thin walled, vertically elongated and having well-defined intercellular spaces among them. This zone is an assimilatory tissue and contains abundant chloroplasts. Inside the photosynthetic zone there is a broad zone consisting of four to five layers of sclerenchymatous cells and represents the main mechanical tissue of the plant. Inside the sclerenchymatous zone there lies a zone of thin walled parenchymatous cells without intercellular spaces.

The well marked endodermis surrounds the stele. There lies a core (pith) of sclerenchymatous cells in the center of the stele which is surrounded by a narrow band of xylem elements. The xylem is exarch and the protoxylem lies at the tip of each ray. The metaxylem tracheids are composed of scalariform xylary elements while the narrow protoxylem elements show spiral thickenings. In between the endodermis and the xylem there lies a mass of thin-walled cells that represent the phloem. The pericycle is ill-defined (Fig. 3.5).

**Leaf:** The leaves receive no vascular tissue. They possess a very simple structure. It remains surrounded by a typical cuticularized epidermis. The stomata are not present. Inside the epidermis there lies the parenchymatous tissue which possesses well developed (e.g., in *P. nudum*) or little developed (e.g., in *P. flaccidum*) intercellular spaces (Fig. 3.6).

**Rhizome:** The epidermis is inconspicuous. All the cells of the outermost cortical layer extend into two celled absorptive rhizoids. The major portion of the cortex is thin-walled and mycorrhizal. The stele is of protostelic type. It has no pith and the xylem mass is usually circular in outline and do not bear any protoxylem rays. There is very little phloem and the endodermis is conspicuous (Fig. 3.7).

## Reproduction

**1-Vegetative propagation:** The vegetative reproduction takes place by means of gemmae. These vegetative structures develop both on rhizomes (sporophyte) and prothalli (gametophyte).

### 2-Sexual reproduction

**The Synangia:** The sporangia are borne in triads on minute appendages subtended by a bract (Fig 3.8). The sporangia remain fused with one another, and therefore, the group is called a synangium. The sporangia seem to be borne on the adaxial side of the appendage at the point of dichotomy and are slightly raised on broad short stalks. The synangium is three lobed and remains divided into three chambers. The wall is composed of several layers of cells. There is no true tapetum. The spores within the sporangium are bean-shaped with finely reticulated walls.

**Development of synangium:** The development is apparently of the eusporangiate type. The earliest stages of development have shown that each locule arises separately from a single epidermal cell of the sporangiophore. The primary initial divides periclinally separating a **jacket initial** and an **archesporial initial**. The jacket initial gives rise to wall three to five cells in thickness, while the archesporial initial produces a central mass of sporogenous cells which give rise to spores.

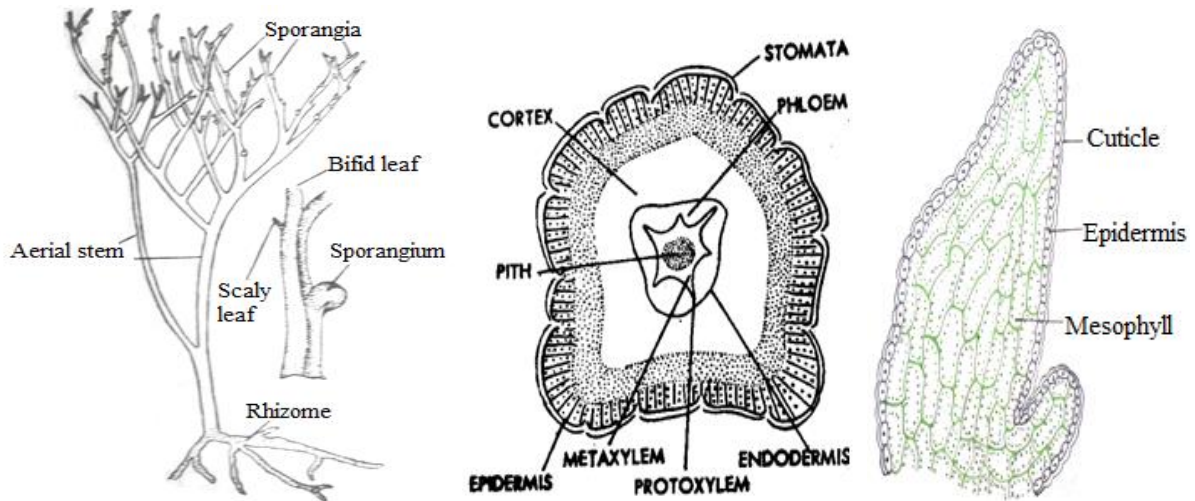


Fig.3.4: A complete plant of *Psilotum nudum* showing synangia; Fig. 3.5 T.S. *Psilotum* stem (Diagrammatic); Fig.3.6: L.S. leaf of *Psilotum nudum*

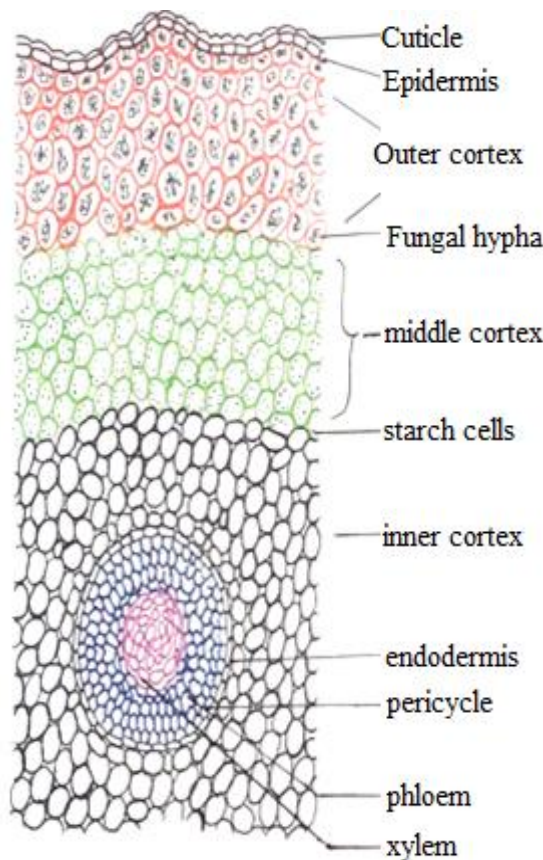


Fig. 3.7: T. S. rhizome of *Psilotum nudum*

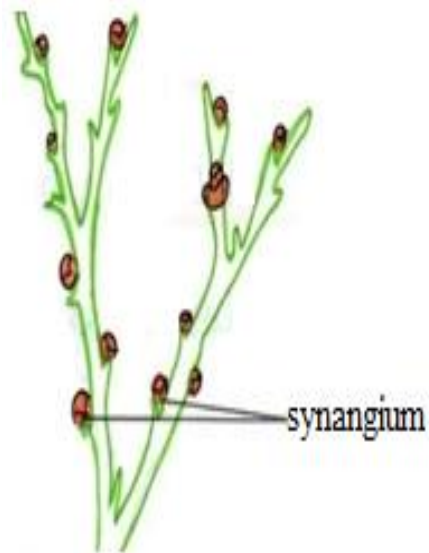


Fig. 3.8: Synangia of *Psilotum*

### The Gametophyte

**Germination of spore:** The spores are of equal size. The spores germinate after about four months by rupture of its wall along the median slit and the spore contents project as a small protuberance covered with a thin membrane, the intine. Later on the extruded portion is cut

off by a transverse wall so that the basal portion remains within the spore wall as a large spherical cell. The apical cell divides by oblique walls and a club-shaped filament is resulted. An apical meristem is established which apparently continues growth resulting in a cellular body. This elongates into a cylindrical, slightly branched prothallus, covered with brown rhizoids. The prothallial tissue is colourless, saprophytic and mycorrhizal as in the sporophyte but it lacks vascular tissue, though cases are on record (Holloway, 1939) in which tracheids are found in large prothalli. The gametophyte is monoecious as it bears both antheridia and archegonia (Fig 3.9). The sex organs are irregularly distributed on the prothallus.

### Development of sex organs

**Development of antheridia:** The antheridia appear first. They are prominently projecting, spherical bodies, with a wall of single layer of cells. The antheridium arises from a superficial cell of the gametophyte (Fig. 3.10 A). The antheridial initial divides periclinally into an outer cell, the jacket initial and an inner cell, the primary androgonial cell. The primary androgonial cell divides and redivides forming a considerable number of androgonial cells, the last generation of which are androcytes. The androcytes metamorphose into spirally coiled multiflagellate anthrozoids. In the mean time jacket initial also divides anticlinally forming a jacket layer one cell in thickness which lies outside the androgonial tissue. There lies a triangular opercular cell in the center of the antheridium which by its disintegration provides an opening for the escape of anthrozoids.

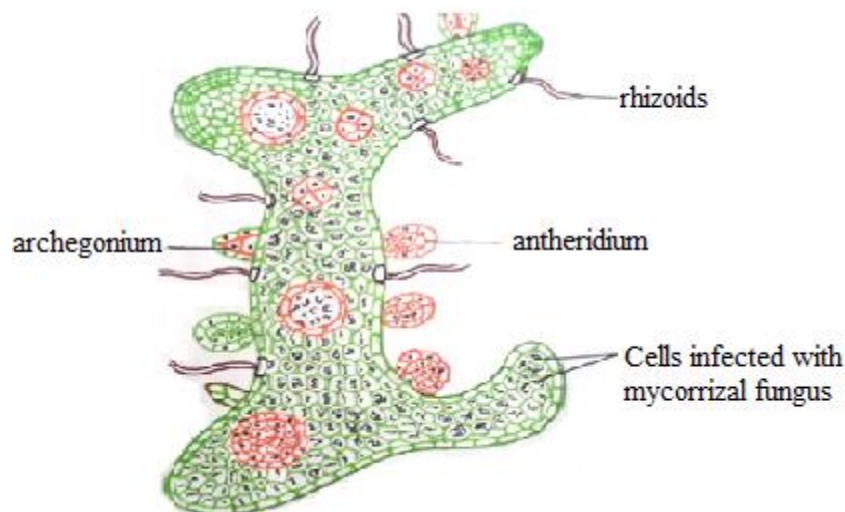


Fig.3.9: *Psilotum nudum*, A mature gametophyte

**Development of archegonium:** The archegonium develops from a superficial cell of gametophyte. (Fig. 3.10 B) and divides periclinally forming a primary cover cell and a central cell. The primary cover cell divides anticlinally twice giving rise to four quaderately arranged neck initials. Now these initials divide periclinally forming an archegonial neck four to five cells in height and composed four vertical rows of cells. In the mean time the central cell also divides periclinally forming a primary canal cell and a primary ventral cell. As the archegonia approach maturity, the cell walls of the lowermost tier of neck cells become cutinized and thickened and the sloughing off of the upper portion the neck takes place. Simultaneously the neck canal cell also disintegrates bearing a passage way for the entrance of anthrozoids in the

venter of the archegonium. One of the antherozoids penetrates the egg and the fusion of male and female nuclei takes place forming the oospore.

**Development of embryo:** The development of embryos very simple. The fertilized egg enlarges downward. Zygote divides by transverse wall into an upper epibasal cell or shoot cell and a hypobasal cell below which will develop into foot, which sends out finger-like projections into the prothallial tissues. No root or cotyledon is formed. The epibasal cell gives rise to the shoot system. There is a marked line of division between axis (upper) and foot (lower). When the developing axis breaks the surface of the prothallus, the foot and the axis separate, the foot remains attached to the prothallus. The first division in the development of epibasal cell into a foot is vertical. Thereafter the division takes place in an irregular sequence in the two halves of the foot (Fig.3.11). As development of the foot continues it becomes a cylindrical structure of equal length and width. Superficial cells of the foot elongate into projection that enter the prothallus like haustoria.

The protruding portion of the sporophyte soon develops rhizoids on its surface and becomes infected with a mycorrhizal fungus. Now this becomes a new independent plant.

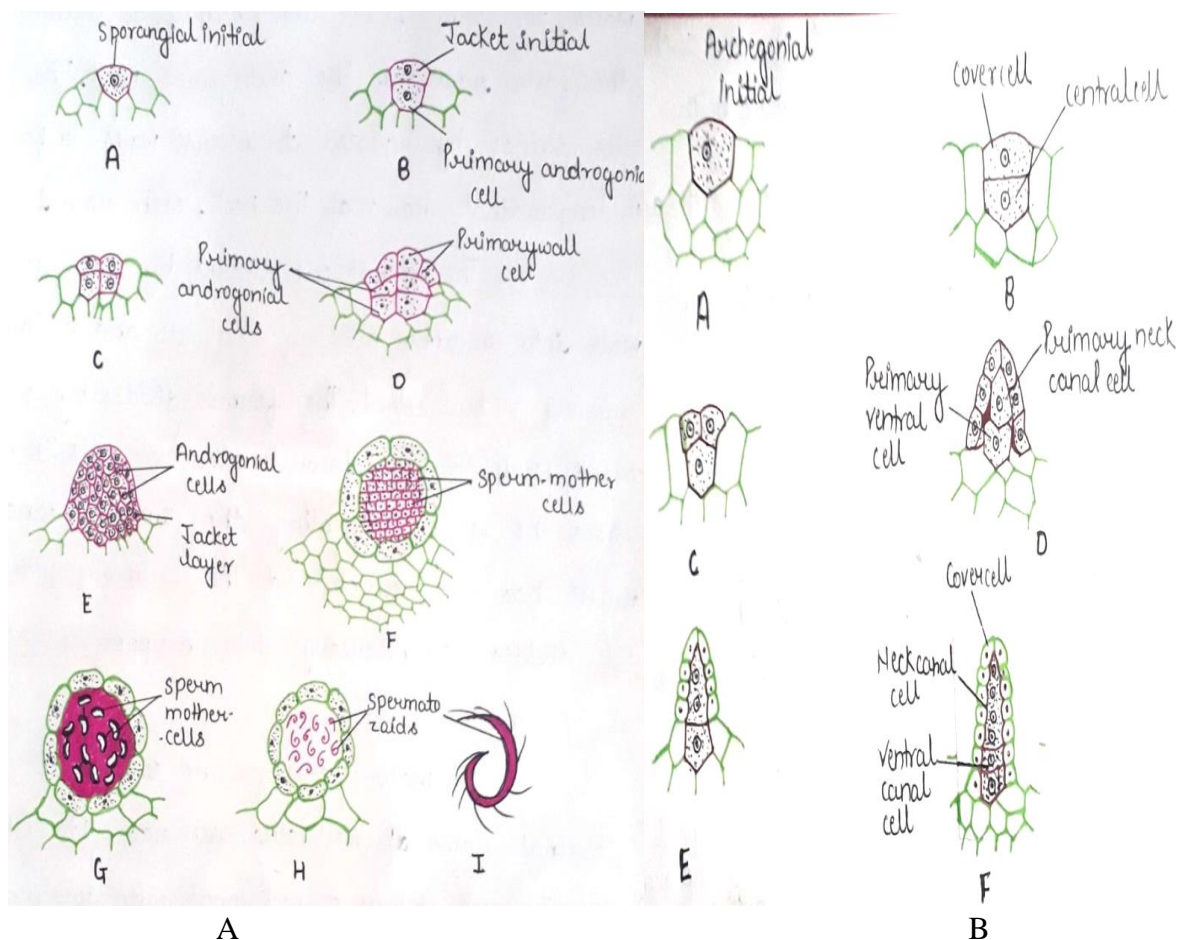


Fig.3.10: *Psilotum nudum*, (A) Stages in the development of Antheridium and (B) Archegonium

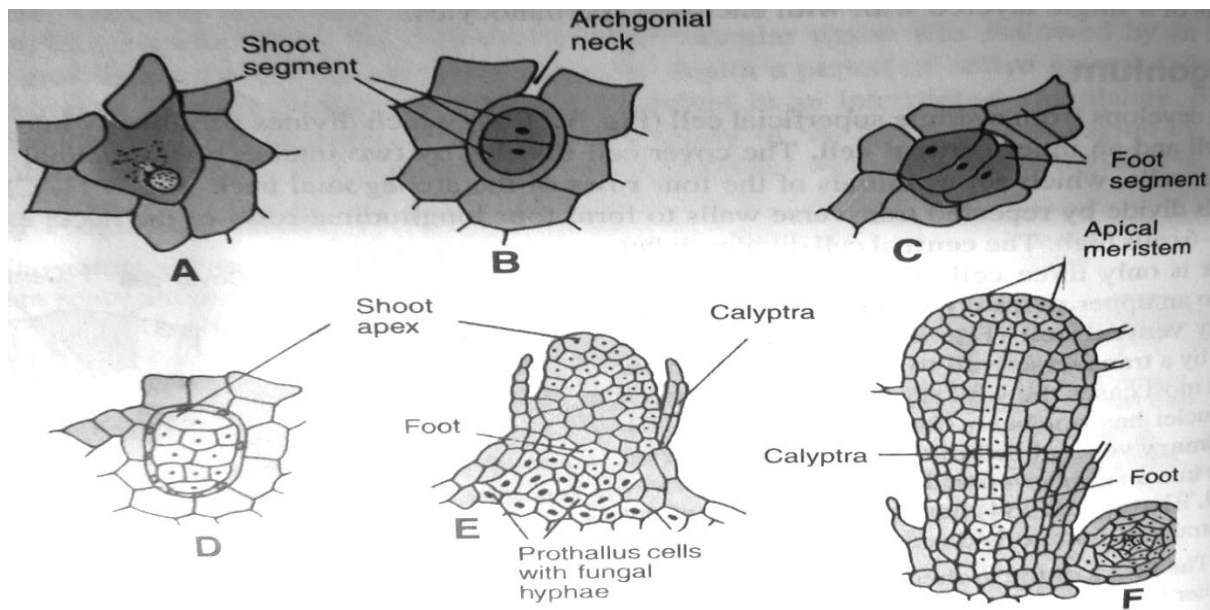


Fig.3.11: *Psilotum nudum*, Stages in the development of embryo

### 3.3.3: *Lycopsidea*

#### General characteristics

1. It includes both fossil (*Lepidodendron*) and living pteridophytes (*Lycopodium*).
2. The sporophyte plant body is differentiated into definite root, stem and leaves.
3. The sporophytes are dichotomously branched.
4. The leaves are usually small (microphyllous). Simple with a single mid vein and usually arranged spirally, in opposite fashion or in whorl.
5. In some members leaves are ligulate (*Selaginella*) and ligule is present at the base of each leaf while some members are eligulate also (*Lycopodium*).
6. The stele may be either protostele, siphonostele or even polystele. The xylem in stem is exarch.
7. Sporangia are quite large and borne singly on the adaxial (upper) surface of the sporophylls.
8. The sporophylls are loosely arranged and form strobilus.
9. The spores may be either one type i.e. homosporous (e.g. *Lycopodium*) or two types i.e. heterosporous (e.g. *Selaginella*). The spores develop into gametophyte
10. Antherozoids are biflagellate or multiflagellate
11. Heterosporous forms have endosporic gametophyte while in homosporous forms the gametophyte is exosporic.

#### 3.3.3.1 *Lycopodium*

**Habit and Habitat:** *Lycopodium* is commonly known as ‘club moss’ due to their moss like appearance and club shaped strobili. It has about 400 species, which are cosmopolitan in distribution. They are found in colder arctic region as well as in temperate, tropical and sub-

tropical regions but they are abundantly found in tropical zones. Thirty three species of *Lycopodium* have been reported from India. Mostly it is found growing in moist and shady places which are rich in humus and other organic matters. Some of the common species are *L. clavatum*, *L. phlegmaria*, *L. cernuum*, etc. On the basis of habit *Lycopodium* is sub-divided into two sub genera: (i) *Urostachya*—stem erect branching dichotomous and roots originate from the base of the stem.(ii) *Rhopalostachya*—stem prostrate with erect branching and roots arise adventitiously from all along the stem.

Mostly the tropical species are epiphytic (e.g., *L. phlegmaria*) and grow hanging from the tree trunks. The temperate species may be erect and shrubby (e.g., *L. reflexum*), creeping (e.g., *L. clavatum*) or erect form (e.g., *L. cernuum*) etc.

**Morphology:** The herbaceous plant body is sporophytic. Usually they may have either prostrate stem with erect leafy branches or weak pendent stem (epiphytes).The plant body is distinctly differentiated into Stem, Roots, and Leaves. (Fig.3.12 A-C). Usually small, adventitious roots are present. Leaves are simple, sessile, small in size, eligulate and possess a single unbranched midrib and are known as microphylls.

### Internal Structure:

**Stem:** A transverse section (T.S.) of the stem of *Lycopodium* is somewhat circular in outline.Epidermisis the outermost layer which is single cell in thickness. The epidermis is cutinised on the outer side and interrupted at places by the presence of stomata. Inner to the epidermis is present a wide zone of cortex which may be homogeneous and made up of parenchymatous cells with small or large intercellular spaces (e.g., *L. selago*) or made up of sclerenchymatous cells, without intercellular spaces. In some species e.g.- *L. clavatum*, the cortex is differentiated into outer and inner sclerenchymatous tissue and middle parenchymatous tissue (Fig. 3.13 A) or differentiated into outer and inner parenchymatous cells and middle sclerenchymatous cells (e.g., *L. cernuum* Fig. 3.13 B). Next to the cortex is present a single layer of well-defined cells known as endodermis with conspicuous casparian strips but at maturity the endodermis may or may not be a distinct structure. Endodermis is followed by pericycle which is composed of one or more layers of compactly arranged parenchymatous cells.

Steleis a protostele i.e., pith is absent and situated in the center. The arrangement of xylem and phloem tissues is different in different species. In case of *L. serratum*, *L. phlegmaria* etc. the xylem is star shaped (actinostele) with a protoxylem situated at the periphery (protoxylem exarch Fig. 3.14 A). In *L. annotinum* the furrows in the xylem are more deep and show stellate arrangement (Fig. 3.14B).The phloem is present in the space between the xylem rays. In case of *L. clavatum*, *L. volubile* etc. xylem appears to be in the form of separate plates arranged somewhat parallel, with phloem in between them. This type of stele is known as plectostele (Fig. 3.13A, 3.14 C). In case of *L. cernuum*, *L. drummondii* etc. xylem and phloem are uniformly distributed i.e. it appears as if strands of xylem are embedded in the phloem. This type of stele is known as mixed protostele (Fig. 3.13 B, 3.14 D).

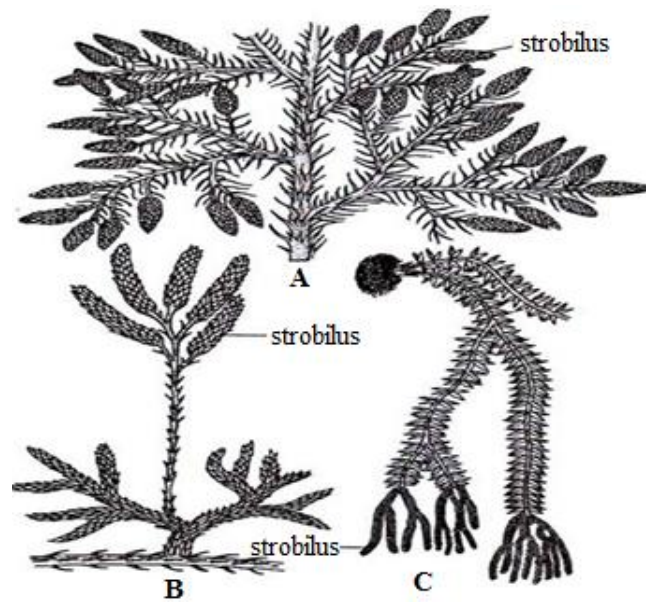


Fig.3.12: *Lycopodium* sporophyte, A- *L. cernuum* (terrestrial), B- *L. clavatum* (terrestrial) C- *L. phlegmaria* (epiphytic)

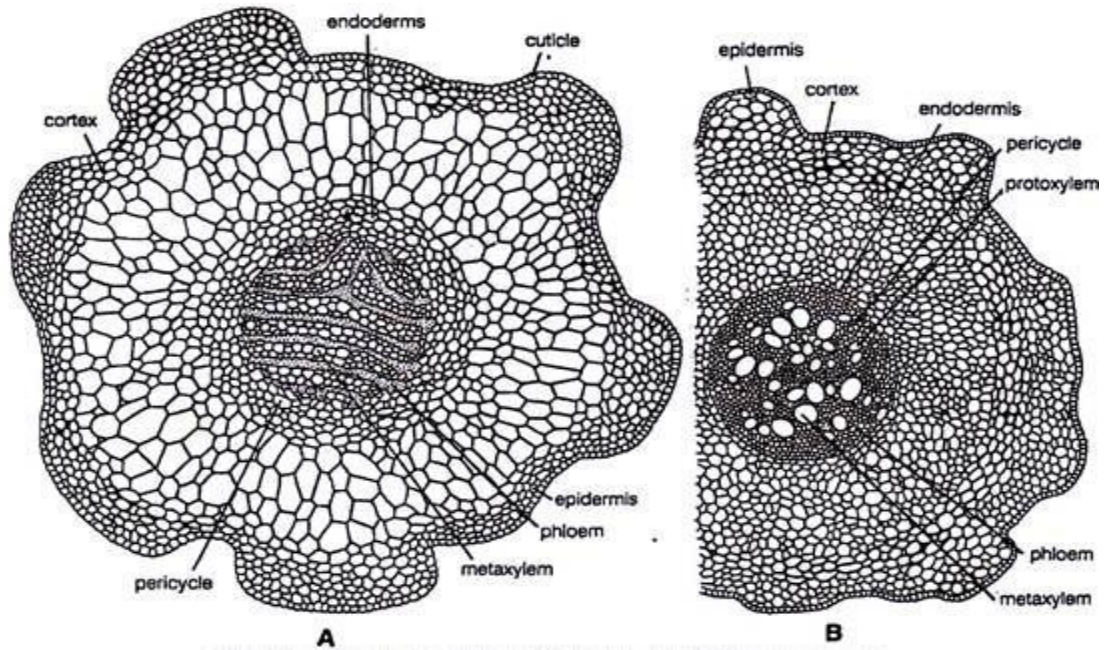


Fig.3.13: T.S. *Lycopodium* stem. A. *L. clavatum* B. *L. cernuum*

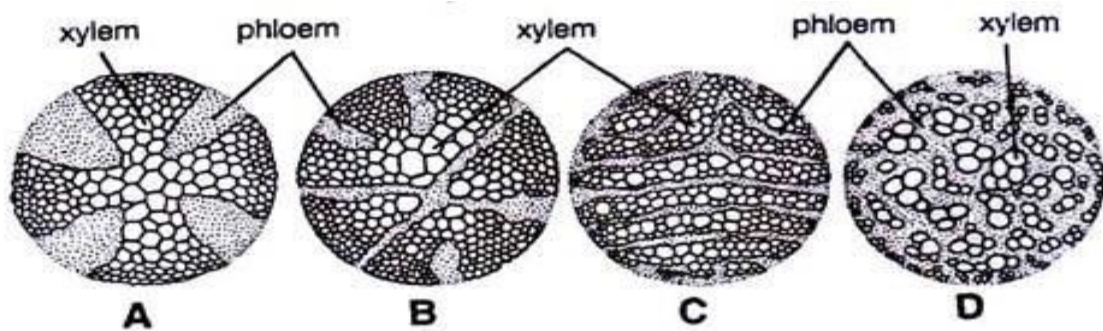


Fig 3.14. Various types of steles in *Lycopodium* stem. A. Actinostele, B. Stellate stele, C. Protostele, D. Mixed protostele



**Root:** The roots are adventitious. A transverse section (T.S.) of the aerial root of *Lycopodium* is somewhat circular in outline. Epidermis the outermost covering layer and is only one cell thick and provided with numerous root hairs present in pairs. Just below the epidermis is present a wide zone of cortex. It is differentiated into outer sclerenchyma and inner parenchyma. Stele may be di-, tetra-, or polyarch with exarch xylem. In prostrate species it is polyarch i.e., having 6-10 plates of xylem arranged radially (star shaped). The phloem is present between the radiating arms of xylem. In erect or pendent species stele is diarch or tetrarch. In *L. selago*, *L. serratum* it is diarch and xylem is C, U or crescent shaped. The phloem is present only in one group between the 2 ends of xylem, (Fig. 3.15 A). The cortical roots are exactly similar in their internal structure to that of aerial roots, except that the epidermis and root hairs are absent. The endodermis and pericycle are indistinct structure at maturity. Pith and cambium are absent (Fig. 3.15 B).

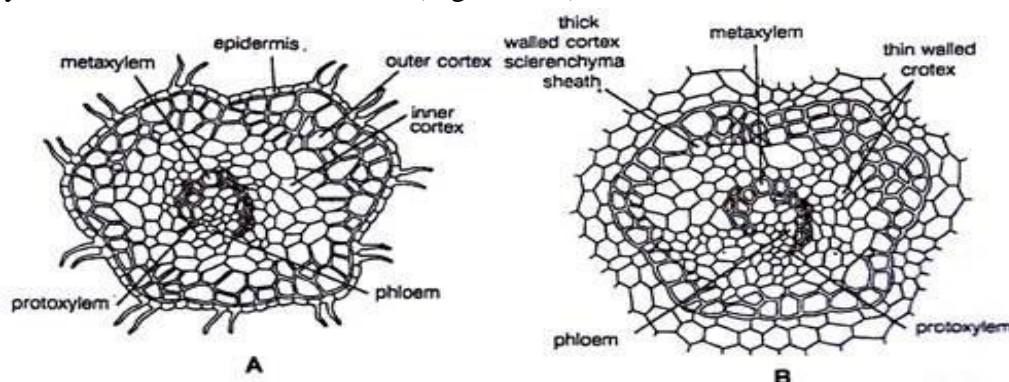


Fig.3.15: T.S. of *Lycopodium* root. A. Aerial root, B. Cortical root

**Leaf:** T.S. of the leaf shows epidermis, mesophyll tissue and a single median vascular bundle. The outermost surrounding layer is only one cell in thickness. The cells of epidermis are parenchymatous and cutinised on their outer side. The epidermis is also interrupted by the presence of stomata. In homophyllous (isophyllous) species the stomata are present on outer as well as inner epidermis (amphistomatic) but in heterophyllous (anisophyllous) species the stomata are mostly restricted on the lower epidermis (hypostomatic). Mesophyll occupies a wide zone between the epidermis and the vascular bundle. It is usually made up of thin walled chlorenchymatous cells which may be with or without intercellular spaces. In the center of the leaf is situated only a single concentric vascular bundle made up of xylem and phloem. The vascular bundle is surrounded all around by a sclerenchymatous sheath (Fig. 3.16).

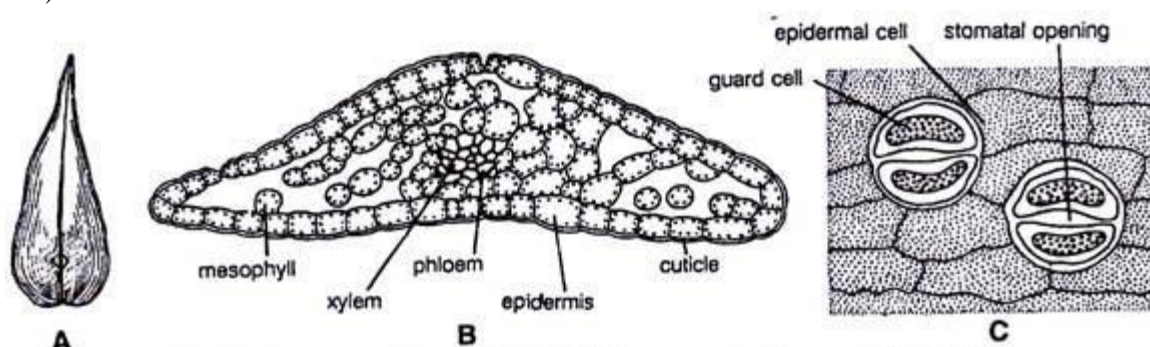


Fig. 3.16. *Lycopodium*, A- A leaf, B- T.S of leaf, C- Stomata on leaf surface

## Reproduction

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

**(i) Gemmae or bulbils:** In a few species like *L. selago*, *L. lucidulum* etc. certain buds like structures known as gemmae or bulbils are usually produced in large numbers on new stem tips annually.

**(ii) Death and decay:** Species with creeping stem reproduces vegetatively by the death and decay of older parts of the stem at the point of branching. This separates the branches which later on grow independently.

**(iii) Resting buds:** In *L. inundatum* the whole of the plant body except the growing tip of rhizome is dead during winter. This tip portion of the rhizome acts as resting bud which in the coming spring season resumes growth and develops into a new plant.

**(iv) Fragmentation:** In several epiphytic species fragments of the plant body are capable of giving rise to new plants.

## 2. Sexual Reproduction

**Spore Producing Organs:** The plant is homosporous i.e., produces only one type of spore. These spores are produced in sporangia which, in turn, are produced on fertile leaves known as sporophylls. Usually the sporophylls are grouped together to form a compact structure known as strobilus or cone which are terminal in position (Fig. 3.17 A).

**Strobilus:** The sporophylls are loosely arranged and may be of the same size or of different size from the foliage leaves. The arrangement of sporophylls is same on the central axis as that of the vegetative leaves on the stem i.e., spiral, whorled or decussate etc. Longitudinal section (L.S.) of strobilus shows the presence of a strobilus axis in the center. On the strobilus axis are present sporophylls (Fig. 3.17 A). Each sporophyll bears only one sporangium (Fig. 3.17 B). All the sporangia are similar in structure and are arranged acropetally in a strobilus i.e., the youngest are at the top (Fig. 3.17 C).

**Structure of Sporangium:** Sporangia are sac-like structures but usually kidney shaped in appearance (Fig. 3.17 B). Sometimes they are sub-spherical in appearance. Their colour varies from orange to yellow. Each sporangium consists of a basal short massive stalk i.e., sub-sessile, with an upper globular unilocular body containing numerous spores. The body of the sporangium consists of 3 or more layers of wall surrounding a cavity. The inner most layer of the wall of sporangium is called as tapetum (Fig. 3.18 F) which is nutritive in nature and persists till maturity. In the young sporangium inside the wall is present a mass of sporogenous cells which in due course of development form spore mother cells which by meiotic divisions, produce haploid tetrad of spores. The spores at maturity separate from each other.

The wall of the sporangium is provided with a transverse strip of cells known as stomium from where the sporangium at maturity splits into 2 valves and the spores are dispersed away in the air. Each spore is provided with a triradiate ridge (Fig. 3.17 D, E) and is somewhat

yellow in colour. A small amount of chlorophyll may or may not be present in spores. Reserve food is in the form of oil in the spores.

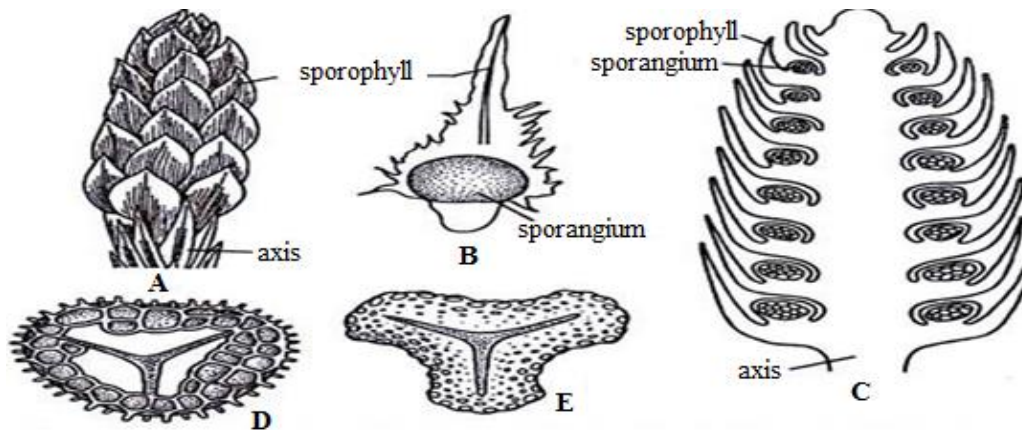


Fig. 3.17. *Lycopodium strobilus*: A- A strobilus, B. A sporophyll showing sporangium on adaxial surface, C. L.S. of strobilus, D-E. Spores

### Development of sporangium and formation of spores

The sporangium develops from a small group of superficial cells arranged in a transverse row on the adaxial side of the sporophyll near the base (Fig. 3.18 A, B). These cells divide by periclinal divisions forming an outer and inner layer of cells. The outer cells divide periclinally and anticlinally forming three celled thick wall of the sporangium (Fig. 3.18 A-F). The inner layer or archesporial cells divide in all directions forming a group of cells known as sporogenous tissue which finally gives rise to spore mother cells. Each spore mother cell undergoes meiosis producing a tetrad of spores (haploid) with tetrahedral arrangement. As the sporangium approaches towards maturity, a transverse row of cells is differentiated near the apical portion from the wall of a sporangium known as stomium. . As the sporangium loses water, it creates a pressure on the wall which leads to the appearance of slit in the stomium as a result of which the wall splits into two halves and the spores are disseminated by air current.

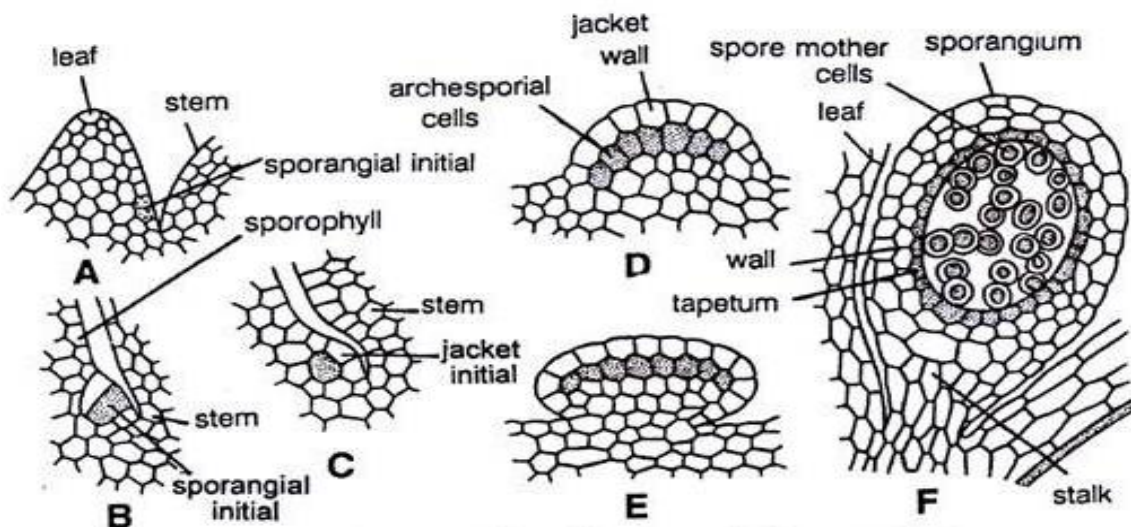


Fig.3.18: *Lycopodium*, Stages in the development of sporangium

## Gametophytic Generation:

The development of the gametophyte (prothallus) takes place from the haploid spores which are the unit of gametophytic generation. Each spore is unicellular, uninucleate haploid structure, 0.03 mm in diameter and surrounded by 2 layers, with a triradiate ridge at the surface (Fig. 3.19 D, E). Chlorophyll may or may not be present in different species both the male and female reproductive organs are produced on the same gametophyte. Germination of spore is depicted in Fig. 3.19.

**Structure of the Mature Gametophytes:** The form and structure of the gametophytes varies greatly in different species. In general they have been grouped under three categories:

**Type I or Cernuum type:** Gametophyte is partly aerial and partly in soil. The prothalli are usually 2 to 3 millimeter in height and 1-2 millimeter in diameter. The gametophytes (prothalli) grow at the surface of the ground and consist of a colourless basal portion buried in soil and a conspicuous upright, fleshy, green aerial portion having lobes (Fig. 3.20 A). The sex organs develop between the green expanding lobes. The underground part contains endophytic fungus e.g., *L. cernuum*, *L. inundatum* etc.

**Type II or Clavatum Type:** The gametophyte is wholly subterranean and totally saprophytic i.e., non- green structure. It is tuberous and without lobes. It may be one to two centimeter long or wide and is top shaped, conical or discoid in shape (Fig. 3.20 B, C). The endophytic fungus is present. Sex organs are formed on the upper surface e.g. *L. annotinum*, *L. complanatum*, *L. clavatum* etc.

**Type III or Phlegmaria type:** The gametophyte is subterranean, saprophytic and colourless. This type of prothallus is seen in *L. phlegmaria* and other epiphytic species. The prothallus is about 2 millimeter in diameter and monopodially branched (Fig. 3.20 D). Sex organs are borne on upper surface of large branches and are interspersed with slender filaments known as paraphyses.

**Development of antheridium:** A single superficial antheridial initial cell situated just away from the meristematic cells gives rise to an antheridium (Fig. 3.21). The triangular opercular cell becomes mucilaginous as a result of which an opening is formed at the apex of antheridium through which water enters into it. The antherozoids absorb water and swell up as a result of which a pressure is created on the wall of antheridium which finally ruptures and the antherozoids are liberated.

**Development of archegonium:** Just like antheridium, the archegonium also arises from a single superficial cell called archegonial initial, situated just away from the meristematic cells at the apex (Fig. 3.22). The archegonium is a sunken flask shaped structure with neck projecting out of the prothallus.

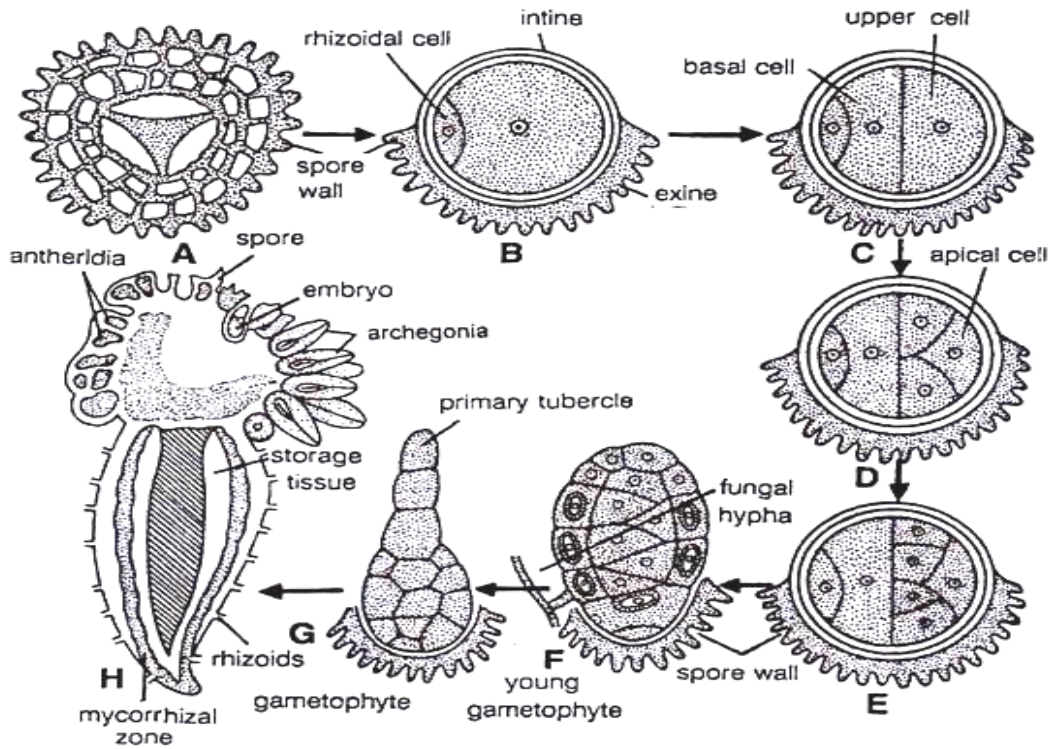


Fig. 3.19: *Lycopodium*, Successive stages in the development of prothallus

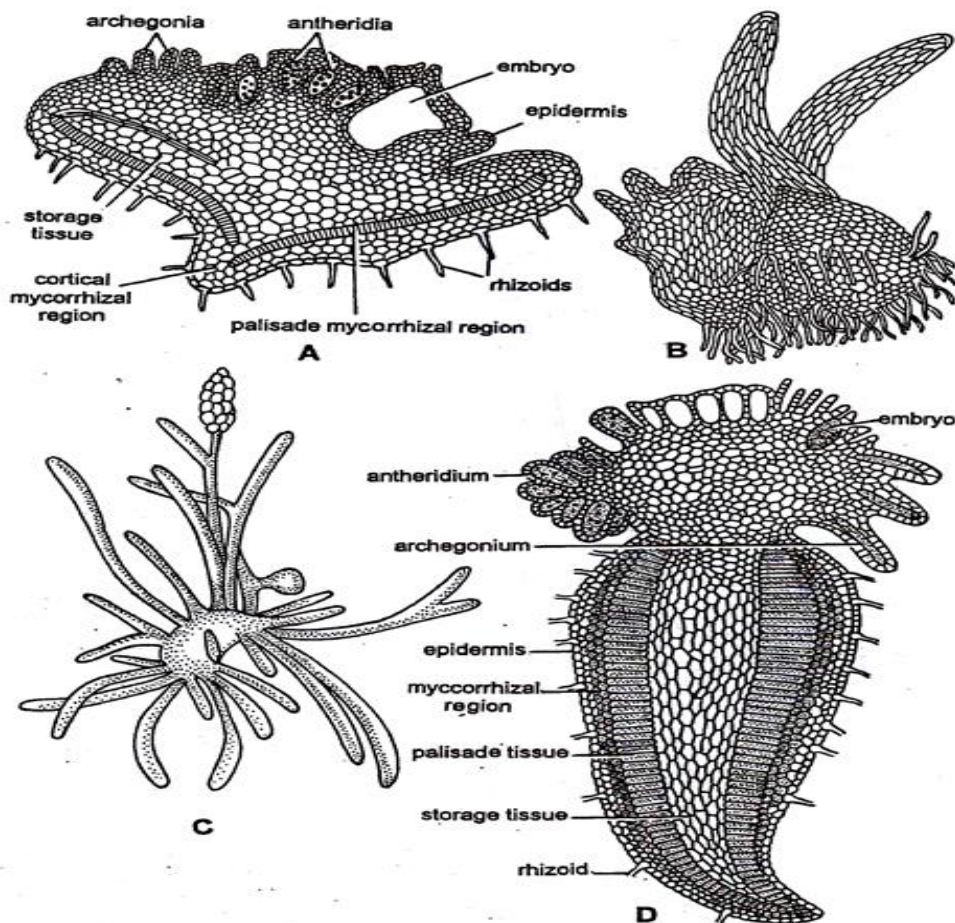


Fig. 3.20: *Lycopodium* prothallus, A. *Cernuum* type, B-C. *Clavatum* Type, D. *Phlegmaria* type

**Fertilization:** At the time of fertilization the neck canal cells and the ventral canal cell disorganise and the cells of the upper-most tier of neck slightly separate apart forming a passage upto the egg (Fig. 3.22 H). The biflagellate antherozoids reach the archegonium by swimming in water on the surface of prothallus and enter the archegonium through neck and reach the egg. Only the nucleus of one antherozoid fuses with the egg nucleus thus forming a diploid structure-known as oospore (2x). The act of fertilization ends the gametophytic generation and the initial stage of sporophytic generation is formed.

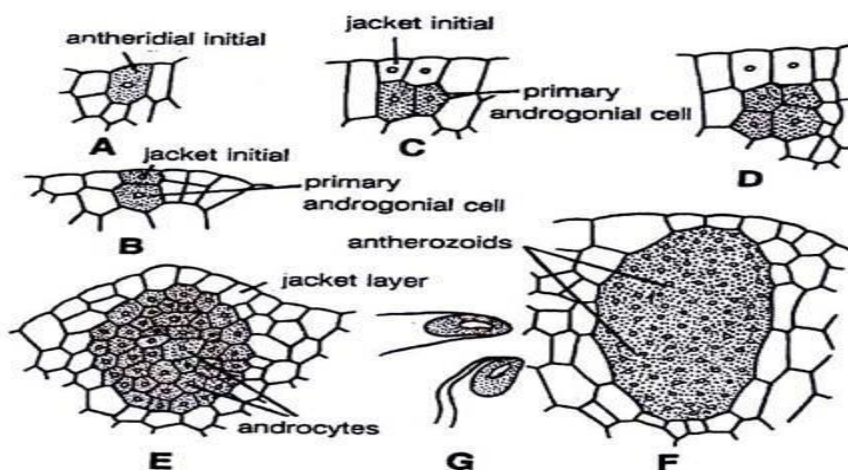


Fig. 3.21: *Lycopodium*, Stages in the development of antheridium

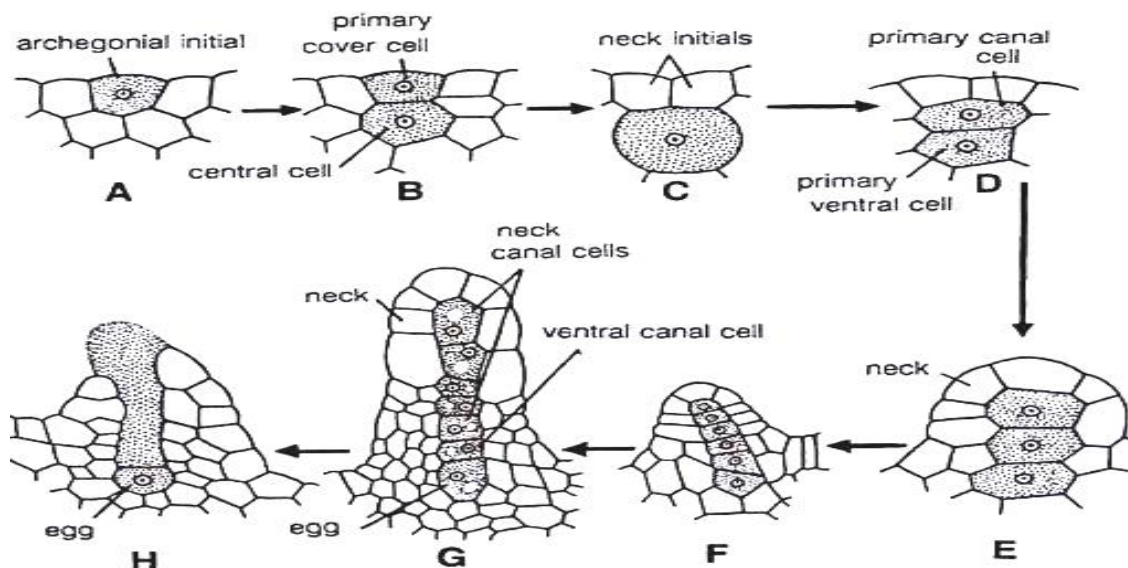


Fig. 3.22: *Lycopodium*, Stages in the development of archegonium

**Embryo Development (Young Sporophyte):**

In *Lycopodium* embryo develops downward into the gametophytic tissue instead of developing upward i.e., towards the neck of archegonium. The first division of the oospore is always transverse, forming an upper cell (epibasal) and a lower cell (hypobasal) known as embryonic cell. The upper cell does not divide further and behaves as suspensor. The oospore normally divides transversely forming suspensor and embryonic cell. The embryonic cell

forms an octant. The tier which gives rise to stem, leaf and primary roots, develops into a massive spherical structure of parenchymatous cells, known as protocorm (Fig. 3.23 K, L). It grows through the gametophyte, becomes green and develops rhizoids on its lower surface. The upper surface of the protocorm gives rise to a few to many erect outgrowths which are leaf like and are known as protophylls. At this stage the protocorm separates from the gametophyte. Now at the upper side of protocorm a region is differentiated which develops into stem.

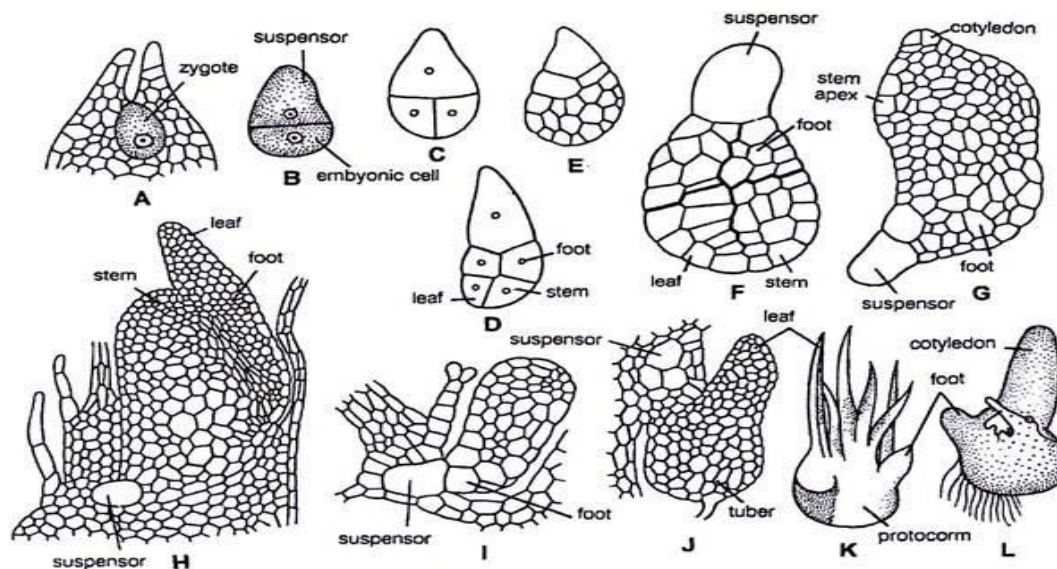


Fig.3.23. *Lycopodium*, Stages in the development of embryo

### 3.3.3.2 *Lepidodendron*

#### Habit and Habitat

The *Lepidodendron* was a large tree (50-60 m tall) with a prominent trunk (up to 35 m height). The ultimate dichotomies formed the leaves. The branches and the foliage formed a spreading crown bearing cones at their tips. The plant had bipolar growth, thus the main axis developed branches at both ends. The aerial branches formed three-dimensional dichotomies bearing branches and foliage, similarly the basal branches formed three-dimensional dichotomies bearing stigmarian root system (Fig. 3.31).

#### Structure:

#### Anchoring and Water-Absorbing Structure:

*Stigmaria ficoides*, the commonest species of *Stigmaria*, was a large trunk base that divided dichotomously into four large massive descending axes (Fig. 3.24). These four axes penetrated the substrate of the swamp shallowly and again formed repeated dichotomous branches in the horizontal plane. The *Stigmaria* spread over an area of about 20 ft (6 m) across. The younger portions of the *Stigmaria* had spirally arranged roots, known as Stigmarian rootlets, while the older portions are marked by spirally arranged root scars that might have abscised.

Anatomically, the main Stigmarian axis showed a distinct primary vascular system with endarch xylem. Secondary growth has been observed by the unifacial activity of cambium which only formed secondary xylem, while abundant extrastelar secondary cortical tissues were produced from the diffuse phellogen. In T.S., the free roots and root trace strand showed a monarch collateral vascular bundle comprised of protoxylem, metaxylem and phloem in centripetal sequence. The root trace, surrounded by inner cortex, is slightly eccentrically placed within the large cavity formed by the dissolution of the middle cortex, which is again delimited by an outer cortex. The Stigmarian rootlets are comparable with the roots of *Isoetes*.

**Stem:** The stem form-genus is called *Lepidodendron* which has been reported mostly as casts or compressions. In most species, the trunks attained a height up to 98-115 ft (30-35 m), because the first branching at a distal end appeared up to 30-35 m in height. At the base, the trunks are known to be 3.3 ft (1 m) in diameter. Numerous leaf cushions arrange spirally on the stem surface. The leaf cushions are rhomboidal in shape and broader in their vertical dimension than their transverse length (Fig. 3.25). A leaf scar is situated just above the middle line of the cushion. The leaf scar comprised of a vascular bundle scar at the center and is flanked by two parichnos scars on either side of the bundle scar just above the middle of the cushion. A ligule pit scar is situated just above the cushion. Two more parichnos scars (intrafoliar parichnos) are situated on either side of the leaf scar at lower level. The parichnos were the longitudinal channels traversing the length of the leaf parallel to the vein which are believed to be aerating organs.

## Anatomy

**Stem:** T.S. of the permineralised stem shows a protostele or a siphonostele (Fig. 3.26). The primary xylem is situated just outside the pith, comprised of metaxylem tracheids. The small protoxylem tracheids form vertical ridges at the periphery and leaf traces develop spirally at the steep angle from these protoxylem ridges. In most species, secondary growth is characteristic of the genus, which was initiated by the unifacial activity of the cambium. Thus, only secondary xylem was produced externally and the cambium did not produce secondary phloem. There was massive extrastellar secondary growth by the meristematic activity of cortical parenchyma.

The periderm thus formed composed of secondary cortex which forms the massive volume of the stem, and exceeds 50% of the volume of the stem. The tracheids are scalariform and have delicate strands of secondary wall material extending between adjacent bars and are termed as fimbrials. The periderm provided the main mechanical support to the stem and branches. **The primary cortex is divided into three regions, viz.:** (i) The outer cortex, just outside the secondary cortex, bearing leaf cushion, (ii) Middle cortex consisting of homogeneous mass of parenchyma cells, interspersed with leaf traces, and (iii) The narrowest inner cortex having parenchyma cells. Some of the cells aggregated to form secretory cells.

**Leaf:** The leaves were microphyllous ligulate, generally linear, acicular or awl-shaped and were borne on the small penultimate or ultimate branches. The leaves were deciduous and



had swollen photosynthetic bases (leaf cushion) that remain attached even after the shedding of laminae. The size of the leaf cushion was related to the diameter of the shoots, the smallest twigs bore smallest leaf cushions. T.S. of the leaves shows two prominent furrows on the abaxial surface (Fig. 3.27). Several rows of stomata were arranged parallel to the long axis on the furrow region. There is a thick-walled, well-developed hypodermis all around the leaf, except the furrows and thin-walled mesophyll cells in the center that encircled the sheathed vein. The sheath is composed of transfusion cells, perhaps made up of tracheidal parenchyma. The center is occupied by a vascular bundle made up of scalariform xylem and phloem cells.

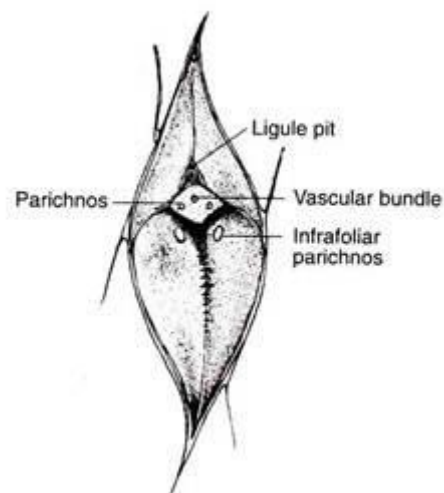
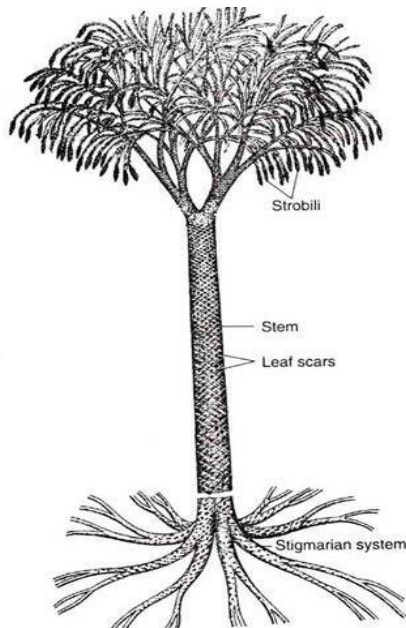


Fig. 3.24: Reconstruction of *Lepidodendron*

Fig. 3.25: Leaf cushion of *Lepidodendron*

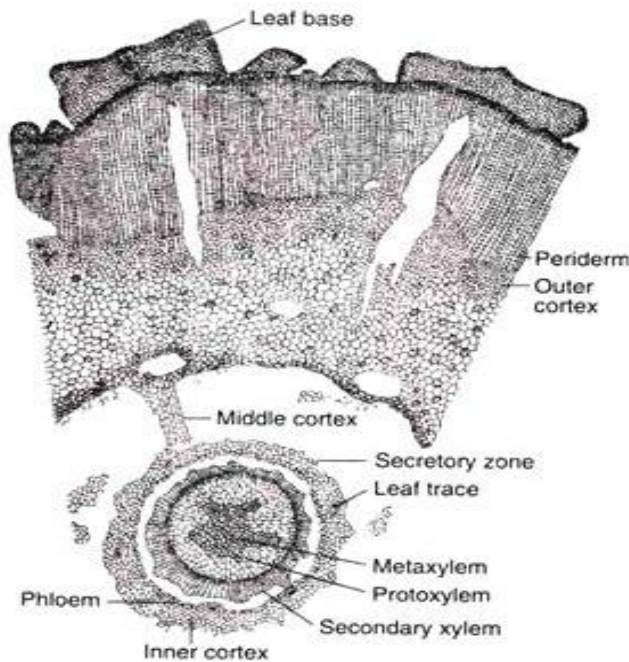


Fig.3.26: T.S. of *Lepidodendron* stem

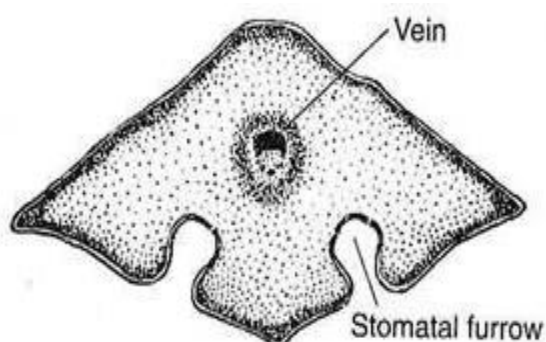


Fig.3.27. Cross section of *Lepidodendron* leaf

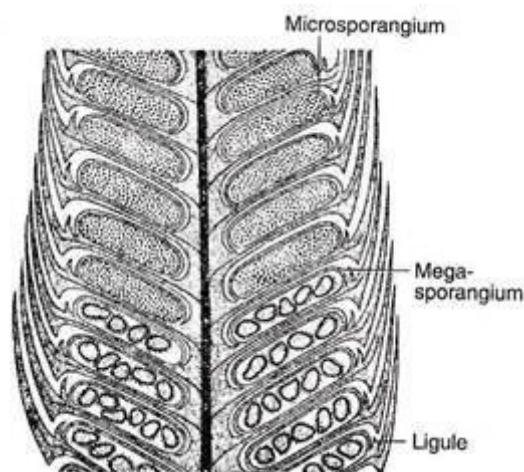


Fig.3.28. L.S of *Lepidostrobus*

## Reproductive Structure

*Lepidodendron* formed bisporangiate cones called *Lepidostrobus* that were borne terminally. The sporophylls were helically attached to the central cone axis. The microsporophylls bearing microsporangia were usually borne in the apical portion, while megasporophylls bearing megasporangia occupied the basal portion of the cones (Fig. 3.28). Morphologically, both the sporophylls were identical, except for their spore content. The microspores were small, about 25 micron in diameter, with smooth or granular exine. Megaspores were spherical, slightly elongated, showing trilete aperture with echinate (spinous) exine. Prothallus formed rhizoids and interdispersed archegonia comprised of one to three tiers of neck cells.

### 3.3.3.3 *Selaginella*

**Habit and Habitat:** *Selaginella* is the only living genus of the order Selaginellales and is commonly known as ‘spike moss’ or ‘small club moss’. Mostly the species prefer moist and shady places to grow but a few species are also found growing in xerophytic conditions e.g., *S. lepidophylla*, *S. rupestris* etc. A very few species are epiphytes e.g., *S. oregana*. Some of the common Indian species are *S. repanda*, *S. biformis*, *S. denticulata*, *S. monospora*, *S. semicordata*, *S. adunca* etc.

**Morphology:** The sporophyte is an evergreen, delicate herb. Its size varies greatly from species to species i.e., from a few cm. to 20 meters. Plant 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 Stem, Leaves, Ligules, Rhizophore and Roots (Fig.3.29). Stem is profusely branched, delicate and evergreen. Leaves are usually small, simple and lanceolate with a pointed apex.

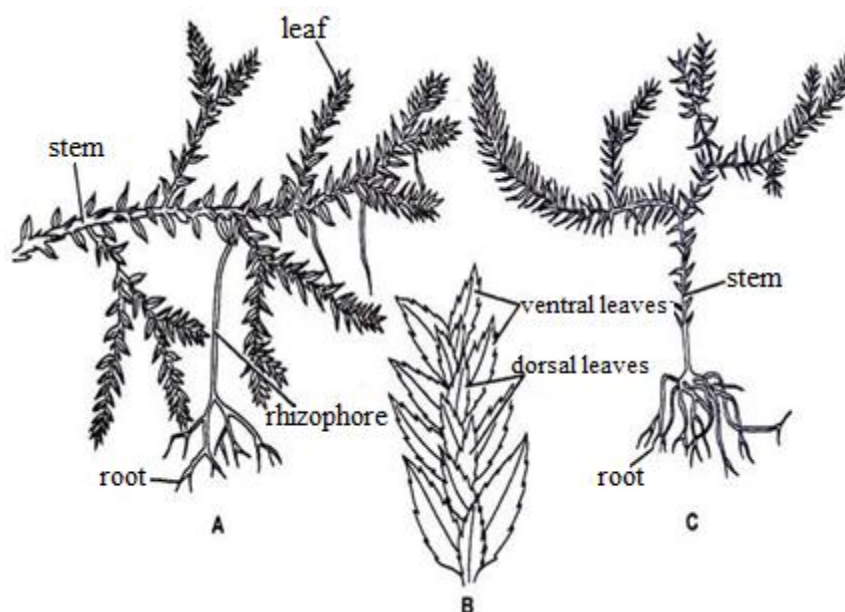


Fig. 3.29 *Selaginella*, External features: A-*S. kraussiana*; B-Leaf arrangement in *S. kraussiana*; C-*S. spinulosa*

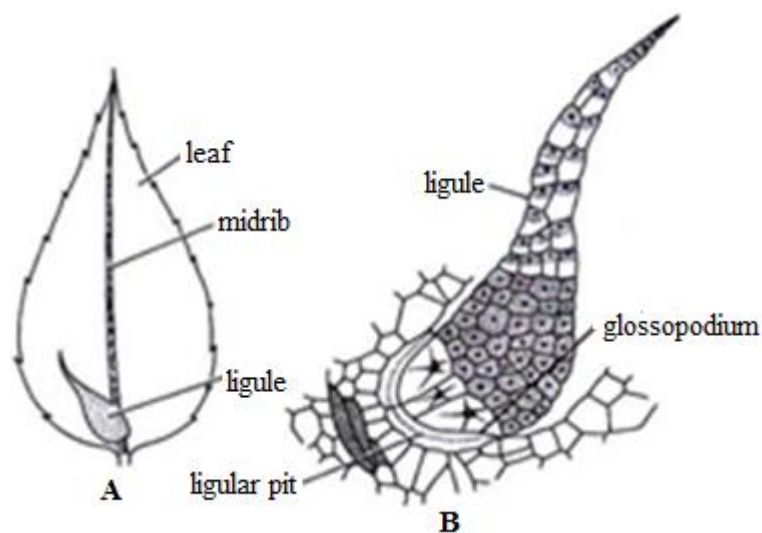


Fig. 3.30: *Selaginella*- Structure of ligule, A. Leaf with ligule, B. L.S. of ligule

Each leaf is provided with a single unbranched midrib. In the sub-genus *homoeophyllum* all the leaves are of 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 (Fig. 3.29 B). Usually the leaves near the apical portion of the branch, bear sporangia (micro-or mega) and are called as sporophylls (micro-or mega) respectively. The sporophylls are usually aggregated into a condense structure which is known as strobilus. On the adaxial side of the leaf, near the base is present a small membranous out-growth known as ligule. It is embedded at the base of a leaf in a pit like structure known as ligule pit. The structure of the ligule can be differentiated into two parts, glossopodium and the body of the ligule (Fig. 3.30 A, B). The function of the ligule is not well known. It may be a water secreting or water absorbing or protective organ.

Rhizophore arises from the prostrate axis at the point of dichotomy and elongates downward. It is a colourless, leafless, unbranched and cylindrical structure. As soon as the free end of rhizophore touches the soil it develops a tuft of adventitious roots at its free end. It differs from root in having no root cap and from stem in having no leaves. Roots originate either from the tips of rhizophores or directly from the stem or from the swollen base of hypocotyl (Fig. 3.29 A).

### Internal Structure

**Stem:** A transverse section (T.S.) of the stem of *Selaginella* is somewhat circular in outline and differentiated into epidermis, cortex and stele (3.31 A). Epidermis is the outer most covering layer which is single cell in thickness. Inner to the epidermis is present a well-defined zone of cortex. In 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 (Fig.3.31 B).The central portion of the stem is occupied by a well-developed protostelic type stele. The stele remains suspended in the center by radially elongated tubular, unicellular structures known as trabeculae formed by the radial elongation of the endodermal cells and are provided with conspicuous casparian strips. In between the trabeculae are present large spaces known as air spaces. 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 surrounded on all sides by phloem which consists of sieve cells and phloem parenchyma. Companion cells are absent in phloem.

**Root:** T.S. of the root is somewhat circular in outline (Fig. 3.32).Epidermis is the outermost covering layer and is only one cell in thickness. The cells are large and the unicellular root hairs arise from them. Just below the epidermis is present a wide zone of cortex which 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. Endodermis is usually not well defined but in some species e.g. *S. densa*, endodermis is followed by one to three layered parenchymatous pericycle. Stele is a typical protostele. The xylem is exarch and monarch. Xylem is surrounded by phloem on all sides.

**Rhizophore:** The internal structure of rhizophore is almost similar to that of root (Fig. 3.33). Epidermis is single layered and the outer wall of epidermal cells is covered with a thick cuticle. Root hairs and stomata are absent.Inner to the epidermis is a wide zone of cortex differentiated into outer sclerenchymatous and inner parenchymatous zones.Endodermis is ill defined single layered structure followed by a single layered parenchymatous pericycle. Stele is typically a protostele. The xylem is surrounded by phloem.

**Leaf:** T.S. of the leaf shows epidermis, mesophyll and a single median vascular bundle. Epidermis 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 cells of the epidermis are provided with chloroplasts. Mesophyll occupies a wide zone between upper and lower epidermis. In some species (e.g., *S. concinna*) the mesophyll is distinguished into upper palisade and lower spongy parenchyma. 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. 3.34).

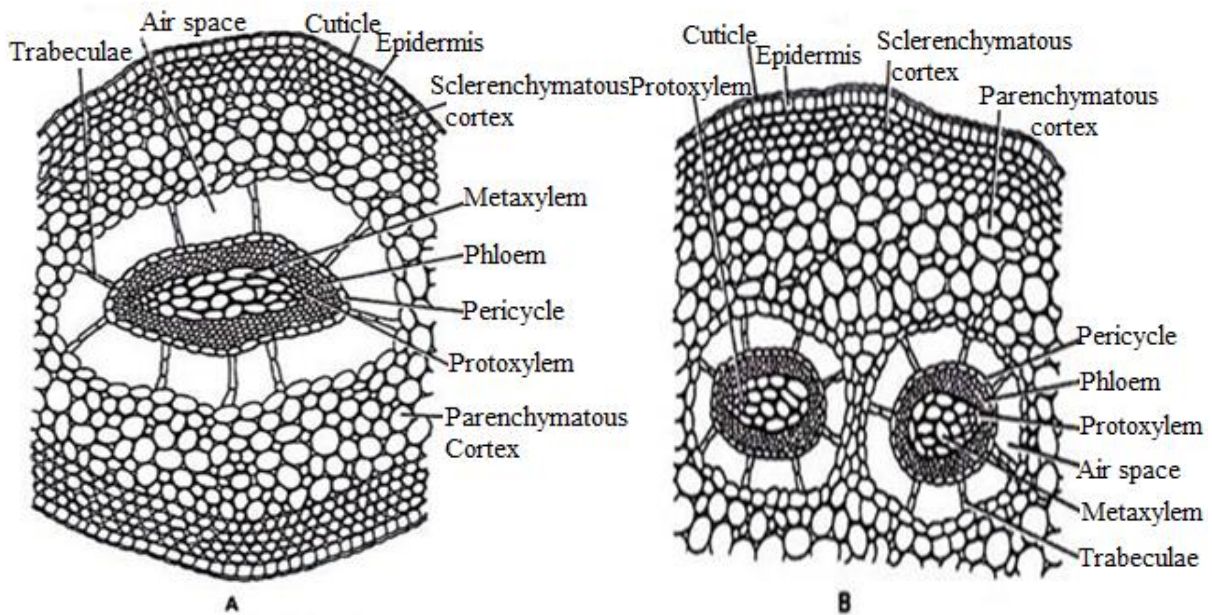


Fig. 3.31: *Selaginella* T.S. stem, A. Monostelic stem (*S. spinulosa*); B. distelic (*S. kraussiana*) stem

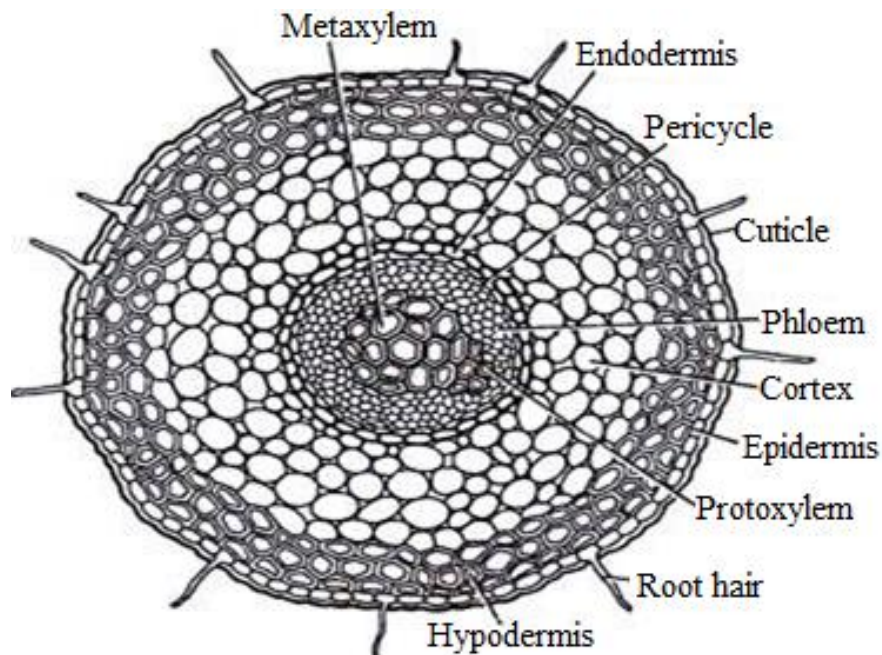


Fig. 3.32: *Selaginella*- T.S. of root

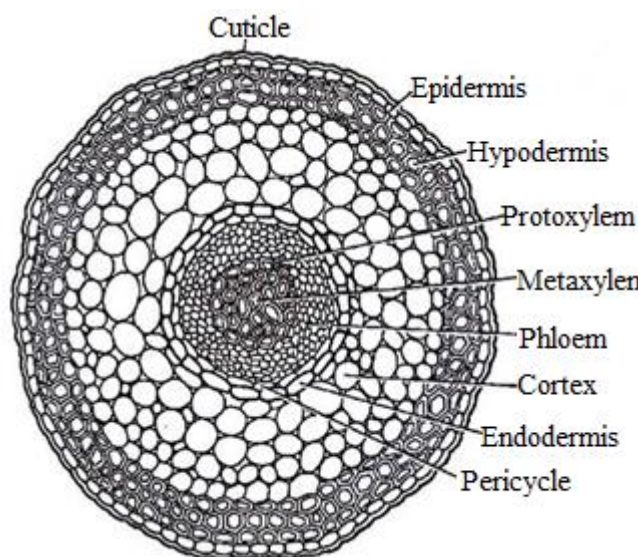


Fig. 3.33: *Selaginella*. T.S. of rhizophore

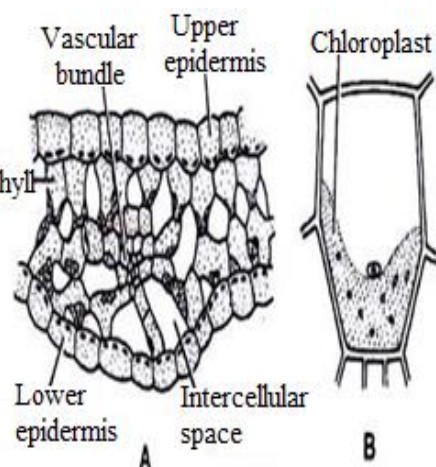


Fig.3.34: A-Internal structure of leaf. B- A mesophyll cell

## Reproduction:

**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:** The tubers may be aerial, developing at the apical end of aerial branches (e.g., *S. chrysocaulos*) or subterranean (e.g., *S. chrysorrhizos*). Under favourable conditions tubers germinate into a new plant.

**(iii) Resting buds:** These are the compact structures which develop at the apical end of some aerial branches.. These resting buds are capable to pass on the unfavourable conditions. Under favourable conditions these buds give off rhizophore that bear roots at their tips.

## 2. Sexual Reproduction:

**Spore producing organs:** 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 together to form a compact structure known as strobilus which is usually a terminal structure (Fig. 3.35 A).

**Strobilus:** It is a reproductive structure formed by the aggregation of ligulate sporophylls at the apex of the branches of stem (Fig. 3.35). 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. 3.35C, D; 3.35 A). *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 similar to a vegetative leaf. The microsporangium produces large number of microspores whereas megasporangium produces usually 4 megaspores.

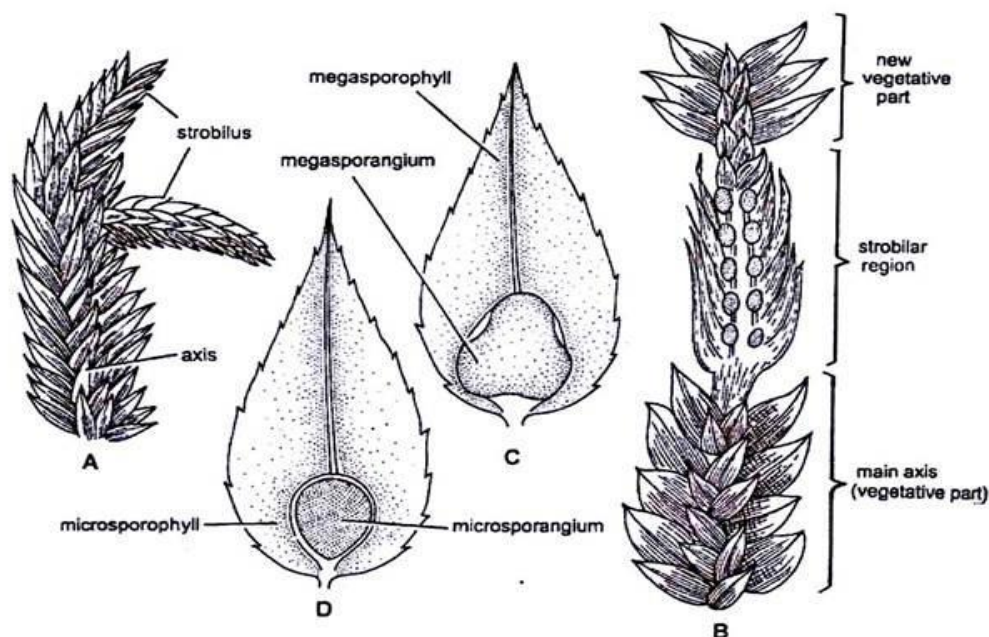


Fig.3.35. *Selaginella*: Structure of strobilus. A- a branch bearing strobilus; B- A branch changing into vegetative region after formation of strobilus; C- A megasporophyll; D- microsporophyll

**Microsporangium:** Each microsporangium is a stalked, globular or elongated structure (Fig. 3.36 D). Its colour varies from red, yellow to brown in different species. The wall is 2 layered thick which is followed by a conspicuous tapetum (Fig. 3.36 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 on by meiotic divisions produce numerous haploid tetrads of microspores.

**Megasporangium:** Each megasporangium is also a stalked but lobed structure and somewhat bigger than the microsporangium. Its colour varies from whitish yellow to red. Its wall is also 2 layered thick and followed by a single layered tapetum (Fig. 3.36G). 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 on by meiotic division produces only 4 haploid megaspores. Sometimes less than 4 megaspores are produced inside each megasporangium. As for example, *S. rupestris* produces only one megaspore per megasporangium.

**Development of sporangium and formation of spores:** 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 (Fig. 3.36 A). These cells divide periclinally forming outer jacket initials and inner archesporial initials (Fig. 3.36 B). The jacket initials by further periclinal and anticlinal divisions form the jacket which is 2 celled thick (Fig 3.36 E). The archesporial initials divide in all directions forming a group of cells known as sporogenous tissue. The cells of the outer most layer of sporogenous tissue divides periclinally forming a single

layered tapetum just inner to wall of sporangium. It is a nourishing layer (Fig 3.36 C-E). Tissue at the base of sporangium divides to form the sporangial stalk. The cell of sporogenous tissue in case of microsporangium finally gives rise to microspore mother cells and in case of megasporangium gives rise to megaspore mother cells. In microsporangium all the microspore mother cells are functional and each one divides reductionally forming a tetrad of 4 haploid microspores, as a result of which a large number of tetrads of microspores are formed inside microsporangium. In megasporangium all the megaspore mother cells degenerate except one which divides reductionally forming a tetrad (Fig. 3.36 D) of 4 haploid megaspores. By the drying of unsplitted portion, the spores are forced out and then they are dispersed away by wind.

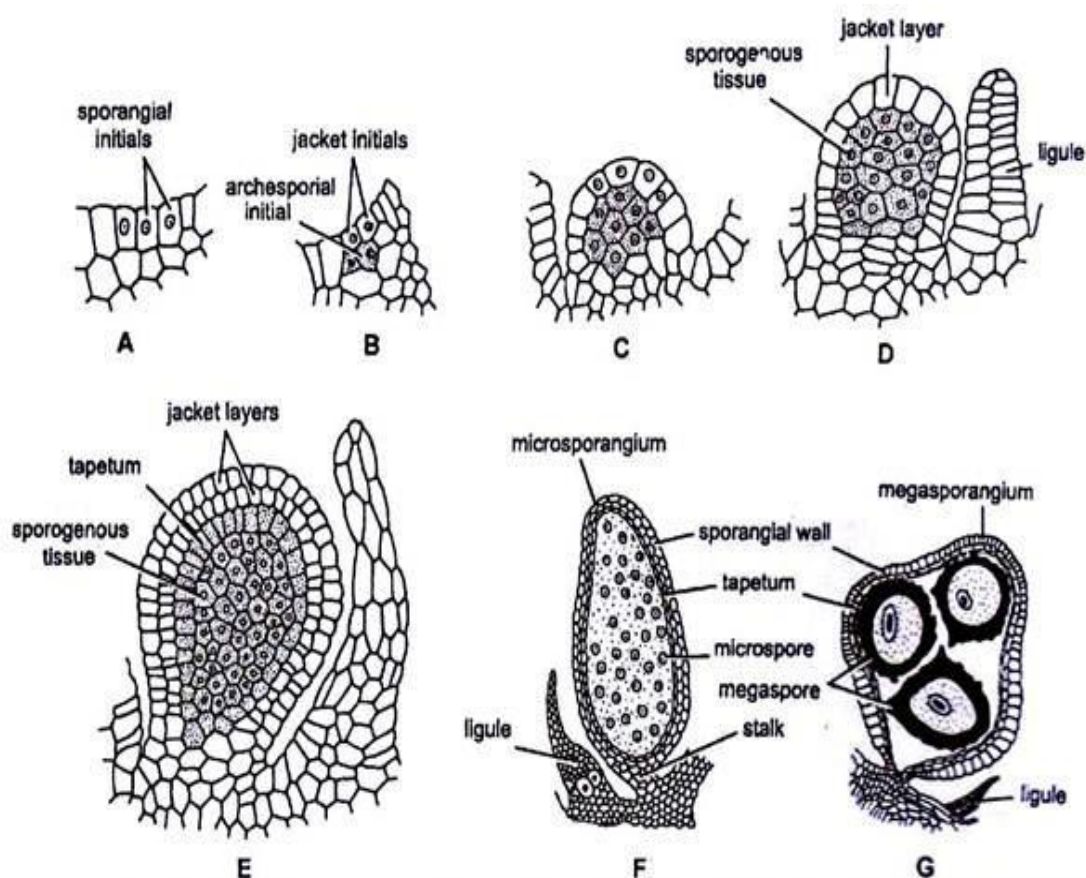


Fig.3.36 (A-G). *Selaginella*. Development of sporangium (A-E). Successive stages in the development of microsporangium in *S. kraussiana*. F. Mature microsporangium; G. Mature megasporangium.

**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 millimeter in diameter, spherical or round in shape and double layered structures. The outer wall is thick and known as exospore (exine). While inner wall is thin and is called endospore (intine). The microspores on germination give rise to male prothalli and megaspores to the female prothalli.



**Development of male gametophyte:** 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. 3.37 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. 3.37B). At this stage the young gametophyte consists of 3 cells (2+1 cell, Figs. 3.3 A, B).

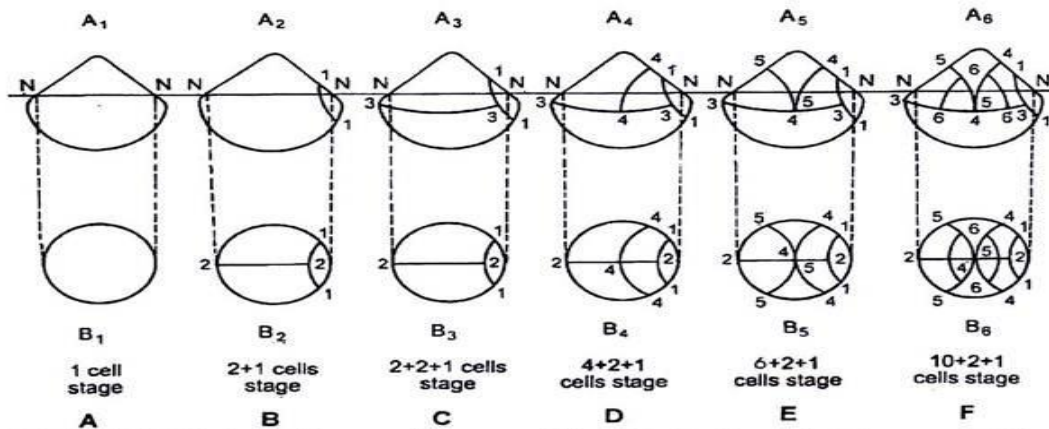


Fig.3.37 I (A-F): *Selaginella*, Diagrammatic representation of the development of microgametophyte

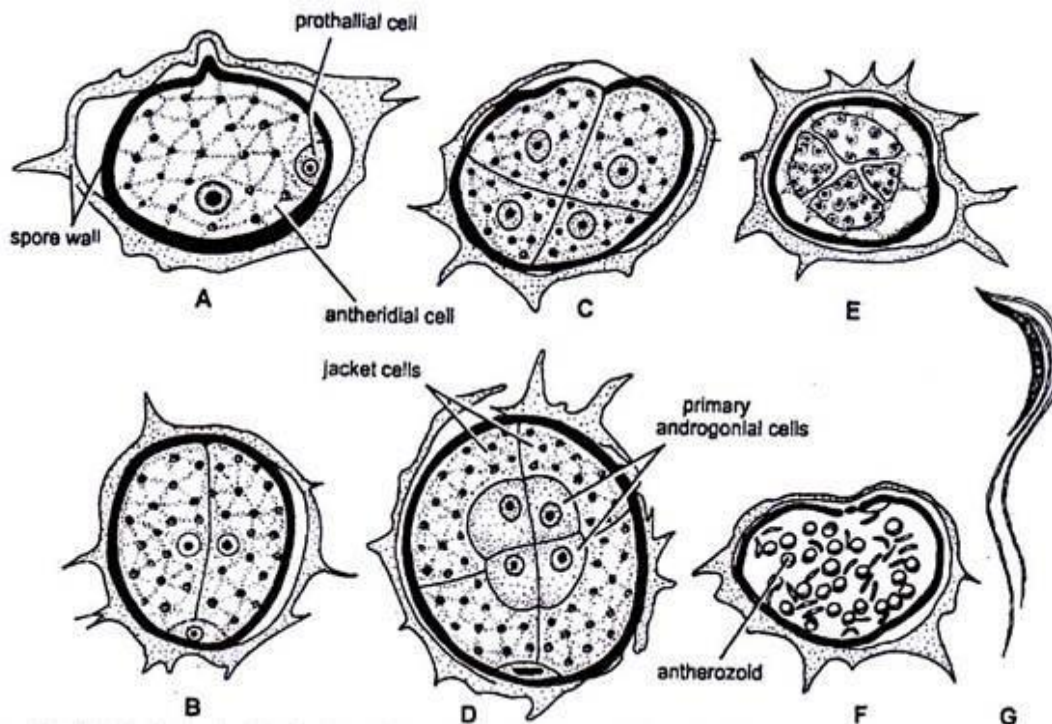


Fig. 3.37 II (A-F): *Selaginella*. Schematic representation of the development of male gametophyte

Two primary cells thus formed divide transversely (3-3 Figs. 3.37 C) and gametophyte consists 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. Upper two cells divide further by curving or arching wall (4-4, Fig. 3.37 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. 3.37 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. The middle four cells divide by periclinal walls (6-6, Fig. 3.37 F; 3.37 D) to form 4 primary androgonial cells and 8 jacket cells. The gametophyte now consist 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. 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. 3.37 F, G) which is a spirally coiled, uninucleate and biflagellate structure.

**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 of all 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 as a result of which a big central vacuole appears (Fig. 3.38 C). Now nucleus divides by free nuclear divisions, forming a large number of nuclei. First the nuclei are equally distributed in the cytoplasm but later on more nuclei collect in the apical region. At this stage wall formation starts from the apical region downwardly thus forming an upper cellular region known as female prothallus and a lower non-cellular region known as storage region (Fig. 3.38 D).

**Fertilization:** Water is necessary to carry out the process of fertilization. The swimming antherozoids reach the egg through the neck of archegonium and the nucleus of 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.

**Development of embryo:** Oospore is the initial stage of sporophytic generation. During development of the embryo, the oospore first divides by a transverse division into an upper suspensor initial (epibasal) and a lower (hypobasal) embryo initial (Fig. 3.39 A, B). The suspensor initial further divides in all directions forming a multicellular suspensor which pushes the developing embryo deep into the female gametophytic tissue to absorb food for further development of embryo. The embryo initial divides by 2 vertical divisions at right angle to each other thus forming 4 cells (quadrant. Fig. 3.39 C). One of these 4 cells divides by an oblique wall forming a shoot initial (Fig 3.39 D). Later by further divisions it forms a multicellular structure which gets differentiated into foot, rhizophore, stem and cotyledons (Fig. 3.39 E-J).

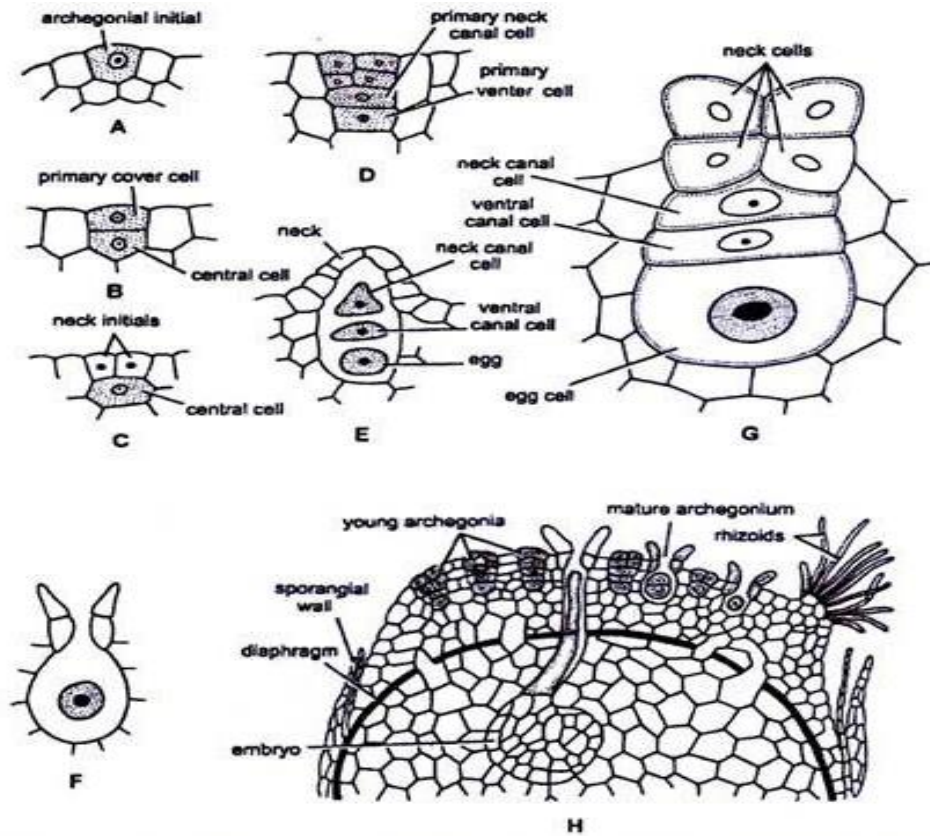


Fig. 3.38 (A-H). *Selaginella*: A-F .Stages in the development of archegonium

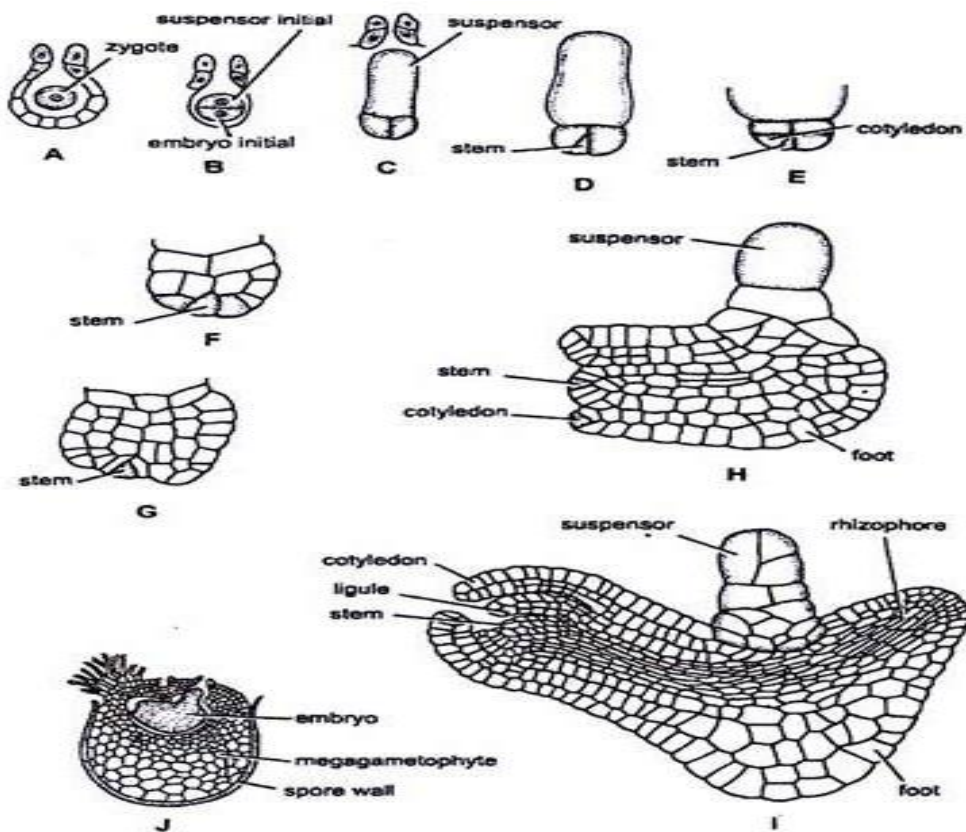


Fig. 3.39 (A-J). *Selaginella*: A-I .Stages in the development of embryo

### 3.3.3.4-Isoetes

**Habit and Habitat:** The genus *Isoetes* has about 65 species reported from many parts of the world. Some of the common Indian species are *I. coramandaliana*, *I. dixitii*, *I. panchananii*, *I. sahyadrii* etc. *Isoetes* is popularly called ‘Quill wort’ or ‘Merllyn’s grass’. The former name is due to the quill like nature of the leaves. The plant body usually grows in swampy regions. Sometimes the plant may grow in aquatic or amphibious habitats. Certain species like *I. butleri* grows on dry soil.

## Sporophyte

### External Morphology

The plant body consists of a condensed, lobed (two or three) structure called the axis or corm (Fig.3.40). The axis or corm is a fleshy structure having complex morphology and anatomy. The corm on its upper surface bears a number of long, quill like, ligulate leaves. The leaves are two to several centimeters long and are crowded in a closed spiral fashion forming a sort of a fascicle. Sometimes the leaves may be as long as 0.5 meter (*I. cormanandaliana*) to 1 meter (*I. japonica*). The leaves have broad spoon shaped bases and tapering tips. The outermost leaves are sterile; successively within them are found mega-sporophylls, micro-sporophylls and sporophylls with immature sporangia. From the lower surface of the corm are produced a number of roots. The roots branch dichotomously.

### Internal Structure

**Corm:** Anatomically the corm exhibits many interesting features, the notable being the peculiar type of secondary growth. A vertical section of the axis shows a central vascular cylinder surrounded by a broad parenchymatous cortex (Fig.3.41). The vascular cylinder in its shape resembles an anchor or a vegetable chopper. The stele is protostelic, the central region of the vasculature consists of xylem, en-sheathed by phloem. The xylem consists of parenchyma intermixed with tracheids. Leaf traces depart from the stele but there are no leaf gaps. The cortex is parenchymatous and has starch filled cells. A peculiar type of secondary growth occurs in *Isoetes*. This is brought about by the activity of a cambium that arises external to the phloem (The normal position of a fascicular cambium is between xylem and phloem). In a corm, after the secondary growth has taken place the following tissues are seen (Fig.3.42). In the center is a mass of primary xylem. Next to this is the primary phloem. Outlining the phloem is the prismatic tissue. External to the prismatic tissue is the cambium, following cambium is the secondary cortex and then is found the primary cortex. The cortex is very broad.

**Root:** The root grows by an apical meristem; sometimes the apical meristem divides, as a result there is branching of the root. New sets of roots are formed every year from the growing point and the older roots are pushed further back from the growing point. The roots may persist more than a year or may be sloughed off by an abscission layer.

A transverse section of the root shows an outer epidermis, middle cortex and central stele. The epidermis is single layered. Cortex is parenchymatous and has a large 'C' shaped cavity (Fig.3.43). This cavity results due to the breakdown of the cortical cells. The presence of this cavity recalls a similar thing found in the stigmarian rootlets of *Lepidodendrales*. The stele is a monarch protostele. The xylem and phloem are collateral and are arranged in such a way that the phloem is on the side away from the rhizome. Surrounding the vasculature is a well defined endodermis.

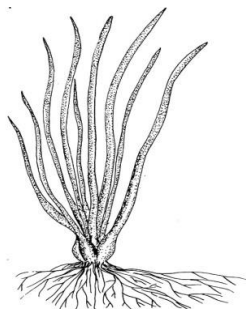


Fig.3.40: External morphology of *Isoetes*

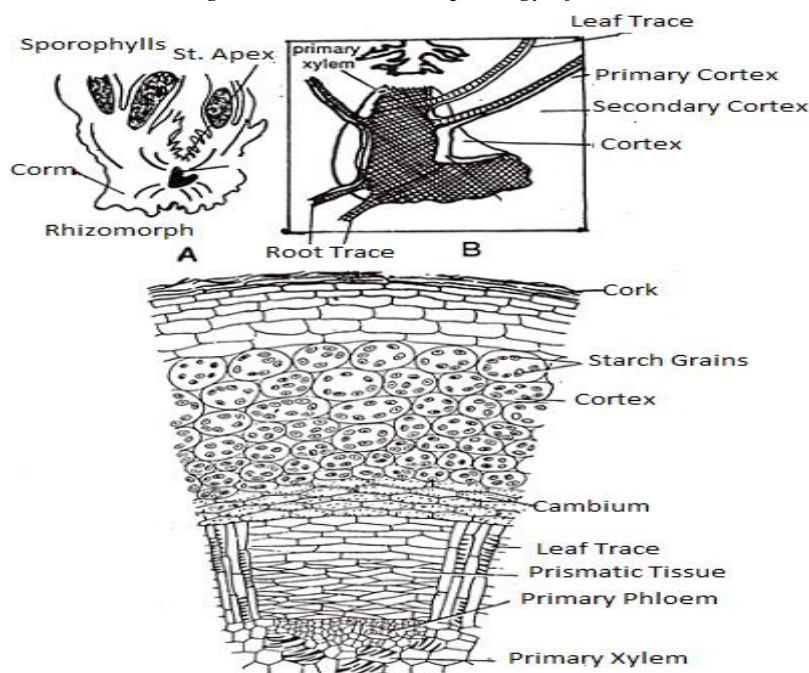


Fig. 3.41. *Isoetes*- Structure of rhizome: A. V.S. of corm, B. A part of the vasculature enlarged, C. T.S. of corm showing cellular details

**Leaf:** The leaves develop from the apical meristem. Each leaf bears a single ligule at the junction of the cylindrical and the basal wider portion of the leaf. Like roots the leaves are also produced every year. Internally, the leaf shows a single vascular bundle surrounded by an undifferentiated mesophyll.

The outermost layer is the epidermis in which stomata are found (except in submerged species). The mesophyll may consist of only parenchyma, sometimes sclerenchyma may also be located. There are four cylindrical air chambers in the mesophyll separated by parenchymatous partitions. Here and there, the air chambers are closed by means of a

diaphragm to offer mechanical support to the leaf. The vascular bundle of the vein is mostly collateral but may become concentric towards the tip of the leaf (Fig. 3.44).

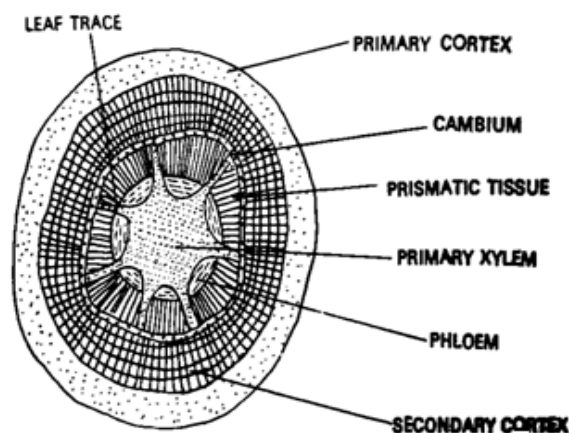


Fig. 3.42- T.S. of corm showing secondary growth

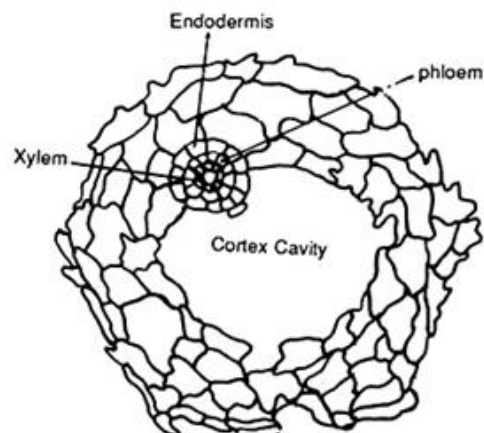


Fig. 3.43. *Isoetes*- T.S. of Root

**Reproduction:** The main method of reproduction is by the formation of spores. However, sometimes gemmae or vegetative buds may be produced.

**Spore Production:** *Isoetes* is heterosporous. The micro and megasporophylls are arranged spirally on the corm. There is also no distinction between the foliage leaves and sporophylls. Those leaves which bear the sporangia constitute the sporophylls. There is no strobilar organisation in *Isoetes*. The sporophylls bear a single flattened sporangium between the ligule and leaf base on their adaxial surface. Completely or incompletely covering the sporangium will be a membranous outgrowth called Velum that arises just below the ligule.

**Structure and Development of the Sporangia:** The micro and mega-sporangia are similar in their development up to the spore mother cell stage. A group of initial cells arise a little below the ligule. These are the sporangial initials. A periclinal division in these cells results in forming an upper layer of jacket cells and an inner layer of archesporial cells. At the same time, some of the cells between the sporangial cells and the ligule divide and project out forming the velum. Subsequently the velum grows downwards completely or incompletely over arching the sporangium. The jacket initials divide and constitute the single layered jacket of the sporangium. At later stages the jacket may become 3-4 layered.

The archesporial cells divide in all the planes and produce a mass of sporogenous tissue. At the time of the formation of spore mother cells bands of sterile cells are differentiated separating the fertile spore mother cells. These bands constitute the trabeculae that divide the sporangium completely or incompletely. The sporogenous cells adjacent to the trabeculae and to the sides of the sporangium differentiate into a two layered tapetum. In a sporangium that is destined to become a microsporangium, most of the spore mother cells are functional and undergo reduction division and produce tetrads of haploid spores (Fig. 3.45). The spore output is enormous and varies from one to three lakhs per sporangium.

In a sporangium that is to become a mega-sporangium, all the spore mother cells except about 40-80, degenerate (Fig. 3.46). The surviving ones undergo reduction division and produce haploid megaspores. Each mega-sporangium of *Isoetes indica* is known to contain megaspores ranging in number between 703-2345.

A peculiar type of sporangium called mixed sporangium has been described in some individuals of *Isoetes coromandaliana*. A mixed sporangium is defined as “a sporangium possessing monolete microspores, trilete megaspores and alete sterile spores”.

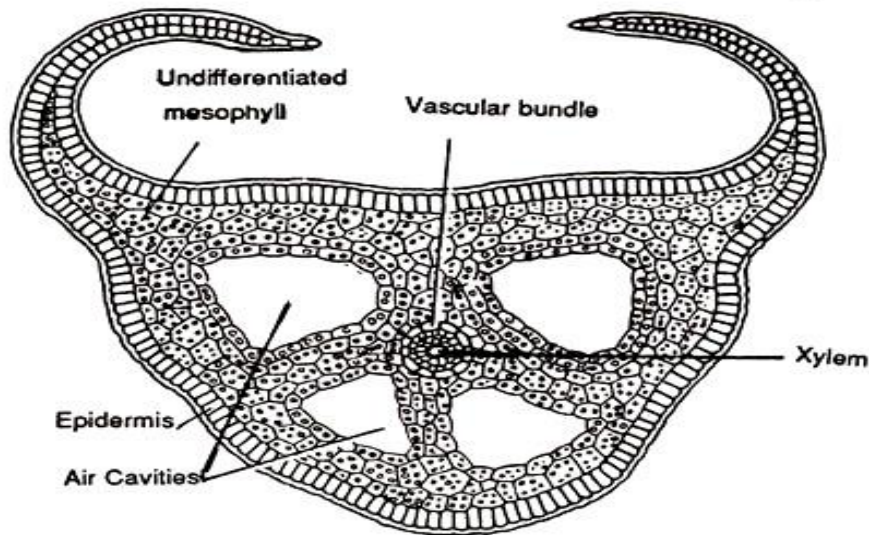


Fig 3.44- *Isoetes*: T.S. of leaf

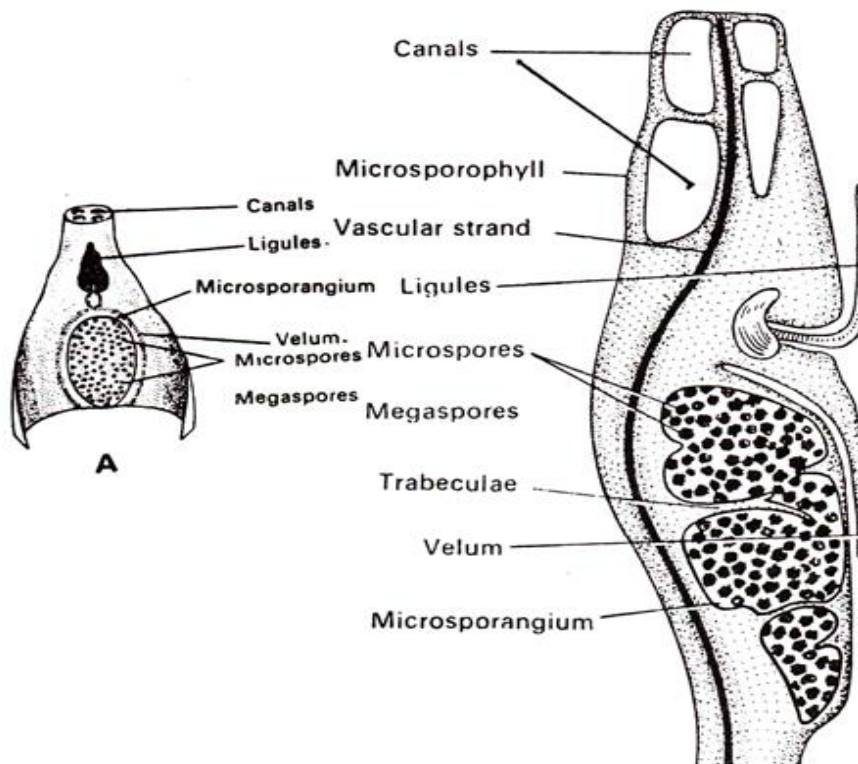


Fig. 3.45: *Isoetes*. A. Microsporophyll and B. L.S. of microsporangium

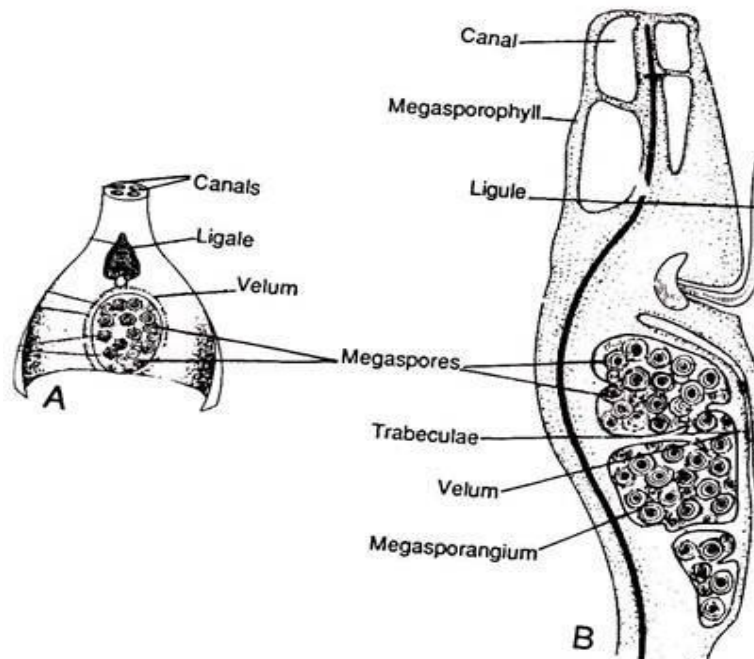


Fig.3.46: *Isoetes*, A. Megasporophyll. B. L.S. of Megasporophyll

**Dehiscence of the Sporangia:** The sporangia remain indehiscent for a long time. Liberation of the spores takes place only upon the decay of the sporophyll. Spore dissemination is mostly by wind. According to a report, worms may also help in the dispersal of spores. On liberation, the spores develop into gametophytes.

**Gametophyte:** As *Isoetes* is heterosporous, two types of gametophytes are produced. Both the gametophytes are endosporic and highly reduced.

**Structure of the microspore and development of the male gametophyte:** The microspores are bilateral or tetrahedral in shape, very minute, brownish in colour and have a diameter ranging from 20 to 45 $\mu$ . The wall is two layered. As the spore liberation is delayed for quite a long time, the germination is immediate and a mature gametophyte is formed within a few days. The first sign of germination is the migration of the microspore nucleus to one side, when it divides asymmetrically to give rise to a small prothallial cell and large antheridial initial.

The antheridial initial first divides diagonally to form two cells; of these, the cell nearer to the prothallial cell will not divide but forms the first jacket cell of the antheridium; the other cell divides at right angles to the previous plane of division. Of the two cells thus formed, the one away from the prothallial cell forms the second jacket cell. The other cell divides in a plane almost parallel to the preceding plane of division. Of the two cells, one forms the third jacket cell and the other one divides periclinally to form the fourth jacket cell and the primary androgonial cell. The primary androgonial cell divides twice to form four androcytes which metamorphose into cork screw shaped, multi-flagellate (nearly fifteen flagella attached to one pole) antherozoids. When the antherozoids are mature, the microspore wall disintegrates liberating the antherozoids.



**Structure of the Megaspore and Development of the Female Gametophyte:** The megaspores are very huge (in comparison with the microspores) having a diameter of 250-900 $\mu$ . They are tetrahedral in shape with prominent triradiate ridges. The colour of the spore is white, gray or black. The spore wall is three layered with the outer layer marked with crusts, spines or ridges. The first sign of germination is the migration of the nucleus towards one side where it undergoes a series of free nuclear divisions to produce about 40-50 nuclei distributed towards the periphery. However, there is no central vacuole as in *Selaginella*. During the later stages many nuclei accumulate towards the apical region where wall formation sets in, first. Subsequently the lower portion also becomes cellular.

After the formation of a cellular gametophyte the megaspore wall breaks open along the triradiate ridge to expose the prothallus. The prothallial tissue is devoid of chlorophyll but may develop a number of rhizoids. Archegonia develop from the apical tissue of the prothallus. Generally two or three archegonia are formed at first. If these are not fertilized, a few more archegonia are produced from the apical tissue. Formation of archegonia continues until their fertilization or the exhaustion of reserve food in the gametophyte. An archegonial initial periclinally divides to form an upper primary cover cell and a lower central cell. The primary cover cell divides twice to form four neck initials which in turn divide to form a three to four celled high neck. The central cell divides to form a primary canal cell and a primary venter cell. The primary canal cell may divide, but wall formation may not take place. The division of the primary venter cell produces a venter canal cell and an egg cell.

**Fertilization:** In a mature archegonium, the neck opens apart and the mucilage formed by the disintegrating neck canal cells and ventral canal cells comes out. Many antherozoids enter the archegonium, but one succeeds in fusing with the egg.

**Embryogeny:** Embryogeny in *Isoetes* differs from that in other lycopods in the lack of a suspensor and in early differentiation of the embryonal parts. The first division of zygote is obliquely vertical (about 20°) to the long axis of the archegonium. Both these cells divide transversely to form four cells (Fig.3.47a, b). In the four celled embryo, root and stem tip are formed from the epibasal half and cotyledon and foot are formed from the hypo basal half (Fig.3.47c). This type of embryogeny is similar to what is seen in some ferns, but differs from them in having the epibasal half giving rise to stem and root instead of cotyledon and root. Cell divisions taking place in the embryo result in its longitudinal differentiation with cotyledon at one pole and the primary root at the other. In the beginning, the embryo is diagonal to the archegonium but later becomes perpendicular to it.

Further development is very rapid. Within about a week after fertilization, the cotyledon comes out of the gametophyte with the primary root growing downwards. The growth of the stem is slow in the beginning. It forms a ligule like structure called the “**cotyledonary sheath**” (Fig.3.47 d). With the formation of root, the young sporophyte becomes independent. Some experiments conducted on the influence of gravity on the four celled embryo have shown that gravitational force has no influence on the parts into which the four initials of the embryo grow.

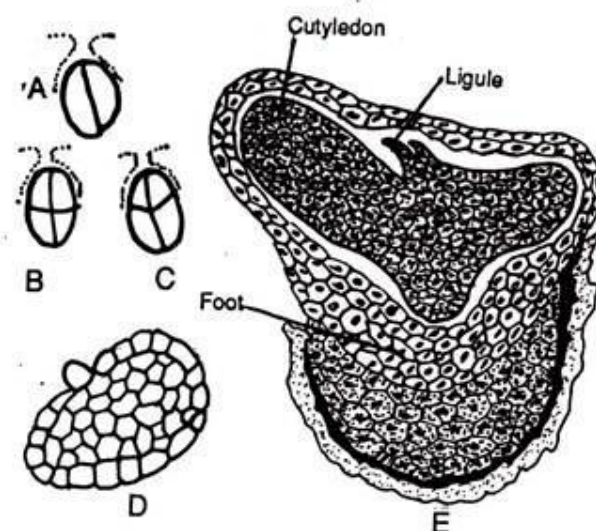


Fig.3.47. *Isoetes*- Stages in embryogeny

### 3.4 SUMMARY

The living members of class Lycopsidea are the representative of the group which during the Carboniferous period formed the chief vegetation. Many of the genera then growing were large trees (e.g. *Lepidodendron*). The modern representatives are small and herbaceous plants. On the basis of presence or absence of ligule this class is divided into two sub classes viz. Ligulatae and Eligulatae. Out of the six genera described in this unit, two (*Rhynia* and *Lepidodendron*) are fossil plants while rest four (*Psilotum*, *Lycopodium*, *Selaginella* and *Isoetes*) are living. *Rhynia* was described by Kidston and Lang (1917,1921). The plant was discovered from Old Red Sandstone Beds of Middle Devonian *Rhynia* is represented by two species *R. major* (now known as *Agalophyton major*) and *R. gwynne-vaughani*. Both the species were herbaceous plants consisted of dichotomously branched horizontal rhizome and erect aerial stem with terminating sporangia. The internal structure of rhizome and stem was quite similar. The genus *Psilotum* has two well defined but polymorphic species (*Psilotum nudum* and *P. flaccidum*). The sporophytic plant is shrubby and possess green, ridged and dichotomously branched stem. Roots are absent and leaves are scale-like. The sporangia are borne in triads on minute appendages and remain fused with one other to form synangium. The gametophyte is colourless, saprophytic and monoecious and sex organs are irregularly distributed on the prothallus. The development of embryo is very simple.

The species of *Lycopodium* are world- wide in distribution. They are commonly known as ground pines, club moss and trailing evergreens. All species of *Lycopodium* possess small, herbaceous or shrubby sporophyte. The leaves are small, simple, sessile, numerous and cover the axis closely. There is great variation in the organization of vascular tissue in stems. It may be an actinostele, plectostele or mixed protostele. The leaf has mid ribs which consist of a single concentric amphicribal bundle. In most of the species sporophylls are arranged in well defined strobili which may be simple or branched. The sporophyll produces single sporangium which remains adaxial in its position and found near the base of the sporophyll. The small spores are uniform in size and shape (i.e. homosporous). There is great diversity in

form and structure of mature gametophyte in different species of *Lycopodium*. There are three main types of prothalli (*L. clavatum*) (*L. complanatum*) (*L. selago*). In certain cases embryo get differentiated into leaf, foot and tuber (protocorm). The rhizoids develop on the lower surface of the protocorm and the upper surface of protocorm gives rise to erect conical outgrowths known as protophylls. These structures are leaf like in function and the protocorm differentiates a meristematic region which gives rise to stem of adult plant.

The sporophyte of *Lepidodendron* was a tree attaining a height of 30 m or more with a diameter of about 2 m near the base. Characteristic leaf bases are found on the stem. There was considerable variation in stellar anatomy of the main trunk from species to species and also in different parts of the same plant ranging from a solid protostele to a siphonostele but the primary xylem was always exarch and polyarch. Some species showed abundant secondary xylem produced by vascular cambium (*L. pettycureuse*) and other had none at all (*L. hickii*). The ligulate leaves known as *Lepidophyllum* were spirally arranged on the stem. They were simple 1 to 20 cm long.

*Selaginella* is world-wide in distribution and comprise of about 700 species. The sporophytic plant body varies in size and shape from species to species. In each case the stem is covered with four rows of leaves. The leaves may be of same size or of different size depending upon the species and in every case the leaves are ligulate. In many species, the prostrate axis bears an elongate, colourless, leafless, cylindrical, downwardly growing structure known as rhizophore. At the terminal end of rhizophore, a tuft of adventitious roots develops. The organization of stele varies from species to species ranging from simple protostele to a complex polycyclic siphonostele. Most of the species of *Selaginella* possess the radially elongated endodermal cells having well developed spaces among them known as trabeculae. In majority of species, the sporophyll are arranged in the strobili or spikes at the terminal ends of the branches. Each sporophyll bears a single stalked sporangium situated in the axil of it, on the adaxial surface between ligule and its base. There are two kinds of sporangia viz. megasporangia and microsporangia which produces megaspore and microspore, respectively. The fertilization takes place while the megagametophytes are still in the megaspore situated in megasporangia which may have fallen on the ground. The young sporophytes remains attached to the megagametophyte for some time and later become independent by establishing its roots into the soil.

The genus *Isoetes* comprising 60 to 70 species is world-wide in distribution (6 species are reported from India). Majority of species grow in aquatic environment or in swampy areas. The sporophytes are small herbaceous, perennials and have short, fleshy, upright corm like subterranean axes with highly specialized structure. The roots arise from the lower portion of axis and are arranged in 2 to 5 groups as axis is 2 to 5 lobed. The upper surface of axis is covered by the bases of crowded leaves. Each leaf has a thickened and expanded colourless base and a tapering distal portion. A persistent ligule is seated in a concavity on the adaxial surface at some little distance from the base. In the center of corm is a protostelic vascular cylinder. Associated with the unique morphology of the axis there is very uncommon mode of secondary growth involving an anomalous lateral meristem, the cambium. The root of *Isoetes* has a single monarch vascular strand which is attached to the cortex along the side of the central air cavity. The sporophyte is heterosporous and every leaf is potentially a sporophyll because each bears a sporangium. The sporophyll are not aggregated into a

definite strobilus. A single large flattened sporangium is situated on the adaxial surface between ligule and expanded base. The sporangia are of two types viz. micro and megasporangia and produce monolet microspores and trilete megaspore, respectively. The submerged sporangia remain indehiscent and the spores are liberated by the decay of sporophyll and sporangium wall.

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### 3.5 GLOSSARY

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**Abaxial:** The side of a lateral organ away from the axis (dorsal)

**Adaxial:** The side of a lateral organ nearest to the main axis (ventral)

**Actinostele:** Protostele having xylem core in the form of radiating ribs

**Archegonium:** The female sex organ of bryophytes, pteridophytes and gymnosperms

**Dorsiventral:** An organ having distinct dorsal and ventral surfaces which usually show difference in structure or colour.

**Endodermis:** The layer of tissue situated between cortex and stele.

**Eusporangiate:** Pertaining to relatively large sporangium developing from a group of initials.

**Fertilization:** The union or fusion of two similar or dissimilar gametes to form a diploid zygote.

**Fossil:** The remains of organism, which existed in prehistoric time or direct evidence of their presence preserved in rocks.

**Heterospory:** The condition of producing two kinds of spores differing in size

**Homospory:** The condition of producing one kind of spores only

**Leptosporangiate:** Pertaining to relatively small sporangium developing from a single initial.

**Ligule:** A membranous, narrow outgrowth from the base of the leaves on the adaxial surface of some some Lycopside e.g., *Selaginella*

**Megaspore:** The larger of the two kinds of spores which produces the female gametophyte in the heterosporous plant.

**Megasporophyll:** A modified leaf bearing the megasporangium.

**Megasporangium:** A diploid spore sac containing only large asexual spores, the megaspore.

**Microspore:** The smaller of the two kinds of asexual haploid spores which produces the male gametophyte in the heterosporous plant.

**Microsporangium:** A diploid spore sac containing only small asexual spores, the microspore.

**Microsporophyll:** A modified leaf bearing only the microsporangium.

**Mesarch:** Of xylem groups or strands when both centripetal and centrifugal xylem are formed and protoxylem lies in the center.

**Protoxylem:** The first formed elements of primary xylem.

**Reconstruction:** A picture drawn out by joining up various fragments or organs apparently belonging to some fossil plant in their presumed position.

**Rhizome:** An elongated underground horizontal stem

**Rhizophore:** a leafless branch intermediate in character between root and stem which bears the roots.

### 3.6 SELF ASSESSMENT QUESTIONS

#### 3.6.1 Select the correct answer:

1. Spike moss is the common name of  
 (a) *Lycopodium* (b) *Selaginella*  
 (c) *Adiantum* (d) *Pteris*
2. *Lycopodium* is commonly known as  
 (a) Horse tail (b) Club moss  
 (c) Quill wort (d) Stone wort
3. Actinostele is found in:  
 (a) *Lycopodium complanatum* (b) *L. clavatum*  
 (c) *L. phlegmaria* (d) *L. cernum*
4. Which of the following is commonly called Quillwort  
 (a) *Psilotum* (b) *Lycopodium*  
 (c) *Selaginella* (d) *Isoetes*
5. *Rhynia* was described by  
 (a) Birbal Sahni (b) Arnold  
 (c) Kidston and Lang (d) Smith
6. The antherozoids in *Isoetes* are  
 (a) Uniflagellate (b) Biflagellate  
 (c) Multiflagellate (d) Aflagellate
7. Trabeculae in *Selaginella* is modified  
 (a) Pericycle cells (b) Cortical cells  
 (c) Endodermal cells (d) None of the above
8. The antherozoids of *Selaginella* are  
 (a) Aflagellate (b) Uniflagellate  
 (c) Multiflagellate (d) Biflagellate
9. Protostele with mixed pith is present in  
 (a) *Lycopodium* (b) *Selaginella*  
 (c) *Lepidodendron* (d) *Isoetes*
10. Three chambered sporangium is present in  
 (a) *Selaginella* (b) *Lepidodendron*  
 (c) *Isoetes* (d) *Psilotum*

#### 3.6.2 Fill in the blanks:

1. The photosynthetic organ of *Rhynia* was \_\_\_\_\_ .
2. There are \_\_\_\_\_ fundamental types of prothallus in *Lycopodium*.
3. The two sub groups of *Lycopodium* are \_\_\_\_\_ and \_\_\_\_\_ .
4. *Selaginella* is \_\_\_\_\_ as two types of spores are produced.

5. The microspores of *Selaginella* are shed at \_\_\_\_ celled stage.
6. *Psilotum* belong to the order \_\_\_\_\_ and family \_\_\_\_\_ .
7. Protocorm formation occurs in \_\_\_\_\_.
8. At maturity the microspore of *Isoetes* is \_\_\_\_\_ .
9. The underground axes of *Lepidodendron* are known as \_\_\_\_\_ .
10. The leaves of *Lepidodendron* are known as \_\_\_\_\_ .

**Answer Key-3.6.1:** 1. (b), 2.(b), 3.(b), 4. (d), 5.(c), 6.(c), 7.(c), 8.(d), 9.(c),10.(d)

**Answer Key-3.6.2:**1. Stem, 2.Three, 3.Urostachya and Rhopalostachya, 4. Heterosporous, 5. Thirteen, 6. Psilotales and Psilotaceae, 7. *Lycopodium*, 8. Kidney shaped, 9. *Stigmaria*, 10. *Lepidophyllum*.

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### 3.7 REFERENCES

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### 3.8 SUGGESTED READINGS

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- College Botany Volume II By H.C. Gangulee and A.K. Kar. New Central Book Agency 8/1 Chintamani Das Lane, Calcutta 9, India.

- Botany for degree student Pteridophyta by P.C. Vashishta, A.K. Sinha and A. Kumar.S. Chand and Company Private Ltd. Ram Nagar, New Delhi
- The morphology of Pteridophytes(The structure of ferns and allied plants).By K.R. Sporne. Hutchinson and Company Ltd.178-202 Great Portland Street, London
- The Biology and Morphology of Pteridophytes. By N.S. Parihar. Central Book Depot, Allahabad.

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### 3.9 TERMINAL QUESTIONS

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#### 3.9.1: Short answer type Questions:

- Q1. Microsporophyll and megasporophyll of *Isoetes*.
- Q2. Stigmarian axes of *Lepidodendron*
- Q3. Leaf cushion of *Lepidodendron*
- Q4. Corm of *Isoetes*
- Q5. Types of steles in *Lycopodium*
- Q6. Secondary growth in *Isoetes*

#### 3.9.2: Long answer type Questions:

- Q1. Describe external and internal structure of *Selaginella*
- Q2. Explain the types of gametophytes in *Lycopodium*
- Q3. Describe internal structure of aerial shoot and reproductive structure of *Rhynia*
- Q4. Describe the life- cycle of a homosporous and a heterosporous pteridophyte. How do they differ? Which is more evolved and why?
- Q5. Give an illustrated account of sporophyte of *Psilotum*
- Q6. Write a comparative account of cones of *Lycopodium* and *Selaginella*

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## UNIT-4- SPHENOPSISIDA AND PTEROPSISIDA

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- 4.1 Objectives
- 4.2 Introduction
- 4.3 Salient features of important classes and life cycle of some genera
  - 4.3.1 Sphenopsida
    - 4.3.1.1 *Hyenia*
    - 4.3.1.2 *Sphenophyllum*
    - 4.3.1.3 *Equisetum*
  - 4.3.2 Pteropsida
- 4.4 Summary
- 4.5 Glossary
- 4.6 Self assessment questions
- 4.7 References
- 4.8 Suggested readings
- 4.9 Terminal questions



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## 4.1 OBJECTIVES

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This unit describes salient features of class Sphenopsida and Pteropsida, characteristic features of *Hyenia* and *Sphenophyllum* and life cycle of *Equisetum*. After reading this unit you will be able to:

- Understand important features of class Sphenopsida and Pteropsida.
- Describe systematic position, habit, habitat and general features of *Hyenia*, *Sphenophyllum* and *Equisetum*.
- Explain morphological features of *Hyenia*.
- Describe morphological and anatomical features of *Sphenophyllum*
- Discuss life cycle of *Equisetum*.
- Understand plant body, gametophyte, classification of class Pteropsida

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## 4.2 INTRODUCTION

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In the previous unit you have read the characteristic features of class Psilophytopsida, Psilotopsida and Lycopsidea. Present unit describes two fossil (*Hyenia* and *Sphenophyllum*) and one living (*Equisetum*) member of class Sphenopsida and general characteristics of class Pteropsida. The class Sphenopsida is represented today only by the herbaceous *Equisetum* but included magnificent trees in geological times. They arose in the lower Devonian, attained the climax of their evolution during carboniferous when they grow into trees of 30 meter height and then began to dwindle in the Permian and since Jurassic only *Equisetum* and some of its immediate associates are known.

The class Sphenopsida is well defined in certain morphological features. The stem is articulated with nodes and internodes and sometimes with a longitudinally ribbed stem surface. The leaves are borne in whorls at the nodes and the branch buds are not axillary but alternate with the leaves. The sporangia are borne in unique structure called sporangiophores arranged in strobili except *Hyenia*. Heterospory possibly developed the least in this class.

The class Pteropsida described in the present unit, represent the most highly evolved group among the lower vascular plants. This group included some most beautiful and familiar plants commonly known as Ferns. It is the most predominant group of the Pteridophytes today with 305 living genera and more than 10,000 widely distributed species according to various estimates (Holttum 1949). This group probably arose in the Lower Devonian almost at the same time as the other groups of Pteridophyta but did not attain the prominence of Lycopsidea and Sphenopsida in the Carboniferous period. They become numerous only during the Triassic and Jurassic period when other major Pteridophytes were getting extinct. Most of the families of class Pteropsida evolved very late. Their successful invasion on varied habitats, their diverse habit, and their supremacy in vegetative propagation and their remarkable success in competition with modern seed plants stamp the Pteropsida as having reached the highest point in the homosporous evolution. A unique feature of Pteropsida (ferns) is that their

persistent basic characters are still sufficiently flexible to be receptive to the environmental fluctuations.

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### 4.3 SALIENT FEATURES OF CLASSES AND LIFE CYCLE OF IMPORTANT GENERA

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#### 4.3.1 Distinguishing features of class Sphenopsida

1. It includes both fossil (*Calamophyton*, *Sphenophyllum*) as well as living plants (*Equisetum*). It is represented by only one living genus *Equisetum* and about 18 fossil forms.
2. The plant body is sporophytic and differentiated into root, stem and leaves.
3. The stem and branches in majority of members are long, jointed with nodes and internodes and ribbed i.e. having ridges and furrows.
4. The leaves are extremely reduced and borne in whorls at the nodes of stems and branches.
5. Branches also arise in whorls from the axil of the scaly leaves.
6. The stem has a solid protosteles (*Sphenophyllum*) or solenosteles (*Equisetum*). Secondary thickening was observed in some extinct forms (*Sphenophyllum*)
7. The sporangia develop on a peltate appendage called sporangiophore. Sporangial walls are thick.
8. Most of the members are homosporous including *Equisetum*. However, some extinct forms were heterosporous (e.g. *Calamostachys*).
9. The gametophytes are exosporic and green.
10. Spermatozoids are large and multiflagellated.
11. The embryo is without suspensor and is exosporic in nature.
12. This class is divided into four orders:

#### Order 1. Hyeniales

Family 1. Protohyeniaceae: *Protohyenia*

Family 2. Hyeniaceae: *Hyenia*

#### Order 2. Sphenophylales

Family 1. Sphenophyllaceae: *Sphenophyllum*, *sphenophyllastachy*, *Bowmanites*, *Eviostachya*

Family 2. Cheirostrobaceae: *Cheirostrobis*

#### Order 3. Calamitales

Family 1. Asterocalamitaceae: *Asterocalamites*, *Archaeocalamites*

Family 2. Calamitaceae: *Protocalamites*, *Calamites*, *Annularia*, *Asterophyllites*,  
*Protocalamostachys*, *Calamostachys*, *Palaeostachya*

#### Order 4. Equisetales

Family 1. Equisetaceae: *Equisetites*, *Equisetum*

#### 4.3.1.1 *Hyenia*

**Division:** Sphenophyta  
**Class:** Sphenopsida  
**Order:** Hyeniales  
**Family:** Hyeniaceae  
**Genus:** *Hyenia*

**Distribution and Habit:** *Hyenia* is the largest genus with three species. *H. elegans* - From the Upper middle Devonian from Germany, *H. Sphenophylloides* from the Upper middle Devonian from Norway and *H. banksii* From the Upper middle Devonian from the Hamilton group of orange county New York. *H. elegans* is the best known species with a horizontal rhizome bearing roots and aerial stem (Fig.4.1A). The erect stem is usually unbranched, upto 30 cm in height and less than 1 cm in diameter (when branched in digitate manner). Some branches are sterile while others are fertile. Sterile branches bear whorls of narrow repeatedly forked leaves which are from 1-2.5 cm long (4.1B).

In *H. banksii* upright stem bears spreading lateral branches of only slightly smaller diameter. Leaves are 7-11 mm long, usually two but sometimes three times forked. Fructifications are described for *H. elegans* only. The upper portion of fertile branches are transformed into spikes bearing short-forked sporangiophores arranged same as leaves. Leaves are not present among the sporangiophores and the entire stem tip is fertile. The bifurcated tips are recurved and each bears 2-3 oval spore (4.1C). The spores have not been observed.

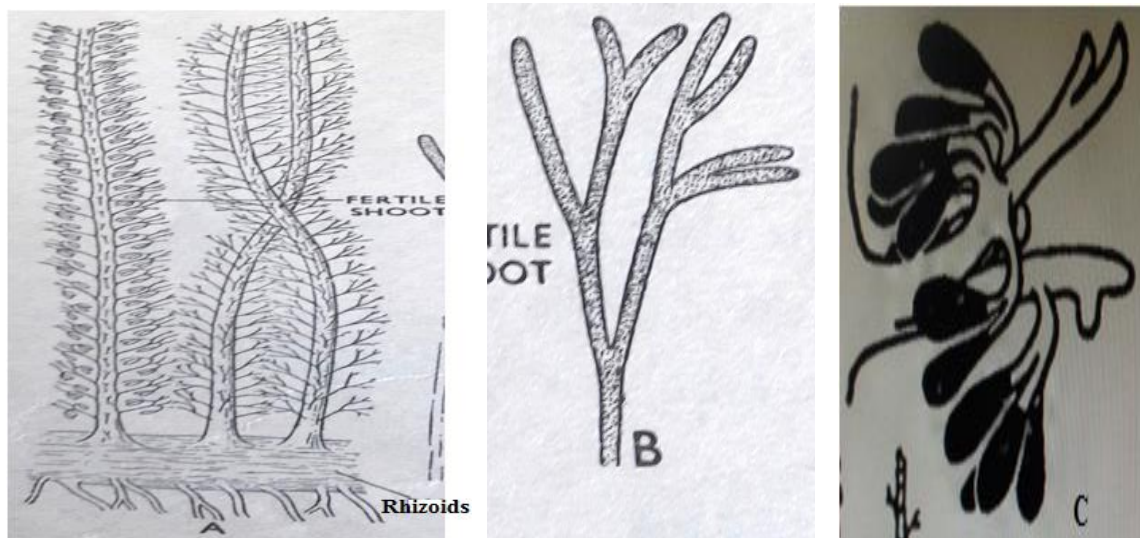


Fig.4.1: *Hyenia elegans*. A. Sporophytic plant, B. Sterile appendage, C. Fertile appendage

**Anatomy:** Very little is known about the vascular system of *Hyenia* that might help in determining its relationship. We depend on external morphology. There are 4 characteristics that suggest that the genus belonged to a group that was ancestral to the class Sphenopsida:

- Small sterile telome trusses of determinate growth that functioned as leaves.
- Sporangioophores with recurved tips bearing terminal sporangia.
- Aggregation of sporangioophores into lax cone like structure.

- A tendency of fertile and sterile appendages to be arranged in shallow spiral or pseudowhorl as might be accepted to occur in ancestors of the Sphenopsida.

The position of the sporangia suggests affinities with Psilophytales. It is possible that the Hyeniales constitute a side line of the Psilophytalean complex from which sphenopsids evolved later on.

#### 4.3.1.2 *Sphenophyllum*

**Division:** Sphenophyta  
**Class:** Sphenopsida  
**Order:** Sphenophyllales  
**Family:** Sphenophyllaceae  
**Genus:** *Sphenophyllum*

**General morphology:** As originally conceived by Brongniart in 1828 the genus *Sphenophyllum* applied to compression fossils of a herbaceous Carboniferous plant with whorls of wedge shaped leaves attached to distinct jointed stems. The exact habit of the *Sphenophyllum* is not known. In general, present evidence (Eggert and Gaunt 1973, Batenburg 1977) indicates a plant with a scrambling habit where slender aerial axes were several meters long but not more than 7mm in diameter.

The small diameter in proportion to the great length indicates that they were unable to support their own weight and must have been prostrate on the ground or must have depended on other plants for support. It is quite possible that the aerial shoots were borne on the rhizome. The shoots are known to branch dichotomously at the distal portion and bear lateral branches, usually one per node (4.2 A). However, several branches per node have also been reported.

The leaves of *Sphenophyllum* showed a wide range of shapes and structure, some being deeply cleft, while others were entire and deltoid (Fig.4.2 B); yet all received a single vascular supply, which dichotomized very regularly within the lamina. Some species were markedly heterophyllous, and in the setae deeply cleft leaves were usually near the base, while the entire ones were at the upper regions on lateral branches, an arrangement that suggests that the former might represent juvenile foliage. The leaves were sessile, wedge shaped, entire or dichotomously divided and with a dichotomously branched venation (4.2 B).

The number of leaves per node is usually 6 or 9 and is related to the trimerous internal structure of the stem. In some cases where leaves are small up to 18 leaves may be present at a node. The leaves are usually less than 2 cm long. They are supplied at the constricted base with one or two vein that dichotomize two to six times, before reaching the distal extremities of the leaf. The leaves of *Sphenophyllum* vary in external morphology from those that have the appearance of a sterile telome truss without webbing to those which are completely webbed leaves. *S. emarginatum* provides an excellent example of leaf polymorphism (heterophylly), ranging from simple leaves with a single unbranched vein to webbed leaves where the vein dichotomises up to four times.

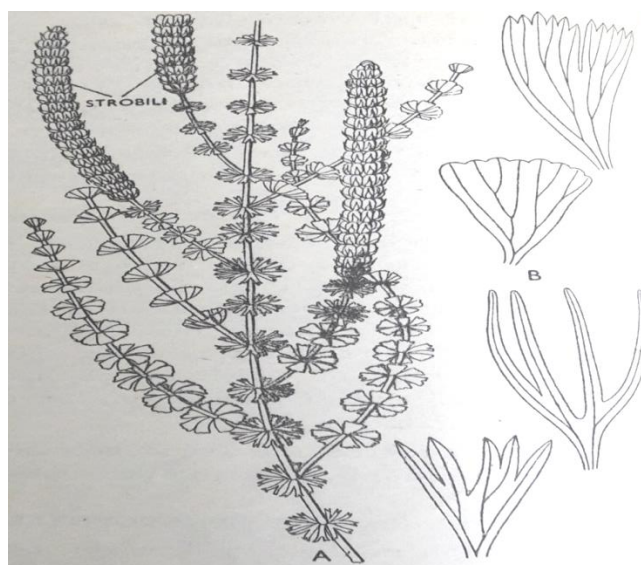


Fig.4.2 A. Shoot of *Sphenophyllum* (redrawn after Hirmer); B. Leaf forms in *Sphenophyllum*

### Anatomy

**Stem:** The primary vascular cylinder of stem in internode was an actinostele and the primary xylem is a three ribbed (triach) exarch protostele. This anatomy of the stem was most peculiar in its resemblance to that of a root. In the Lower Carboniferous species, *S. insigne* the strands of protoxylem located at the tip of each radiating arms of actinostele occasionally break down to leave a lacuna in mature stems and an important characteristic of Sphenopsida (Fig. 4.3 A), but in the Upper Carboniferous species this rarely happened. The small exarch cells of protoxylem are annual, helical or scalariform tracheides. The larger centripetal metaxylem tracheides may bear multiseriate bordered pits. There was primary phloem around it but it is not well preserved. The cortex around the stele is formed of thin walled cells on the exterior.

Outside the primary wood *Sphenophyllum* stem is provided with a bifacial vascular cambium (Eggert and Gaunt, 1973) (Similar to woody stem of angiosperm). The vascular cambium first divide between the arms of the actinostele and completed later around the tips of the arms. Cichan and Taylor (1982) and Cichan (1985) demonstrated that the secondary xylem production is unique. The secondary xylem opposite to protoxylem is less well developed and composed of smaller tracheids than in other parts. This resulted in a characteristic pattern (dimorphic secondary wood) which is recognizable at a glance in transverse sections (Fig.4.3B). In young stems primary phloem is present while in older stems small amount of secondary phloem and secondary ray tissue is present.

The primary wood consisted entirely of tracheids (i.e., without any admixture of parenchyma) and they bore multiseriate bordered pits on their lateral walls. The tracheids of the secondary wood also bore multiseriate pits, but they were restricted to the radial walls. Between the tracheids, there were wood rays. These were continuous in *S. insigne*, but were interrupted in *S. plurifoliatum* where they were represented only by a group of parenchyma cells in the angles between adjacent tracheids. Large stems had a considerable thickness of cork on the outside, formed from a deep-seated phellogen.

In older stems the primary tissue of the cortex are lost because of the activity of a phellogen and production of periderm (phellogen is a lateral meristem that originates in the parenchyma of the cortex where it forms a continuous ring. It gives rise to phellum tissues composed of radial files of cells that are similar in their appearance to the cork cells of modern seed plants). Leaf traces diverge singly or in pairs from the parenchyma at the tips of the radiating arms. As they pass horizontally to the leaf base they may divide dichotomously or remain unbranched.

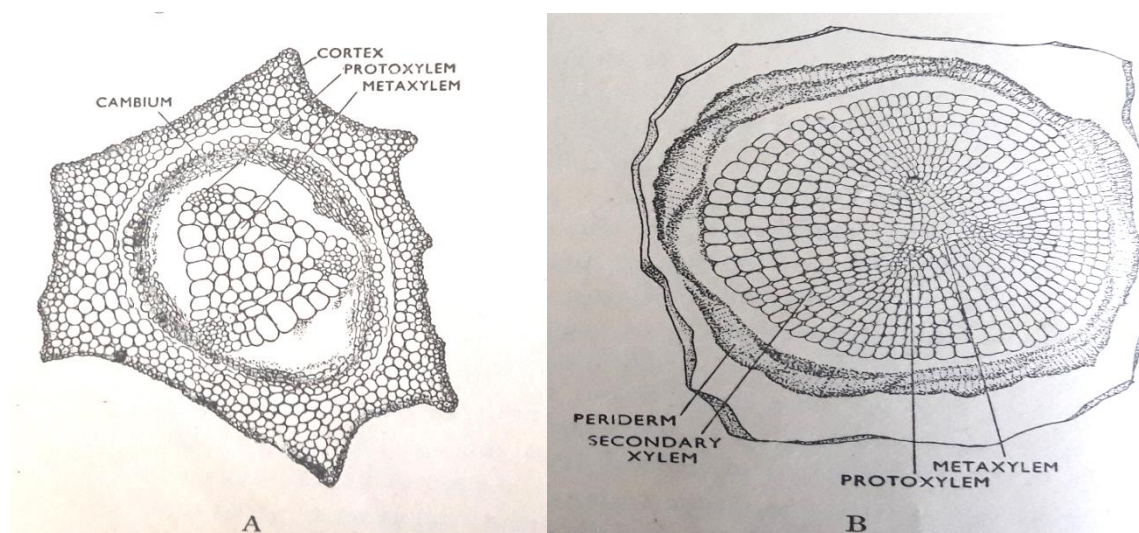


Fig. 4.3 A. Primary stem of *Sphenophyllum*, B. *Sphenophyllum* stem showing secondary growth

**Leaf:** The internal anatomy of leaf varies with the location at which the section is taken. The epidermal cells with their sinuous wall outline are found not only on leaves, but on bracts, sporangiophores and sporangia of *Sphenophyllum* (Reed 1949, Baxter 1950, Leisman 1964). Sunken stomata are abaxial. In the distal portion of the leaf they are confined to two rows, one on each side of abaxial furrows. Below the epidermis especially on the upper side, is a sclenchymatous hypodermis. At the midpoint of a leaf there may be several veins more or less evenly spaced except near a dichotomy. Each vein is a concentric bundle with centrally placed group of protoxylem cells surrounded by a layer of thin walled cells interpreted as phloem. Around this vascular bundle is a layer of thin walled cells with dark contents that make up a melasmatic layer (a layer of storage cells, Good 1973). The mesophyll is composed of thin walled parenchyma with large intercellular space (Fig 4.4).

**Roots:** *Sphenophyllum* roots were adventitious and produced at the nodes, often with leaves. This suggests that as the stems of *Sphenophyllum* increased in length and basal portions assumed a horizontal position on the floor of the swamp. The roots are much smaller than the stem that bore them; they have essentially the same internal structure except for the primary xylem which is usually diarch instead of triach. Unlike stem secondary elements radial to the protoxylem were not smaller than the others (Fig.4.5). The roots also had a well developed periderm formed by a cork cambium which arise in the pericycle and relatively narrow cortex persisted after the periderm was well develop.

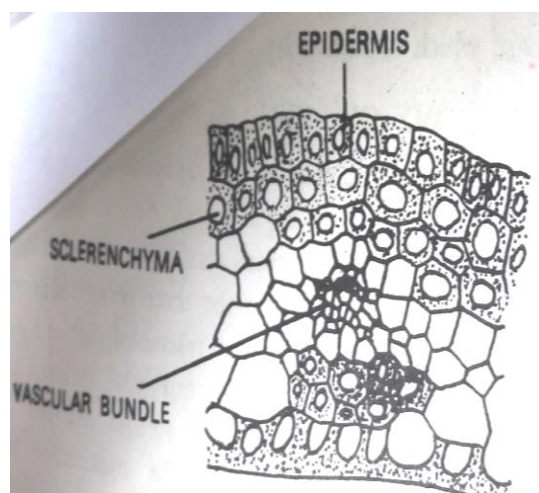


Fig.4.4 Cross section of *Sphenophyllum* leaf

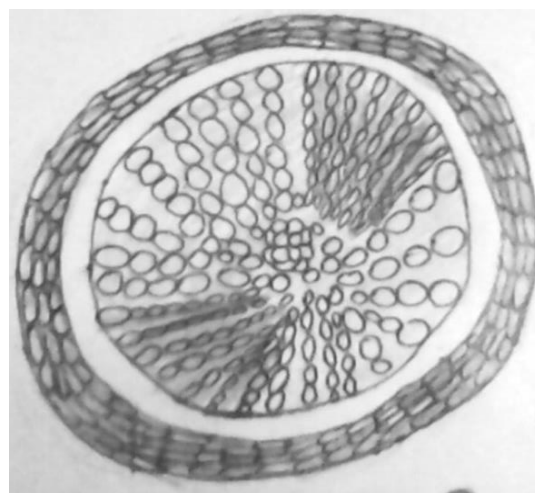


Fig 4.5.T.S. root of *Sphenophyllum*

### Reproductive structure (Cones or Strobili)

A number of cones, referred to the genus *Sphenophyllostachys* or *Bowmanites* have been found attached to the parent plant, others found detached, are placed in these genera on the basis of their general similarity. Many compressions, impression fossils of *Sphenophyllum* stems with attached cones have been described (Boureau 1964). Attachment also has been confirmed by Good (1978) who found premineralized cones attached to *Sphenophyllum* stems with leaves. Most species of cones assigned to the *Sphenophyllum* consist of whorls of bracts that are usually fused tangentially to some part of their length to form a shallow disc like structure. Immediately above the whorl of bracts and partially fused to their adaxial surface are sporangiophores with terminally borne sporangia.

The number of bracts per whorl, the number of sporangiophores and the orientation of their terminal sporangia varies even within a single cone (Good, 1978). However, features of the spores (including the presence of a distinctive perispore) are characteristic of most species. The principal organ genus for cones of *Sphenophyllum* is *Bowmanites*. Some authors (Boureau 1964, Sporne 1965) adopted the name *Spherophyllum*. Hoskins and Cross (1943) pointed out *Bowmanites* has priority over *Sphenophyllostachys* therefore these authors placed all cones in the genus *Bowmanites* with its species. Some of the strobili represent the most complex cones in the whole plant kingdom.

#### *Eviostachya* sp.

Some paleobotanists believe that the *Sphenophylls* evolved from middle Devonian ancestors belonging to the Hyeniales. Much of the evidence for this interpretation is based on the characteristics of an upper Devonian fossil called *Eviostachya* described by Leclercg (1951) in detail. Less than 6 cm long and less than 1cm in diameter the compressed and premineralized specimen represent small cones on a peduncle with a whorl of six bracts below the fertile region. Above this were whorls of sporangiophores, six in each whorl. Each sporangiophore was itself highly complicated (Fig. 4.6 G) and branched in a very characteristic way bearing a total of twenty-seven sporangia in are flexed position (Fig.4.6H). Each sporangiophore bears both sporangia and sterile processes. Sporangioophores in

successive whorls stood vertically above each other, as is characteristic of the Sphenophyllales, but there were no bract. A triarch protostele not unlike that of *Sphenophyllum* was found in the cone axis. This gives off traces from the arms that supply whorls of six sporangiophores. The similarity of *Eriostachya* with its trichotomizing and then dichotomizing recurved branches each terminated by a cluster of three sporangia resemble the complex sporangiophores of Hyeniales.

***Sphenophyllostachysfertilis* = *Sphenophyllum fertile*=*Bowmanitiesfertilis***

It is reported from Lower Carboniferous period. Cone is up to 6 cm long and 2.5cm in diameter. It was made up of whorls of superimposed sporangiophores, six in a whorl, each subtended by a pair of sterile appendages (possibly homologous with one bifid bract). Each sporangiophore bears a distal cluster of 16 branches, each terminating in a petiole like structure with tworeflexed sporangia (Fig. 4.7). This complex structure can be interpreted as a stage in the sterilization of a fertile telome truss to produce bracts that subtend a sporangiophore or as a stage in the reduction of sterile and fertile telome truss accompanied by recurvation as suggested by Zimmermann is telome theory. Taylor (1969) suggested that the general trend in the evolution of the sphenopsid cone has been from complexity to simplicity in organization of the bract-sporangiophore unit with the *B. fertilis* representing the primitive type. Only detached cones of *B. fertilis* have been reported and are presumed to belong to the members of Sphenophyllales because of the triarch or hexarch arrangement of primary xylem in axis.

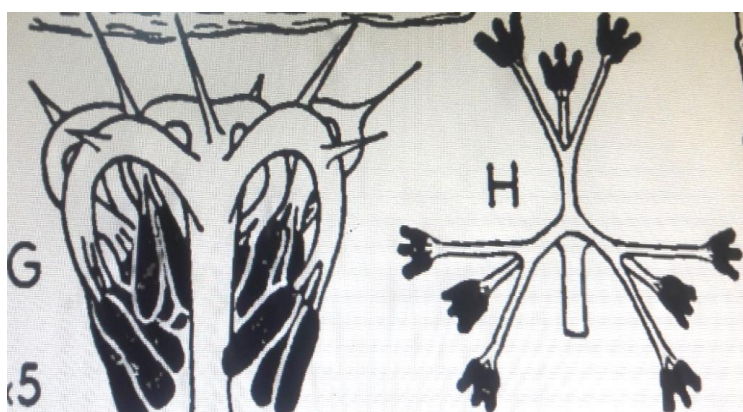


Fig.4.6: *Eviostachya*. G. Sporangiphore. H. Mode of branching

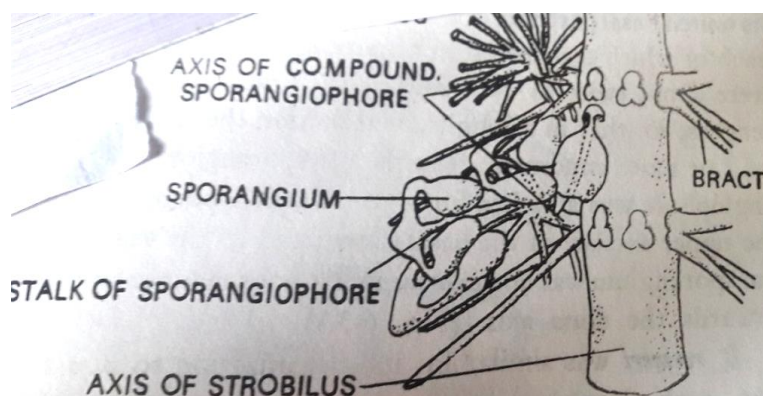
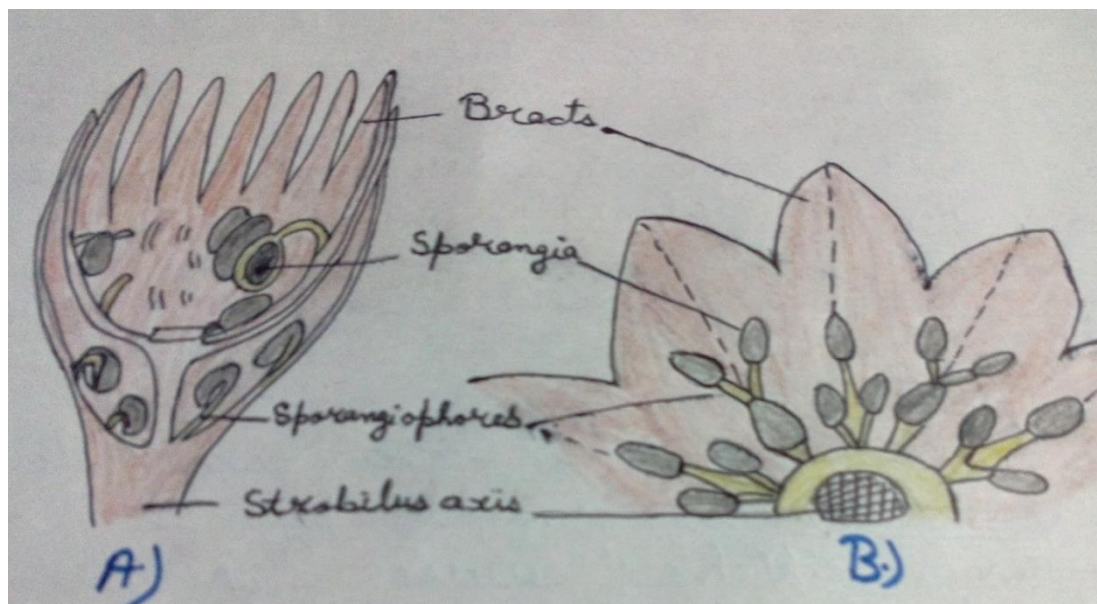


Fig. 4.7: *Sphenophyllostachys (Bowmanites) fertilis* (After LeClereq)



*Sphenophyllostachys dawsoni*= *Bowmanites dawsoni*

Cone is known to have been borne on stems like those of *Sphenophyllum plurifoliatum*. It is about 1cm in diameters and upto 12 cm in length and bore whorls of bracts fused into a cup near the base but with free distal portions. In the axils of these bracts and fused with them to a certain extent were branched sporangiophores (Fig 4.8). One sporangiophore is shorter than the other, so that two concentric rings of sporangia are produced in the whorl. The vascular stand of the cone axis is an exarch actinostele, which may be triarch as in the stem or with additional radiating arms confirming to the hexarch condition. The vascular supply to the bracts and sporangiophores originates from the tips of the arm of the protostele. In one type (form $\alpha$ ) each sporangiophore had three branches (with two long distal and one short median) each terminating in a single reflexed sporangium. In other form (form $\gamma$ ) there were six branches. The bract number is variable (14-22) as is the number of sporangiophores. In some specimen there were 3 sporangiophores per bract while others have 1:1 ratio.

**4.3.1.3 Equisetum**

**Division:** Sphenophyta  
**Class:** Sphenopsida  
**Order:** Equisetales  
**Family:** Equisetaceae  
**Genus:** *Equisetum*

**Habit and Occurrence:** This genus comprises of about 30 species and is of world-wide distribution except Australia and Newzealand. It grows in a wide variety of habitats. Some species grow in ponds and marshy places, e.g. *E. palustre*, *E. hyemale*; some species are shade loving and grow in damp shady places, e.g. *E. pretense*, whereas some other species grow in relatively dry and exposed conditions e.g. *E. arvense* . The common Indian species

are: *E. debile*, *E. arvense* and *E. ramosissimum*. *E. debile* is found along the banks of the rivers, canals and pools in the Indian plains.

The species of *Equisetum* are commonly known as pipes, horsetails and scouring rushes. These species vary greatly in size. The tallest South American living species with a diameter of few centimeters grows to a height of 40 feet. The Indian species *E. debile* has a diameter of 0.5 cm only when growing in swamps and reaches a height of 10 to 15 feet. However most of the species are smaller seldom reaching a height of few feet only. *E. scirpoides* is the smallest species.

## The Sporophyte

### External structure

**Rhizome and aerial stem:** The plant is herbaceous and branched. It consists of horizontal underground branching rhizome which is conspicuously differentiated into nodes and internodes (Fig 4.9A). It penetrates the soil and upright aerial sterile and fertile branches as well as whorl of adventitious roots arise from each node of rhizome. The sterile green branches have a whorl of lateral branches at their nodes and the lateral branches in turn possess small branchlets thus giving a bushy appearance. Depending upon the species the fertile branches may be green or colourless, branched or unbranched. The fertile branches bear strobili at their apical ends, such branches die as soon as the spores are shed (Fig. 4.9 B).

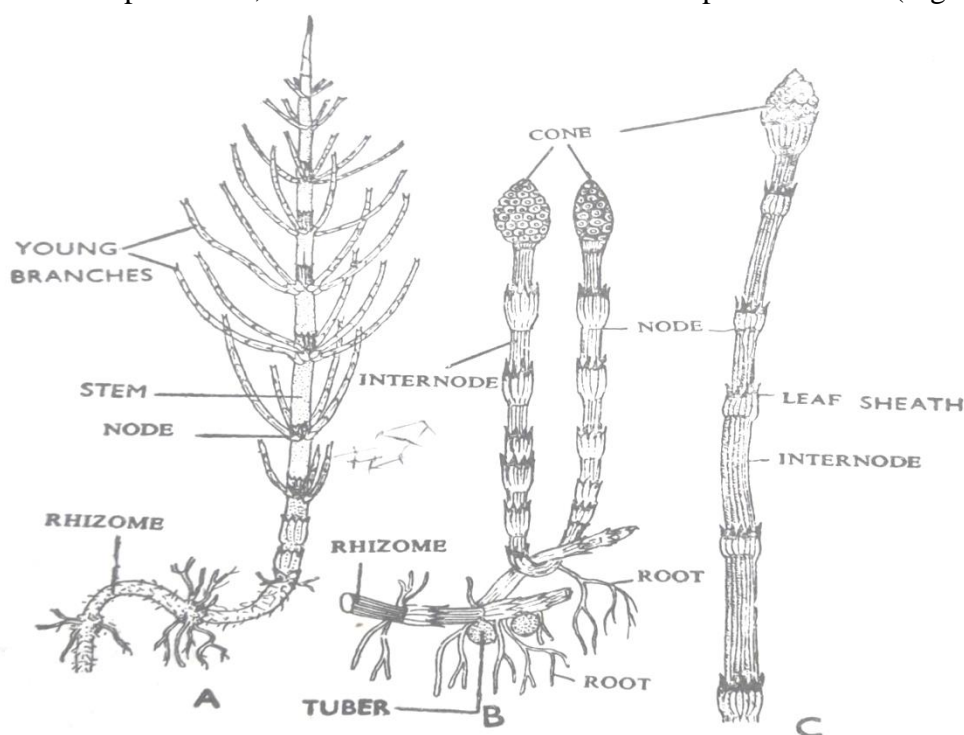


Fig. 4.9 A. Habit of *Equisetum arvense* showing underground rhizome, roots and young branches; B. *E. hyemale* with terminal strobilus and, C. Surface view of a node with leaf sheath.

The aerial stems have conspicuous nodes dividing the stem into jointed sections. On each node of aerial branches whorl of scale like leaves are present which are more or less united at the base to form a brown sheath. Each internode is marked by longitudinal ridges and grooves

and ridges of successive internode alternate with each other. Stem is the main and dominant organ of the plant body and may branch freely as in *E. arvense*, or remain unbranched as in *E. hyemale*. Some species like *E. palustre* develop three types of branches: (i) sterile green branches; (ii) fertile non green short lived branches and iii. Intermediate type which are fertile, non green and unbranched in the beginning but become green and persist after disorganization of strobili.

**Leaves:** The leaves are arranged in whorls at each node of the aerial branches (4.9 C). They are simple, scaly, slender, unnerved brownish and more or less fused at their base laterally to form a sheath around the base of the internode, the leaf apices are free and pointed. The number of the leaves in each whorl ranges 3-40 from species to species. The leaves of successive nodes are arranged in alternate fashion. At first, the leaves are green and remain photosynthetic for a short period, but soon become brownish, dry and scale-like and are only protective in function. The bases of leaves fused and give an appearance of a collar.

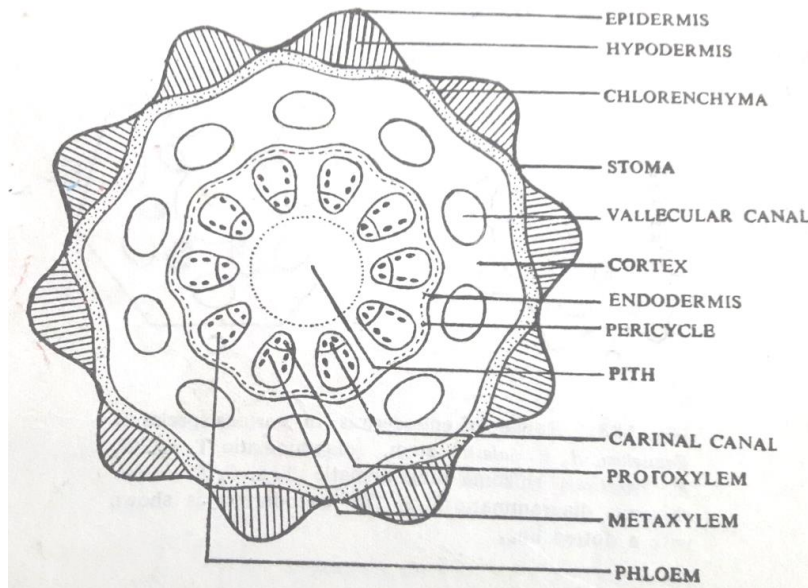
**Roots:** The roots are adventitious and arise in whorl at the nodes of the subterranean rhizome (4.9 B). They are slender, fibrous and endogenous in nature.

### Anatomical structure

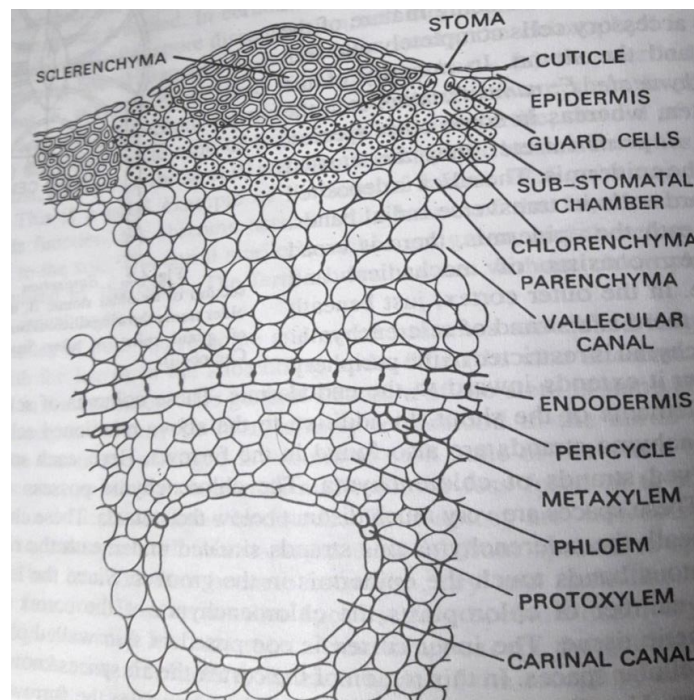
**Aerial stem- T. S. through internode:** The T.S. of aerial stem passing through internode exhibits distinct ridges and furrows (Fig. 4.10 A). The outermost layer is single-layered epidermis that consists of elongated thick walled cells, the epidermis is impregnated with a thick layer of silica hence the stem is hard and rough to touch. On account of silica deposit the ash of plant is used for polishing purposes and plants as such used to clean utensils and earned the name 'scouring rushes'. The stomata are found in the furrows, each stoma consists of 4 cells, two inner sunken guard cells and two outer accessory cells. In majority of the species the stomata are sunken, e.g. *E. hyemale* and *E. ramosissimum*; while in *E. palustre* and *E. pratense*; they are localized on the surface of epidermis. The stoma opens into intercellular space bordered by chlorenchymatous cells. Just underneath the epidermis there is broad cortex. The cortex consists of mechanical and assimilatory tissues and divided into outer and inner cortex. In the outer cortex, just beneath each of the ridges, there is a strand of sclerenchyma; the strands of sclerenchyma are also found in furrows; here each strand is situated in between the curved strands of chlorenchyma. The chlorenchymatous bands are found beneath the sclerenchymatous strands situated underneath the ridges and possess well developed intercellular spaces.

The inner cortex is composed of thin-walled parenchyma with well developed inter-cellular spaces. In this region of the cortex the air spaces known as vallecular canals are present; usually the vallecular canals are found below the furrows in the deeper tissue of the cortex, they are alternate to the vascular bundles. The endodermis is the last layer of the cortex. In *E. arvense*, *E. telmateia*, *E. palustre* etc. the endodermis surrounds the entire stele. Just beneath the endodermis there is single layered pericycle. The vascular skeleton, i.e., stele of *Equisetum* is siphonostelic. The vascular bundles are of collateral type and are arranged in a ring. The vascular bundles are situated below the ridges and alternate to the vallecular

canals. In each internode, as many vascular bundles are found as there are leaves at the node; the vascular bundles alternate to each other in their position in the vascular nodes. Each vascular bundle contains both metaxylem and protoxylem. A cranial canal is developed in each bundle, because of the disintegration of the early formed tracheids of the protoxylem. The remaining protoxylem elements are composed of few tracheids which are found to be arranged on the margin of canal; protoxylary elements are composed of spiral and annular tracheids. The metaxylem elements are found in two groups, these two groups are arranged on the margin of cranial canal in a 'V' shaped manner (Fig.4.10B).



A



B

Fig.4.10: T.S. Equisetum stem, A. diagrammatic. B. Detailed structure

**Aerial stem- T.S. through node:**

- There is a continuous ring of vascular bundles.
- The bundles at the nodes do not have cranial canal.
- Here the protoxylem elements are intact and completely occupy the lacuna or cranial canal.
- At the node, the pith is not hollow and it forms a diaphragm spreading the two successive internodes.

**Rhizome:** The anatomy of rhizome is similar to stem but differ from it in showing a simple cortex without assimilatory cells and stomata and with poor development of mechanical tissue and solid pith. The ridges and grooves are not so marked as in the aerial stem.

**Leaves:** The leaves do not serve as photosynthetic organ but protect the lateral buds. In transverse section leaf reveals a very simple structure. There only one simple collateral vascular bundle surrounded by endodermis. The xylem is poorly developed and without carinal canals.

**Roots:** The adventitious roots also show a very simple structure (Fig 4.11 A). It has an outer unicellular piliferous layer from which sparse root hairs are given off. Below epidermis is a thick multilayered cortex divisible into two zones: The outer zone consists of three to four celled exodermis formed of highly lignified cells. The inner zone is parenchymatous in nature and contains a large number of intercellular air spaces. The endodermis is peculiar in that it is two layered and consist of outer layer of large cells and inner layer of small cells. Pericycle is absent. Lateral roots arise from inner layer of endodermis and casparian bands are present only in outer endodermis. The stele is protostelic and usually tri or tetrarch (Fig. 4.11 B). In the center there are large tracheids representing meta xylem with variable number of protoxylem towards periphery. Each protoxylem consists of a single spirally thickened tracheid. In between the angles of protoxylem phloem is present. The phloem is composed of phloem parenchyma and sieve tubes.

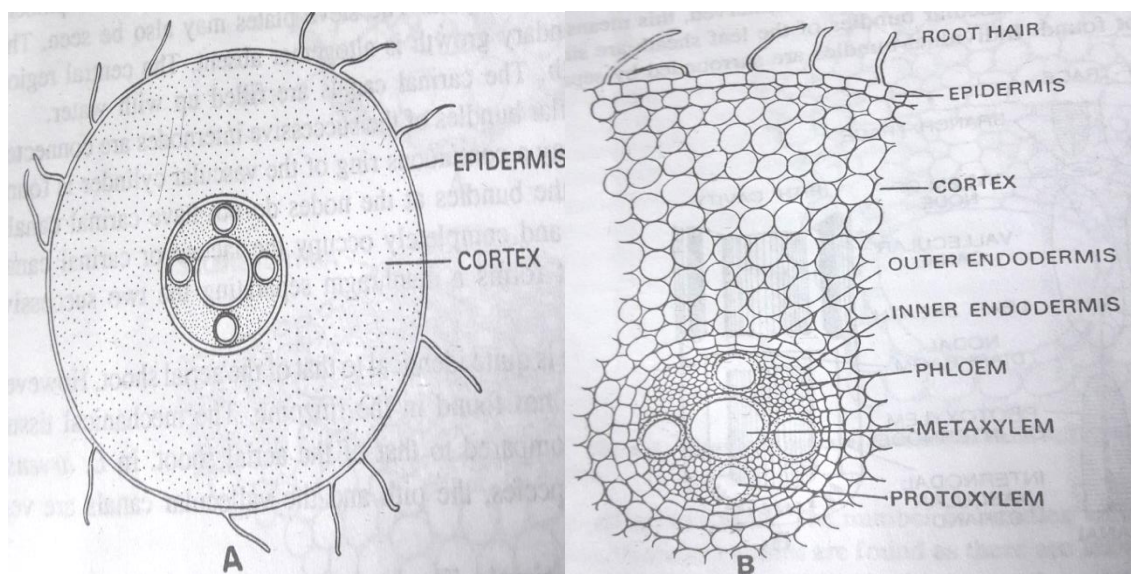


Fig.4.11: T. S. of *Equisetum* root, A. Diagrammatic. B. Detailed structure

**Vegetative propagation:** The ovoid or pyriform tubers are found on the rhizome (Fig 4.9 B). Tubers may also be pear shaped as in *E. arvense*. Each such hard and food filled structure is capable to develop into a new sporophyte when detached from the rhizome of mother plant. Some species under favourable conditions develop rudiments of buds at their nodes which develop new plants as in *E. limosum*, and *E. arvense*.

## Reproduction

Equisetum is homosporous and reproduces by means of spores. The spores are formed in sporangia which develop on the underside of the peltate, hexagonal disc part of sporangiophores. Sporangiophore consists of two parts: stalk and peltate disc. The clusters of whorled sporangiophores are arranged in compact cones or strobili which develop at the tips of aerial branches (Fig.4.9 B).

**Spore Producing Organ (Strobilus):** Each strobilus consists of a thick axis, bearing several whorls of deeply/densely crowded sporangiophores (Fig. 4.12 A). Each whorl is composed of twenty sporangiophores or so. Immediately below the sporangiophores, the central axis of the strobilus bears a small ring-like outgrowth, the annulus. Each sporangiophore is composed of a single slender stalk of which the terminal end is expanded into a flattened peltate disc situated at right angles to the stalk (4.12 B, C). The peltate disc is usually hexagonal in outline in its surface view. Each peltate disc bears a ring of 5 to 10 isolated pendent sporangia on its underside. Each sporangium is elongated, sac like and rounded at apex. On maturity, the sporangia open by longitudinal slits for the dispersal of the spores. The mature sporangium contains spores within it. The mature sporangium remains surrounded by a single-layered intact jacket layer. Each spore is surrounded by a wall composed of four concentric layers. The outermost layer is known as exosporium and the innermost endosporium. Outside the exosporium there is a cuticle layer. On the extreme outside of the spore there lies epispore which later on develops into four strips which get separated from rest of the wall but for one common point of attachment; these strips are spoon-like elaters (Fig 4.12 D, E). Each spore contains nucleus and many small chloroplasts.

**Development of Sporangium:** The sporangium develop by eusporangiate method of development. The sporangial initial divided periclinally into an outer cell which forms sporangial wall and an inner cell which give rise to a part of archesporium or the sporogenous tissue (Fig. 4.13). The sporangial wall varies from two to several cells in thickness. The innermost layer of sporangial wall become glandular and forms the tapetum. The cells of archesporium separate and round off. About one third of them disorganize forming a nourishing liquid to be utilized by the remaining two third surviving spore mother cells. The tapetum also breaks down forming a nourishing medium for the spore mother cells. The diploid spore mother cells undergo reduction division and four haploid spores are formed in tetrahedral fashion (4.13 J).

**Dehiscence of sporangia:** After maturation the internodes of the strobilus elongate separating sporangiophores. The stalk of sporangiophore shrinks and ultimately falls down exposing sporangia. Mature sporangium possesses a single layered wall composed of spirally

thickened cells, these cells lose moisture on exposure to air and shrink on drying and sporangia dehisce by a longitudinal slit, down the side next to the stalk of the sporangiophores.

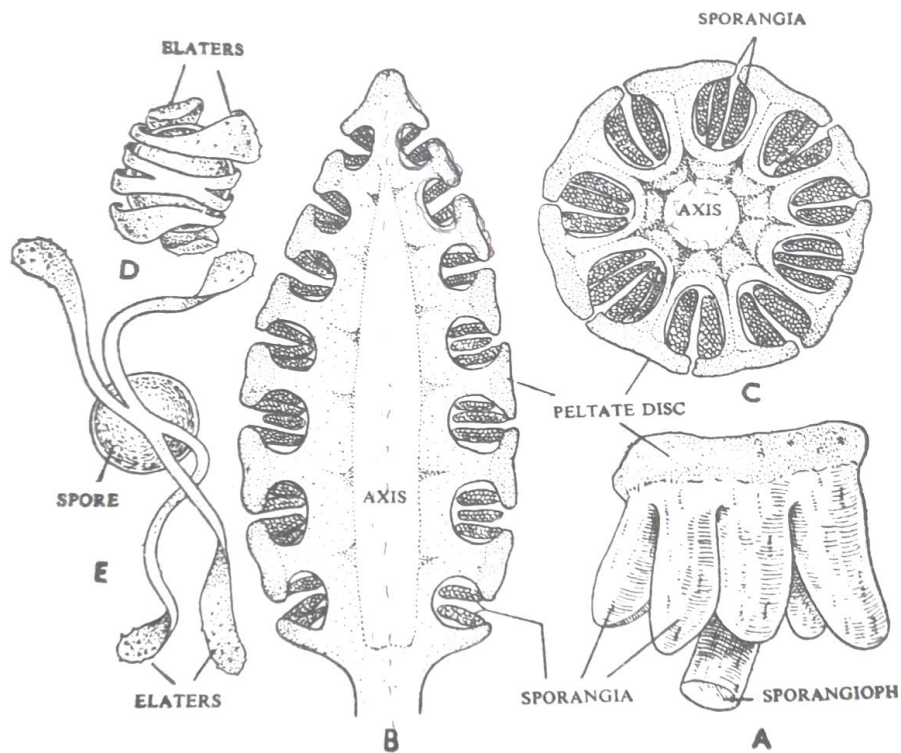


Fig. 4.12: *Equisetum arvense*: A. Sporangiophore showing pendent sporangia; B. L. S. of Cone; C. T.S. of Cone; D. Spore with coiled elaters; E. Spore with uncoiled elaters

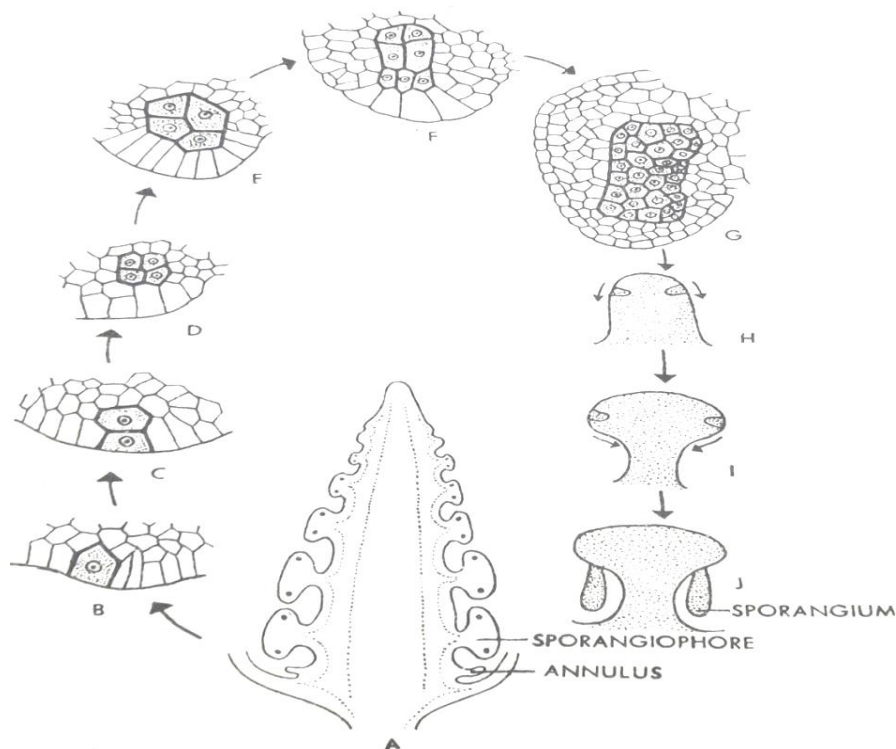


Fig. 4.13-(I): Development of sporangium in *Equisetum*, A. L.S. of Strobilus.; B. Sporangial initial; C-G Development stages; H-J Stages in development of sporangiophore and inversion of sporangia.

## The Gametophyte

**Spore:** The spores are green as they contain numerous chloroplasts (Fig 4.14). According to Beer (1909) the wall of spore consists of four layers (Fig. 4.14 A). Each spore besides an innermost yellowish intine and a light blue exine, contain a third delicate cuticular layer enclosed by an outermost colourless layer, the perispore. This is thick and split along spiral lines into long bands which remain attached to the wall of the spore at the middle point so as to appear as four distinct appendages with flat spoon like tips (Fig. 4.13E). These peculiar structures are known as elaters and remain completely wrapped around the spore till maturation. Elaters are hygroscopic and unwind themselves as the spores dry. The spores are light and carried away easily by wind currents. Each spore is large and contains centrally placed nucleus and many chloroplasts.

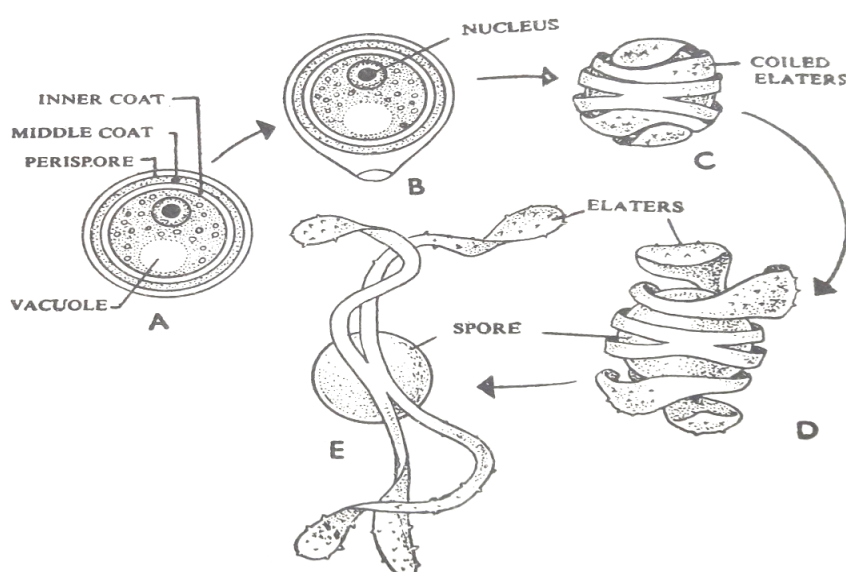


Fig. 4.13 (II) Development of spores of *Equisetum*: A. Unripe spore with three covering; B Spore with outer coat being detached; C Formation of elaters from perispore; D Splitting of perispore into spirally coiled elaters ; E Spore with uncoiled elaters.

**Germination of spore and development of Gametophyte (Prothallus):** The spores are delicate and remain alive for only few days. Under favourable conditions they germinate immediately and a small cell is cut off by a transverse wall within 10 to 12 hours. The spore loses its spherical shape and gives off its spore wall. The chloroplast disappear from smaller cell which develop the first rhizoid (Fig 4.14 B ) The larger cell remains green and produce prothallus or gametophyte. The division which follows in the larger cell may be in any plane, thus there develops a flat plate of green tissue from which many filamentous branches are given out. The tissue is mostly one cell thick and there is no apical growth. The green peculiar prothallus of *Equisetum* differs from fern prothallus both in form and location of sex organs. On maturation prothallus consists of a disc-shaped cushion several cells in thickness. From its upper surface arises irregularly vertical erect lobe-like branches one cell in thickness, while rhizoids arise from the lower surface of disc. The prothallus grows in moist and shady places and its size varies from a pin head to eight mm in diameter. The prothalli



are of two types, small male prothalli which produce only antheridia and large hermaphroditic prothalli which produce antheridia and archegonia both. The question whether *Equisetum* is monoecious or dioecious is a controversial issue. When plants develop in field condition they are generally monoecious e.g., *E. debile*. In such cases archegonia develop first and antheridia later on. The cultivated species are dioecious due to artificial unfavourable condition. *E. arvense* produces spores half of which develop male gametophyte and rest half female gametophyte. The male prothallus is small, deep red in colour and the lobes bearing antheridia are more or less folded (4.15 I). The female prothalli are large and green in colour (Fig.4.15 II).

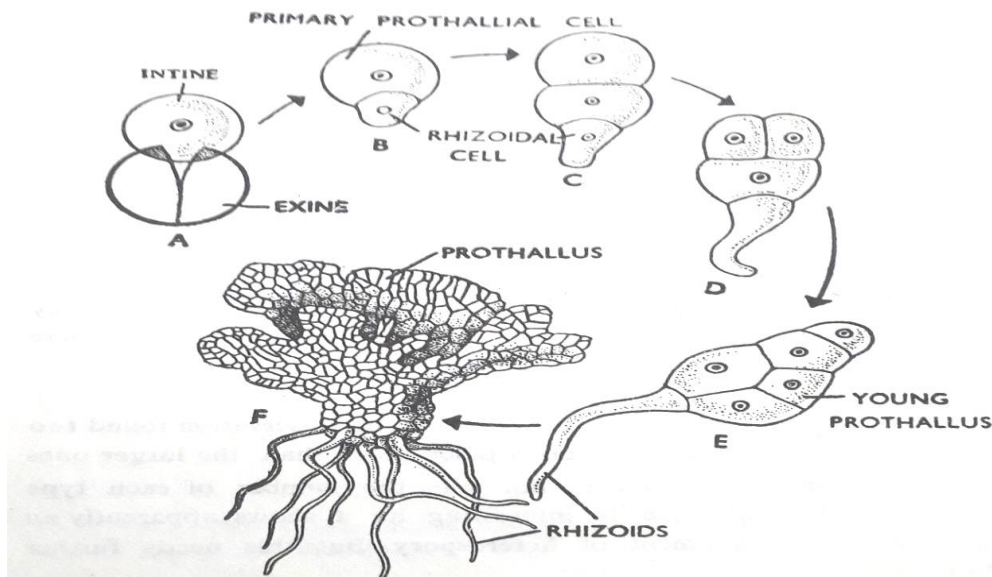


Fig. 4.14- Germination spore of *Equisetum* and development of gametophyte: A. Rupture of wall; B. Division into outer primary prothallial cell and inner hyline primary rhizoidal cell; C-D. Division of primary prothallial cell to form a filamentous gametophyte

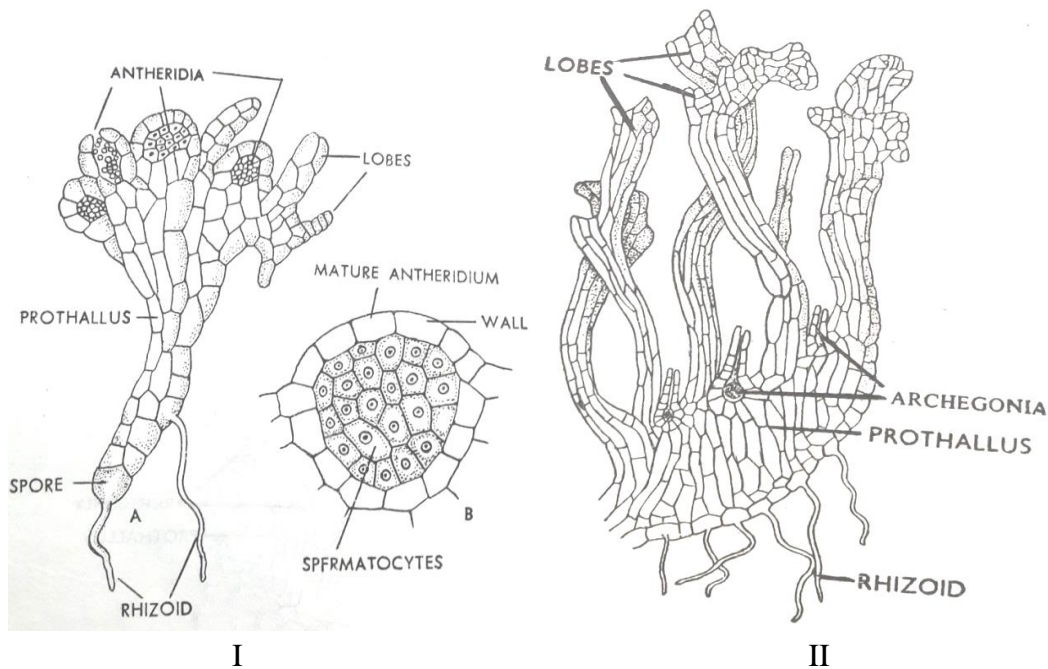


Fig.4.15: Male (I) and female (II) prothallus of *Equisetum arvense*

## Development of sex organs

**Development of Antheridium:** The antheridia develop in the expanded lobes of the uncrowded prothalli after the development of archegonia and on crowded prothalli when they are 20 to 30 days old. The antheridia are of two types:

(i) Sunken or embedded type formed on the massive part of the plants and (ii) projecting type formed on the margins or apex of delicate lobes. The antheridium arises from a superficial cell of the prothallus which divides periclinally into an outer jacket initial and an inner androgonial cell (Fig. 4.16 A). Each antheridium remains surrounded by a single layered jacket; the jacket covers the androcytes, each androcyte metamorphoses into a spermatozoid or sperm. There are 100-150 multi flagellate spirally coiled spermatozoids. The sperm consist of an homogenous spirally coiled body derived from the

nucleus of the spermatocyte and its numerous cilia originating from its cytoplasm (Fig.4.15 III).

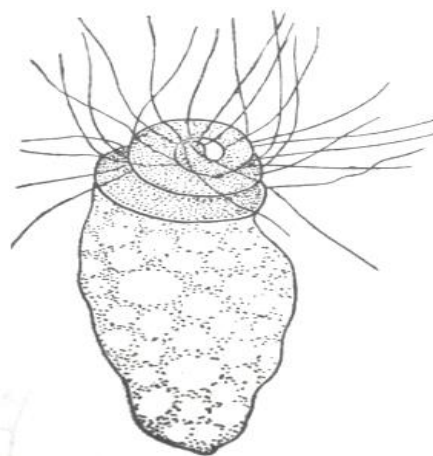
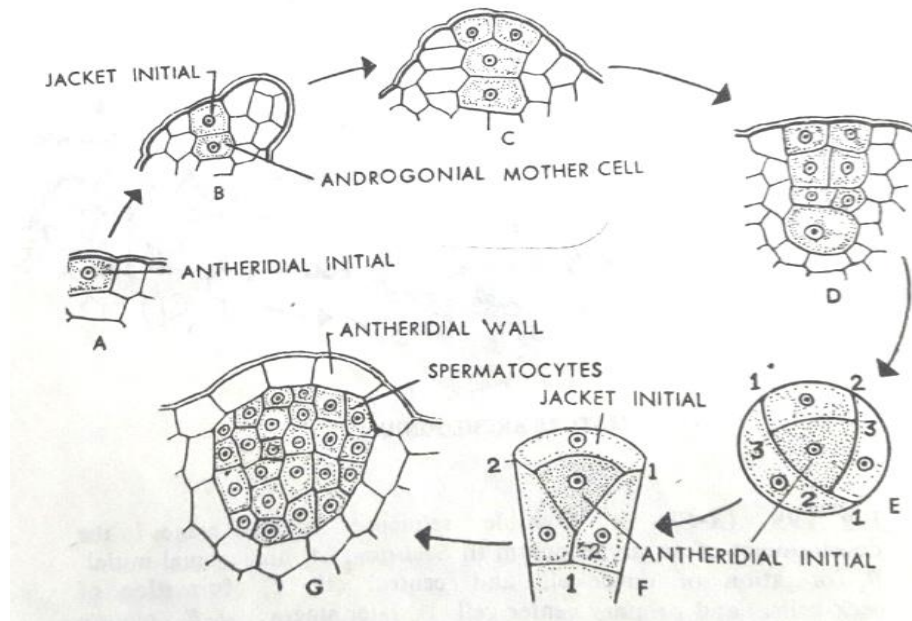


Fig.4.15 (III)- a multiciliated sperm

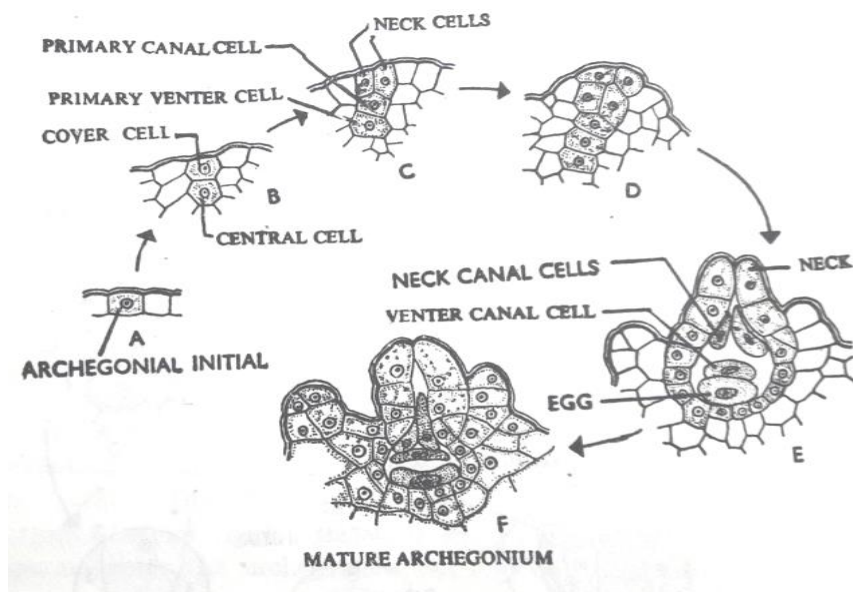
They are attached to a narrow band, the blepharoplast, which lies against the anterior end of the antherozoids. The sperm of *Equisetum* are large as compared to other cryptogams. They are explosively discharged through a small opening in the outer wall when the mature antheridia are moistened.

**Development of Archegonium:** The archegonia appear in the meristematic region where upright lobes are about to develop. At first archegonia point downwards, but on subsequent development of fresh lobes they turn upward. The archegonia arise from superficial cell which divide periclinally forming an outer cover cell and an inner central cell (Fig 4.16 B). The former develops a few neck cells whereas the later gives rise to primary canal cell which develops to two boot shaped cells and a primary venter cell. The latter forms an egg and a venter canal cell. The neck is composed of four vertical rows of cells, each row is two to four cells in height; the terminal cells of the archegonial neck are quite long, which become separated and curved outward on maturity. The axial row consists an egg cell, a ventral canal cell and one or two neck canal cells. A mature archegonium consists of a sunken base in the prothallus, and a projecting neck (4.16 B).

**Fertilization:** The multiciliated sperms are attracted toward the neck of archegonium which secretes malic acid as the neck canal cells and venter canal cells undergo disorganization. A number of sperms enter the archegonium but only one penetrates the egg. In *Equisetum* a number of eggs may be fertilized and may develop into embryonic sporophyte, a feature rarely seen in pteridophytes. An oospore is formed as a result of fertilization which is beginning of the diploid sporophytic generation.



A



B

Fig.4.16: Stages in the development of antheridium (A) and archegonium (B)

**Development of Embryo:** The first division of the oospore is transverse followed by a division at right angle to it. This four celled stage is the quadrant stage of the embryo (Fig. 4.17). From the upper (epibasal) half of the quadrant, the larger cell forms the stem initial cell and smaller one give rise to leaf. The larger cell of hypobasal half forms the root and smaller one forms a weak foot (Fig 4. 17 C). Suspenser is absent and entire structure becomes the embryo proper. In a mature embryo (Fig. 4.17 E) the apical cell of stem and primary root are organized very early in development. Due to rapid growth the embryonic root burst through the gametophytic tissues into the soil establishing the independent young sporophyte.

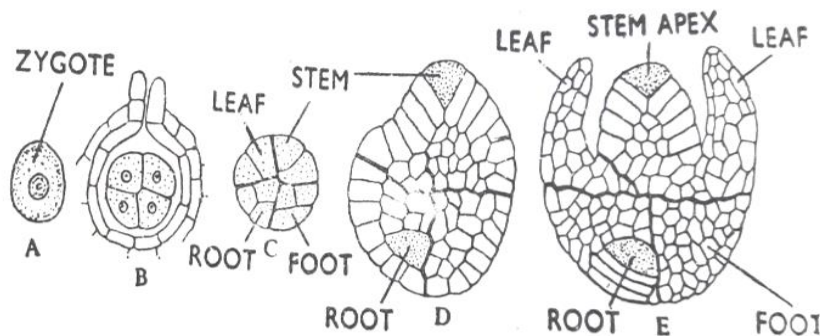


Fig.4.17-(A-E): Stages in the development of embryo in *Equisetum*

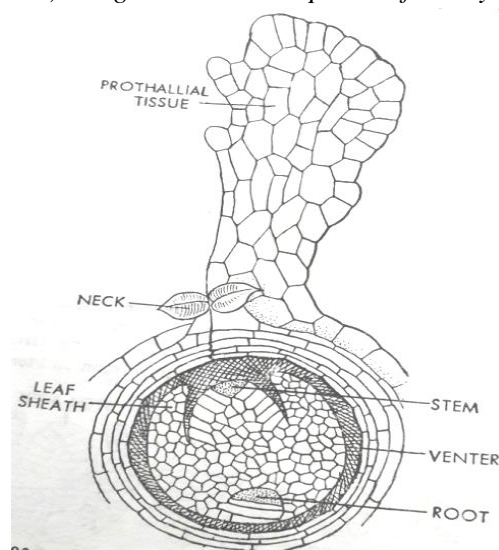


Fig.4.18: Mature embryo of *E. arvense*

The stem portion of the embryo burst through the neck of archegonium and form the calyptra growing upright (Fig.4.18). The primary stem grows straight until it has differentiated into a dozen nodes each bearing three leaf sheaths. Soon a more vigorous branch arises from the base of this primary stem, and this in turn is replaced by another branch and the process is repeated. The third or four series of these branches enter the soil and remain underground and form the rhizome of the mature plant. During the course of development the primary root withers and its function is taken up by adventitious roots which develop from the base of the stem. The embryo develops into a young sporophytic plant body whose stem is differentiated into nodes and internodes with whorl of scale leaves at node and a rhizome with unlimited growth. The primary (embryonic) stem is peculiar because it shows a protostelic structure with well developed xylem without carinal canals but the first branch revealed a siphonostelic structure. This structure persists at nodes while at internodes a eustelic or polyfascicular siphonostele is present.

**Life cycle of *Equisetum*:** The complete life-cycle of *Equisetum* consist of two generations which are morphologically different (i.e. heteromorphic) and they alternate each other. The haploid spore on germination gives rise to a relatively small and inconspicuous structure-the prothallus which bears directly the sex-organs. This is the gametophyte or sexual generation. As a result of fertilization a diploid zygote is formed. It enlarged, undergoes a series of

divisions and forms a conspicuous, highly developed plant provided with stem, leaves and roots. After an initial vegetative phase, sporangia develop and spores are liberated. This is the sporophyte or asexual generation. During spore formation reduction division takes place and spore thus formed are haploid. The spore germinates and the life-cycle commences again (Fig.4.19).

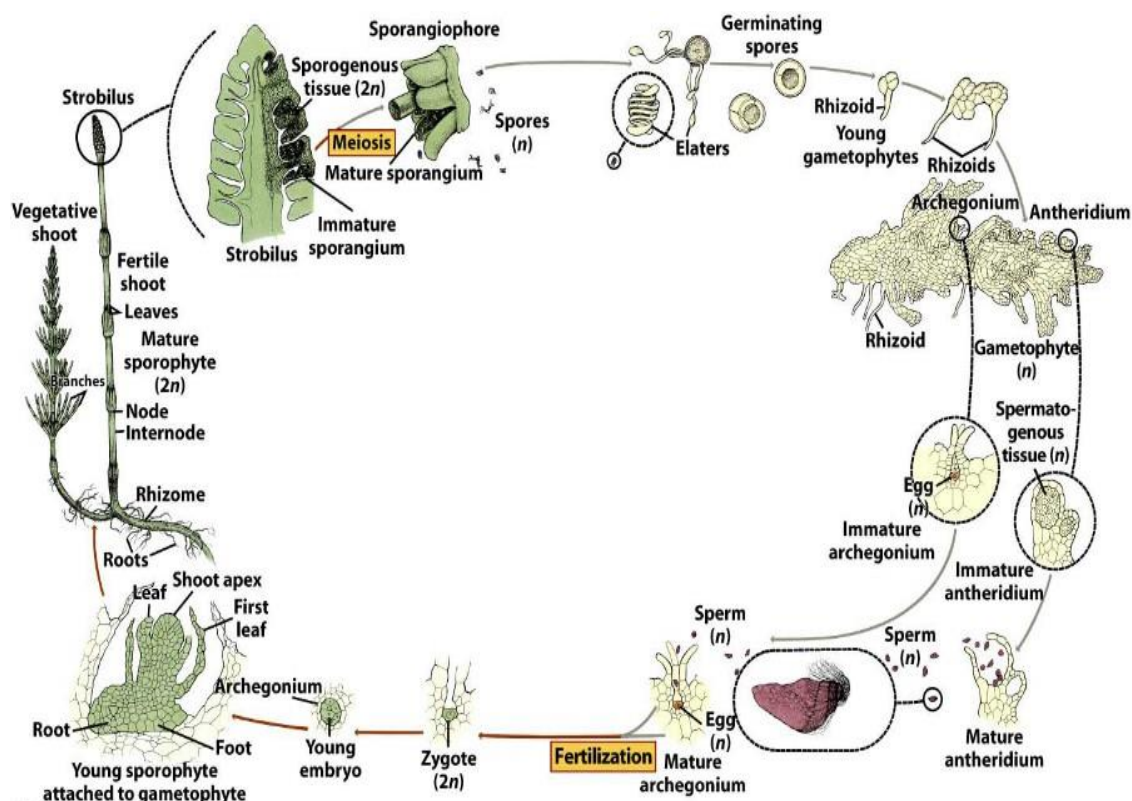


Fig.4.19. Diagrammatic representation of Life-cycle of *Equisetum*

### 4.3.2 Class Pteropsida

1. This class includes the plants which are commonly known as Ferns. It is represented by about 305 genera and more than 10000 species.
2. The sporophytes are usually perennial in nature and differentiated into roots, stem/ rhizome and spirally arranged leaves. Majority of members (except some tree ferns e.g. *Angiopteris*, *Cyathea*) have short and stout rhizomes. The rhizome may be creeping, upright or growing above the soil.
3. Most of the members are terrestrial and prefer to grow in moist and shady habitats. Some members are epiphytic (*Asplenium nidus*), aquatic (e.g. *Marsilea*, *Azolla*), xerophytic (*Adiantum emarginatum*), halophytic (*Acrostic humaureum*) or climbers (*Stenochlaena*).
4. Some members are very small (*Azolla*) while some members are tall tree like (*Angiopteris*, *Cyathea*)
5. The leaves range in size from 2-5 cm in *Anogramma leptophylla* to large tree ferns of family Cyatheaceae.

6. The leaves may be simple (e.g. *Ophioglossum*), entire or lobed, pinnately or palmately compound (most of the ferns) or highly dissected with reticulate or dichotomous venation and described as fronds.
7. Leaf dimorphism is quite common in many genera (e.g. *Vittaria*). Young leaves show circinate vernation (i.e. coiling of leaves) except *Ophioglossum*.
8. Leaves are exstipulate (e.g. Filicales) while stipulate in some other groups.
9. The rachis is covered with brown hairs (ramenta). Leaf trace is usually C-shaped with adaxial curvature.
10. The stele shows a wide variety of types e.g., protostele, dictyostele, solenostele or poly cyclic stele.
11. Vegetative reproduction takes place by fragmentation (e.g., *Adiantum*, *Pteridium*), stem tubers (e. g. *Marsilea*) adventitious buds (*Asplenium bulbiferum*).
12. The sporangia are grouped in distinct sori and arise in groups from a swollen cushion of cells called the placenta.
13. The sori are protected by true (*Marsilea*) or false (*Adiantum*, *Pteris*) indusium and develop on the margins or abaxial surface of the leaves (sporophyll) or leaflets.
14. The sporangia in most cases possess a distinct annulus and a stomium.
15. The sporangial development may be Eusporangiate type (*Ophioglossum*) or Leptosporangiate type (*Osmunda*)
16. Majority of ferns are homosporous but a few like *Salvinia*, *Azolla*, *Marsilea*, *Pilularia*, *Regnelidium* are heterosporous.
17. Sopes on germination form autotrophic prothalli (gametophyte). The development of gametophyte may be exosporic (in homosporous plants) or endosporic (in heterosporous plants).
18. The gametophytes are monoecious in homosporous types and dioecious in heterosporous types. The antheridia and archegonia are usually embedded in the gemetophytic tissue and have a structure similar to other vascular cryptogames.
19. Embryo may or may not have suspensor.

**Classification: Class Pteropsida is divided into four sub classes (Sporne1965):**

**Sub class 1. Primofilices:** This sub class is divided into two orders:

Order 1: Cladoxylales

Order 2: Coenopteridales

**Sub class 2: Eusporangiatae:** This sub class is divided into two orders:

Order1: Marattiales

Order 2: Ophioglossales

**Sub class 3: Osmundidae:** This sub class has only one order:

Order 1: Osmundales

**Sub class Leptosporangiatae:** This sub class is divided into three orders:

Order 1: Filicales

Order 2: Marsileales

Order 3: Salviniiales

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#### 4.4 SUMMARY

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The class Sphenopsida is also known as Arthrospida and Calamopsida. This class is well defined in certain morphological features. The stem is articulated with nodes and internodes and sometimes with a longitudinally ribbed surface. Heterospory possibly least developed in this group. Of the four orders of this class, Hyeniales is the most primitive as well as the simplest. The Sphenophyllales are protostelic and the leaves are megaphyllous with dichotomous venation. In the Equisetales the stem is siphonostelic and the leaves are microphyllous with single unbranched vein. The leaf in Sphenopsida is not as simple as in Lycopsidea where it is uniformly microphyllous. Though the living form of Sphenopsida (e. g., *Equisetum*) does not show secondary growth, some extinct forms (e. g. *Sphenophyllum*) possess secondary thickenings. Sporangia develop on special stalked structures known as sporangiophores. Except *Hyenia* sporangiophores form compact strobilus. The living forms are homosporous but some extinct forms (e.g. *Calamostchys*) were heterosporous. The gametophyte is green and autotrophic. It is exosporic i.e. develops outside the spore wall. Antherozoids were multiflagellate.

The class Peropsida commonly known as Ferns is an assemblage of vascular cryptogams that have established themselves most successfully to life on land. They are characterized by the presence of megaphyllous and pinnately compound leaves except *Ophioglossum* (with simple leaves). Anatomically the stem exhibits complex structure and range from a simple to highly dissected protostele, or a siphonostele or a dictyostele to poly stelic conditions. The plants are homosporous and heterosporous and spores are formed in sporangia. Sporangia develop in groups called sori on the ventral surface (*Gleichenia*) or on the margins(*Hymenophyllum*) of leaves. In some species (e.g. *Marsilea*) sporangia are borne in special structure called sporocarp. The sporangium develops either from a single initial cell (leptosporangiate) or from a group of initials (eusporangiate).The sporangium exhibits a greater range in shape, form and structure. The plasmodial fluid in sporangium of *Azolla* forms characteristic structures called massulae. The germination of spore follows a different course in the homosporous and heterosporous ferns. Generally five types of adult prothalli (cordate, filamentous, strap shaped, ribbon shaped and tuberous) have been reported in homosporous ferns. The sex organs develop on the gametophyte and are always multicellular and jacketed. The embryo has distinct root and leaf initials with poorly developed foot.

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#### 4.5 GLOSSARY

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**Abaxial:** Located on the side away from axis; e.g., lower leaf surface; contrasting with adaxial.

**Adaxial:** Located on side towards axis; e.g., upper leaf surface; contrasting with abaxial.

**Annulus:** A row or patch of partially or entirely thick walled cells of the capsule which contracts and forces the capsule to open and to discharge its spores.

**Articulate:** (a) Jointed or with a visible discontinuity or place of separation.

**Dimorphic, Dimorphism:** Occurring in two forms (two types).

**Epiphyte:** A plant growing on another plant for physical support only and not parasitic.

**Extinct:** No longer in existence; descriptive of a species for which living representatives no longer exist. Locally extinct refers to extinction in a given geographic region.

**False Indusium:** An introse, reflexed or revolute lamina margins that protects young sporangia

**Ferns:** The pteridophytes with feather like fronds

**FronD:** The photosynthetic organ of ferns usually consisting of a stipe and lamina.

**Herbaceous:** (a) Referring to the aerial shoot of a plant that does not become woody; typically dying back to the ground each year; (b) of a soft texture, as green leaves.

**Indusium:** A usually thin, often scale like, epidermal membrane subtending and/or covering the sorus that partially or fully protects the young sporangia.

**Petiole:** (= Stipe) Stalk of a leaf/frond supporting the blade.

**Pinna:** (plural pinnae, adjective pinnate) - a stalked or sessile, primary division of a compound lamina that is at least narrowed at the base.

**Pinnule:** a stalked or sessile division of a pinna that is at least narrowed at the base.

**Strobilus (plural strobili):** A compact reproductive structure borne at the tips of branches or axes consisting of a central axis bearing closely spaced, spirally arranged sporophylls or sporangiophores.

**Synangium (plural synangia):** A group of sporangia partially or entirely fused laterally, as in *Psilotum* and in members of family Marattiaceae.

**Solenostele (adjective solenostelic):** A siphonostele with only one parenchymatous gap at a single level (as seen in cross section).

**Sorus (plural sori, adjective soral):** A cluster of sporangia.

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## 4.6 SELF ASSESSMENT QUESTION

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### 4.6.1 Select the correct answer:

- Sori bearing leaflets known as:
 

(a) Prophyll	(b) Sporophyll
(c) Both	(d) Microphyll
- The development of sporangium from a group of initials is known as
 

(a) Complex	(b) Leptosporangiate
(c) Simple	(d) Eusporangiate
- In ferns spore germinate to form
 

(a) Zygospore	(b) Oospore
(c) Prothallus	(d) Embryo
- The spores with elaters are found in



- (a) *Selaginella* (b) *Rhynia*  
 (c) *Equisetum* (d) *Lycopodium*
5. The common name of *Equisetum* is  
 (a) Club moss (b) Water fern  
 (c) Quillwort (d) Horsetail
6. Dimorphic secondary wood is a characteristics feature of  
 (a) *Sphenophyllum* (b) *Hyenia*  
 (c) *Equisetum* (d) *Calamites*
7. *Eviostachia* is a name given to  
 (a) Stem (b) Root  
 (c) Reproductive organ (d) Leaf
8. Carinal canals are formed due to disintegration of  
 (a) Phloem (b) Protoxylem  
 (c) Metaxylem (d) Cambium
9. *Hyenia* is a member of class  
 (a) Psilopsida (b) Lycopsida  
 (c) Sphenopsida (d) Pteropsida
10. Heteromorphic leaves are present in  
 (a) *Hyenia* (b) *Sphenophyllum*  
 (c) *Equisetum* (d) *Lycopodium*

#### 4.6.2 Fill in the blanks:

- The cavities present in the cortex of *Equisetum* are known as \_\_\_\_\_ .
- The *Equisetum* is characterized by the presence of \_\_\_\_\_ in spore.
- \_\_\_\_\_ is characteristic feature of ferns young leaves.
- The group of sporangia is known as \_\_\_\_\_.
- A special outgrowth protecting sorus in ferns is known as \_\_\_\_\_.
- Hyenia* is a member of order \_\_\_\_\_ and family \_\_\_\_\_ .
- Bowmanites* is a cone associated with \_\_\_\_\_ .
- Recurved sporangia is a characteristic feature of \_\_\_\_\_.
- Presence of triarch and exarch xylem in stem of *Sphenophyllum* is characteristic feature of \_\_\_\_\_.
- Green spores are present in \_\_\_\_\_ .

**Answer Keys-4.6.1:** 1-(b),2-(d),3-(c),4-(c),5-(d),6-(a),7-(c),8-(b),9-(c),10-(b)

**Answer Keys-4.6.2:** 1.Vellicular canals, 2.elaters, 3.circinate venation, 4.sori, 5. annulus, 6.sphenopsida, hyniaceae, 7.Sphenophyllum, 8. Hyenia, 9.root, 10.*Equisetum*

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## 4.8 SUGGESTED READINGS

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- College Botany Volume II By H.C. Gangulee and A.K. Kar. New Central Book Agency 8/1 Chintamani Das Lane, Calcutta 9, India.
- Botany for degree student Pteridophyta by P.C. Vashishta, A.K. Sinha and A. Kumar. S. Chand and Company Private Ltd. Ram Nagar, New Delhi
- The morphology of Pteridophytes (The structure of ferns and allied plants). By K.R. Sporne. Hutchinson and Company Ltd. 178-202 Great Portland Street, London

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## 4.9 TERMINAL QUESTIONS

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Q1- Explain the following:

- (a) Dimorphic wood  
(c) Prothallus
- (b) Sorus  
(d) Antherozoid
- Q2. Describe the following:  
(a) Morphology of *Hyenia*  
(b) Range of stele in Pteropsida
- Q3. Define the following:  
(a) Sporophyll  
(c) Gametophyte  
(e) Heterosporous  
(b) Annulus  
(d) Elater  
(f) Megaspore
- Q4. Differentiate between:  
(a) Sphenopsida and Pteropsida  
(b) Abaxial and Adaxial  
(c) True Indusium and False indusium  
(d) Root and stem of *Sphenophyllum*
- Q5. Write short notes on:  
(a) *Hyenia*  
(c) Leaf of *Sphenophyllum*  
(b) Adoptative characters of *Equisetum*  
(d) Gametophyte of *Equisetum*
- Q6. Draw well labeled diagram to illustrate the structure of following:  
(a) T.S. of *Sphenophyllum* stem  
(b) L.S. of *Equisetum* strobilus  
(c) Sporangiohores of *Hyenia*  
(d) *Eviostachia*
- Q7. Describe salient features of class Pteropsida and differentiate it from class Sphenopsida.
- Q8. Describe the internal structure of internode of *Equisetum* stem with the help of suitable diagram.
- Q9. Describe fructifications associated with *Sphenophyllum*.
- Q10. Describe classification of class Pteropsida.

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**UNIT-5-EUSPORANGIATAE AND LEPTOSPORANGIATAE**

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- 5.1 Objectives
- 5.2 Introduction
- 5.3 Eusporangiatae
  - 5.3.1 Ophioglossales
  - 5.3.2 Marattiales
- 5.4 Protoleptosporangiatae
  - 5.4.1 *Osmunda*,
  - 5.4.2 *Leptopteris*
- 5.5 Leptosporangiatae
  - 5.5.1 Filicales-*Hymenophyllum*, *Adiantum* and *Dryopteris*
  - 5.5.2 Marsileales-*Marsilea*
  - 5.5.3 Salviniales-*Salvinia* and *Azolla*
- 5.6 Summary
- 5.7 Glossary
- 5.8 Self Assessment Questions
- 5.9 References
- 5.10 Suggested Readings
- 5.11 Terminal Questions

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## 5.1 OBJECTIVES

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After reading this unit student will learn about:

- Characteristics features of Ophioglossales and Marattiales.
- Morphology and anatomy of Sporophyte of *Osmunda*, *Leptopteris*, *Hymenophyllum*, *Adiantum*, *Dryopteris*, *Marsilea*, *Azolla* and *Salvinia*
- Gametophyte of *Osmunda*, *Leptopteris*, *Hymenophyllum*, *Adiantum*, *Dryopteris*, *Marsilea*, *Azolla* and *Salvinia*
- Development of sporangia, reproduction and embryology of *Osmunda*, *Leptopteris*, *Hymenophyllum*, *Adiantum*, *Dryopteris*, *Marsilea*, *Azolla* and *Salvinia*

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## 5.2 INTRODUCTION

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In the previous unit you have studied about the general characteristics of class Pteropsida. The subclass Eusporangiatae and Leptosporangiatae are distinguished from the other classes of seedless vascular plants by their possession of large leaves (megaphylls) with branched veins in lamina, in contrast to the small leaves (microphylls) of Lycopsida and Sphenopsida. A wide variety of stele types ranging from simple protostele to complicate polysteles are present in members of these sub classes. Usually the sporangia are borne either upon the margins or upon the abaxial surface of unmodified or modified leaves.

The two orders viz. Ophioglossales and Marattiales joined to constitute the group Eusporangiatae to which some authors gave the taxonomical status of a sub class (Smith 1955, Reimers 1954, Sporne 1965). Some others (Bold 1957, 1967, Parihar 1965) included these orders in class Eusporangiopsida. The Ophioglossales are represented by a few genera of living plants only, to date no fossil progenitors belonging to them are known. They constitute a well defined natural group sharply distinct from other living ferns and are characterized by the presence of fertile spikes. The order Marattiales is a small fairly uniform group of ferns represented today by six or seven genera and about 200 species. Although not conspicuous in the present day vegetation, there are a number of fossil forms dating back to the Carboniferous times which show strong similarity to the extant marattiaceous genera both with regards to anatomy and characters of the sori.

The Osmundales is treated as an order of class Pteropsida but Hirmer (1927) separated it from other ferns and created a new group Protoleptosporangiatae since they are intermediate between Eusporangiatae and Leptosporangiatae in many respects, especially in the origin of sporangia. They are terrestrial ferns with massive, hard, erect or ascending non-paleate stem. The stem shows characteristic C-shaped bundle in cross section. The sporangia are either superficial on the abaxial surface of unmodified fertile pinnules or marginal on much reduced fertile segments. The sporangia are not organized into distinct sori and there is no indusium.

The sub class Leptosporangiatae includes all the leptosporangiate ferns (sporangia develop from a single superficial cell). They grow luxuriantly in the tropical rain forests and also

present in temperate part of the world. Majority of them are perennials and only few are annuals. They range in size from extremely small forms like *Anogramma leptophylla* (4 to 5 cm in height) to huge tree-like forms like *Cyathea*. The wall of sporangia is one cell in thickness and encloses a definite number of spores. The antheridia are small and more or less project above the surface of prothallus. The leaf is usually circinate in buds. This is the largest sub class of class Pteropsida and contained great majority of ferns whose delimitation and classification is very difficult.

This unit describes characteristics features of sub classes of class Pteropsida and important genera of these sub classes.

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### 5.3 *EUSPORANGIATAE*

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This subclass includes ferns having eusporangiate type of sporangial development and divided into two orders Viz. Ophioglossales and Marattiales.

#### 5.3.1 *Ophioglossales*

This group is represented by a few genera of living plants only; to date no fossil progenitors surely belonging to this order are known. This order has a single family Ophioglossaceae which includes three genera of living plants viz.: *Ophioglossum*, *Botrychium*, and *Helminthostachys*

**Distribution and Habitat:** This group of plants, completely without any early fossil record, is represented by about eighty species, belonging to three genera. *Botrychium* (thirty-five species) is cosmopolitan in distribution and *Ophioglossum* (forty-five species) is nearly so, but *Helminthostachys* (monotypic) is restricted to Indo-Malaysia and Polynesia. Two species are fairly common in the British Isles, *Botrychium iwiiaria*, 'Moon- wort' which grows in dry grassland and on rocky ledges, and *Ophioglossum vulgatum*, 'Adder's Tongue' in damp grassland, fens and dune-slacks, while a third species, *O. lusitanicum*, is restricted to grassy Off tops in the Channel Islands and the Scilly Isles.

#### **Sporophyte**

**External features:** The sporophyte is differentiated into a subterranean rhizome with roots and spirally arranged leaves bearing sporangiferous spike. Where the stem is erect, the leaves arise in a spiral sequence, but in temperate regions it is normal for only one leaf to be produced each year (Fig.5.1). In *Helminthostachys*, the leaves are borne in two ranks along the rhizome; they are large and alternately compound (Fig.5.2), but in the other two genera they are usually much smaller. In *Botrychium* leaves are pinnately compound (Fig.5.3) and in *Ophioglossum* are simple or lobed. At the base of the petiole there is a pair of thin stipules which enclose the apical bud; and, when leaf begins to grow, it breaks its way through the thin sheath covering it. Unlike all other living ferns their leaves are not circinately coiled

when young. In all three genera, the fertile fronds have two distinct parts, the fertile part being in the form of a spike which arises at the junction of the petiole with the sterile lamina, on its adaxial side. The roots are peculiar in being completely without root hairs, a feature which is possibly connected with their mycorrhizal habit.

## Anatomy

**Rhizome:** The stem of the young sporeling is protostelic, but soon becomes medullated. Later on the stem of *Botrychium* becomes solenoxyllic, i.e. there are leaf gaps in the xylem, but not in the single external endodermis (Fig.5.3 C). *Botrychium* is the only genus of living ferns to show secondary cambial activity, and in some species it may give rise to a considerable thickness of secondary wood, composed of tracheids and wood-rays. Rhizomes of *Helminthostachys* pass through much the same stages of stellar organization, but the largest specimens go one stage further and achieve true solenostely, with an internal as well as an external endodermis (Fig.5.2B).

*Ophioglossum* varies considerably in its anatomy, according to species. Some possess an outer endodermis, but in most species it is absent, even at the young stage. The leaf gaps in the xylem overlap one another, giving rise to a network of meristemes, which form a rudimentary kind of dictyostele (Fig.5.4). The xylem is endarch in *Botrychium* and *Ophioglossum*, but mesarch in *Helminthostachys*.

**Leaf:** Majority of the temperate species produce only one leaf each year, but several tropical species are known to produce up to five leaves in a year. Each leaf has a thin stipule at its base and is differentiated into petiole and a lamina (Fig.5.5A). A T.S. of the petiole shows an epidermis, ground tissue and a number of vascular bundles (Fig.5.5A). A single leaf trace arises at the base of the petiole which divides into two strands and enters the leaf. In some species (*O. palmatum*) each leaf gap is associated with two leaf traces. The epidermis is composed of single layer moderately thick-walled cells. Stomata are absent in the epidermis. The ground tissue is made up of thin-walled spongy parenchymatous cells. The basal part of the petiole shows a single median vascular bundle, but there are many bundles in the upper part of the petiole. The vascular bundles are collateral and arranged in C-shaped arc with xylem facing the adaxial side (Fig.5.5A). Bundle sheath is absent. Some of the bundles enter the lamina and others supply the fertile spike.

The T.S. of the lamina shows an upper and lower epidermis (Fig.5.5 B). Both the epidermises are single-layered and interrupted by the presence of stomata (amphistomatic). The mesophyll is not differentiated into spongy and palisade parenchyma. Large numbers of intercellular space occur between these cells. Vascular bundles are collateral and endarch and surrounded by a distinct bundle sheath.

**Root:** Roots are often branched, heavily infested by mycorrhizal fungi. Roots are perennial and devoid of root hairs. The T.S. of root shows a single-layered epidermis, a massive cortex and a broad central stele (Fig. 5.6). The outer cortex contains endophytic mycorrhiza. Stele may be monarch or diarch or triarch or tetrarch or even pentarch.

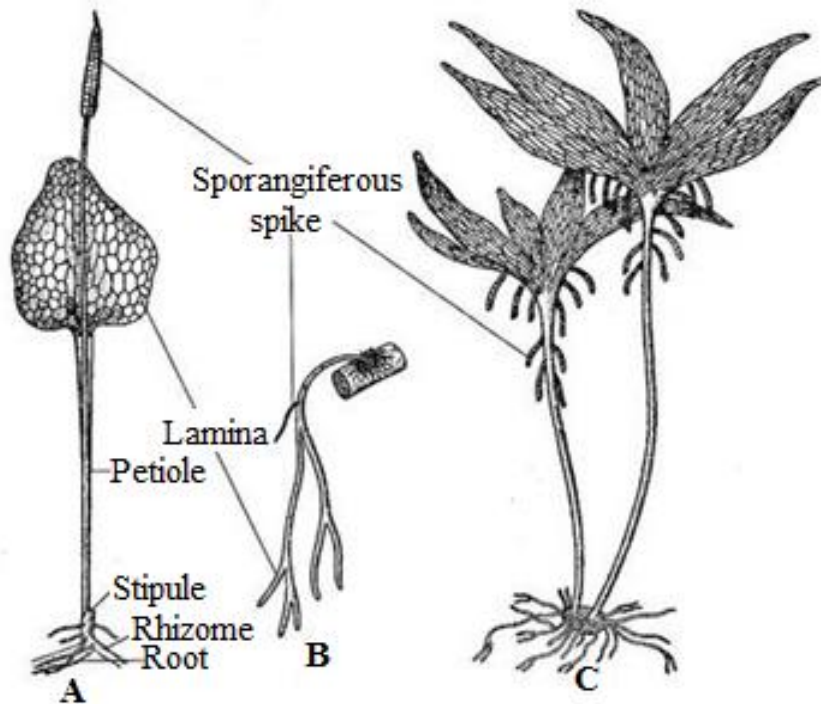


Fig. 5.1: *Ophioglossum*: Habit of sporophyte. A. *O. vulgatum*, B. *O. pendulum*, C. *O. palmatum*

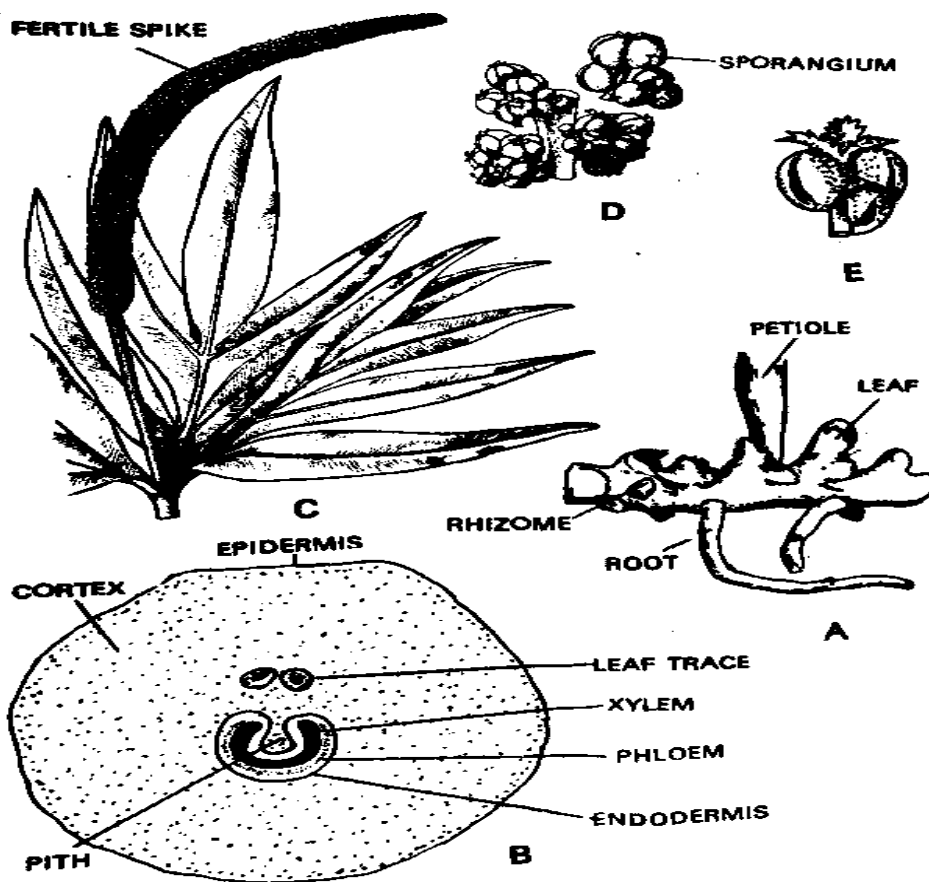


Fig. 5.2: *Helminthostachys*. A. Rhizome; B. T.S. of rhizome; C. Top of the leaf showing sterile and fertile region; D. Part of fertile spike ;E. Branch of fertile spike with a group of sporangia



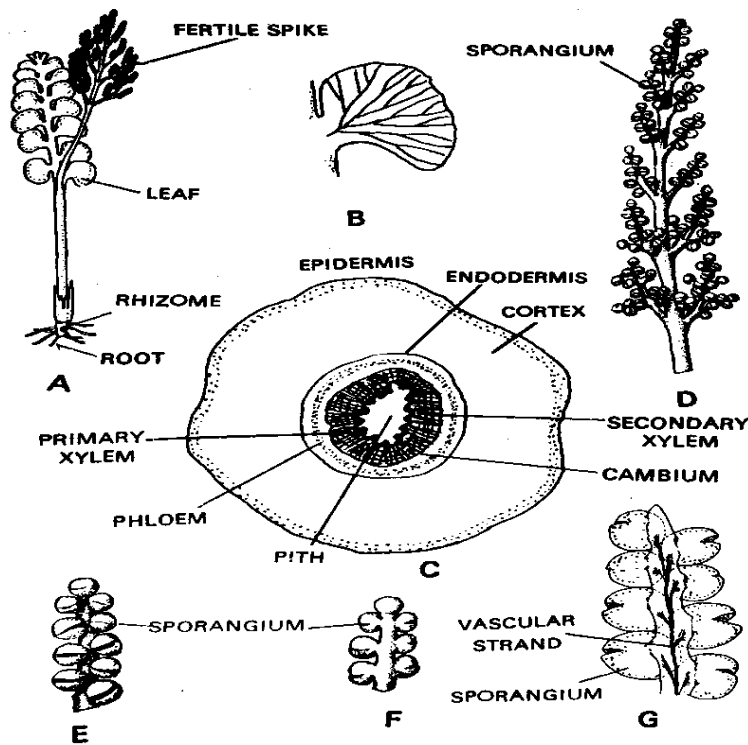


Fig. 5.3: *Botrychium*: A. Sporophyte; B. A pinna showing venation; C. T.S. of Rhizome; D. Fertile spike; E-F. Portion of spike from dorsal and ventral side; G. Portion of spike showing vascular supply to sporangia.

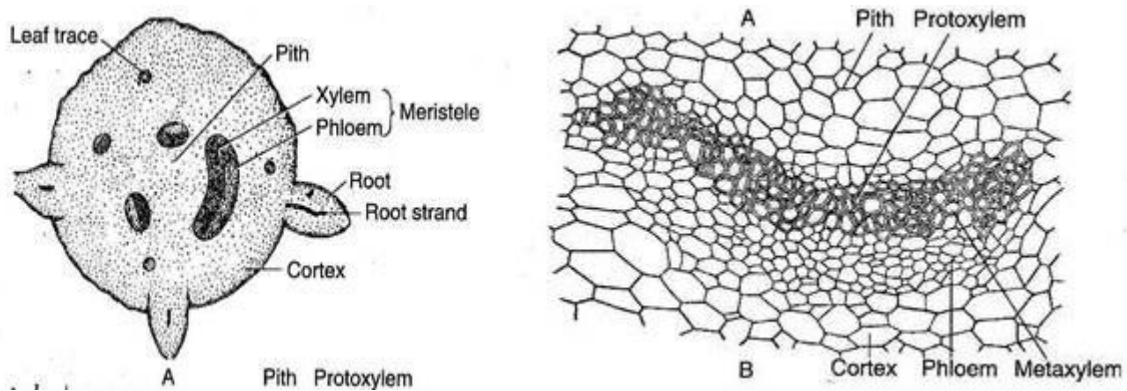


Fig.5.4: *Ophioglossum*: A. T.S. of rhizome; B. A meristele enlarged

## Reproduction

Majority of *Ophioglossum* species reproduces by means of spores. Spores are of same size and shape i.e., homosporous. However, some species e.g., *O. pendulum*, *O. vulgatum*, *O. reticulatum*, *O. nudicaule* and *O. aitchisonii* reproduce vegetatively by means of adventitious buds formed on roots.

**Spore producing organ:** The spores are present in sporangia. The sporangia in all three genera are 'marginal' in position. In *Botrychium*, they are borne in two rows along the ultimate pinnules of the fertile spike (Fig. 5.7) and each receives its own separate vascular

supply from a vein running into the pinnule (Fig.5.7B). In *Helminthostachys*, the axis of the fertile spike bears numerous 'sporangiohores' in several rows, each bearing several sporangia and a few tiny green lobes at the tip (5.2 D). The spike is a simple, somewhat cylindrical and stalked structure (Fig. 5.7A). 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. A number of vascular strands run longitudinally along the axis and from these strands many lateral branches develop which lead to the sporangia (Fig. 5.7B, 5.3G).

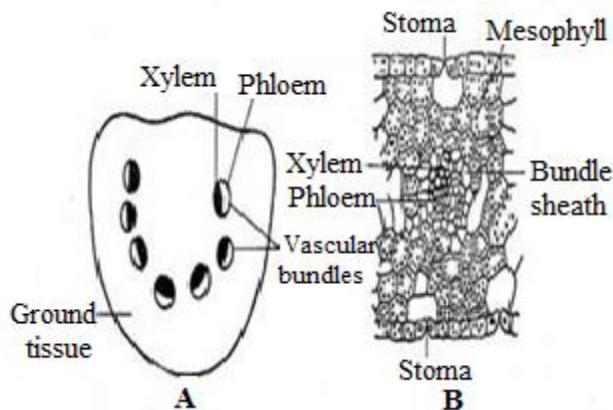


Fig.5.5: *Ophioglossum vulgatum*.  
(A). T.S. of petiole; (B).T.S. of a part of lamina

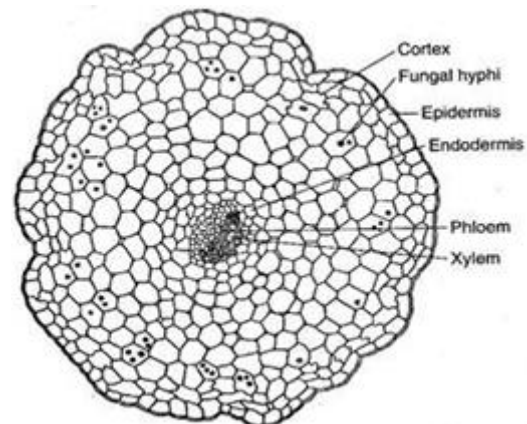


Fig.5.6: *Ophioglossum vulgatum*.  
T.S. of root.

**Structure of the Sporangium:** The development of sporangium in *Ophioglossum* is of eusporangiate type, a single initial cell undergoes a periclinal division, the inner half giving rise ultimately to the archesporial tissue, while the outer half forms part of the sporangium wall. 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 sporangiogenic band (Fig. 5.7C); the hypodermal cells of each band now differentiate into alternate groups of fertile (archesporial) and sterile cells (Fig. 5.7D). The archesporial cells mature into sporogenous cells, thus representing a future sporangium. Adjacent cells contribute further to the wall, which is very massive and several cells thick at maturity. A tapetum of several layers of cells is formed from the inner regions of the sporangium wall, which breakdown to form a continuous plasmodium in which the spores develop (fig. 5.7 E). The sporangia have no specialised dehiscence mechanism. The annulus, a characteristic structure of other fern sporangia is absent in Ophioglossales. Dehiscence of the sporangium is transverse in *Botrychium* and *Ophioglossum* (Fig 5.7 B), but longitudinal in *Helminthostachys*, and large numbers of spores are released (more than 2,000 in *Botrychium* and as many as 15,000 in *Ophioglossum*).

## Gametophyte

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

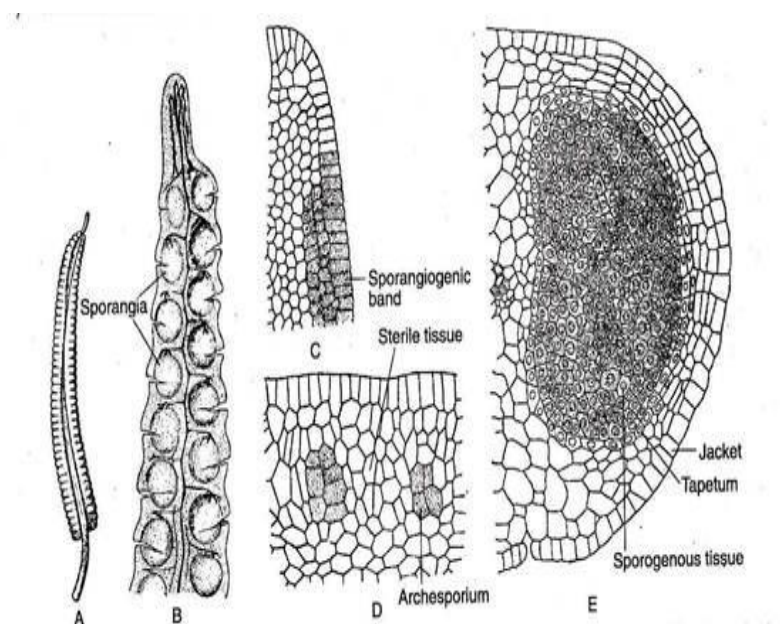


Fig. 5.7: *Ophioglossum*: A- A sporangiferous spike; B. A mature spike showing dehiscence; C-D. Sporangial development. E. A mature sporangium.

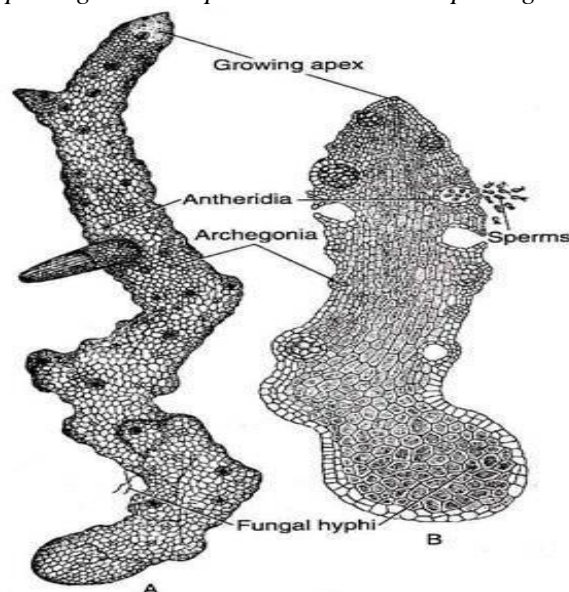


Fig. 5.8: A. Gametophyte surface view B. L.S. of gametophyte

**Development of Gametophyte:** The spores, on germination, produce a subterranean gametophyte (Fig. 5.8 A, 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 into a 3-celled stage. Further development only proceeds if it gets infected with mycorrhizal fungi. Indeed, the presence of the appropriate fungus is essential for the growth of the prothallus beyond the first few cell divisions. In most cases the prothallus is deeply buried in the soil and lacks chlorophyll, but cases have been reported of superficial prothalli, in which some chlorophyll was present. Some have abundant rhizoids, but others are completely without them. The prothallus of *Botrychium virginianum* (Fig.5.8) is a flattened

tuberous body, upto 2cm long. The prothallus of *Ophioglossum vulgatum* differ being cylindrical, and may be as much as 6 cm long (Fig. 5.8 A). Frequently, there is an enlarged bulbous base, in which the bulk of the mycorrhizal fungus is located (5. 8 B).

**Sex Organs:** The gametophytic prothallus 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. Antheridia appear first and are deeply sunken.

**(i) Antheridia:** The antheridium develops from a single superficial cell of the derivatives of apical meristem called antheridial initial (Fig. 5.9 A-F).

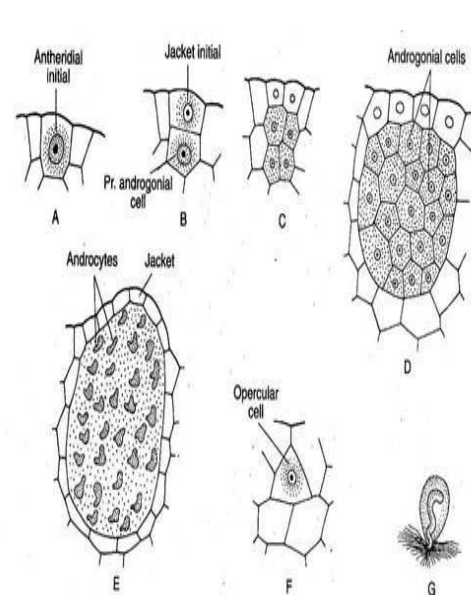


Fig. 5.9. The stages in the development of antheridium

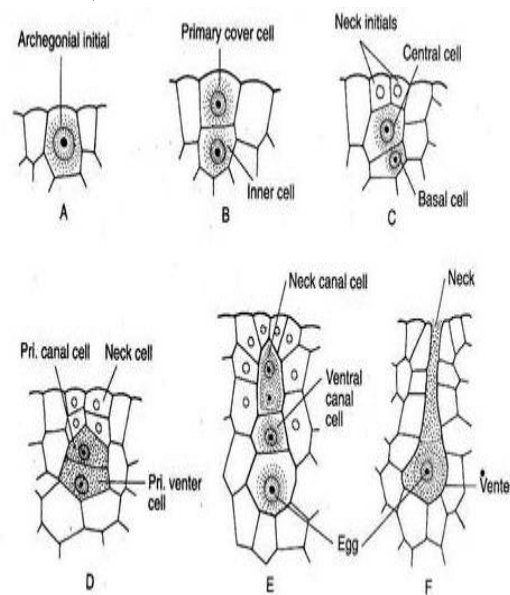


Fig. 5.10. The stages in the development of archegonium

**(ii) Archegonia:** The archegonium is also initiated in the derivatives of apical meristem (Fig. 5.10 A-E).

**Embryogeny:** The first division of the zygote is in a plane at right angles to the archegonial axis. In *Helminthostachys*, the outer (epibasal) hemisphere undergoes a second division, so as to produce a suspensor of two cells, while the hypobasal hemisphere gives rise to a foot, a root and, later, the stem apex. The embryo is thus, endoscopic, but during its further development its axis becomes bent round through two right angles, so as to allow the stem to grow vertically upwards. The embryo of some species of *Botrychium* is likewise endoscopic and has a small suspensor, but in others including *B. lunaria*, there is no suspensor and the embryo is exoscopic, and this is true of all species of *Ophioglossum*. A vertical cell division of the apical and the basal cells results in the formation of four cells, the quadrant stage of embryogeny. Subsequent cell divisions are irregular and indefinite. In all cases there is considerable delay in the formation of the stem apex, and in some species it may be several years before the first leaf appears above the ground, by which time many roots may have been formed. These long delays suggest that the mycorrhizal association is an

important factor in relation to the nutrition, not only of the prothallus, but also of the young sporophyte.

### 5.3.2-Marattiales

The Marattiales is a small, fairly uniform group of ferns represented today by six to seven genera and about 200 species. Sporne (1965) recognized nine genera grouped in five families. Family Asterothecaceae includes fossil genera only.

**Distribution and Habitat:** The Marattiales are represented at the present day by about 200 species, placed in six (or seven) genera, most of which are confined to the tropics. *Angiopteris* (100 species) is a genus of the Old World, extending to Madagascar, while *Danaea* (thirty-two species) is confined to the New World. *Marattia* (sixty species) is pan-tropical and extends as far south as New Zealand. *Christensenia* {=*Kaulfussia*} is monotypic and is confined to Indo- Malayan region. *A. evecta* is a common species found in India

### Sporophyte

**Morphology:** Most species have massive erect axes, but they never attain the dimensions of the fossil *Psaronius*. The largest, although reaching a diameter of 1 m, seldom exceeds this in height. *Christensenia* and some species of *Danaea*, however, have creeping horizontal axes. The fronds of some species are larger than in any other living ferns and may be as much as 6m long, with petioles 6cm in diameter. They may be as much as five times pinnately compound or, in some species, only once pinnate, like a Cycad leaf, while a few species have a simple broad lamina. In *Angiopteris* plant body consist of an upright, tuberous, conical, fleshy, rhizomatous stem. The stem is quite thick and resembles a tree fern and bears a crown of graceful, stately leaves (Fig. 5.11 A). *Christensenia* is peculiar in having a palmately compound frond, as the specific name, *C. aesculifolia*, implies. It is also peculiar having reticulate venation, for all the other genera have open dichotomous venation. With the exception of *Danaeatric homanoides*, all the living members of the group have very leathery pinnules in whose ontogeny several rows of marginal initials are active (instead of a single row of marginal initial cells, as is more usual in leaves of other plants). In all species there are thick fleshy stipular flanges at the base of the petiole (Fig. 5.11B, C). After the frond has died and has been shed, the stipules and the leaf base remain attached to the axis and contribute much to its overall diameter.

### Anatomy

**Rhizome/Stem:** A transverse section of the stem of *Angiopteris* (Fig.5.12 b) shows an outer epidermis, a broad cortex and a central region of vasculature. The cortex is parenchymatous and mucilage ducts are seen. A number of concentric rings of meristemes which, in a dissection are seen to be part of a series of complex and irregular mesh works lying one within the other, yet interconnected by 'reparatory strands'. The whole system may be described as a highly dissected poly- cyclic dictyostele. Although each meristeme in the sporeling is surrounded by an endodermis, in the adult state the endodermis is completely

lacking. In *Marattia* stem outermost layer is a distinct epidermal layer whose cells are thick-walled in mature rhizomes. The entire cortex is parenchymatous. A ring of mucilage canals and tannin filled cells is present in the outer layers of the cortex (Fig 5.12 a). The stellar organisation in the younger or earlier formed portions of the rhizome is protostelic. The protostele becomes medullated and later at a level where the third or fourth leaf arises, the medullated protostele or the uninterrupted siphonostele becomes interrupted by the departure of a leaf trace that leaves a gap. A characteristic feature of the stellar organisation of Maratiaceae is presence of a central commissural strand in the stem. This strand traverses across the pith at a level where the protostele changes to a siphonostele. In the older rhizomes of *Marattia* the central commissural strand breaks up into a number of separate strands in the center of the stem. These strands appear as a ring of vascular bundles internal to the siphonostele of the rhizome. The siphonostele becomes broken up into a number of separate strands in older portions of the rhizome. This is due to the appearance of overlapping leaf gaps left by the departing leaf traces. So in the older portions of the stem, the vasculature becomes a dictyostele (Fig. 5.12 C).

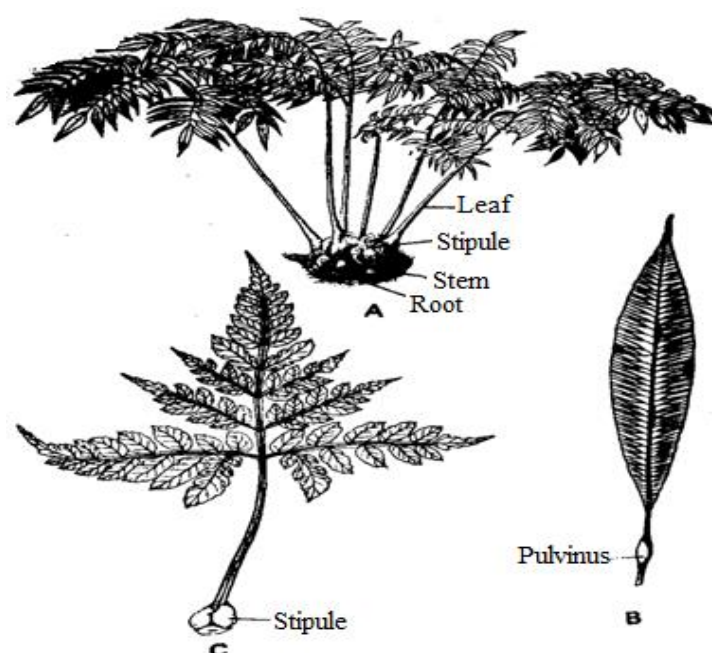


Fig. 5.11: *Angiopteris erecta*: A. Sporophyte; B. Pinna showing pulvinus at the base; C. *Marattia alata* Leaf

Each leaf, in a mature plant, receives a number of traces which arise from the outermost system of meristeles, but the root traces may arise from the innermost regions of the stele, threading their way through successive cones on their way to the cortex (cross-hatch). Species with erect axes, the roots may emerge from the cortex some distance above the ground, so forming prop- roots (Fig.5.12a).

**Petiole:** In *Angiopteris* petiole shows much the same structure as in the stem. There is palisade parenchyma below the upper epidermis and a loose spongy parenchyma above the lower epidermis. The leaf trace may be C-shaped. In *Marattia* distinct collenchymatous

hypodermis is present below the epidermis (Fig 5.13 A). There are two or more concentric circles of vascular bundles. Endodermal boundaries are lacking around the meristeleles.

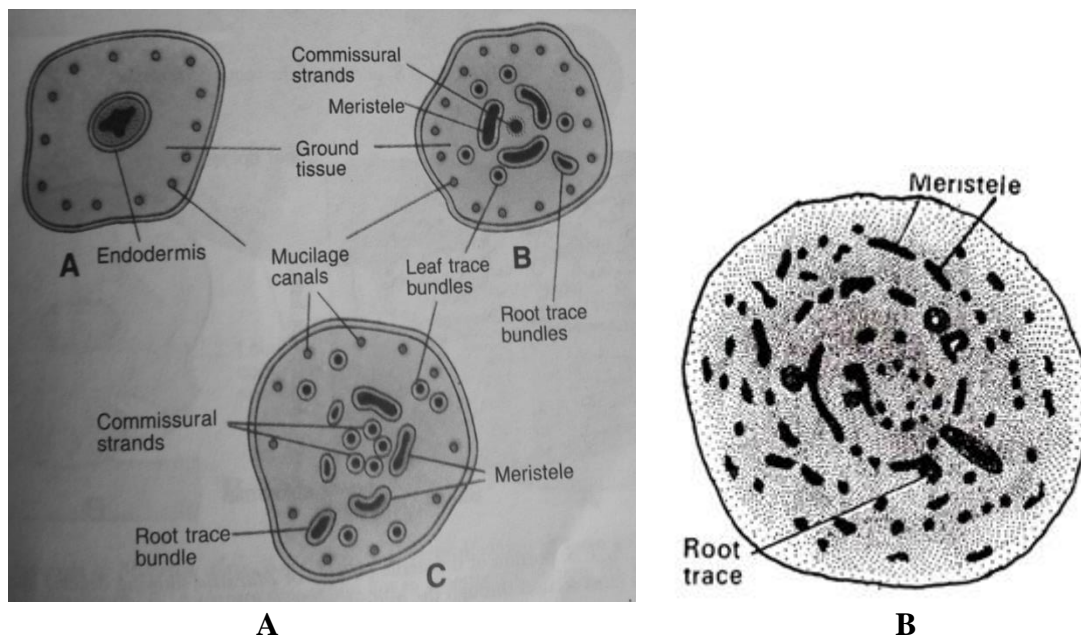


Fig.5.12: T.S. rhizome/stem a. *Marrattia* stem; b. *Angiopteris* stem

**Root:** In *Marattia* the roots have a many layered and parenchymatous cortex. The cortex contains numbers mucilage canals. An endophytic fungus has been reported in the younger roots. It is absent in the older roots. The stele consists of up to twelve xylem bundles alternating with the same number of phloem bundles. Tanin cells are also present in the parenchymatous bands that separate the system bands. The xylem is exarch (Fig.5.14 A). In *Angiopteris* the cortex has parenchyma as well as sclerenchyma. Stele is an exarch, polyarchactinostele (Fig. 5.14 B).

## Reproduction

Sporophyte reproduces vegetatively as well as by spore production. Dormant buds are formed on the rhizome whereas the stipules join the petiole. When the stipules are ultimately shed from the plant, the bud develop into new individuals.

**Spore producing organs:** In all genera, the sori are borne in a superficial manner, i.e. on the dorsal surface of the lamina, and beneath a vein or a veinlet. *Christensenia* has circular sori irregularly distributed between the main veins (Fig.5.15) but, in all other genera, the sorus is more or less elongated beneath a lateral vein. In *Angiopteris* the sporangia are free from each other and arranged in two linear rows (Fig. 5.15 F), but in *Marattia*, *Danaea* and *Christensenia* they are fused into a synangium (Figs. 5.15 and 5.16). *Danaea* is peculiar in having fleshy flanges of tissue projecting between the adjacent synangia (or, according to some, in having the synangia sunken into a very fleshy pinnule) (Fig. 5.16).

The first stage in the development of a sporangium is a periclinal division of a single epidermal cell, of which the inner half gives rise ultimately to the archesporial tissue, while

the outer half gives rise to part of the sporangium wall, the rest of the wall being produced by the activity of adjacent cells. At maturity, the sporangium wall is many cells thick and the tapetum formed from the innermost wall cells. The occurrence of numerous stomata in the sporangium wall is an important feature.

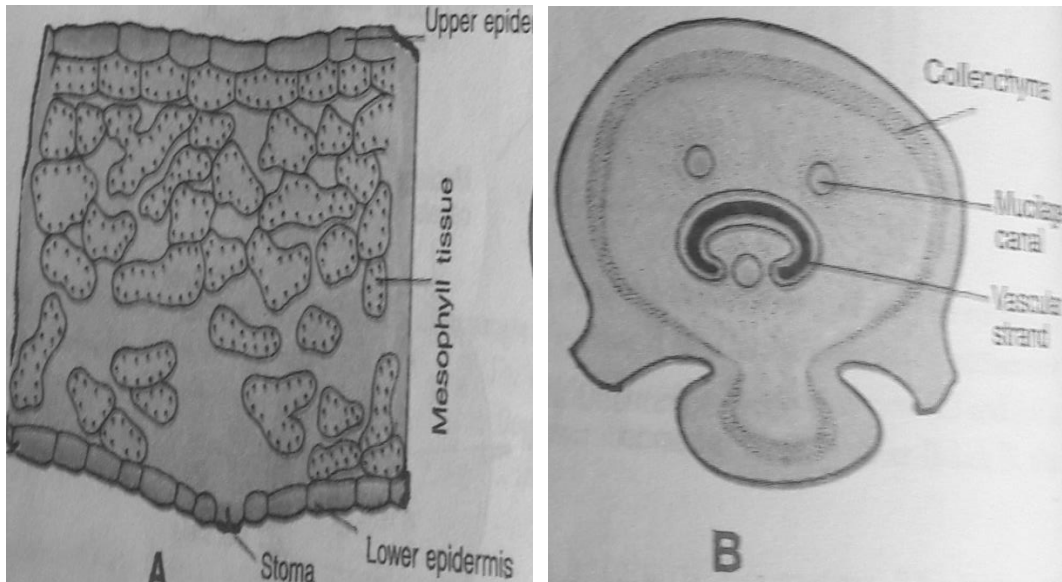


Fig. 5.13. *Marattia*: A. T. S. portion of a sterile pinnule; B. Cross section through mid-rib region of pinnule

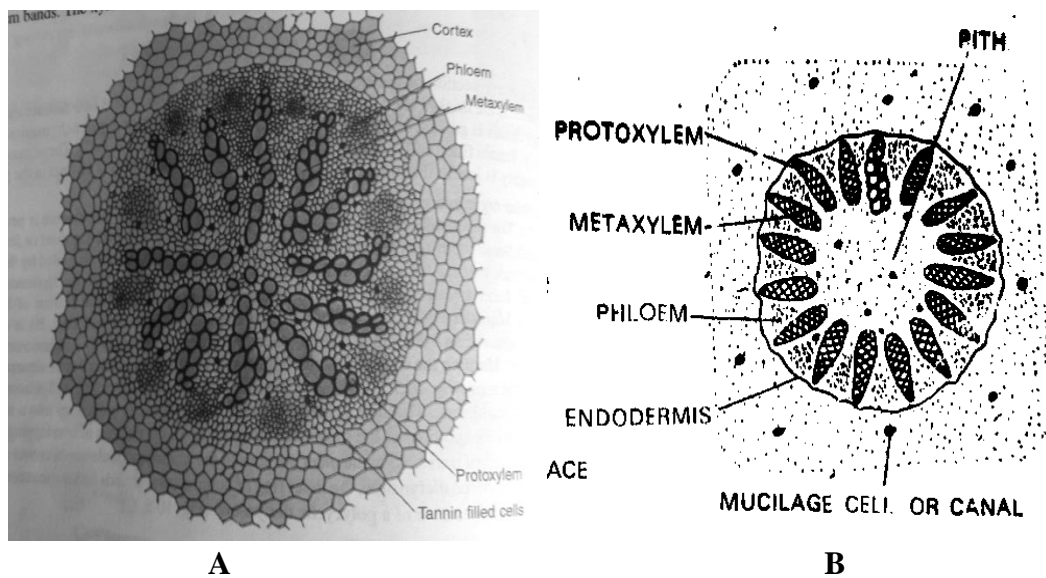


Fig. 5.14: T.S portion of the root A. *Marattia*; B. *Angiopteris*

**Gametophyte:**

Germination of the spores is rapid, occurring within a few days of being shed, and they develop directly into a massive dark green thalloid prothallus, which is mycorrhizal and is capable of living for several years. An old prothallus may be several centimeter long and may resemble closely a large thalloid liverwort (Fig. 5.17).The prothallus is monoecious but,



while the antheridia occur on both the upper and lower surfaces, the archegonia are confined to the lower surface only, where they occur on the central cushion along with rhizoids. Both types of gametangia are sunken beneath the surface of the prothallus and the antheridium is large and massive. The archegonium (Fig. 5.17 J) has a large ventral canal cell (except in *Danaea*) and a neck canal cell with two nuclei. The antherozoids are coiled and multiflagellate, as in other ferns (5.17 L). The structure and development of antheridium (Fig. 5.18 I) and archegonium (Fig. 5.18 II) are similar to that of *Ophioglossum*. In *Marattia* the ventral canal cell is distinct and not transitory as in *Ophioglossum*. Interesting feature rarely found else where and presumably associated with its massive structure.

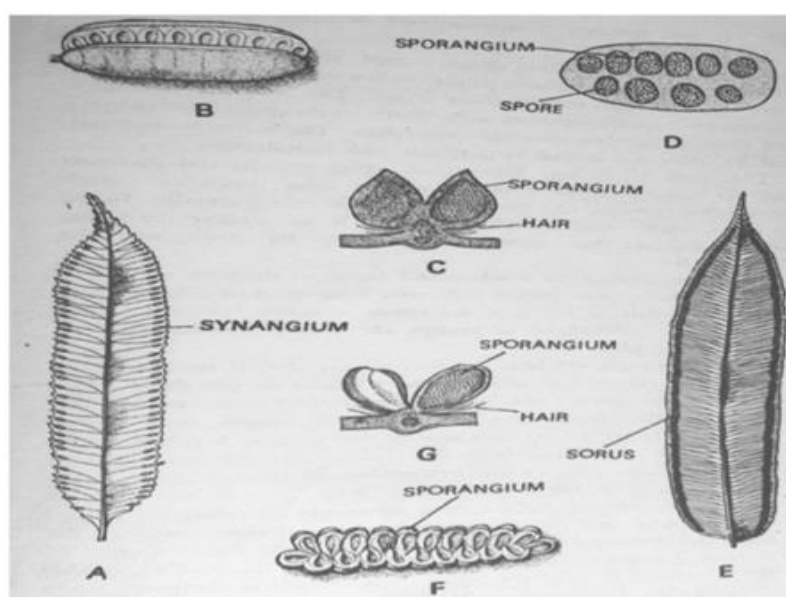


Fig. 5.15 A-D. *Marattia*. A. Fertile pinna; B. Synangium; C. T.S. of synangium; D. L.S. of synangium. E-G. *Angiopteris* E. Abaxial view of fertile pinna; F. Sorus; G. T.S. of sorus

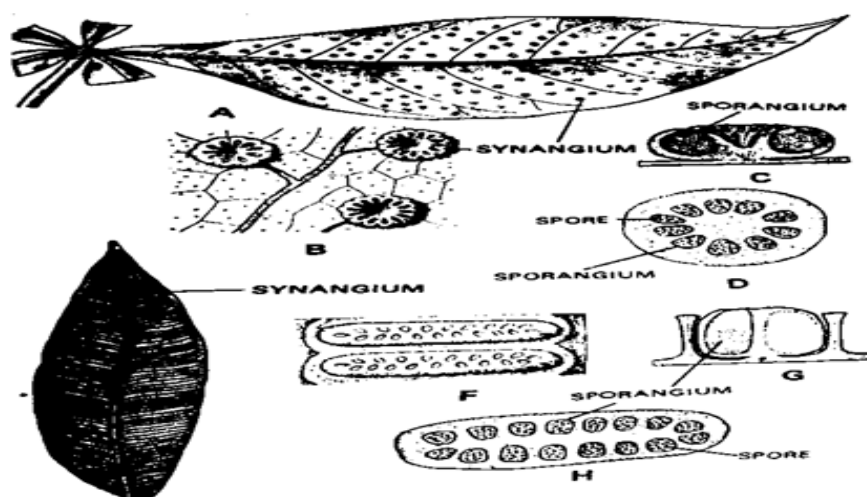


Fig. 5.16.A-D: *Christensenia*. A. Leaf with one pinna intact and other cut; B. Surface view of pinna showing three synangium; C. Cross section of synangium; D. Horizontal section of synangium. E-H. *Danaea*. E. fertile pinna; F. Surface view of two sporangia; G. Cross section of synangium; H. L.S. of synangium

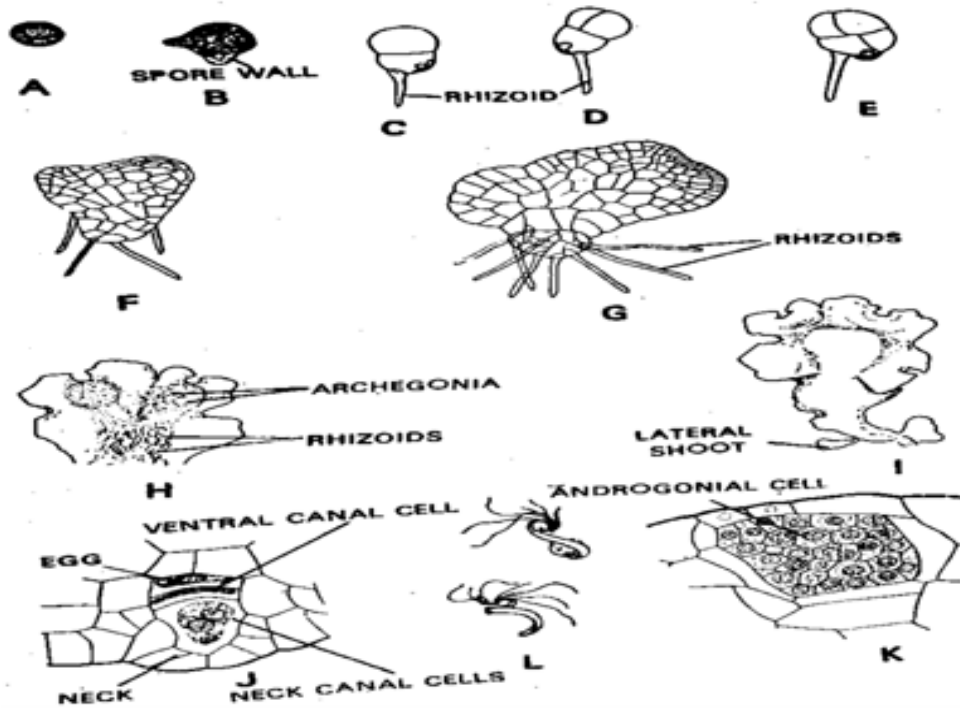


Fig.5.17: *Angiopteris*. A-G Stages in the development of the gametophyte. H-L *Marattia*. H-I. Mature prothallus; J. Mature archegonium; K. Mature antheridium; L. Antherozoids

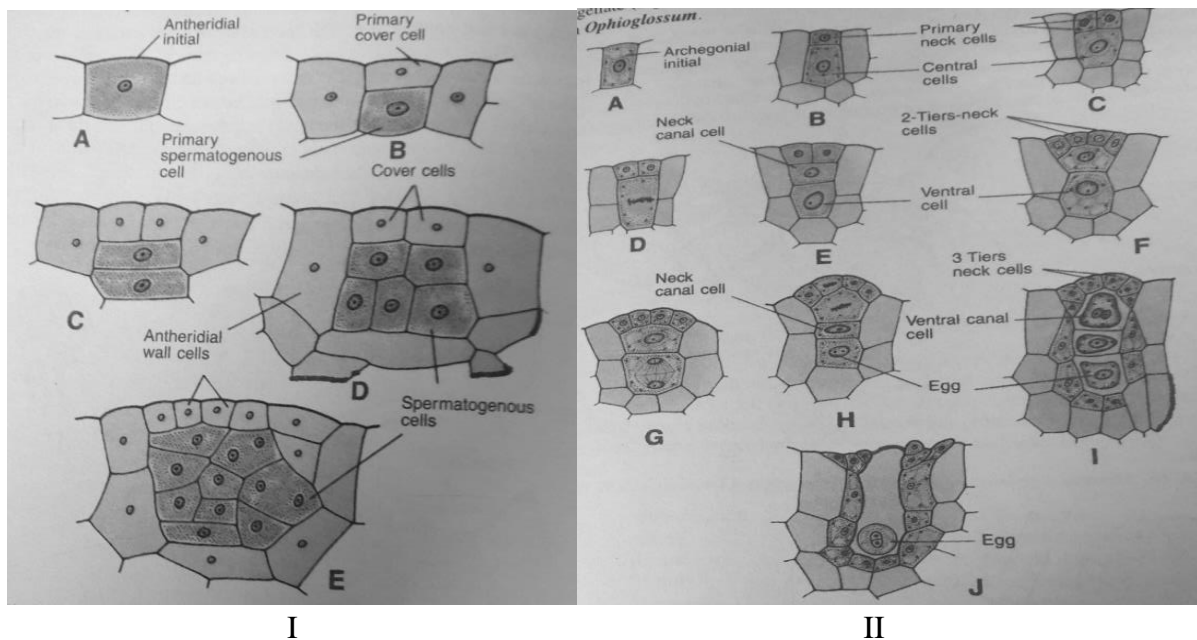


Fig.5. 18. *Marattia*: I. Various stages in the development of antheridium; II. Various stages in the development of archegonium

**Embryogeny:** The first division of the zygote is at right angles to the axis of the archegonium, and the embryo is endoscopic. Thus, since the archegonial neck is directed downwards, the embryo is orientated with its shoot uppermost and, as it grows upwards, it bursts its way through the tissues of the prothallus. A minute suspensor is present in *Danaea* and in some species of *Angiopteris*, but *Marattia*, *Christensenia* and most species of

*Angiopteris* are completely without a suspensor. This lack of constancy is paralleled in the Ophioglossales and has led to speculation as to its phylogenetic implications. A suspensor is generally held to be a primitive character and its presence even if not universal in the Eusporangiatae, places them at a lower level of evolution than the remaining ferns, from which it is completely absent.

The epibasal hemisphere gives rise to the shoot apex (x) and the first leaf, but there is no regular pattern of cell divisions and the hypobasal regions gives rise to a poorly developed foot and, somewhat later, to the first root (Fig. 5.19 F).

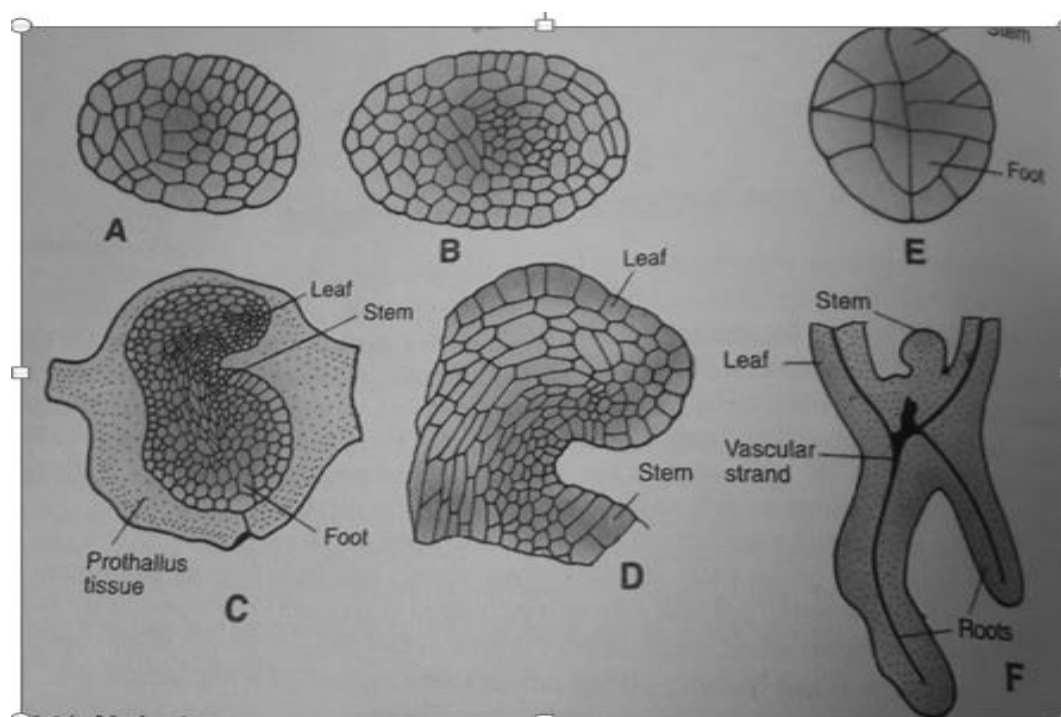


Fig.5.19. *Marattia*. A-E. Stages in the development of embryo; F. Young sporophyte

## 5.4 PROTOLEPTOSPORANGIATAE

The sub class Protoleptosporangiatae is an assemblage of interesting ferns. The class includes both living and fossil members all of which are included in a single order Osmundales with the single family Osmundaceae. The modern representatives of the Osmundales occupy an isolated position among the ferns, intermediate in many respects between the Eusporangiatae and the Leptosporangiatae but not necessarily, therefore, linking the two groups phylogenetically, for they are an extremely ancient group with an almost complete fossil history extending as far back as the Permian. Those that have survived to the present day can truly be described as 'living fossils'.

### 5.4.1-*Osmunda*

**Distribution and Habit:** It is a widely distributed genus and is found in both tropical and temperate regions of the world. *Osmunda* (fourteen species) is wide- spread in both

hemispheres. Only one species, *Osmunda regalis* the 'Royal fern' is represented in the British flora. Its stems are massive and branch dichotomously to form large hummocks.

**External Features:** All the species of *Osmunda* are medium sized ferns, a few like *O. cinnamomea* achieve a height of 2-3 meters. The rhizomes are wholly subterranean and appear as short-sized, hard and stumpy structure that is sparingly branched. The branching is dichotomous. Numerous endogenously developed adventitious roots arise from the rhizome near the bases of leaves and fix it to the substratum. The leaves of *O. cinnamomea* and a few other species may reach a length of 2-3 meters. The proximal portions of the petiole in the older leaves are hard and stout, whereas in the young leaves they are herbaceous. The leaflets of the lamina are usually leathery in texture and may be entirely or variously incised. The leaves may be monomorphic (*O. regalis*, *O. claytoniana*) or dimorphic (*O. cinnamomea*, *O. japonica*). In *O. claytoniana* two types of leaves appear on the stem (Fig. 5.20 A). These are the sterile leaves which appears late in the season and the fertile leaves which appear earlier. The fertile leaves do not possess green lamina. Some of the pinnae or the pinnules are sterile and others are fertile. In such leaves there is a segregation of photosynthetic and reproductive functions in the same leaf (Fig. 5.20 B).

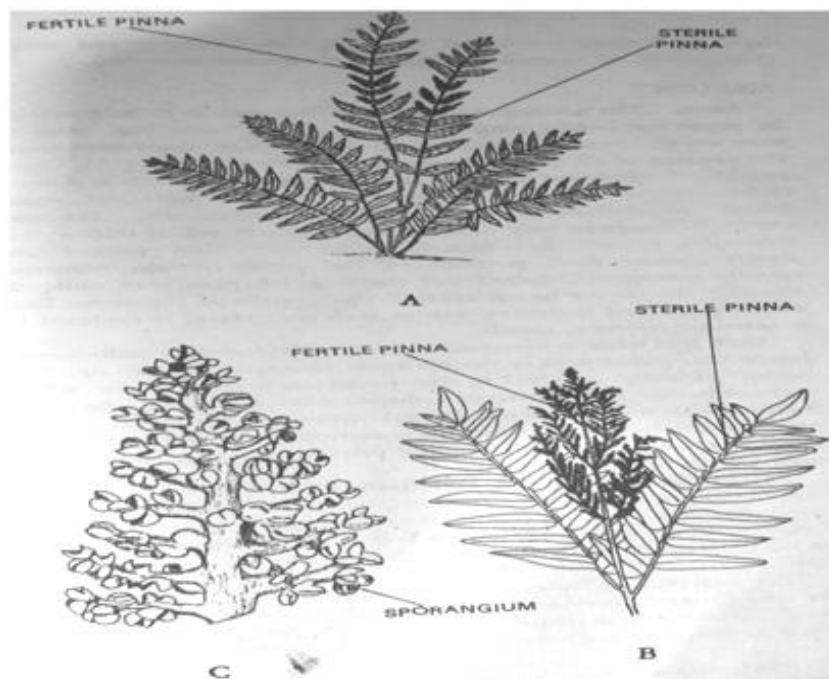


Fig.5.20: *Osmunda*- Sporophyte showing habit. A. *O. claytoniana*; B. *O. regalis*; C. *O. cinnamomea*

**Leaves:** The pinnate or bipinnate compound leaves grow in tufts from the apices of the stem branches and are 0.30 to 3 m in length. The leaf has a stout petiole with a stipule like expansion at the base covered with glandular hairs. The leaves are annular and die at the end of the season, but the leaf bases are persistent and surround the stem. The lamina is a usually leathery in texture with open-dichotomous venation. The arrangement of leaves on the stem is spiral.

## Anatomy

**Stem:** The cortex is distinguished into two well defined regions: Outer and Inner cortex (Fig. 5.21 A). The outer cortex extensive and is composed of several layers of dark brown, thick-walled sclerenchymatous cells. The boundary of the outer cortex is irregular due to the presence of the persistent leaf bases. There is no definite layer of epidermis bounding it as all the cells are sclerenchymatous. The inner cortex is comparatively narrow and composed of thin-walled colourless parenchymatous cells which are often packed with starch grains. Both the portion of cortex contains numerous spirally arranged C-shaped leaf traces which pass very obliquely through the cortex to the centrally lying stele of the stem (Fig. 5.21 B).

Each leaf trace is surrounded by a well developed endodermis followed by pericycle of two or three layers of cells. Internal to pericycle is phloem which surrounds the solid horse-shoe shaped mass of xylem with the convex side turned outside. The xylem is made up of large scalariform tracheids constituting the metaxylem and there is usually a small protruding protoxylem mass in the concave side towards the stele of stem.

Next to the inner cortex is the endodermis. The endodermal cells possess distinct casparian bands on their radial walls. Pericycle forms 2-4 layers of parenchymatous cells next to the endodermis. The stele consists of a varying number of C-shaped or horse shoe-shaped xylem bundles surrounded by a continuous ring of phloem elements. The outer cells of phloem constitute the protophloem. The phloem is composed of distinct sieve tubes with sieve plates on their lateral wall. Next to the phloem sheath is the several layered xylem sheath which is made up of parenchymatous cells.

Pith is quite conspicuous and may be entirely parenchymatous (*O. claytonian*) or a few sclerenchymatous strands may be present (*O. regalis*, *O. cinnamomea*). The stele in *Osmunda* has been designated as dictyostele by some workers. Sporne (1966) regards it as dictyoxyletic. Due to the presence of continuous endodermis, pericycle and phloem layers internal to the xylem, it does not fulfil the conditions met with in the dictyostele. The individual xylem strands can also not be regarded as meristemes. A meristeme in its essentials has its own separate phloem, pericycle and endodermis. Nevertheless, the stele was still strictly a protostele, since there was a continuous zone of phloem (and, presumably, endodermis) round the out- side.

**Petiole:** A transverse section of the petiole reveals a distinct layer of epidermis, which in younger leaves is covered with numerous simple and multicellular hair. Next to the epidermis is a few layers thick sclerenchymatous hypodermis. The hypodermis encircles a broad central ground tissue. The ground tissue is composed of thin-walled cells. In it is embedded a single petiolar bundle. The bundle is crescentic or horse-shoe shaped and has a central xylem core surrounded on all sides by phloem. Endodermis is not very clear. The xylem has several protoxylem groups along concave.

**Leaflet:** A cross section of leaflet reveals the presence of two epidermal layers. The stomata are present on the lower epidermis.

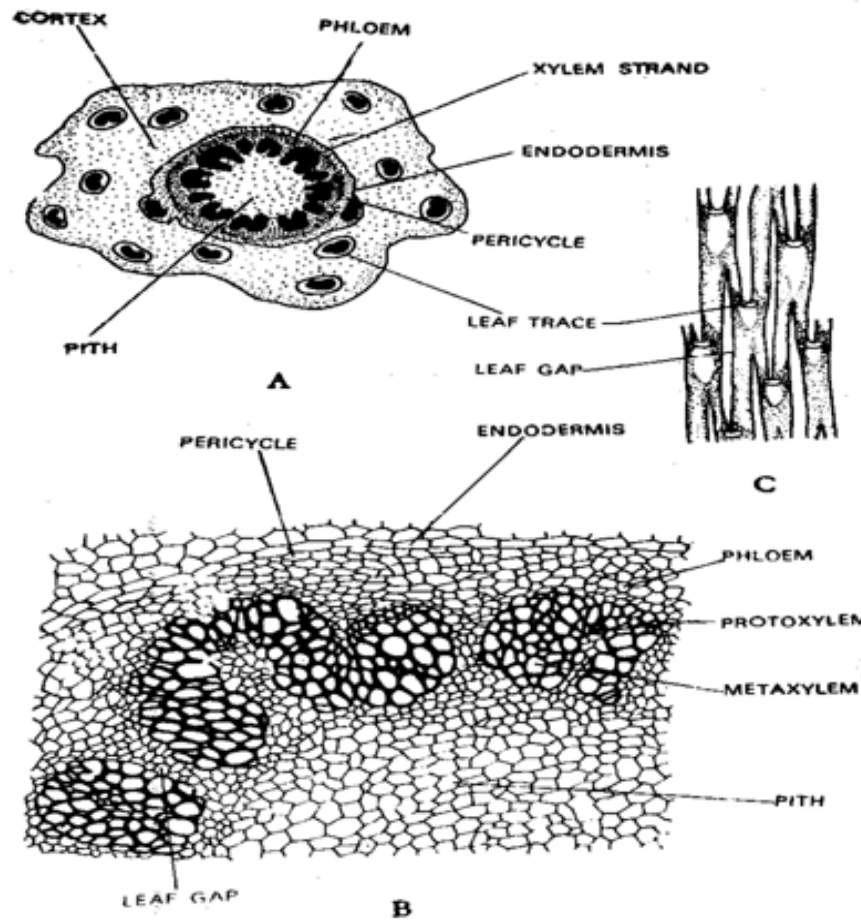


Fig.5.21. *Osmunda*: A. T.S. of Stem; B. Portion of stele enlarged; C. stereodiagram of a portion of a stele

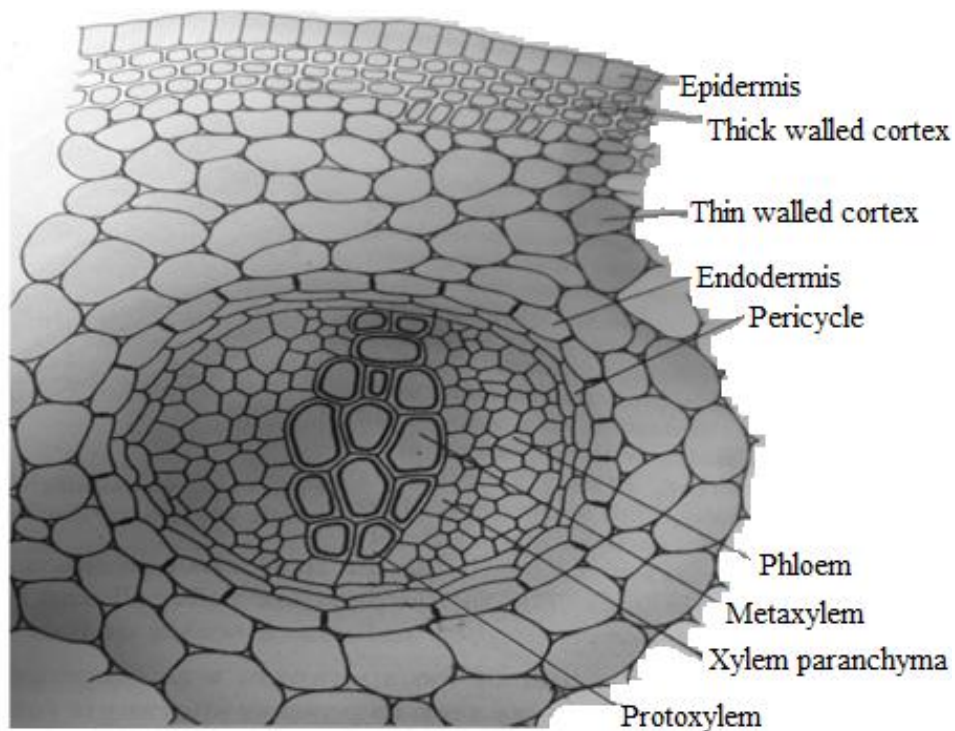


Fig. 5.22 *Osmunda*: T.S. root

**Root:** The roots arise endogenously from the rhizome. There is distinct outer layer or the epidermis in the young roots. It is later replaced by the outermost layer of the cortex called exodermis. Next to the epidermis is a few-layered hypodermis which is made up of thick-walled cells. The rest of the cortex is parenchymatous. There is a distinct endodermis surrounding the central stele. The endodermis of the root is continuous with that of the rhizome and the petiole. Next to the endodermis are two layers of thin-walled cells. They constitute the pericycle. The stele is usually diarch or triarch (Fig.5.22). The protoxylem is exarch in position and represented by two groups on either side of the ellipsoidal xylem mass. There is no pith. Phloem forms two patches on either side of the xylem. There are a few layers of thin-walled cells between the xylem and phloem bundles.

## Reproduction

*Osmunda* is a homosporous fern, sporangia do not form sori.

**Development of sporangium:** *Osmunda* is intermediate between eusporangiate and leptosporangiate ferns therefore, known as protoleptosporangiate fern (Fig. 5.23). The sporangial initial divides periclinally into an outer jacket initial and an inner archesporial cell. The archesporial cell is tetrahedral or cubical. Jacket initial and daughter cells divide only anticlinally a one cell thick wall of the sporangium is formed.

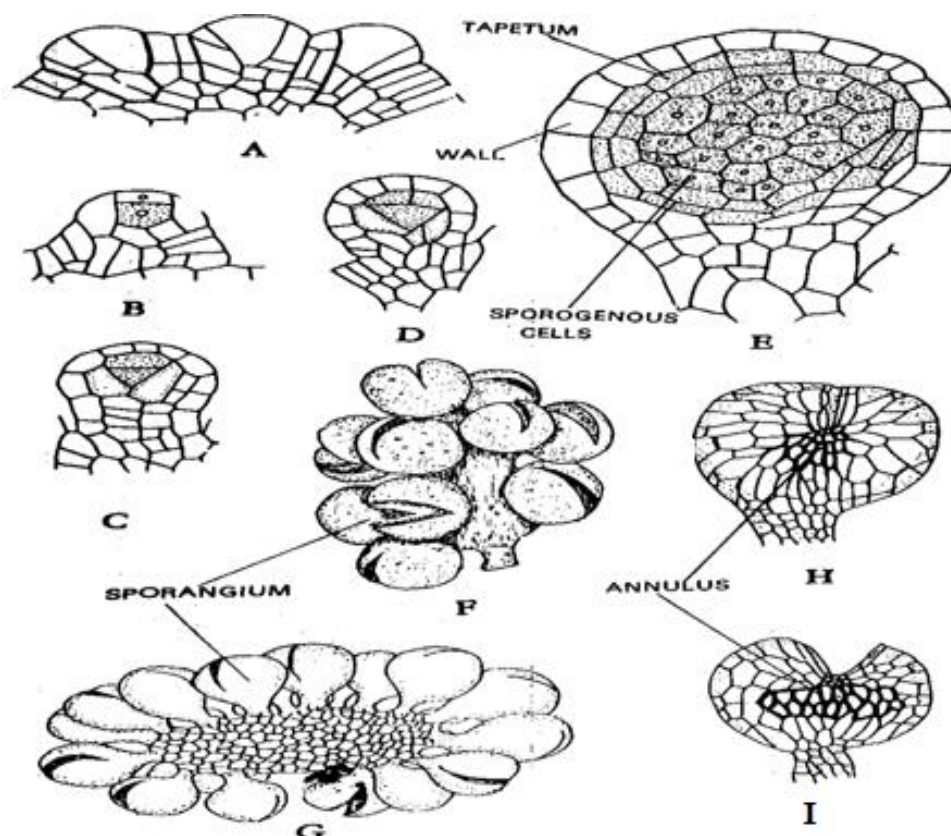


Fig.5.23: *Osmunda*: A-E. Stages in the development of sporangium. F. Portion of marginal tassal. G. Cross section of tassal showing arrangement of sporangia. H-I. Sporangia showing form, dehiscence and annulus. (After Bower 1899 and Willams 1927)

**Structure of mature sporangia:** A mature sporangia of *O. regalis* and most other species of *Osmunda* is a massive, short stalked and a pyriform structure. The capsule has a single layer of sterile jacket cells. Next to it there are two layers or rarely three layers of tapetal cells surrounding a central mass of 32 to 128 spore mother cells. The tapetal cells do not disorganise to form the nourishing plasmodial fluid. There are two layers of tapetal cells. The inner layer is derived from the sterile sporogenous cells and later disorganises to form the plasmodial fluid. They elongate and push their way in between the spore mother cells. Their walls disintegrate and their protoplasts fuse with each other to form a network like plasmodial fluid. It disappears during the maturation of spores. The outer layer of tapetal cells is derived from the primary archesporial cell. It is made up of a single layer of flattened cells and persists throughout the life of the sporangium. It may be regarded as a functionless second wall layer. The spore mother cells undergo meiosis and produce 128-512 spores. The wall of the sporangium splits over the apex and down the opposite side along the line of thin walled cells and the sporangium open widely (Fig. 5.23 H-I).

### Gametophytic Generation

It starts with the spore whose structure and germination is described below:

**Spore:** The spore is almost spherical in shape and possess a distinct triradiate mark (5.24 A). The spore wall consists of the usual two layers: the outer exine and an inner thin intine. The intine grows out in the form of a small conical papilla. The protruding spore protoplast divides by a transverse wall into a small primary rhizoidal cell and a large primary prothallial cell (5.24 B). The rhizoidal cell contains a few chloroplasts which later on, as it push its way down into the soil as a first rhizoid; disappear. The larger prothallial cell contains numerous chloroplasts which move towards the periphery of the cytoplasm. The prothallial cell grows exactly opposite to the first rhizoid (bipolar germination). The apical cell cuts off segment towards its right and left in a regular, alternate manner. The segments cut off by apical cells divide each by a transverse wall to form an outer and an inner cell. The inner cells divide by horizontal walls. This adds to the thickness of the prothallus in the middle portion which becomes distinct as a midrib.

The outer cells divide rapidly and overgrow the apical cell structure thus, giving the young prothallus a heart shaped appearance (Fig. 5.24 E). An apical cell is soon established in this mass and by its activity give rise to a flat and cordate prothallus (5.24 G). The prothalli are dark green in colour.

**Sex Organs:** The monoecious prothalli are protandrous and bear antheridia after about weeks (*O. cinnamomea*) to one month (*O. claytoniana*) of their development from the spore. The antheridia usually appear along the margins or on the ventral surface along the wings. The archegonia appear late and develop either along the margins of the thick midrib (*O. cinnamomea*) or are scattered along over its surface (*O. claytoniana*).

**Antheridium:** The antheridia are of projecting or emergent type. They are large and globular structures and vary in position from terminal to marginal or even to the ventral side of the prothallus. The antheridia may or may not have a distinct stalk. The body of the antheridium



has a single-layered wall made up of many curved cells that contain chloroplasts (5.25 J). A triangular cell at the apex of the antheridium on one side is the opercular cell. It is thrown off during dehiscence thus permitting the spermatozoids to come out and get dispersed. The spermatozoids are coiled and multiciliate structure. It has two coils. Posterior coil is slightly broader than the anterior.

**Archegonium:** The archegonia are always produced on the ventral surface and have necks that project in a horizontal direction from the median cushion. The neck consists of 4 vertical rows of cells, each row 6 cells in height i.e., it consists of 6 tiers of 4 cells each (5.25 R). The neck encloses a single binucleate neck canal cell. The venter is embedded in the prothallus tissue and is not surrounded by its own wall. It contains a single ventral canal cell and a large egg cell.

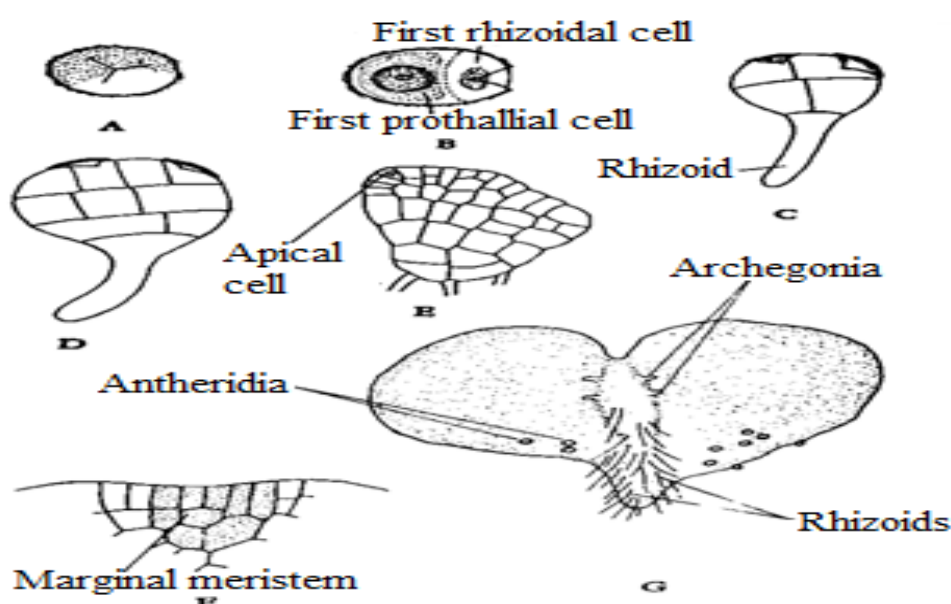


Fig.5.24: *Osmunda*: A-F. Stages in the development of prothallus; G. Mature prothallus with antheridia and archegonia. (After stroke and Atkinson)

**Fertilization:** Before fertilization, the neck canal cells and the ventral cell disorganise and become mucilaginous. The mucilaginous absorbs water, swell up and forces the apical tier of cells apart, thus making an open passage for the sperms to enter. The mucilage drop oozes out and attracts the spermatozoids.

**Embryogeny:** As a result of fertilization a diploid zygote is established. It is surrounded by a dense cytoplasm, which secretes a wall, thus establishing a diploid cell called the zygote or the oospore. It is lying in the venter and is protected by the surrounding prothallial tissue. The zygote divides (Cross, 1931) by a wall parallel to the long axis of the archegonium (Vertical wall) into two almost equal cells. The two cells thus formed divide each by a wall at right angles to the first wall to form four cells. This is the quadrant stage (Fig. 5.26 C).

The epibasal quadrants give rise to the leaf and the stem and the two hypobasal ones give rise to the foot and the root.

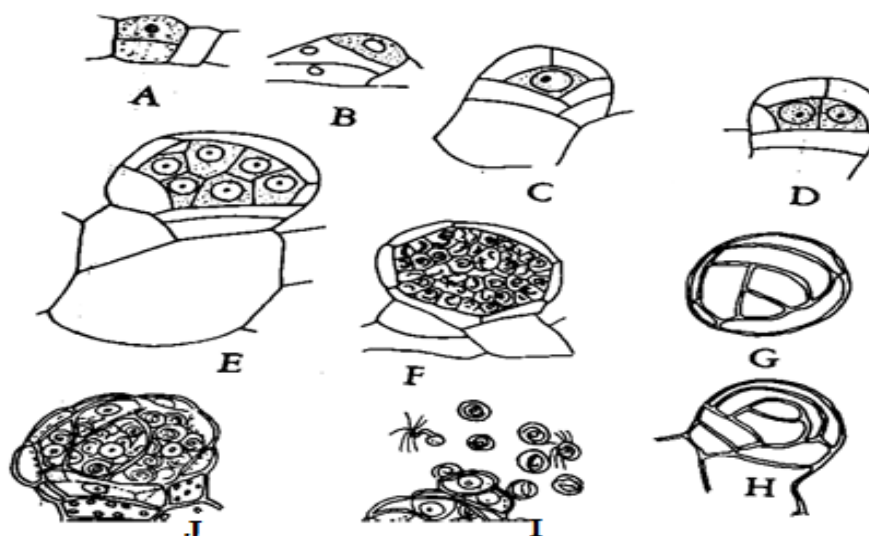


Fig.5.25: *Osmunda*: A-F stages in the development of antheridium; H-I. Surface vies of mature antheridium; J. Mature antheridium ready to discharge (After Campbell 1892)

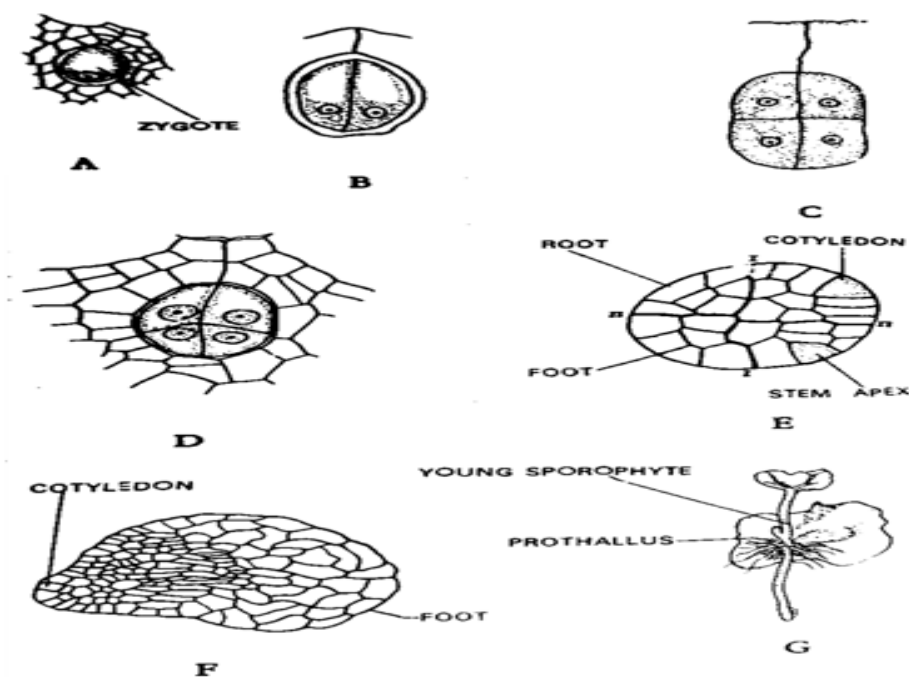


Fig. 5.26. *Osmunda*: Stages in the development of embryo. A. Fertilized egg; B. Two celled embryo; C. Quadrant stage; D. Octant stage ; E. Older embryo ; F. Horizontal section of advanced embryo; G. Young sporophyte still attached to prothallus. (After Cross 1931 and Campbell 1892)

The quadrants divide transversely a form an octant stage (Fig. 5. 26D). Subsequent divisions are not very regular. The foot is well-developed and may perform haustorial functions. The root apical initial appears endogenously and by its activity gives rise to the primary root. The development of the embryo is slow and it retains its globular form for a sufficiently long time. The young leaf soon appears as a conical protuberance on one side (Fig. 5. 26G).

### 5.4.2-Leptopteris

*Leptopteris* (six species) is confined to Australia and the South Sea Islands. *Leptopteris hymenophylloides* may have a free-standing trunk 1 m or more high, while one species of *Leptopteris* from New Caledonia attains a height of 3m. The leaves of *Leptopteris hymenophylloides* are comparable with those of the Hymenophyllaceae (filmy ferns) and have a thin pellucid lamina, only two or three cells thick, from which stomata are completely lacking. During their development the leaves of all species exhibit circinate vernation and are covered with hairs. The base of the petiole is broad and winged in a manner reminiscent of the Eusporangiatae and, after the frond has been shed, the leaf base is persistent, adding considerably to the diameter and the mechanical strength of the stem.

The fronds of *Leptopteris hymenophylloides* are large and many times pinnate, with the superficial sporangia scattered sparsely along the vein and veinlets of unmodified pinnules (Fig.5. 27 A). The bipinnate leaf is exceedingly thin being only 2 or 3 cell layers thick and devoid of mesophyll and stomata. There is no marked difference between the bipinnate fertile and sterile leaves. In no case is there any tendency for the sporangia to become aggregated into sorus, nor is there any sign of an indusium.

The sporangium is not strictly leptosporangiate, for several cells play a part in its initiation and, at maturity; it is relatively large and massive with a stout short stalk. There is some variation in the shape of the archesporial cell, for it may be tetrahedral, as in leptosporangiate ferns or it may be cubical, as in the Eusporangiatae. The tapetum is formed from the outermost layers of the sporogenous tissue, unlike that of the Eusporangiatae, and there is also a layer of tubular cells, formed from the same regions, which becomes appressed to the inner side of the sporangium wall. For this reason, at maturity, the wall appears to be two cells thick. There is a primitive kind of annulus, formed by a group of thick-walled cells, on one side of the sporangium and a thin-walled stomium, along which dehiscence occurs, extends from it over the apex of the sporangium (5.27B). Relatively large numbers of spores are released from each sporangium (e.g. about 128 in *Leptopteris*). The spores contain chlorophyll and must germinate rapidly if they are to do so at all.

The prothallus is large, fleshy and dark green, resembling a thalloid liverwort, up to 4 cm long. The antheridia project from the surface as in Leptosporangiatae, but are larger, have more wall cells and produce a greater number of antherozoids than do most of them. The archegonia are borne along the sides of the midrib; they have projecting necks and differ from those of leptosporangiate ferns only in the number of neck cells (six tiers, instead of the usual four).

The embryology of the young sporophyte, too, shows some features which distinguish the Osmundales from the Leptosporangiatae. Not only is the first division of the zygote is vertical, but also the second one is vertical. It is the third division which is at right angles to the axis of the archegonium, instead of the second. Subsequent divisions are somewhat irregular and the embryo remains spherical for a relatively long time. Ultimately, however, a

shoot apex, cotyledon, root and a large foot appear, but there is some irregularity in their derivation from the initial octants.

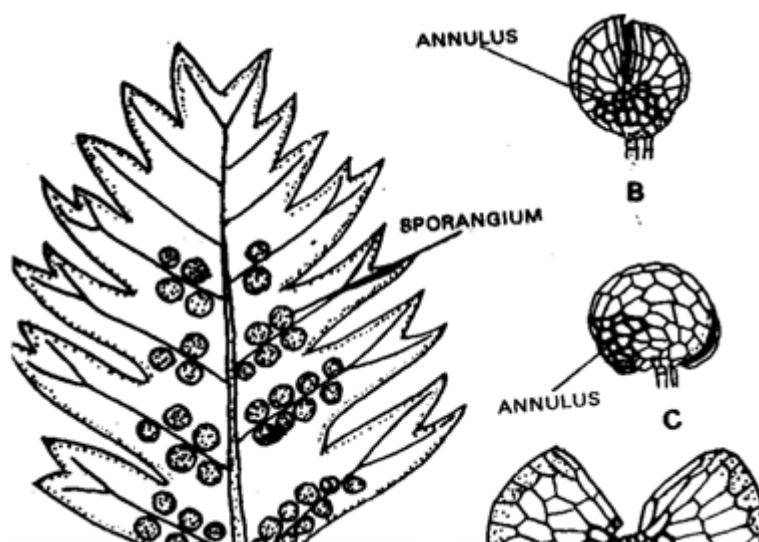


Fig.5.27. *Leptopteris*: A. Fertile pinnule; B-C. Sporangia

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## 5.5 LEPTOSPORANGIATE

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### 5.5.1 Filicales

#### 5.5.1.1 Hymenophyllum

**Distribution and Habit:** This group is commonly referred to as '**the filmy ferns**', because of their delicate fronds, the lamina of which is usually only one cell thick. There are some 300 species of *Hymenophyllum*, of which two occur in the British Isles. Because of their delicate nature, almost all of them are confined to moist habitats, and most of them are restricted to the tropics, where they commonly grow as epiphytes. The British species *H. tunbrigense* may be seen growing on rocks constantly wetted by the spray from waterfalls. About 8 species of *Hymenophyllum* have been recorded from India.

**External Features:** Most filmy ferns have a thin wiry creeping, protostelic rhizome, from which the fronds arise in two rows (Fig. 5. 28A). The plant body rarely exceeds 8-10 cm in size. But in *H. pulcherrimum* the pendant fronds may be 0.5-1 meter in length. Branching of the rhizome is axillary. Roots are adventitious (lacking in some smaller forms) and are produced in pairs at the base of each leaf. But sometimes roots may be seen between the leaves. This is due to the failure of leaf primordium to develop above the region where the roots are produced.

The leaves of *Hymenophyllum* are characteristically true to the name filmy ferns and are objects of beauty. The translucent leaves when growing in close mats may easily be mistaken for bryophytic thalli. Leaves are produced in acropetalous succession and show circinate vernation. But it is not uncommon to find sometimes, the unfolding of a young leaf between

two mature leaves. This shows that many leaf primordia may remain dormant and may resume growth at a later stage. The leaves have a flattened petiole. The lamina may be simple (*H. cruenta*) or dissected into unequal dichotomies as in the majority of species. It is mostly one celled thick and has an open dichotomous venation. In each shank of dichotomy there is single vein. In *H. cruenta* there are a series of veins reaching the margin of the simple lamina. Sori are borne along the margin (Fig.5.28B) or at the apex of each dichotomy. The leaves are pale green in colour and together with the roots they also seem to take part in absorption.

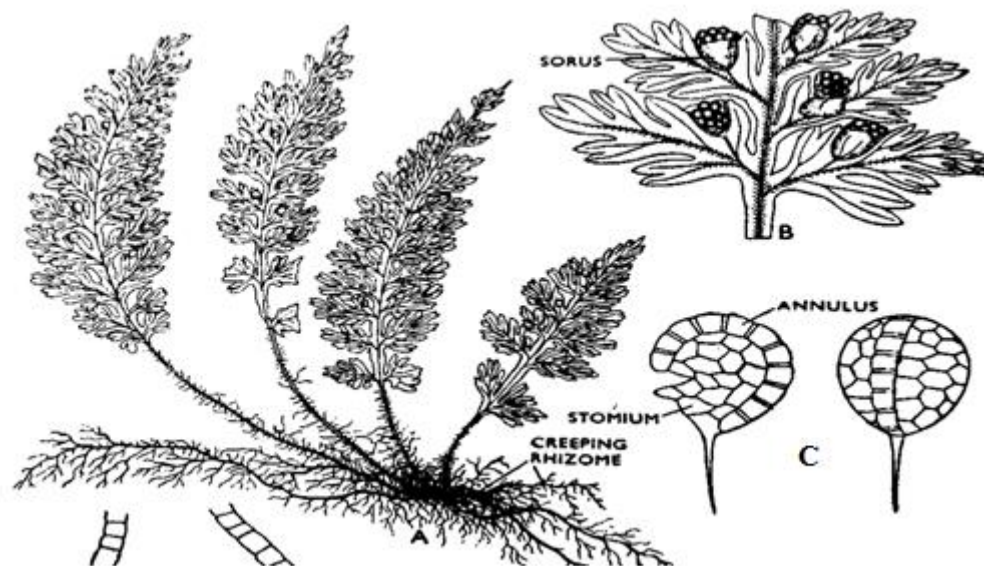


Fig.5.28. *Hymenophyllum*: A. Morphology; B. Fertile pinnae; C. Sporangia

## Internal Structure

**Rhizome:** A transverse section shows an epidermis, a relatively narrow cortex surrounding a central stele. The cortex may be wholly sclerotic or partly thin walled (outer cortex) and partly thick walled (inner cortex). Vascular cylinder is protostelic even in the mature plant, a feature unusual to ferns, but not unusual in the background of its habitat. There is an outer endodermis surrounding the vasculature (Fig. 5.29 A). Internal to the endodermis is the pericycle one or many cells thick. Phloem surrounds the xylem but the two are separated by conjunctive parenchyma. The architecture of the xylem is variable in different species.

In *H. demissum* there is a ring of metaxylem surrounding a parenchymatous region in which is embedded the protoxylem. In *H. scabrum* the metaxylem ring is broken at two points to form two arcs, in *H. cruenta* one of the arcs (ventral) may be absent. Leaf traces that depart from the vascular cylinder do not leave any gap. Branch traces are connected to the leaf traces or more often arise from it.

**Root:** There is no root cap; the vascular cylinder is protostelic as in other Leptosporangiatae. Xylem may be monarch or diarch.

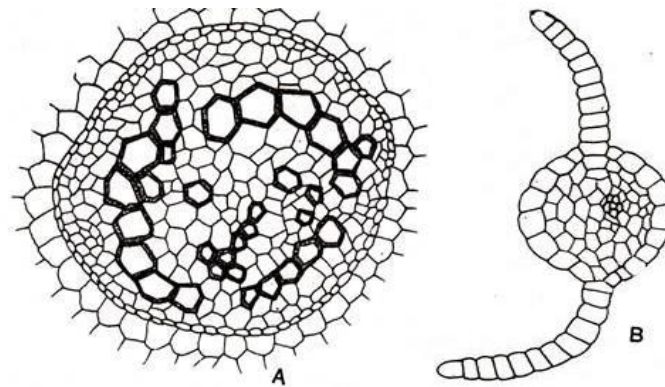


Fig. 5.29. *Hymenophyllum*: A. T.S. Stem showing stele; B. T.S. of leaf

**Leaf:** Leaf blade is one cell in thickness (Fig. 5.29 B) towards the margin but many celled thick towards the central vein. In *H. dilatatum* leaf blade also is many celled thick. The vein consists of poorly developed xylem and phloem.

### Reproduction

Vegetative propagation may be brought about by the fragmentation of the rhizome when each portion grows into a new individual.

**Spore Producing Organs:** The characteristic method of reproduction of the sporophyte is by the spore formation. The sori are marginal, and most species are strictly gradate (Fig. 5.30 B). The sorus has a fertile tissue called 'receptacle' from which sporangia are produced. Receptacle development on the lamina is associated with the development of two flaps of tissue from the axial and abaxial surface of the leaf. The vein leading to the sorus continues into a columnar receptacle. The receptacle of *Hymenophyllum* has more limited power of growth or may lack them altogether. In such species, the sporangia are produced simultaneously, but, where the receptacle can grow, new sporangia arise in basipetal sequence true to the gradate nature of the sorus. Surrounding the sorus is a two-lipped indusium (Fig. 5.30B). The sporangium has a relatively thin stalk and an oblique annulus, which brings about dehiscence along a lateral line (Fig. 5.30C).

**Development of Sporangia:** Sporangial initials are first differentiated towards the apex of the receptacle. Succeeding ones appear in basipetalous fashion. Early stages of sporangial development resemble those of Osmundaceae. A sporangial initial (leptosporangiate type) functioning like an apical cell cuts off one or two stalk cells and then divides periclinaly to form an inner primary archesporial cell and an outer primary wall cell. The latter by undergoing only anticlinal divisions builds up the single layered wall, while the former produces the archesporium, the cells of which form the spore mother cells. These divide meiotically to produce haploid spores. All spores are of the same type. The spore output varies from 128 or 256 in *Hymenophyllum*. The dehiscence of the sporangium is brought about by an oblique vertical annulus (Fig. 5.30 C) by a process of slow opening, followed by rapid closure as a gas phase suddenly appears in the cells of the annulus. This mechanism is found throughout the more highly evolved members of the Filicales, and results in the

forcible ejection of the spores. Splitting of the sporangium is transverse. Spores are wind dispersed.

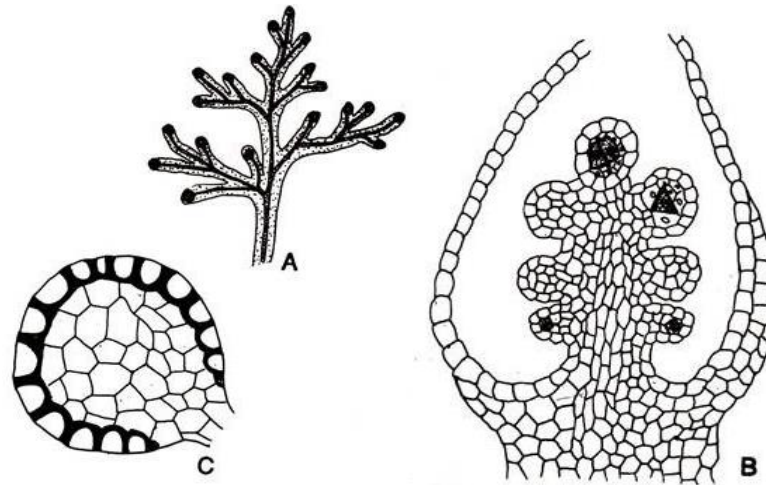


Fig.5.30: *Hymenophyllum*: Spore bearing organ, A. Tip of fertile leaf; B. L.S of receptacle; C. A mature sporangium showing annulus

## Gametophyte

**Structure and Germination of the spore:** Spores have a triradiate shape because of the tetrahedral arrangement. They are minute in size and have a two layered wall. Early stages of germination take place in situ. The spores divide into three radiately arranged cells (Fig. 5.31A), when they are still within the sporangia. Further development takes place after shedding. Each of the three cells divides transversely resulting in a six celled germling (5.31 B). Further growth is independent in the three arms. Very soon growth ceases in two arms by the transformation of their terminal cell into a rhizoid. In the third arm an apical cell is established with two cutting faces. This is later replaced by a transverse row of cells. The prothallus of *Hymenophyllum* is a strap-shaped filamentous, ribbon like and dichotomously branched or lobed thallus, often only one cell thick. Rhizoids are produced from the ventral surface. Some of the branches of the gametophyte may grow erect (5.31D).

**Sex organs:** Sex organs are mostly formed on the ventral side. Antheridia are borne near the margins of the branches. They are scattered all over the thallus. A mature antheridium has a single layered jacket (Fig. 5.31 F). There is a triangular opercular cell at the apex to facilitate the exit of the antherozoids. Archegonia are borne on short upright, special branches along the margin. Their development is typical of other ferns (see *Ophioglossum*). The neck is six to nine cells in height. The axial row consists of a bi-nucleate neck canal cell, a venter canal cell and an egg cell (Fig.5.31 E).

**Embryogeny:** Nothing is known about the embryo development in *Hymenophyllum*. The first division is transverse (unlike in other Leptosporangiates). Embryonal parts are differentiated only at a later stage. The orientation of the embryonal organs is typical to leptosporangiate forms.

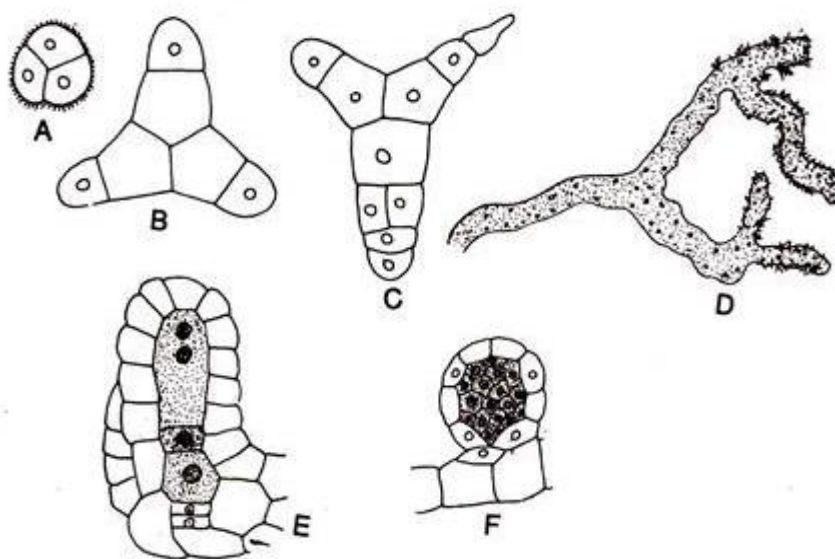


Fig. 5.31: *Hymenophyllum*: A-C. Stages in the development of gametophyte; D-F. Part of mature gametophyte; E. Archegonium; F. Antheridium

### 5.5.1.2 *Adiantum*

**Occurrence and distribution:** *Adiantum* is popularly called ‘**Maiden hair fern**’ because of the shiny black rachis of the leaves. It is one of the most widely distributed genus of the family growing luxuriantly in both tropical and sub tropical regions of the world. It grows ubiquitously wherever nature offers a moist, shaded locality. There are nearly 200 species. Some of the common Indian species are: *A. capillus-veneris*, *A. petdatum*, *A. incisum*, *A. caudatum*, *A. venustum*, *A. lunulatum*, *A. edgowrthii* etc. Species of *Adiantum* are commonly cultivated in green houses because of their attractive foliage.

### Sporophyte

**Morphology:** The sporophytic plant body consists of an underground rhizome from which are produced leaves and roots (Fig. 5.32 A). The rhizome is covered with chaffy scales (Paleae). It may be erect (*A. caudatum*), semi erect (*A. petdatum*), or creeping (*A. capillus-veneris*). The rhizome may be hard or soft and brown in colour. The chaffy scales that cover the rhizome are of various shapes and sizes. From the undersurface of the rhizome arise a number of adventitious roots. The roots are stiff and black in colour. The leaves are produced in acropetalous succession on the creeping rhizome. They show circinate vernation typical of ferns. The rachis of the leaf is hard, wiry, shiny and black or dark brown in colour, has a medium dorsal groove, and is covered with paleae at the basal region. In addition to this, glandular hairs may also be present. The leaves may be unipinnate (*A. xaudatum*) or bi or tri-pinnate as in, *A. capillus – veneris* (Fig. 5.32 B). The pinnae are stalked and have a dichotomous venation. The rachis may terminate in a pinna or may bear a bud. There is no distinction between fertile and sterile leaves in *Adiantum*. The whole leaf may be sporangiferous or only certain pinnae may bear sporangia. Sori are borne on the ventral surface of the pinnae.



**Anatomy**

**Rhizome:** A transverse section reveals the usual three zones: epidermis, cortex and stele (Fig.5.33). The outline of the section would be wavy. Epidermis is single layered and the cells may be thin walled or thick walled. There is a cuticle external to the epidermis. Cortex lies internal to the epidermis. It may be wholly parenchymatous (*A. rubellum*), (Fig. 5.33 A) or it may have sclerenchyma and parenchyma. In *A. pectinatum*, scattered masses of sclerenchyma are found embedded in the parenchymatous ground tissue. In *A. caudatum*, sclerenchyma constitutes the hypodermal region. The central vascular cylinder exhibits great variety. In *A. capillus veneris*, it is a dictyostele consisting of a ring of meristoles (Fig. 5.33 B). In the young condition the stele may be a solenostele. In *A. rubellum* the stele is a typical amphiphloic solenostele, with characteristic features such as outer endodermis, outer pericycle, outer phloem, xylem, inner phloem, inner pericycle and inner endodermis lining the parenchymatous pith.

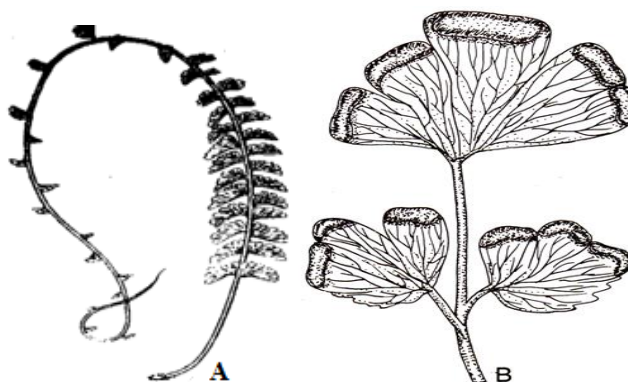


Fig.5.32. *Adiantum*: A. Sporophyte; B. Fertile leaflets of *A. capillus veneris*

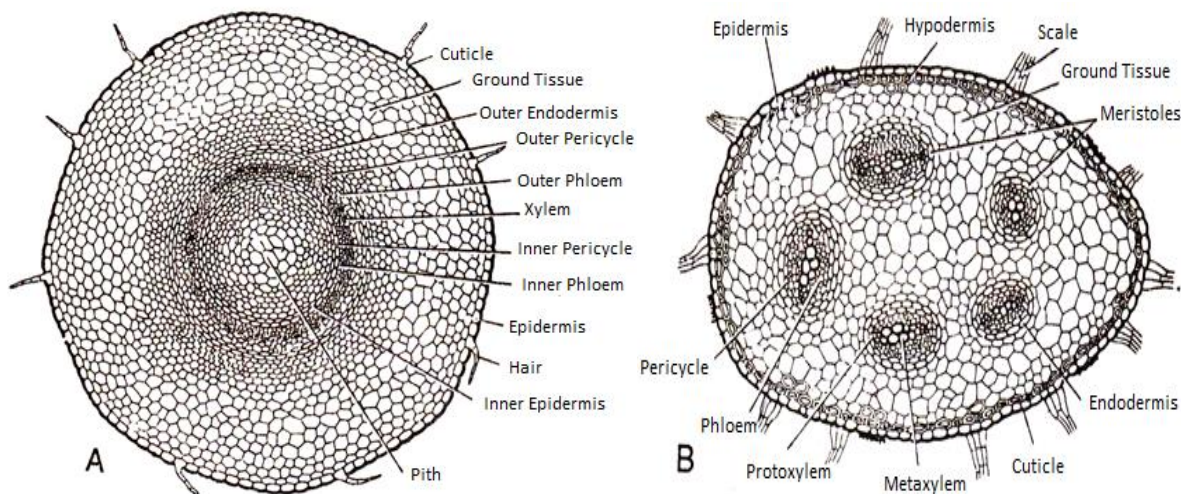


Fig.5.33. *Adiantum*. Anatomy of rhizome. A. Siphonostele in *A. rubellum*; B. Dictyostele in *A. capillus veneris*

**Leaf:** The petiole shows an epidermis, parenchymatous cortex and the vascular tissue (Fig. 3.34). There is a thick walled hypodermis next to the epidermis. The number of leaf traces entering the leaf, varies. It is single in *A. caudatum* and others and double in *A. capillus – veneris*. The xylem is concave at the base but triradiate higher up with three protoxylem groups. Xylem is exarch. The lamina shows the two epidermal layers upper and lower and the mesophyll is generally undifferentiated. It is highly reduced in *A. capillus – veneris*, *Apedatum*, etc., having only two layers of cells. In *A. pedatum*, in some regions the mesophyll is totally absent and at such places the two epidermal layers are closely appressed to each other. The mesophyll (when present) as well as the epidermal layers are chlorophyllous. The stomata are scattered throughout the surface of the leaf. Paleae or ramenta may be borne even on the epidermis of the lamina. The vein may or may not have a bundle sheath.

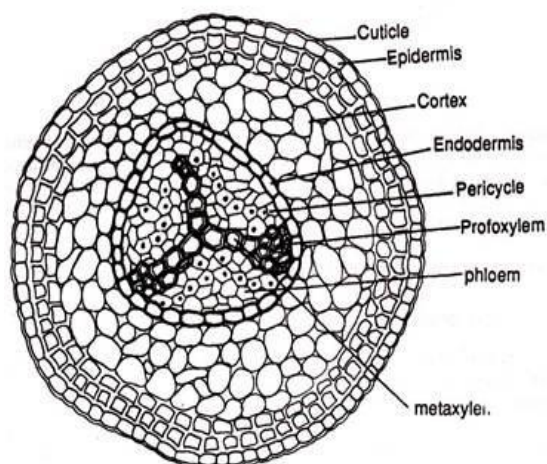


Fig.5.34: *Adiantum*: T.S. petiole

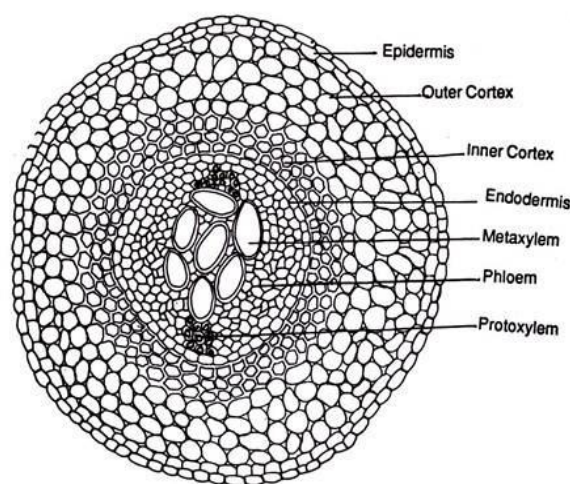


Fig.5.35: *Adiantum*: T.S. root

**Root:** A transection of root shows a very prominent piliferous layer, a two zoned cortex and the central protostele (Fig. 5.35). The piliferous layer has brown coloured cell wall. Cortex has an outer parenchymatous zone and an inner sclerotic zone. Surrounding the stele is a conspicuous endodermis with prominent casparian thickenings. The xylem is exarch and diarch, phloem completely surrounds the xylem. External to phloem is a single layered pericycle.

## Reproduction

Vegetative propagation is brought about by buds produced at the leaf tips. The buds enter the ground when the leaf bends and touches the soil. There they develop into a new individual. This, in turn may repeat the process leading to the walking Habit. Walking habit is seen in *A. caudatum*.

**Spore producing organs:** As has already been said there is no distinction into fertile and sterile leaves. The sori are born at the distal end of the pinnae. But the sori are not exactly marginal. They are borne a little behind the tip of the veins (sub marginal). The sorus bearing

margin of the leaf curls inwards and forms the false indusium. In some cases sporangia may develop at the distal ends of the veins (*A. phillippense*). In the sori paraphyses may be present in between the sporangia as in *A. rubellum*, *A. tenerum*, etc. The sorus is of the mixed type.

**Development and structure of the sporangium:** The development is similar to what is seen in *Pteris*. A mature sporangium has a stalk made up of three rows of cells. The stalk terminates in a globose or biconvex capsule. The wall is single layered. There is an oblique vertical annulus (Fig.5.36) of 12-24 cells long. The annulus is separated from the stalk by two or three cells. The stomium also is separated from both the stalk, and the annulus. The rest of the sporangial wall is composed of a few large cells. The sporangium dehisces transversely liberating the spores. All the spores are of the same type.

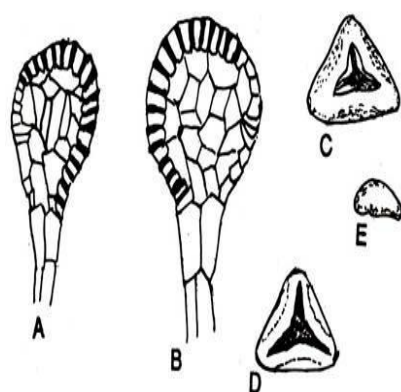


Fig.5.36: A-B. Sporangia and C-E. Spores

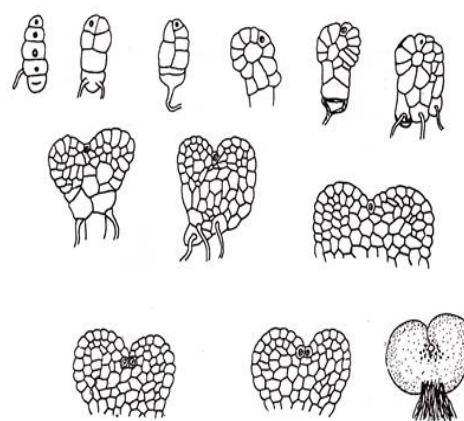


Fig.5.37: Development of gametophyte

## Gametophyte

**Structure and germination of the spores:** Spores are tetrahedral in shape (Fig.5.36). The wall is two layered. Exine is thick and smooth and has a brownish tinge. On falling upon a suitable substratum the spore germinates. The first sign of germination is the rupturing of exine and the protruding out of the germ tube. The germ tube undergoes several transverse divisions to form a short filament. The lowest cell forms a lateral rhizoid. The terminal cell becomes an apical cell with three cutting faces. By the division of the apical cell, a spatulate prothallus is formed first. (Fig. 5.37). The mature prothallus is cordate, photosynthetic, dorsiventrally flattened and aerial. The growing point is situated in the apical notch. All the cells in the prothallus are parenchymatous. The prothallus is one celled thick towards the margins but many celled thick towards the center. In some species collenchyma may be found at the corners. Rhizoids are produced from the ventral surface (Fig. 5.37).

**Sex organs:** The prothalli are monoecious. Antheridia are found in between the rhizoids towards the ventral surface. Archegonia are found near the growing point towards the ventral surface. Structure and development of sex organs is same as in *Pteris*.

**Embryogeny:** The first division of the zygote is vertical. The epibasal half (next to the archegonial neck) forms the leaf and root while the hypo basal half forms the stem' apex and

foot. Embryogeny is essentially similar to what is seen in *Pteris*. Generally only one sporophyte is formed per prothallus. During embryogeny the root and juvenile leaves make their appearance first, with the stem differentiating late. The primary root penetrates the soil and establishes itself. Apogamy has been reported in *A.philippense*.

### 5.5.1.3 *Dryopteris*

**Distribution and Habit:** 41 species of *Dryopteris* are found in India. They grow well in Western, Northern, Western and Eastern Himalayas. *D. ramose* and *D. blanfordii* are very common in Kashmir. *D. chryscoma* is very common in India and frequently in exposed places and hill tops between 1540-2700 meters above sea level. *D. hirteps* and *D. pulvinulifera* are other common species met in the Eastern Himalayas. *Dryopteris filix-mas* commonly known as Male Shield fern is a cosmopolitan species.

### The Sporophyte

**Morphology:** The plant represents the sporophytic generation and is distinguished into root, rhizome and the leaves. Leaves or fronds are the only above ground portions of the plant. The other organs are subterranean. The sporophyte has a partly horizontal and partly erect rhizome densely covered with brown, soft, broad and often fimbriated scales and adventitious roots. The fronds (leaves) are large and attain a height of 15-50 centimeter or more (may exceed one meter in length) and pinnately compound and there is usually an annual flush of a cluster of such fronds on the top of the rhizome, the leaf bases persisting when the older leaves perish. A characteristic feature of the leaves is that they are coiled in a circinate manner when young and as they grow old they unfurl into a pinnately compound leaf (Fig. 5.38 A). The lower portion of rachis is paleaceousie covered with numerous scales which are brown in colour and known as ramenta. The older and pinnately compound leaves are clearly distinguished into a petiole and the lamina. The primary root is short-lived and is replaced by adventitious roots that arise endogenously from the rhizome. They are branched and possess a root cap. They are thin, black wiry structures that anchor the rhizome to the substratum and also absorb water and other nutrients from the soil.

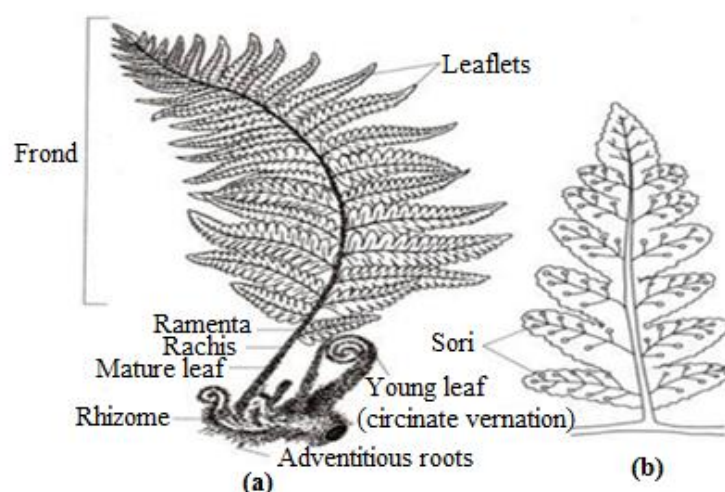


Fig. 5.38: (a) External features of *Dryopteris*, (b) Ventral view of pinna showing sori

## Anatomy

**Rhizome:** The outer most layer epidermis is a single layer of rectangular cells that become sclerenchymatous in the older rhizome. The cuticle is thick. Below epidermis is a brown zone of outer cortex made-up of a few layers of sclerenchymatous cells that form hypodermis and give mechanical strength to the rhizome followed by the thin walled parenchymatous inner cortex forming ground tissue (Fig. 5.39 A). The cells are polygonal in outline and enclose small intercellular spaces. They store food material in the form of starch and proteins. Some tanniferous cells are also present in this region. The vascular cylinder is a typical dictyostele composed of a varying number of oval or circular meristemes arranged in leaf gap interrupted ring in the ground tissue. The stele, if extracted as a whole from the ground tissue, appears as a cylindrical meshwork of vascular strands (Fig 5.39 B). There is no definite node in the rhizome and the numerous leaf traces are present in inner cortex everywhere. The stem stele gives off leaf traces to the leaves and the leaf trace bundles from the base of petiole give off vascular strands to the roots.

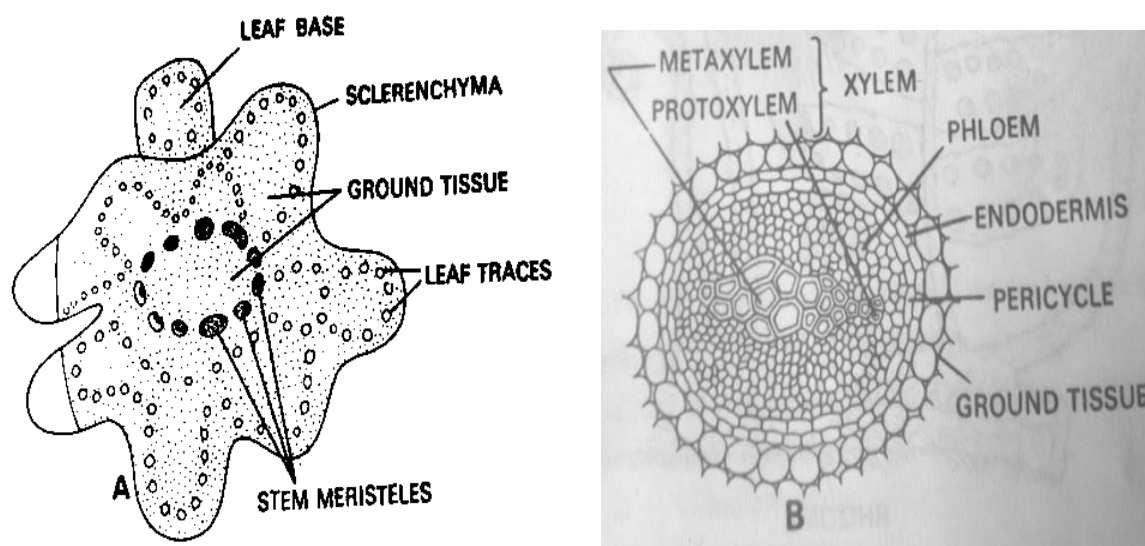
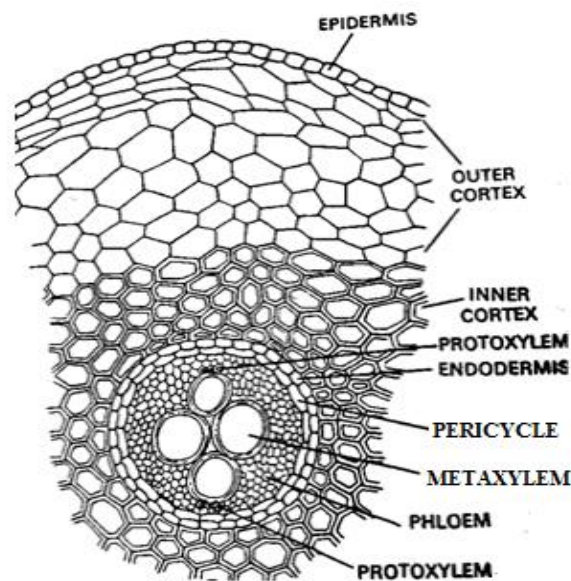


Fig.5.39. *Dryopteris*. T. S. of rhizome showing  
A. Meristemes and leaf traces. B. Detailed structure of meristeme

An individual meristeme is bordered by a layer of endodermis followed by a single layer of pericycle (Fig 5.39 B). Both of these layers are made up of parenchymatous cells. The cells of endodermis have distinct casparian strips and store food in the form of starch grains. Next to pericycle is phloem tissue which completely surrounds the central mass of xylem. The phloem can be distinguished into protophloem and metaphloem. The former occurs as a single layer of sieve cells and parenchyma next to the pericycle, whereas the latter forms two or three layers of sieve cells and phloem parenchyma. The xylem is also distinguishable into protoxylem and metaxylem. The former has smaller tracheids that are spiral or reticulate. It is surrounded by metaxylem tracheids that are larger in diameter and are pitted.

**Rachis:** The rachis has a similar arrangement of tissues like rhizome but the large number of vascular strands is arranged in the horse-shoe shape and not in the ring.

**Root:** The original epidermal layer is sloughed off during downward growth of the root through soil. It is replaced by the outermost layer of the cortex. This is usually termed as exodermis or rhizodermis or piliferous layer. It is made up of thin walled cells that bear unicellular root hair in the root hair zone. Below epidermis is cortex made up of several layers of cells and is distinguishable into two zones: (i) Parenchymatous cortex which is next to the epidermis and consists of 5-7 layers of thin walled, polygonal cells that enclose small intercellular spaces. The cells store food and also help in translocation of water absorbed by root hair to the stelar region (Fig.5.40). (ii) Sclerenchymatous cortex that forms the central mechanical cylinder external to the vascular region. These cells possess pitted thickenings and are polygonal in shape. They are devoid of cytoplasmic contents.



*Fig.5.40: T.S of Dryopteris root*

Endodermis is distinct and is made up of barrel shaped cells that filled with starch and possess casparian strips on the radial and inner horizontal walls. Pericycle is made up single layer of thin walled cells. Roots are provided with single central stele which is diarch and exarch (Fig 5.40). It consists of central plate of xylem with metaxylem in the center and protoxylem at either ends. Phloem forms two conspicuous groups alternating with the xylem. Pith is absent. Secondary growth is absent. The lateral roots originate from definite cells of the endodermis that are opposite to protoxylem groups.

**Leaf:** The internal structure of the leaf will be considered separately for the pinnule and petiole.

(i) **Pinnule-** A vertical section of sterile pinnule reveals the two epidermal layers (dorsal and ventral) whose cells are parenchymatous and contain chloroplasts. The stomata may be restricted to the lower epidermis or may be present on both the layers (5.41 A).

(ii) **Petiole-** Transverse section of petiole is almost semi-circular in outline due to the presence of a groove on one side. It reveals an outer epidermis which bearsramenta or the scales. Next to it is 3-7 layered hypodermis which is wholly sclerenchymatous and forms a peripheral mechanical cylinder that resists the bending strain. The rest is the ground tissue is parenchymatous.

## Reproduction

Reproduction takes place by vegetative means as well as by formation of spores, which are produced within sac-like structures called the sporangia. The sporangia are grouped into definite structures called the sori (singular sorus). The sori are borne on the ventral surface of the pinnules which are called the sporophylls.

Vegetative propagation takes place by two methods: (i) by fragmentation and (ii) by the formation of adventitious buds on the petioles.

**Reproduction by spores:** When the leaves are mature they bear sporangia on the ventral surface of fertile pinnae. Usually whole frond produced at this time are sporophyll and there is no segregation between fertile and sterile leaves. The leaves are capable of performing the dual functions of reproduction and photosynthesis. *D. cochleata* is an exception because in this species there is a segregation between sterile and fertile parts of a leaf.

**Structure of sporangium:** In *Dryopteris*, the sori are borne in two rows on two sides of the median vein of a pinnule in between margin and the mid rib (Fig 5.41A). Each sorus is covered by a kidney shaped indusium which is basal in origin and raised on a cushion of tissues forming an umbrella shaped structure covering the sorus. In the center of sorus the vein ends in a placental tissue from which a number of sporangia arise without any order of development (mixed type). The sporangium in *Dryopteris* can be distinguished into two parts (i) Stalk or the pedicle and (ii) Capsule or the spore sac. The stalk is composed of three rows of elongated cells and bears a water gland. The capsule or the spore sac is more or less oval in shape and appears like biconvex lens. The mature sporangium has a single-layered wall that encloses forty-eight bilateral and monoete spores. The cells of the sporangial wall or the jacket layer are thin-walled, flattened, transparent and have wavy cell walls along the two flattened sides of the sporangium. They are polyhedral in shape. Around the edge of the capsule is a vertical row of about 16 specially differentiated cells with specially thickened walls. It is the annulus. It extends over about two-thirds of the circumference of the capsule connecting the sides and forms an incomplete ring of large cells. The annulus is incomplete at the base of one side where the cells are somewhat transverse and form stomium (5.41 B).

**Development of sporangium:** A sporangium develops from a single initial cell in a typical leptosporangiate way. The superficial sporangial initial project out the surface of receptacle and divide transversely. The outer cell gives rise to the sporangium and forms a short filament with an apical cell with three lateral cutting faces. A three rowed stalk is developed from its base and the upper part ends in a flat outer jacket initial and an inner tetrahedral archesporial cell. The jacket initial forms one layer thick jacket. The archesporial cell forms a two layered nutritive tapetum on the outside and the sporogenous cell inside.

The sporogenous cell develops 16 spore mother cells but some of them may abort so that the number of spores after reduction division may be 64 or less. The process of differentiation of haploid spore from the diploid spore mother cell is called sporogenesis. The spore mother cells round off and separate from one another. The tapetal cells start disorganising. Each

spore mother cell undergoes meiosis to form four haploid nuclei. As a result of simultaneous laying down of the walls between the nuclei, tetrads of haploid cells are called the spore tetrads and are tetrahedral in form. Later the spores secrete their own walls and separate from each other

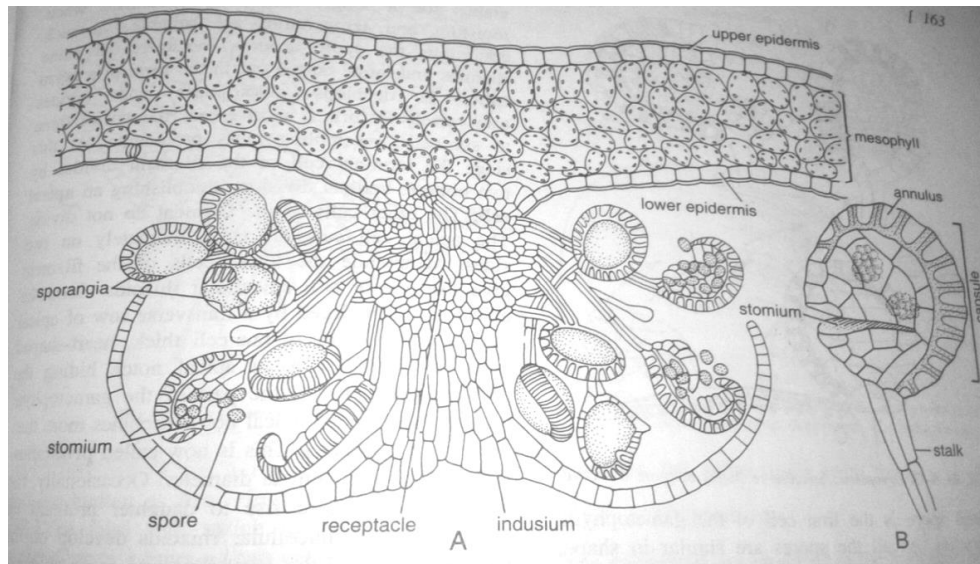


Fig. 5.41. *Dryopteris*: A. Vertical section through sorus (also showing leaf structure) B. A sporangium

**Dehiscence of sporangium:** The sporangia normally open in the dry weather. The annulus and stomium are directly concerned in the process. The mature sporangium dries out. It loses water all over its surface including the annulus cells consequently their thin outer walls are drawn inwards. The combined suction forces set up the entire annulus causes tension bending the annulus backwards. As a result the stomium ruptures between the lip cells. In the second stage the annulus suddenly snaps back to its original position like a spring hurling the spores into the air. As drying continues a stage is reached when the cohesive force of water within the annulus cells is not so great as to hold the outer thin walls in a sucked in position. Consequently they are pushed outward explosively. As a result the annulus along with the ruptured upper part of the capsule snaps back to its original position throwing the spores with a jerk, into the air forcibly. The spores are carried away by the wind. They remain viable for a long period. The dry conditions are essential for spore dispersal.

## Gametophyte

**Spores:** Spore is more or less tetrahedral, monolete, bilateral, minute, dusty and dark coloured and surrounded by two coats called (i) The outer exine or exosporium and (ii) inner intine or endosporium. The exine is covered by another coat called the perine or perispore. The cytoplasm store food but has no chloroplast.

**Germination of spore:** Under suitable conditions of moisture and temperature the spore germinates to produce the prothallus. It absorbs water and swells up, the latent cytoplasm rejuvenates and a metabolic activity starts. The exine ruptures and the intine protrudes out



along with enclosed contents in the form of a small germ tube. The germ tube elongates and its cytoplasm develops chloroplast and divides into an upper large cell and lower small cell. The lower cell loses chloroplasts and act as the primary rhizoidal cell. It gives out the first rhizoid which establishes contact with the substratum. The upper cell is called the prothallial cell and contains many chloroplasts. By further transverse division and elongation it develops into a green, uniseriate filament 3-5 or even more cells in length.

**Structure of mature prothallus:** The adult prothallus is a small, green, flat, thallus like structure which is somewhat heart shaped in outline (Fig.5.42). It varies in size from 5 or 6 to 13 mm in diameter. It is several celled thick but thin in texture. The cytoplasm forms a thin lining layer within the cell wall and contains a single nucleus, many small discoid chloroplasts and a central vacuole. Many delicate, brown, hair like thin walled unicellular unbranched rhizoids arise from the lower surface of the cushion. Being green the prothallus is autotrophic in its mode of nutrition thus, it is self supporting haploid plant of the gametophytic generation and concerned with the sexual reproduction.

**Sex organs:** The prothallus is monoecious and bears sex organs on the ventral side. The antheridia (male sex organs) arise among the rhizoids towards the posterior side of the prothallus and are emergent. The archegonia develop in central cushion behind the apical notch. The necks of archegonia are bent towards the antheridia and protrude above the surface of the prothallus. The ventral position of the sex organs exposes them directly to moist air and water, which are necessary for their development and dehiscence. The monoecious prothalli are always protandrous. This device is helpful in bringing about cross fertilization. The antheridia are small, sessile and globular structures. Each antheridium consists of a wall and is made up of three tubular cells. These three cells are called (i) first ring cell, (ii) second ring cell and (iii) an opercular or cap cell. The antheridial wall encloses about thirty-two spermatozoids

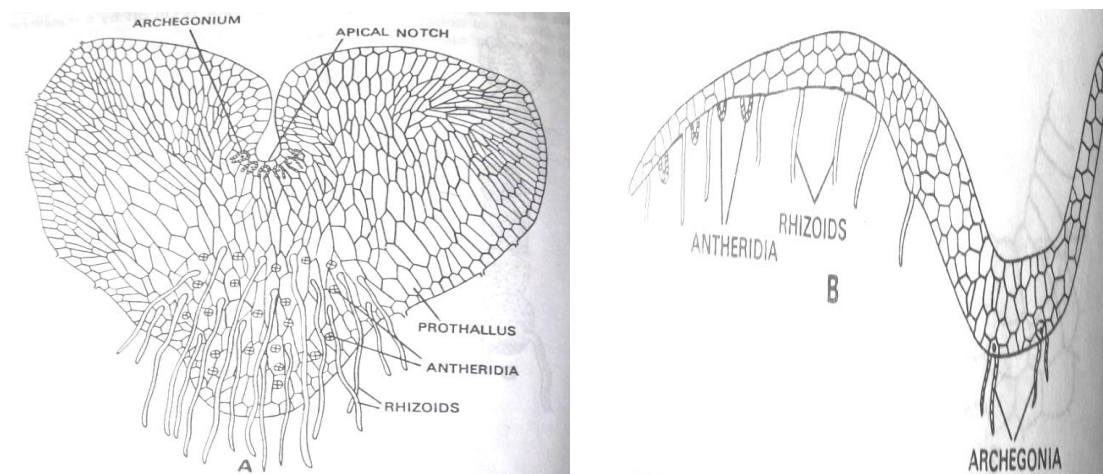


Fig.5.42. *Dryopteris*: A. A mature prothallus. B. Vertical longitudinal section of prothallus showing archegonia and antheridia

**Development of antheridium:** In the development of antheridium, a superficial antheridial initial divides transversely. The outer cell is pushed in by turgidity to form a

funnel cell penetrating the inner one which then becomes a ring cell (Fig 5.43 B). The funnel cell cuts off a peripheral dome cell and an inner primary androgonial cell (Fig 5.43 C). The mature antheridium bulges out of the prothallus and at maturity the cover cell is pushed off and sperms are liberated. Dehiscence is affected in the presence of water which is absorbed by the mucilaginous antheridial wall and consequently by the spermatid walls. This results in swelling of spermatids and antheridial wall. The membrane soon dissolves and the spermatozoids become free to swim.

**Archegonium:** Each archegonium that projects from the lower surface of the prothallus is a flask shaped organ. It consists of a swollen base, the venter and a projecting short slender neck. The venter is sunk in the tissue of the prothallus. The neck cells enclose a central neck canal.

**Development of archegonium:** The archegonium develops by the division of archegonial initial into a primary cover cell, a central cell and a basal cell (5.43 F). Primary cover cell forms four neck initials which divide transversely to form a neck of 5 to 7 cell high. The central cell gives rise to a binucleate neck canal cell, a ventral canal cell and an egg. The basal cell divides to form a few celled base (5.43 G).

**Fertilization:** It occurs in the presence of water between the lower surface of the prothallus and the soil. Both kinds of sex organs are in contact with the moist earth and open on the lower surface of the prothallus. During fertilization the ventral canal cell and neck canal cell along with the tip of the neck disintegrate and passage become full of mucilage and chemicals like malic acid. This chemical attracts large number of sperms and some of them make their way down in the venter to the egg (Fig.5.43 H). One of these enters the egg to accomplish fertilization. The male and female nuclei fuse. The fertilized egg secretes a wall around it becomes a zygote or oospore.

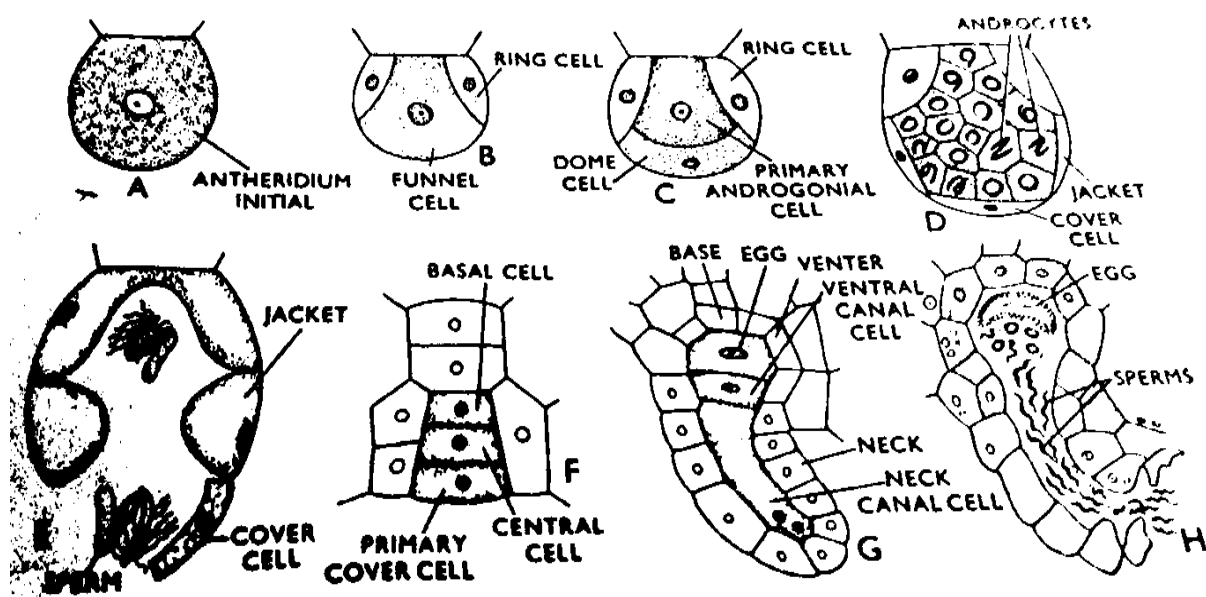


Fig.5.43 *Dryopteris*: A-E Stages of development of antheridium; F-H. Stages in the development of archegonium

**Development of embryo:** The zygote divides by a wall parallel to the long axis of the archegonium forming two unequal cells. The smaller cell which is towards the apex of the prothallus is epibasal cell and the larger is hypobasal cell. The second wall is laid in the transverse plane and forms a quadrant stage (Fig5.44B).

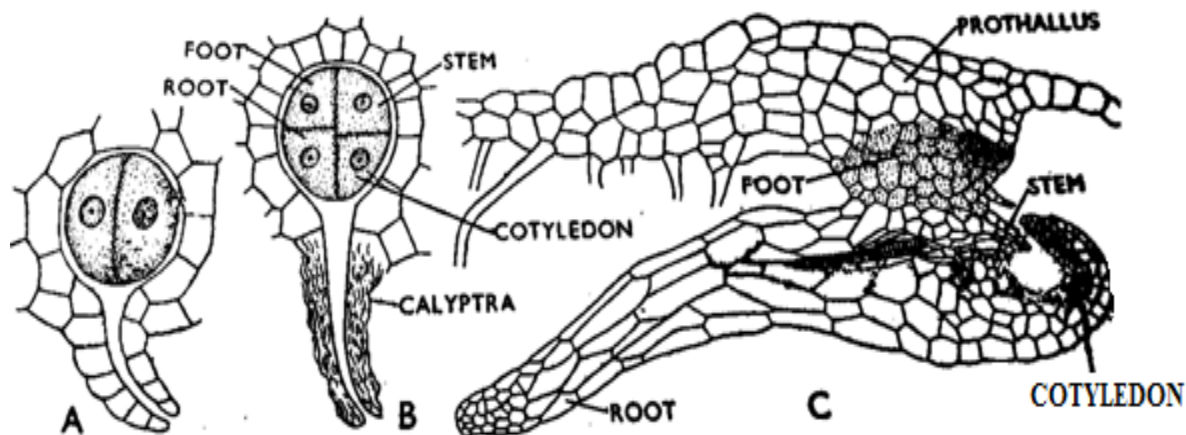


Fig.5.44: *Dryopteris*: Stages of development of embryo

During further development the root grows rapidly and pierces through the calyptra and establishes contact with the soil. Later the first leaf emerges through the apical notch of the prothallus. It turns green and starts photosynthesis. The shoot grows slowly and becomes evident after the young sporophyte has produced a few young and juvenile leaves and primary roots. The shoot grows underground and bears adventitious roots and young fronds.

## 5.5.2- Marsileales

### 5.5.2.1 *Marsilea*

**Distribution and habitat:** The plants are herbaceous with rhizomatous stem, creeping on or just below the soil surface. The species of *Marsilea* are generally aquatic or amphibious in nature with their roots embedded in mud or damp soil. The aquatic species viz. *M. minuta* and *M. quadrifolia* occur in fresh water ponds, shallow water, or in mud or damp soil. *M. condensata* and *M. rajasthanensis* are near xerophytic forms which grow in dry soil.

### Sporophyte

**External features:** The sporophytic plant body of *Marsilea* shows differentiation of stem, leaves and roots (Fig.5. 45).

**Stem:** The stem is long, slender and freely-branched rhizome of indefinite growth that grows on or just below the soil surface. It is differentiated into nodes and internodes. The internodes are generally long in aquatic species but are short in sub-terrestrial or terrestrial species. The production of underground tubers on rhizome has been reported only in *M. hirsuta*.

**Leaves:** The leaves arise from the nodes and are arranged alternately in two rows on the upper side of the creeping rhizome. The leaves are long petiolate and palmately compound, each having four leaflets in many species, but sometimes the number of leaflets varies from 3-8. A young leaf shows circinate vernation. At maturity the pinnae are extended perpendicular to the petiole. The venation is of closed reticulate type.

**Root:** The primary roots are short-lived (ephemeral) and are replaced by adventitious roots. Roots usually arise at nodes on the lower side of the rhizome. However, in some species (e.g., *M. aegyptiaca*) the roots arise from the internodal region of the rhizome.

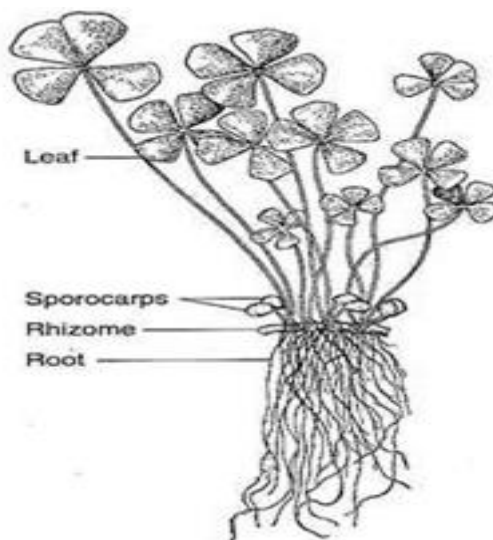


Fig.5.45: External features of Marsilea

## Anatomy

**Rhizome/stem:** A T.S. of the rhizome (stem) shows epidermis, cortex and the stele from periphery to the center (Fig. 5.46). The outermost layer is epidermis, composed of compactly arranged thick-walled cells and is devoid of stomata. The cortex is extensive and differentiated into three layers viz., outer cortex, middle cortex, and inner cortex. The outer cortex is parenchymatous with large air spaces. The air chambers are separated from each other by a single-layered septum. The middle cortex is sclerenchymatous, while the inner cortex is made up of compactly arranged parenchymatous cells. The air spaces are absent in xerophytic species (e.g., *M. aegyptiaca*). The stele is amphiphloic solenostelic which occupies the centre of the rhizome. Xylem occurs in the form of a ring and is surrounded on either side by phloem. The central part of the stele is occupied by pith which is parenchymatous in aquatic species and sclerenchymatous in xerophytic species (e.g., *M. aegyptiaca*). The stele is bounded externally by outer pericycle and outer endodermis, while it is bounded internally by inner pericycle and inner endodermis.

**Petiole:** In T.S., the petiole differentiates into epidermis, cortex and stele (Fig. 5.47). The epidermis is cutinized and composed of single-layered rectangular cells. The cortex is differentiated into outer and inner cortex. The outer cortex consists of aerenchyma having many air-cavities separated by one-celled thick septa. The stele is protostelic with diarch and

exarch xylem. The xylem has two large metaxylem elements at the center and protoxylem elements at each end towards the periphery. Phloem bands are present on either side of xylem (Fig. 5.47).

The vertical section of the leaflet shows epidermis, stomata, mesophyll and vascular bundles. Stomata are present in the upper epidermis (in submerged species) or on both the upper and lower epidermis (in terrestrial and amphibious species). Mesophyll tissue is differentiated into palisade and spongy parenchyma and generally associated with vertical airspaces. The vascular bundles are concentric with a central core of xylem surrounded by phloem. Each vascular bundle is separated from the mesophyll tissue by a layer of endodermis.

**Leaflet:** A layer of upper epidermis on the upper surface and lower epidermis on the lower surface is present. The vascular bundles are concentric. The xylem is surrounded by phloem and a layer of endodermis (Fig. 5.48).

**Root:** In transverse section, the root shows three distinct regions: the epidermis, the cortex, and the stele (Fig. 5.49). The epidermis is composed of single-layered parenchymatous cells, outer walls of which are thickly cuticularised. The cortex is differentiated into three zones, viz., the outer cortex, the middle cortex, and inner cortex. The outer cortex is aerenchymatous with many air spaces separated by radially elongated septa. The middle cortex is parenchymatous. The inner cortex is thick-walled, sclerenchymatous, internally bounded by the successive layers of endodermis and pericycle.

## Reproduction

**i. Vegetative reproduction:** Under some unfavourable circumstances the subterranean branches of the rhizome form tubers. These structures have reserve food in the form of oil globules which help them to overcome the unfavourable conditions. On return of the favourable conditions, these tubers germinate and form new plant body (e.g., *M. hirsuta*, *M. minuta*, *M. erosa*).

**ii. Reproduction by spores:** *Marsilea* is a heterosporous fern. It produces two types of spores i.e., the microspores and the megaspores. The microspores and megaspores are produced in microsporangia and megasporangia, respectively, and the sporangia are enclosed in special bean-shaped structures called sporocarps. When young, the sporocarps are soft and green, but turns dark brown and hard at maturity. The sporocarp develops at the short branch of petiole called pedicel or stalk. In most species they occur singly, but in some species the number varies from two to twenty.

The sporocarp wall is hard, thick, thus resistant against mechanical injury. Anatomically, the wall is differentiated into three layers. The outer layer is epidermis made up of single-layered cuboidal cell with sunken stomata. The middle layer is made up of radially elongated compactly arranged thick-walled palisade cells. This is followed by second palisade layer which is comprised of more elongated thin-walled palisade cells. A vertical longitudinal

section (VLS) of sporocarp away from the plane of the stalk reveals many sori arranged in vertical rows (Fig. 5. 50 A). In this plane of section either megasporangia or microsporangia are visible. Each sorus is surrounded by an indusium. The development of sori is of gradate type. The gelatinous mucilage ring is more prominent in dorsal side.

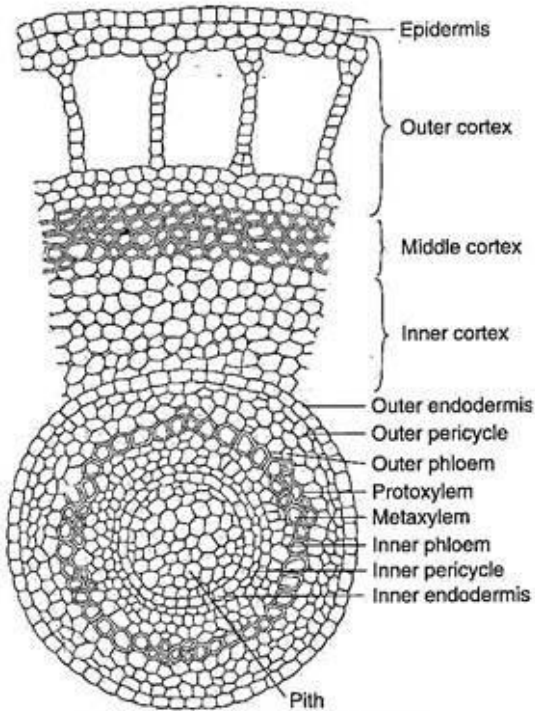


Fig.5.46. Marsilea: T.S. rhizome/stem

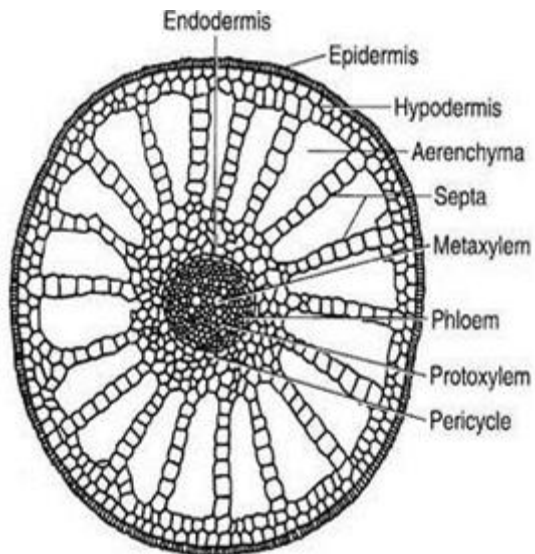


Fig.5.47. Marsilea: T.S. petiole

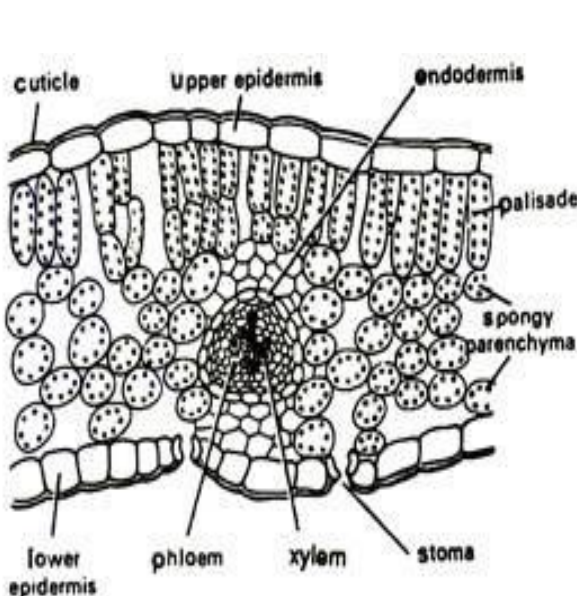


Fig.5.48 Marsilea: T.S. leaflet

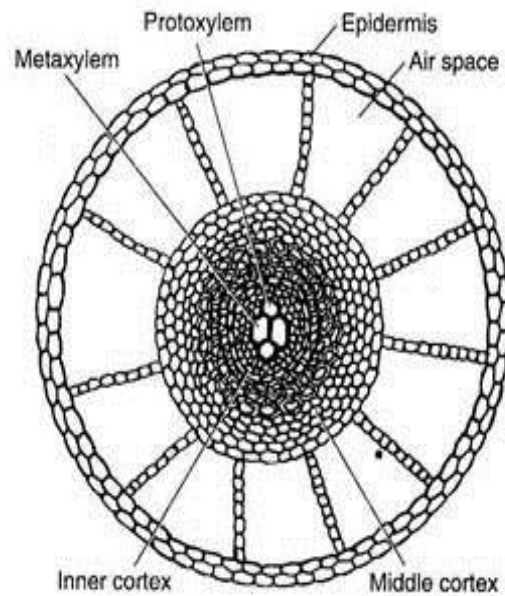


Fig. 5.49. Marsilea: T.S. root

A horizontal longitudinal section (HLS) cuts each sorus transversely and it is seen that each sorus is an elongated structure, covered by a delicate indusium. The sori are gradate, basipetal in arrangement with a row of largest sporangia (megasporangia) at top and two rows of

smaller sporangia (microsporangia) on two sides (Fig. 5. 50 B). The mucilage ring is present in the form of two masses, one in the dorsal and the other in the ventral sides.

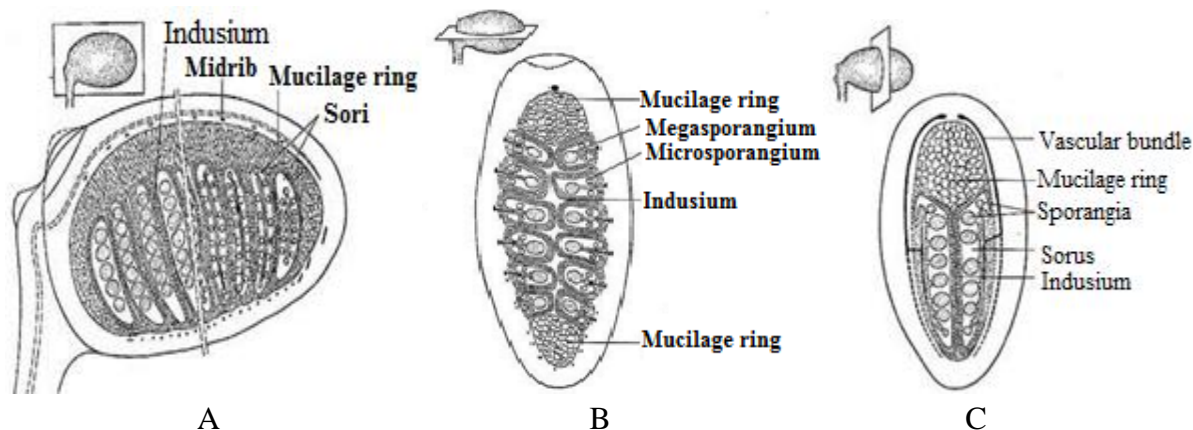


Fig.5.50: *Marsilea*: L.S. of sporocarp, A. Vertical. B. Horizontal C. Vertical

A vertical transverse section (VTS) of the sporocarp shows only the sori on two sides (Fig. 5.50 C). Both the sori contain megasporangia if the section is taken through the megasporangia or the sori contain only microsporangia if it is taken through the microsporangia. The sporophore is seen in the form of two masses on either side. The mucilage ring is present only on the dorsal side.

**Development of sporangium:** Sporangial development is of the leptosporangiate type. The development of both the micro- and megasporangia is almost alike. The sporangial initials for megasporangium and microsporangium are formed at top and at the sides of the receptacle, respectively. The initial cell divides periclinally (transversely) into an outer and an inner cell. The inner cell does not take part in further development. The outer cell undergoes three successive diagonal divisions and forms a tetrahedral apical cell with three cutting faces. This apical cell cuts off two segments along each of its three cutting faces which form the stalk of the sporangium. Now the apical cell divides with the help of an arched periclinal wall towards its outer face and forms an outer jacket initial and an inner tetrahedral archesporial cell. The outer jacket initial divides anticlinally to form a single-layered jacket.

The archesporial cell divides periclinally to form an outer tapetal initial and an inner primary sporogenous cell. Anticlinical and periclinal divisions of the tapetal initial forms a two-layered thick tapetum. The primary sporogenous cell divides to form a mass of either 8 or 16 spore mother cells. Spore mother cells ( $2n$ ) undergo meiotic division to form 32 or 64 haploid spores ( $n$ ). The developments of both the sporangia are similar up to this stage. In megasporangium, only one megaspore survives to become a large functional megaspore, while all the microspores are functional in microsporangium.

**Opening of the sporocarp:** The sporangium wall of *Marsilea* shows no sign of cellular specialization (e.g., formation of annulus) required for dehiscence of sporangium. The tissues slowly swell up by absorbing water in natural conditions. Thus the swelling puts pressure on the wall of the sporocarp and eventually it splits open along its ventral side into two halves. Splitting is followed by the emergence of a long, worm-like gelatinous structure to which the

sori are attached (Fig.5.51). The mucilaginous cord may become ten or fifteen times larger than the sporocarp. Following the release of the sori from the sporocarp, the indusia and the sporangial wall disintegrate and the spores are liberated.

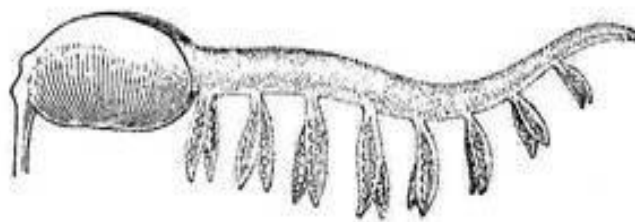


Fig.5.51: *Marsilea*: Extrusion of the sori on the mucilaginous cord

## Gametophyte

*Marsilea* is heterosporous i.e., they produce microspores and megaspores which eventually germinate to form the male and female gametophytes, respectively.

**Male Gametophyte:** The microspores are small, globose structures with a thick outer ornamented exine and inner thin intine. The outer exine is covered by a thin layer called perispore. The microspore contains a distinct haploid nucleus and its cytoplasm is rich in starch grains. The microspores germinate inside the spore wall (endosporic type) almost immediately after its release. It divides asymmetrically to form a small prothallial cell and a large apical cell (1-1). A division (2-2) of apical cell diagonal to prothallial cell forms two antheridial cells. Then both the antheridial cells divide diagonally (3-3) with curving wall forming the first jacket cell and large wedge-shaped cell. The jacket cells do not divide, but the wedge-shaped cell divides periclinally (4-4) to form smaller inner cell (2nd jacket) and a large outer cell. Further, the periclinal division (5-5) of outer cell forms 3rd jacket and primary androgonial cell. At this stage the male gametophyte consists of one prothallial cell, 6 jacket cells and 2 androgonial cells. After several divisions of the primary androgonial cells, sixteen androcytes are formed surrounded by jacket cells. Later the prothallial cell and the jacket cells disintegrate and the two groups of androcytes, representing the two antheridia, float freely in the cytoplasmic mass within the original spore wall. Each androcyte becomes a motile antherozoid by dissolution of the androcyte membrane. The antherozoids multiflagellate structure characterised by the presence of a large posterior cytoplasmic vesicle.

**Female Gametophyte:** The megaspore is an oval or elliptic structure, the wall of which imbibes water and expands to form a gelatinous mass around the megaspore. The spore wall expands to form a small papilla (protuberance) at the apical end where the nucleus is located in a dense part of cytoplasm. The remaining portion of the spore is filled with a frothy cytoplasm full of starch grains. Development of megagametophyte is depicted in Fig.5.52.

**New Sporophyte (The Embryo):** The zygote is the mother cell of the next sporophytic generation. The first division of the zygote is vertical (in relation to the neck of the



archegonium) followed by a transverse division resulting in the quadrant stage (four-celled stage) of the embryo (Fig. 5.53A, B). Subsequent development of the upper two cells forms the root and leaf, whereas the lower two cells give rise to the foot and shoot apex (Fig. 5.53 C, D). With the development of the embryo the vegetative cells of the surrounding gametophyte divides periclinally and form a two- to three-layered sheath (calyptra) around the embryo. The primary root grows vertically and establishes the sporophyte in the soil. The young sporophyte has a well-developed primary root and leaf.

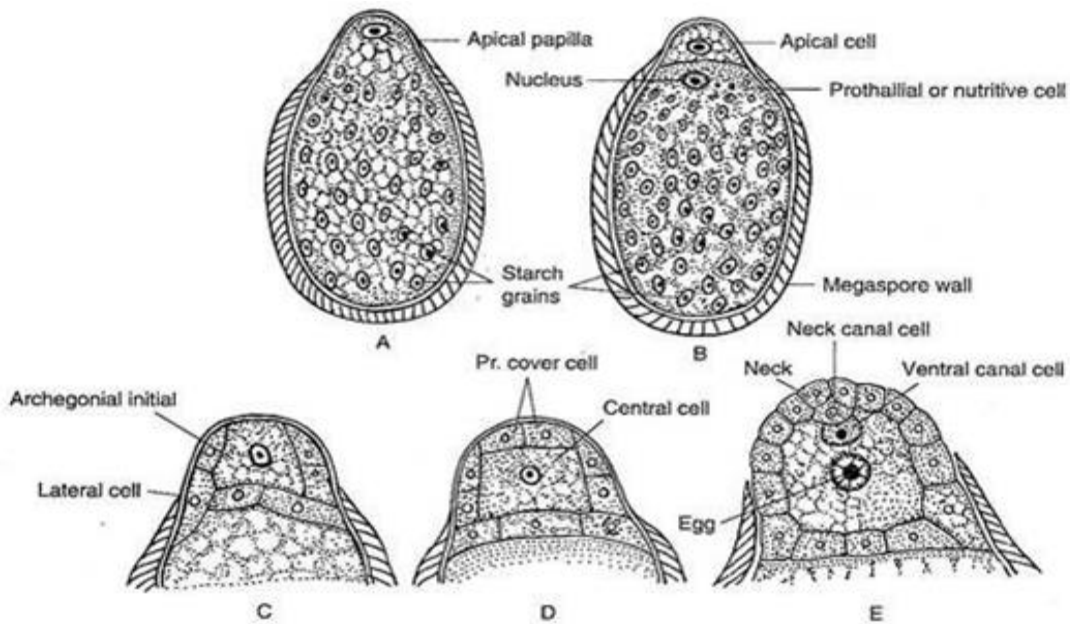


Fig.5.52. Marsilea: A. Megaspore, B-D. Stages in the development of megagametophyte and E. A mature archegonium

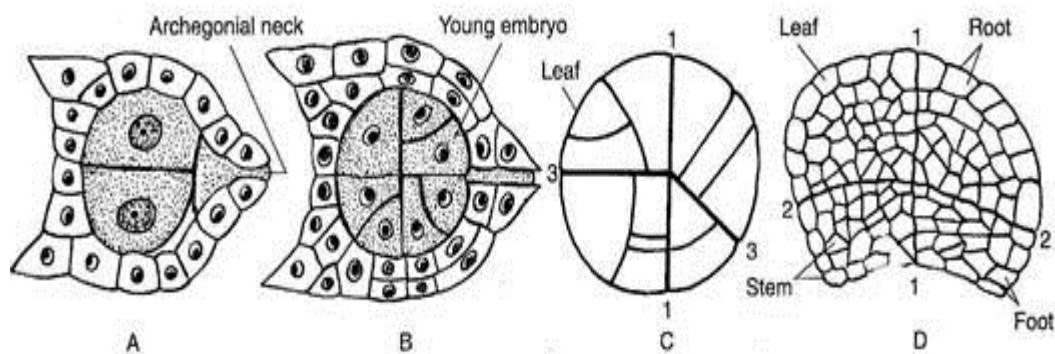


Fig.5.53. Marsilea: A-D The stages in the development of embryo

### 5.5.3-Salviniales

#### Salvinia

**Occurrence and distribution:** The genus *Salvinia* has 12 species most of which are found to be distributed in the African continent. The genus is represented in India by two species

namely *S. natans* and *S. auriculata*. *S. natans* is found in Kashmir. Of the several species of *Salvinia*, *S. natans* is the only annual.

### **Sporophyte**

**Morphology:** The sporophytic plant body consists of a long slender floating rhizome which grows horizontally. The rhizome is completely covered by whorls of leaves.

**Leaves:** Leaves are oblong or sometimes hemispherical. They usually arise in groups of three. Of the three leaves, two lateral ones float on the surface of water while the third one is submerged. There is a distinct morphological difference between the submerged and floating leaves. The submerged leaves are highly dissected, long and filiform. They resemble very much with the roots. But it is not certain whether they also function like roots. **It is very often suggested that the function of fill form leaves is:** (i) To protect the sporocarp and(ii) To act as a ballast or a stabilizer in preventing undue drift of the plant.

The floating leaves are green and ovate or oblong. They are covered with stiff hairs that prevent wetting. Besides the hairs, papillate projections are also found. The members of the leaf whorl alternate at successive nodes, so that there are actually six rows of leaves though the arrangement apparently suggests three rows.

**Stem:** The stem is divided into nodes and internodes and a branch initial is always produced at every node. But the stem is sparsely branched because of the non-functioning of many of the branch initials.

**Roots:** There are no roots in the sporophyte. Absorption is mainly carried out by the general surface. It is suggested that the hair like structures found on the submerged filiform leaves may help in the absorption of water and nutrients. These hairs however are different from root hairs in being multicellular.

### **Anatomy**

**Rhizome:** A transverse section of the rhizome shows the following features. Outermost layer is epidermis. It is distinct; single layered and is made up of thin walled cells. Epidermis on its outer surface is covered by a thin cuticle. Stomata are absent. Next to the epidermis is the cortex. It consists of a number of lacunae or air cavities (Fig. 5.54A). In the central region is found the stele. The stele is surrounded by an endodermis and a pericycle (Fig. 5.54B). True to the hydrophytic nature, the rhizome shows poorly developed vascular elements. Central region of the stele consists of parenchyma within which are found many tracheids. Xylem is surrounded by phloem. The vascular arrangement suggests an ectophloic siphonostele.

**Leaf:** Anatomically, the floating leaves show a bifacial arrangement. There are two epidermal layers surrounding a mesophyll with plenty of air cavities. The mesophyll is undifferentiated. The epidermal layers are studded with multicellular hairs. The submerged leaves, anatomically exhibit a siphonostele near their base. A little higher up, the single

vascular strand first breaks up into two and ultimately into a number of small ectophloic steles. Surrounding the vasculature, pericycle and endodermis are distinguishable.

## Reproduction

The sporophyte reproduces by means of sporangia. As in *Marselia*, the sporangia are aggregated into sporocarps. The details of reproduction have been studied extensively in *S. natans*. The sporocarps appear in clusters ranging in number from 4 to 20. The sporocarps are usually borne on the inner segments of submerged leaves. In arrangement, the sporocarps are sympodial. The shape of the sporocarp varies from globose to ovoid, occasionally flattened also with ridged surfaces. The wall of the sporocarp is made up of two layers of cells. The outermost layer when young is clad with hairs. Externally all sporocarps are alike. But unlike in *Marselia*, the sporocarps are unisporangiate. The first one or two sporocarps in each cluster are megasporangiate whereas all the later formed ones are microsporangiate. The sporocarp at its base has a stout columnar receptacle which carries the vascular supply into the sporocarp. The receptacle is unbranched in the megasporangiate sporocarps of *S. natans*.

**Development of sporocarp:** The entire sporocarp is traceable to a single apical cell (Fig. 5.55A). This apical cell with its two cutting faces cuts off cells towards its left and right. Very soon a sorus primordium is resulted. A little later, an outgrowth surrounds the sorus primordium. This later develops into the indusium completely covering the sorus. The derivatives of soral primordium gives rise to sporangial initials, which later develop into the sporangia (Fig. 5.55 B-E).

**Structure of a Mature Sporocarp:** A sectional view of mature sporocarp shows a well-developed wall enclosing the, sporangia. In a megasporangiate sporocarp, only about 25 megasporangia are seen whereas in a microsporangiate sporocarp, the number is much larger because of the branching of the receptacle (Fig. 5.56 F).

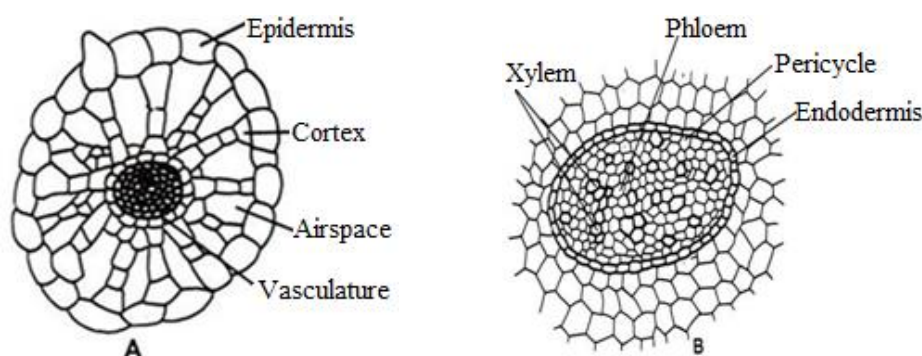


Fig.5.54: *Salvinia*: A. T.S. of stem; B. Stellar portion enlarged

**Structure and development of sporangia:** The sporangial initials whether of micro or mega-sporangium arise on the distal end of the soral primordium (Fig. 5.55E). The development of sporangium is of the leptosporangiate type. The first division of the sporangial initial is transverse resulting in two superposed cells. Of these, the upper one develops into the wall whereas the lower one gives rise to the sporogenous tissue. The

sporangial development upto the sporocyte stage is similar in both micro and mega-sporangia. While only a few spore mother cells survive in megasporangium while quite a large number do so in microsporangium.

The mega-sporangium consists of a short stalk and a generally ovoid capsule. The capsule is made up of a single layer of cells. Internal to the wall of the capsule is a layer of tapetum. Enclosed by the tapetum are found 8 mega-sporocytes which divide meiotically to produce 32 megaspores. Of these spores, all except one degenerate. The degenerating spores and the tapetum harden and surround the functional megaspores in the form of a thick layer. This is often called the 'perispore' or 'episporium'. The perispore towards the apex of the sporocarp forms a triangular chamber, which very much simulates the pollen chambers of gymnosperms. Arising from the floor of the pollen chamber is a central mound of tissue with three flaps. These three flaps get separated during the germination of megaspore.

The microsporangia are basically similar to mega-sporangia in their construction. Enclosed in the sporangium are 16 microspore mother cells and consequently 64 microspores are formed. All the spores attain maturity and survive. The microspores are embedded in the cytoplasmic fluid derived from the tapetum. As the spores mature, the tapetal cytoplasm encompassing the spores gets hardened and forms a mass called 'massula'. The microspores are extremely small, triradiate in appearance and have two wall layers. There is a single nucleus in each microspore.

**Dispersal of sporocarp:** After the maturity of sporangia, the sporocarps get detached from the leaves and sink to the bottom of the pond. In annual species, this generally takes place during September, when the plant breaks up into bits. The sporocarps open up due to the mechanical decay of their walls. This results in the release of spores. In most of the cases the spores that float on the surface of water are still surrounded by the sporangial walls.

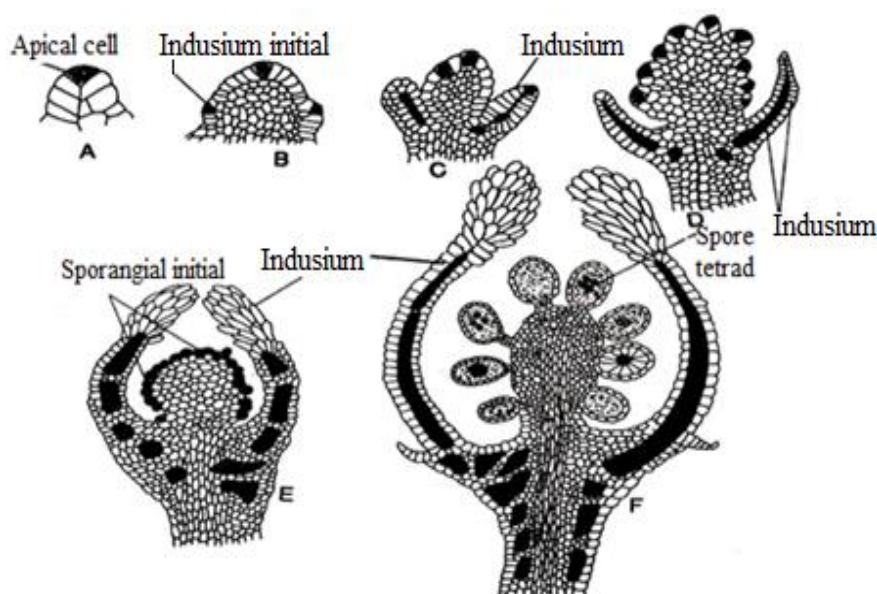


Fig.5.55. *Salvinia*: Stages in the development of sporocarp and sporangia. A. Sorus primordium with apical cell; B. Initiation of Indusium; C-D. Developmental stages; E. L.S. of young sporocarp; F. L.S. of mature sporocarp

## Gametophyte

Two types of gametophytes may be expected since *Salvinia* is heterosporous. In both micro and mega gametophytes the development is endosporic. The gametophytes begin their development much earlier to the dehiscence of the sporangium.

**Structure and development of megagametophyte:** The megaspore generally floats on the surface of water in a prone position. Prior to the first division, the nucleus migrates to the apical portion of megaspore. First division of the nucleus results in forming two unequal cells. The upper cell is small and lenticular while the lower cell is very large and is filled with plenty of nutrition. Most of the gametophyte is derived from the upper lenticular cell, while in the lower large cell there are only free nuclear divisions. This multinucleate cell functions as a store house of reserve food material. The upper lenticular cell by means of several divisions forms a lobed apical cushion which comes out penetrating the spore wall and perispore. Archegonia appear on this apical cushion. Generally, two to four archegonia develop in the apical cushion. The archegonia are deeply sunken in the apical cushion. They have a very short neck, an egg cell, a ventral canal cell and a bi-nucleate neck canal cell.

**Structure and development of micro-gametophyte:** The microsporangium does not dehisce; hence the microspores develop within the microsporangium. As the first sign of development, the microspore gets divided into three cells. Of these, the lowest divides slightly obliquely to form a prothallial cell. Further divisions are restricted only to the upper two cells. From these two cells, by successive divisions, two spermatogenous cells and four sterile cells are formed. The four sterile cells constitute the jacket cells. The two spermatogenous cells by further divisions form eight spermatocytes which appear in two clusters separated by means of a sterile cell. When the gametophytes are mature the sterile cells (Jacket cells) disintegrate, releasing the multi-flagellate spermatozoids which develop from the spermatocytes.

**Fertilization:** The female gametophyte at maturity exposes the archegonia. In the archegonium, the neck canal cell and ventral canal cell disorganize to facilitate the entry of the sperms. A large number of sperms enter into the neck of the archegonium while only one succeeds in fusing with the egg. The resultant zygote develops into embryo.

**Embryogeny:** The first division of the zygote is longitudinal i.e., parallel to the long axis of the neck of the archegonium the next division is transverse resulting in the formation of a quadrant. Vertical division of the quadrant cell results in the octant stage. The basal cells of the octant form a foot which is haustorial in nature. Of the remaining upper four cells of the octant, the two anterior ones develop into the first leaves. Of the remaining two cells, one gives rise to the stem apex while the other is functionless. There are no roots in *Salvinia*. Further divisions from the octant stage onwards are bit difficult to follow. From the octant cells, a cell plate is formed, which functioning like a column that connects the foot with the leaf and stem apex. According to some workers the foot plus the column represents a

vestigial root. The leaf segment enlarges and grows into a cordate leaf. The stem apex divides actively and forms the rhizome.

## *Azolla*

### Sporophyte

The sporophyte is extremely small when compared with *Marsilea* and *Salvinia*. It is distinguishable into stem, leaves and roots. The stem is often called the rhizome. It is profusely branched and its upper surface is covered with dense leaves (5.56 A). The leaves are alternate and are arranged in two rows. Each leaf has two lobes, the upper lobe being aerial and green in colour. The lower lobe is thin and colourless and is completely submerged in water. The dorsal lobe encloses large mucilage filled cavities. Inhabiting these mucilage cavities is found a Cyanophycean alga-*Anabaena azollae* (Fig. 5.56 C). According to Oes (1913), the relationship between alga and *Azolla* is symbiotic. While the alga provides nitrogen to the plant the latter gives it shelter. The same species of *Anabaena* occurs in *Azolla* all over the world. The rhizome on its lower surface produces simple roots either singly or in clusters. These roots help in stabilising the plants in water.

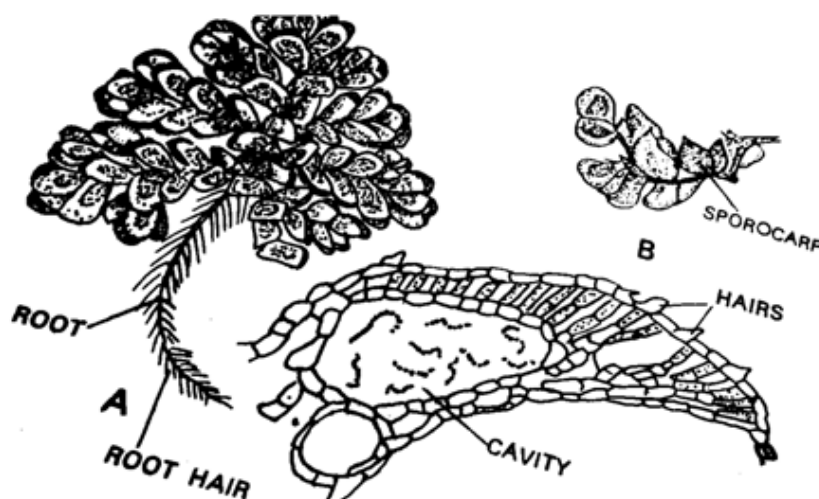


Fig.5.56. *Azolla*: A. Sporophyte; B. Sporocarp; C. Leaf

### Anatomy

**Rhizome:** The rhizome, anatomically resembles other ferns. A cross section shows an epidermis, a middle cortex and a central stele (Fig. 5.57). Epidermis is single layered and it encloses a cortex which is 4-8 cells broad. There are no air cavities in the cortex as in *Salvinia*. The stele is surrounded by an indistinct endodermis. Internal to the endodermis is the pericycle. The vascular elements are greatly reduced. There are a few tracheids surrounded by phloem elements.

**Leaf:** Anatomically, the dorsal lobe of leaf shows two epidermal layers enclosing a thin mesophyll (Fig. 5.58). Stomata are found on both the epidermal layers. The upper epidermis is composed of one to two celled layers. The mesophyll is made up of loosely arranged cells.

Within the mesophyll is found a mucilage filled cavity containing *Anabaena*. It has been suggested that the hormogones of *Anabaena* enter into the cavity through a small pore and get themselves established.

**Root:** A cross section of the root shows a thin walled epidermis enclosing a two layered cortex. Next to the cortex is the endodermis and xylem made up of six tracheids surrounded by four phloem elements.

## Reproduction

The main method of reproduction in *Azolla* seems to be vegetative which is by fragmentation. The lateral branches get separated and develop into new individuals.

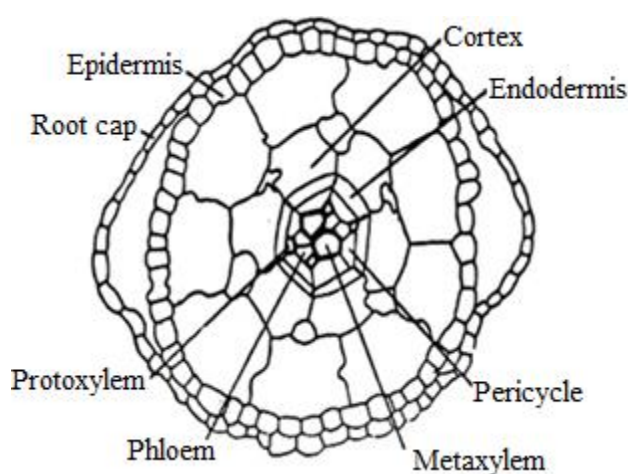


Fig. 5.57. *Azolla*: T.S. of root

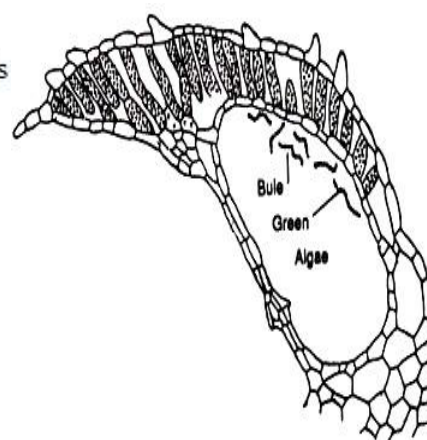


Fig. 5.58. *Azolla*: Internal structure of Leaf showing endophytic blue green alga

**Spore production:** The spores in *Azolla* are produced in sporangia which in turn are enclosed in sporocarps as in *Marsilea* and *Salvinia*. The sporocarps are usually borne on the first leaf of the lateral branch. In fertile leaves, the submerged lobe is usually divided only twice, and on each a sporocarp is produced terminally. The upper lobe of the leaf forms a marginal flap covering the sporocarp. The sporocarps are unisporangiate. They have either microsporangia or megasporangia. There is a size difference also between mega-sporocarps and micro-sporocarps. The former are small and have only one megasporangium, while the latter are large and have a number of microsporangia. The wall of sporocarp is two layered. In a mega-sporocarp, the mega-sporangium arises on a small receptacle at the base. The sporangium is covered by a two layered indusium. In a microsporocarp there is a central cushion like receptacle which gives rise to a number of microsporangia.

The development of the sporangium is of the leptosporangiate type. As the sporangia begin to emerge, a ring of meristematic tissue surrounds the sporangium and forms the sporocarp wall. The wall ultimately becomes two layered thick. In some cases the filaments of *Anabaena* which are commonly present above the stem apex may get enclosed in the top of the sporocarp cavity. In a megasporangium there are usually eight mega-sporocytes surrounded by a layer of tapetum. The tapetal cells break down and form a plasmodium within which is

enclosed the sporocytes. The mega-sporocytes undergo reduction division and produce 32 spores of which all but one degenerate. The disorganising tapetal cells by now form four massulae. Of these one contains the functional megaspore while the other three hold together the remaining 31 abortive spores.

At maturity the wall of the sporocarp as well as of the sporangium break open helping in the further development. The development of the microsporangium is similar to that of mega-sporangium until the sporocyte stage. In the microsporangium all the 32 spores are functional. These spores get enclosed by the tapetal plasmodium. Here also the plasmodium forms four massulae, each containing more than one microspore. In *Azolla filiculoides* and *A. caroliniana*, many hooked processes arise from the massulae. These are called 'Glochidia'. Soon after the maturation, the sporangial wall dehisces and massulae with microspores lie freely in the cavity of the sporocarp. Subsequently, when the sporocarp wall ruptures, the massulae with the spores come out. The glochidia help in the attachment of the microspore massulae to the megaspore massulae.

### **Gametophyte**

The mature sporocarps usually sink to the bottom of the pond where the release of the massulae from the sporocarp takes place.

**Development of male gametophyte:** The microspore germinates within the massula. The spore wall breaks open and a small projection comes out. This projection is cut off by a cross wall at its base. The large cell filling the spore cavity cuts off a small lenticular basal cell. The outer cell divides into three, by cross walls. Of these, the outer and inner cells do not divide and they develop into the cap and basal cells of the antheridium. In the central two cells, periclinal divisions take place forming a central cell and two jacket cells. A division in one of the outer cells ultimately results in a total of five jacket cells surrounding a central cell. By further divisions the central cell produces eight spermatocytes. The spermatocytes metamorphose into spermatozoids.

**Development of Female Gametophyte:** Germination takes place in situ. The gametophyte never comes out of the confines of the spore. In the early stages of development *Azolla* resembles *Salvinia*. The first division forms a large basal cell and a terminal lenticular cell. The lenticular cell by further divisions forms an apical cushion from which an archegonium is formed. At this stage, the spore wall breaks open and the gametophyte bulges out a little. The archegonium in its structure and development resembles that of *Salvinia*. The lower large cell undergoes free nuclear divisions and serves as a store house of reserve food material.

**Fertilization:** Fertilization is affected when the sperms released from the micro-gametophyte reach the archegonium.

**Embryogeny:** The first division of zygote is transverse (Fig. 5.59 A). Subsequent divisions form the quadrant, from which develop the four primary organs of the plant namely, foot, root, stem, and leaf. The lower quadrant forms the root and foot while the upper quadrant



forms the leaf and stem (Fig. 5.59 H). The foot is cylindrical. It does not have further growth. The other three organs grow by means of an apical cell. The first leaf is like a funnel and it surrounds the stem apex. The development of the root is very slow. As the embryo continues its growth, the upper portions of the sporocarp and massulae are thrown off. The embryo rises to the surface of water when air chambers develop within the first leaf.

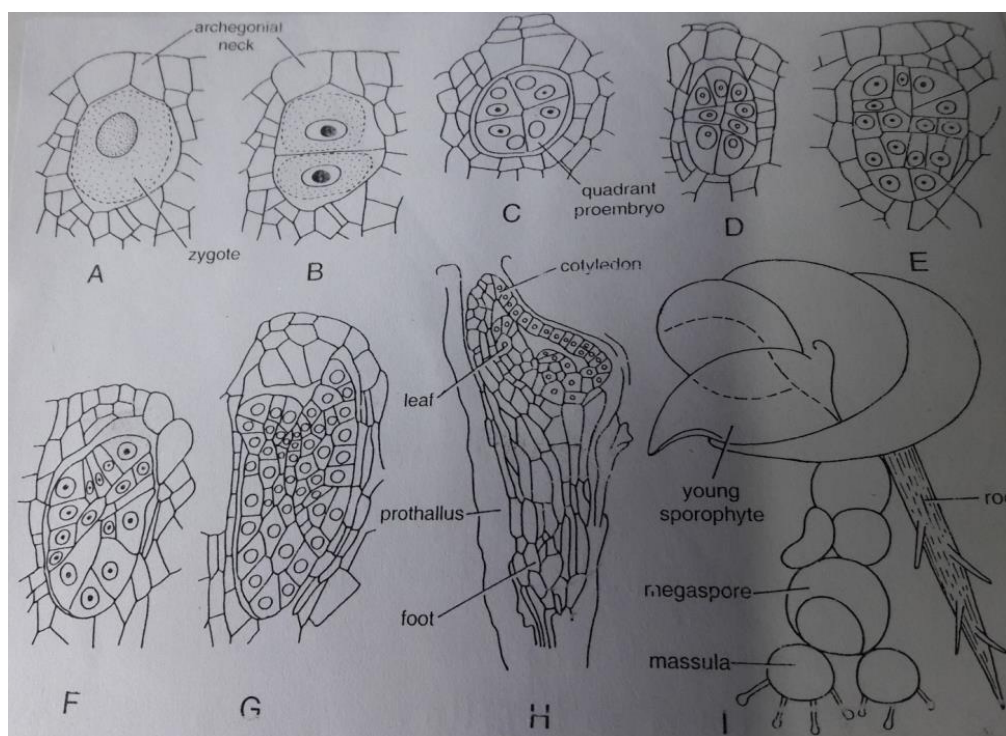


Fig.5.59. *Azolla*: Stages in the development of embryo

## 5.6 SUMMARY

This unit describes salient features of three subclasses (Eusporangiatae, Protoleptosporangiatae, and Leptosporangiatae) of class Pteropsida. The Eusporangiatae is represented by two orders viz. Ophioglossales and Marattiales. The members of Ophioglossales have herbaceous sporophyte with short, fleshy, naked rhizome which is buried in the substratum and are attached by thick radiating fleshy roots. The leaves have a straight (non-circinate) vernation and stipular sheath. The sporangia are borne on an outgrowth the fertile spike which usually arise from the adaxial surface of leaf usually near the junction of the lamina and petiole. The large sporangia are marginal in position and each is provided with a vascular supply at the base. The sporangia lack annulus and their wall is more than one cell in thickness. The spores are of one kind and give rise to tuberous, colourless, mycorrhizal, subterranean prothalli living saprophytically. The numerous sex organs are scattered on the prothallus. This subclass has a single order, Ophioglossales which in turns has a single family Ophioglossaceae including three genera of living plants: *Ophioglossum* and *Botrychium* (20 to 30 species each) are widely distributed genera and the monotypic *Helminthostachys*.

The order Marattiales includes nine genera grouped in five families. The living genera have sporophyte that possesses either short massive tuberous erect stems (*Angiopteris*, *Marattia*) or a creeping horizontal rhizome that are mostly dorsiventral (*Christensenia*, *Danaea*). The leaves range from a few centimeters in length in *Danaea* to 6 m long in *Angiopteris*. At the base of long petiole are two conspicuous thick fleshy stipules. The venation is open dichotomous in all genera except in *Christensenia* which has reticulate venation. In young stems the stele is an amphiphloic siphonostele with distinct gaps (solenostele) while in older stem it can be called apolycyclic perforated dictyostele. The sporangia are borne on the abaxial surface of the pinnule or simple leaf lying along the vein near to the margin as in *Angiopteris* or on the each side of groove as in *Marattia* or extended from the midrib to margins as in *Danaea* or are irregularly distributed between the main vein as in *Christensenia*. The sporangia in a sorus are either free as in *Angiopteris* or fused together to form synangia as in *Marattia*, *Danaea*, and *Christensenia*. The large sessile sporangia are eusporangiate in origin and spores are of one kind. The gametophytes are monoecious and large consisting of a dorsiventral, flat, several-celled thick green prothallus provided with an endophytic fungus.

The subclass Protileptosporangiateae is represented by a single order Osmundales which in turn has a single family Osmundaceae. It is considered as a connecting link between Eusporangiateae and Leptosporangiateae. The representative genera of this family, *Osmunda* and *Leptopteris* are terrestrial ferns with massive hard, erect or non-paleate stem. The pinnate or bipinnate compound leaves grow in tufts from the apices of the stem. In *Osmunda* the leaves are leathery in texture while in *Leptopteris* the bipinnate leaf is exceedingly thin. In *Osmunda*, the xylem forms a circle of horse-shoe shaped oval of irregular strands separated by parenchymatous rays that passes outwards from the large pith. The xylem strands vary in number from 15 in *O. regalis* to 40 in *O. claytoniana*. The sporangia are usually grouped in sori or protected by an indusium. The sporangia are attached to the margins of fertile segment forming marginal tassels. The development of sporangia is intermediate between the eusporangiate and leptosporangiate type of development. The mature sporangium is large, reddish brown, pyriform body with stout short stalk and spore contains many chloroplasts. On germination spore gives rise to an elongated cordate shaped, dark green and monoecious prothallus.

The sub class Leptosporangiateae includes all the ferns with leptosporangiate type of sporangial development (sporangium develops from a single superficial cell). The ferns under this sub class have been variously classified. Sporne divided this sub class into Filicales, Marsileales and Salviniiales. This unit described three representative genera of order Filicales (*Hymenophyllum*, *Adiantum* and *Dryopteris*), one member of Marsileales (*Marsilea*) and two members of Salviniiales (*Salvinia* and *Azolla*). In members of this subclass the wall of sporangium is one cell in thickness and encloses usually a definite number of spores. The antheridia are small and more or less project above the surface of prothallus. The main features of life-history of most of the Leptosporangiate members are fairly uniform throughout with a few exceptions. The variations are observed in the structure of the sporophyte, form and insertion of sori, the shape of indusium when present, structure of

receptacle, shape of spore and form of leaf etc. The *Marsilea*, *Salvinia* and *Azolla* are heterosporous plants and sporangia are enclosed in a special structure known as sporocarp. In *Marsilea* the sori contain both microsporangia and megasporangia and the sporocarps are interpreted as highly specialized pinnae. In *Salvinia* the sporocarp are typically monosporangiate. In *Azolla* though the sporocarps are potentially bisporangiate but during development the microsporangial initial abort in megasporocarp and megasporangial initial abort in microsporocarp. The germination of spore takes place either under water as in case of *Salvinia* or on the surface of water as in *Azolla*.

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## 5.7 GLOSSARY

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**Annulus:** a row or patch of partially or entirely thick-walled cells of the capsule of the leptosporangium which contracts and forces the capsule to open and to discharge its spores.

**Antheridium:** The male sex organ of pteridophytes borne on the gametophyte and producing spermatozoids.

**Apomixis:** The formation of a sporophyte from a gametophyte by direct, asexual development, rather than by fertilization of gametes.

**Apophysis:** A swelling on which a sorus is located.

**Archegonium:** The female sex organ of pteridophytes borne on the gametophyte and producing eggs.

**Bulbil:** A small, usually persistent, globose, usually hairy or scaly, asexual propagule borne on a root, rhizome, or frond and capable or not capable of forming a plantlet, as in *Dryopteris*.

**Coenosorus:** A compound sorus composed of several contiguous sori fused end-to-end.

**Dictyostele:** A siphonostele with more than one parenchymatic gaps at a single level (as seen in cross section).

**Frond:** The photosynthetic organ of ferns, usually consisting of a stipe and lamina; synonyms leaf, megaphyll.

**Heterosporous:** Producing spores of two sizes, each of which develops gametophytes having gametangia of a single sex.

**Indusium:** A usually thin, often scale like, epidermal membrane subtending and/or covering the sorus, that partially or fully protects the young sporangia.

**Leptosporangium:** A thin-walled, thin-pedicelled sporangium bearing usually 64 spores and formed usually from a single epidermal initial cell.

**Massula:** In *Azolla*, a structure derived from the contents of the microsporocarp that contains the microspores and has glochidia (minute barbed hairs) protruding from its surface.

**Monolete:** Bilaterally symmetrical spores, with a linear, unbranched laesura.

**Rachis:** The principal, central axis of a pinnately or more compound lamina.

**Stipe:** The structure of a frond that connects the base of the lamina to the point of its attachment to the rhizome.

**Stipule:** In the Marattiaceae, each one of a pair of lateral, fleshy, starch-bearing, persistent, partially or entirely vascularized outgrowths of the rhizome that clasp the base of the stipe.

**Trilete:** Radially symmetrical spores, (spherical or tetrahedral) with a laesura with three radiating branches.

**Paraphysis:** A minute, unicellular or multicellular (resembling a simple hair), usually elongate and sometimes glandular structure borne on the soral receptacle, on the sporangium capsule or pedicel.

**Pinna:** A stalked or sessile, primary division of a compound lamina that is at least narrowed at the base.

**Primordium:** A part (e.g., a frond) in its most rudimentary form or stage of development.

**Rhizome:** In pteridophytes, a scaly or hairy (rarely glandular or glabrous) anchoring stem that bears roots and fronds.

**Sorus:** A cluster of sporangia.

**Sporocarp:** The hard, short- to long-pedunculate, nutlike structure containing the sporangia, apparently a highly modified leaflet e.g. *Marsilea*, or a thin, short-stalked, globose structure containing the sporangia, apparently a modified indusium e.g. *Azolla* and *Salvinia*

**Sporophyll:** A leaf or frond bearing sporangia.

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## 5.8 SELF ASSESSMENT QUESTIONS

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### 5.8.1 Select the right answer

- The sori of *Hymenophyllum* are borne on the:
  - Margins of the sporophylls
  - Dorsal surface of the sporophylls
  - Ventral surface of the sporophylls
  - The rachis of the sporophylls
- Maiden hair fern is the name given to
  - Pteris*
  - Adiantum*
  - Polypodium*
  - Dryopteris*
- Sori are not protected by indusium in
  - Lycopodium*
  - Selaginella*
  - Polypodium*
  - Osmunda*
- Stele of rachis in *Dryopteris* is
  - Protostele
  - Siphonostele
  - Dictyostele
  - Plectostele
- Dimorphic leaves are present in
  - Osmunda regalis*
  - O.cinnamomea*
  - O. javanica*
  - O. claytoniana*
- In *Marattia*, the sporangia are
  - Borne separately
  - Fused to form Synangia
  - Present in pairs
  - Absent
- Which of the following is monotypic
  - Ophioglossum*
  - Botrychium*

- (c) *Helminthostachys* (d) *Equisetum*
8. Sporangia of *Ophioglossum* are seen in the form of  
 (a) Strobilus (b) Sporophylls  
 (c) Spike (d) Tassel
9. Osmundales is link between  
 (a) *Selaginella* and *Lycopodium* (b) Leptosporangiate and Eusporangiate  
 (c) Eligulatae and Ligulatae (d) Pteridophyte and Gymnosperms
10. Sporocarp of *Marsilea* is  
 (a) Unisporangiate (b) Bisporangiate  
 (c) quadrisporangiate (d) Multisporangiate

### 5.8.2 Fill in the blanks:

- The middle cortex in *Marsilea* is\_\_\_\_\_.
- Glochidia are present in\_\_\_\_\_.
- Members of family \_\_\_\_\_are known as Filmy ferns.
- In *Dryopteris* antherozoids are\_\_\_\_\_.
- In *Osmunda* antheridia are of \_\_\_\_\_.
- \_\_\_\_\_is commonly known as Adder's Tongue fern.
- The asexual reproductive bodies of *Marsilea* are known as\_\_\_\_\_.
- The characteristic feature of stele organisation of *Marattia* stem is presence of\_\_\_\_\_.
- Petiole or Whole leaf hypothesis was proposed by \_\_\_\_\_ to explain morphological nature of sporocarp in *Marsilea*.
- The stele of *Osmunda* root is usually\_\_\_\_\_.

**Answer Keys: 5.8.1:** 1.(a), 2.(b), 3.(d), 4.(c), 5.(b), 6.(b), 7.(c), 8.(c), 9.(b), 10.(b)

**5.8.2:** i. aerenchymatous, ii. *Azolla*, iii. Hymenophyllaceae, iv. multi ciliate and coiled, v. projecting or emergent type, vi. *Ophioglossum*, vii. sporocarp, viii commissural strand, ix. Johnson, x. Diarch.

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## 5.9 REFERENCES

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- Stokey A.G. and Atkinson, L.R. 1956. The gametophyte of Osmundaceae. Phytomorphology. 6 : 1940
- Bower, F.O. 1899. Studies in the morphology of spore-producing members. IV. The leptosporangiate ferns, Phil. Trans. Roy. Soc. London. 162 B: 29-138.
- Williams, W. 1927. Sporangial variation in Osmundaceae. Trans. Roy. Soc. Edinburg. 55: 795-805.
- Bower, F.O. 1926. The ferns (Filicales) Vol 2. Cambridge.

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## 5.10 SUGGESTED READINGS

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- College Botany Volume II By H.C. Gangulee and A.K. Kar. New Central Book Agency 8/1Chintamani Das Lane, Calcutta 9, India.
- Botany for degree student Pteridophyta by P.C. Vashishta, A.K. Sinha and A. Kumar.S. Chand and Company Private Ltd. Ram Nagar, New Delhi
- The morphology of Pteridophytes (The structure of ferns and allied plants).By K.R. Sporne. Hutchinson and Company Ltd.178-202 Great Portland Street, London
- The Biology and Morphology of Pteridophytes. By N.S. Parihar. Central Book Depot, Allahabad.

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## 5.11 TERMINAL QUESTIONS

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### 5.11.1 Write short notes on:

- i. Mature prothallus of *Adiantum*
- ii. Prothallus of *Dryopteris*
- iii. Habit of *Angiopteris*
- iv. Embryogeny in *Marattia*
- v. Sorus of *Angiopteris*
- vi. Development of sporangium in *Osmunda*

### 5.11.2 Differentiate between:

- i. Fertile fronds of *Botrychium* and *Osmunda*
- ii. Sporangia of *Marattia* and *Angiopteris*
- iii. Prothallus of *Dryopteris* and *Hymenophyllum*
- iv. Structure of stele in rhizomes of *Marsilea* and *Adiantum*
- v. Sporocarp of *Salvinia* and *Azolla*

### 5.11.3 Draw well labeled diagrams of:

- i. Male and female gametophytes of *Salvinia*
- ii. L.S. of *Marsilea* sporocarp
- iii. Sori of *Hymenophyllum*
- iv. T.S of *Osmunda* stem/rhizome
- v. Fertile spike of *Ophioglossum*

### 5.11.4 Long answer type Questions:

- Q1. Explain structure of sporocarp in *Marsilea*.
- Q2. Give a brief account of the sporophyte of *Osmunda*.
- Q3. Give an illustrated account of sporocarp of *Azolla*.
- Q4. Discuss brief account of the gametophyte of *Salvinia* and *Azolla*.
- Q5. Describe the genus known as Filmy fern.
- Q6. Describe the life-cycle of *Adiantum* with the help of well labelled diagrams.

- Q7. Describe the salient features of the fertile pinna of *Dryopteris*.
- Q8. Osmundaceae is intermediate between Leptosporangiatae and Eusporangiatae..
- Q9. Describe the systematic position and distinguishing feature of *Ophioglossum*.
- Q10. Give a brief account of reproduction in *Marattia*.

## **BLOCK-2 GYMNOSPERM**



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**UNIT-6-GENERAL CHARACTERISTICS,  
CLASSIFICATION, DISTRIBUTION,  
REPRODUCTION, EVOLUTIONARY TRENDS  
AND ECONOMIC IMPORTANCE OF  
GYMNOSPERMS**

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- 6.1. Objectives
- 6.2. Introduction
- 6.3. General Characters of Gymnosperms
- 6.4. Classification
- 6.5. Distribution
- 6.6. Reproduction
- 6.7. Evolutionary trend
- 6.8. Economic importance of Gymnosperms
- 6.9. Summary
- 6.10. Glossary
- 6.11. Self Assessment Question
- 6.12. References
- 6.13. Suggested Readings
- 6.14. Terminal Questions

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## 6.1 OBJECTIVES

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After reading this unit students will be able-

- To study the general characteristics, classifications, distributions and reproduction of Gymnosperms.
- To study the evolutionary trends and economic importance of Gymnosperms.

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## 6.2 INTRODUCTION

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The word Gymnosperm, (“*Gymnos*”= naked and “*Sperma*”= seed) was first used by Theophrastus, a pupil of Aristotle in his famous book “*Enquiry into Plants*”. He used this term for all the plants having unprotected (without covering) seeds. On the basis of their seeds with or without covering flowering plants are grouped into two major categories namely- Angiosperms and Gymnosperms. Thus the group of seed plants or Spermatophyta is divided into two sub groups Angiosperms and Gymnosperms.

The ovules of gymnosperms are freely exposed before and after fertilization, while in case of angiosperms the ovules are enclosed within the ovary. Due to this, the angiosperms are considered as the most advanced in plant kingdom. Compared to angiosperms, the gymnosperms are less advanced and they have some specific characteristic features.

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## 6.3 GENERAL CHARACTERS OF GYMNOSPERMS

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1. They are slow growers and lacks vegetative means of propagation such as by cuttings, layering etc.
2. They are unable to grow under varied habitats as they are able to grow on some specific habitats and conditions.
3. They have limited means of dispersal of seeds and can be dispersed only by wind, animals or by human beings.
4. Most of the gymnosperms are terrestrial and unable to grow in aquatic habitats except a few.
5. They lack vessels in xylem (with few exceptions) and companion cells in phloem.
6. Most of the gymnosperms are unisexual, thus due to absence of bisexuality, chances of self- pollination reduces.
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 are complete absence of herbs and climbers. Vegetative propagation is not reported in this group but reproduction by bulbils is known in *Cycas*. Generally plant possesses tap root 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 on the basis of their branching system. Leaves are present at their apices of dwarf shoot. Dwarf shoot with leaves is collectively known as 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*). 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 in nature, while pycnoxylic wood is the characteristic feature of Coniferophyta as this wood is compact, 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 stem are conjoint, collateral, endarch and open.

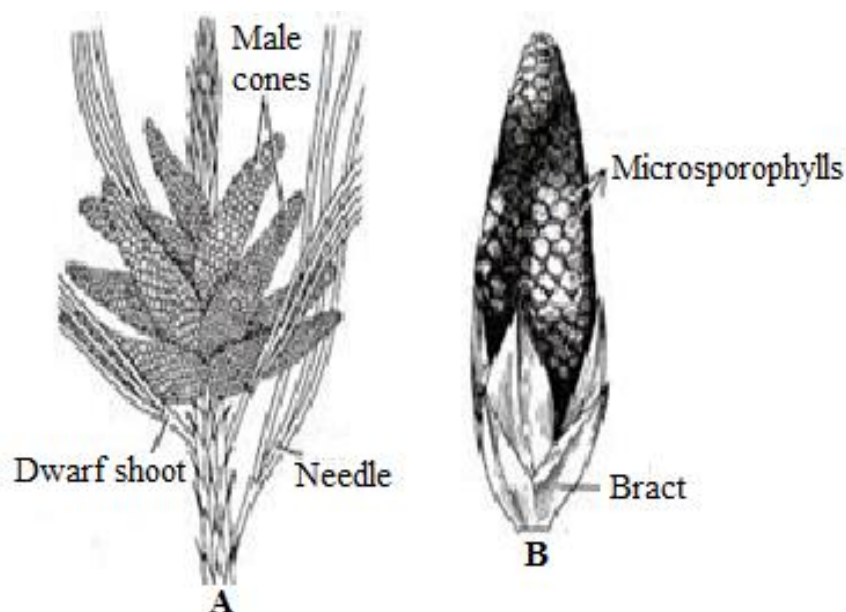


Fig.6.1 *Pinus wallichiana*, A- Cluster of male cone B- A single male cone



Fig.6.2 Naked seeds of Gymnosperm– (A) *Ginkgo biloba*, (B) *Cycas*

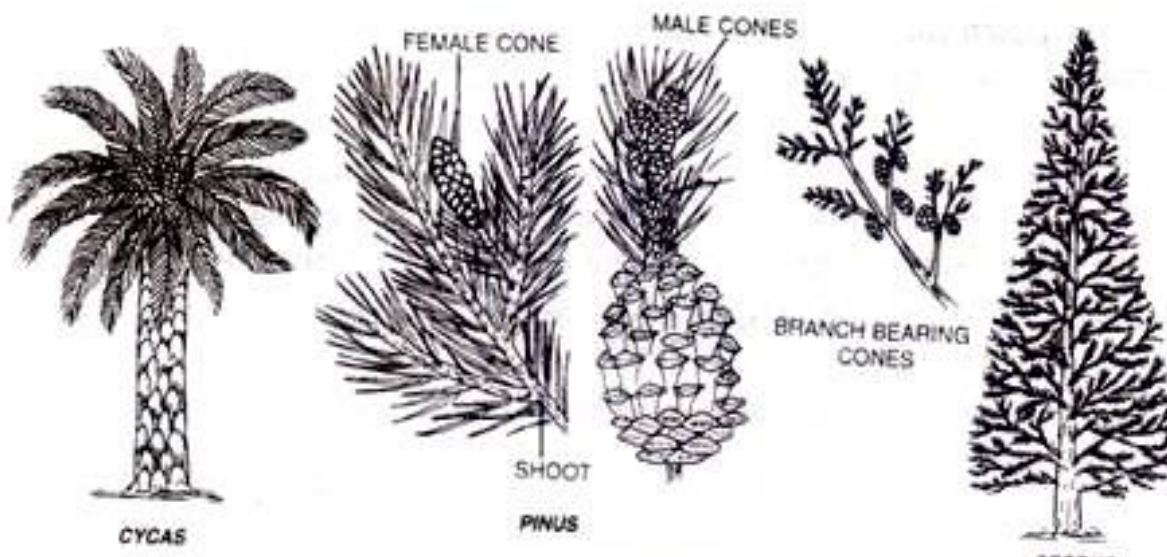


Fig.6.3: Habit sketch of some Gymnosperms

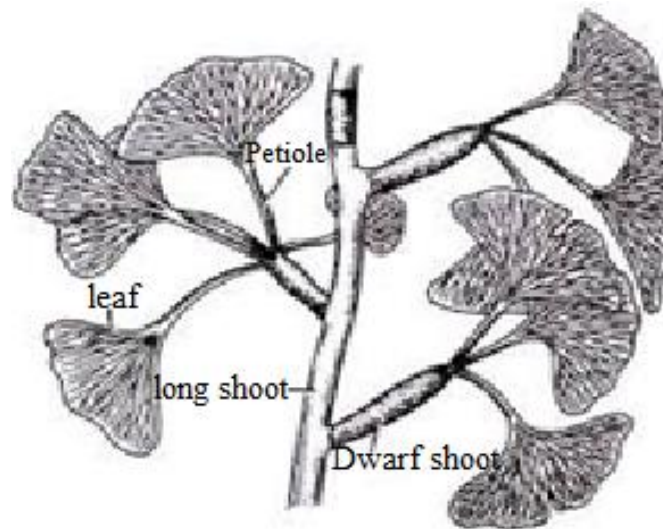


Fig.6.4: *Ginkgo biloba* along shoot bearing a dwarf shoots

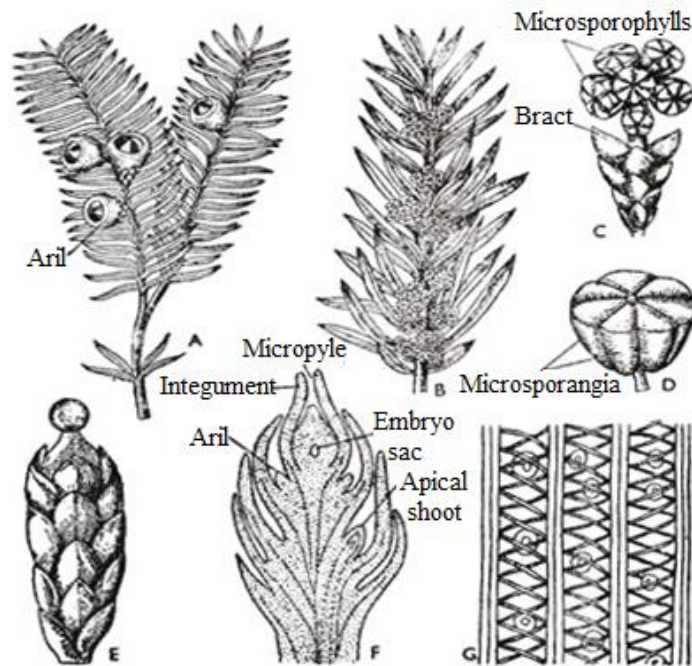


Fig.6.5 *Taxus baccata*: A. Shoot bearing seeds, B. Male shoot, C. A male strobilus, D. A microsporophyll, E. A female flowering shoot, F. Median L.S. of female flowering shoot, G. L.S. of *Taxus* wood showing tracheids with tertiary spiral thickening in addition to bordered pits

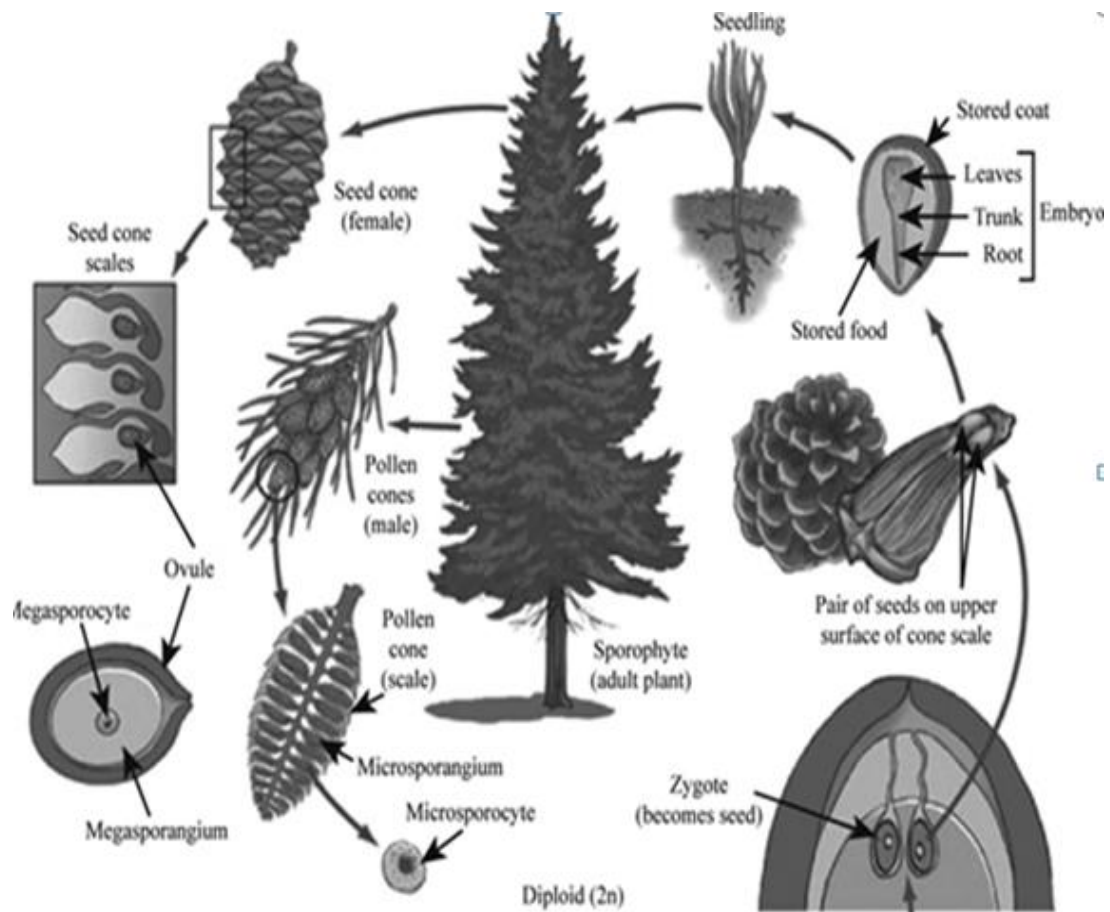


Fig.6.6 Life cycle of a Gymnosperm plant

## 6.4 CLASSIFICATION

The Gymnosperm is a very large group which 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 with 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 apollen tube. It included two orders-

1. **Order Coniferales**- It included living genera e.g. *Pinus*, *Cedrus*, *Taxus*, *Podocarpus*, *Taxodium* etc. and also included fossil genera.
2. **Order Gnetales**- Included *Ephedra*, *Gnetum* and *Welwitschia* and many fossil genera.

On the basis of composition of wood the gymnosperms were divided into two classes-

- i) 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, 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 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) had proposed a classification in which the Gymnosperm is divided into three divisions as:

- i) Cycadophyta
- ii) Clamydospermatophyta
- iii) Coniferophyta

Coniferophyta, Clamydospermatophyta and Coniferophyta were further divided into classes and orders.

Raizada and Sahni (1958-61) have classified Gymnosperms after the discovery of a new and unique group of Jurassic period- 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 as-

- 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 further divided into orders-

### 1. Cycadopsida-

**Order 1. 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

**Order 1. 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.



3. 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. Protopytales

##### **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 organ 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, Bennettiales 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

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**6.5 DISTRIBUTION**

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Certain groups of gymnosperms are entirely extinct, while others are represented by living as well as fossil forms. Still there are some groups chiefly within living gymnosperms that extend throughout the temperate, tropical and even in arctic zones. Most of the living gymnosperms are evergreen xerophytes. The total number of living gymnosperms in the world is approximately 70 genera and 725 species. A total of 16 genera and 53 species were reported from India (M. B. Raizada and K. C. Sahni, 1960), While Maheshwari listed only 14 genera. Gymnosperms are mainly dwellers of temperate regions in India. They form extensive forests and grow luxuriantly in the Himalayan ranges and that is why most of the gymnosperms are distributed in eastern and western Himalayas besides some other regions of India.

Members of order Cycadales, Coniferales, Ephedrales and Gnetales are reported from India. The Cycadales is represented by 4 species of *Cycas* in India. In the vast peninsular India they are represented by a few species of *Cycas*, *Podocarpus*, and *Gnetum*, However, in the extra peninsular Himalayas and to some extent in the connected ranges of Kashmir, Assam, and Arunachal Pradesh Gymnosperms are represented only by conifers and covering extensive tract of forest land.

Among different groups of gymnosperms, most densely populated group is Coniferales. This group is represented by *Pinus*, *Cedrus*, *Abies*, *Larix*, *Picea*, *Cupressus*, *Tsuga*, *Juniperus*, *Taxus*, *Araucaria*, *Thuja*, *Podocarpus*, *Cephalotaxus*. Conifers are found predominantly in the Himalayas and are particularly rich in the north- west Himalayas (Uttarakhand, Kashmir, Himachal Pradesh etc.) Their distribution is generally governed by altitude which ranges

from 1800- 3300masl. While some species of *Pinus* (*P.insularis*-700- 1,850 m asl and *P. merkusii*-150- 600 m asl.) are reported from Khasya region of Assam and on the hillocks in East Bengal.

Among Cycads only *Cycas* occurs in India and the genus is represented by four species viz. *C. circinalis*, *C. beddomei*, *C. pectinata* and *C. rumphii*, beside this another species *C. revolute*, which is a native of Japan is commonly cultivated in Indian gardens. Species of *Zamia*, *Macrozamia*, *Encephalartos* and *Stangeria* are exotic and occasionally cultivated in Indian gardens. Similarly a few plants of *Ginkgo biloba*, a native of China, occur in India under cultivation in gardens. Gnetales are represented in India by a number of species of *Ephedra* and *Gnetum*. Out of seven species of *Ephedra* only one, *E. foliate* occurs in the plains of Rajasthan and Punjab while rest six species are confined to the north- west Himalayan regions.

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## 6.6 REPRODUCTION: (LIFE-CYCLE)

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Gymnosperms possess two different types of spores and hence referred as hetrosporous. The microspores are smaller and there may not be any difference in the size of the spore while another spore larger in size called megaspore. These two kinds of spores on germination produce two different kinds of gametophytes. The microspore or pollen grain produces male gametophyte, while the larger one, megaspore produces female gametophyte, which bears two or more archegonia or female sex organs. These spores are produced within the sporangia that 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 same tree as in *Pinus* or on different trees like *Cycas* and *Ginkgo*. The microsporangium contains numerous small microspores where as the megasporangium contains only one large megaspore. Both micro and megaspores are haploid and develop as a result of 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.

**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. Integument grows all around except the apical part leaving a small pore i.e. micropyle and this end is known as micropylar end. The nucellus is having a single megaspore mother cell at later stage which undergoes meiosis and form 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 into large number of free nuclei. This transforms into 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) inner fleshy layer or inner sarcotesta. Thus integument of 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 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 apical end. Depending upon 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 as a result of which the female gametophyte become a cellular structure. The female gametophyte or prothallus gets differentiated into an upper reproductive region, middle storage region and the lower basal haustorial region. Generally in gymnosperms the female gametophyte has cellular tissue at its lower end while few free nuclei remains at its upper end. a. After fertilization the apical end however, becomes cellular (exception is *Welwitschia*)

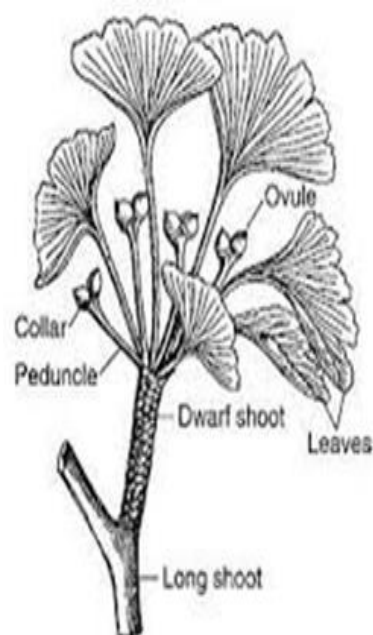


Fig.6.7 *Ginkgo biloba*- a female dwarf shoot

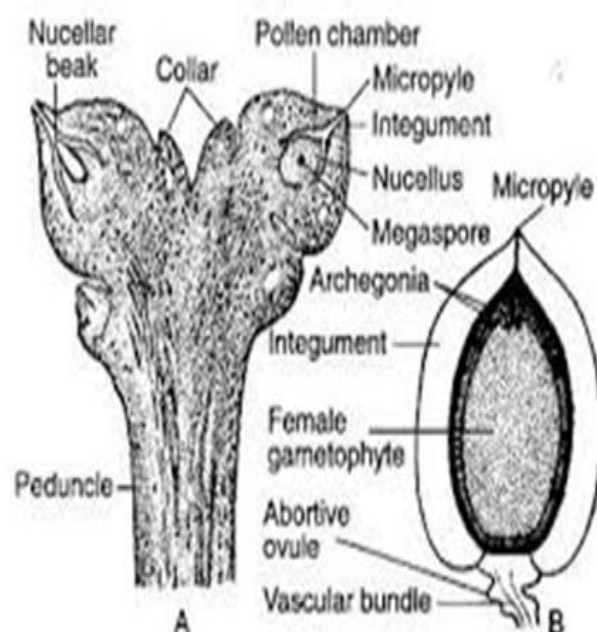


Fig.6.8 *Ginkgo biloba*- A median L.S. of female cone, B- Median L. S. of an ovule

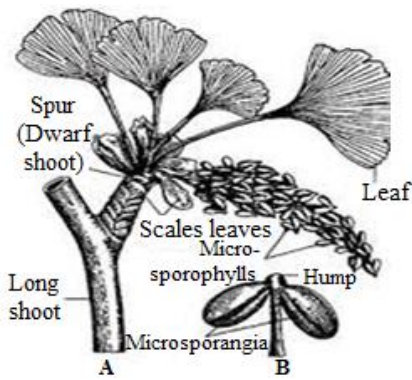


Fig.6.9 *Ginkgo biloba* -A- male dwarf shoot

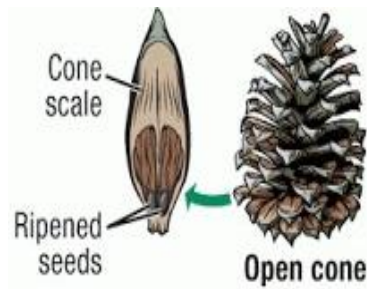


Fig.6.10: *Pinus* open cone and ripened seeds with microsporophylls

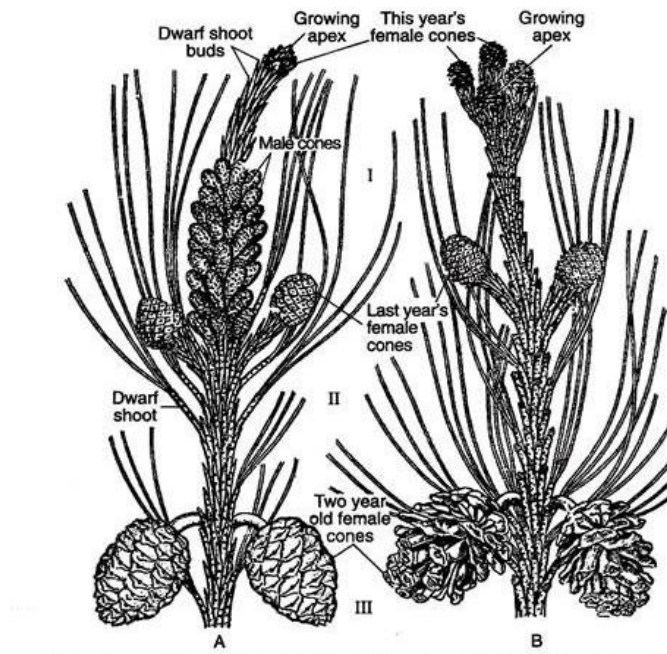


Fig.6.11 *Pinus*: Male and female cones: A- at early spring showing male cones, B- at the end of spring (rains) male cones disappear

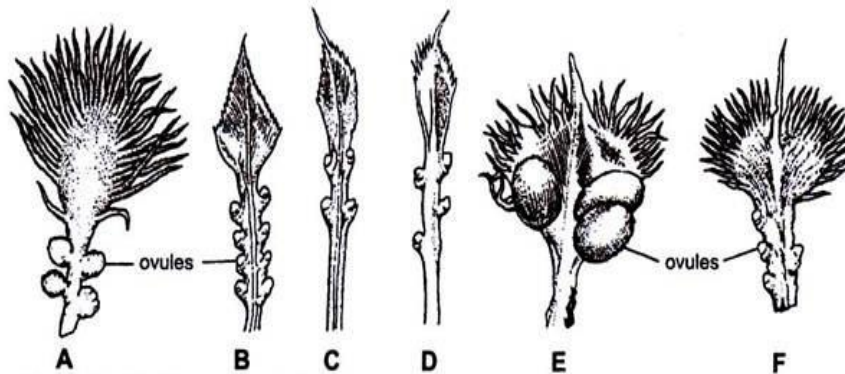


Fig.6.12: A-F, Megasporophylls of *Cycas*: A) *C. revolute*, B) *C. circinalis*, C) *C. rumphii*, D) *C. beddomei*, E) *C. pectinata* and, F) *C. sinensis*

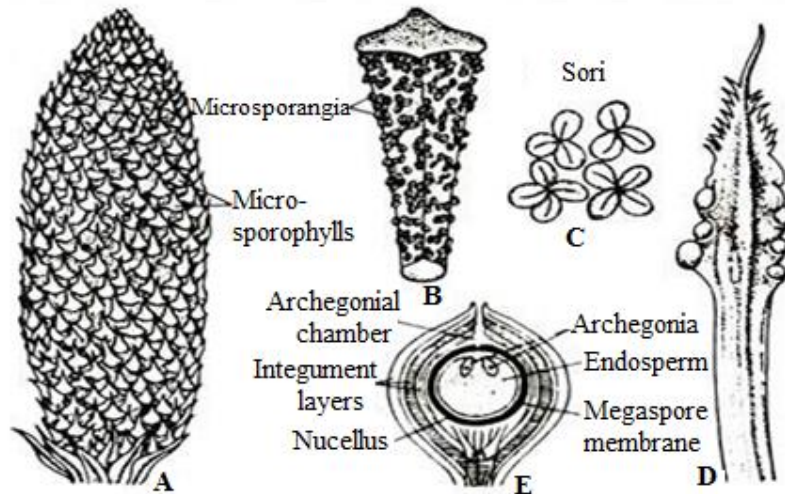


Fig.6.13 *Cycas sp.*, A-E, A) Male cone, B) Microsporophyll, C) Sori, D) Megasporophyll, E) V.S. through ovule

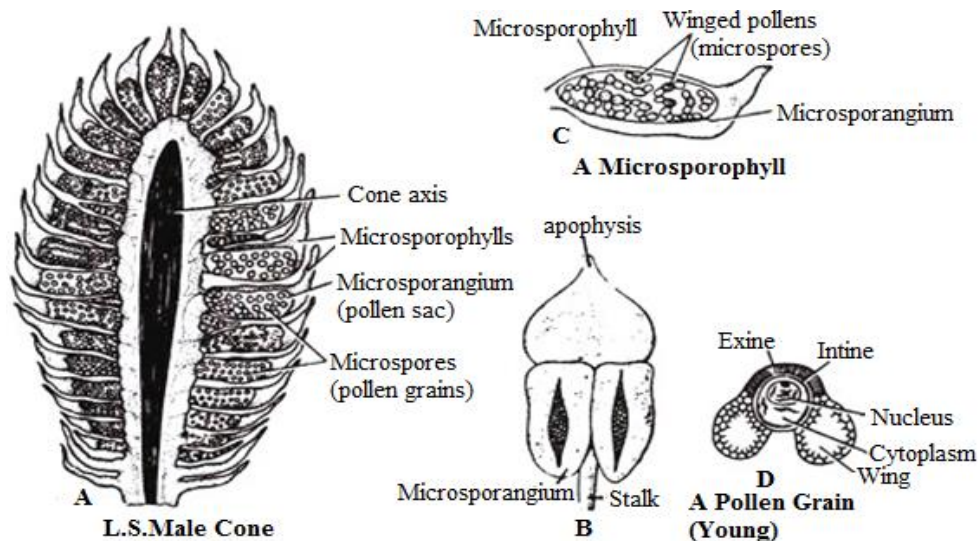


Fig.6.14: *Pinus*: A-L.S. male cone, B -A single microsporophyll in surface view; C- A microsporophyll; D- A young pollen grain

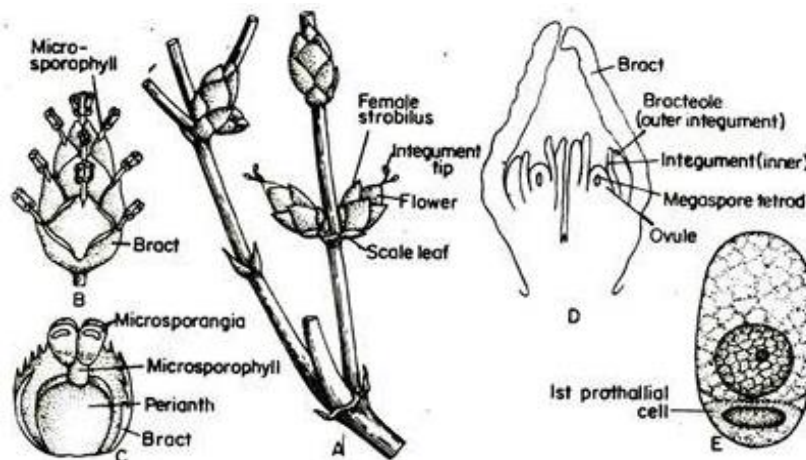


Fig.6.15: *Ephedra sp.* A- fertile bract, B- a male cone, C- Single male flower, D- V. S. through female cone, E- young female gametophyte

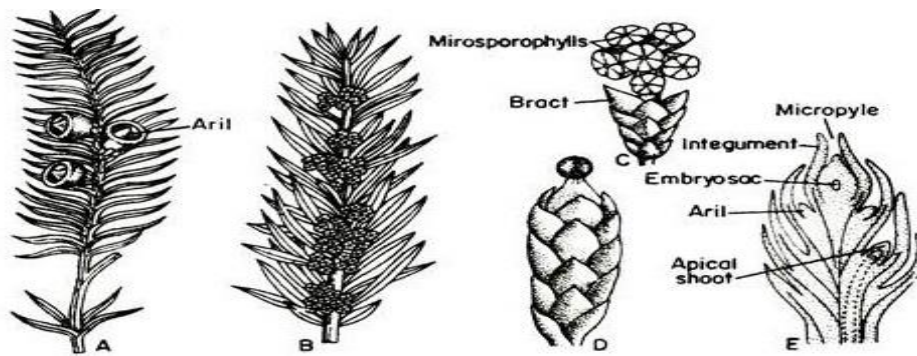


Fig.6.16: *Taxus sp.* A- A fertile twig with female cone, B- A fertile twig with male cone, C & D male cone magnified, E- V.S. through female cone

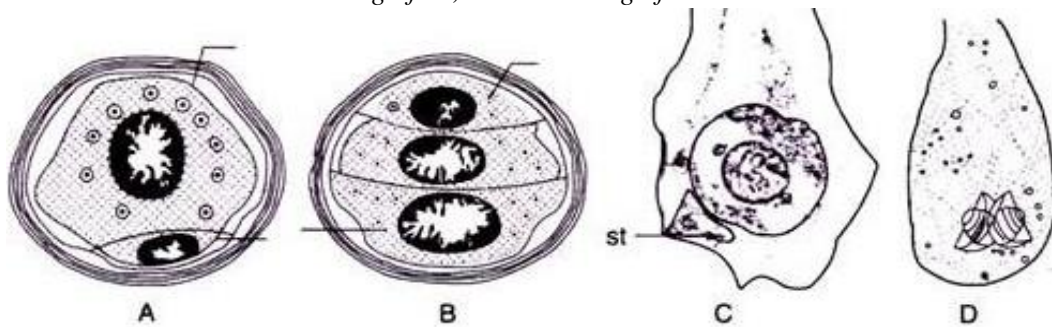


Fig.6.17: *Cycas* microspores showing development of male gametophyte A- Two celled pollen showing prothallial cell and a large antheridial initial, B- 3 celled-pollen at shedding stage, with prothallial cell, antheridial cell and tube cell, C- pollen tube showing large spermatogenous cell, small tube nucleus, prothallial cell and stalk cell, D- Spermatozoids (Fig. A, B after Pant, Fig. C, D after Maheshwari)

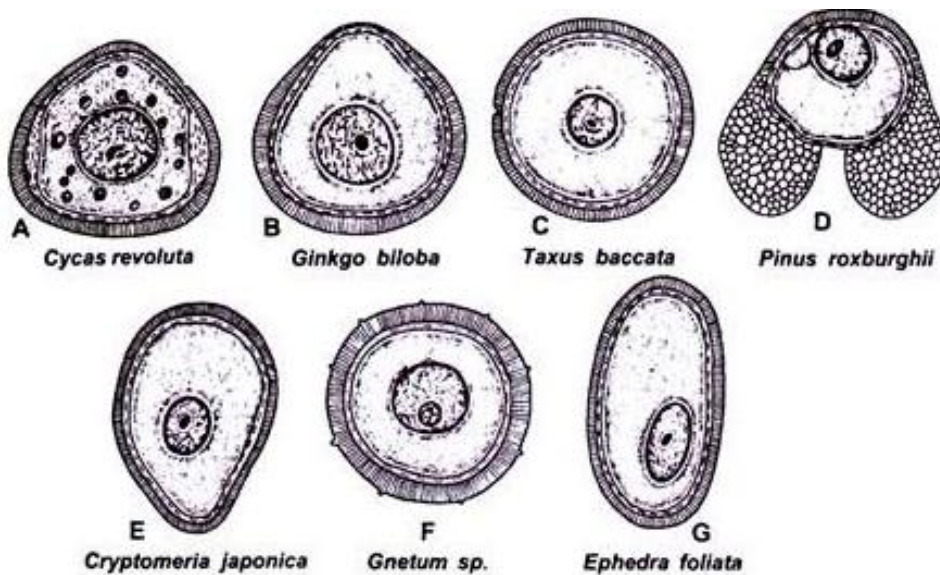


Fig.6.18: Pollen grains in gymnosperms, A- *Cycas revoluta*, B- *Ginkgo biloba*, C- *Taxus baccata*, D- *Pinus roxburghii*, E- *Cryptomeria japonica*, F- *Gnetum ula*, G- *Ephedra foliata*

**Microspores:** The pollen grains or microspores are unicellular and haploid structures developed within specific structures, the microsporangia. They differ in shape and sizes 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*), may be almost spherical (*Ginkgo*), may be winged (saccate), and may be having reticulate exine (*Abies pindrow*, *Cedrus deodara*, *Pinus roxburghii* and *P. wallichiana*, *Picea smithiana* etc.) whereas in *Ephedra* the pollen grains are inaperturate, elongated with palcate exine surface. *E. foliata* pollen grains showing 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 relationship of *E. foliata* with Coniferales and Cordaitales as there is a minute sac in the pollen grains of the former one.

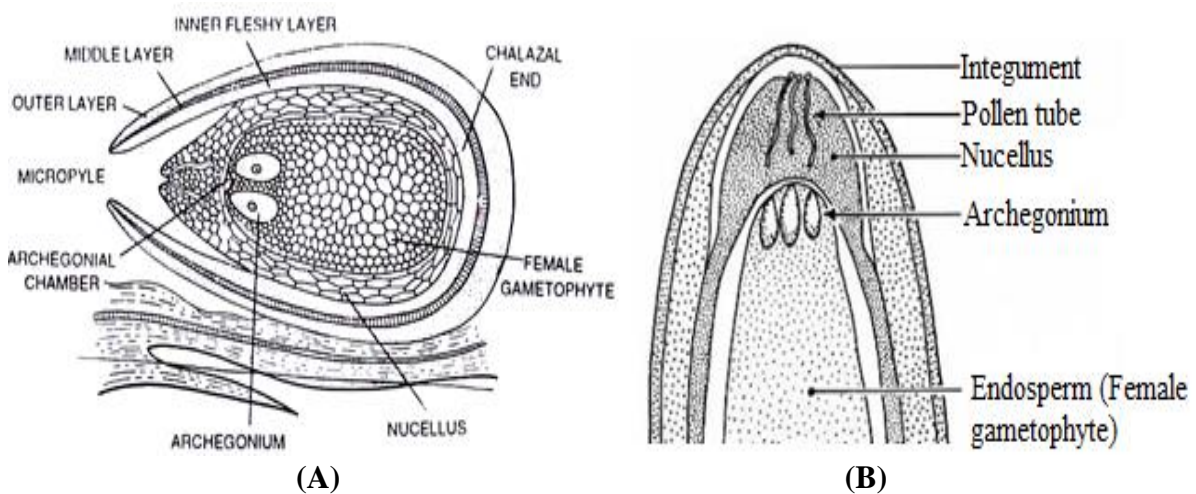


Fig.6.19- (A-B) *Pinus roxburghii*: L.S. of mature ovule showing archegonia

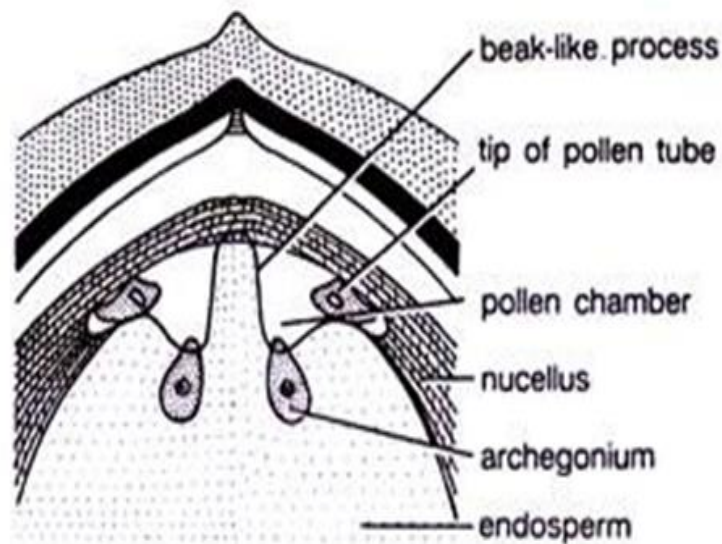


Fig.6.20- L.S. of ovule (upper part)



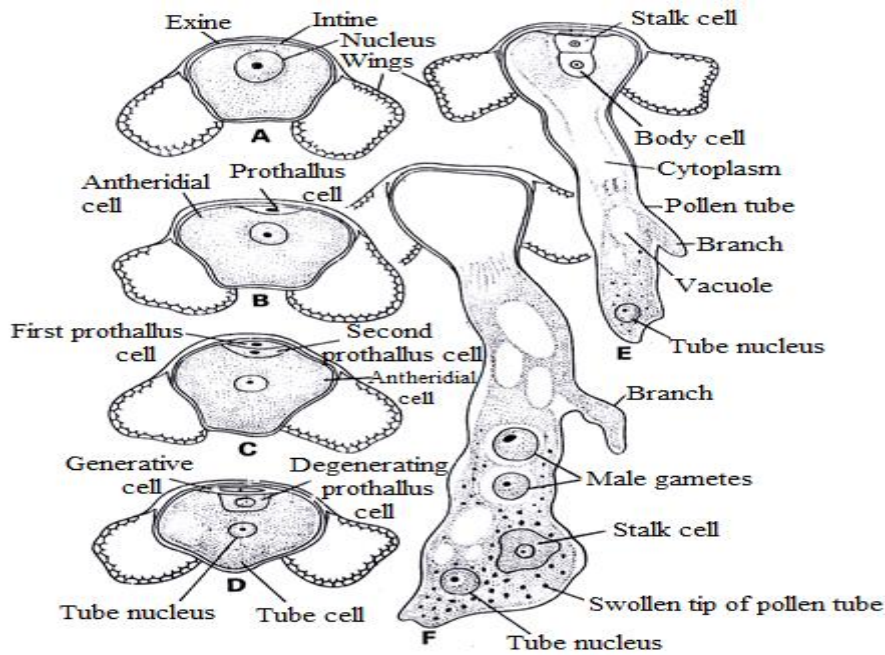


Fig.6.21: *Pinus sp.* Development of male gametophyte, A – a pollen grain; B-D successive stages in the development; E- pollen tube with nucleus; F- two unequal male gametes, stalk nucleus, tube within pollen tube

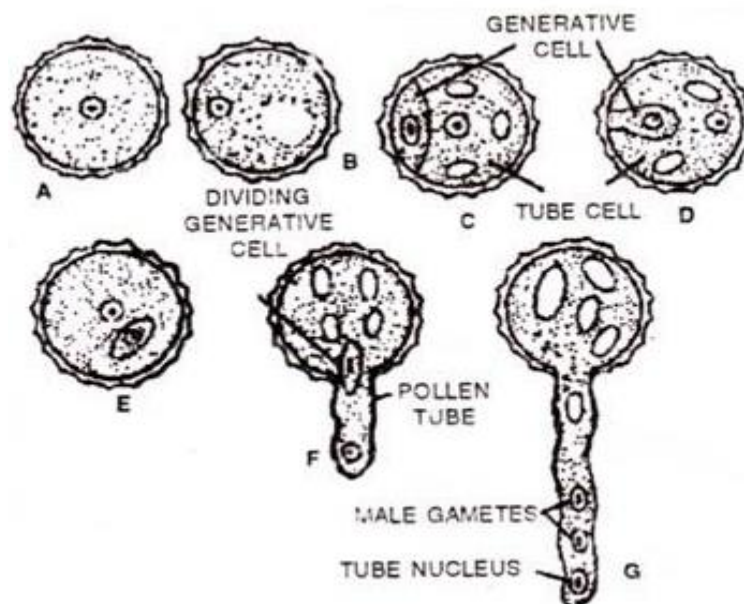


Fig.6.22 Germination of pollen grain and development of male gametes (A-G)

**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 completes 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 haustorial in nature than a sperm carrier. While in *Microcycas*, the stalk cell divides into 10 or 11 body cells or spermatogenous cells. These all cells divide to produce 20 or 22 spermatozoids. 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 anticlinally.

**Bennettiales (cycadeoids): Fossil seeds of extinct gymnosperms**

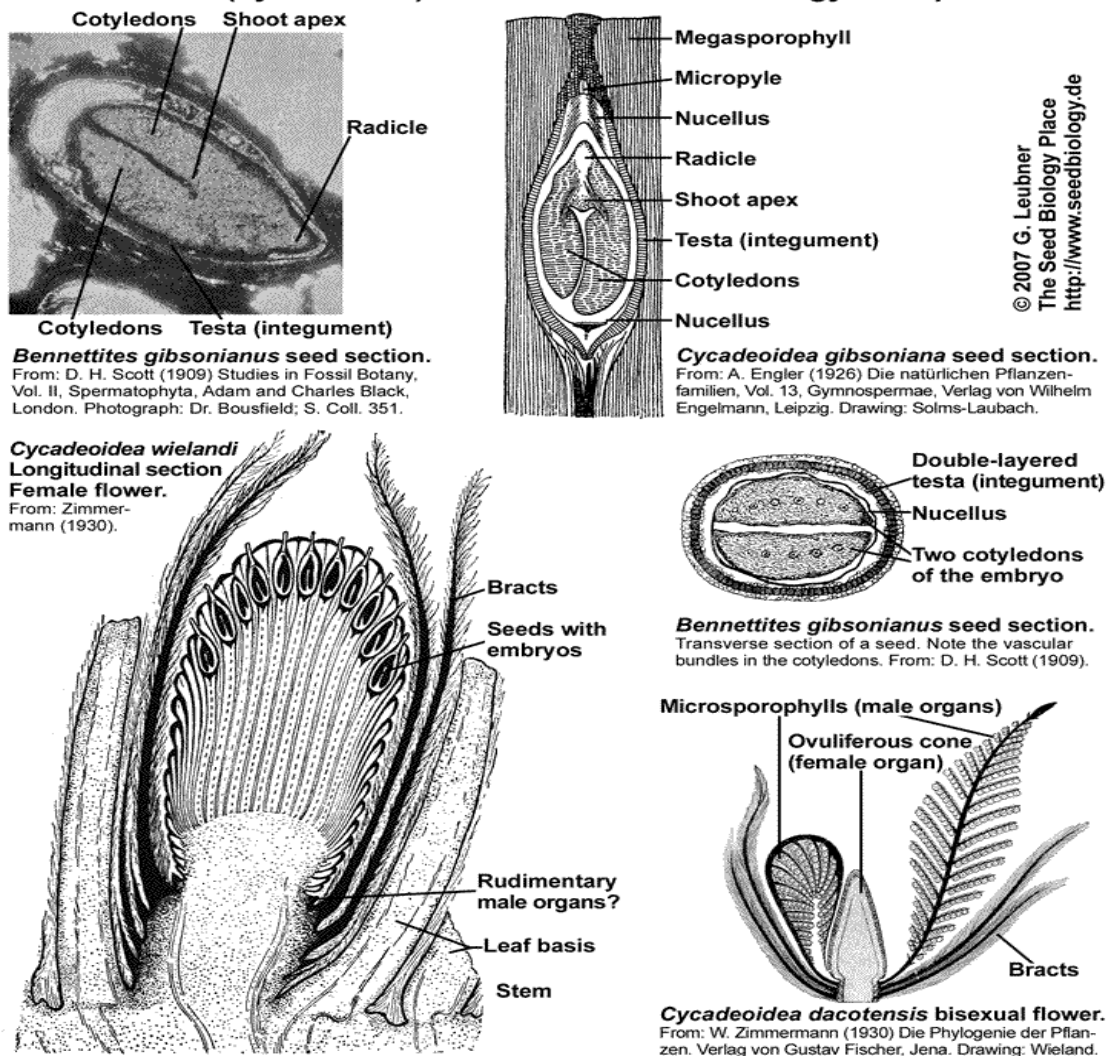


Fig.6.23: Fossil seeds of members of Bennettiales

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 remain 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 difference of opinion regarding the male gamete. According to some workers the two male gametes areas two nuclei of binucleate sperm cell, 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, Chawdhury (1960) have 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 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 acts as antheridial cell and may divide into generative cell and tube cell before pollination. Based on studies, in *Cupressus semipervirens* the body cells divides 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 equalin size. In the members of Podocarpaceae the number of male prothallial cells may be 1-8 in *Podocarpus*, 3-6in *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 for 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 cell or body cell.
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 of the gymnosperms, the pollen grains are caught into a pollination drop secreted at the micropylar end of the ovule. After drying of pollination drop, the microspores in semi-germinated 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.) While in Conifers and other gymnosperms the semi- germinated pollen grains come in direct contact with the nucellar beak. Contrary to this in the palaeozoic 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 pollen tube as a tubular outgrowth that grows through the nucellar tissue. In Cycads and *Ginkgo* the pollen tubes mainly acts as the haustorial organ and grows for long time (several months) into the nucellar tissue and 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 mega gametophyte. At that time the sperms swims to the archegonial neck and enters into 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 sperm carrier. The male gamete along with stalk and tube nucleus migrate to tip of the pollen tube. The tube grows through the nucellar tissue, reaches to the archegonial neck and enters through it and after bursting liberates the male gametes. Among them, one fuses 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 **Zooidiogamy**. In 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 transformed 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 that in conifers only four nuclei formed, so in this case all the four cells of the young embryo separates after wall formation and develop into 4 embryos, but only one completes further development while others abort.

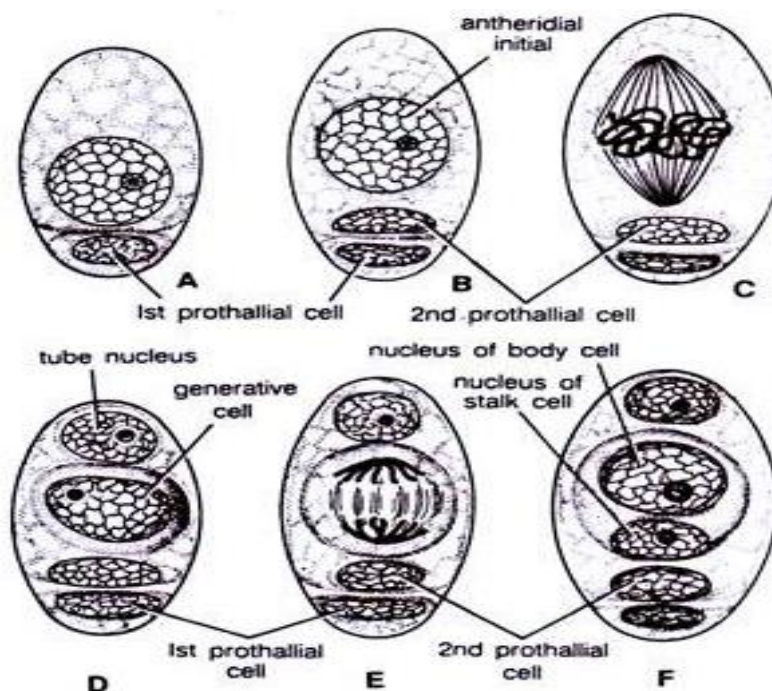


Fig.6.24 *Ephedra trifurca*: Development of male gametophyte

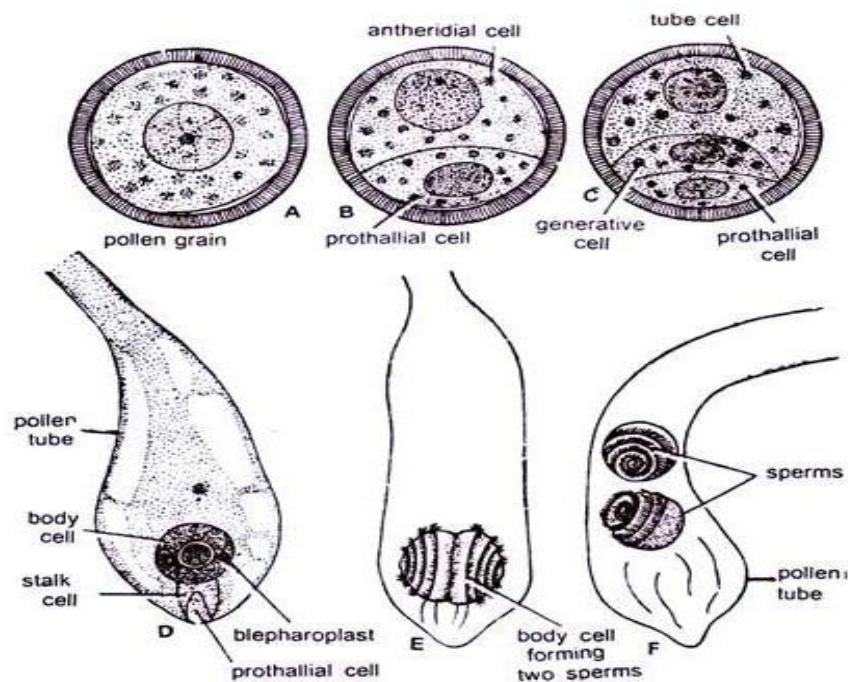


Fig.6.25: A-F, *Cycas*: Development of male gametophyte

In *Thuja* no cleavage Polyembryony 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 forming 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 initial 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 majority of 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 upper most tier ends are in open contact with the egg cytoplasm. This end is apparently active in transmission of nutrients to the growing embryos.

The number of cotyledons varies indifferent 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*, the 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 case of Cupressaceae, the genus *Actinostrobus* shows Cleavage Polyembryony and shows somewhat different pattern of development. Here 4 free nuclei are formed. Wall formation results in forming 4 cells among which two vertically placed cells below 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 show 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 embryonal cell are 9-12 in *Podocarpus spicatus* and 1-2 in *P. toterra*, *P. nivalis* and *P. macrophyllus*. *Podocarpus spicatus* has 9-12 and *P. macrophyllus* has 14-15 pro-suspensor cells. The embryo has two cotyledons.

Development of embryo in the members of Gnetales is different than above mentioned cases. In *Ephedra trifurcate* 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 wall which become globular later. All these globular cells are pro-embryos, an example of polyembryony. Later the globular pro-embryo develops into an embryo with the massive embryonal mass at the distal end and a number of 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 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.

On the basis of comparative studies of embryonal development in gymnosperm, it is concluded that there is no close relationship or resemblances between the embryogeny of pteridophytes, gymnosperms and angiosperms. This suggests parallel evolution among these

groups rather than evolved 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 fertilized ovule and its consequent enlargement is known as seed. The zygote develops into an embryo while the endosperm persist 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 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 complete its development. In *Taxus* a fleshy aril develops from the basal cup- shaped structure. Except *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 trifurcate* **Vivipary** has been reported. All the gymnosperms represent **heterologous alternation of generation**.

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## 6.7 EVOLUTIONARY TRENDS

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Geological history revealed that the gymnosperms are the most ancient seed plants that evolved during Upper Devonian and Lower Carboniferous periods in the Palaeozoic era around 350 million years ago. They flourished well during the period of 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 Palaeozoicera. 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 Carboniferous period and are an evidence of the origin of gymnosperms from fern or an ancient fern like ancestor. These plants had fern like general appearance and foliage but also had primitive type of seed. The gymnosperms morphologically also resemble so much with the ferns or pteridophytes that this period generally known as “**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 Mesozoic and showed striking resemblances with modern Cycads.

The third line of evolution, which is also a group of extinct members, is Cordaitales that emerged during Upper Devonian and reached its full development in the Upper Carboniferous period and disappeared by the end of 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 Tertiary period. Evidently this group is of recent origin and possibly offshoot of some Coniferales.

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## **6.8 ECONOMIC IMPORTANCE OF GYMNOSPERMS**

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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, 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 feast in China and Japan, to promote digestion and lowering the effect of drinking wine. Seeds of *Pinus gerardiana* (Chilgoja) used as dry fruit.

Seed kernels of *Gnetum ula* yield oil for illumination and massage in rheumatism. Bark of *Taxus baccata* is used as main ingredient of 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 vegetable. The famous "Sago" starch is obtained from the stem / seeds of *Cycas* and used as food. This stem starch obtained from *Macrozamia spiratis* is an important source of food for poultry, dairy animals and pigs. The seeds of *Cycas* are used as paste and eaten as cakes in Nicobar island.

**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 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 pleasant smell and used for packing cases, match wood, wood wool, aircraft work, plywood, light camp furniture and also used as household materials. *Juniperus* 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 smooth glossy surface. Beside this, wood of *Araucaria cunninghamii* used for plywood manufacture.

**6-Resin:** Conifers exudate resins, this make 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 mounting medium for microscopic objects and as cements 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 also used with the oil immersion lenses of the microscope. The oil obtained from *Cedrus atlantica* possesses medicinal properties and used against bronchitis, tuberculosis, skin diseases and gonorrhoea.

The essential oils are used extensively in preparation of deodorants, room sprays, disinfectants, perfumery and 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 also used for paints. The Tail Oil obtained as a by-product 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, hiccough, epilepsy and for indigestion. **Taxol** (from *Taxus brevifolia*) is found effective against ovarian cancer, breast cancer, and 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 cold, respiratory disorder and hay fever. An aromatic beverage, known as **Mormon tea** is also brewed from the species of *Ephedra* in south western United State.

**11-Amber:** It is a fossil, water insoluble tree resin which was secreted by the now extinct pine, (*P.succinifera*). It is yellow, brown to black, hard and brittle with an aromatic odor.

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## 6.9 SUMMARY

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Gymnosperm is a small group of plants, which constitutes a sub- division of Phanerogams. All gymnosperms are found in four major divisions of Ginkgophyta, Cycadophyta, Coniferophyta and Gnetophyta. They have a vascular system used for the transportation of water and nutrients. The name ‘Gymnosperm’ means ‘naked seed’ which is the major distinguishing factor between gymnosperms and angiosperms, the two distinct seed plants. Most of the plants are perennial and woody. They are xerophytic with sunken stomata and thick cuticle. The xylem is without vessels. Beside this they do not produce flowers but form seeds .The group constitutes most valuable tree species of multipurpose uses and producers of highly valuable medicines like “**Taxol**” and “**Ephedrine**”.



*Ginkgo biloba: Medicine used for brain function support*

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## 6.10 GLOSSARY

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**Amber:** It is a fossil, water insoluble tree resin, secreted by now extinct pine (*P. succinifera*), yellow, brown and black in color and hard, brittle with aromatic odor.

**Aril:** Fleshy and sometimes hairy outgrowth of seed regarded as modified outer integument.

**Epigeal:** Germination of seed where cotyledons are raised above the ground surface by considerable elongation of hypocotyl.

**Embryo:** Young individual formed after fertilization.

**Endosporic:** Gametophyte that develops within the spore.

**Gametophyte:** vegetative structure representing gamete producing generation in the life-cycle of plant.

**Generative Cell:** One of the cells found in pollen of seed plants. In gymnosperms it gives rise to a body cell and a stalk cell.

**Gum:** Substance that swells in water to form gels or sticky solutions.

**Heteromorphic alternation of Generation:** Type of alternation of generation where morphologically different gametophytic and sporophytic generations alternate with each other to complete the life cycle of an organism.

**Heterospory:** Plants producing two different types of spores.

**Hypocotyl:** Part of the embryo lying between cotyledons and radicle.

**Hypogeal:** Type of seed germination in which cotyledons remain buried in the ground at the time of germination.

**Living Fossil:** Only living plants whose all the allies have become extinct. (viz., *Ginkgo biloba*).

**Pollen Chamber:** A cavity at the micropylar end of nucellus in some gymnosperms into which pollen grains settle after the pollination.

**Pro- Embryo:** Young stage of embryo formed after fertilization not before its differentiation into embryo and suspensor tissue.

**Polyembryony:** Condition of formation of more than one embryo in an ovule.

**Prothallus:** Free living gametophyte of certain lower vascular plants.

**Sporophyll:** A modified leaf that bears sporangia

**Sporophyte:** Individual of diploid phase of life cycle that produces spores.

**Tegmen:** The inner fleshy layer of integument which persists as a thin layer of seed coat.

**Testa:** The middle stony layer of integument which changes into a hard layer in a seed.

**Vivipary:** Phenomenon of germination of seeds *in situ* on the maternal plant.

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## 6.11 SELF ASSESSMENT QUESTIONS

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### 6.11.1 Multiple Choice Questions:

- Pinus* commonly occurs -
  - In plains
  - On hills
  - Near sea shore
  - In water
- “Chilgoja” edible seeds are obtained from-
  - P. insularis*
  - P. merkussi*
  - P. gerardiana*
  - P. excelsa*
- Turpentine is obtained from which part of *Pinus*-
  - Root
  - Stem

- (c) Leaf (d) Fruit
4. The gymnosperm occurring in deserts is  
 (a) *Cycas* (b) *Pinus*  
 (c) *Gnetum* (d) *Ephedra*
5. The stem is photosynthetic and the leaves are minute in-  
 (a) *Cycas* (b) *Pinus*  
 (c) *Gnetum* (d) *Ephedra*
6. Which of the following is a living fossil?  
 (a) *Ginkgo biloba* (b) *Pinus*  
 (c) *Cedrus deodara* (d) *Abies*
7. Both *Cycas* and *Pinus* have-  
 (a) Motile sperms (b) Motile and non- motile sperms  
 (c) Non-motile sperms only (d) Non- motile and motile sperms
8. Gymnosperms are recognized as a distinct group of plants by  
 (a) J. D. Hooker (b) Robert Brown  
 (c) Birbal Sahni (d) Coulter and Chamberlain
9. A Coniferous family Taxaceae for the first time was raised to the rank of order by  
 (a) Engler (b) Eichler  
 (c) Florin (d) Sporne

### 6.11.2 Fill in the blanks

1. Presence of -----canals is characteristic feature of conifers.
2. Absence of pollen tube formation and direct release of spermatozoids in archegonial chamber is known as-----
3. *Ginkgo biloba* is considered ----- fossil.
4. The germination of seed in *Cycas* is-----
5. The first cell during the development of male gametophyte of gymnosperm is-----
6. Winged pollen grains are found in -----
7. Naked ovules and absence of vessels in xylem are characteristic of group-----

**6.11.1 Answer key:** 1-(b), 2- (c), 3-(b), 4-(d), 5- (d), 6-(a), 7- (a), 8-(b), 9-(c)

**6.11.2 Answer key:** 1-Resin, 2-Zoodiogamy 3-Living, 4-Hypogeal, 5-Microspore, 6-*Pinus*, 7-Gymnosperms

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### ***6.13 SUGGESTED READINGS***

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### ***6.14 TERMINAL QUESTIONS***

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- Q1. Describes briefly the salient features of gymnosperms
- Q2. Discuss briefly the system of classification of gymnosperms proposed by Pant.
- Q3. Describe briefly various systems of classification of gymnosperms.
- Q4. Write short notes on-
- a) Male gametophyte of gymnosperms.
  - b) Female gametophyte of gymnosperms.
  - c) Embryogenesis in gymnosperms
  - d) Evolutionary trends in gymnosperms.
- Q5. Discuss the characteristic features of gymnosperms.
- Q6. Describe briefly various systems of classifications of gymnosperms.
- Q7. Discuss briefly reproduction in gymnosperms.
- Q8. Give an account of distribution of living gymnosperms in India.
- Q9. Write an account of economic importance of gymnosperms.
- Q10. Discuss briefly:
- a) Geographical distribution of Cycadales.

- b) Source and use of resin.
- c) Medicines obtained from gymnosperms.
- d) Source and uses of Canada balsam.
- e) Geographical distribution of Coniferales in India

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## **UNIT-7-PTERIDOSPERMALES AND PENTOXYLALES**

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- 7.1 Objectives
- 7.2 Introduction
- 7.3 Brief account of Pteridospermales and its families
  - 7.3.1 Lyginopteridaceae
  - 7.3.2 Medullosaceae
  - 7.3.3 Caytoniaceae
  - 7.3.4 Glossopteridaceae
- 7.4 Brief account of Pentoxylales
- 7.5 Summary
- 7.6 Glossary
- 7.7 Self Assessment Questions
- 7.8 References
- 7.9 Suggested Readings
- 7.10 Terminal Questions



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## 7.1 OBJECTIVES

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After reading this unit students will be able:

- To study characteristic features of Pteridospermales.
- To study about different families of Pteridospermales.
- To know about Pentoxylales and its affinities with other plant groups.

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## 7.2 INTRODUCTION

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Pteridospermales are Gymnosperms with fern like foliage (also called as seed ferns) having unprotected seeds. Pteridospermales appeared during upper Devonian period of Paleozoic era and existed throughout Carboniferous and Permian periods and became extinct during Mesozoic Era. Pteridospermales were first of all discovered by Grand Eury in 1877.

### Characteristic features

1. The plants possess erect, slender or weak stem
2. Leaves are large, pinnately compound and frond like.
3. Primary xylem is present in form of solid or medullated protosteles.
4. Primary xylem is usually mesarch and rarely exarch. Polystelic condition has also been reported.
5. Secondary wood has been found to be manoxylic and was formed in small amount.
6. Multiseriate pits were present on radial walls of tracheids of secondary wood.
7. Seeds were borne directly either on modified or unmodified foliage.
8. Seeds exhibited similarity with that of cycads.
9. Ovules do not contain annulus and were surrounded by cupules.
10. A distinct pollen chamber was present in the ovule and the integuments were either free or fused with nucellus.
11. Integuments were vascularized and nucellus was also vascularized in some ovules.
12. Microsporangia were grouped into synangia.
13. Pollen grains were either monolete or trilete and lacked pollen tube.
14. Leaf traces were mesarch.

Pteridospermales have been reported to occupy intermediate position between the ferns and Cycadophytes. They have been kept in gymnosperms as they produce naked seeds. Pteridospermales have been known to exhibit similarity with Pterophytes and Cycadophytes. These similarities are:

### Similarities of Pteridospermales with Pterophytes:

1. Both possess large and pinnately compound leaves.
2. Lateral veins are dichotomously branched.
3. Gametophytes are endosporic (in aquatic ferns).
4. Xylem is mesarch (rarely exarch).

5. Xylem vessels are absent and phloem lacks companion cells.
6. Megaspores lacks thick wall.
7. Archaeogonia present
8. Spermatozoids are motile and multiflagellate.

### Similarities of Pteridospermales with Cycadophytes

1. Presence of manoxylic wood.
2. Presence of pinnately compound leaves
3. Most of the Cycadales and some Pteridospermales possess extensive cortex.
4. Spermatozoids are multiciliate and motile.
5. Presence of pollen chamber in ovules.
6. Presence of similarity in vascular supply of ovules.

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## **7.3 BRIEF ACCOUNT OF THE FAMILIES OF PTERIDOSPERMALES**

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**Arnold (1948) divided Cycadofilicales or Pteridospermales into three families**

- a) **Lyginopteridaceae:** Representative of this family were characterized with monostelic stem, petioles generally with single strand and small seeds e.g. *Lyginopteris*
- b) **Medullosaceae:** Representatives of this family exhibit polystelic stem, large petiole, large seed and number of scattered bundles. e.g. *Medullosa*
- c) **Calamopityaceae:** This family is characterized to be the largest family of Pteridospermales, with monostelic stem and large number of bundles. e.g. *Calamopitys*

**Sporne (1974) classified** Pteridospermales into seven families. Out of these the first three families, Lyginopteridaceae, Medullosaceae, Calamopityaceae are confined to Paleozoic era and the remaining four families belong to Mesozoic era. Mesozoic era families were characterized with pinnate leaves, pollen and seed organs. The four families have been identified as Glossopteridaceae, Peltaspermaceae, Corystospermaceae and Caytoniaceae.

### 7.3.1-Lyginopteridaceae

Characteristic features of Lyginopteridaceae include:

1. Members have been reported from both the Upper and the Lower Carboniferous periods of Palaeozoic era.
2. The plants were not very large and attained a maximum height of two metres.
3. Several plants were lianas (woody climber) or vine-like in their general habit.
4. They had axillary branching fronds with bifurcate rachis.
5. The leaves were highly dissected and produced along the stem at widely separated intervals.

6. Petioles had a V-or W-shaped trace, formed as a result of the fusion of several smaller traces.
7. A large amount of secondary xylem was present in the stem.
8. Cauline vasculature was generally monostelic.
9. Due to the monostelic stems, it was always difficult for the stems to support the weight of their large fronds, and, therefore, the plants must have had a straggling growth habit.
10. The tracheal pitting was usually of the multiseriate, elliptical bordered type.
11. A “dictyoxylon cortex” was present in some members, i.e. anastomosing longitudinally oriented bands of sclerenchyma were present in the outer cortex.
12. Often one or two massive traces were seen going into the leaves.

### External Features of Lyginopteridaceae

The plants have been recognized to be climbers. The stem was long and aerial ranging from 2 mm to 4 cm in diameter. Branching has been reported in some cases. Walton (1940) has specifically reported axillary branching (specifically in one case). Presence of adventitious and prop roots have been reported to be present in weak stems. Plants contain large number of spirally arranged leaves which were bi-pinnate to tri-pinnate. Presence of spines is a characteristic feature which perhaps helps in climbing. Spines were present both on stem and leaves. The pinnae had pinnules or leaflets, and were present at right angles to the rachis. The petiole and the rachis were attached with capitate glands.

### Anatomy of Lyginopteridaceae

**Stem:** The stem pieces are well preserved in the European and American coal balls in the form of petrifications and compressions. A reconstruction of the transverse section of the stem clearly depicts presence of a mesarch siphonostele alongwith a well-developed centrally located pith (Fig.7.1).

Separate regions of secondary wood and thick cortex have been identified. The outer cortex contains radially broadened fibrous strands which form a net-like structure. The inner cortex consists of parenchymatous cells. Pericycle is located inner to the cortex. Five mesarch primary vascular bundles, separated by parenchymatous areas, constitute the primary structure of the stem. The primary phloem is present towards the outer side in each vascular bundle. The cambium is preserved between phloem and xylem in some of the specimens. The xylem consists of tracheids.

The protoxylem tracheids have spiral thickenings. Centripetal tracheids of the metaxylem have multiseriate bordered pits while the centrifugal tracheids are scalariform. The pith is large and parenchymatous. Some thick-walled cells, called *sclerotic nests* are scattered throughout the pith.

Several distinctly mesarch leaf traces are quite prominent. One leaf trace traverses through the petiole and branches into two parts to supply to the forking rachis. The secondary

structure of the stem exhibits the presence of periderm just inner to the two cortical layers. The primary phloem gets crushed and inner to this is present the cylinder of the secondary vascular tissue, which surrounds the primary xylem. Presences of many secondary medullary rays have been reported. Secondary vascular tissues are interrupted by leaf traces. Several large and small cells are alternately present in the secondary phloem. Cambium and secondary xylem are located inner to secondary phloem. Secondary xylem consists of large tracheids with multiseriate bordered pits which were arranged on radial walls.

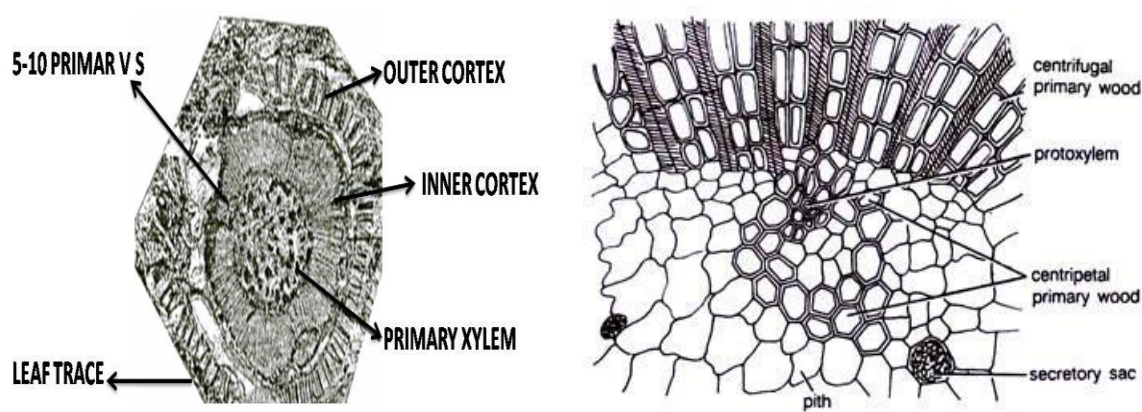


Fig 7.1: Part of T.S. of stem (*Lyginopteris oldhamia*)

**Leaf:** Leaf of *Lyginopteris oldhamia* was described as *Sphenopteris hoeninghausii* before the connection between stem and leaf was discovered. Impressions of *Sphenopteris* clearly depicted that the rachis was forked and possessed strong pinnae, which were further divided pinnately. The leaves were reported to be about 50 cm in length. Leaves were circinate rolled with petiolar base. Entire leaf was covered with hairs and glands. Epidermis of leaf was cutinised on the adaxial (upper) surface and stomata were present only on abaxial (lower) surface. Mesophyll was differentiated into palisade and spongy parenchyma (Fig. 7.2).

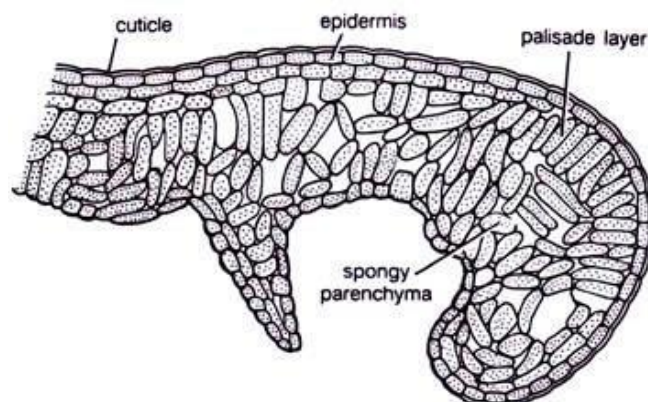


Fig. 7.2: T.S of part of Pinna of *Sphenopteris hoeninghausii*

**Root:** Transverse section of root shown that cortex is divided into outer and inner cortex. The 2 to 3 layered outer cortex contains thin walled cells while the inner cortex is 4-6 layered and consists of several cells of mucilaginous nature. The outer cortex of *Lyginopteris* root has been compared with the velamen of orchid root by Scott. The stele has been reported to be tetrarch with each arm of xylem having a small amount of protoxylem towards the outer side.

Rootlets exhibit diarch condition. The protoxylem is made up of spiral tracheids. The phloem groups alternate with the xylem. In the prepared sections the endodermis and pericycle are clearly observed. Development of secondary wood occurs in larger roots, however presence of pith has not been reported (Fig.7.3).

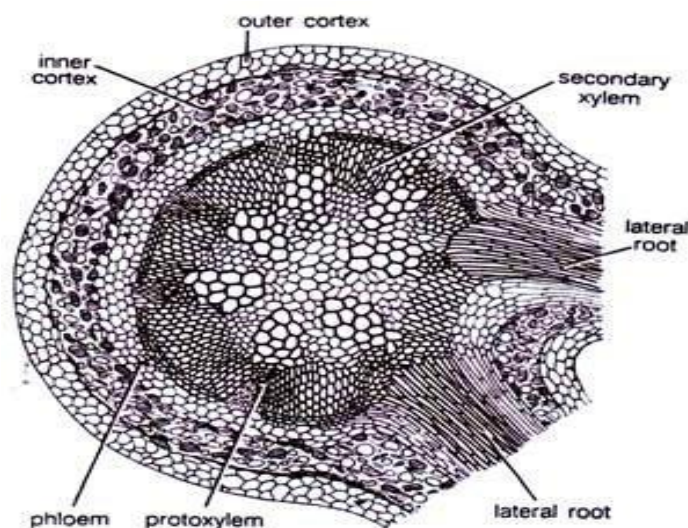


Fig. 7.3: T.S of root of *Lyginopteris oldhamia* (after Scott)

### Reproductive Organs:

*Lyginopteris oldhamia* has been reported to be heterosporous, with its ovules enclosed within cupules. Kidston (1905) discovered the impressions of *Crossotheca* in connection with the leaves of *Sphenopteris hoeninghausii*, and hence it was found that *Crossotheca* is the microsporangium of *Lyginopteris* because the leaves of *Lyginopteris* were described under the name *Sphenopteris hoeninghausii*. The ovules and seeds of *Lyginopteris* were described under the name *Lagenostoma lomaxi*. Arnold (1947) stated that the microsporangiate structures of *Lyginopteris* belong to *Telangium*.

**Microsporangium:** *Crossotheca hoeninghausii* has been characterized as the microsporangia-bearing member of *Lyginopteris*. About 6-7 bilocular and pendant microsporangia have been identified to be present on peltate fertile pinnules called as microsporophyll (Fig. 7.4). Each microsporangium was about 3 mm. in length and its dehiscence was longitudinal. Microspores were located in cavities of microsporangia, at times in tetrads. Each microspore possessed a thick rough exine with a diameter of 50 to 70  $\mu$ . Chamberlain (1935) suggested that pollen grains must have shed in a similar manner as observed in *Isoetes*, *Selaginella* and other water ferns. Stidd et al., (1985) in their study characterized Schopfiangium having synangia similar to the pollen organs of *Lyginopteris*. Taylor & Taylor (1987) described a new pollen organ as *Phacelotheca*.

**Ovule and seed:** Seed were characterized to be small, barrel-shaped structure ranging 5-6 mm in length and 4 mm in width. Every seed was covered and protected by a cupule present at the end of the slender rachis. Rachis was itself covered by glands and hair as seen in leaves

and stem. The seeds and the cupules have been reported only in a petrified condition. Single vascular bundle of the rachis divided into about 10 vascular strands. These vascular strands traversed laterally into the cupule. Several glands have been found to be present on outer surface of the lobed cupule. The seed named as *Lagenostoma lomaxi* was found to be orthotropous. The nucellus was free at the tip however during later stages of development it was surrounded by a bell-shaped pollen chamber or lagenostome. The ovule was surrounded by two layers an outer hard stony layer and an inner fleshy layer. Seeds have also been reported to exhibit similarity with seeds of Cycad.

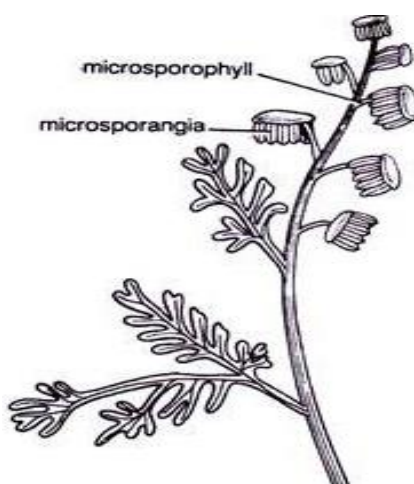


Fig. 7.4: *Crossotheca hoeninghausii* with microsporophyll

**Other fossil studies pertaining to Lyginopteridaceae:** Several stems, fronds, seeds and pollen bearing organs belonging to Paleozoic era studied by different scientist have been reported to belong to family Lyginopteridaceae.

### *Heterangium*

It is a stem genus and is represented by 12 species. It is another important member of Palaeozoic Cycadofilicales belonging to family Lyginopteridaceae. It has been reported from Upper and Lower Carboniferous beds and the best characterized species is *Heterangium grievii*. The genus has been discovered in the form of compressions and petrifications. The largest stem of this genus was about 4 cm in diameter and rarely branched. Transverse section depicts longitudinal ribs of sclerenchyma to be present in the outer cortex. Several stone cells embedded in the parenchymatous inner cortex have been reported. Many strands of tracheids which were separated by the parenchymatous bands were present in the vascular column. The stele was reported to be solid. Single protoxylem was present in the leaf trace. The plant body of *Heterangium grievii* exhibits similarity with that of *Calymmatotheca hoeninghausii*.

### *Tetrastichia*

*Tetrastichia* has been identified as monotypic genus of Lyginopteridaceae and is represented by only one species *T. bupatides*. Its existence has been reported from the Lower

Carboniferous of Scotland along with another monotypic genus (*Tristichia ovensii*) of the family.

Structure of its stem closely resembles with that of ferns however, cortical bands of sclerenchyma and its secondary wood exhibit similarity with the stems of Pteridospermales. Branching has been reported to be in an opposite decussate manner. The primary xylem was usually four-armed but sometimes five-armed also and made of a solid protostele. Tracheids present in the protostele were either reticulate or scalariform pitted. Parenchyma cells were completely absent. Presence of mesarch protoxylem group has been identified in the middle region of each branch of stem. From this protoxylem group originated several branch-trace protoxylems. Some researchers consider lateral branches of the stem to as petioles. A narrow zone of secondary wood was present in some of the branches while in other branches the secondary thickenings were absent. The tracheids possessed reticulate thickenings. The rays were both uniseriate as well as multiseriate. "Sclerotic nests" or group of stone cells were reported to be present in the region of inner cortex and network of plates of fibres was present in the region of outer cortex.

### 7.3.2-Medullosaceae

Medullosaceae is another group of pteridosperms occurred during lower and upper carboniferous and were persistent upto Permian period. Fossil remain of roots, stem and leaves of Medullosaceae have been reported from coal balls. The most prominent evidence is the presence of leaf organ genera, *Neuropteris* and *Alethopteris* which reveals Medullosaceae to be the predominant family of coal age. Medullosaceae family is characterised by massive trees whose stems contained more than one vascular segment. The plants of the family possessed secondary thickening and the ground parenchymatous tissue is believed to have retained ability of meristematic activity throughout the life of plant. Due to such meristematic activity primary as well as secondary vascular tissue exhibited continuous growth.

Anatomical details of several specimens of Medullosaceae have been studied by Delevoryas (1955). He reported stem and vascular segments to increase in size with growth of plant. This increase was attributed to formation of secondary xylem around every segment. Parenchymatous tissue (in primary bundle), rays in secondary wood and cortical parenchyma were also reported to increase in size. Delevoryas depicted a correlation between size of primary and secondary wood in specimens of all age groups. According to him such a relation could have been existed only if primary wood grew continuously throughout the life of plant.

For several years stems of *Medullosa* were considered to be polystelic. Basinger *et al.*, (1974) characterised the stems to be monostelic. In their study it was reported that separate stele have evolved by dissection of single prostele. Individual vascular cylinder represents a vascular segment (not a stele). All the vascular segments combined for form eustele. Also sympodia represents protoxylem points (or strands) and not vascular segment as such. In *M.*

*noei* there was reported 5-6 sympodia for 2-3 vascular segment. Another example is of *M. primaeva* which possesses 13 sympodia for 4-5 vascular segments (Fig. 7.5).

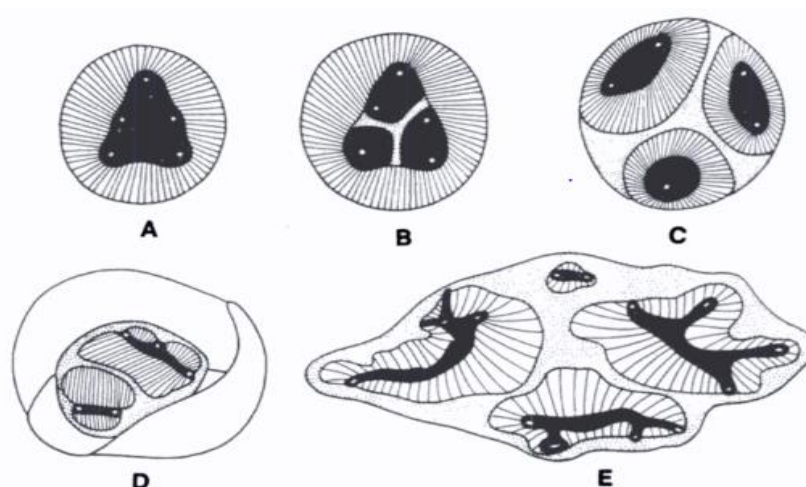


Fig 7.5: Hypothetical stages in evolution of *Medullosa* stem. A- Three ribbed protosteles showing mesarch xylem, B- Dissection of protosteles into three segments, C- Each vascular system is invested secondary xylem, D-T.S of *M. noei*, E- T.S of *M. primaeva*



Fig.7.6: Reconstruction of *Medullosa noei*

Other characteristic features (beside the stem discussed above) include

1. Fronds possessing bifurcating large petioles
2. Non cupulate ovules
3. Integuments free from nucellus (except base)
4. Comparatively simple pollen chamber.
5. Large male reproductive structure.
6. Presence of tubular sporangia along with monolete pollens.



Stewart and Delevoryas (1956) reconstructed the *Medullosa* plant (Fig. 7.6) with following mentioned characteristic features. *M. noei* resembles with a tree with an appropriate height of 3 -4.5 m, presence of pinnately compound leaves, leaf bases are spirally arranged and get thrown off during later stages, development of adventitious roots from lower part of stem. The stem is represented by four genera i.e. *Medullosa*, *Sutcliffa*, *Colpoxylon* and *Quaestora*.

**Stem:** The diameter of stem varies from 7-8 cm. Large number of spirally arranged leaf bases are present. There are several complete vascular segments and the most common number of vascular segment is 3. Every vascular segment is surrounded by monoxyletic secondary xylem and ground tissue of parenchymatous cells. Cortex is divided into inner and outer zone. Outer cortex is characterised by presence of sclerenchymatous tissue and leaf trace strands along with scattered distribution of accessory vascular strands. Leaf traces divide (split) into several small collateral bundles with exarch xylem. The collateral bundles associated with sclerenchymatous tissues that were either present in ring or otherwise scattered in ground tissue of petiole.

Number, shape and size of vascular segments are specific characters. The number of vascular segments could vary from 2-20 in *M. primaeval*, two vascular segments upon proliferation give rise to many subsequent segments. In *M. Leuckartii* there was the presence of three tangentially expanded vascular segments along with several smaller segments in ground tissue (Fig. 7.7). Delevoryas (1955) explained the complete vascular cylinder present in *M. Stellata* might have evolved as a result of fusion of peripheral vascular segments of *M. leuckartii* species.

*Sutcliffa* is another genus of Medullosaceae characterised by plants with bigger stems with large central vascular system along with subsidiary vascular systems which branch from central vascular system (Fig. 7.7). *Sutcliffa* is regarded to be intermediate between *Medullosaceae* and *Lyginopteridaceae*.

Upto 1980 medullosaceae included stem having more than one vascular system. Maper and Rothwell (1980) reported *Quaestora* from upper Mississippian of Arkansas possessing single vascular system in stem and was included in Medullosaceae. *Quaestora* possessed several features which differed from medullosaceae as it contained cruciform protosteles, decussately arranged leaves and absence of internal periderm. Petiole structure and leaf trace production in *Quaestora* resembled to that of medullosa. Overall studies revealed that *Quaestora* was a transitional stage or intermediate between *Calamopityaceae* and *Medullosaceae*.

**Leaves:** *Alethopteris* and *Neuropteris* are regarded as the two most common leaf types of genus *Medullosa*. A characteristic feature of such leaves was the association of pollen bearing or seed like structure with these leaves. These genera have been discovered from coal balls of America and Europe. Andrew (1945) figured out structure of *Alethopteris* showing unequal branching of rachis. Delevoryas (1955) reported axes of *Myeloxylon* exhibited unequal branching in lower parts and concluded that regular pinnate arrangement was attained in distal region of the frond.

*Alethopteris* is characterized to be compound frond which was constructed on pinnate plan, borne on main rachis (fig.7.8A). The main rachis was reported to exhibit dichotomous branching. Fronds possessed pinnae which were divided into linear pinnules having a decurrent base. Pinnules were traversed by a mid rib which reaches till the apex and give rise to secondary veins which were forked at the ends (fig.7.8A). The decurrent base is supplied with veins directly arising from pinna. In upper portion of frond pinnules are replaced by lamina (simple, entire or lobed). Zeiller studied portion of cuticle from upper surface of pinnule and reported presence of polygonal epidermal cells. Cells present above veins were rectangular in shape. He also reported presence of group of cells encircling a pore, which was regarded as sunken stomata.

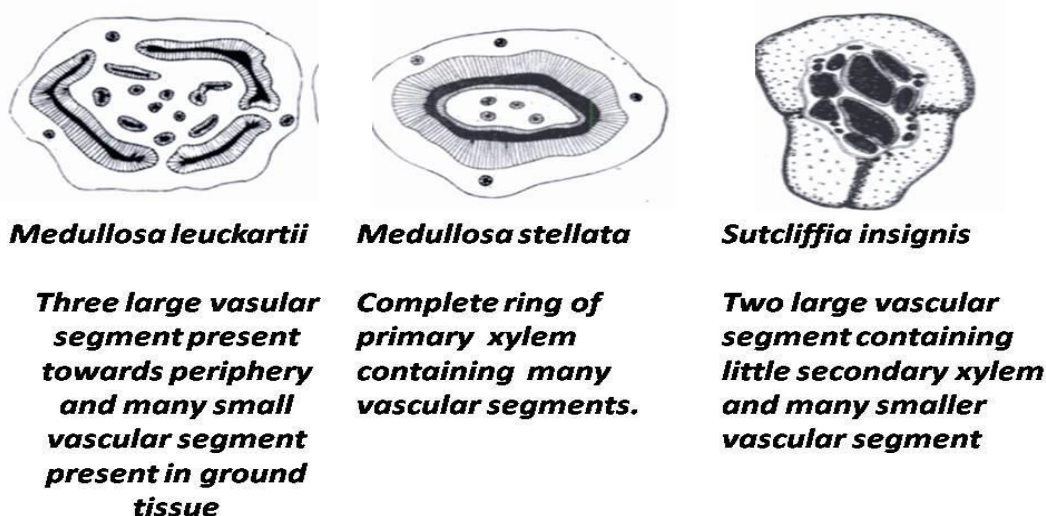


Fig. 7.7: T.S. of stem of three species to depict vascular segment

*Neuropteris* genus was first of all described by Brongniart and was initially classified under ferns. Later the genus was found to belong to Pteridosperms and is presently considered leaf genus of Medullosaceae. Fronds of *Neuropteris* may range upto 10 m in size and may be bi or tri pinnate. Rachis may have dichotomous branching. Rachis and petioles possess single pinnule. Pinnules are generally entire they are rarely lobed. Brongniart reported presence of small pedicel in pinnules of *N. grangeri*. Mid rib does not reaches up to apex of pinnules. Secondary veins were arched and forked repeatedly.

**Root:** Development of adventitious roots have been reported in *Medullosa*. Roots have been characterized to be either triarch or tetrarch. Free branching occurs in roots and diameter of roots was more than one cm. In *M. angila* root was reported to be triarch which means it possesses three groups of primary xylem alternating with same number of phloem groups. In *M. noei* root was found to be tetrarch. The primary xylem is surrounded by secondary xylem except opposite to the protoxylem. Cortex was well preserved in older roots, along with a clear zone of thick periderm. Rothwell and Whiteside (1972) reported the presence of several distinctive root fragments in carbonate petrified material from middle Pennsylvanian of Illinois. The fragments were either incompletely developed small rootlets or mature axes which measured over 2 cm in diameter/. These root axes also exhibited development of

secondary tissue. In small roots pericycle was surrounded by endodermis and parenchymatous cortex. Mature roots developed a periderm at outer margin of pericycle. Secondary xylem (completely surrounding primary xylem) was well developed in larger specimens.

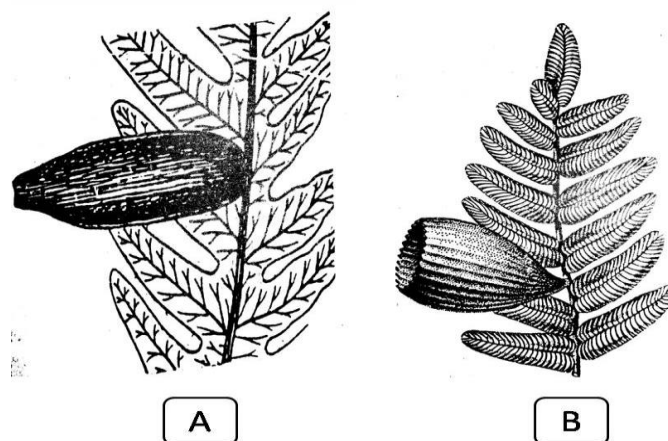


Fig. 7.8: A- Leaf of *Alethopteris* bearing fructification, B- Leaf of *Neuropteris* bearing fructification

**Male fructification:** Male fructification in Medullosaceae have been found in the form of impressions. Halle (1933) reported that some of the structures which were earlier described as seeds were actually pollen organs containing microspores. Halle also succeeded in preparing microtome sections of carbonised material. Large number of sporangia fused side by side to form a cup shaped structure. In the centre was present a hollow cavity with wide opening. In compressed state they appeared like leaves. The pollen grains have been characterized to be large and elliptical when flattened. *Dolerotheca* is one of the largest pollen organ of Medullosaceae (Fig. 7.9). It comprises of four identical synangia, all of which are fused to form a compound structure. Each microsporangium has a vascular trace and dehisces longitudinally. *Codontotheca* represents basic radial symmetry of medullosan pollen organ. It comprises of six fingers like structures (segments) which are fused at the base. Separation of sporangia is partial in *Codontotheca*. The complete synangium is quite slender. *Autotheca* is oval, elongated and much more slender tapering towards apex. About 6-9 sporangia remain fused to form a hollow synangium which contains a narrow opening. Genus *Parasporotheca* described by Dennis and Eggert (1978) consists of cluster of ventrally curved lamina like synangia. Every synangium consists of uniseriate row having 14 -20 sporangia, which contain bisaccate and large prepollens. These prepollens are also called as parasporites. As seen in above description the pollen bearing organs depict variation but still there exists uniformity in pollen grains. The pollen grains are large, prolate and have a suture on proximal surface.

**Female fructification:** Seeds of medullosa have been grouped under *Trigonocarpels*. Nucellus is free from integument except for basal region (Fig.7.9). Seed coat comprises of outer fleshy sarcotesta and inner stony sclerotesta. Three prominent ridges are present in sclerotesta. Independent vascular bundles are present in nucellus and integument. *Trigonocarpus parkinsonii*, the well known seed is now known as *Pachytesta olivaeformis*. Seeds exhibit considerable amount of variation in size. The largest seed reported measure

11cm in length and 6cm in diameter. The smallest seed reported in *P. Berryvillensis* is 6.8mm long and 5.2 mm in width. *Pachytesta hexangulata* exhibits a well developed female gametophyte having three oval archegonia present below pollen chamber.

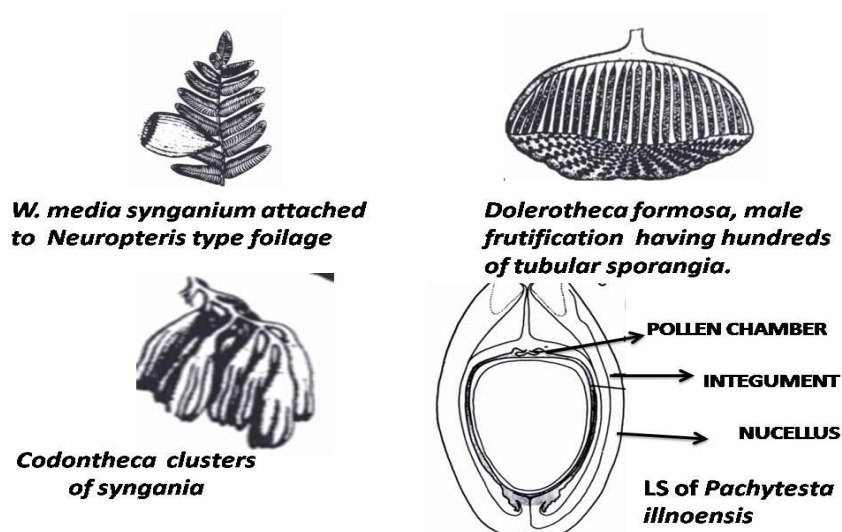


Fig.7.9: Male and female fructification in *Medullosa*

*Pachytesta obvlivatoris* (belongs to stem genus *Medullosa anglica*) is also a large seed with lower portion cylindrical in shape and upper portion flat. Micropyle is long occupying almost half the length of seed. Seed coat consists of three layers, sarcotesta (outer fleshy), sclerotesta (middle stony layer) and endotesta (inner thin layer). Seed coat encloses massive nucellus with epidermis and a pollen chamber (Fig.7.9).

### 7.3.3-Caytoniaceae

Thomas discovered this group of plants from middle Jurassic rocks of Cayton Bay in Yorkshire coast of England. The group is characterized by presence of

- Leaves (*Sagenopteris*)
- Seed bearing organs (*Caytonia*)
- Pollen bearing organs (*Caytonanthus*)

**Leaves (*Sagenopteris*):** Leaves are palmately compound possessing 3-6 (in most of the cases four) lanceolate leaflets. Length of each leaflet varied from 2-6cm. Petiole carries these leaflets in two parts at its tip. Leaflets are characterized by the presence a prominent midrib and reticulate venation. Similar pattern is also reported in *Glossopteris* in which several lateral veins arise which fork and rejoin to form a mesh, however, veins end freely at margin. Leaves are also characterised by presence of palisade tissue and elongated transfusion tissue. Stomata (as observed in most of gymnosperms) are haplocheilic and present only on lower surface. After formation of well defined abscission layer leaflets and entire leaf is shed. Stems are represented by small branched twig on which bud of *Sagenopteris* are present. Stem, as reported through studies conducted by different workers were not thick and also leaves were not directly borne on tree trunk.

**Male reproductive structure:** Pollen bearing organs or microsporangiate fructification was named as *Caytonanthus*. Initially they were studied by Phillips in 1829 and were described as leaves. Later Harris (1964) characterised it to be modified pinnate microsporophyll. Dorsoventral rachis or central axis bears opposite pinnae. Pinnae exhibit irregular branching and apex of every branchlet contain single, pendant, tubular and quadrilocular synangium. Pollen sacs or sporangia upon dehiscence get separated (except at the tip) and pollen grains are released. Pollen of *Caytonanthus* have been characterised to be small, bisaccate with terminal aperture. It has smooth surface with irregular pits. Sporoderm consists of two layers, inner layer is thick lamellate while outer layer is alveolate.

**Female reproductive structure:** Megasporophyll of Caytoniales was initially characterized through the genus *Caytonia* and *Gristhorpia*. However, it was later found that the difference between the two genera was inconsistent. As a result the characters of the two genera were merged to the genus *Caytonia*. The species *C. seawardii*, *C. nathorstii* and *C. thomas* have been assigned to the genus *Caytonia*. *C. seawardii* have been characterized with foliage *Sagenopteris colpodes* and *C. nathorstii* with foliage *S. Phillipsii*. Seeds are completely closed in fruit, which is a small sac like structure having an outgrowth called as lip (flange) present near stalk (Fig.7.10). A minute opening called mouth is located in between lip and stalk. Except the mouth region, remaining part of epidermis is cuticularized. Mouth remains closed in mature fruit but it is believed that mouth would have remained open during pollination. The number of seeds in three identified species *C. seawardii*, *C. nathorstii* and *C. thomas* have been reported to be 8, 15 and 30 respectively.

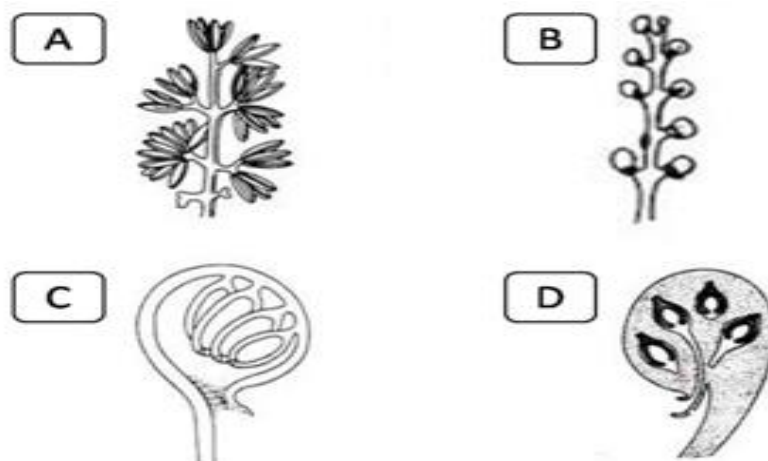


Fig.7.10: A- Microsporophyll of *Caytonia*, B- Megasporophyll showing pinnately arranged cupules, C- L.S of cupule showing position of seeds inside, D- Vertical L.S of fleshy fruit of *Caytonia*

Presence of pollen grain on lip of *C. nathorstii* was reported by Thomas (1925). Hence this particular part was believed to function as stigma. Harris found pollen grains to be present in micropyle of seeds. Size of each seed was about 2mm X 1mm, seeds were oval in shape and unitegmic. Except base region integument is free from nucellus. Nucellus is covered by a thick cuticle except for micropyle end and chalaza opening. No trace of presence of vascular bundle in integument has been reported. Harris (1951) reported presence of small channels through which each seed is connected to mouth. Maturation of seed occurs inside the fruit.

Pollen grains were trapped through pollination drop formed at the tip of mouth. The pollen grains float in the drop and travel through the channel to reach nucellus. The two bladders of pollen grain act as floating device.

### 7.3.4-Glossopteridaceae

Distinctive vegetation of Palaeozoic found in Gondwana land during Carboniferous and Permian period is known as Glossopteris flora. The fossils of Glossopteris have been reported from India, South America, South Africa, Australia and Antarctica. All these regions which are now separate due to continental drift were joined at that time and are hypothetically called as Gondwana land. Most of the fossil records of Glossopteris flora are in the form of impressions and compression of leaves and detached reproductive organs. Different scientists have studied about fossil records of Glossopteridaceae. Brongniart (1828) first of all recognized leaves of *Glossopteris*. Gould and Delevoryas reported presence of petrified woods and reproductive organs from region of Australia. Zeiller (1902) first of all recognized reproductive organs of *Glossopteris*. Major contribution to presently available knowledge about Glossopteridaceae have been provided through the work conducted by Plumstead, Pant, Surange and Chandra.

Royle (1883) characterized the axis under genus *Vertebraria*, including two species *V. indica* and *V. radiate*. Studies conducted by other workers reported the two species to be two different aspects of axes of same kind. Walton and Wilson (1983) and Pant (1956) in their respective studies have described about the structure of stem. Pant and his co workers have given anatomical description of leaves of *Glossopteris*. Leaves of *Glossopteris* are tongue shaped and are characterised by presence of prominent midrib with reticulate venation (Fig.7.11). Leaves have been reported to have considerable variation in size and shape i.e. leaves may be small or large in size and wide or narrow in shape. Leaves were sessile however petiolate leaves have been reported (rarely) in species such as *G. petiolata*. Leaves were dorsiventral, hypostomatic, stomata have been described to be haplocheilic, sunken and distributed irregularly in between the veins. Mesophyll was characterised by presence of both palisade and spongy parenchyma. Hypodermis was reported to be present in some of the species. Tracheids of midrib and subsidiary veins exhibited scalariform thickenings Bordered pits were present in few tracheids in the midrib region. Midrib shows large number of longitudinal veins which may or maynot anastomose. Pant (1982) during their work included leaf form of *Gangamopteris*, *Rubidgea*, *Paleovittaria*, *Euryphyllum* and *Rhabdotaenia* in Glossopteridaceae due to their similar form, similar pattern of venation and cuticular structure.

**Male reproductive structure:** Male fructifications have been named as *Eretmonia*, *Glossotheca* and *Nesowalesia*. All the three reported genera possessed sporangia of Arberia type. *Eretmonia* consist of stalked lamina in upper half of which were borne two branches on each of which were borne whorls of microsporangia (Fig.7.12 C). Microsporangium was purse shaped with an opening (present due to longitudinal rupture). Through this opening pollen grains were released. Pollen were reported to be striated and

bisaccate and means of pollination was anemophilous as reported by Pant (1987). Lacey, (1974, 1975) have reported only one species (*E. Natalensis*) whereas Surange and Maheshwari (1970) reported of *Eretmonia* from India. *Glossotheca* described by Surange and Maheshwari (1970) and Surange and Chandra resembles *Eretmonia* with the difference that in *Glossotheca* are present more sporangia bearing pedicels. Three or even more pedicels are borne on stalk of leaves. Each pedicel divides to give out two branches and each of this branch further divides dichotomously and sporangia are borne on terminal branches. Sporangia of *Glossotheca* have been described to be of Arberiella type. *Nesowalesia*, the third genus was reported to be closely associated with *Glossopteris*.

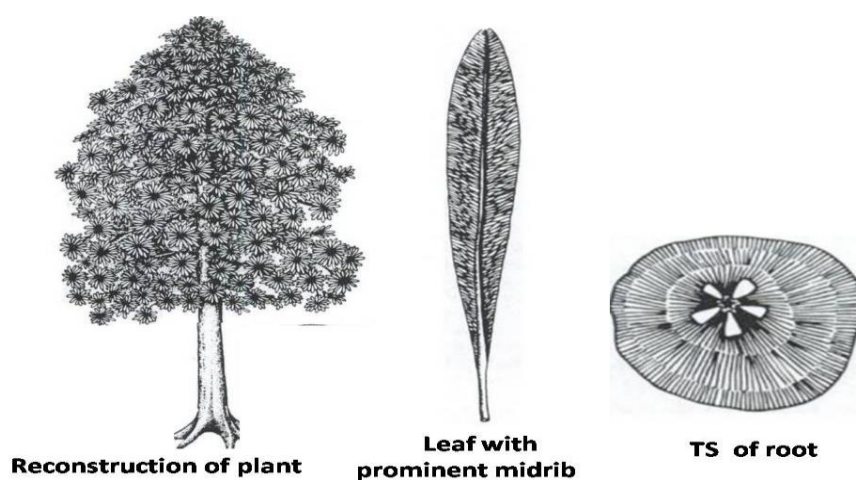


Fig. 7.11: Reconstructed *Glossopteris* plant with leaf and T.S of root

**Female reproductive structure:** Several workers have studied and reported a number of female fructifications. Which were found in the form of compression and impressions only. Some of the female reproductive structures have been found to be attached to unmodified leaf (as in *Dictyopteridium*, *Ottokaria*, *Scutum*, *Austroglossa*, etc) or they may be attached to modified leaf or bract (as found in *Partha*, *Mooia*, *Lidgettonia*, *Denkania* etc).

Plumstead (1952) reported female reproductive structure in *Glossopteris* to be leaf borne based upon studies conducted on fossils from Africa. Surange and Chandra described the genus *Denkania indica* having several long pedicels (Fig.7.12A). These pedicels were attached to adaxial surface of midrib and contains seed like bodies named as uniovulate cupules (Fig. 7.12). Lacey., (1975) also reported presence of similar reproductive structure from Africa however, they have not described presence of any such cupules. Instead only two seeds were borne on two scales which in turn were attached to lamina base. They specifically named it *Rusangla elegans*. Surange and Chandra described another type of fructification and named it as *Partha*. In this type of fructification the stalks do not terminate in single seed, there were present a disc like structures (cupules) beneath which were borne four seeds. Lacey *et al* have also described *Mooia*, which was characterised by presence of fertile leaf having 2-4 stalked cupules. Single seed was present in each cupule.

Thomas (1958) reported *Glossopteris* like scales containing cupules which were named as *Lidgettonia*. Thomas found presence of seeds as well as sporangia around the plant and reported some plants of the group to be seed bearing and others to be sporangia bearing. However, Surange and Chandra characterized *Lidgettonia* to be seed bearing. Gould and Delevoryas (1977) have also studied seed bearing organs alongwith their relationship with leaves from several specimens reported in Permian beds in Australia. They reported seed bearing organs to be always borne in axil of leaves. Seed bearing organs were named as ovulate capitulum. Microscopic structure of ovulate capitulum is similar to that of leaves hence they were regarded as megasporophylls. Megasporophyll possesses revolute margin and partially enveloped ovules (Fig.7.12D). Ovules are numerous, small, oval shaped and borne on lower surface of megasporophyll. Integument is free of nucellus except at chalazal end. Pollen chamber is present at micropylar end. Taylor and Taylor (1992) characterised that the seeds are borne adaxially on megasporophyll. They studied reproductive organs of specimens from late Permian deposits in Beardmore, Glacier region of central transantarctic mountains. Female frutifications of *Glossopteris* also exhibited gradual reduction in number of ovules with increase in their protection. Dispersed seeds of *Glossopteris* does not show presence of embryo. In this respect Pant (1987) reported its resemblance with present day Cycads and *Ginkgo* seeds, as *Glossopteris* were also shed after fertilization and embryo development occurred on ground. Occurrence of dicotyledonous seedlings in *Glossopteris* also supports the concept described by Pant.

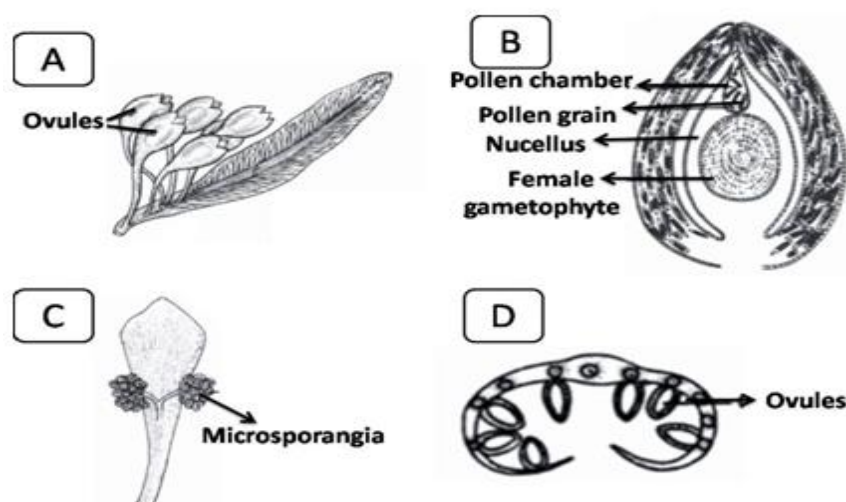


Fig. 7.12: A- Ovules arising in a row on adaxial surface of leaf of *Denkania indica*, B- L.S. section of seed, C-Fertile leaf bearing microsporangia in clusters, D-Section through ovuliferous capitulum of *Glossopteris* to show position of ovules

## 7.4 PENTOXYLALES

Birbal Sahni a well-known Indian Palaeobotanist in 1948 proposed a name Pentoxylales to represent a group of fossil plants which were discovered from Rajmahal hills in Amrapara District (Santhal Parganas) of Eastern Bihar, India. Pentoxylales have been reported to exist during Jurassic period. Pentoxylales were also reported from Newzealand by Harris (1962).



Several scientists have carried out research to provide morphological and physiological details about Pentaxylales, Table 7.1 represents contribution of eminent scientists.

### Characteristic features of Pentoxylales

1. Pentoxylales have been characterized to be shrubs or trees of small size.
2. Pentoxylales possessed two types of branches long shoots and dwarf shoots.
3. They have been named so (Pentoxylales) because their stems were polystelic with 5 or 6 primary steles. Beside this each stele was characterized to possess its own ring of cambium.
4. Leaves of Pentoxylales were simple, lanceolate, thick and had spiral arrangement.
5. Venation in leaves was open and rarely reticulate.
6. Secondary medullary rays were uniseriate.
7. Secondary wood possessed exocentric development.
8. Pentoxylales possessed unisexual reproductive organs which were borne on terminal end of branches.
9. Male reproductive organs of Pentoxylales were characterized to be a whorl of branched sporangiophores which were fused at base to form a disc.
10. Sporangiophores bear microsporangia on its short branches.
11. Female strobili were mulberry like in appearance.
12. Female reproductive organs lacked interseminal scales and were composed of thick central axis with ovules attached to the axis spirally.
13. Ovules were sessile.

**Table 7.1: Contribution of scientist towards discovery and study of Pentoxylales**

S.No.	Name of scientist	Contribution
1-	Birbal Sahni (1948)	Discovered Pentoxylales
2-	Sahni and Srivasava (1948)	Carried out research on leaves, stem and seed bearing organs of Pentoxylales.
3-	Vishnu Mittre (1953)	Described about pollen bearing organs of Pentoxylales
4-	Sporne (1965)	Characterized Pentoxylales as separate order

### Anatomy

Stem of Pentoxylales were polystelic with five primary steles. Each stele was described as a concentric structure having its own cambium. The cambium has been reported to be active in young stems but in older stems, it produced secondary tissue directed towards centre and hence secondary wood in these plants was characterized to be exocentric. Vascular strands were located external to cambium and comprised of primary xylem and primary phloem. Both primary xylem and primary phloem were present in the form of internal rings. These vascular strands run longitudinally and also gave rise to leaf traces. Beside five main vascular strands were present five smaller strands alternating with main strands. Sahni has characterized these small strands to be strands of lateral shoots Vishnu Mittre reported variation in number of primary strand at different levels along the length of stem. Presence of three strands was

traced in lower part of stem whereas five such strands were found to be present in middle region of stem. The number of strands increased to six in the upper (top) part of stem. In *Nipanioxylon guptai* single vascular cylinder was reported to be present at the lower (near base) part of stem, the number of strands was found to increase to 5-7 in upper region of stem. However, at apex of stem these strands coalesced to give rise to single vascular strand.

Secondary xylem in Pentoxylales was pycnoxylic which indicates that the wood of these plants was very compact, a character which is also found in conifers. Tracheids of Pentoxylales were similar to the tracheids found in living *Araucaria*. Tracheids contained bordered pits which were present on radial wall. Also tracheids were described to be uniseriate or biseriate. Alongwith this, secondary medullary rays were also characterized to be uniseriate and were arranged in height from one to five cells. Secondary wood developed more towards centre and contained growth rings, however, it is not clearly defined whether these rings can be regarded as annual rings.

The leaves have been described under the name *Nipaniophyllum raoi*. Leaves were found to be attached with the shoots i.e. *Pentoxylon sahnii* (Fig.7.13). Leaves have been characterized to be simple, petiolate, star-shaped. Presence of prominent midrib along with many parallel lateral veins is characteristic feature of leaves of pentoxylales. Leaf traces were reported to contain vascular bundles having centrifugal and centripetal xylems. Hence the leaf traces resemble Cycadalean pattern. Six strands arising from stele enters each leaf base. Stomata of pentoxylales were characterized to be syndetocheilic, a character similar to Bennettitales. However, Vishnu Mittre (1957) reported stomata to be of both types, he also reported presence of haplocheilic stomata.

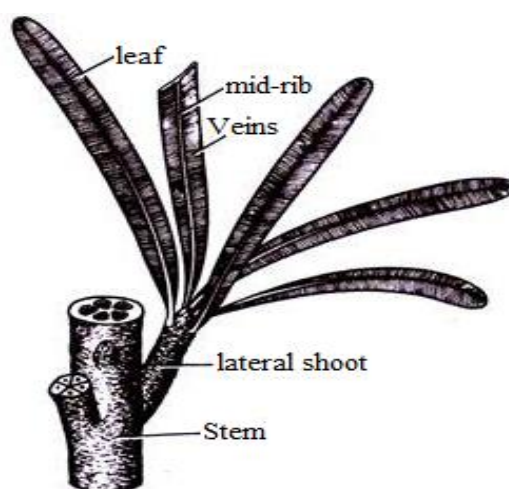


Fig. 7.13: *Pentoxylon sahnii*, reconstruction of stem and leaves

## Reproductive organs

The female cones or seed-bearing organs have been described under the name *Carnoconites*. Two species namely *C. compactum* and *C. laxum* have been reported. Seed-bearing organs were forked and were found to be attached terminally on lateral dwarf shoots (Fig.7.14B). They were mulberry-like in appearance and their length was about 1.8 cm in *Carnoconites*

*compactum*, 3 cm in *C. laxum*. About 20 sessile ovules were attached on the receptacle. Presence of sporophyll-like structure has not been reported. Also there were no inter seminal scales present. Ovules were covered by a single integument and nucellus was free from integument.

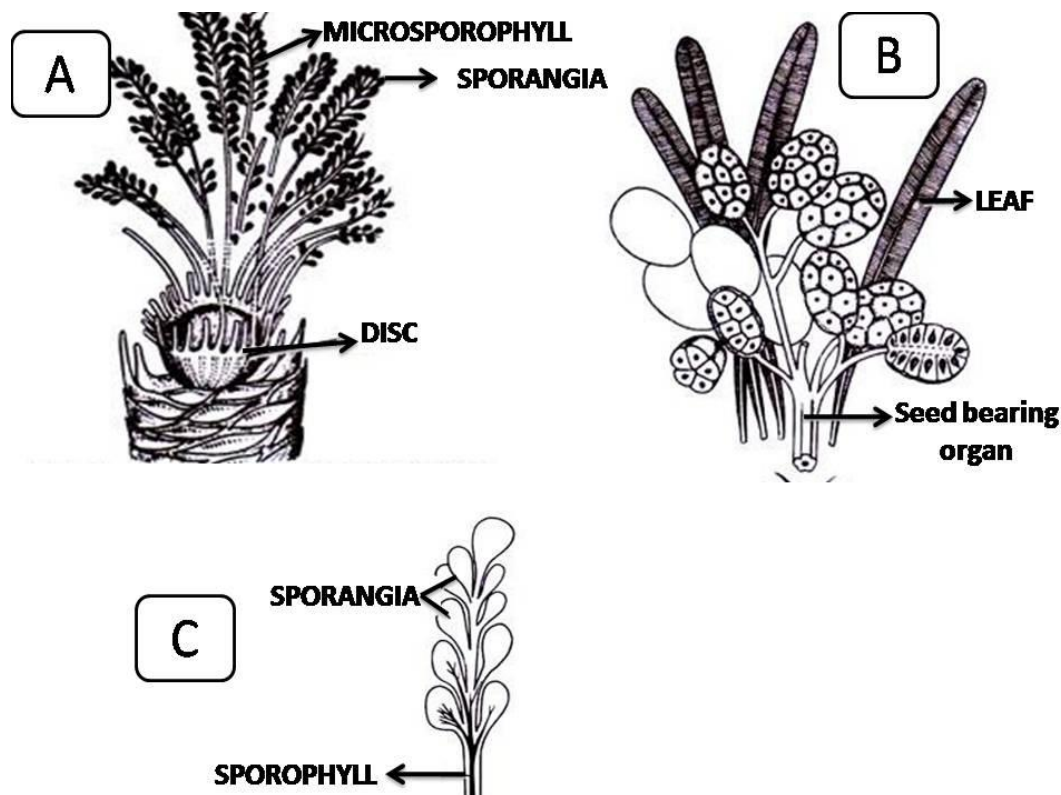


Fig.7.14: A- *Sahnia nipaniensis*, reconstruction of male flower (after Vishnu Mittre), B-*Carnoconites compactum* showing female cones (after Sahnii), C- *Sahnia nipaniensis*, a detached microsporophyll

Vishnu-Mittre (1953) described male organs (microsporangiate) of Pentoxylales as *Sahnia nipaniensis*. These microsporangiate structures were present terminally on the shoot, and were fused at base to form a shallow disc Fig.7.14A). Presence of about 24 such pollen-bearing organs was reported. Each microsporophyll possessed many pear-shaped, unilocular sporangia. Several monocolpate and boat-shaped pollen grains were present in each microsporangium.

## Affinities of Pentoxylales

Pentoxylales have been reported to exhibit structural and functional similarities with other plant groups. Some of the possible affinities of pentoxylales include:

### I. Affinities of Pentoxylales with Cycadales:

1. Presence of direct leaf trace in Pentoxylales and also in seedlings of some cycads
2. Anatomy of leaf traces exhibits diploxylic nature of their respective vascular bundles
3. Presence of haplocheilic stomata

4. Occurrence of vestigial polystely in seedling stages of some of the modern cycad
5. Similarity between nature of wood and pittings of Pentoxylales and cycads.
6. Presence of more or less similar type of pollen grains.
7. Similar kind of structure of seeds as well as peduncles.

Along with, above mentioned similarities, Pentoxylales differ from cycads in several aspects as vascular bundles found in Pentoxylales are not arranged the way they are arranged in Cycads. Moreover, there is no similarity between the polystelic condition of *Pentoxylon* and mature modern cycads.

## II. Affinities of Pentoxylales with Conifers:

1. Presence of Pycnoxylic wood
2. Tracheids with circular bordered pits arranged in uniseriate or bi-seriate manner.
3. Presence of Uniseriate wood rays
4. Reported dimorphism in stems of *Pentoxylon sahnii* and which is also found in many conifers.

Beside the above mentioned similarities the general anatomy of stem of Pentoxylales is not similar to conifers as described by Sahnii (1948). Pentoxylales have been reported to be stachyospermous (which means that both male and female organs were borne on stems and not on leaves) whereas conifers are partly phyllosperrmous and partly stachyospermous.

## III. Affinities of Pentoxylales with Medullosaceae:

Pentoxylales have been reported to resemble with members of family Medullosaceae of order Pteridospermales (Palaeozoic Pteridospermales).

1. Presence of polystelic primary vasculature in stems of both the groups.
2. Secondary wood of *Pentoxylon* was characterized to be pycnoxylic, a character also found in some species of *Medullosa*.
3. Mode of branching found in Pentoxylales and Medulosaceae have been reported to be similar. Nature of stele of both the groups is also similar.
4. Presence of Coniferous type of pittings have been reported in stems of *Pentoxylon* and in some *Medullosa* species.

## III. Affinities of Pentoxylales with Bennettitales:

1. Presence of syndetocheilic stomata, in addition to haplocheilic ones.
2. Vascular bundles having diploxylic nature.
3. Presence of whorled microsporangioophores.
4. Male flowers of Pentoxylales and Bennettitales exhibited superficial similarity.
5. Stachysporous nature of male and female organs of pentoxylales resemble with Bennettitales.
6. Both the groups share several common characters in their dwarf shoots.
7. Existence of direct leaf traces.

However, the polystelic condition of the stems of *Pentoxylon* and *Nipanioxylon* has no similarity with that found in Bennettiales. In Pentoxylales, 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 Bennettiales these structures were completely different. They had circinate dorsiventral pinnate sporophylls with a sterile and synangium-bearing portion.

### Features Unique to Pentoxylales:

Besides having above mentioned similarities with different groups there are some unique characteristic features possessed only by Pentoxylales.

1. One of the key unique feature of Pentoxylales is presence of mulberry-like female cones or inflorescences of Pentoxylales (*Carnoconites compactum*) having over twenty sessile ovules which are attached to central receptacle.
2. Moreover, these inflorescences neither had any inter-seminal scales, nor any other structure which could be regarded as sporophyll, which is another unique feature of Pentoxylales.
3. The sporangiophores of Pentoxylales had spirally arranged branches and the sporangia were unilocular and terminal.

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## 7.5 SUMMARY

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1. Pteridospermales are the gymnosperms with fern like foliage
2. Pteridospermales appeared during upper Devonian period of Paleozoic era and existed throughout Carboniferous and Permian periods and became extinct during Mesozoic era.
3. Pteridospermales have been reported to occupy intermediate position between the ferns and Cycadophytes.
4. Arnold (1948) divided Cycadofilicales into three families, Lyginopteridaceae, Medullosaceae and Calampityaceae.
5. Sporne (1974) classified Pteridospermales into seven families Lyginopteridaceae, Medullosaceae, Calampityaceae, Glossopteridaceae, Peltaspermales, Corystospermaceae and Caytoniaceae.
6. The group Lyginopteridaceae was represented in upper and lower Carboniferous periods of Paleozoic era
7. Lyginopteridaceae are fern-like plants with weak, aerial and well branched stems.
8. Leaves of Lyginopteridaceae were bi or tri-pinnate and large.
9. Xylem in stems is mesarch in Lyginopteridaceae.
10. Leaf traces in Lyginopteridaceae develop by tangential division of cauline strands.
11. In Lyginopteridaceae secondary xylem is soft- textured and contains a high proportion of ray tissue and long tapering tracheids.
12. In Lyginopteridaceae the secondary growth is manoxylic.
13. In Lyginopteridaceae secondary xylem is exocentric in development.

14. *Crossotheca hoeninghausii* has been characterized as the microsporangia-bearing member of *Lyginopteris*.
15. Seeds were characterized to be small, barrel-shaped structure ranging 5 - 6 mm in length and 4 mm in width.
16. Several stems, fronds, seeds and pollen bearing organs belonging to Paleozoic era were studied by various scientists which were reported to belong to Lyginopteridaceae
17. In Medullosaceae plants are small trees with fern-like appearance.
18. Stems of Medullosaceae are aerial, erect and unbranched. Leaves of medullosaceae are bi-pinnate or tri-pinnate, large.
19. In Medullosaceae stems are polystelic, advanced types having a complete cylinder with smaller vascular bundles.
20. Xylem in Medullosaceae stems is mesarch and similar to that found in Lyginopteridaceae.
21. Medullosaceae steles possessed well-developed ground tissue.
22. Each stele is surrounded by pericycle separately in medullosaceae.
23. The secondary growth in medullosaceae is manoxylic.
24. The fossils of *Glossopteris* have been reported from India, South America, South Africa, Australia and Antarctica
25. Roots of *Glossopteris* are called *Vertebraria* and roots are flattened and grooved.
26. *Glossopteris* leaves are simple, entire, sessile with a prominent midrib and exhibit variation in size.
27. Male fructifications are *Eretmonia*, *Glossotheca* and *Nesowalesia*. All the three reported genera possessed sporangia of *Arberiella* type
28. Female reproductive structures are found attached either to unmodified leaf or to modified leaf.
29. Pollination was reported to be anemophilous.
30. Caytoniales were discovered from middle Jurassic rocks of Cayton Bay in Yorkshire coast of England.
31. Stems of Caytoniales are represented by small branched twig on which bud scales of *Sagenopteris* are present.
32. Pollen bearing organs or microsporangiate fructification was named as *Caytonanthus*.
33. Pentoxylales are shrubs or trees of small size and possess either dwarf or long branches.
34. Pentoxylales have been named so because their stems were polystelic.
35. Pentoxylales possessed unisexual reproductive organs which were borne on terminal end of branches.
36. Male reproductive organs of Pentoxylales were characterized to be a whorl of branched sporangiophores which were fused at base to form a disc
37. Female reproductive organs lacked interseminal scales and were composed of thick central axis with ovules attached to the axis spirally.
38. Pentoxylales have been reported to exhibit structural and functional similarities with other plant groups such as Cycadales, Coniferales, Pteridospermales and Bennettitales.

39. Pentoxylales possessed several unique features such as presence of mulberry-like female cones or inflorescences, the sporangiophores had spirally arranged branches and the sporangia were unilocular and terminal.

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## 7.6 GLOSSARY

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**Fossils:** A fossil is any preserved remains or impression or trace of any living thing from a past geological age.

**Pedicel:** A pedicel is a stalk that attaches a flower to the inflorescence.

**Dictonomous branching:** In dichotomous branching, the branches form as a result of an equal division of a terminal bud (i.e., a bud formed at the apex of a stem) into two equal branches that are not derived from axillary buds

**Venation:** The arrangement of veins in a leaf

**Anemophilous:** Pollination by wind.

**Lamina:** The lamina is the expanded portion of a blade of leaf and it is an above ground organ specialized for photosynthesis.

**Haplocheilic stomata:** A type of stoma in which the guard cells are derived from a single mother cell and the subsidiary cells are derived from a different initial.

**Nucellus:** the central parenchymatous part of an ovule.

**Syndetocheilic stomata:** A type of stoma in which both guard cells and the subsidiary cells are derived from a single mother cell.

**Manoxylic wood:** It is non compact wood with large amount of parenchyma mixed with less amount of xylem tracheids.

**Rachis:** a stem of a plant, bearing flower stalks at short intervals.

**Adventitious roots:** Such roots arise from an organ except radicle.

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## 7.7 SELF ASSESSMENT QUESTION

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### 7.7.1 Choose the most appropriate option for the following:

- Female reproductive structure in *Glossopteris* were
 

(a) Leaf borne	(b) root borne
(c) Stem borne	(d) none of the above
- Uniovulate cupules are
 

(a) Modified leaves	(b) seed like bodies
(c) Underground stem	(d) root like structures
- Thomas characterized *Glossopteris* to be
 

(a) Only seed bearing	(b) only sporangia bearing
(c) Both seed and sporangia bearing	(d) neither seed nor sporangia bearing.

4. Which of the following represents similarity between pteridophytes and pteridospermales
- (a) Endosporic Gametophyte and mesarch xylem.
  - (b) Xylem vessels are absent and phloem lacks companion cells.
  - (c) Presence of Archegonia
  - (d) All the above represent similarities between pteridophytes and pteridospermales
5. In *Partha* number of seeds borne beneath the cupules were
- (a) Five
  - (b) Numerous
  - (c) One
  - (d) Four
6. Ovules of *Glossopteris* were
- (a) Large, oval, numerous and borne on upper surface of megasporophyll.
  - (b) Small, oval, numerous and borne on lower surface of megasporophyll
  - (c) Small, oval, few and borne on lower surface of megasporophyll
  - (d) Small, oval, numerous and borne on upper surface of megasporophyll
7. In which of the following female reproductive structure is not attached to modified stem
- (a) *Partha* and *Denkania*
  - (b) *Mooia* and *Lidgethonia*
  - (c) *Ottokaria* and *Scutum*
  - (d) All the above
8. Which of the following is not a characteristic feature of Pentoxylales
- (a) Pentoxylales have been characterized to be shrubs or trees of small size.
  - (b) Pentoxylales possessed two types of branches long shoots and dwarf shoots.
  - (c) Their stems were monostelic.
  - (d) Leaves of Pentoxylales were simple, lanceolate, thick and had spiral arrangement.
9. Which of the following is not true about vascular strands of Pentoxylales
- (a) Vascular strands were located internal to cambium and
  - (b) comprised of primary xylem and primary phloem.
  - (c) Both primary xylem and primary phloem were present in the form of internal rings.
  - (d) Beside five main vascular strands there were present five smaller strands alternating with main strands.
10. Pteridospermales are
- (a) Angiosperms with fern like foliage and protected seed
  - (b) Angiosperms with fern like foliage and unprotected seed
  - (c) Gymnosperms with fern like foliage and protected seed
  - (d) Gymnosperms with fern like foliage and unprotected seed

### 7.7.2 State whether following statements are true or false

1. Stem of *Pentoxylon* is monostelic.
2. Pollen bearing organs of Caytoniaceae are called as *Caytonanthus*.



3. Maturation of seeds occurs inside fruit in Caytoniales.
4. *Pentoxylon* was dioecious in nature.
5. Reproductive organs were formed on terminal positions of lateral shoots in pentoxylales.
6. Female reproductive structure in *Glossopteris* was either attached to modified or unmodified leaf.
7. Medullosaceae are characterized by small plants.
8. Pentoxylales were monoecious in nature.
9. In Caytoniales integument remains attached to nucellus except base.
10. Seeds of *Medullosa* does not exhibit any variation in size.
11. In *Partha* each fructification stalk terminates in single seed.
12. Development of secondary wood in *Pentoxylon* is exocentric.
13. Pentoxylales were first of all discovered by Prof. Birbal Sahni (1948).

### 7.7.3 Fill up the following blanks:

1. The name pentoxylales was proposed by \_\_\_\_\_.
2. Leaves of pentoxylales are known by name \_\_\_\_\_
3. Sporangioophores bear \_\_\_\_\_ on the tips of its short branches.
4. Caytoniaceae group of plants were discovered by \_\_\_\_\_.
5. \_\_\_\_\_ is regarded as intermediate between Medullosaceae and Lyginopteridaceae.
6. Sporangia of *Glossotheca* have been described to be of \_\_\_\_\_ type.
7. *Partha* is a type of \_\_\_\_\_.
8. Pentoxylales resembled \_\_\_\_\_ in having pycnoxylic wood.
9. Vishnu Mittre described pollen bearing organs of \_\_\_\_\_
10. Stem of Pentoxylales are \_\_\_\_\_

### 7.7.4 Very short answer type questions:

1. Describe Pentoxylales.
2. Name the type of stomata found in pentoxylales.
3. Mention a similarity between Pentoxylales and Cycadales.
4. What kinds of leaves were found in Pentoxylales?
5. Which is the most prominent evidence of existence of Medullosaceae?
6. From where and by whom Caytoniaceae was discovered?
7. What do you understand by *Pentoxylon sahnii*?
8. Name four stem genera of Medullosaceae.
9. Mention a characteristic feature of Pentoxylales which was different from other gymnosperms.
10. Explain the term mooia.
11. How does seeds of *Glossopteris* resemble seeds of Cycads and *Ginkgo*?
12. Why are Pentoxylales called so?
13. Explain the term parasporites.

**7.7.1 Answers Key:** 1- (a), 2-(b), 3- (c), 4- (d), 5-(d), 6-(b), 7-(c), 8-(c), 9- (a), 10-(d)

**7.7.2 Answers Key:** 1-False, 2-True, 3-True, 5-True, 6-True, 7-False, 8-False, 9-False, 10-False, 11- True, 12-True, 13-True

**7.7.2 Answers Key :** 1-Birbal Sahni, 2- *Nipaniophyllum raoi* 3-Microsporangia, 4 – Thomas, 5- Sutcliffia, 6-Arberiella, 7- fructification, 8- Conifers, 9- Pentoxylales, 10- polystelic.

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## 7.10 TERMINAL QUESTIONS

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### 7.10.1 Short answers type questions:

1. Enlist contribution of different scientist who studied Pentoxylales.
2. How does *Quaestora* resembles and differs from members of Medullosaceae?
3. Write a short note on Megasporephyll of Caytoniales.
4. Briefly describe about female fructification in *Medullosa*.
5. What were the characteristic features of leaves of Caytoniaceae?
6. Write an explanatory note on *Glossotheca*.
7. Briefly describe about stem of Medullosaceae.
8. Define Pteridospermales. Discuss their similarities with Pterophytes and Cyacadophytes.
9. Mention about unique characteristic features of Pentoxylales.
10. Differentiate between *Alethopteris* and *Neuropteris*.

### 7.10.2 Long answer type questions:

1. Describe Caytoniaceae in detail.
2. Enlist characteristic features of Medullosaceae.

3. Explain about anatomy of leaf, stem and root of Lyginopteridaceae.
4. Explain the different parts of *Pentoxylon*.
5. Describe in detail about reproductive organs of Lyginopteridaceae.
6. Give a detailed account of Glossopteris.
7. Mention the affinities of Pentoxylales with Cycadales, Bennettiales and Pteridospermales.
8. Enlist characteristic features of Pteridospermales.

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## **UNIT-8-GENERAL ACCOUNT OF BENITTITALES, CYCADALES, CORDAITALES AND GINKGOALES**

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- 8.1 Objectives
- 8.2 Introduction
- 8.3 Bennettiales (or Cycadeoidales): General features, anatomy, reproductive structures and affinities
- 8.4 Cycadales: General features, anatomy, reproductive structures and affinities
- 8.5 Cordaitales: General features, anatomy, reproductive structures and affinities
- 8.6 Ginkgoales: General features, anatomy, reproductive structures and affinities
- 8.7 Summary
- 8.8 Glossary
- 8.9 Self Assessment Question
- 8.10 References
- 8.11 Suggested Readings
- 8.12 Terminal Questions

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## 8.1 OBJECTIVES

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After reading this unit students will be able:

- To study about origin, distribution and general characters of Bennettiales, Cycadales, Cordaitales and Ginkgoales
- To understand about the anatomical features of stem, leaf and root of these gymnosperm groups.
- To learn about the reproductive structures of these gymnosperm groups
- To understand the relationship (similarities / differences) between different gymnosperm groups.

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## 8.2 INTRODUCTION

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Gymnosperm is a large group which includes several fossil as well as living forms. In this chapter we will study about different groups (orders) of gymnosperms including Bennettiales, Cycadales, Cordaitales and Ginkgoales. Cycadales represent lower living gymnosperms and possess peculiar resemblance with pteridophytes. Members are woody sporophyte having palm like appearance. Important representatives of the order are *Cycas*, *Microcycas*, *Zamia*, *Stangeria*, etc. *Ginkgoales* include only one living species *Ginkgo biloba*. It is regarded as oldest living seed plant. Ginkgoales comprise one of the higher living forms of gymnosperms. Bennettiales is an order having extinct forms. They were characterized by complex reproductive system. These have been reported to have flourished through Triassic to lower cretaceous period of Mesozoic era. Cordaitales also comprised of extinct members. They were woody plants with characteristic cone like reproductive structures. In this chapter we will study about the geological periods during which these groups originated and flourished. We will also study about their characteristic features, anatomy, reproductive structures and their similarities and differences with different plant groups.

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## 8.3 BENETTITALES

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Bennettiales (or Cycadeoideales) is a fossil group which was prevalent during the Triassic to Lower Cretaceous periods of Mesozoic era. Bennettiales have been discovered either in the form of compressions or petrifications. **Bennettiales** have been named so in honour of J.J. Bennett, an English botanist. First representative specimen of Bennettiales was collected from Great Britain (1825) in form of fossilized trunk of genus *Bucklandia*. About ten petrified trunks were discovered from iron ore beds of Potomac formation between Baltimore and Washington. *Bennettites gibsonianus* of Lower Carboniferous was discovered in the form of silicified petrifications from Isle of Wight and Portland of South Coast, England. *Williamsonia gigas* was discovered by Williamson from Jurassic of Yorkshire in 1868. Birbal Sahni (1932) reported *Williamsonia seawardiana* from the region of Upper Gondwana beds of India. Several representatives of Bennettiales have been discovered from Rajmahal

Hills of Bihar (India). Some of the members include *Bucklandia sahnii*, *B. indica*, *Dictyzamites*, *Otozamites benghalensis*, *Cycadinocarpus rajmahalensis*, *Sahnioxylon rajmahalensis*, *Williamsonia indica*, *W. sahnii* and *W. seawardiana*.

Due to Cycad-like form of their fronds and the presence of short stems covered with an armour of persistent leaf bases Bennettiales (Cycadeoideales) have been treated under Cycadophyta by some workers. However, the two groups are quite distinct from each other and maintain their independent identity. Several palaeobotanists believe Bennettiales to have originated from Pteridospermales. However, presence of stalked ovules in Bennettiales strongly opposes such a theory.

Unique characteristic features of Bennettiales include:

- (i) Presence of Bisporangiate strobili
- (ii) Synangium-bearing fused microsporophylls
- (iii) Close occurrence of ovules and interseminal scales
- (iv) Stalked ovules.

### Characteristic features of Bennettiales

1. These plants existed during Triassic to Cretaceous periods.
2. The stems were stout or slender with a wide pith.
3. The stem grew very slowly and had manoxylic wood.
4. Leaves were mostly pinnately compound (occasionally simple) with open (rarely closed) venation.
5. Stomata were syndetocheilic.
6. The wall of the epidermal cells was sinuous.
7. Reproductive organs have been reported to be present in the form of hermaphrodite (e.g. *Cycadeoidea*) or unisexual (e.g. *Wielandiella*) flower.
8. Flowers developed in the axil of leaves and were protected by bracts.
9. Male reproductive organs were borne in a whorl. They were free or fused, entire or pinnately compound.
10. Microsporangia were present abaxially in the form of synangia.
11. Microsporophylls sometimes surrounded megasporophylls forming hermaphrodite flowers.
12. Ovules were stalked, produced in large numbers on a conical, cylindrical or dome-shaped receptacle.
13. Presence of several interseminal bracts on the ovule containing receptacle.
14. Seeds were dicotyledonous.

### Classification

**Walton (1940) recognized two families of Bennettiales**

- a. **Williamsoniaceae:** This family was characterized by fully exposed flowers which were present on slender stems. e.g. *Williamsonia*, *Wielandiella*

**b. Bennettiteae:** This family is characterized by flowers which are deeply sunk among persistent leaf bases and were present on thick short trunk. e.g. *Cycadeoidea*.

**Arnold (1948)** classified Bennettiales into two families viz. Williamsoniaceae and Cycadeoideaceae while **Sporne (1965)** divided it into following three families:

1. Williamsoniaceae, e.g. *Williamsonia*, *Pterophyllum*.
2. Wielandiellaceae, e.g. *Wielandiella*, *Williamsoniella*.
3. Cycadeoideaceae, e.g. *Cycadeoidea* = (*Bennettites*)

The family as constituted by Sporne is represented by about thirty species of single genus *Cycadeoidea*. The species has been reported from U.S.A., Russia, Europe, Belgium, France, Isle of Wight and Portland.

### External Feature

1. The genus *Cycadeoidea* possesses short branched or un-branched, spherical or conical to irregular trunk.
2. The surface of petrified trunk was marked by several rhomboidal leaf bases having multicellular hair in between.
3. The height of the trunk rarely reaches a meter and diameter of trunk is about 50 centimeters.
4. Wieland in his book 'American Fossil Cycads,' has illustrates structural organization of these trunks.
5. The trunks exhibit slow growth and those profusely branched give the impression of bunch of pineapples.
6. At the apex of trunk a crown of pinnately compound leaves is present (Fig.8.1). These leaves were found in a partially developed condition in organic connection with some silicified trunks.

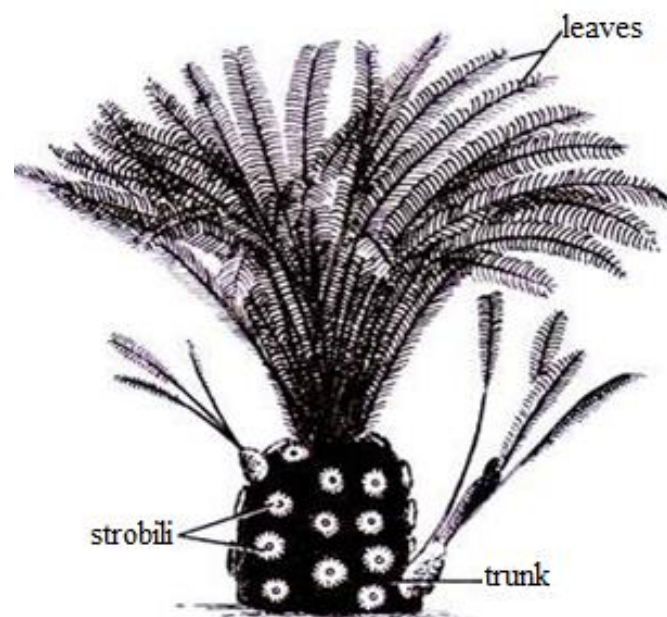


Fig.8.1: External features- *Cycadeoidea dacotensis*

## Anatomy

A cross section of the stem shows roughly a circular outline. The epidermis is not well preserved due to the heavy armour of leaf bases with hair like ramenta wedged in between them. The wide cortex is entirely parenchymatous and is traversed by numerous leaf traces and mucilage canals (Fig. 8.2). The primary vasculature consist of a ring of endarch, collateral, conjoint and open vascular bundles encircling the wide parenchymatous pith. Ray like extensions of the pith pass between the vascular bundles, which therefore appear discrete.

The secondary wood encircles the primary xylem and consists of tracheids with scalariform and circular bordered pith. The secondary medullary rays traverse the secondary xylem and the secondary phloem. They are uniseriate as well as biseriate. The tracheids appear rectangular in a cross section. A distinct cambium is visible between the secondary xylem and phloem.

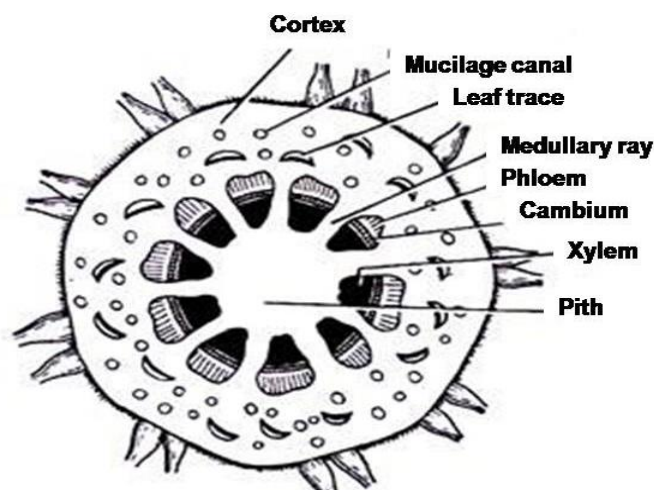


Fig. 8.2: T.S. of stem (*Cycadeoidea*) showing primary structure

**Structure of flower:** Flower is bisexual and consists of short stalk which extends from main stem into armour of leaf base. Around 100-150 elongated hairy bracts arise in close spiral present below apex of shoot. The function of these bracts is to provide protection to micro and megasporangiate flowers. Apical region of stalk function as receptacle. In species such as *C. gibsoniana* and *C. wielendii* it is convex in shape and in other species such as *C. dacotensis* it is conical in shape (Fig. 8.3).

**Androecium (microsporophyll):** Wieland interpreted microsporophyll to consist of central rachis which bears several pinnae that alternate with one another. Pinnae bears two rows of pollen capsules or synangia which are bean shaped and have short stalk (Fig. 8.3 A&B). Contrary to this concept, Delevoryas (1963) reported that microsporophyll was not expanded. He observed tip of microsporophyll to be fused to its base in *C. colosalis* and *C. dacotensis*. Fertile region of microsporophyll contained trabeculae which connect outer wall of microsporangium to inner wall. Along these trabeculae, synangia or pollen capsules were born. According to this concept the entire microsporophyll might have shed as a single unit. William L Crepet (1972) studied bisporangiate cone of *Cycadeoidea* and reported self pollination to be the means of pollination. He supported Delevoryas's interpretation of



bisporangiate cone. Each pollen capsule measures about  $3.5 \times 2.5$  mm and carries 20-30 pollen sac or microsporangia. These pollen sacs are separated by distinct walls. Synangium contains a several layered thick wall. Outer wall is thick and is composed of palisade like cells while inner layer is made up of thin walled cells. Microsporangia dehisce longitudinally and microspores are released into synangial cavity. At maturity synangia opens to release microspores.

**Gynoecium:** Gynoecium consists of conical or spherical receptacles which contains several ovules and interseminal scales (Fig. 8.3D). Harris characterized ovules to possess single integument which is fused with nucellus except at apex. Ovules are stalked, has a pollen chamber and nucellar beak. The stalk of ovules may be short (*C. dacotensis*) or long (*C. wielendii*). Ovules are orthotropus having a long micropylar beak which extends beyond the pores in surface plate (this surface plate is formed by union of flattened ends of interseminal scales). Fused tips of interseminal scales form a protective covering (pericarp) surrounding the seeds. Crepet and Delevoryas (1972) reported presence of many bisporangiate cones of *Cycadeoidea* from cretaceous of black hills. They obtained young ovules which were probably in pregametophytic developmental stage. These ovules were found to be similar to that of *C. wellsii*.

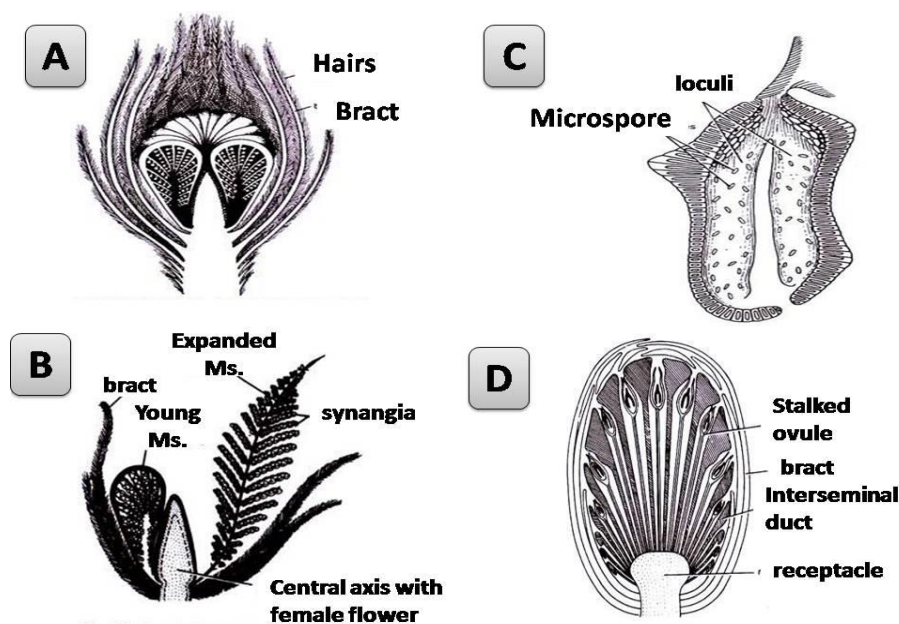


Fig. 8.3: A-Unexpanded stobilus, B- Apical part with curved microsporophyll and central axis (Ms= Microsporophyll), C- LS of sporangium with two locules having microspores, D- Female stobilus

They were stalked, urn-shaped and widest in the middle. A distinct constriction appears below funnel shaped micropyle. Micropyle is lined with large epidermal cells. Integument is single, develops rapidly and consists of three layers. Outer layer of integument consist of axially elongated cells and middle layer possesses thick walls. Nucellus is free of integument. Cells of integument are elongated at micropylar region. They probably close micropyle after pollination. Young nucellus is made up of thin walled cells. These cells are smaller at chalazal end and comparatively large at micropylar end. However, cells of micropylar end are much elongated. A single cell having pointed tip terminates nucellus during early stages of

development. On each side of nucellar tip cells bend outwards to form outline of nucellus. In their study Crepet and Delevoryas (1972) also observed presence of linear tetrad or a row of three cells below middle of nucellus. They possess thin transverse walls and thick longitudinal walls. Seeds possess two cotyledons and are oval in shape.

### Affinities of Bennettitales

#### Similarities between Bennettitales and Ferns

- (i). Bennettitales possessed multicellularramenta on their entire body, a characteristic similar to ferns.
- (ii). Presence of direct leaf traces.
- (iii). Presence of scalariform tracheids.
- (iv). Presence of large pith in both the groups.

#### Similarities between Bennettitales and Cycadales

- (i). Similar structure of their fronds.
- (ii). Presence of short stems covered with an armour of persistent leaf bases.
- (iii). Presence of barrel-shaped trunk.
- (iv). Presence of very thick cortex, thin wood and large pith in the stem.
- (v). Presence of manoxylic wood.
- (vi). Monocolpate pollen grains and orthotropous ovules.
- (vii). Dicotyledonous embryo.

Due to above mentioned similarities, Chamberlain (1935) suggested that both Bennettitales and Cycadales arose by parallel evolution from a common ancestor. However, due to several differences (Table-2) between Bennettitales and Cycadales it will not practically be possible to visualize any phylogenetic connection between two groups. Andrews (1961) concluded the groups to have evolved along different and independent evolutionary lines.

**Table-1: Differences between Bennettitales and Cycadales**

S.No.		Bennettitales	Cycadales
1	Stomata	Syndetocheilic	Haplocheilic
2	Secondary wood	Manoxylic	Polyxylic .
3	Fructifications	Flower-like	Strobilar
4	Flowers	Bisporangiate	Monosporangiate
5	Plants	Monoecious	Dioecious
6	Microsporophyll	Arranged in whorls, fused at the base	Such arrangement is not found
7	Seeds	Exalbuminous	Albuminous

#### Similarities between Bennettitales and Pteridospermales

- (i). Presence of ramental hairs
- (ii). Syndetocheilic stomata
- (iii). Direct leaf traces

- (iv). Similarity in anatomical structure
- (v). Leafy nature of microsporophyll
- (vi). Presence of cupule.

The bisporangiate flower of Bennettiales can be compared with bisporangiate fronds of Pteridospermales. It is believed that there existed two lines of evolution from Pteridospermales. Out of these two lines of evolution one gave rise to Bennettiales possessing both uni- and bisporangiate forms while from other line of evolution formation of monosporangiate forms of cycads occurred.

### Similarities between Bennettiales and Angiosperms

- (i). Endarch siphonostelic vasculature of Bennettiales shows similarity with sympetalous angiosperms.
- (ii). Presence of frequent scalariform tracheids in both the groups
- (iii). Flowers of several primitive angiosperms (e.g. Magnoliaceae) also exhibit similarity with strobili of Bennettiales.

Bennettiales exhibited significant amount of dissimilarity with angiosperms which includes:

- (i). Stamen of both the groups differ from one another.
- (ii). Differences in carpel of *Magnolia* and ovule of *Cycadeoidea* which is typically gymnospermous.
- (iii). Ovules of Bennettiales are naked while it is not so in angiosperms.
- (iv). Marginal cells are absent in wood rays of Bennettiales while they are present in angiosperms.
- (v). General habit and floral morphology of the two groups also differ from one another.

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## 8.4 CYCADALES

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Order Cycadales includes living as well as extinct forms which originated in the upper Triassic period of early Mesozoic era. The group flourished through Jurassic and Cretaceous period after which their decline began. In the present scenario about 10 genera with around 110-117 species are known to be distributed in regions of Australia, Central America, South Africa and Eastern Asia including India. Extinct forms have been reported from mid Jurassic Cayton Bay beds on Yorkshire coast. Cycadales have been classified by different workers differently.

I- Pilger and Melchior included all living genera into five subfamilies.

- (a) *Cycadoideae* (b) *Stangerioideae* (c) *Bowenioideae* (d) *Dioonoideae* (e) *Zamioideae*.

II- Sporne classified the order Cycadales into two families

- (a) *Nilssonaceae* – All living forms were included into this family.
- (b) *Cycadaceae* – This family included one fossil genus, *Palaeocycas* and ten living genera.

III- Cycadales were classified into three families by Bierhorst

- (a) *Cycadaceae* – This family includes *Cycas*.

(b) Stangeriaceae – This family includes *Stangeria*.

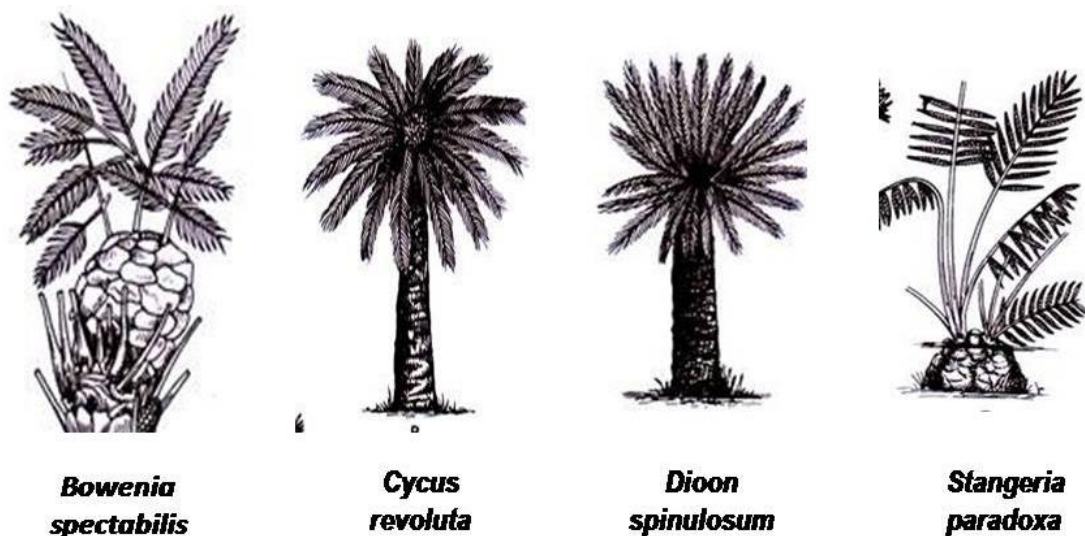
(c) Zamiaceae – This family is represented by eight genera; *Zamia*, *Lepidozamia*, *Macrozamia*, *Encephalartos*, *Dioon*, *Microcycas*, *Bowenia*, and *Ceratozamia*.

## Distribution of Cycadaceae

Cycadaceae was almost worldwide in distribution in the past ages, and the members of this family have been in existence for at least past 200 million years. The members are, however, now restricted to four main regions in the world, namely Central America, South Africa, Eastern Asia and Australia (Table-2).

**Table- 2: Geographic distribution of different members of Cycadaceae**

S.No.	Geographical region	Member of Cycadaceae
1-	South Africa	<i>Encephalartos</i> and <i>Stangeria</i>
2-	Australia	<i>Bowenia</i> , <i>Lepidozamia</i> and <i>Macrozamia</i>
3-	Indian sub-continent, China, Japan, Australia, Madagascar	<i>Cycas</i>
4-	Mexico	<i>Ceratozamia</i> and <i>Dioon</i>
5-	Cuba	<i>Microcycas</i>
6-	Mexico, West Indies, North-western South America and Florida	<i>Zamia</i>
7-	Columbia	<i>Zamia</i>



*Fig.8.4: Some of the important representatives of Cycadales*

## External Features of Cycadaceae

1. Plants of the family have been reported to exhibit slow-growth and have a general appearance of a palm tree with thick, stout, cylindrical and generally unbranched stem (Fig.8.4).
2. The height of stem in species such as *Macrozamia* and *Dioon* reaches upto 10-15 meters.

3. The stem is either spherical or tuberous in *Bowenia* and *Zamia*. Large stem apices are found in cycads and tunica is absent in Cycads.
4. A crown of pinnate leaves is present at the apex (Fig.8.4). The leaves are large, unipinnate or bipinnate and have spiral arrangement.
5. Some of the genera possess incurved rachis and leaflets are enrolled in the bud condition showing circinate vernation as in *Cycas*.
6. The rachis of the young fronds shows sub-circinate vernation in *Stangeria*, *Bowenia* and *Ceratozamia*.
7. Midrib is absent in several genera however, a distinct midrib is reported to be present in leaflets of *Stangeria* and *Cycas*.
8. Genera which do not contain midrib have open dichotomous venation.
9. The leaves are long-lived and persist on the stem for several years. When the leaves are shed a scar is left on the stem.

## Anatomy

**Stem:** Owing to the presence of persistent leaf bases, the cycadaceous stems are roughly circular in outline. Both centrally located pith and the peripheral cortex are large and well-developed, and contain mucilage canals. The endodermis and pericycle are not clearly demarcated. The primary vascular bundles are conjoint, collateral, open and endarch. The leaf traces are cauline i.e. develop singly from the vascular cylinder of the stem. They completely girdle the stem cortex. Presence of such girdling bundles is a characteristic feature of the family (Fig. 8.5). In many cycads leaf traces after entering the petiole, form either an omega-shape or horse-shoe-shaped pattern. Both centripetal and centrifugal xylems are present in the leaf trace bundles, i.e. they are diploxylic (Fig. 8.5).

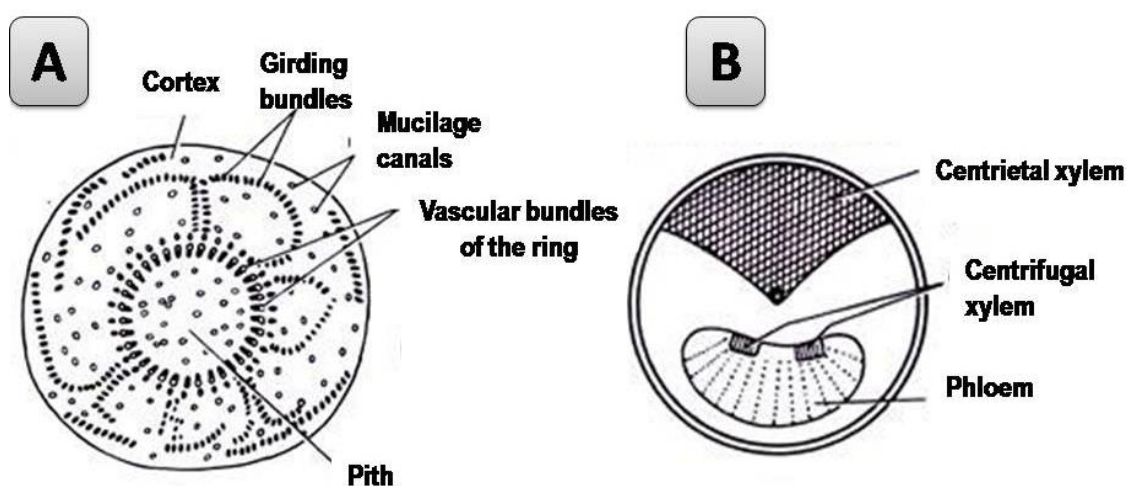


Fig .8.5: A- T.S. of stem of *Zamia floridana*, B- Leaf trace bundle of *Cycas revoluta* (showing diploxylic condition)

Well developed, strong, stout and large trunk has been found in many members of Cycadaceae however, secondary wood is surprisingly small. Persistent leaf bases provide mechanical strength to such strong trunks. Cycadaceae generally possess single persistent

cambium, but in many species of *Cycas* and some species of *Encephalartos*, *Macrozamia* presence of successive cambial layers have been reported. Such cambial layers form co-axial cylinders of secondary xylem and phloem. Presence of scalariform tracheids in the secondary wood, a primitive characteristic feature, is present in the stems of *Stangeria* and *Zamia*. The wood in Cycadaceae is diffused and contains 1-7 cells wide medullary rays.

**Leaf:** The leaves of cycads are covered with a thick cuticle. Leaves contain haplocheilic type of sunken stomata. The vascular bundles are diploxylic, i.e. two types of xylem (centripetal and centrifugal) are present. Usually the centripetal xylem is triangular with a single protoxylem group. Two types of xylem are separated by parenchymatous region.

**Root:** Roots of cycads are usually polyarch. Xylem bundles are known to alternate with the equal number of phloem bundles. The number of bundles gradually decreases towards the apex which results into a diarch condition at the tip of the root. Concentric cylinders of secondary wood are produced by the accessory cambial rings in the older roots. The primary xylem is exarch.

## Reproduction

Members are dioecious as male and female reproductive parts are present on different individuals of the same species. In some genera including *Cycas* sex of individual is determined by X and Y chromosomes.

**Microsporophylls and male cones:** The male cones are a compact structure which consists of a central cone axis which is covered by several spirally arranged microsporophylls. The microsporophylls are triangular or conical structures which bear definite sterile and fertile portions (Fig.8.6D). The sterile portion is distal in position and produced into a single spinous projection as in *Macrozamia*, *Dioon* and *Cycas*. Most of the genera contain thousands of microsporangia (grouped in sori) located in lower or abaxial surface of the microsporophyll. However, number of sporangia ranges from 20-50 in *Zamia*.

The development of microsporangium in all members of Cycadaceae is eusporangiate. Mature microsporangium is surrounded by a massive sporangial wall which is made up of several layers. Cells of the outermost layer are thick and function as epidermis. The sporangial wall encloses sporogenous tissue, outermost cells of this, function as single-layered tapetum. The sporogenous tissue metamorphoses to form diploid microspore mother cells. Each microspore mother cells forms four haploid microspores (pollen grains) through meiosis.

**Megasporophylls and female cones:** The reproductive organs are borne in the form of compact cones in all living genera. However, in *Cycas*, loose megasporophylls are spirally arranged and alternate with the cataphylls and vegetative leaves. Megasporophylls in the female cone are spirally arranged around the cone axis. Generally only one female cone is produced at the apex but sometimes two cones may also develop due to development of another meristem. Smallest female cones (about 2-3 cm in length) of Cycadaceae develops in

*Zamiapygmea*, in *Macrozamia denisonii* length of female cone is upto 60-75cm. In *Dioon spinulosum* length of female cone reaches up to 50-60 cm in length. Megasporophyll of *Cycas* are leafy in nature and regarded to be the most primitive one. It is believed that during evolution distal foliar part of megasporophyll of cycadales gradually reduced in the size along with reduction in number of the ovules on the megasporophyll. Hence, megasporophylls of *Cycas revoluta* having leafy distal part and many pairs of ovules represent the most primitive form while megasporophylls of *Macrozamia* and *Zamia* bearing only two ovules with their distal part not leaf like represent the most advanced form (Fig 8.6 B&C). Hence, ovules are foliar in origin and Cycadales are phyllospermous. Contrary to this some workers believe Cycadales to be stachyospermous. Botanists in favour of this view believe that peltate megasporophylls of *Zamia* and *Macrozamia* with two ovules are most primitive, and the entire series has progressed in an opposite direction. According to them, leaf-like megasporophylls of *Cycas revoluta* having several ovules represent the most advanced stage.

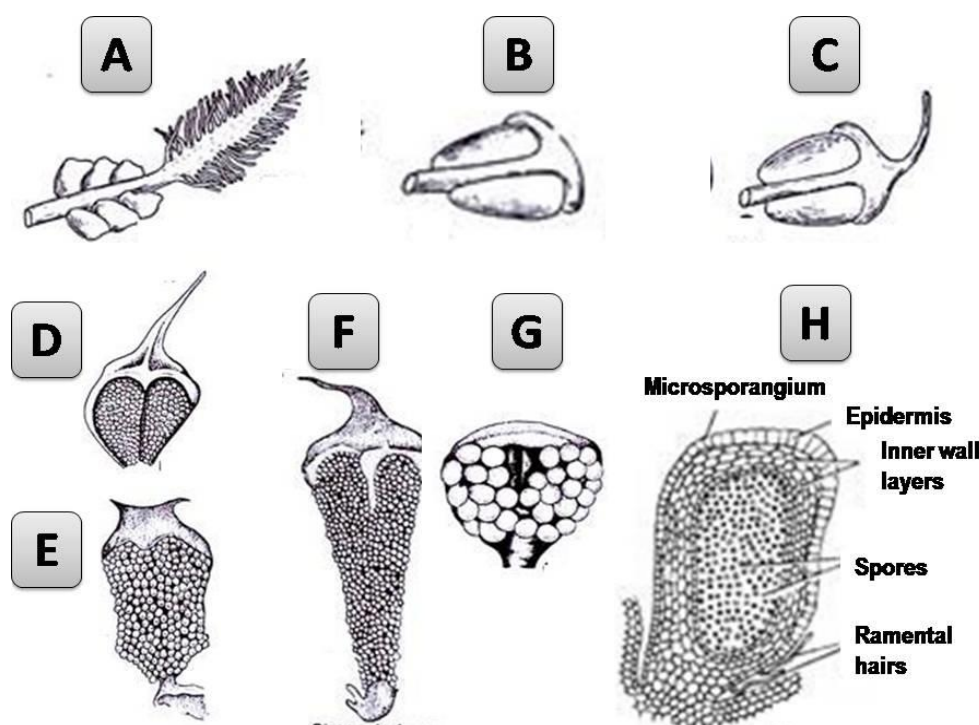


Fig. 8.6: Megasporophyll: A- *Cycas revoluta*, B- *Zamia*, C- *Macrozamia*; Microsporophyll: D- *Macrozamia*, E- *Ceratozamia*, F-*Dioon*, G-*Zamia*, H- Sporangium of *Stangeria*

**Pollen grain and male gametophyte:** Microspores (pollen grains) are haploid structures each of which develops into a male gametophyte. Microspore is uninucleate with an outer thick exine and inner thin intine. The exine is thick at the bottom and thinner at the top. A single prominent nucleus of the microspore is centrally positioned and is surrounded by dense cytoplasm which contains some reserve food.

Germination of microspore is precocious i.e. starts within the microsporangium before dehiscence microspore divides into smaller prothallial cell and a large cell. The larger cell divides again to form a generative cell and tube cell (Fig. 8.7 A-C). Microspore (at three

celled stage) are released from microsporangium and further germination occurs on the nucellus after pollination. Some of the pollen grains reach up to the micropyle of the ovule and get entangled in the pollination drop. Through the micropyle such young pollen grains reach up to the pollen chamber of the ovule where each pollen grain germinates by producing a pollen tube that penetrates through the nucellar tissue. After few weeks, the generative cell divides into a stalk cell (which remains in contact with prothallial cell) and a body cell, which divides into two cells and these two cells metamorphose into two multi-flagellate spermatozoids.

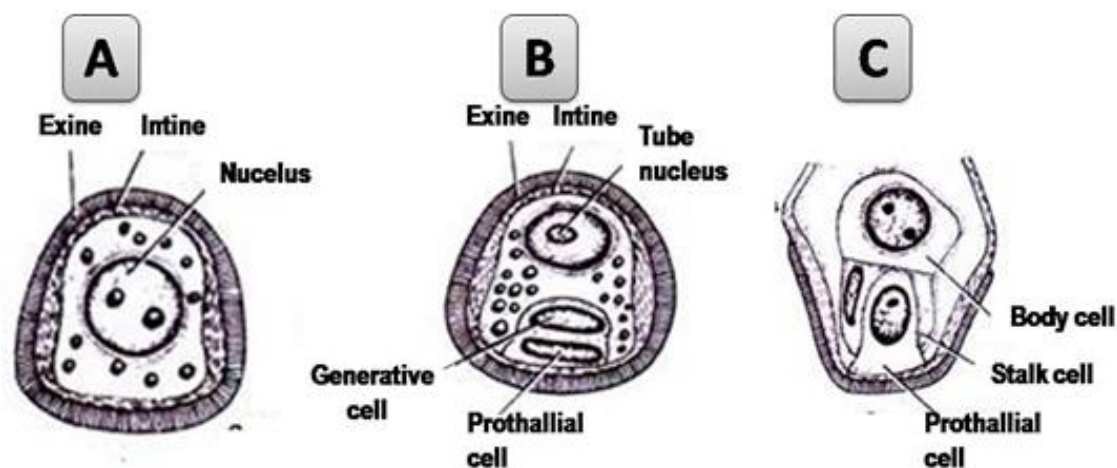


Fig.8.7: A-Pollen grain B & C- Developmental stages of male gametophyte of *Dioon edule*

**Ovule and female gametophyte:** Cycadaceous ovule is a sessile structure and is surrounded by a single integument. The integument consists of three layers, among which outer and inner layers are fleshy (sarcotesta) and middle one is stony (sclerotesta) in nature. A distinct micropyle is present at the distal end. The nucellus consists of parenchymatous cells. A megaspore mother cell gets distinguished in the nucellus. This mother cell undergoes meiosis to form 4 haploid megaspores. Out of these three gets degenerated and one megaspore remains functional. This functional megaspore undergoes free-nuclear divisions followed by wall formation and develops into cellular female gametophyte. A vascular strand enters through the basal part of the ovule and constitutes its vascular supply. In some members the vascular strand divides before it enters the ovule. Two concentric vascular systems (outer and inner) are found at the base of the ovule. The outer vascular system consists of twelve vascular strands which traverse upwards through the outer fleshy layer from chalazal end to micropylar end of the ovule. The strands of the inner vascular system also moves upwards through the part of ovule where the inner fleshy layer is in close contact with the nucellus. Stomata-like structures (with guard and subsidiary cells) have been reported to be present on outer surface of the nucellus in ovules of *Ceratozamia*, *Cycas*, *Encephalartos* and *Zamia*. Female gametophyte contains a cavity which represents the pollen chamber. One or more archegonial initials appear at the micropylar end of the female gametophyte. Each of these initials develops into an archegonium.

**Seed:** Outer fleshy layer of integument of the ovule forms coloured seed coat. Middle stony layer forms its hard testa. The inner fleshy layer is converted into papery layer called as



tegmen. The micropyle is present as such in the seed. The nucellus forms a nucellar cap at the micropylar end. As soon as seeds fall from the plant they begin to germinate if conditions are favorable. Hence there is no resting period. Germination is hypogeal.

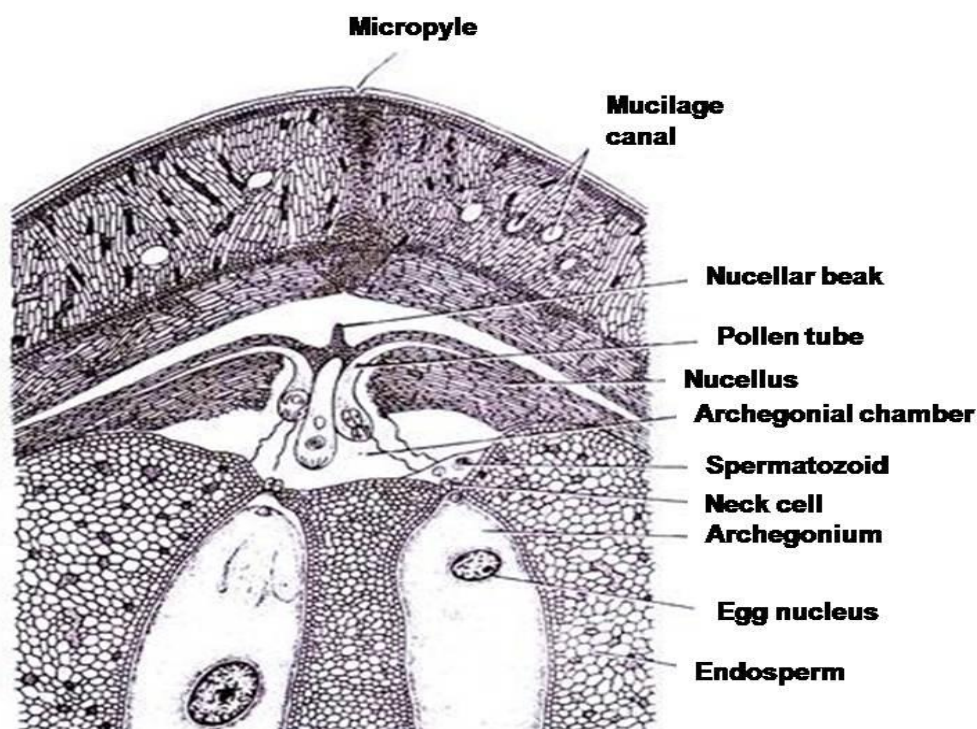


Fig.8.8: V.S. of ovule (*Dioon edule*)

### Economic Importance

1. Pith of *Encephalartos* is utilized for beverage by tribal people of Central Africa.
2. Hats, mats, baskets and several other similar articles are prepared from the leaves of *Encephalartos* in some African countries.
3. Underground stem of *Bowenia spectabilis* are cooked and eaten by native people of Queensland.
4. Bread is prepared by starch of *Encephalartos*, *Macrozamia* and *Zamia*.
5. Ramental hairs obtained from the leaf bases of *Macrozamia* are used as stuffing fibres.
6. Seeds of *Macrozamia* yield an oil used as palm oil by some native people.
7. Sago starch or "arrowroot" is obtained from the seeds and stems of *Macrozamia*, *Zamia* and *Encephalartos* which is used in laundering and several other purposes.

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## 8.5 CORDAITALES

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Cordaitales represent most ancient order of class Coniferopsida. The Cordaitales is a group of fossil tall trees of Palaeozoic era which existed from Devonian through Carboniferous upto the Permian period. The group started declining during Permian period and became extinct by the end of the period. Cordaitales have been reported to have occurred alongside with Pteridospermales. They have been named in honour of Australian botanist, A.J. Corda. Most

of the Cordaitales were tall, large-leaved trees reaching a height of about 30 meters or more with a diameter of about 3 feet. They have been known to form the first great forest of the world. Fossils of Cordaitales have been reported from regions of North and South America, China, Europe, India, Russia, Africa and Australia. Such widespread occurrence indicates their world-wide distribution during Devonian and Permian periods.

### Distinguishing Features

1. The plants of Cordaitales were tall trees having slender trunks with a crown of many well- developed branches (Fig.8.9A).
2. These plants existed from Devonian to Permian periods of Palaeozoic era.
3. Leaves were simple, arranged spirally and were either strap-shaped, grass-like or paddel-like.
4. Leaves possessed parallel venation and the length of leaves was about 1 meter or even more.
5. Presence of scanty primary wood has been reported.
6. Secondary wood was mostly pycnoxylic (in mature stem).
7. Compound unisexual cones were present.
8. Each compound cone had a main axis with bracts subtending with secondary fertile shoots possessing fertile and sterile appendages.
9. Megastrobili possess sterile appendages below and ovule-bearing fertile appendages above (Fig. 8.9 B).
10. One to four ovules were present on each female fertile appendage.
11. Microstrobili had sterile appendages below and pollen-sac containing fertile appendages above (Fig. 8.9 B).
12. Each male fertile appendage contained 4–6 terminally located pollen sacs.
13. Sperms have not been reported, but presence of pollen chambers suggests that motile sperms might have been formed.

### The order has been divided into following three groups:

- (a) **Poroxylaceae:** Represented by single genus *Poroxylon*. Stems were slender with long internodes and collateral exarch primary bundles, pith was large, and double leaf traces for each leaf along with thick parallel venation in leaves.
- (b) **Pityaceae:** Also represented by single genus *Pitys*. Vascular bundles were mesarch, wood possessed multi-ciliated pits.
- (c) **Cordaitaceae:** It was represented by several genera, among which the best characterized genus remains to be *Cordaites*. *Cordaites* has been subdivided into three sub- genera
  - (i) Eu- Cordaites - leaves were spatulate with obtuse apices.
  - (ii) Dory - Cordaites – leaves lanceolate with pointed apices.
  - (iii) Poa-Cordaites – leaves grass like

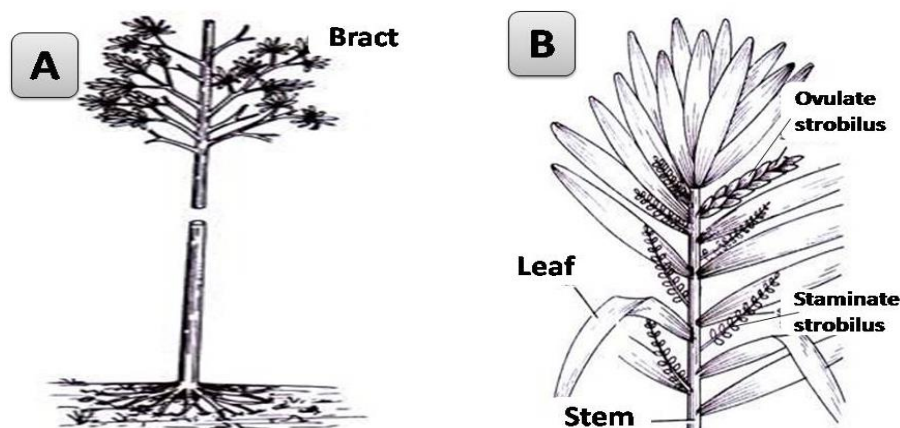


Fig 8.9: *Eu-Cordaites*, A- reconstruction of plant, B- Reconstruction of Branch

Some workers classified Cordaitales into three families as 1-Cordaitaceae, 2-Eristophytaceae and 3- Poroxylaceae

### Anatomy

**Stem:** The stem resembled closely with Conifers. Stem of cordaitales have been described under several genera including *Mesoxylon*, *Cordaites*, *Metacordaites*, *Parapitys*, *Coenoxylon*, *Cordaicladus* and *Artisia*. Both *Cordaites* and *Mesoxylon* possessed a large central pith and cortex (Fig.8.10A). The wood was scanty in some species while in others it developed a large vascular cylinder, and in still other cases distinct growth rings were present. The primary wood was endarch but in *Mesoxylon* it was mesarch. The secondary wood consisted of pitted tracheids having multiseriate pittings (Fig.8.10B). The tracheids were long and slender. Bordered pits were present, and they were confined mainly on the radial walls. In older tracheids, however, the pits were also present on the tangential walls. Medullary rays were one or two cells wide. The bordered tracheids were hexagonal in outline and the large pith was characteristically discoid. *Mesoxylon* differed from *Cordaites* in the structure of the leaf trace. A network of sclerenchyma, present in the outer cortex of *Mesoxylon*, was absent in *Cordaites*. The genus *Metacordaites* lacked air chambers on pith and xylem was endarch. In *Parapitys* xylem was mesarch. Due to secondary growth compact or pycnoxylic secondary wood was formed.

**Root:** The roots of Cordaitales are known as *Amyelon* and resembled very much with the modern Conifers. Cridland (1964) studied the root system of *Amyelon* and found it to be shallow and highly branched forming stilt roots supporting the stem. They were diarch or triarch in structure. The protoxylem had spiral tracheids while the metaxylem was scalariform in structure. Tracheids had multiseriate bordered pits. The cortex was quite large and divisible into outer and inner cortex. The secondary cortex and cambium were also quite distinct (Fig. 8.11A). Another root genus was *Premnoxylon* which was exarch with xylem poles varying from two to seven in different specimens. Pith possessed sclerenchymatous patches, secondary xylem formed distinct ring and the cortex was divided into outer and inner region. Ectotrophic mycorrhizal association was present on the roots.

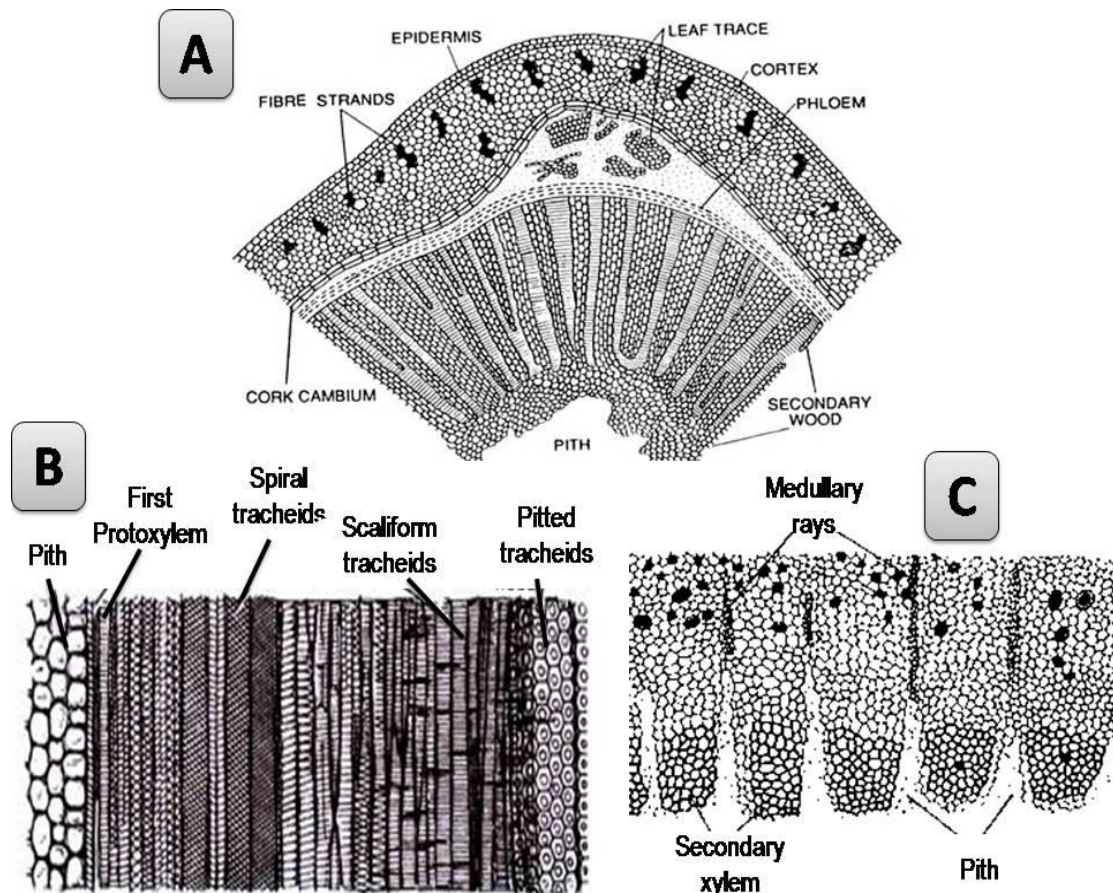


Fig: 8.10: A- T.S. of stem, B- L.S. of stem (*C. brandiingii*) from pith to beginning of secondary growth, C- Secondary xylem showing medullary rays and pith

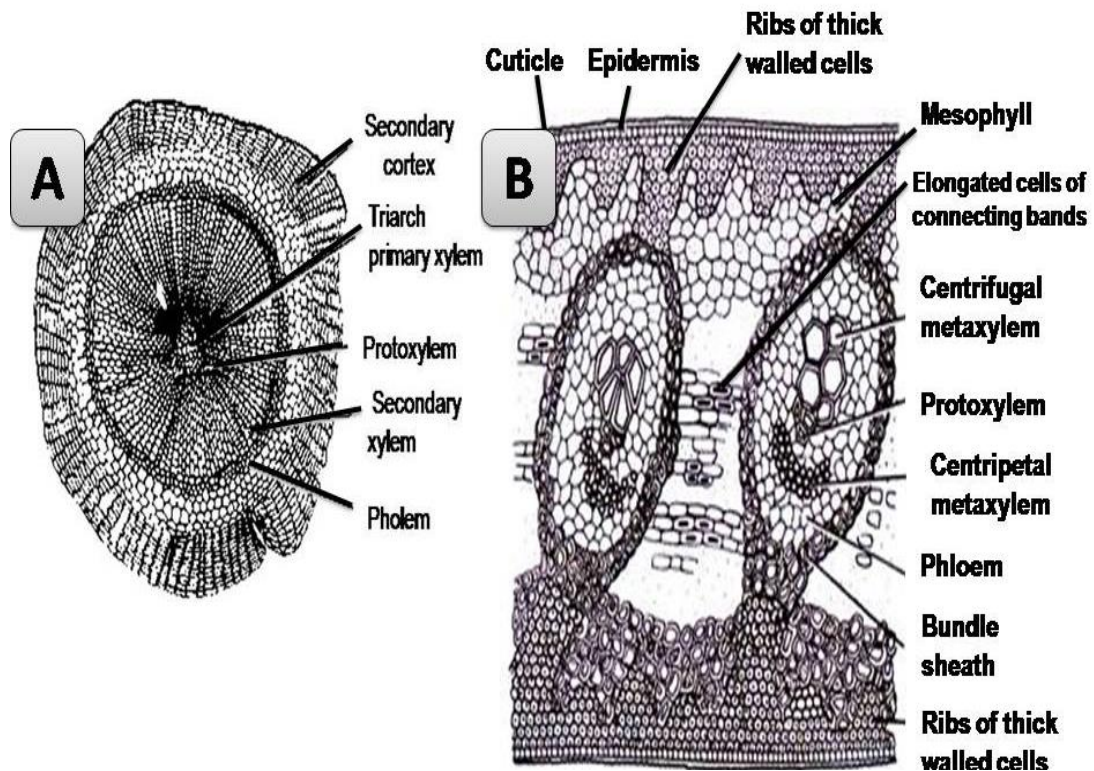


Fig: 8.11: A- T.S. of root (*Amyelon radicans*), B- T.S. of leaf (*Cordaites angulostriatus*)

**Leaf:** Leaf is described by the name *Cordaites* and is characterized by the presence of xerophytic characters. Well defined epidermis was present on upper and lower surfaces of leaves. The epidermal and hypodermal cells were thick-walled. Vascular bundles were mesarch and were surrounded by a thick-walled bundle sheath. The mesophyll comprised of palisade and spongy parenchyma (Fig.8.11 B). Stomata were present along entire length of leaf arranged in distinct bands and guard cells were surrounded by four to six subsidiary cells.

**Reproductive Structures:** The Cordaitales were monoecious or dioecious however, strobili were always monosporous (never bisporangiate). The male and female strobili were borne separately on the lateral sides of axis. Since these strobili were enclosed by bracts (when young) so outwardly it was difficult to differentiate unless sections were cut and examined.

**Male strobilus and male gametophyte:** The male strobilus contains a thick axis which bears spirally arranged bracts and some microsporophyll (Fig.8.12 A&B). These bracts possess stamens on them. Stamens may be either solitary or grouped near the apex. Sterile bracts are present between the stamens. Every stamen contains a cluster of 3 -6 terminally located sporangia. Different opinions have been put forward regarding male catkin of *Cordaites*. Some workers believe whole strobilus to act as a single male flower which contains large number of stamens, the stalk is filamentous and bears several pollen sacs. Other workers have characterized this male catkin to be inflorescence, in which each catkin bears a flower itself. Filament represents stalk of the flower and the pollen sacs represent stamens.

Much is not known about the male gametophyte of Cordaitalean members. Only the upper part of the nucellus provides some picture of the male gametophyte (Fig. 9.12). The inner structure was multicellular and the mature pollen grains were present in the micropylar canal. It could, however, not be ascertained that whether the cells of the multicellular region were vegetative or spermatogenous in nature. Most probably, both vegetative and spermatogenous tissues were present in the pollen grains.

**Female strobilus and female gametophyte:** As seen in male strobilus, female strobilus also possesses stout axis which bears large number of spirally arranged bracts. Female strobilus contains more number of bracts than male strobilus. Dwarf shoots are present in the axils of some of the bracts. Terminal ovule was present at the tip of shoot (Fig.8.12C). Not much is known about the structure of female gametophyte and embryo. Andrews and Flix (1952), however, observed some seeds with well-preserved female gametophyte in *Cardiocarpus*. In a few specimens, they also observed archegonia. The elongated gametophyte in such specimens had only two archegonia, each of which exhibits a beaklike projection of the endosperm. Darrah (1938) reported the embryo of Cordaitales from the coal balls of Iowa, USA, and if his observations were actually cordaitalean then it is perhaps the first Palaeozoic embryo so far recognized. In many seeds, well-preserved gametophytes with megaspore wall, a tent pole and two archegonia near micropyle have been observed by many workers. Even the starch grains have been reported in the ovule of *Cardiocarpus spinalus* by Baxter (1964).

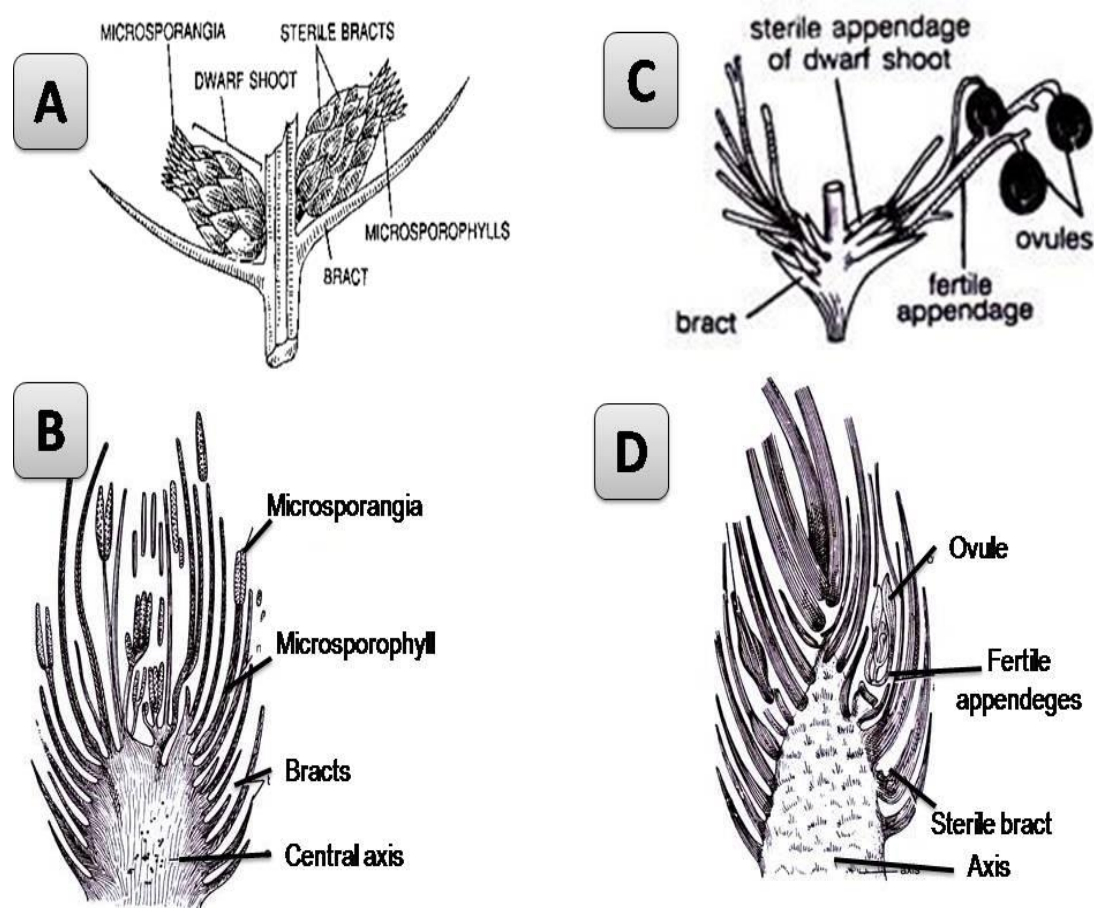


Fig.8.12: A- Two male strobili, B-L.S. of male strobilus of *Cordaianthus penjonii*, C-A part of female inflorescence of *C. pseudofluitans*, D-L.S. female strobilus of *C. williamsonii*

**Ovule:** Ovule was surrounded by two coats out of which outer coat was thick and fleshy and inner coat delicate in young ovule and hard in older ovules. Nucellus was completely free from integument. At the base of micropyle the nucellus formed a prominent nucellar beak and pollen chamber. In *Cordaianthus williamsonii*, a single ovule was present on each fertile appendage (Fig. 8.12 D). Two groups have been described by Dr. Sahni based upon the position of ovules:

- **Phyllospperms:** In which ovules borne on leaves as also found in Pteridosperms and *Cycas*.
- **Stachysperms:** The ovules born on axis (stem) as seen in Cordaitales, Ginkgoales and Coniferales.

**Seed:** It is believed that *Cordaianthus* type of strobili possessed seeds known as *Cardiocarpus*. *Mitrospermum* and *Kamarospermum* are the other two seed-genera of Cordaitaceae. Seeds were heart shaped, bilaterally symmetrical and crassinucellate. Central nucellus was surrounded by a two-layered envelope, of which the outer layer was probably expanded in the form of a wing. In *Cardiocarpus spinatus* the seeds were large and surrounded by five distinct layers, including two layers each of sarcotesta and sclerotesta and a layer of endotesta.

**Affinities of cordaitales:** Presence of unique and characteristic features justifies Cordaitales to be independent group, but still Cordaitales exhibit several resemblances with different plant groups such as Pteridospermales, Cycadales, Ginkgoales, Coniferales and Ephedrales.

**Some of these unique characteristics include**

- (i). Arborescent habit
- (ii). Scanty primary wood
- (iii). Pycnoxylic secondary wood
- (iv). Multiseriate pittings on the tracheid-walls
- (v). Absence of resin canals
- (vi). Simple but very long (up to 1 metre) leaves with parallel venation
- (vii). Compound unisexual cones
- (viii). Fertile female appendages with one to four ovules
- (ix). Bilateral seeds.

**Similarities between cordaitales and Pteridospermales**

- (i). Presence of large pith in stems
- (ii). Walls of tracheids of both the group possess multiseriate pittings.
- (iii). Centripetally developed xylem in their primary wood
- (iv). Presence of double leaf traces
- (v). Similarity in structure and vascularization of ovules
- (vi). Seeds of cordaitales as well as pteridospermales lack embryo.

**Differences between cordaitales and Pteridospermales**

- (i). A seed-bearing inflorescence, is reported to be present only in Cordaitales, and is not known in Pteridospermales
- (ii). Cordaitalean leaf and pteridospermic frond show significant variation.
- (iii). Pycnoxylic nature of wood of Cordaitales whereas manoxylic wood in Pteridospermales.

**Similarities and differences between Cordaitales and Cycadales**

- (i). Xerophytic nature of both plant groups.
- (ii). Presence of large pith and centripetal wood in stems
- (iii). Large amount of sclerenchyma in leaves
- (iv). Motile spermatozoids
- (v). Simple and large seeds
- (vi). Similar vasculature of ovules

Cordaitales differ from Cycadales in having simple leaves with parallel venation, straight leaf traces, pycnoxylic wood and compound nature of their strobili. Whereas Cycadales have pinnately compound leaves in which venation is not parallel, leaf traces not straight, the wood is monoxylic, and the strobili are not compound.

### Similarities and differences between Cordaitales and Ginkgoales

- (i). Double leaf-trace,
- (ii). Motile sperms
- (iii). Similar anatomy of leaves
- (iv). Endospermic beak in their ovules.

The two groups differ in their respective origin of leaf traces, In Ginkgoales, the double leaf traces originate from two separate protoxylem groups while in Cordaitales they originate from the same group of the protoxylem.

### Similarities between Cordaitales and Coniferales

- (i). Arborescent habit of both groups.
- (ii). Simple leaves and parallel venation
- (iii). Sclerenchymatous hypodermis in the leaves
- (iv). Pycnoxylic wood
- (v). Bilaterally symmetry of ovules
- (vi). Compound strobili of Cordaitales also show similarity with cones of Pinaceae.

### Similarities between Cordaitales and Ephedrales

- (i). Presence of parallel venation in leaves.
- (ii). Presence of two leaf traces.
- (iii). Haplocheilic stomatal apparatus.
- (iv). Pycnoxylic wood.
- (v). Long and slender tracheids with tapering ends.
- (vi). Occurrence of flattened microsporophylls in *Cordaianthus* and also in some species of *Ephedra*.
- (vii). Terminal sporangia.
- (viii). One to six microsporangia in each microsporophyll
- (ix). Reduced number of ovules and shortened megasporophylls.

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## 8.6 GINKGOALES

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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 of all introduced the name “Ginkgo” in 1690. The same name was adopted by Linnaeus (1771). Due to the presence of several primitive characters, and also 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*, *Psymphyllum* 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 number.
14. Integument comprises of outer fleshy orange coloured portion and hard inner stony layer. Fleshy coat is rich in butyric acid and produced 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 female tree. *Ginkgo biloba* is also known as maidenhair tree.
15. Spermatozoids are motile.

### Anatomy

**Root:** 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. 8.13). 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.

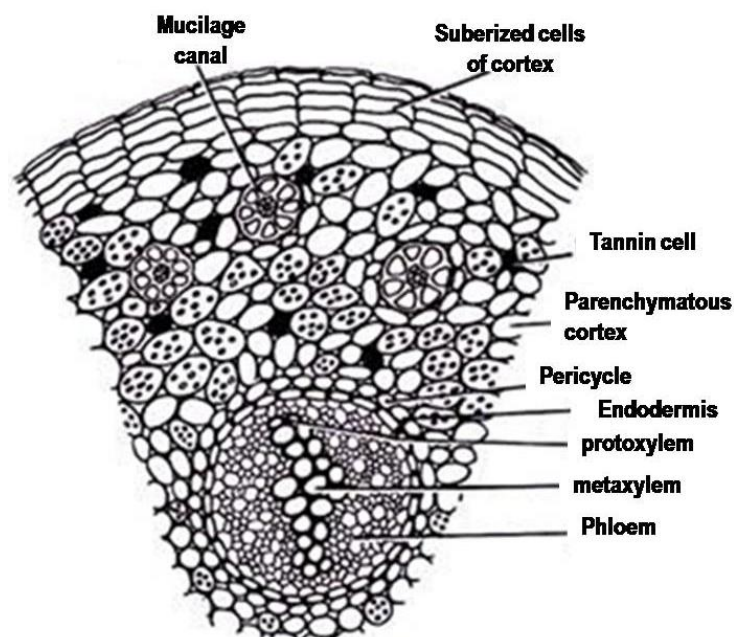


Fig.8.13: *G. biloba*: T.S. of young root

**Stem:** The young stem is more or less circular in outline. Outermost layer is the epidermis is single-layered made of brick-shaped cells and covered by thick cuticle (Fig.8.14 A). In older stem epidermis is replaced by periderm which originates from cortex. Cortex layer next to 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 also 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. 8.14B). Uniseriate medullary rays are present which are 1-5 cells high in dwarf shoots and 1-15 cells high in long shoots. 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 and large in dwarf shoots and narrow in long shoots. Pith contains mucilage canals and calcium oxalate crystals.

**Secondary growth in stem:** Secondary growth takes place through activity of single ring of cambium which remains active throughout the plant life. The wood is characterised to be pycnoxylic as well as manoxylic. Cambium after developing a complete ring cuts off secondary phloem elements towards outside and secondary xylem towards pith. Cambium is made up of fusiform initials (which give rise to vascular elements) and ray initials (which give rise to uniseriate rays). Secondary phloem is made up of sieve elements, parenchyma and phloem fibres. Companion cells are however, absent. Secondary xylem is made up of tracheids and possess weakly developed annual rings. Tracheids have moderately thick wall and most of tracheids end at 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 outer cortex and forms periderm which replaces epidermis. Cambium also forms secondary cortex towards innerside (Fig. 8.14 B).

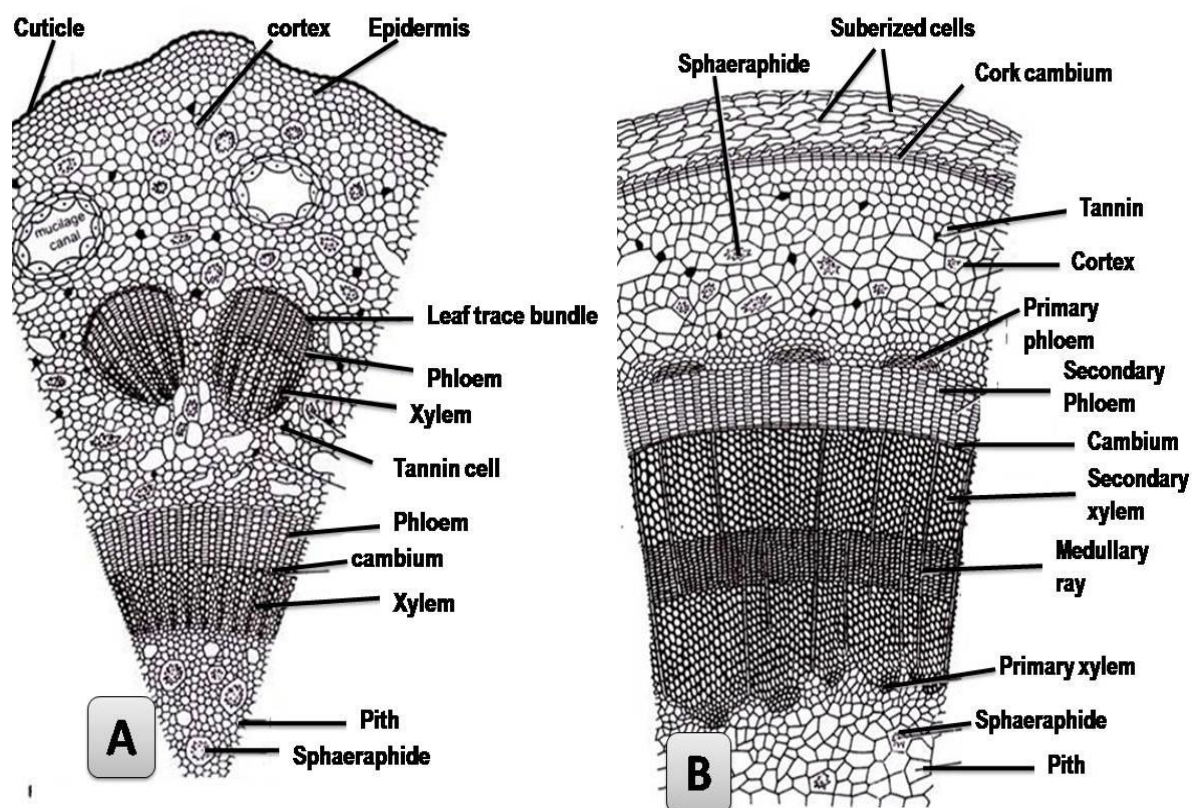


Fig. 8.14: *G. biloba*: (A)-T.S. of young and (B) mature stem

**Leaf:** Upper as well as lower surface of leaf are lined by layer of epidermis covered by cuticle. Epidermal cells are polygonal between the veins and rectangular over the vein. Stomata are haplocheilic type and present only on 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. Guard cells of stomata are surrounded by accessory cells which may be 4-6 or 7 in number. 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. Large number of loosely arranged chloroplasts are present in the mesophyll cells. Loose arrangement of chloroplast allows air spaces to be enclosed between them (Fig 8.15A).

**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.8.15 B). Vascular bundle is surrounded by a sclerenchymatous bundle sheath. Protoxylem contains spiral thickenings. Xylem is traversed by uniseriate rays. Medullary rays of xylem are continuous with those of phloem.

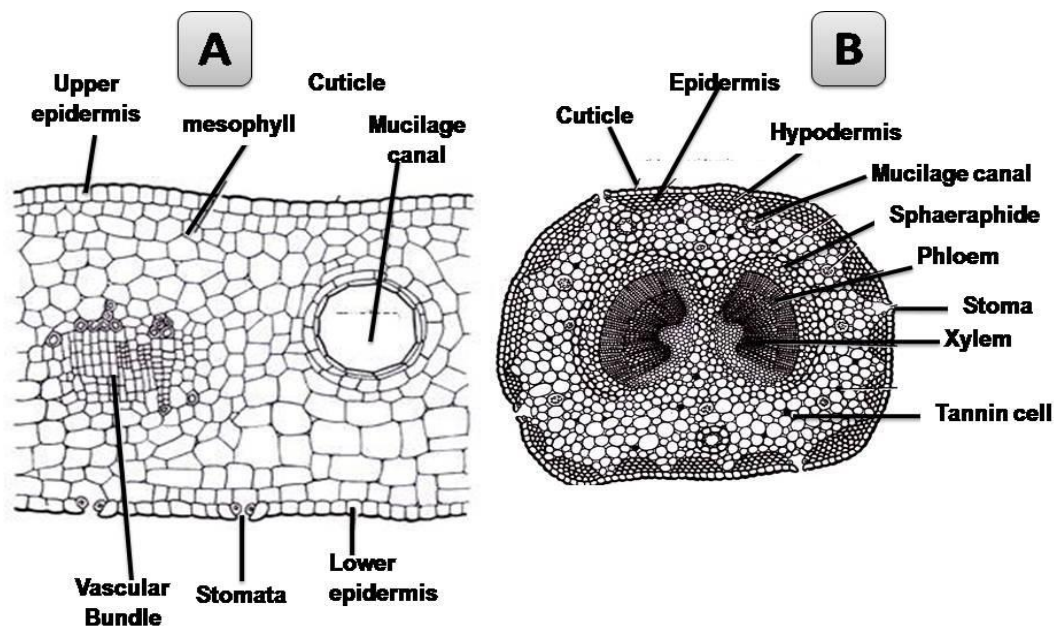


Fig. 8.15: A- T.S. of leaf of *G. biloba*, B- T.S. of petiole of *G. biloba*

**Reproductive 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 male and XX in female). Reproductive bodies of *Ginkgo* are most primitive among living seed plants except 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.8.16A). 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.8.16B). 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 wall. Outermost layer 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., single archesporial cell divides by a periclinal wall forming primary wall cell and primary sporogenous cell. The former develops into wall of microsporangium while the latter develops into sporogenous tissue. Sporangium dehisces by means of a longitudinal slit.

**Female Strobilus:** Megasporangiate organs are borne on dwarf shoots of female tree. They arise in axils of foliage or scaly leaves at apices of dwarf shoots (Fig.8.17A). These are much reduced structures, each having a long stalk or peduncle. Ovules are borne on long stalk or peduncle. Each long stalk possesses 2 or 3 (rarely more) ovules at the tip (Fig.8.16B). 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 increase in number of ovules vascular traces doubles. For example if 3 ovules are present then number of vascular traces will be six. The leaves surrounding the ovules do not show their bilobed character.

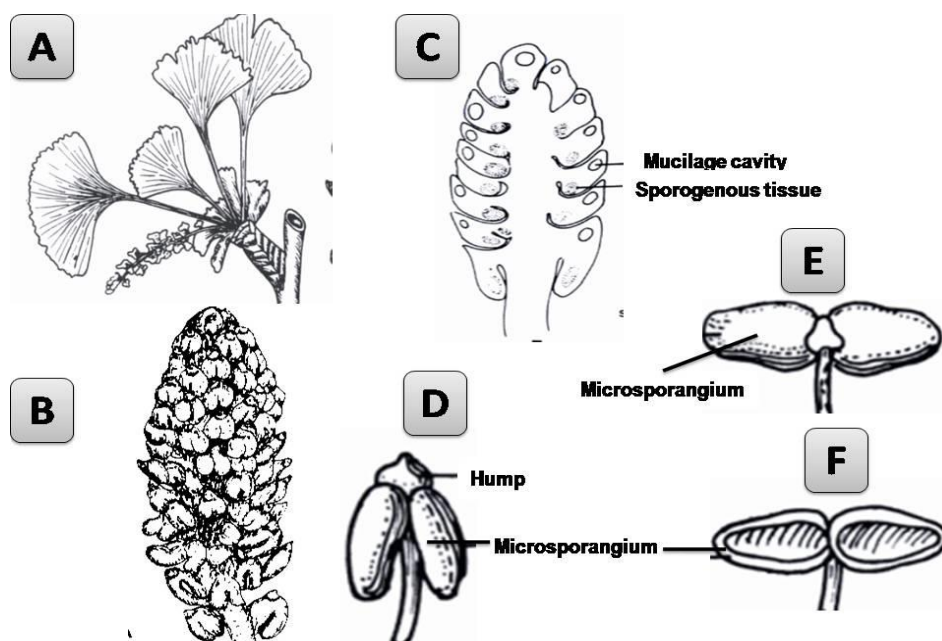


Fig. 8.16: *G. biloba*: A- Part of long shoot bearing short shoot and male strobilus, B- Male strobilus showing arrangement of sporophylls, C-L.S. of male strobilus, D-Microsporophyll with two pendant sporangia, E-Mature sporangia pulled apart due to dehydration, F- Condition after sporangia has dehisced

The development of ovule, mega-sporogenesis and structure of the mature ovule is similar to 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 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 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 ovule, a hump-like outgrowth at apex of microsporophyll, presence of tent pole at the tip of the female gametophyte and absence of suspensor in its embryo.

Beside 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.

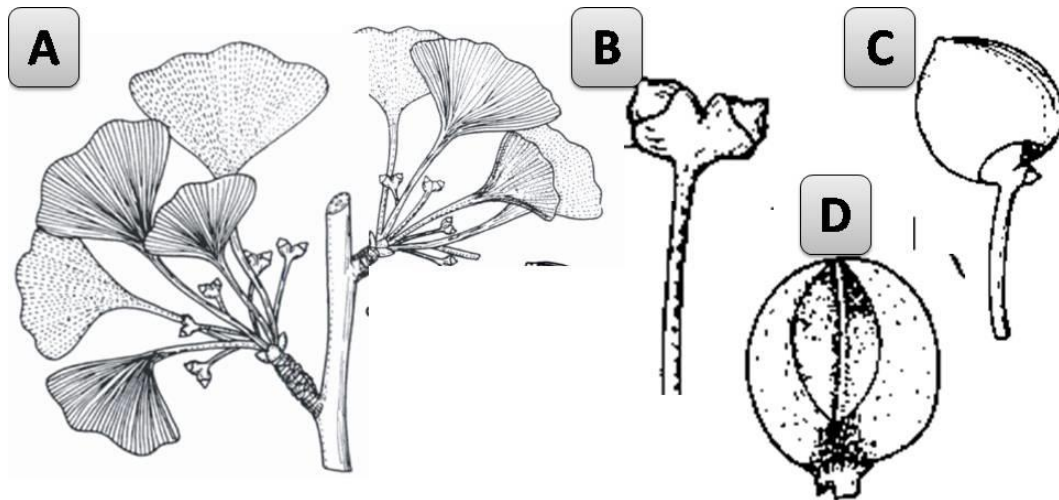


Fig. 8.17: *G. biloba*: A- Long shoots with dwarf shoots bearing leaves and female strobili, B- Axis with a pair of sessile ovules, C- Later stage with one mature ovule (other aborted), D-Seed

### Similarities between Ginkgoales and Pteridospermales

- (i). 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). Collar at the base of the ovules in *Ginkgo* can also be compared to cupule in ovules of some members of Pteridospermales.

### Similarities between Ginkgoales and Filicales

- (i). Structure of primary xylem, secondary xylem and periderm of *Ginkgo* exhibit similarity with some ferns.
- (ii). Leaves of both the 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 arranged uniseriately along the radial walls of the tracheids
- (ix). Microsporangia show longitudinal dehiscence
- (x). Sessile nature of ovule.

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## **8.7 SUMMARY**

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1. Bennettiales (or Cycadeoideales) is a fossil group which was prevalent during the Triassic to Lower Cretaceous periods of Mesozoic era.
2. Stems of Bennettiales were stout or slender with a wide pith and manoxylic wood
3. Leaves of Bennettiales were mostly pinnately compound (occasionally simple) with open (rarely closed) venation with syndetocheilic stomata.
4. Reproductive organs in Bennettiales have been reported to be present in the form of hermaphrodite (e.g. *Cycadeoidea*) or unisexual (e.g. *Wielandiella*) flower.
5. Male reproductive organs were borne in a whorl.
6. Ovules were stalked, produced in large numbers on a conical, cylindrical or dome-shaped receptacle.
7. Order Cycadales includes living and extinct forms which originated in upper Triassic period of early Mesozoic era.
8. At present the members are restricted to four main regions of the world (Central America, South Africa, Eastern Asia and Australia).

9. Cycadales exhibit slow-growth and have a general appearance similar to that of a palm tree with thick, stout, cylindrical and generally un-branched stem.
10. Stems of Cycadales are roughly circular in outline. Both centrally located pith and the peripheral cortex are large and well-developed, and contain mucilage canals.
11. Well developed, strong, stout and large trunk with small secondary wood has been found in many members of Cycadaceae.
12. The leaves of cycads are covered with thick cuticle and contain haplocheilic stomata and diploxylic vascular bundles.
13. Roots of cycads are usually polyarch.
14. Cycadaceae are dioecious and possess male and female reproductive structures on different individuals.
15. The reproductive organs are borne in the form of compact cones.
16. Microspores (pollen grains) are haploid structures which develop into a male gametophyte.
17. Cordaitales represent the most ancient order of class coniferopsida
18. Cordaitales comprise a fossil group of Palaeozoic tall trees of gymnosperms which existed from Devonian through Carboniferous up to the Permian periods.
19. Stem of Cordaitales has been described under several genera and their stem resembled with that of conifers.
20. The roots of Cordaitales are known as *Amyelon* and they also resemble with roots of modern Conifers.
21. Leaf is described by the name *Cordaites* and is characterized by presence of xerophytic characters.
22. Cordaitales exhibit several resemblances with different plant groups such as Pteridospermales, Cycadales, Ginkgoales, Coniferales and Ephedrales.
23. Ginkgoales is represented by only one living member, i.e. *Ginkgo biloba*.
24. Ginkgo is regarded as a **living fossil**.
25. Leaves are fan shaped and possess open type of dichotomous venation.
26. In young stem epidermis is single layered made of brick-shaped cells and covered by thick cuticle. In older stem epidermis is replaced by periderm which originates from cortex.
27. Mature roots are surrounded by suberized cells of cortex. Young roots possess extensive cortex which is made up thin walled cells.
28. Secondary growth in stem is due to activity of single ring of cambium which remains active throughout the plant life.
29. *Ginkgo biloba* is dioecious. Male and female plants are, however, difficult to be differentiated, when young.
30. Beak like protuberance develops from female gametophyte at micropylar end. This protuberance is called tent pole and is characteristic of *Ginkgo biloba*.

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## 8.8 GLOSSARY

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**Arborescent habit:** A treelike plant with an erect trunk, side branches and a distinct crown



**Cambium:** A layer of actively dividing cells between xylem (wood) and phloem (bast) tissues that is responsible for the secondary growth.

**Catkin:** a downy, hanging flowering spike.

Dichotomous venation: vascular arrangement in leaves in which veins are forked with each vein dividing at intervals into smaller veins of almost equal size.

**Dioecious plant:** A dioecious plant is one where the male and female reproductive systems occur on separate plants.

**Eusporangiate:** Plants in which sporangia arise from a group of cells.

**Inflorescence:** Arrangement of flowers on a plant.

**Leaf trace:** a strand of conducting tissue extending from the stem to the base of a leaf.

**Manoxylic wood:** It is non compact wood made up of large amount of parenchyma.

**Micropyle:** a small opening in the surface of an ovule, through which the pollen tube penetrates

**Monoecious plant:** These plants have male and female flowers on the same plant.

**Nucellus:** The central part of an ovule made up of parenchymatous cells.

Phellogen: Also called cork cambium is similar to cambium in function forming phellem outside and phelloderm inside.

**Petrifications:** The process by which organic matter exposed to minerals over a long period is turned into a stony substance

**Pycnoxylic wood:** It is compact wood with large amount of xylem tracheids and less amount of parenchyma.

**Sclerenchyma:** Cells with thickened lignified walls.

**Siphonostele:** Stele consisting of a core of pith surrounded by concentric layers of xylem and phloem.

**Tap root:** a straight tapering root growing vertically downwards and forming the center from which subsidiary rootlets spring.

## 8.9 SELF ASSESSMENT QUESTION

### 8.9.1 Choose the most appropriate option from the following:

- Cordaitales are
  - Tall trees with slender trunk and crown of branches
  - Dwarf trees with slender trunk and crown of branches
  - Tall trees with lateral branches arising throughout the length of trunk.
  - Small trees with lateral branches arising throughout the length of trunk
- Smallest female cones of Cycadaceae develop in
 

(a) <i>Zamiapygmea</i>	(b) <i>Dioon</i>
(c) <i>Macrozamia</i>	(d) <i>Ceratozamia</i>
- Bennitttales resemble Cycadales in having
 

(a) Haplocheilic stomata	(b) Monosporangiate flowers
(c) Polyxylic secondary wood	(d) None of these

4. Which of the following is NOT true about leaves of Cycadaceae
  - (a) Presence of Haplocheilic stomata
  - (b) Diploxylic xylem
  - (c) Leaves covered with thin cuticle
  - (d) Vascular bundle diploxylic
5. In *Ginkgo biloba*
  - (a) Fibrous root system is present
  - (b) Plants are dioecious
  - (c) Leaves arise in groups on terminal branches
  - (d) Wood is manoxylic
6. Which of the following is not true about *Bennettitales*
  - (a) Syndetocheilic stomata
  - (b) Bisporangiate flowers
  - (c) Polyxylic secondary wood
  - (d) Exalbuminous seeds
7. Cordaitales have been named in honour of
  - (a) A.J Corda
  - (b) Birbal Sahnii
  - (c) Stout Corda
  - (d) None of these
8. *Mitrospermum* and *Kamarospermum* are two seed genera of
  - (a) Pteridospermales
  - (b) Cordaitales
  - (c) Bennettitales
  - (d) Cycads
9. Which of the following is unique characteristic feature of *Cordaitales*
  - (a) Arborescent habit and scanty primary wood
  - (b) absence of resin canals
  - (c) Compound unisexual cones
  - (d) All the above
10. Which of the following is not a *Cycadales*
  - (a) *Bowenia*
  - (b) *Ginkgo*
  - (c) *Lepidozamia*
  - (d) *Macrozamia*

### 8.9.2 Fill in the blanks:

1. \_\_\_\_\_ in stem of Cycadaceae are diploxylic
2. \_\_\_\_\_ is only living member of Ginkgoales
3. \_\_\_\_\_ in Cordaitales were always monosporous
4. Germination of \_\_\_\_\_ in Cycadaceae is precocious
5. Cycadaceae \_\_\_\_\_ are usually polyarch
6. Microsporangiate strobili of *Ginkgo* resemble with \_\_\_\_\_ inflorescence.
7. Trachieds of cordaitales contain \_\_\_\_\_ bordered pits
8. \_\_\_\_\_ represent ovules borne on leaves
9. \_\_\_\_\_ formed first great forest of world
10. \_\_\_\_\_ is also called Maiden fair tree.

### 8.9.3 Very Short answers type questions:

1. What are Benittitales?
2. How *Cordaitates* and *Ginkgo* differ from one another?
3. Give an example of living fossil.
4. Mention two unique characteristics features of Benittitales.

5. Why Mesozoic era is called age of Cycades?
6. How does Benittiales differ from Pteridospermales?
7. What are phyllospperms and stachyosperms?
8. Which group of plants formed first great forest of world?
9. Name the regions of the world where fossils of cordaitales have been obtained.
10. What do you understand by the term *Cardiocarpus*?
11. Mention two differences between young and mature roots of Ginkgoales.
12. Why some workers treated Benittiales under Cycadophyta?

#### 8.9.4 Short answers type questions

1. With the help of diagram explain about stem anatomy of Cycads.
2. Enlist characteristic features of Cordaitales.
3. How does Benittiales resemble with Angiosperms and Pteridospermales?
4. Differentiate between Benittiales and Cycadales.
5. Write short note on features of Benittiales.
6. What are the characteristic features of Ginkgoales and coniferale? Mention characteristics common between these groups.
7. Describe about anatomy and secondary growth of stem of *Ginkgo*.
8. Classify Cordaitales according to various Scientists.
9. Briefly describe the distribution of Cycads.
10. Mention about the classification of Cycadales.
11. What are the similarities and difference between Cordaitales and Pteridospermales?
12. Briefly describe about male and female strobili of *Ginkgo biloba*.
13. Describe stem anatomy of *Cycas*.

**8.9.1 Answer Key:** 1-(a), 2-(a), 3-(d), 4-(c), 5-(b), 6-(c), 7-(a), 8-(b), 9-(d), 10-(b)

**8.9.2 Answer Key:** 1- Xylem, 2-*Ginkgo biloba*, 3- Strobili, 4- Microspore, 5- roots, 6-catkin, 7- Multiseriate, 8- Phyllospperms, 9- Cordaitales, 10- *Ginkgo biloba*

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### 8.12 SUGGESTED READINGS

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## 8.13 TERMINAL QUESTIONS

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### 8.13.1 Long answers type question

- Q1. With well labelled diagram describe anatomical features of *Cordaites*.
- Q2. Describe about reproductive structures of Cycads.
- Q3. Mention the affinities of Cordiales with different plant groups.
- Q4. Describe reproduction in *Ginkgo biloba*.
- Q5. With self-explanatory diagram explain about anatomy of stem and leaf of Cycads.
- Q6. Explain about strobilus of Cordiales.
- Q7. Describe general Characteristics features of Bennettiales.
- Q8. With the help of diagram explain about reproductive structure of Cycads.

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## **UNIT-9-GENERAL ACCOUNT OF CONIFERALES, TAXALES, EPHEDRALES, WELWITSCHIALES AND GNETALES**

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- 9.1 Objectives
- 9.2 Introduction
- 9.3 Coniferales
- 9.4 Taxales
- 9.5 Ephedrales
- 9.6 Welwitschiales
- 9.7 Gnetales
- 9.8 Summary
- 9.9 Glossary
- 9.10 Self assessment questions
- 9.11 References
- 9.12 Suggested readings
- 9.13 Terminal questions

## 9.1 OBJECTIVES

After reading this unit student will be able-

- To know about origin, distribution and general characters of Coniferales, Taxales, Ephedrales, Welwitschiales and Gnetales
- To understand anatomical features of stem, leaf and root of the members of these orders.
- To know about reproductive structures of different plants mentioned here.

## 9.2 INTRODUCTION

In the present chapter we will study about Coniferales, Taxales, Ephedrales, Welwitschiales and Gnetales. Coniferales includes living and extinct forms and were found from carboniferous period to present times. Taxales order has been separated from Coniferales due to variation in reproductive parts. Class Genopsida is considered to include one order Gnetales with three families Ephedraceae, Welwitschiaceae and Gnetaceae. This was due to presence of some common features. However, owing to presence of several morphological differences Eames (1952) suggested to split Gnetales into three different orders Ephedrales, Welwitschiales, and Gnetales, each with a single family and a single genus.

## 9.3 CONIFERALES

Conifers are tall trees with foliage and branches which have a cone like appearance. Coniferales are known as dominant forest-makers of the world. They comprise of about 54 living genera having more than 570 species. They are widely distributed in areas of Northern and Southern hemispheres. In India conifers are represented by genera like *Pinus*, *Abies*, *Picea*, *Cedrus*, *Tsuga*, *Cupressus*, *Juniperus*, *Araucaria* and *Podocarpus*. They are found from Carboniferous to the present times. Conifers have been classified into different families, Table 9.1 represents brief outline of different families of conifers:

**Table 9.1: Brief summary of families of Coniferales**

S.N	Family	Brief overview
1	Lebachiaceae	Earliest conifers, Based on the genus <i>Lebachia</i> and formed by Florin out of Upper Carboniferous and Permian fossils. <i>Lebachia</i> was a tree with pinnately arranged branch-lets on which very small needle-like leaves were borne spirally in an imbricate manner. There were separate male and female cones. Lebachiaceae is the best known of the earliest conifers
2	Voltziaceae	The Voltziaceae (after taking out the Lebachiaceae) shows a group of fossils from the Permian to the Jurassic.
3	Palissyaceae	Represented by two genera <i>Palissya</i> and <i>Stachyotaxus</i> . <i>Palissya</i> is well represented in the Indian Upper Gondwana by <i>P. conferta</i> , <i>P. indica</i> and <i>P. jabalpurpsis</i> from the Rajmahal, Kota and Jabalpur Stages

4	Cheirolepidaceae	Is a family of Triassic-Jurassic fossils which is very close to the Podocarpaceae and also related to the Araucariaceae. Only the female cones are known.
5	Protopinaceae	Protopinaceae represents an assorted group of coniferous wood fossils from the Jurassic and Cretaceous periods which show affinities with Pinaceae, Taxodiaceae, Cupressaceae and Podocarpaceae.
6	Taxodiaceae	Includes 10 genera and 18 species. It is a family of monoecious trees which vary in size from small to huge size, small needle-like to falcate or scaly leaves borne spirally (rarely opposite). Cones are small with spiral members. Bracts and ovuliferous scales are almost completely fused. There may be 2 to 9 ovules on an ovuliferous scale. Pollens are wingless.
7	Cupressaceae	Largest family with 20 genera and 148 species. Is a family of small or large trees. Leaves are persistent, small, scale-like, opposite or in whorls. No shoot dimorphism, Male strobili are small, female cones arise on short branches. Number of ovules varies from 3-30 (rarely 1-2), wingless pollen,
8	Araucariaceae	Is a family of beautiful trees with branches in whorls. Leaves linear or broad and spirally arranged, Male cones large, catkin-like. Female cones woody, large, with spiral scales. There are two genera <i>Agathis</i> (monoecious) and <i>Araucaria</i> (dioecious) with about 35 species.
9	Podocarpaceae	Family includes 7 genera and 150 species, shrubs or trees with linear or lanceolate leaves. Male strobilus with microsporophylls each with two microsporangia. Pollens are winged. Definite female cones in some species, in others it is very much reduced. This is an ancient family with fossils clearly known up to Upper Triassic.
10	Cephalotaxaceae	Represented by six species of genus <i>Cephalotaxus</i> , found in subtropical forest of Japan, China and Eastern Himalayas. Shrubs or small trees, dioecious, spirally arranged leaves, and male cones arise in clusters.

### General Characters of Coniferales

1. Plant body is sporophytic and the sporophytes are richly branched trees or shrubs
2. Their growth habit varies from extremely tall trees to miniature forms.
3. Branches may be of one kind or they may be dimorphic as in *Pinus*.
4. Stems contain small pith and the secondary wood is pycnoxylic and consists of tracheids with large uniseriate or rarely multiseriate pits on their radial walls.
5. Resin canals are distributed in pith, cortex and sometimes also in wood.
6. Leaves are of two types, i.e. foliage leaves and scaly leaves.

7. Plants are either monoecious or dioecious.
8. The sporophylls are generally arranged in the form of cones.
9. The micro-strobili or male cones are simple and contain many scales like microsporophylls.
10. The female cone or mega-strobili consist of many sterile bract scales and fertile ovuliferous scales.
11. Female gametophyte is completely dependent on the sporophyte.
12. Oospore has the ability to produce more than one embryo, hence conifers show polyembryony.
13. Seeds are endospermic and winged with hard testa.
14. Members of conifers have economic value as they are source of timber, pulp, wood, oils, resins, turpentine etc.

### Structure and anatomy of leaves of conifers

Leaves of Conifers are either scale like or they possess well developed lamina. Leaves are simple and a prominent midrib present in most of Conifers. Table-9.2 represents shape of leaf in different families of conifers.

**Table 9.2: General shape of leaves in conifers**

Family	Shape of leaf
Pinaceae	Needle like, linear
Taxodiaceae	Linear, scale like
Araucariaceae	Broad
Cephalotaxaceae	Linear
Cupressaceae	Scale like
Podocarpaceae	Linear, scale like

In general leaves are linear and needle like. Most of the Conifers are evergreen. In *Araucaria* the foliage (leaves) remain green for about 10-15 years. However genera such as *Taxodium*, *Metasequoia*, *Larix* etc are deciduous and in these leaf fall occurs in every autumn. Considering the small size and single vein, leaves of conifers are regarded to be microphyllous but in other view if it is believed that leaf traces leave leaf gap in stem stele, then the leaves of Conifers are megaphyllous. Phyllotaxy (arrangement of leaves) in most of Conifers is alternate or spiral. Family Cupressaceae however, possesses whorl and opposite phyllotaxy. In Pines needle like green leaves are borne on spur shoots. Spur shoots arise from axillary bud of a scale leaf. Needles fall along with the spur and hence are deciduous.

Leaf is characterized by thickly cuticularized well defined epidermis and cells have a thin cell wall. Stomata are sunken, haplocheilic and are generally present in parallel rows forming vertical band on each side of midrib. There is no regular arrangement of stomata in *Cedrus*, *Cupressus* and *Cryptomeria*. Pinaceae is characterized by needle like leaves and stomata are present on all sides of leaves (amphistomatic). The arrangement of stomata in *Tsuga*, *Podocarpus*, *Abies* is hypostomatic hence stomata are found on abaxial surface only. Contrary to this arrangement of stomata in *Thuja*, *Juniperus* and *Cupressus* stomata are



present only on adaxial surface and hence are hyperstomatic. Leaves of *Cephalotaxus* and *Tsuga* specifically lack hypodermis. Whereas hypodermis is present in distinct patches in *P. roxburghii* and *P. merkusii*. Sclerenchyma is uniformly present in *Abies*, *Cedrus*, *Cryptomeria*, *Agathis* etc. Well developed palisade tissue and spongy parenchyma is found in *Agathis* and *Podocarpus* (Fig.9.1A). Such distinction is not seen in other members. Cells of mesophyll tissue in *Pinus* contains foldings and mesophyll tissue of *Cryptomeria* is characterized by presence of well developed air spaces. Distribution of resin canal varies from genera to genera and species to species. In *Cryptomeria* a big resin canal is present above vascular bundle. Leaf trace is double in living Pinaceae and single in Cupressaceae.

A characteristic feature of leaves of Conifers is the presence of transfusion tissue. In *Pinus* transfusion tissue consist of two types of cells:

- Transfusion tracheids which are dead cells having thick, lignified walls and circular bordered pits.
- Second type of cells are transfusion parenchyma cells which are living cells and contain tannin like contents.

Both cell types are present in vascular region enclosed by endodermis. They function to conduct water and food material between vascular bundle and mesophyll tissue.

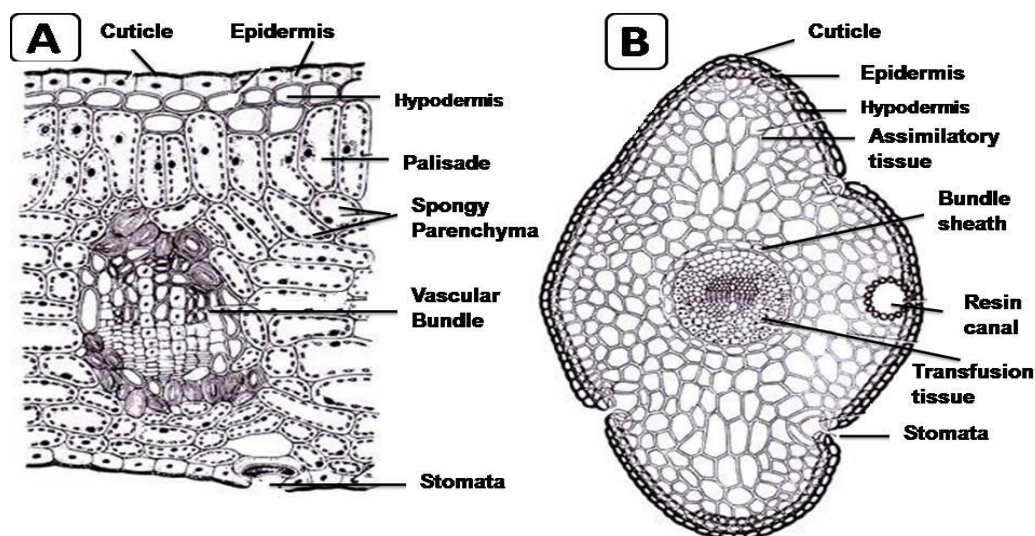


Fig. 9.1 A- T.S. of leaf of *Agathis robusta*, B- T.S. of leaf of *Picea excelsa*

## Anatomy

**Stem:** Shoot apices of conifers exhibit similar development as found in other gymnosperms. However, variation occurs in seasonal distribution of growth. For example shoot apices of *Sequoia* exhibit slow but continuous growth over long periods. However, in some Conifers such as *Pinus*, *Pseudotsuga* and *Torreya* annual shoot development occurs during a specific seasonal phase. In the shoot apex there are different zones which differ from one another in mitotic activity, direction of growth and cellular constitution. In Pinaceae, the apical meristem shows nuclear distinction between tunica and corpus. Initially group of apical cells divide (anticlinally and periclinally) to form lateral derivatives and central mother cell zone. At the center of this zone, cells having meristematic activity gradually differentiate to give

rise to peripheral zone. From this peripheral zone arise leaf primordia (in part), cortex, procambium and epidermis. The central mother cell gives rise to rib meristem which eventually produces pith. Central mother cell is also found in *Sequoia*, *Araucaria* and *Pseudotsuga*, however, central mother cells are absent in most of the conifers including *Pinus*. From the peripheral zone arise pro-vascular strands which differentiate into vascular bundles. Vascular bundles (strands) are conjoint, collateral, open and endarch and form a ring around the central pith. Conifers contain large vascular cylinders and small area of pith and cortex. Cortex as well as pith contains resin passages. Leaf traces may be single or double.

A characteristic feature of Conifers is that in them cambial activity begins very early. All xylem elements are radially aligned from the pith outwardly. A few bundles of the ring arise at later stage. These are entirely derived from cambium and contain protoxylem elements. As the stem matures the cambium forms a complete ring and cambium cells tangentially divide to form secondary xylem and phloem. There exists a remarkable similarity in structure of xylem and phloem in almost all families of conifers. Secondary wood in Conifers is pycnoxylic. Except for medullary rays which are heterogenous while rest of wood has homogenous texture. Xylem contains tracheids which are long, narrow and contains circular bordered pits having distinct tori. Pits are generally present on radial walls and are uniseriate however, biseriate pits are found in *Agathis*, *Araucaria*, *Microbiota*, *Cedrus* and *Keteleria*. Vessels are absent in xylem. Medullary rays are uniseriate and few cells high. Secondary phloem is made up of sieve elements or sieve cells and undifferentiated parenchyma. Sieve cells have small, rounded and separated sieve areas confined to radial walls. Companion cells are absent. *Pinus* contains two types of phloem rays one which dies with rest of phloem and other which is starch filled and remains alive even when the rest of phloem is dead. Cambium remains active for hundreds of years. Annual rings are distinct however; false rings may also arise because of abnormal cambial activity (Fig.9.2).

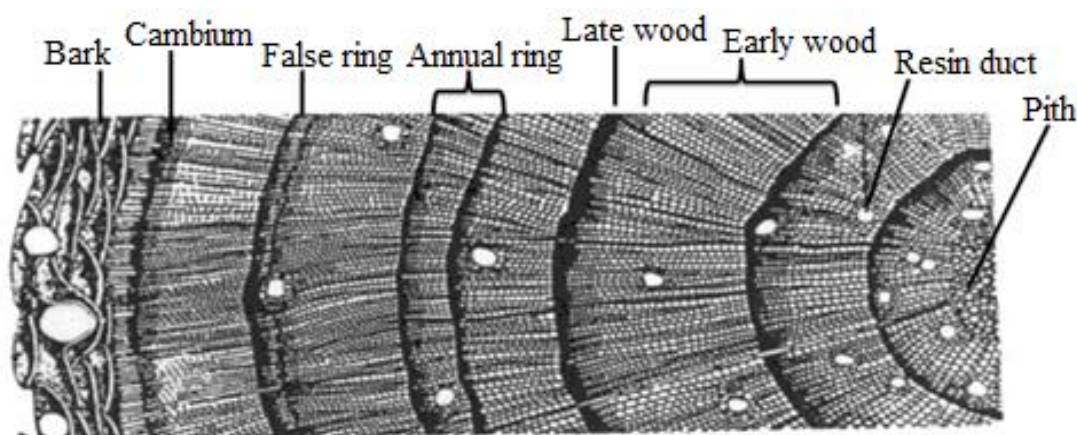


Fig.9.2: Cross section of Conifer stem

Outer cortex contains cork cambium, whose cells divide horizontally to cut off cork cells (or phellem cells) outwardly and secondary cortex (or pheloderm cells) within. As a result of regular increase in growth of secondary wood and phloem the outer cork layer are shed (sloughed) off and new layers arise by activity of cork cambium. Hence in older stems bark of tree comprises of periderm, made up of cork layer, cork cambium and secondary cortex

and a nonfunctional secondary phloem. A specific term rhytidome is used to describe fissured or wrinkled and furrowed portion of bark. In *Sequoias* bark of trees can be as thick as 2 feet and it forms an effective insulating tissue which provides protection from heat of forest fires. This is considered to be most important reason for survival of conifers for thousands of years.

**Root:** At the root apex are present apical initial cells which repeatedly divide to form cells which contribute to root cap zone and stelar mother cell zone. These initial cells divide to form several verticals rows of cells which form one core of root cap. Core cells divide to form cortex and lateral cells of root cap. From this it becomes clear that cortex and root cap have a common origin because of which there is no well defined dermatogen and periblem present at root tip. Cells of stelar mother cell zone divide transversely to form pro cambial cells. These pro cambial cells elongate and divide longitudinally to form a distinct procambial zone. Generally a diarch stele is present in root but triarch and tetrach stele are also commonly found (Fig9.3). *Taxodium imbricatum* specifically contains pentarch roots. Xylem is exarch and in *Pinus* protoxylem is Y shaped which contains a resin duct in arms of Y. Pericycle and endodermis are clearly visible. Primary cambium is very active and divides to form secondary vascular tissue. Due to secondary growth continuous layers of secondary xylem and phloem are formed. Endodermal cells are characterized by the presence of casparian strips. Annual rings are not prominent. Internal organization of roots of old plants looks similar to that of stem.

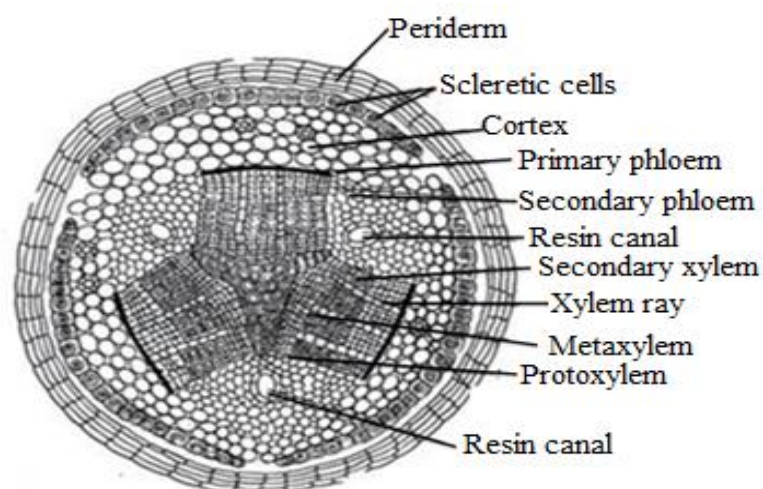


Fig.9.3- T.S. of triarch root of *Pinus*

## Reproduction

There exists a great amount of variation in reproductive structures of members of different families of conifers. Here we will discuss reproductive structure of member of family Pinaceae (Fig.9.4 A).

**Male reproductive structure:** Microsporoangiate cones bear spiral sequence of microsporophylls (Fig.9.4 B). Each microsporophyll contains a sterile distal flap and a pair of elongated microsporangia (Fig.9.4 C). Microsporangia dehisce by longitudinal split however, oblique and transverse dehiscence has rarely been reported. Male cones take the place of

short shoots and are aggregated in *Pinus*. Wall of mature sporangium is made up of 2-6 layers. Tapetum is present and in species such as *P. roxburgii* it originates from innermost layer. Tapetum alongwith all wall layers except for the outer layer or epidermis degenerate during meiosis and microspore maturation. Cells of epidermis develop tanniferous contents. Their walls become thick and a thick cuticle develops on outer tangential walls. Microspores of Pinaceae contains two wings. Microspores in genus *Tsuga* are wingless except *T. martensiana*. Young microspores consists of a three layered exine (outer ectine, middle mesine and inner endine) and inner intine whose outer layer is well developed and inner layer does not develop in young grains but is prominent in mature grains as pectocellulosic tissue. Germination of pollen grains begins within microsporangium and are shed at 4 (*Pinus*, *Keteleeria davadiana*) or 5 (*Abies*, *Larix*) celled stage.

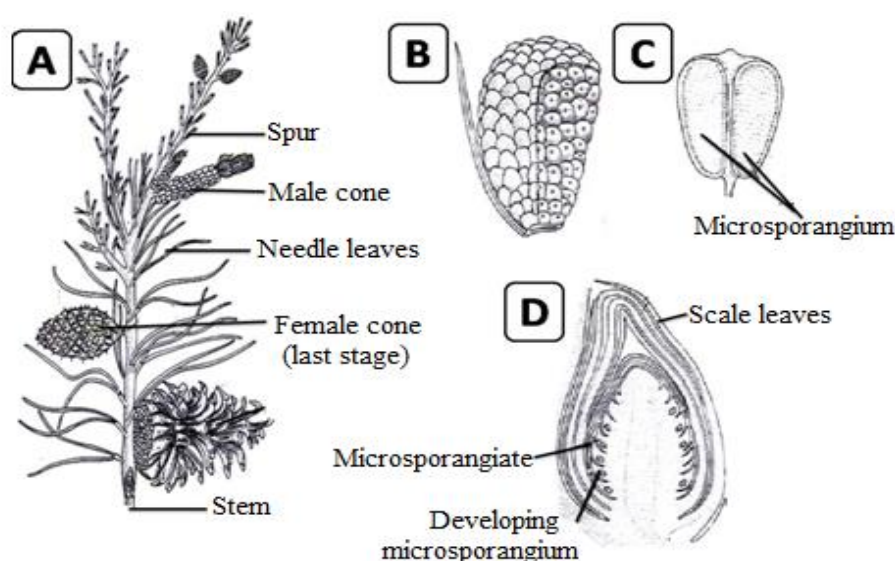


Fig. 9.4: A- *Pinus* showing male and female cones, B- Mature male cone, C- Microsporophyll with 2 undeveloped sporangia, D- VS of young male cone

**Female reproductive structure:** Megasporangiate cones are composed of number of spirally arranged bracts, in axil of these bracts are produced ovuliferous scales. In each of these scales two ovules are present. Ovules are unitegmic i.e., have single integument which is made up of three layers, outer and inner fleshy and middle stony. Integument is fused to nucellus except for its upper part. Nucellus is thick, well developed and is known as megasporangium. In most of Pinaceae a deeply seated cell inside nucellus acts as megaspore mother cell. Konar reported that in *P. roxburghii* a hypodermal archesporial cell undergoes differentiation and division to form outer primary parietal cell and inner sporogenous cell. This sporogenous cell functions as megaspore mother cell. Three to four megaspores are formed due to reduction division. In *Keteleeria* functional megaspore enlarges and its nucleus divides to form 512 free nuclei, there is no resting period. However in *Cedrus deodara* a resting period of four months has been reported before the start of division of nucleus. The number of free nuclei produced varies from species to species. Megaspore remains surrounded by a spongy tissue during free nuclear stage, this layer however, disappears after formation of complete female gametophyte. Free nuclear division is followed by wall formation. Development of archegonia occurs from superficial cells of female gametophyte present at micropylar end.

Their number varies from one genera to another for e.g. 1-5 in *Larix deciduas*, 3-5 in *Cedrus deodara*, 7-12 in *P. roxburghii*, etc. An archegonial chamber is formed by neighbouring tissue of gametophyte. Archegonium contains a short neck and long venter. Neck consists of neck cells however, neck canal is absent. Venter contains a small ventral canal cell which may degenerate before fertilization or may persist for some time after fertilization. Cytoplasm of egg contains vacuoles or para-nuclei which play a nutritive role. Female cones take the place of long shoots and takes three years for development (Fig.9.5A-C).

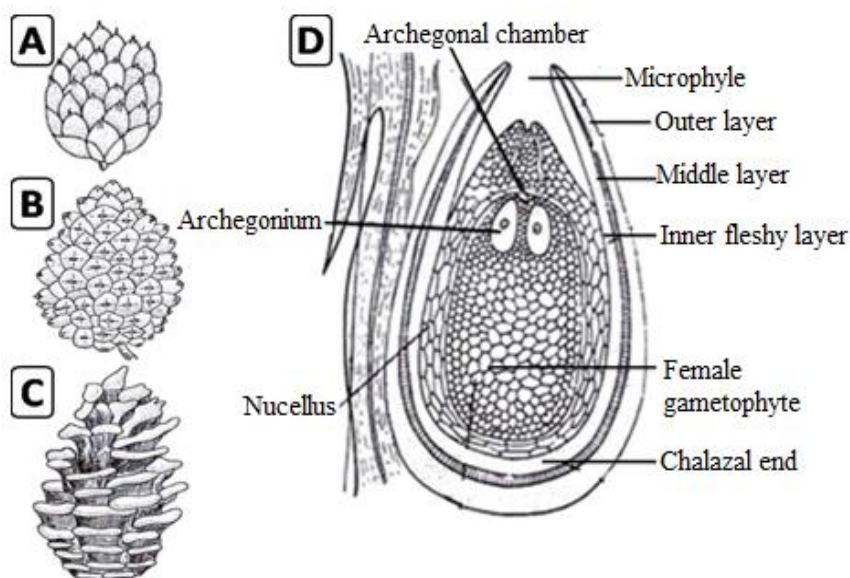


Fig. 9.5 A- First year female cone, B-Second year female cone, C- Third year female cone, D- L.S. of ovule of *Pinus roxburghii*

## 9.4 TAXALES

The order is represented by single family Taxaceae, which has been separated from conifers and placed in a new order-Taxales due to differences in reproductive organs. Engler and Prantl (1889) recognized only one species, *Taxus baccata*, under *Taxus*, while Dallimore and Jackson (1948) and Sporne (1965) included 9 species viz. *Taxus baccata*, *T. brevifolia*, *T. canadensis*, *T. chinensis*, *T. cuspidata*, *T. jioridana*, *T. globosa*, and *T. media*. *Taxus* is widely represented in North and South America, Europe, Philippines, Algeria, Morocco and India extending even up to Malaysia. In India, *Taxus* occurs both in the eastern as well as western Himalayas in Khasi and Naga hills, Assam, Manipur, Shimla and several other areas at an altitude of about 1800 meters or more above sea level. Raizada and Sahni (1960) recognized a tenth species of *Taxus* (*T. wallichiana*) growing in Himalayas.

The family is characterized by evergreen small trees or shrubs. They show extensive branching. Leaves are simple, solitary and spirally arranged. Secondary wood is pycnoxylic. There is no distinction of shoot apex into tunica and corpus. Wood rays are homogenous and have thick walls. Trees are generally dioecious however, monoecious trees are also known. A terminally borne single ovule represents female strobili. Male strobilus consists of small

central axis at the apex of a dwarf shoot. Seeds are endospermic. *Taxus baccata*, a small tree is an important representative found in Himalayas in India.

## Morphology

1. *Taxus baccata* is an evergreen tree with a height of 9-20 meters. It is commonly known as 'Yew' tree.
2. *T. baccata* possesses a huge trunk; stem is profusely branched and is covered with a thin brown coloured bark.
3. All branches exhibit unlimited growth and form a very dense canopy, which makes *T. baccata* a shade providing tree. It differs from *Pinus* in not possessing dimorphic branches.
4. Only the green leaves are present on vegetative branches. The upper surface is dark green while the lower surface is pale or rusty red in colour.
5. Leaves are linear, small (2-3 cm long), spirally arranged and shortly stalked.
6. Each leaf contains a single strong vein and recurved margins.
7. The apex is sharply pointed mainly because of accumulation of silica.
8. The scaly leaves present on the fertile shoot are opposite and decussate.
9. Well developed tap root system is present. Roots are deep-feeders and highly branched.

## Anatomy

**Stem:** In transverse section the stem exhibits similarity with *Pinus* in structure. It is surrounded by a single-layered epidermis having a thick cuticle. Next to epidermis is present parenchymatous cortex which possesses tannin-filled cells. Inner to cortex region is present endodermis and sclerenchymatous pericycle (Fig.9.6A). The young stem shows a ring of conjoint, collateral, open and endarch vascular bundles enclosing a distinct pith in the centre. The protoxylem consists of spiral tracheids, and the phloem contains sieve cells with sieve plates and phloem parenchyma. Companion cells are absent. The cambium is persistent and develops a thick vascular cylinder due to secondary growth. The cambium cuts off secondary phloem towards outer side and secondary xylem towards inner side. The secondary wood lacks resin canals and wood parenchyma (Fig.9.6B). Uniseriate bordered pits are present only on their radial walls of tracheids. The tracheid possesses spiral thickenings. The medullary rays are uniseriate and homogeneous however in *Taxus baccata* they have been reported to be biseriate. The wood is strong and dense. Due to the presence of tertiary spirals, the wood is elastic in nature. Phellogen may develop in the older stems showing extrastelar secondary growth.

**Root:** Root has an outer layer called epiblema in younger roots where epidermal cells possess long and unicellular root hairs. A thin cuticle is also present. Next to epidermis is present parenchymatous cortex which is several layers thick. These cells enclose intercellular spaces. A distinct endodermis is present. Pericycle contains resin canals and is multilayered except opposite protoxylem. Stele is diarch and exarch and protoxylem lacks resin passages. There

is no pith present as it is occupied by plates of metaxylem tracheids. Secondary growth is similar to the one seen in *Pinus*.

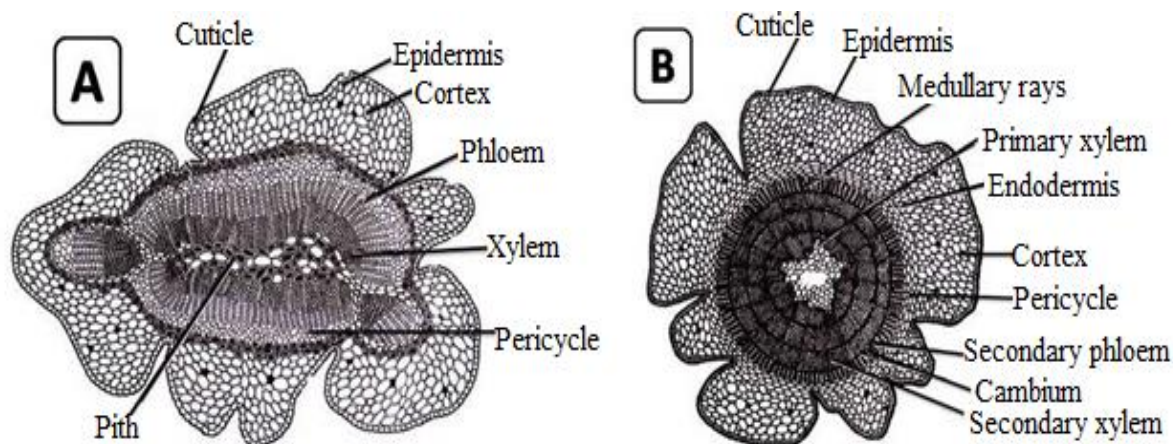


Fig. 9.6: Stem of *Taxus baccata*, A- T S of young stem, B- T S of old stem

**Leaf:** The leaf is dorsiventral and exhibits xerophytic characters. Cells of both upper and lower epidermis are rectangular in shape and thickly circularized. The cuticle is comparatively thin on the lower surface. Sunken stomata are present only to the lower epidermis. Stomata show haplocheilic development. The mesophyll is differentiated into two layered palisade and spongy-parenchyma. Single vascular bundle is present in the mid-rib region. Enclosed by a distinct endodermal layer or bundle sheath the collateral vascular bundle contains phloem towards the lower side and xylem towards the upper side (Fig.9.7). On both the sides of the vascular bundle is present transfusion tissue. Resin canals are generally absent. In the above mentioned description presence of thick cuticle, sunken stomata, transfusion tissue and differentiation of mesophyll into palisade and spongy parenchyma comprise xerophytic characters of leaves.

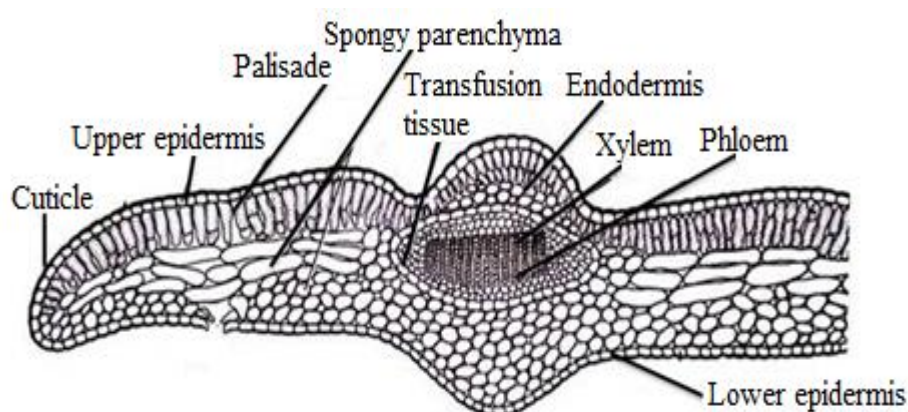


Fig. 9.7: V.S. of leaf of *Taxus baccata*

## Reproduction

*Taxus* is usually dioecious; however, monoecious species have also been reported. The male and female plants have no difference in their vegetative organisation, and they can be

differentiated only when the plants begin to flower or in fruiting stage. The reproductive structures become prominent on the plant during February-March.

**Male strobilus or Male flower:** Male strobili are yellow coloured which develop in the axil of foliage leaves (Fig.9.8A). Each strobilus consists of several overlapping sterile bracts. Some of these bracts towards the tip region of strobilus are replaced by stamens or microsporangiohores (Fig.9.8B). Stamens are short-stalked with a peltate disc having 4-8 pendant microsporangia. The stalk is completely surrounded by microsporangia. The axis of the male strobilus contains a broad apex which is consumed in the formation of a stamen (Fig.9.8C). In young male strobilus microsporangia are compactly arranged but at maturity they get loosened and undergo dehiscence. Presence of peltate micro-sporangiophores is an important characteristic feature of *Taxus*. Mature microsporangium is surrounded by an epidermal layer followed by two wall layers and sporogenous tissue. The outermost sporogenous cells differentiate into a tapetum layer. The sporogenous cells function as microspore mother cells and undergo meiosis to form microspores or pollen grains. These microspores are arranged isobilaterally or tetrahedrally for some time. Microsporangium is similar to that of *Pinus* and exhibit eusporangiate development. Four to eight archesporial cells develop hypodermally. These cells divide to form above mentioned wall layers and sporogenous tissue.

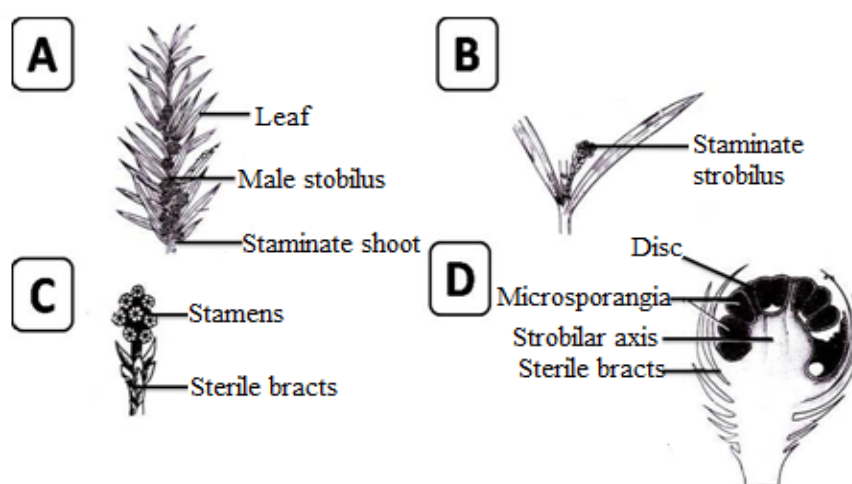


Fig.9.8: A- Male shoots of *T. baccata* with staminate stobili, B-Single branch with male strobilus, C- Male strobilus with many stamens, D- L.S. of male strobilus

**Female strobilus or female flower:** The female strobili in *Taxus* are greatly reduced and they hardly appear as cones or strobili (Fig.9.9 A). They arise in the axils of leaves early in the season but mature in the next season. Each female reproductive organ comprises of a short primary axis containing scaly leaves or bracts which are arranged in opposite decussate manner. A short secondary axis which develops from the axil of upper three scaly leaves contains few pairs of scaly leaves and a terminal ovule (Fig.9.9 B).

The ovule is orthotropous and rounded or oval in shape contains thick integument which is present upto the base of ovule forming a long micropyle. Integument is free from nucellus and is differentiated into outer and inner fleshy and middle stony layers. Two vascular strands enter the integument from the base of the ovule and reach up to the top. A ring-like outgrowth



called aril or cupule develops from the base of the integument which surrounds the entire ovule. At young stage aril is green and saucer-shaped but after maturity it becomes red and cup-shaped. Aril is also supplied by two minute and rudimentary vascular bundles. Pollen chamber and nucellar beak are absent. The apex of the female gametophyte changes into a flask-shaped structure called tent-pole which however, disappears at the later stages. In general about 10 archegonia develop in a female gametophyte but sometimes the number may reach up to 25. During development in the young ovule develops an archesporial initial which divides periclinally to form an outer parietal cell and an inner primary sporogenous cell. The primary sporogenous cell further divides to form many sporogenous cells, out of which one or more functions as megaspore mother cells. The megaspore mother cell undergoes meiosis to form four megaspores arranged in linear tetrad. Out of these lowermost megaspore remains functional while others degenerate. The functional megaspore nucleus divides and develops into multicellular gametophyte.

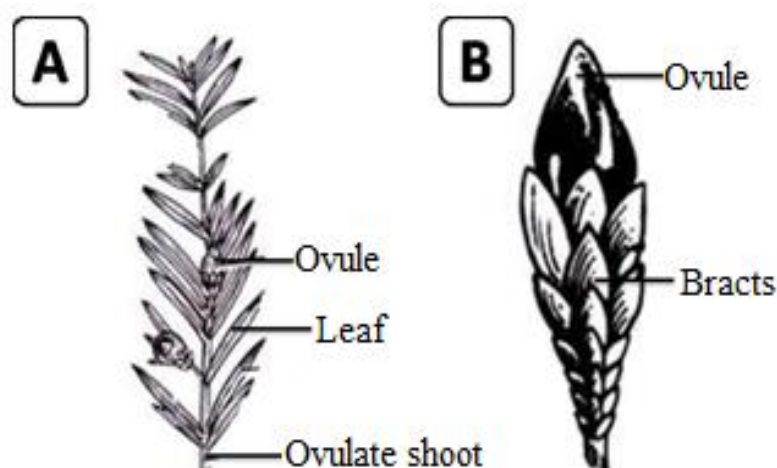


Fig.9.9: A- An ovulate shoot of *T. baccata*, B- Female strobilus with terminal ovule

**Male gametophyte:** Microspore develops into a male gametophyte. At the time of shedding or dispersal it is uninucleate, Microspores are carried away by wind, few microspores reach up to the micropyle, where they are caught into pollination drop. Microspores are then taken up to the nucellus where germination occurs. During germination, the microspore nucleus divides to form a tube cell and a generative cell. The exine gets ruptured and the intine protudes out to form a pollen tube. The tube nucleus moves towards the tip of the pollen tube. The generative cell divides into a stalk cell and a body cell. Body cell later divides to form two unequal male gametes.

**Female Gametophyte:** The functional megaspore develops into the female gametophyte. It enlarges in size and its nucleus divides by many free-nuclear divisions to form about 256 nuclei. A central vacuole develops after which free nuclei become parietal in position. Centripetal wall formation starts later on due to which the whole of the tissue ultimately becomes cellular. Certain archegonial initials are differentiated towards the micropylar end of the cellular female gametophyte. Each archegonium contains 2 to 4 neck cells with a large venter containing an egg nucleus. Venter canal cell is absent. The cytoplasm of egg cell contains small and large cytoplasmic inclusions, a zone of mitochondria and lipid globules.

**Fertilization and Embryogeny:** Fusion of functional male nucleus (larger one) and the egg nucleus occurs to form a zygote. The tip of the pollen tube present near the neck of the archegonium, bursts, both the male gametes, along with stalk nucleus and tube nucleus, are liberated into archegonial venter after which fertilization occurs. As already stated the remaining three nuclei (stalk nucleus, tube nucleus, smaller male cell) degenerate. Because there are several archegonia present in female gametophyte, many eggs may be fertilized, which results in simple polyembryony. However, only one embryo attains maturity to form one embryo. The zygotic nucleus divides to form 16 to 32 nuclei. Only 16 free-nuclei are formed in *Taxus baccata* according to Sterling (1948). After division, cell formation begins and the entire structure becomes cellular. Some of the cells present at the tip of this pro-embryo develop into embryo while the cells above it elongate to suspensor. Complete endosperm is absorbed by developing embryo; hence the seed is non-endospermic. Mature embryo is dicotyledonous.

**Seed:** Seed coat is three-layered. The outermost layer is thin, brown and detaches soon, middle layer is hard and stony and the innermost layer is fleshy. The mature seeds are covered by a red coloured aril. The aril serves to attract birds and help in seed dispersal. The germination is hypogeal.

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## 9.5 EPHEDRALES

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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.

### *Ephedra*

1. The vegetative plant body is represented by roots, stem and leaves and exhibit xerophytic characters.
2. Shrubby plant body usually remains less than two meters in height in most of the species. *Ephedra compacta* attains 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.9.10).
5. Branches are green and photosynthetic.
6. The leaves are small, scaly and rudimentary. They are present in opposite and decussate manner, or in 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.

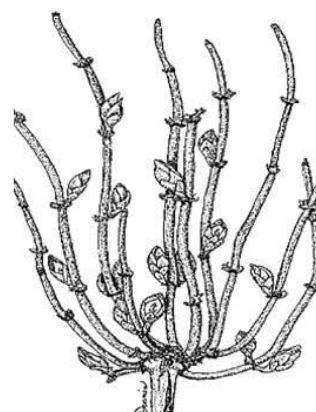


Fig. 9.10 Images of *Ephedra viridis* and *E. coryi*

## Anatomy

**Leaf:** T.S of 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 tissue are present. Major remaining part of the scaly leaf is filled with cells of spongy parenchyma (Fig.9.11). 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.9.11).

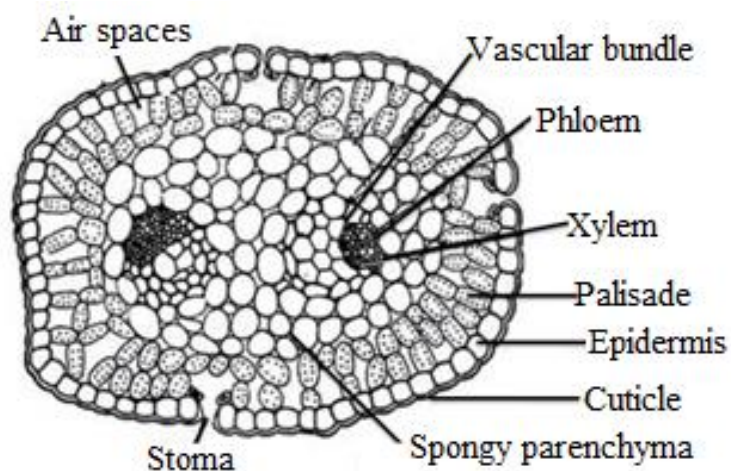


Fig.9.11. L. S. of leaf of *Ephedra*

**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 clearly 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.9.12A).

Secondary growth occurs due to vascular cambium present in between primary xylem and phloem. When a complete ring of cambium is formed, it cuts secondary phloem towards outer side and secondary xylem towards inner side. Formation of distinct annual rings occurs due to varied activity of cambium in different seasons. Secondary xylem is made of vessels, tracheids 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. Largest vessels are formed in spring but the size eventually decreases in the later part of the season. The bordered pits some time become simple perforations as they may lose the torus and border of the pits (Fig.9.12 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 on 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.

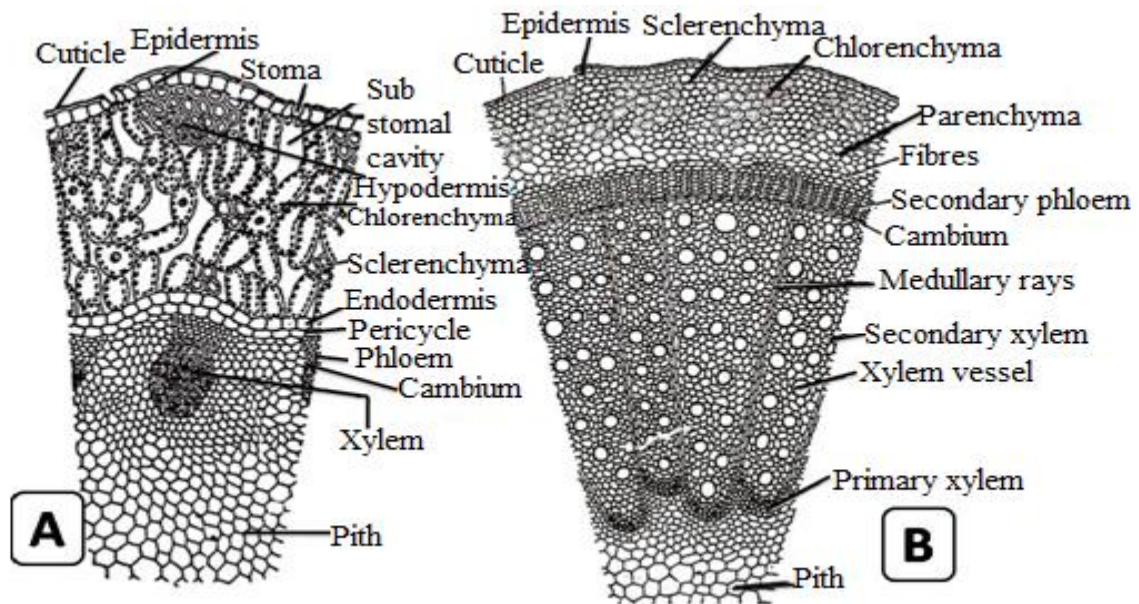


Fig.9.12: Stem of Ephedra, A- T S of young stem, B- T S of old stem

**Male strobilus:** Male strobilus is round or ovoid compound structure which arises in clusters at the node of the branches (Fig.9.13A). 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.9.13B). The stalk continues into a short axis or microsporangiphore which bears terminally located about two to eight or even more microsporangia. Microsporangia are sessile and are bilocular or trilocular (Fig.9.13C).

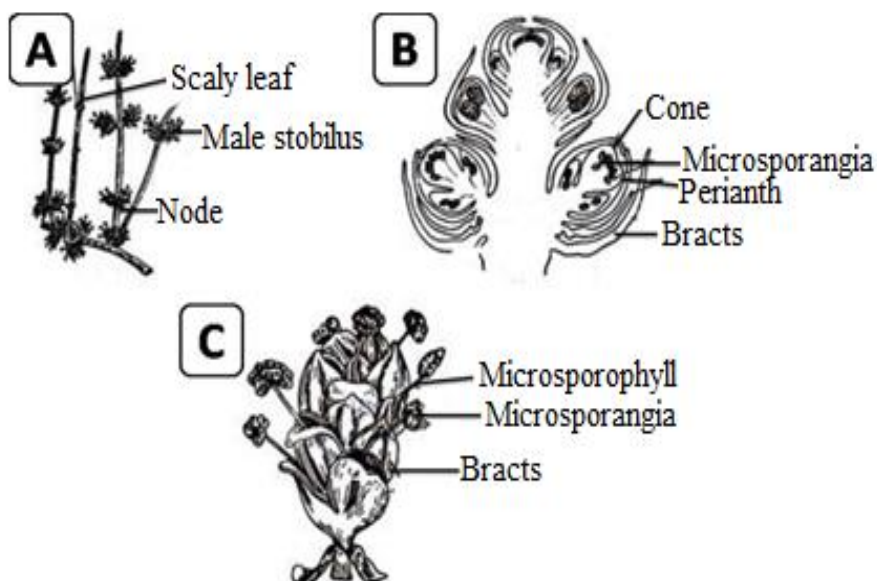


Fig.9.13 A-Shoot of Ephedra with male strobili, B- L.S. of Male strobilus, C- Complete male strobilus

**Development of Microsporangium:** 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 tapetum (one cell thick). However, Singh and Maheshwari (1962) have reported primary wall layer to function directly as 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.9.14). The latter divide meiotically to form spore tetrads. The haploid microspores later on get separated. Rarely, the spores are arranged iso-bilaterally.

**Male Gametophyte:** The microspore is the first cell of male gametophyte. Microspore is wingless, inaperturate and contains a thick exine. Germination of microspore begins within the microsporangium, 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.

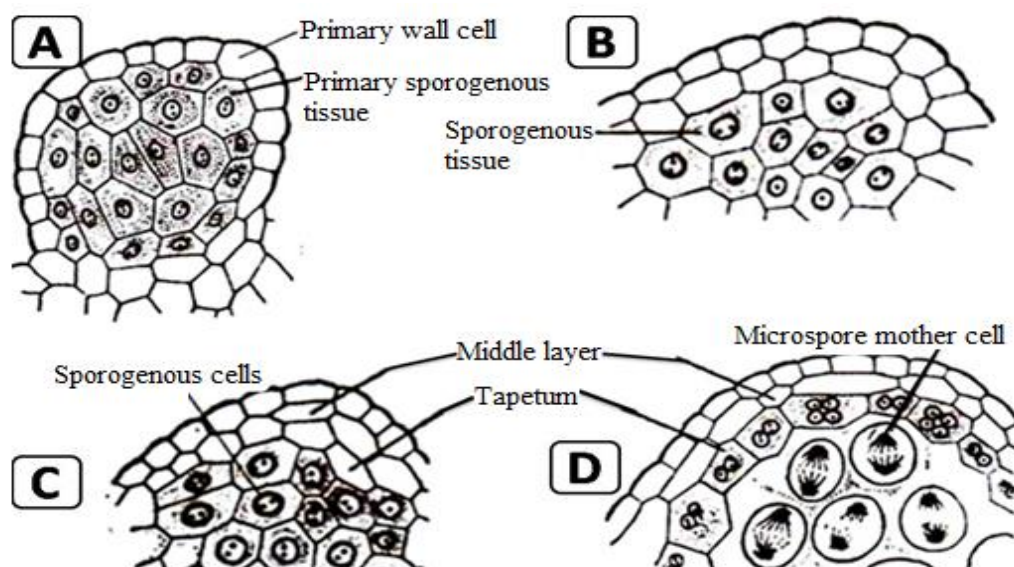


Fig.9.14 Different stages during microsporogenesis in *Ephedra*

**Female or megasporangiate strobilus:** Female strobili arise in pairs at nodes, in the axil of leaves. Sometimes 3-4 strobili 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.9.15A). Lower bracts are sterile while upper two bracts bear an ovule in the axil of each bract. Ovule has a short stalk and this stalk with ovule is known as female flower (Fig.9.15 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. 9.15 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 comparatively 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 2 archegonia but the number varies from 1-3. An archegonial initial is differentiated in the upper reproductive region of female gametophyte. Archegonial initial divides periclinally 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 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 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 embryony:** During the process of fertilization, pollen tube penetrates into archegonium and releases its contents into the egg cytoplasm. One out of two male nuclei fuses with the egg nucleus and forms 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

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.

**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.

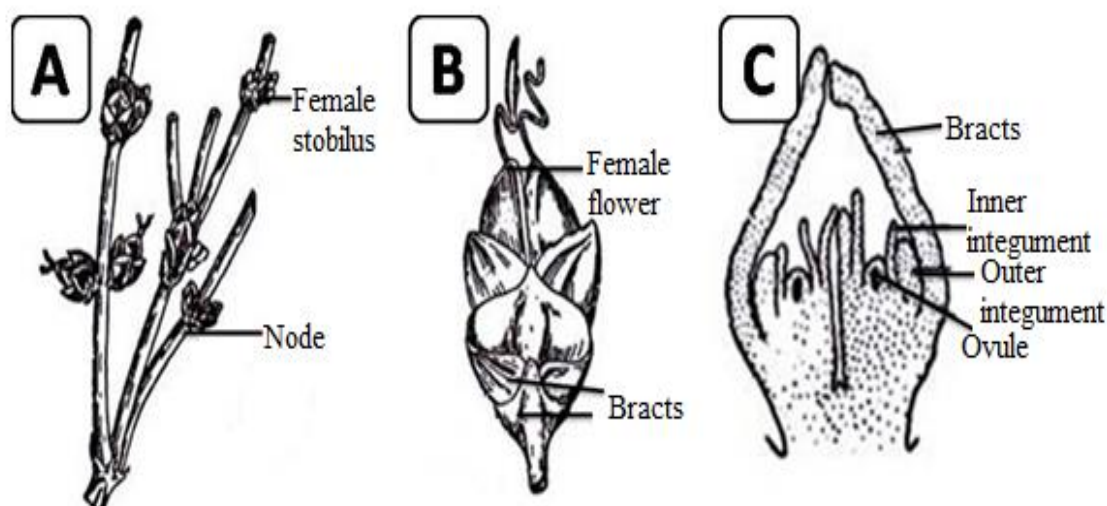


Fig.9.15 *Ephedra* female strobilus, A- Ovulate shoots, B- Female strobilus, C- L S of ovule

## 9.6 WELWITSCHIALES

The order has single family Welwitschiaceae which is represented by genus *Welwitschia* having single species *Welwitschia bainesii*. The plant has a restricted distribution and the plant is found in narrow coastal belt of South West Africa, a region where rainfall is extremely scanty. The plant represents an extreme xerophytes and usually grows on sand, on bare rocks, rocky beds of streams (which are almost dry). The successful survival of plant in such adverse dry conditions is attributed to the presence of well developed tap root system. Austrian physician and botanist Dr. Friederich Welwitsch discovered *Welwitschia* in 1859 from African country Angola. Hence the genus was named in honour of Dr. Welwitsch.



## *Welwitschia*

1. *Welwitschia* is considered one of the most bizarre or strange plant because the plant appears like a gigantic wooden radish or turnip.
2. *Welwitschia* plants have a very long life, sometimes as long as 1000 years or even more.
3. Major part of its stem remains buried in the sandy soil and the exposed part of the stem consists of a well-developed, woody concave disc bearing two very large, up to 2 meters long, strap-shaped leaves (Fig.9.16).
4. Both the leaves are thick, leathery and opposite, with parallel veins and grow continuously from a basal meristem.
5. Three pairs of foliage organs are produced during the entire life of the plant. First is a pair of cotyledons that are short lived, second is a pair of large leaves and third is two leaf promordia.
6. Leaf promordia form scaly bodies which are regarded as buds by some workers and cones by others.
7. Leaves stand erect in young plants but they grow along the substratum in old plants.
8. Young leaves are entire but as they grow old they split along their length.
9. The region of split becomes corky so as to prevent any damage to the plant due to split.
10. Portion of the stem above the leaves is called as crown and the part of stem below the leaves is called stock (Fig.9.16A).

## **Anatomy**

**Leaf:** Leaves are characterized by the presence of thick cuticle on lower and upper epidermis. Below the epidermis (on both sides) is present palisade tissue alternating with sclerenchymatous patches. Space between palisade layers is filled with spongy tissue. Sclereids or spicular cells are also present in the spongy tissue. The stomata are syndetocheilic. Row of collateral vascular bundles are present with their xylem facing towards upper epidermis and phloem towards lower epidermis. Vascular bundles are surrounded by transfusion tissue and a fibrous cap formed by thick-walled cells is present on both the ends of vascular bundles (Fig.9.16 C).

**Stem:** Upper surface of stem is covered by a thick and ridged corky layer. A ring of conjoint, collateral, open, endarch vascular bundles is present in the young stem it also contains a centrally located distinct pith. Cortex and pith contains thick-walled spicular cells which are encrusted with calcium oxalate crystals. Older stems contain a saucer-shaped mass, from which arises vascular traces which are given out to the leaves, tap root and inflorescences. Primary cambium is short lived, it becomes functionless after producing ring of secondary phloem and xylem. Later rings of cambium appear outside primary ring and forms successive incomplete rings of secondary vascular bundle separated by medullary rays (Fig.9.17). Cork cambium is subepidermal in position and it cuts off thick layer of cork. Hence the secondary wood is polycyclic. Stem also contains vessels which consist of about a dozen cells which are present in the form of coiled, worm-like masses. Tracheary elements which develop early

have circular bordered pits. Vessels contain singly occurring pores present on end walls and lateral walls. Pores can be either transversely or obliquely oriented. In few cases vessels contain pores in pairs and rarely a foraminated plate having three pores may also occur. In later formed xylem elements walls become thick and contain ramiform system of bordered pits. Xylem parenchyma is abundant. Phloem is made up of sieve cells and phloem parenchyma. Each sieve cell possesses a prominent nucleus.

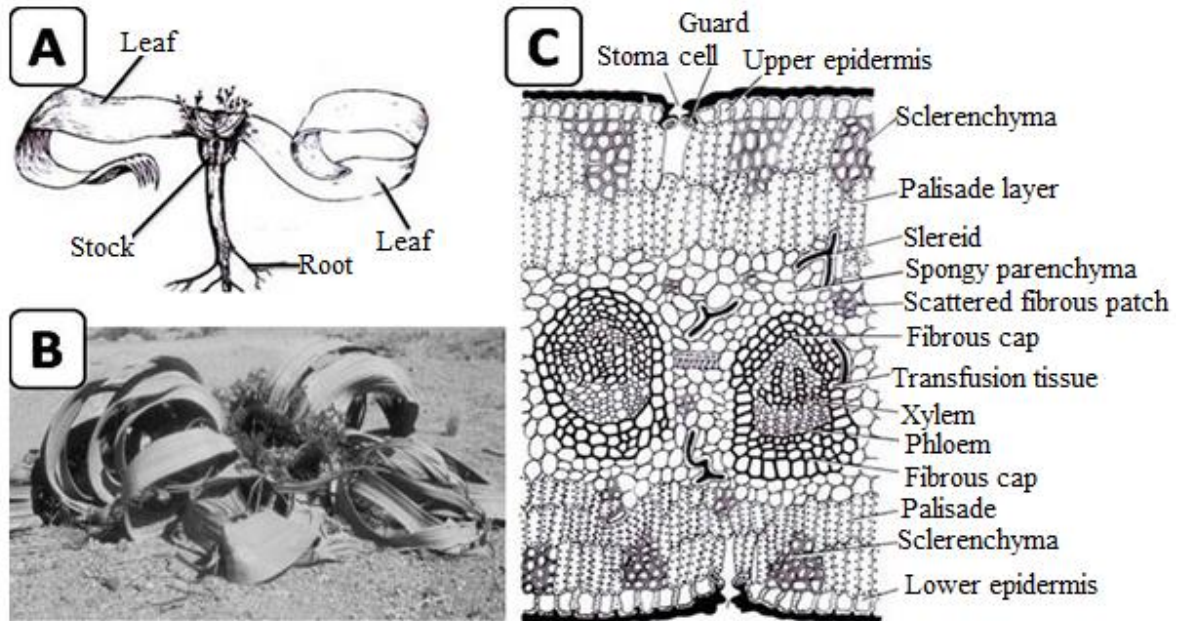


Fig.9.16: A & B- Plant of *Welwitschia bainesii*, C- A portion of T.S. of leaf of *Welwitschia*

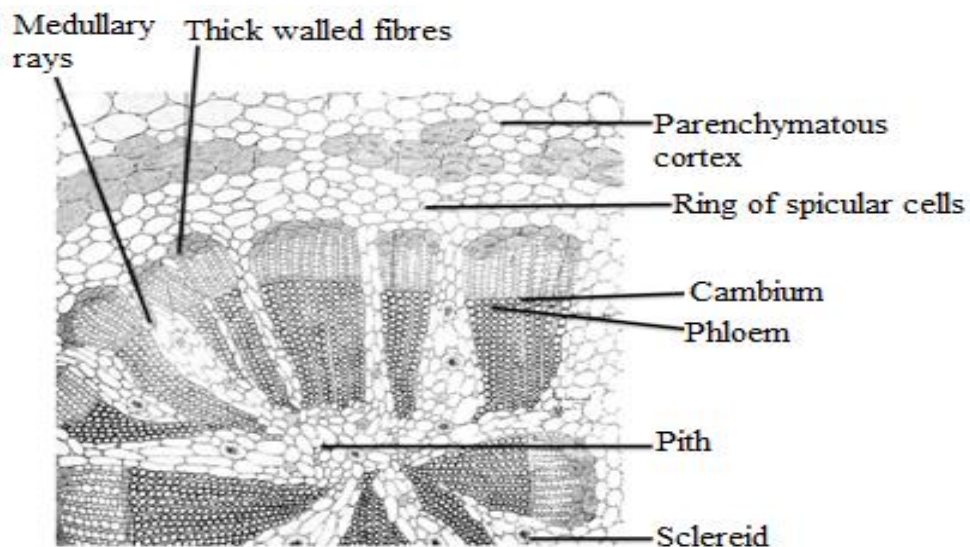


Fig.9.17 T.S. of young stem of *Welwitschia bainesii*

## Reproduction

*Welwitschia* is dioecious. Development of inflorescences occurs from series of several transverse ridges which arise parallel to the leaf bases. Branching in inflorescences is dichasial with each branch ending in a cone. Each cone possesses several bracts (or cone

scales) which are arranged in opposite decussate manner. Cones have an attractive appearance due to crimson or scarlet colour of mature cones.

**Male Strobilus and male flower:** Microsporangiate strobilus or male cone is a compound structure having a quadrangular cone axis. Male cone possesses several bracts (also called cone scales) which are arranged in opposite decussate manner. Each male flower is present in the axil of each subtending bract. Each male flower possesses two lateral bracts. Male flower also contains perianth which is formed from two bract-like anterior-posteriorly placed structures. Inner to the perianth is present a whorl of six micro-sporangiophores which remain fused at the base to form a cup-like structure. At the top of each micro-sporangiophore is present a synangium. Each synangium is formed by the fusion of three microsporangia (Fig.9.18A-B). Each microsporangium contains many pollen grains which are shed through a vertical slit. Pollination is affected either by wind or by insects.

**Male gametophyte:** Pollen grain matures to form a three-celled male gametophyte but there is not much information about the process of development of male gametophyte. This 3-celled stage includes a tube nucleus, a sterile cell and a spermatogenous cell. The sterile cell usually gets aborted even before pollination. The spermatogenous cell gives rise to two male nuclei or sperm nuclei. Bomman (1972) have reported *Welwitschia* to be wind pollinated and Van Jaarsveld (1990) opined it to be insect pollinated.

**Female Strobilus and Female Flower:** The female strobilus, known as ovulate or megasporangiate strobilus or ovuliferous cone is a compound structure as seen in male strobilus. Several decussate bracts or cone scales are present on axis of female strobilus. In the axil of bract is present a female flower. Inside the subtending bract of each female flower are present two small lateral bracts, two envelopes and a single nucellus. The inner envelope functions as a true integument and prolongs in the form of a long tubular micropyle and the outer envelope develops from two posterior-anterior primordia which fuse with each other in the early stages of the development. This fusion product is also called as perianth which expands into a broad wing-like like structure in the mature seed (Fig.9.18 D-E).

**Female Gametophyte:** A single megaspore mother cell develops deep in the nucellar tissue. Diploid nucleus of megaspore mother cell undergoes meiosis, but no cross-wall formation occurs. Also, linear tetrad is not formed, and development of tetrasporic female prothallus occurs directly. Haploid nuclei of young female gametophyte divide and redivide several times mitotically but again no cross-wall formation occurs. These divisions result in formation of thousands of free-nuclei. Now formation of cell wall begins irregularly, and each cell contains varying number of nuclei. In many cells the nuclei fuse to form polyploids (Fig.9.18 E-F). Formation of archegonia has not been reported in *Welwitschia*.

**Fertilization:** Process of fertilization begins with elongation of pollen tubes which grow downwards through the nucellus. Simultaneously the apical cells of female pro-thallus also elongate and form prothallial tubes which grow upwards. Hence, pollen tube and prothallial tube grow in opposite directions come in contact near nucellar cap. Walls between the two tubes get dissolved, male and female nuclei fuse to form a fusion nucleus. It should be noted

that fertilization occurs in the pollen tube and not in archegonium or embryo-sac. Diploid zygotic nucleus divides to form a 2-celled pro-embryo. Upper cells of this pro-embryo develop into a primary suspensor and the lower cell of proembryo divides to form a large number of secondary suspensor cells and a multicellular embryo. *Welwitschia* exhibits polyembryony since many zygotes and young embryos are formed. However, only one embryo matures to form a seed. Germination is epigeal the two permanent leaves appear soon after germination. Cotyledons grow for about six months and finally die. The somatic number of chromosomes in *Welwitschia* is 42.

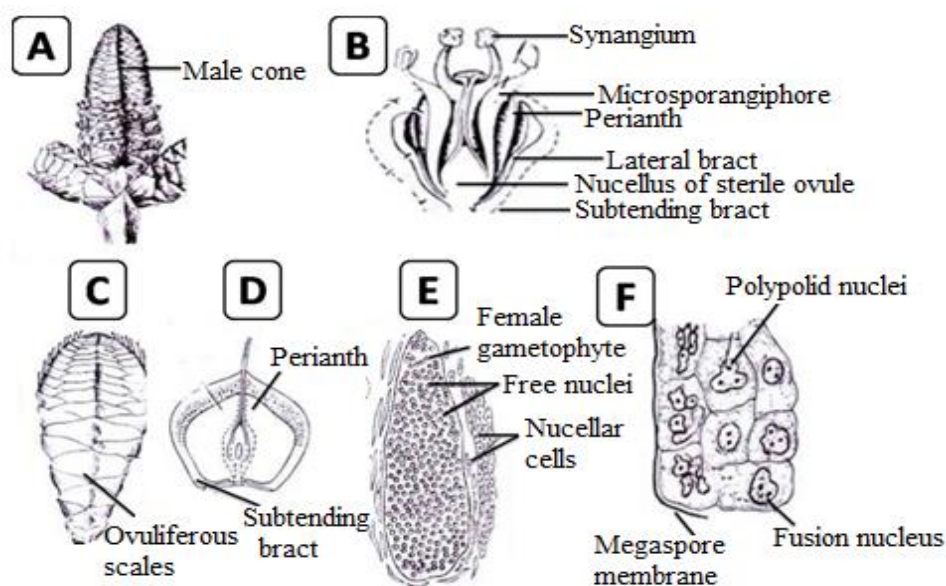


Fig.9.18: Reproductive structures A- Male cone, B- Longitudinal section of male flower, C- Female cone, D- Female flower, E- Free nuclear stage of female gametophyte, F- Wall and polyloid nuclei formation

## 9.7 GNETALES

Order includes single family Gnetaceae having Genus *Gnetum* which includes about 30 -35 species which comprises of woody trees, shrubs and climbers. *Gnetum* species are dioecious and mostly found in rain forests. In India five species are found which includes *G. contractum* which is a scandant shrub found in regions of Kerala and Madras, *G. gnemon* which is a tree and has six varieties out of which two are found in India, *G. montanum* which is a woody climber and distributed in regions of Sikkim, Orissa, Assam, China and Siam, *G. latifolium* has five varieties all of which are woody climbers and *G. ula* is also a woody climber found in various parts of India.

### *Gnetum*

#### Anatomy

**Stem:** In transverse section young stems appears to be roughly circular in outline and are quite similar to a typical dicotyledonous stem. A single layered epidermis is present which

consists of rectangular cells. Some cells of epidermis show papillate outgrowths. Stomata are sunken. Cortex consists of three regions, outer region is chlorenchymatous which is 5-7 cells thick, middle one is parenchymatous region of few cells thick and innermost region is sclerenchymatous which is 2-4 cells thick. Endodermis and pericycle regions are not very clearly distinguishable. Young stem contains several vascular bundles which are arranged in ring (Fig.9.20A). These vascular bundles are conjoint, collateral, open and endarch. Xylem contains both tracheids and vessels. Protoxylem elements are spiral or annular while the metaxylem shows bordered pits which are circular in outline. The phloem consists of sieve cells and phloem parenchyma. Pith is extensive and consists of polygonal and parenchymatous cells.



*Fig.9.19 Gnetum plant*

Secondary growth is observed in old stems of *Gnetum*. The primary cambium is ephemeral, i.e., short-lived. The secondary cambium in different parts of cortex develops in the form of successive rings. The first cambium cuts off secondary xylem towards inside and secondary phloem towards outside. This cambium ceases to function after some time. Another cambium ring gets differentiated along the outermost secondary phloem region, and the same process is repeated (Fig.9.20B). During later stages, excess amount of secondary xylem is produced on one side and comparatively less on the other side due to which formation of eccentric rings of xylem and phloem occurs in the wood. (Such wood is the characteristic feature of angiospermic lianes. Periderm is thin contains lenticels and develops from the region of outer cortex. The cortex also contains chlorenchymatous and parenchymatous tissues and many sclereids. Secondary wood of older stems consists of tracheids and vessels. Tracheids contain bordered pits present on radial walls whereas vessels are characterized by presence of simple pits. Wood xylem and medullary rays can be clearly seen in tangential longitudinal section of stem. . Bordered pits are present on radial as well as tangential walls. Medullary rays consist of polygonal parenchymatous cells and can be either uniseriate or multiseriate. Sieve cells of the phloem contain oblique and perforated sieve plates.

**Leaf:** Leaves of *Gnetum* are bifacial or dorsiventral and show resemblance with a dicot leaf. Upper and lower epidermis is covered with cuticle. Cuticle is thin on lower surface as compared to cuticle present on upper epidermis. Stomata are syndetocheilic and are

distributed all over the lower epidermis except the region of midrib and veins. Maheshwari and Vasil reported stomata in *G. gnemon* and *G. ula* to be haplocheilic. Mesophyll is differentiated into a single-layered palisade and spongy parenchyma. Palaside layer is full of chloroplast. Spongy parenchyma contains loosely-packed lobed cells which contain chloroplast, stellately branched sclereids which have thick and lignified walls, stone cells and latex tubes scattered in midrib region. In the midrib region are present several vascular bundles either in form of an arch or curve. Vascular bundles are conjoint and collateral. The xylem of each vascular bundle faces towards the upper surface and is made up of tracheids, vessels and xylem parenchyma. Phloem faces towards the lower surface and consists of sieve cells and phloem parenchyma (Fig.9.21).

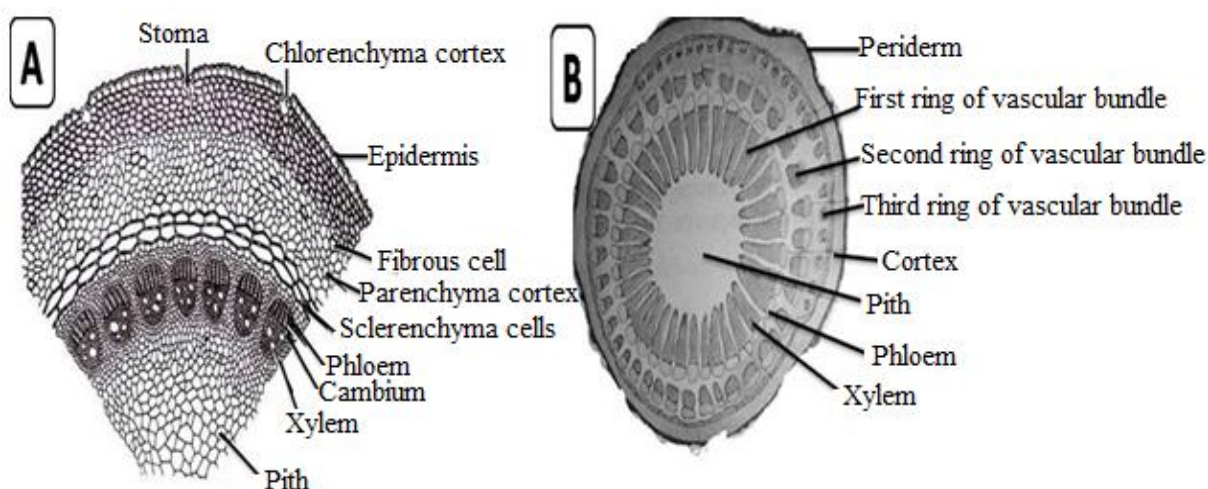


Fig.9.20: *Gnetum*: A- T.S. of young stem, B- T S of old stem

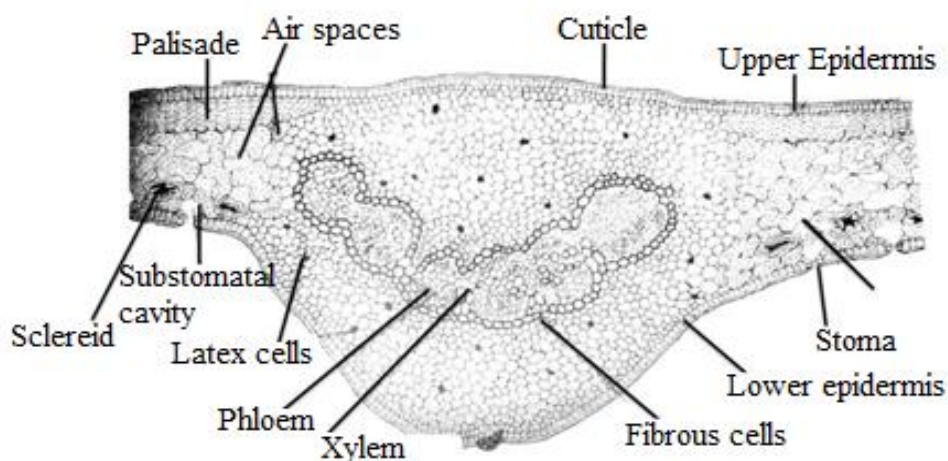


Fig.9.21: T.S. of leaf of *Gnetum*

**Root:** In young roots cortex is made up of several layers of parenchymatous cells. These cells are polygonal in outline and contain starch grains. Among the cortex cells are present groups of sclerenchymatous cells. A distinct endodermis with casparian strips is present. Cells of endodermis also contain starch grains. Pericycle consists of 4-6 layers of parenchymatous

cells. Vascular bundles are diarch and exarch. Primary xylem consists of fewer elements and its identity is lost after secondary growth.

Roots exhibit normal secondary growth and a cambial arc is formed which is internal to phloem and external to xylem. Secondary xylem consists of tracheids, vessels and xylem parenchyma. The tracheids are elongated cells having tapering ends and possess uniseriate bordered pits (present on radial and tangential walls) along with bars of Sanio. Vessels contain simple or small multiseriate bordered pits. Bars of Sanio are absent in vessels. Phloem consists of sieve cells and phloem parenchyma. Parenchyma cells are living and have walls (thick or thin) with simple pits. Parenchyma cells form rows which alternate with those of sieve cells. Secondary medullary rays are multiseriate and made up of thin walled cells due to which wood of roots is soft (Fig.9.22 A-B).

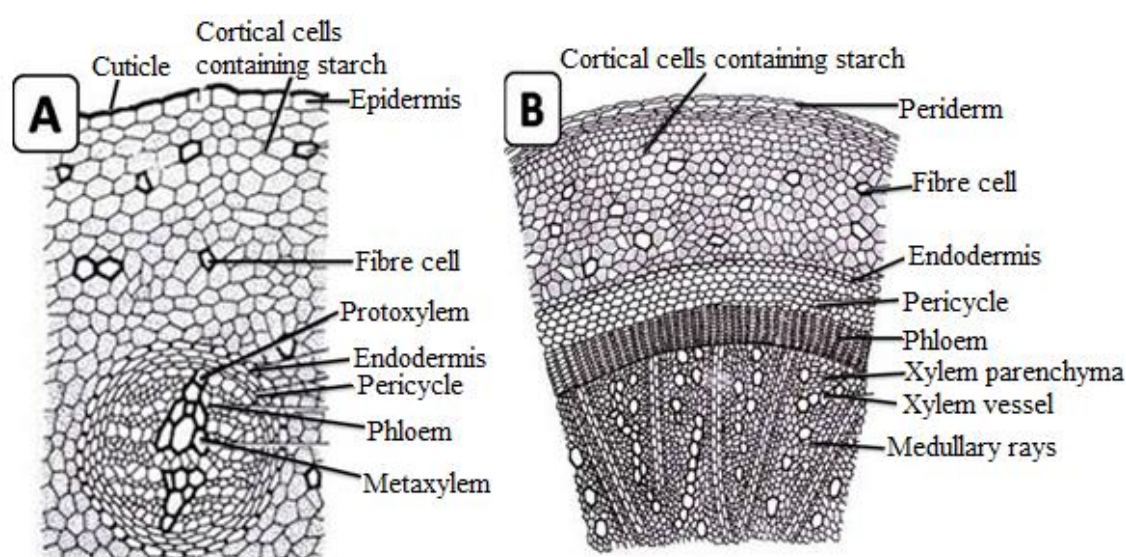


Fig.9.22: *Gnetum*, A- T. S. of young root, B- T. S. of old root

## Reproduction

*Gnetum* is dioecious. Reproductive organs are arranged into cones or strobili. These strobili are further organized into inflorescences. Cones arise in axils of paired and decussate scale leaves. These leaves are fused at base to form boat shaped structure. These are called as bracts. Bracts bear accessory or axillary buds which may also develop into inflorescence.

**Male strobili and male gametophyte:** Male strobili consist of elongated axis having nodes and internodes. Nodes bear scaly bracts arranged in whorls. Bracts fuse to form a cup shaped structure called as cupule or collar. Each node of axis has a collar and above each collar are present 2-6 rings of male flowers and every ring contains a number of male flowers arranged alternately in rings (Fig. 9.23A). Above rings of male flowers is present a ring of abortive female flower or ovules. In *G. africanum* the cone can be bisexual as in this case ovule in the ring becomes fertile.

Male cones are compact and enveloped within bracts. Due to elongation of internodes collar separate from one another. Collars contain sclereids of different shape and size and laticiferous tubes. Each male flower is enclosed within perianth. It contains a stalk and on apex of stalk two anthers are present (Fig.9.23B). Each anther possesses single locule or microsporangium. At the time of maturity (before dehiscence) stalk elongates and emerges out of perianth, as a result of which anthers and stalk become visible. Male flowers are interspersed with uniseriate and multicellular hairs.

Cells present below collar become meristematic and divide to form an annular outgrowth (below collar). Upper cells of this outgrowth differentiate to form initials of ovule which eventually develop into abortive ovule on uppermost ring. Lower cells of outgrowth also differentiate to form primordia which develops rings of male flowers. Initials of male flower divide to form a centrally located cushion of cells which is surrounded by a cellular sheath (which develops into perianth having a slit). The central mass formed deepens and is differentiated into two lobes which develop into anther. From lower cells of central mass is formed a stalk and due to elongation of this stalk, upper part is pushed out through the slit (in perianth). Differentiation of male flowers is basipetalous. A microsporangium develops in each anther. Each anther lobe is surrounded by wall layers. The innermost layer which encloses a sporogenous tissue is called tapetum. Sporogenous cells become loose and known as spore mother cells. These cells undergo meiosis to form spore tetrads.

Male gametophyte is represented by microspore or pollen grain, which is spherical in shape, uninucleate and enveloped by thick and spiny exine and thin intine (Fig. 9.23C). It is wingless and is released at three nucleate stages. Nucleus of microspore divides into two daughter nuclei which are either present free in cytoplasm or a plate is formed between them. One of the nuclei again divides and hence there are present three nuclei which have been named as prothallial nucleus, generative nucleus and tube nucleus. After the release of pollen further development occurs in pollen chamber. Exine gets ruptured and intine grows to form a pollen tube. The tube nucleus is first to move into the pollen tube. Generative nucleus gets surrounded by a membrane and forms generative cell. It also migrates into pollen tube and divides to form two unequal male gametes. Prothallial nucleus never enters pollen tube and it rather disappears before pollen tube is formed. Thomson has however, stated that no such prothallial nucleus is formed in male gametophyte and by first division only tube nucleus and generative cell are formed.

Female strobilus exhibit similarity with male strobili except that in female strobilus only a single ring of 4-10 ovules is present above collar (Fig. 9.24A-B). At younger stages male and female cones cannot be morphologically distinguished, they can only be differentiated when ovules grow and project beyond the collar. Only few ovules attain maturity and rest of them fall down. Ovules contain a centrally located nucellus which contains female gametophyte and is surrounded by three envelopes. Outermost envelope is perianth, middle one is known as outer integument and innermost envelope is called inner integument. The outer two envelopes contain stomata, sclereids and laticiferous ducts. Perianth is thick and fleshy. The



innermost third envelope is fused with the nucellus at the base while its upper portion remains free and forms micropylar tube. The micropylar canal gets closed after pollination.

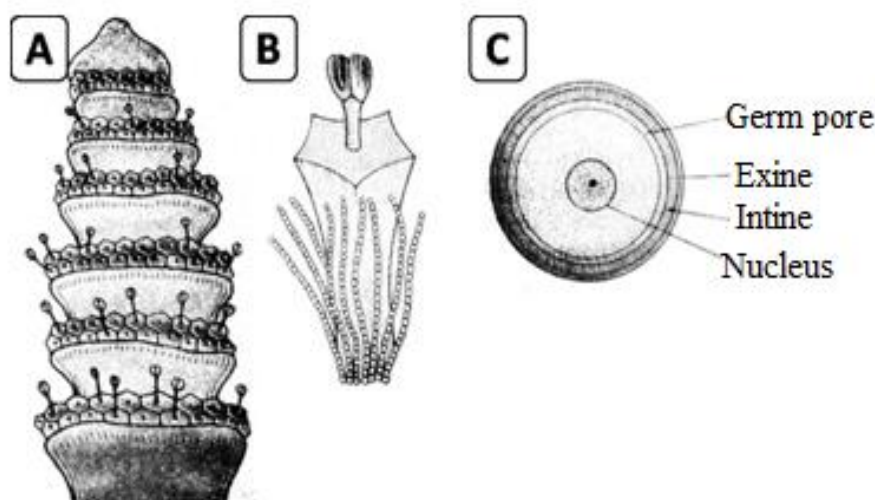


Fig.9.23: *Gnetum ula*, A- Male cone, B- Single male flower, C-Structure of microspore Female strobilus

In the young conditions, an outer epidermal layer can be distinguished in the nucellus. Two to four archesporial cells which develop below epidermis at a later stage divide periclinally to form outer primary parietal cells and inner sporogenous cells. The sporogenous cells divide to form megaspore mother cells. Female gametophyte shows tetrasporic development and 256-1500 free nuclei are formed. Free nuclei get dispersed around central vacuole. *Gnetum* lacks archegonia. One to two nuclei at micropylar end act as egg nuclei. Cells of nucellus of female gametophyte divides to form a tissue called as pavement tissue. The tissue consists of several rows, the tissue however, later gets absorbed. Nucellar cells are rich in starch. Nucellus gets completely absorbed by growing gametophyte except for a small portion from which develops cuticle.

Pollination is mediated by wind. The micropylar tube secretes a fluid in which pollen grains get entangled and finally reach up to the pollen chamber. During fertilization, the pollen tube pierces through membrane of female gametophyte, tip of pollen tube bursts and the male cells are released. One of the male cells enters the egg cell. The male and female nuclei fuse to form zygote.

**Endosperm:** Lower part of gametophyte becomes cellular before fertilization while upper part becomes cellular after fertilization. Zygote is surrounded by cells at different stages of its development into embryo. Female gametophyte after fertilization is known as endosperm in Gymnosperms and usually it is a haploid tissue (contrary to triploid in Angiosperms). But in case of *Gnetum* a peculiar feature of endosperm is that its cells become multinucleate and the nuclei may fuse to form polyploid cells. In some cells two nuclei may fuse and in other more nuclei may fuse, the ploidy level varies from haploid (n) to polyploid (upto 12n).

Gametophyte in *Gnetum* shows variations from other gymnosperms in the following aspects:

- Gametophyte becomes partially cellular before fertilization and cell formation is completed after fertilization. In some species gametophyte may be free nuclear before fertilization.
- Cells are multinucleate and show graded ploidy.
- Since archegonium is absent free nuclei or specialized cells act as eggs.
- Tetrasporic development in gametophyte.

**Seed:** Thoday (1911) has described the structure of seed of *G. africanum* and *G. ula*. The seed contains three envelopes (Fig. 9.25A-B) as described below:

Envelope	Features
Outer envelope	Green in colour, succulent, free from other envelope, made up of parenchymatous cells, contains sclereids and fibers, epidermis punctured by stomata.
Middle layer	Stony layer, main functions to provide protection, stomata, sclereids, fibres, latex tubes present. Palisade like cells present below epidermis,
Inner layer	Made up of parenchymatous cells, lacks stomata, sclereids and laticifers. This layer forms micropylar tube.

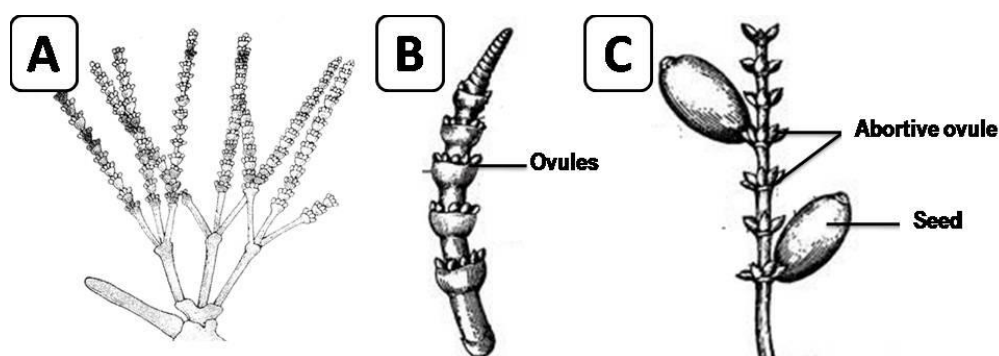


Fig.9.24: *Gnetum latifolium*, A- Branch with female cones, B-Mature female inflorescence, C- Female inflorescence with seeds

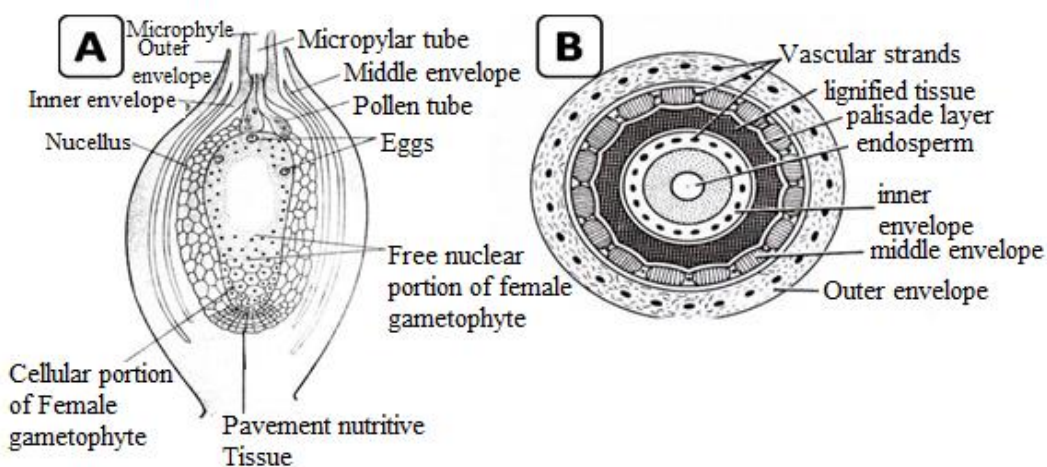


Fig.9.25: *Gnetum*, A- L. S. of ovule, B- T. S. of seed

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## 9.8 SUMMARY

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1. Coniferales include extinct forms and living gymnosperms.
2. They are usually monoecious with distinct male and female cones.
3. Their growth habit varies from extremely tall trees to miniature forms.
4. Stems contain small pith and the secondary wood is pycnoxylic.
5. Leaves are of two types, i.e. foliage leaves and scaly leaves.
6. Pollination is anemophyllous
7. Seeds are endospermic and winged
8. *Taxus baccata* is an evergreen tree and is found in North and South America, Europe and Philippines, Algeria, Morocco and India.
9. *T. baccata* possesses a huge trunk and all branches exhibit unlimited growth.
10. Leaves are linear, small (2-3 cm long), spirally arranged and shortly stalked
11. Well- developed tap-root system is present.
12. Young stem shows a ring of conjoint, collateral, open and endarch vascular bundles
13. *Taxus* is usually dioecious, however monoecious trees have also been reported
14. The female strobili in *Taxus* are greatly reduced and male strobili are yellow coloured which develop in axil of foliage leaves.
15. Pollen chamber and nucellar beak are absent in *Taxus*.
16. Family Ephedraceae is represented by a single genus *Ephedra*
17. *Ephedra* is uniformly distributed in regions of Western as well as Southern hemispheres
18. The leaves are small, scaly and rudimentary, branches are green and photosynthetic.
19. Underground tap root system is present having long and branched and deep roots
20. Secondary growth in stems occurs due to activity of vascular cambium.
21. *Ephedra* is dioecious, (*E. foliata*, is monoecious) and exhibits heterosporous condition.
22. Microsporangia are sessile about 2-8 in number and are bilocular or trilocular.
23. Generally *Ephedra* contains 2 archegonia but the number varies from 1-3.
24. Since more than one embryo is formed, hence *Ephedra* represents polyembryony.
25. Seed germination occurs without any resting period and is of epigeal type.
26. Family Welwitschiaceae is represented by single species *Welwitschia bainesii*
27. *Welwitschia* plants have a very long life, sometimes as long as 1000 years or even more
28. Portion of the stem above the leaves are called as crown and the part of stem below the leaves is called stock.
29. Cones have an attractive appearance due to crimson or scarlet colour of mature cones.
30. Microsporangiate strobilus is a compound structure having a quadrangular cone axis.
31. *Gnetum* includes about 30 -35 species which comprises of woody trees, shrubs and climbers.
32. Secondary growth is observed in old stems of *Gnetum*
33. Leaves of *Gnetum* are bifacial or dorsiventral and show resemblance with a dicot leaf.
34. *Gnetum* is dioecious and reproductive organs are arranged into cones or strobili.

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## 9.9 GLOSSARY

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**Albuminous cells:** It is one of the parenchyma cells adjacent to the sieve cells in gymnosperm wood, distinguished by staining deeply with cytoplasmic stains, and apparently associated physiologically with the sieve cells and joined to them by sieve areas.

**Epigeal germination:** When the cotyledons are brought above the ground due to the elongation of hypocotyl.

**Haplocheilic stomata:** When guard cells and the subsidiary cells are derived from different initials.

**Mycorrhiza:** A mycorrhiza is a symbiotic association between a fungus and the roots of higher plants.

**Oospore:** The thick-walled zygote formed by fertilization of an oosphere.

**Ornamental plants:** Plants that are grown for decorative purposes in gardens and landscape design projects, as *houseplants*.

**Perianth:** The perianth is the non-reproductive part of the flower, and structure that forms an envelope surrounding the sexual organs.

**Pericycle:** A thin layer of plant tissue between the endodermis and the phloem.

**Polyembryony:** The formation of more than one embryo in an ovule.

**Siphonostele:** A stele consisting of pith surrounded by concentric layers of xylem and phloem.

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## 9.10 SELF ASSESSMENT QUESTION

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### 9.10.1 Choose the most appropriate option:

- Fertilization in *Welwitschia* occurs in
  - Archegonium
  - Pollen tube
  - Ovary
  - Embryo sac
- Roots in *Ephedra* are
  - Tap roots, long branched and lack mycorrhiza
  - Tap roots, long unbranched and lack mycorrhiza
  - Fibrous, long branched with mycorrhiza
  - Fibrous long branched and lack mycorrhiza
- Leaves in *W. bainesii* are
  - Two in number, thick, leathery and opposite
  - Two in number, thin, leathery and opposite
  - Four in number, thick, leathery and opposite
  - Four in number, thin, leathery and parallel
- W. bainesii* are able to survive in xerophytic conditions due to
  - Tap root system
  - Fibrous root system
  - Absence of leaves
  - Both (b) and (c) are correct

5. In stem of *T. baccata* phloem is made up of
  - (a) Sieve cell, sieve plate, phloem parenchyma
  - (b) Sieve cell, companion cell, phloem parenchyma
  - (c) Sieve plate, companion cell, phloem parenchyma
  - (d) Sieve cell, sieve plate, companion cell, phloem parenchyma
6. Pollen grains in *Ephedra* are shed at stage
  - (a) Binucleate
  - (b) Trinucleate
  - (c) Tetranucleate
  - (d) Pentanucleate
7. Which of the following is not true about stomata are *Taxus*
  - (a) Stomata are sunken type
  - (b) They exhibit haplocheilic development
  - (c) Stomata are present only on upper epidermis
  - (d) Stomata are present only on lower epidermis
8. Development of microsporangium in *Ephedra*
  - (a) Leptosporangiate
  - (b) Eusporangiate
  - (c) Both
  - (d) None of these
9. Development of female gametophyte in *Welwitschia* is
  - (a) Monosporic
  - (b) Tetrasporic
  - (c) Trisporic
  - (d) Pentasporic
10. In *Taxus baccata*
  - (a) Branches exhibit limited growth
  - (b) Fibrous root system is present
  - (c) A short slender trunk is present
  - (d) *Taxus baccata* is evergreen tree

### 9.10.2 State whether the following statements are true or false

1. *Welwitschia bainesii* is the only representative of family *Welwitschiaceae*.
2. Many zygotes and embryos are formed in *welwitschia*.
3. *Ephedra* is monoecious.
4. *Welwitschia bainesii* possesses large number of leaves.
5. *Ephedra* exhibits polyembryony.
6. Root system in *Taxus baccata* is fibrous type which is well developed and deeply rooted.
7. Male and female plants of *Taxus* can be differentiated based upon their vegetative growth.
8. There is no vegetative reproduction in *Taxus*.
9. *Welwitschia* appears like a gigantic radish or turnip.
10. *Welwitschia* is strictly monoecious.
11. Transfusion tracheids found in *Pinus* are living cells with thick and lignified walls.
12. Stomata in conifers are sunken and haplocheilic.
13. *Gnetum* lacks archegonia.
14. In conifers female cones replaces short shoots.

15. Pollen grains are shed at 5 celled stages in *Pinus*.

### 9.10.3 Fill in the blanks:

1. Germination in *Welwitschia* is \_\_\_\_\_.
2. *Taxus baccata* is commonly known as \_\_\_\_\_.
3. Seeds of *Taxus baccata* possess \_\_\_\_\_ germination.
4. In *Welwitschia bainesii* stomata are \_\_\_\_\_ type.
5. \_\_\_\_\_ of *Taxus baccata* are deep rooted and highly branched.
6. Pholem in the stem of *Taxus baccata* lacks \_\_\_\_\_ cells.
7. Branches of \_\_\_\_\_ are photosynthetic.
8. \_\_\_\_\_ cells divide to form many microspore mother cells.
9. In *Ephedra* \_\_\_\_\_ occurs through wind.
10. An antibiotic \_\_\_\_\_ is obtained from *Ephedra*.

**9.10.1 Answers Key:** 1-(b), 2-(a), 3-(b), 4-(a), 5-(a), 6-(b), 7-(c), 8-(b), 9-(b), 10-(d)

**9.10.2 Answers key:** 1-T, 2-T, 3-F, 4-F, 5-T, 6-F, 7-F, 8-T, 9-T, 10-F, 11-F, 12-T, 13-T, 14-F, 15- F

**9.10.3 Answers Key:** 1-Epigeal, 2-Yew, 3-epigeal, 4-syndetocheilic, 5-roots, 6-companion, 7-*Ephedra*, 8-sporogenous, 9-pollination, 10-ephederin

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## 9.11 REFERENCES

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## 9.12 SUGGESTED READINGS

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## 9.13 TERMINAL QUESTIONS

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### 9.13.1 Very short answer type questions

- Q1. Name different foliage organs of *Welwitschia*.
- Q2. Define crown and stock with reference to *Welwitschia*.
- Q3. What are cone scales?

- Q4. Mention the function of spermatogenous cell.
- Q5. Mention about distribution of *Ephedra*?
- Q6. What is economic importance of *Ephedra*?
- Q7. How does branching of *T.baccata* differ from *Pinus*?
- Q8. Define aril.
- Q9. What is pavement tissue?
- Q10. What type of distribution of stomata is found in conifers?
- Q11. Define the term rhytidome.
- Q12. Mention about economic importance of conifers.

### 9.13.2 Short answer type questions

- Q1. Enlist morphological features of *Welwitschia*.
- Q2. Write short note on female gametophyte of *Welwitschia*.
- Q3. What are the similarities between *Welwitschia* and *Gnetum*?
- Q4. Mention about external characteristics features of *Ehedra*.
- Q5. Describe about gametophytes of *T. baccata*.
- Q6. Briefly describe about female flower and ovule of *Ephedra*.
- Q7. How does double fertilization occur in *Ephedra*?
- Q8. Draw a well labeled self explanatory diagram of T.S of young stem of *Ephedra*.

### 9.13.3 Long answer type questions

- Q1. With well labeled diagrams describe about anatomy of stem and leaf of *Welwitschia*.
- Q2. Describe about reproductive structures of *Welwitschia*.
- Q3. Discuss anatomy of stem of *Ephedra*.
- Q4. Describe the anatomy of stem and root of *Pinus*.
- Q5. Explain about male and female gametophytes of *Ephedra*.
- Q6. Describe in detail about reproduction in *Taxcus baccata*.
- Q7. Describe in detail about reproductive structures found in *Gentum*.
- Q8. Explain the male and female strobili of conifers.
- Q9. Give a brief outline of different families of conifers.

## **BLOCK-3 PALAEOBOTANY**



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## **UNIT-10-FOSSILS: TYPES, FORMATION AND THEIR PRESERVATION**

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- 10.1 Objectives
- 10.2 Introduction
- 10.3 Fossils
  - 10.3.1 Types of fossils
  - 10.3.2 Formation of fossils
  - 10.3.3 Preservation of fossils
- 10.4 Summary
- 10.5 Glossary
- 10.6 Self assessment questions
- 10.7 References
- 10.8 Suggested readings
- 10.9 Terminal questions

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## ***10.1 OBJECTIVES***

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After reading this unit students will be able to:

- To understand about the Fossils and its Types
- To learn about the Formation of fossils
- To know about the Preservation of Fossils
- Discuss about paleobotany

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## ***10.2 INTRODUCTION***

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For the study of plant life of past million years fossils are studied. The fossil means the remains of organism that lived long long ago. The word 'fossil' is derived from the Latin word "Fossilis" which means "to dig up". In the earlier studies, therefore, a large number of things dug out of earth's crust were called fossils. In fact fossils are impressions or casts of the organism or its parts living some time back but now extinct. Although most of the plants of geological periods were decomposed by decomposers like fungi, bacteria etc. But sometimes under certain circumstances a few of them got buried and they did not decompose. Thus the plant parts found preserved in the sedimentary rocks of different ages. These remains are known as fossils.

The study of fossils of plant is called palaeobotany. The prefix paleo comes from the Greek word 'paleon' which means old, so palaeobotany is the study of the plants that lived long ago. It is one half of a larger branch of science called Paleontology which studies the history of both plant and animal life of the geological past. Paleobotany is restricted to the study of fossil plants alone.

Fossil is any evidence of past life. There are two types of evidences - Direct fossil evidences and indirect fossil evidences. The direct fossil evidence provides information about the material from past organisms in its original form, or sometimes in altered form. The indirect fossil evidence gives information about the chemical fossil i.e. organic signatures of past life, Imprints provide impressions of plant parts, Ichnofossil i.e. trace fossils, foot prints. Indirect evidence also provides information about the presence, behaviour and physiology of plants. First fossil record was found in Silurian period of Palaeozoic era. Spores and cuticles were found in Ordovician period. Angiosperms (flowering plants) evolved during the Mesozoic, and early Cretaceous.

### **Importance of Paleobotany**

The study of fossil plants and the facts derived from them are of great importance as evident from the following:

1. They throw light on phylogeny and evolution of plants. The extinct plants tell us some stages through which existing groups have passed during course of their evolution.

2. Palaeobotanical researches may be helpful in determining similarities and dissimilarities of plants of the past and their habitat.
3. Fossil plants give a historical approach to plant kingdom and helpful in classification of plants.
4. Palaeobotanical researches are also helpful in understanding the formation of earth and evolutionary relationship among plants as well as climatic conditions of the past.
5. Fossil plants can be used in the field of descriptive and comparative anatomy.
6. Study of fossils helps in understanding the extinction of huge plants of the past.

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## ***10.3 FOSSILS***

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The study of dead remains of the plants or their imprints preserved in the geological rocks is called palaeobotany. Fossils are the preserved remains of plants and animals. There are two main types of fossils, body fossils and trace fossils. Body fossils are the preserved remains of organisms. Trace fossils are the remains of the activity of an animal, for example- preserved trackways, fossilized egg shells, foot prints, nests etc.

A fossil is the naturally preserved remains or traces of animals or plants that lived a very long time ago. They are usually found in rocks and stones. Fossils provide scientists many clues about Earth's history, offering evidences of Dinosaurs and strange plants that existed in the past.

Plant fossils are normally present in rocks composed of sediments deposited in waters. These stratified rocks are super imposed upon one another in series. These rocks are built of sediments. These accumulated at the bottom of seas, lakes, swamps, flooded valleys, subsiding beaches etc. The rock formation is correlated with the geological approach in the subject paleobotany. In fact fossil are the makers of geologic time.

### **Factors favouring fossilization**

1. **Anoxic environment:** The term anoxia means a total depletion in the level of oxygen. Low oxygen conditions repel scavengers while slowing the rate of bacterial decay.
2. **No bacteria:** Bacteria can completely decompose organic remains, leaving nothing behind to fossilize.
3. **No Scavengers:** Scavengers scatter and destroy organic remains, stopping fossilization before it starts.
4. **High deposition rate:** This allows the organism to be buried before bacteria, scavengers or the environment can take their toll, allowing the fossilization process to begin.

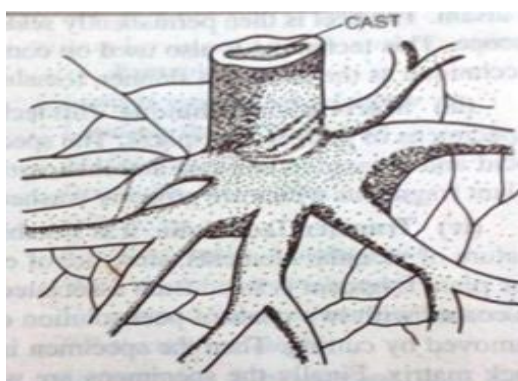
#### **10.3.1-Types of Fossils**

Some of the important types of plant fossils are as follows-

**1. Petrifications or Mineralized plants:** ‘Petrified’ actually means, ‘turned into stone’. Petrification is the process of turning living organic material into stone. This process takes place when the molecules in an organism are replaced with the molecules of minerals. In this type of plant fossil, the original cell of the plant tissue is retained by means of some minerals like silica etc. These minerals have infiltrated the tissues. In this type of fossil sometimes the material of original plant may be preserved e.g. coal balls, silicified wood etc. Petrifications are usually bits of stems, twigs, seeds, sporangia etc. Silicified bits of wood are often found. Calcified fossils are also known (Fig. 10.1).



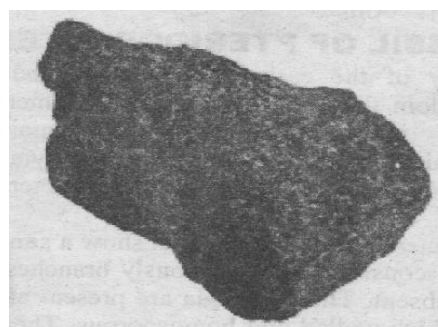
*Fig.10.1 Showing Petrification*



*Fig.10.2 Showing cast of Stigmarian stump*

**2. Cast or incrustations:** In this type of plant fossil the plant part gets covered up by sand or mud. In due course of time the plant material inside rots away leaving a hollow space. This cavity again gets filled up by some rock forming material (Fig. 10.2).

**3. Compressions:** In this type of plant fossil, the external form of plant modifies and leaves impressions on the sediment over which it lies. Compression is only a degree of impression when the organic remain of the plant part actually remains in the fossil but is highly compressed. The great pressure under which fossilization takes place flattens out all round or solid organs so that what remains in the fossil is usually a carbonaceous film. But, in good compressions it has been possible to swell out the organs by some chemical treatments so that some details become visible (Fig. 10.3).



*Fig.10.3 A compression type of fossil (e.g. Zamites) Fig.10.4 Compaction type of fossil*

**4. Compaction or mummified plants:** The process of the formation of fossils in ice-frozen environments of the polar regions is termed as mummification. The moisture of the tissue of

the organism gets converted to very small or microcrystals of ice. It is almost a process similar to deep freezing. There is no or little change in the original organic matter (Fig. 10.4).

**5. Impressions:** In this type of plants fossil, the roots, stems, leaves, fruits and seeds falling on semi-stiff clay easily leave an impression on its surface. It is just an impression made by plant or its part coming in contact with the soft clay. In due course of time this impression becomes permanent when the clay turns into stone. Such impressions are often very clear showing full details of venation, external features etc. It is dark in colour than the rock surface. It is useful in studying the external features of stem, leaf and flower etc. The only drawback is that the cellular details are not available in this type of fossil (Fig.10.5).



Fig.10.5 Impression fossil



Fig.10.6 Amber fossil



10.7 Pseudofossil

**6. Amber:** They are resinous excretions of certain fossil conifers (*Pinus succinifera*) due to injuries caused by insects or decaying branches. They fall on forest floor, get hardened and accumulated over for long periods and shape taken by it is called Amber. Several small insects, animals, small plants are preserved in this resin; amber is also considered as a type of fossil.

The fossilized plant resin secreted by coniferous trees that grew during very early times is called Amber. Certain extinct coniferous plants ooze resin and gum due to injuries. These resin and gum accumulated on the forest floor gradually hardened and become fossilized. This transparent pale yellow buff or reddish substance is the semiprecious substances and called as Amber. Fungal spores, pollen grains, small plants, animals, etc. were trapped in this resin before fossilization (Fig.10.6).

**(7) Pseudofossils:** - Sometimes watery solutions of various minerals recede through the sediments and it takes the shape of some plant part or animal. Their detailed studies, clearly reveal that they are not plants or animals but are mineral depositions mistaken for plant or animal remains. Such specimens are known as Pseudofossils (Fig.10.7).

**(8) Coal balls:** Petrified plant organs of roughly spherical shape are known as coal balls. Coal balls 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.

**(9) Trace fossils:** Trace fossils provide us with indirect evidences of past life. They are tracks left behind by animals or plants. Trace fossils include footprints, burrows, tracks, borings and feces left behind by animals.

**Living Fossil:** The term “living fossils” was first used in 1859 by Charles Darwin in his publication, ‘on the origin of species’. A living fossil is an existing organism that closely resembles to an extinct organism that is only known from fossil archives. Due to adaptation to the environment over times, living fossils do not retain the primitive features of their ancestors. The behaviour and survival instincts of living fossils are much more advanced than their ancestors. An animal or plant, such as the *Coelacanth* and *Ginkgo* and *Equisetum* belonging to groups, most of whose members are extinct. *Ginkgo biloba* is the only surviving species of the Ginkgoaceae. Recovered fossils revealed that *Ginkgo* species have remained unchanged over millions of years and similar trees were alive 170 million years ago during the Jurassic period. Another example of living fossil is a group of plants called the Cycads. Cycads look superficially like palm trees, but they belong to a very different group. This group reached its highest point of evolution in the Mesozoic (about 200 million years ago) and since then declining, although without showing any appreciable changes in their evolution. Fossil cycads from the Paleozoic (about 240 million years ago) have many characteristics similar to the cycads of the present time.

### 10.3.2 Formation of Fossils

The process by which a fossil is formed is called ‘fossilization’. The term ‘fossilization’ refers to complex processes that enable the preservation of organic remains within the geological record. Almost all living organisms can leave fossils, but usually only the hard parts of plants and animals fossilize. Soft internal organs, muscle, and skin rapidly decay and are rarely preserved, but the bones and shells of animals, spores, pollens, seeds, and woody parts are good for fossilization. Certain environmental conditions drastically slow down the decaying process, helping to preserve the tissues. For example high soil acidity (when an organism falls into a Peat bog). Insufficient oxygen e.g. when an organism becomes trapped in amber, low temperatures e.g. when an organism becomes frozen in a glacier.

Fossils can be formed in several ways:

- a. Hard body parts, such as shells, bones and leaves, can be covered by layers of sediments, over time and the parts are gradually replaced by minerals.
- b. Dead animals and plants can be preserved in amber (hardened tree resin), peat bogs, tar pits, or in ice.
- c. Casts or impressions, such as foot prints can be covered by layers of sediments. These eventually become rock, so preserving the casts.

The process of fossilization varies according to tissue type and external conditions:

**1-Freezing (Refrigeration):** In certain parts of the world, where the temperature has remained extremely low for millions of years, so-called ‘frozen fossils’ i.e. entire animal complete with skin, hair and soft body tissues are found from time to time. Frozen fossils

usually occur when an animal becomes trapped in some way in mud, tar, cervices or a pit and the temperature drops rapidly affectively 'flash freezing' the animal. A common example of such fossilization is a woolly mammoth and woolly rhinoceros frozen in a permafrost region of Siberia and Alaska. They probably died during the last ice age. Frozen fossils are only formed in special circumstances, so they are rare and usually dates back to the ice age. Rarely Paleontologists come across mastodons, moose, woolly rhinoceros, horses, bison etc. In Antarctica, where there are now no trees, frozen fossils of tree trunks 3 feet across have been discovered.

**2-Petrification:** Petrification is the process by which organic materials are turned into rock. Petrification occurs when water that is rich with inorganic minerals (silica or calcium carbonate) passes slowly through organic matter replacing its cellular structure with minerals. This process can sometime takes between a few years to millions of years. Wood is one of the most common types to become petrified. One of the most common types of petrified animal fossil is petrified teeth and bone.

**3-Carbonization:** Carbonization is the process where only the residual carbon of the organism remains. In nature this usually happens over time when leaves and some soft body parts of fish, reptiles, and marine invertebrates decompose leaving behind only the carbon. The carbon leaves a residue which shows an outline of the organism. A very common example of carbonization are fossil plants, where only a thin carbon layer is left on a piece of shale. In the carboniferous time period, fern forests created miles of carbon, which we mine today as coal.

**4-Mold and Casts:** A mold fossil is when the organism decays leaving an impression in the rock called a mold. A cast is when that mold has been filled up with rock or minerals. Molds and casts are three dimensional and preserve the surface contours of the organism. A mold preserves a negative imprint of the surface, while a cast preserves the external form of the organism. Most molds and casts do not contain the actual remains of an organism. Shells, bone and wood often form as molds or casts. Some trace fossils also known as ichnofossils, such as tracks and burrows can form as casts or molds. Tracks and burrows can provide clues to the behaviour and biomechanics of an organism when it was alive.

**5-Replacement and Recrystallization:** Replacement involves the complete removal of original hard parts by solution and deposition of new minerals in its place. The minerals in ground water replace the minerals that make up the body remains, after the water completely dissolves the original hard parts of the organism. The Petrified Forest in Arizona is an excellent example of this type of preservation. Here the original organic material (wood) has been wholly replaced by silica. Recrystallization occurs when a solution or precipitate changes the internal physical structure of a fossil. For example some shells are made of aragonite. During the fossilization process aragonite reverts to a more stable form of calcium carbonate called calcite. Thus, recrystallization from aragonite to calcite represents a type of replacement. Some shells are made of layers of calcite and aragonite. The small crystals of

calcite in shells may recrystallize into larger calcite crystals. The overall shape of the shell may remain as such as is evident from the microscopic texture.

### 10.3.3 Preservation of Fossils

The fossil record consists of a number of different organisms that have been preserved for our analysis in many ways. Fossils are preserved with and without alterations. Preservation with alteration includes carbonization, recrystallization, petrification and replacement. Preservation without alteration includes the use of molds and the collection of indirect evidence. Plants and animals may become fossilized in a number of different ways. However, most paleontologists recognize four major types of preservation. In general, the way in which an organism is ultimately preserved will depend upon the composition of the organic remains or the changes which have undergone since their burial.

**1. The Original Soft parts of Organisms:** The most rare type of fossil preservation is where unaltered soft parts are preserved. In order to preserve fossils in this way, the dead organism must be mummified in one way or another, that is, the organism must be entirely removed from any exposure to water, wind, air, oxygen etc. in which the organism is completely surrounded by a seal of the preserving agent and restricted from decay. This normally occurs only in arid or desert regions and in places where the remains have been protected from destruction by scavengers and predators. The best known examples of preserved soft parts of prehistoric animals have been discovered in Alaska and Siberia. In these areas, the frozen tundra has yielded the remains of large numbers of frozen elephant like creatures called mammoths. The bodies of these now extinct creatures, many of which have been buried for as long as 25,000 years ago, are exposed as the frozen earth begins to thaw.

Preservation in amber is another unusual form of fossilization. This process takes place when ancient insects became trapped in the sticky gum that oozed out of certain coniferous trees such as the spruce or pine. With the passing of time this resin hardened, leaving the insect encased in a tomb of amber. Some of these insects have been so well preserved that even fine hairs and muscle tissues may be studied under the microscope.

**2. The Original Hard parts of Organism:** The most common directly preserved fossils are unaltered hard parts of a living organism, like teeth, bones, shells etc. This material is unchanged, except for the removal of less stable organic matter under certain selective conditions, exoskeletons of arthropods and shells of brachiopods, molluscs and bones and teeth of vertebrates are found preserved unaltered at times in their original colour and luster.

**Altered hard parts of organisms:** Altered fossil remains have undergone some sort of changes. The original organic material is partially or fully changed into new material. There are many different types of altered fossil preservation.

**(a) Petrification or permineralization:** Petrification (Petros means stone) occurs in Porous materials such as shells, bones and plants. The material is buried, later the pore spaces may be filled with minerals that precipitate out of ground water. **Permineralization** occurs after burial when empty spaces within the plant containing liquid or gas during life become filled



with mineral-rich ground water and the minerals precipitate from the ground water filling the spaces. The anatomy of leaves is often lost, but occasionally cell walls and even cell contents may be preserved by permineralization. In this process the organic matter is completely replaced by stone minerals and the fossil is turned to stone. This method reproduces the original tissue in every detail. An example of this kind of fossilization is petrified wood. One of the processes involved in petrification is permineralization. Permineralization occurs when the pores of bones and shells are filled by minerals. Not all of the original material is replaced. Permineralized plant fossils reveal cellular level anatomy.

**(b) Carbonization and distillation:** The leaves of plants are frequently reduced to a carbon film in a process known as carbonization or distillation. Carbonized fossil remains may result when organisms are rapidly buried, especially in low-oxygen conditions. Carbonization is a process by which the more volatile substances of plants and animals decay, but leave behind the carbon. Carbonized remains are thin, approximately two-dimensional films of carbon preserved on a flat surface of rock. Crumbly woods of lignite deposits are the examples of carbonization. Distillation, most often referred as carbonization. This process of preservation occurs when volatile elements in organic matter distill away, leaving a thin carbon film as the only fossil record. Many fossils in Arizona are preserved in this way.

**(c) Replacement or mineralization:** Replacement takes place when water dissolves the original hard parts and replaces them with mineral matter. This chemical action may take place slowly, reproducing the microscopic structures of the original organism. The most common replacement minerals are calcite, hematite, silica and pyrite.

**(d) Traces of organisms:** The other types of indirect evidence are collectively called trace fossils. A trace fossil gives a paleontologist some evidence of the organism's behavior. Trace fossils including footprints, burrows and fossilization feces provide scientists with a proof of life. Tracks and trails are produced by an organism crawling, resting, foraging or walking. For instance, dinosaur tracks provide information about how large the dinosaur was, how fast it walked etc. Burrows and boring are the tunnels or burrows left by organism digging into the ground, either on land or water. This may indicate whether the organism was dwelling, feeding or just foraging. Coprolites are fossilized animal excrements. Preserved, fossilized dung provides fossil experts with evidence of ancient food sources and the structure of prehistoric digestive system.

## Levels of Preservation

The preservation takes place at a number of levels and each level contains a different type of information. Usually organic material is to be decomposed to carbon dioxide and water, and recycled into the biosphere. However, some organic matter or its traces escapes these cycles to be preserved in the rock record. Each type of preservation carries different information about the past life.

**(a) Cellular level:** Plant cell walls are far more likely to escape decomposition than internal membranes and organelles. Preservation of cytological details has been reported in fossil plants, but occurrences are rare. Compounds, for example those impregnating or covering cell wall, can also be resistant to decompose, such as sporopollenin, which forms the external shell of spores, pollens, and the resting cysts of some marine algae.

**(b) Tissue level:** The cell walls of xylem are impregnated with decay resistant lignin, while phloem cell walls are cellulosic, that's why xylem is often preserved, while phloem commonly is not. Cuticle, composed of the resistant material cutin and waxes, is more likely to be preserved than actual epidermal cells. Spores and pollen, due to their resistant spore coats, are the most abundant structural remains of vascular plants preserved in the rock record.

**(c) Organ level:** Plants break apart and dispersed parts may be transported before buried and become fossils. Assemblages of plant fossils that have been transported are called allochthonous, assemblages that are preserved close to where their parent plants are known as autochthonous. Whether an assemblage is autochthonous or allochthonous has obvious implications for what sorts of ecological interpretations we can make from it. Reproductive organs such as flowers are delicate, therefore rare in the fossil record. In such cases 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).

**(d) Organism level:** Process of fossilization usually favour large woody plants (with resistant tissues) in comparison to small herbs. Plant preservation depends on removing the organic material from the zone of aerobic decomposition. This is most easily accomplished by burying the plant. Consequently lakes, deltas, swamps, and volcanic areas are good locations for fossilization.

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## ***10.4 SUMMARY***

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Fossil is the naturally preserved remains or impression of a prehistoric plant or animal embedded in rock and preserved in petrified form. The study of plant fossils is called palaeobotany. Palaeobotany research is helpful in solving the problems connected with the formation of earth and evolutionary (gradual development) relationship among plants. Petrifications or mineralized plants, cast or incrustations, compressions, compaction or mummified plants, impressions, amber, coal balls, trace fossils are some important type of plant fossils. There was the occurrence of some fossil like objects known as pseudofossils. The process by which a fossil is formed is called 'fossilization'. Soft internal organs, muscle, and skin rapidly decay and are rarely preserved, but the bones and shells of animals, spores, pollens of plants are good for fossilization. The process of fossilization varies according to tissue type and external conditions such as petrification, freezing, carbonization, mold and casts, replacement and recrystallization, etc. Living fossil is a term used for an organism such

as horseshoe crab or *Ginkgo*, *Equisetum* that has remained essentially unchanged from earlier geologic times and whose close relatives are usually extinct.

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## 10.5 GLOSSARY

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**Fossil:** Fossils are the preserved remains of plants or animals.

**Palaeobotany:** The study of fossil plants.

**Petrification:** The process by which organic materials are turned into rock.

**Amber:** Amber is fossilized tree resin

**Carbonization:** Carbonization is a process occurring within the sediment in the absence of oxygen

**Anoxic:** means a total depletion in the level of oxygen.

**Living fossil:** living fossil refers to life forms which have survived with little change for a long time, and which are still around today while their close allies are extinct.

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## 10.6 SELF ASSESSMENT QUESTION

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### 10.6.1 Multiple choice questions:

- Who studies fossils?
  - Zoologists
  - Biologists
  - Meteorologists
  - Paleontologists
- What is amber?
  - An insect's body
  - Wet, sticky tree sap
  - Hardened tree sap
  - A hard shell
- Which kind of temperature will slow down an organism's decay?
  - Freezing temperature
  - Warm temperatures in a wet climate
  - Cool temperatures
  - Hot temperatures
- Petrified wood is an example of a-
  - Trace fossil
  - Microfossil
  - Carbon film fossil
  - mineral replacement fossil
- Which of the following is an example of a trace fossil?
  - Mold and cast
  - Preserved foot print
  - Hardened tree sap
  - A frozen mammoth
- Which of the following will not make a fossil?
  - Decomposed organic material
  - Plant impressions (casts)
  - Animal footprints
  - Loose animal bones
- Which of the following is called living fossil?
  - Pinus*
  - Ephedra*
  - Ginkgo*
  - None

8. The three types of preservation are-
- Removal, recrystallization, permineralization
  - Replacement, recrystallization, permineralization
  - Replacement, Removal, recrystallization
  - Replacement, Removal, permineralization
9. The fossilization process by which the original material is dissolved and new materials added is called-
- Replacement
  - Carbonization
  - Mineralization
  - Replication
10. Name three trace fossils-
- Tracks, burrows, caprolite
  - Nest, teeth, bones
  - Cast, mold, rocks
  - Eon, era, period, epoch

### 10.6.2 True or False:

- Fossils are remains of ancient plants and animals.
- Organisms are more likely to become fossils if they have many soft parts.
- A cast forms when mud or minerals fill a mold.
- Mold and cast can be preserved in tar, amber or ice.
- Fossils are preserved most often in sedimentary rock.

**10.6.1. Answer Key:** 1-(d), 2-(c), 3-(a), 4-(d), 5-(b), 6-(a), 7-(c), 8-(b), 9-(a), 10-(a)

**10.6.2. Answer Key:** 1-True, 2-False, 3-True, 4-False, 5-True

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## 10.8 SUGGESTED READINGS

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- Palaeobotany and Gymnosperms, A.K.Sharma and Rajeshwari Sharma, 2010, Published by Jagdamba Publishing Co.
- A Text Book of Botany (Diversity of Pteridophytes, Gymnosperms an Elementary Palaeobotany) by K.A. Siddiqui, 2013, Published by Kitab Mahal.

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***10.9 TERMINAL QUESTIONS***

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- Q1. What is Fossil? Discuss different types of fossils.
- Q2. Describe the formation of fossils in detail.
- Q3. Explain levels of preservation.
- Q4. What is living fossil? Discuss about living fossil.
- Q5. What is palaeobotany. Describe preservation of fossils in detail.

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## **UNIT-11- METHODS OF STUDY OF FOSSILS AND GEOLOGICAL TIME SCALE**

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- 11.1. Objectives
- 11.2. Introduction
- 11.3. Methods of study of fossils
- 11.4. Geological time scale
- 11.5. Importance of palaeobotanical research
- 11.5. Summary
- 11.6. Glossary
- 11.7. Self assessment questions
- 11.8. References
- 11.9. Suggested readings
- 11.10. Terminal questions

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## ***11.1 OBJECTIVES***

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After reading this unit you will be able -

- To learn how fossils are studied.
- To know what is geological time scale and its significance.
- To understand What is paleobotany.
- To know the use and significance of paleobotany.

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## ***11.2 INTRODUCTION***

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Fossils are the preserved remains of plants or animals. The oldest fossils on Earth are about 3.8 billion years old or almost a billion years younger than the planet itself. Fossil remains can give us insight into how prehistoric plants and animals obtained food, reproduced and even how they behaved. At times fossils can also provide evidences for how or why these past organisms died. There are mainly two types of fossils, body fossils and trace fossils. The preserved remains of the body of a plant or animal are body fossil while trace fossils are the remains of the activity of an organism, such as footprints, pollens, seeds etc. Plant fossils are normally present in sedimentary rocks. These stratified rocks are super imposed upon one another in series.

Fossils are not used only to understand individual organisms. Geologists also use fossils for the bio-stratigraphic correlation which allows researchers to match layers of rocks in different locations by age based on how similar the fossils in each rock layer are. This information can be used to help to understand the time period of formation of different layers of rock even when large distances separate them.

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## ***11.3 METHODS OF STUDY OF FOSSILS***

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The search for fossils begins with geological surveys. Some areas are more likely to yield fossils than others, and researchers normally concentrate their efforts on regions that have good, fossil-bearing rocks. Although fossils can provide different information about past life but study of fossils is a laborious process which requires much time and patience. Specimens are cut in sections and studies conducted which give an idea of the actual structure of the fossil. These petrified pieces are cut into very fine slices by different methods. Geologists used different methods for fossil study in the field as well as in laboratory:

### **11.3.1 In Field**

**A-Site Preparation:** First the area is surveyed and when a potential site is identified, it is again surveyed thoroughly using different technologies that produce three-dimensional maps and plans of potential fossil-bearing areas. Findings are plotted on virtual maps using a digital Geographical Information System (GIS).

**B-Excavation:** Various methods are used for excavation. The method used mainly depends upon the type of sediment or matrix holding the fossils. For example if fossils are encased in hard breccias (a matrix consisting of mud or sand and stone fragments cemented together by calcium carbonate) is excavated using jackhammer drills driven by compressed air. Blocks are then broken away by driving wedges into the holes.

Technicians carefully uncover fossils from breccia blocks by removing the surrounding rock using delicate drills, including power tools called aircsribes, which use compressed air. Little Foot is being excavated in this way. Areas of decalcified breccia deposits (i.e. where the lime has been dissolved by ground water) are excavated with picks and shovels and carefully sieved so that even small bone can be recovered. Fragmented and crushed fossils can be reconstructed after cleaning.

Blocks of breccia can be removed for preparation in a laboratory. Prior to removal, the position of each block of breccia is recorded in three dimensions, relative to a grid or digital 3D site plan.

Fossils can be prepared in a laboratory using small, pointed chisels and lightweight hammers. Fine cleaning of important fossils is done under a microscope with dental picks and aircsribes. Specimens are numbered and catalogued with reference to their position vertically and horizontally in the site. Photography and making drawings of stratigraphic sections are important activities during the excavation.

### 11.3.2 In the Laboratory

After a fossil has been prepared and cleaned, it is studied in the laboratory. There are many ways of examining fossils in detail. Significant fossils can be measured using callipers. Binocular light microscopes are used to look at surface features. A scanning electron microscope (SEM) is used for detailed high magnification analysis.

Trace element and isotope analysis of soils and fossils provides information about the environment. DNA analysis has the potential to add information on the nature of relationships between organisms.

### 11.3.3 Scientific Techniques

**(i) Radio carbon dating:** Radio carbon dating is a method that provides fossil's age estimates for carbon-based materials that originated from living organisms. The method was developed by an American chemist, Willard Libby in late 1940s and soon became a standard tool for archaeologists. Libby received the Nobel Prize in Chemistry for his work in 1960.

The radiocarbon dating method is based on the fact that radiocarbon is constantly being created in the atmosphere by the interaction of cosmic rays with atmospheric nitrogen. The resulting radiocarbon combines with atmospheric oxygen to form radioactive carbon dioxide, which is incorporated into plants during photosynthesis while animals get this  $^{14}\text{C}$  by eating the plants.



When the animal or plant dies, it stops exchanging carbon with its environment and from that point onwards the amount of  $^{14}\text{C}$  it contains begins to decrease and  $^{14}\text{C}$  undergoes radioactive decay. Measuring the amount of  $^{14}\text{C}$  in geological sample one can calculate when the animal or plant died. The older a sample is, the less  $^{14}\text{C}$  is to be detected. Since the half-life of  $^{14}\text{C}$  (the period of time after which half of a given sample will have decayed) is about 5,730 years, the oldest dates that can be reliably measured by this process date to around 50,000 years ago (Fig.11.1). A special preparation method occasionally permits accurate analysis of older samples. Earlier the measurement of radiocarbon was done by beta-counting devices, which counted the amount of beta radiation emitted but recently, accelerator mass spectrometry has become the method of choice for measuring the decaying  $^{14}\text{C}$  atoms in a sample.

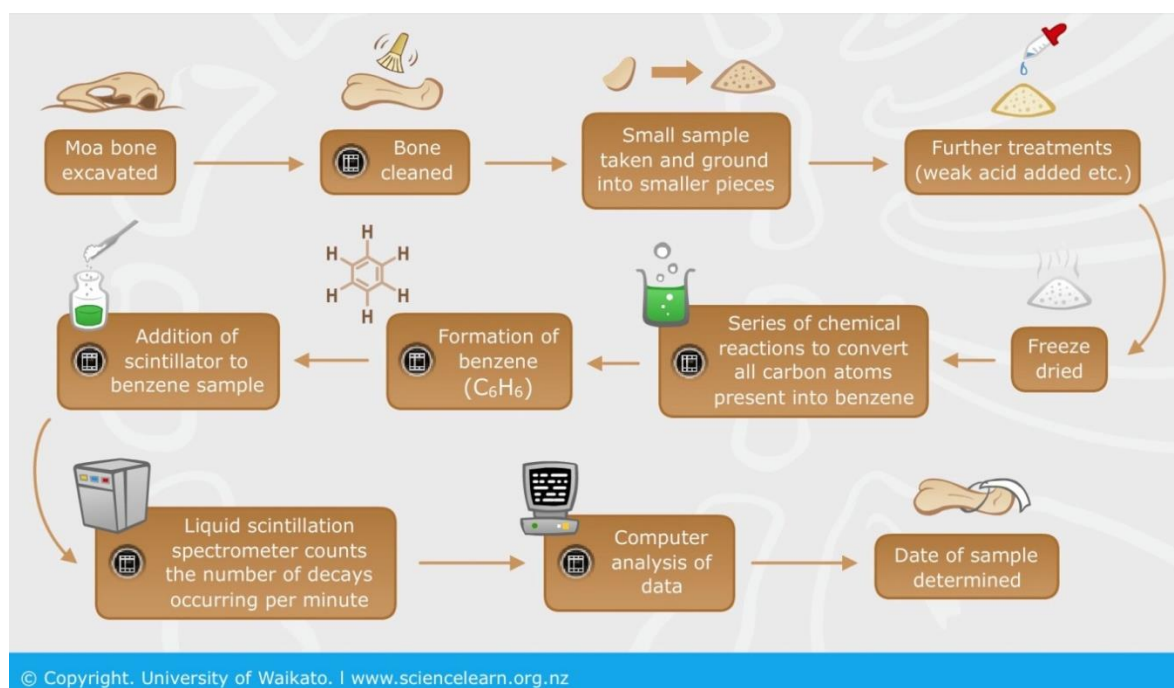


Fig.11.1 C-14 Carbon dating process

**(ii) Ground thin section technique:** This technique is suitable for the study of petrified fossils which preserve cellular details. In this technique the specimen is cut into small-sized sections and surfaces are smoothed. The smooth surface of the section is mounted on a glass slide. Now it is warmed and coated with melted resin. Now the specimen is cut as close to the glass as possible, thus a moderately thin section is obtained.

The thin section fixed to the glass slide is further ground on a revolving lap with 100 carborundum till sufficiently translucent, so that the section can be viewed under the microscope. Finally, the slice is mounted with a cover glass using suitable mounting media.

**Advantages:** A thin section of petrified wood can be made that preserves the cellular structure in an unchanged condition.

**Disadvantages:** This technique have the following disadvantages:

- a) The technique needs extensive labour and is timeconsuming.

- b) A small number of sections can be made from a given specimen, thus a lot of material is wasted.

**(iii) Peel section technique:** This is a conventional and most suitable technique for study of well-preserved petrifications with considerable organic material. In this technique the etching of the fossil surface is done with the help of some mineral acids e.g., 5% hydrochloric acid (if the material has calcium carbonate) and 10% hydrofluoric acid (if the material has silica) for 5 and 10 minutes respectively. The etched surface is gently washed under running water for the removal of acid and is air-dried and then covered with a solution or a thin film of nitrocellulose.

#### **Advantages**

- a) A series of sections can be made from a single specimen.
- b) It is less expensive and quicker to prepare.
- c) The sections (peels) obtained are translucent, thinner and durable.

**(iv) Transfer technique:** It is an important technique for the study of coalified compressions. This technique is most suitable for study as it reveals additional details of venation, epidermal pattern and hairs. In this technique the peel solution is coated on the delicate fossil material adjoining the rock surface. When solution dries, the portion of the rock having fossil material is removed. The face of the specimen adjoining the rock surface is cleaned either mechanically or by washing in an acid for removal of rock particles. The prepared surface of the rock is coated with a solution of nitrocellulose or with a cellulose acetate film. When the film is dried, it is loosened from the rock surface.

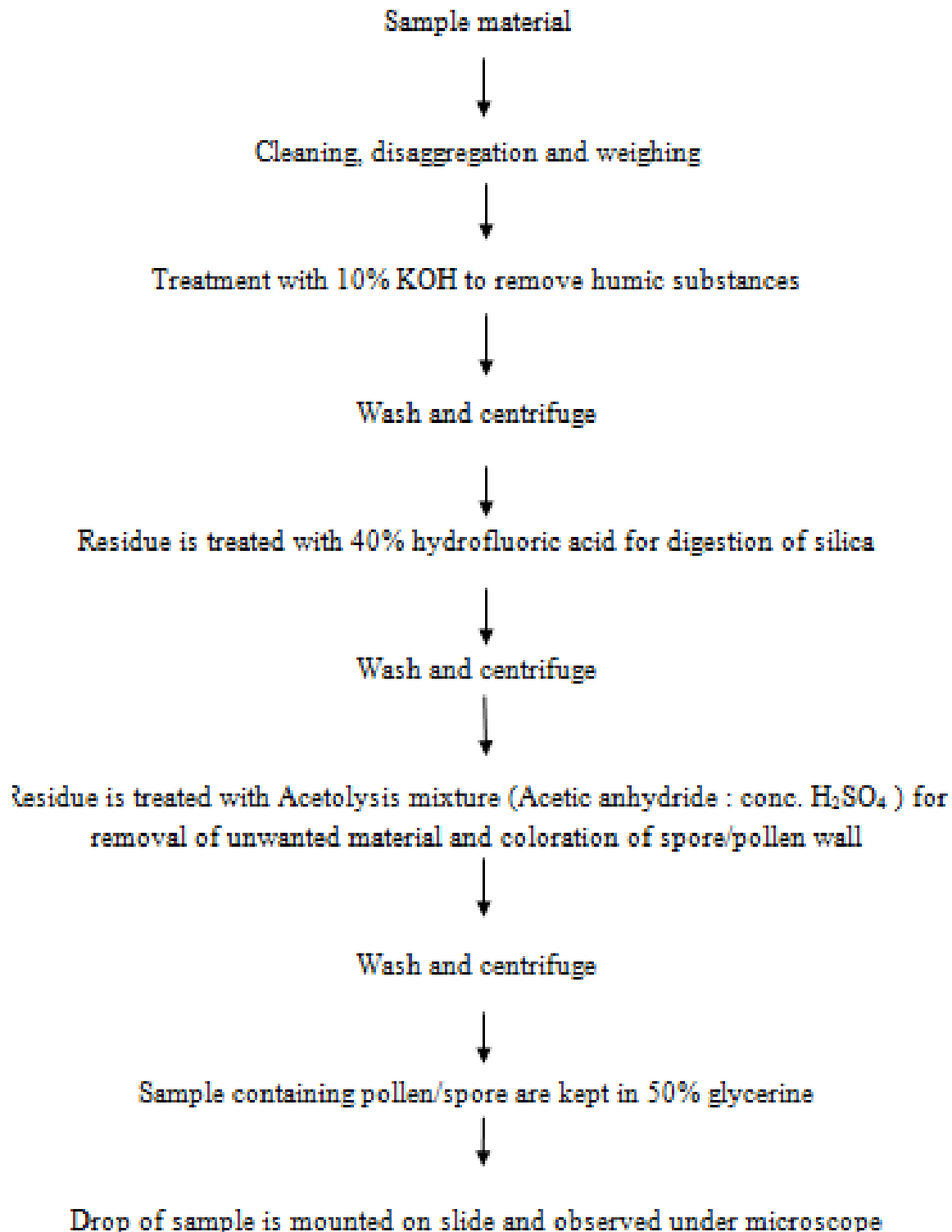
Sometimes coalified materials are adhered to the film. Occasionally, the film is treated with strong oxidizing agent to make the film more transparent. Finally, the film is dried and permanently mounted on the slide with a cover glass using a suitable mounting medium.

**Advantages:** This technique is very useful for the study of coalified compressions. It helps to learn about leaf form, venation pattern, stomatal and epidermal characteristics which are important features used in establishing systematics and phylogeny of extinct plants.

**(v) Maceration technique:** This technique is most suitable for the study of peat, lignite and coal. It is very useful for pollen and spore analysis. The methods of peat, lignite and coal analysis are discussed schematically in flow chart:

#### **Advantages**

1. A small portion of sediment is enough to get considerable amount of pollens and spores.
2. Due to the presence of resistant chemical sporopollenin in exine, pollens and spores are considerably preserved in deposits like peat/ coal/lignite, etc.
3. The maceration process is very simple and reliable.

**PEAT ANALYSIS (ACETOLYSIS TECHNIQUE):**

**LIGNITE AND COAL ANALYSIS:**

**(vi) Modern Techniques:** Nowadays fossils are studied by modern techniques using transmission and scanning electron microscope, interference microscope, phase contrast microscope and by X-ray analysis.

**X-Rays and CT Scans:** Researchers can study the anatomy of fossils without damaging the material by using X-ray analysis (radiography) and CT scans (using computed tomography) which provide detailed internal images of fossil.

**Cave Taphonomy:** Taphonomy is the study of processes which is related to the death of organisms, their burial and decay. It is important to understand these to interpret fossil sites correctly. Bones were once parts of living animals and when animal dies, it naturally decays where it is buried so taphonomy includes the investigation of things like the age of the individual to which the bones once belonged to and how weathering has affected them.

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## ***11.4 GEOLOGICAL TIME SCALE***

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It is assumed that our earth is made approximately 4.6 billion years ago. This extensive interval of time occupied by the geological history of earth, is divided into different time intervals, which extended from 4.6 billion years ago upto the present day. Based on the different methods of the fossil study, the chronological order of the history of the organic evolution was prepared and presented in the form of time scale and this scale is known as Geological Time Scale. Actually, it is a record of the earth's geological history as scientists have come to understand it by studying the layers formed and present in the rocks. The geological time scale is divided into larger and smaller subdivisions, which help us in getting a better sense of how historical events fit together. From largest to smallest time intervals, the hierarchy includes eons, eras, periods, epochs, and ages. This time scale included the history of the earth from the time of its origin.

**Eon:** Eons are the largest intervals of geologic time and are hundreds of millions of years of duration. Two or more geological eras form an eon, which is the largest division of geologic time.

**Era:** Eons are divided into smaller time intervals known as eras. In the time scale one can see that the Phanerozoic is divided into three eras: Cenozoic, Mesozoic and Paleozoic. Very significant events in Earth's history are used to determine the boundaries of the eras.

**Period:** Eras are subdivided into periods. The events that bound the periods are widespread in their extent but are not as significant as those which bound the eras. In the time scale one can see that the Paleozoic is subdivided into the Permian, Carboniferous (Pennsylvanian, Mississippian), Devonian, Silurian, Ordovician and Cambrian periods.

**Epoch:** It is the smallest division of geologic time. The periods of the Cenozoic are frequently subdivided into epochs. Subdivision of periods into epochs can be done only for the most recent portion of the geologic time scale. This is because older rocks have been buried deeply, intensely deformed and severely modified by long-term earth processes. As a result, the history contained within these rocks cannot be as clearly interpreted as the recent ones.

### **11.4.1 Major Events of Geological Time Scale**

The period between the origin of earth (4.6 billion years ago) and the time of earth crust formation is called Azoic era (era of no life). Rest of the time is divided into five different eras i.e. Archaeozoic, Proterozoic, Palaeozoic, Mesozoic and Coenozoic.

Archaeozoic and Proterozoic era grouped together known as Precambrian. The rest three eras are further divided into smaller time spans known as period and period of Coenozoic is further divided into epochs. It is believed that the different eras in the history of the earth started from intense geological disturbances which is also known as revolution or cataclysm. The first great revolution occurred between Archaeozoic and Proterozoic era, followed by second great revolution which occurred between Proterozoic and Palaeozoic eras. The

Appalachian revolution occurred in between Palaeozoic and Mesozoic eras while Rocky Mountain between Mesozoic and Coenozoic eras.

The first record of photosynthetic organisms was recorded around 3000 million years ago from the fossil records of Cyanobacteria which used water as a reducing agent to produce atmospheric oxygen as a by-product. This oxygen oxidized to the dissolved iron which was present in the oceans and precipitated it to the ocean floor to form sedimentary layers of oxidized iron which is known as **banded iron formations (BIFs)**.

These BIFs are part of the geological record of evidence for the evolutionary history of plants by identifying when photosynthesis originated. This also provides deep time constraints upon when enough oxygen could have been available in the atmosphere to produce the ultraviolet blocking stratospheric ozone layer. The oxygen concentration in the ancient atmosphere subsequently raised, acting as a poison for anaerobic organisms and resulting in a highly oxidizing atmosphere and opening up niches on land for occupation by aerobic organisms.

Evidence for Cyanobacteria also comes from the presence of stromatolites in the fossil record deep into the Precambrian. Stromatolites are layered deposits which are mainly of limestone and formed by the growth of blue-green algae (primitive one-celled organisms). These structures are usually characterized by thin, alternating light and dark layers that may be flat or dome-shaped. These layers may trap, bind or cement the sedimentary grains of microbial biofilms, produced by Cyanobacteria.

Chloroplasts in eukaryotic plants evolved and formed by the endosymbiotic relationship between Cyanobacteria and other prokaryotic organisms. These earliest photosynthesizing singlecelled autotrophs later evolved to the group of freshwater green algae. The dominant floras of each time period are described as follow:

## **A - Paleozoic Flora**

The Paleozoic Era, which ran from about 542 million years ago to 251 million years ago, was a time of great change on Earth. The era began with the breakup of one supercontinent and the formation of another. Plants became widespread.

**1- Cambrian Flora:** Plants were small, unicellular or filamentous with soft body tissues and simple branching. Due to soft body nature, these plants decayed and destroyed easily so that a very less record of Cambrian flora is available. Fossil record of calcareous green alga, *Dasycladales* found in the middle Cambrian. Other major groups of green algae had been established by this time, but there were no land plants with vascular tissues until the mid-Silurian.

**2- Ordovician Flora:** The evidence of plant evolution changes dramatically in the Ordovician with the first extensive appearance of spores in the fossil record (Cambrian spores have also been found.). The first terrestrial plants were probably in the form of tiny plants resembling liverworts. This early plant lack conducting tissues and grows in wet and humid places and reproduced with spores. These spores had important dispersal units with hard

protective outer coatings which help it to protect future offspring against the harsh environmental conditions.

**3-Silurian Flora:** The first fossil records of vascular land plants were recorded from Silurian period. The earliest known representatives of this group (mostly from the northern hemisphere) are placed in the genus *Cooksonia*. They had very simple branching with terminal flattened sporangia. By the end of the Silurian much more complex vascular plants, the Zosterophylls, had diversified and primitive lycopods, such as *Baragwanthia* (originally discovered in Silurian deposits in Victoria, Australia), had become widespread.

**4-Devonian Flora:** By the Devonian Period, life was well underway in its colonization of the land. Early Devonian plants did not have roots, leaves or vascular tissues like modern plants. They probably spread largely by vegetative growth, and did not grow much more than a few centimeters.

By the Late Devonian, forests of large, primitive plants had evolved. Most of these plants had true roots and leaves, and many were quite tall. The tree-like *Archaeopteris*, ancestral to the gymnosperms, and the giant *Cladoxylopsid* trees had true wood. These are the oldest known trees of the world's first forests. *Prototaxites* was the fruiting body of an enormous fungus that stood more than 8 meters tall.

By the end of the Devonian, the first seed-forming plants had appeared. This rapid appearance of so many plant groups and growth forms has been called the "Devonian Explosion". The primitive arthropods co-evolved with this diversified terrestrial vegetation structure. The evolving co-dependence of insects and seed-plants that characterizes a recognizably modern world had its genesis in the late Devonian. The development of soils and plant root systems probably led to changes in the speed and pattern of erosion and sediment deposition.

The 'greening' of the continents acted as a carbon dioxide sink, and atmospheric levels of this greenhouse gas may have dropped. This may have cooled the climate and led to a massive extinction event.

**5-Carboniferous Flora:** Early Carboniferous land plants were very similar to those of the preceding Late Devonian vegetation, but new groups also appeared at this time. The main plants of early Carboniferous period belonged to Equisetales (Horsetails), Sphenophyllales (scrambling plants), Lycopodiales (Club mosses), Lepidodendrales (scale trees), Filicales (Ferns), Medullosales (previously included in the "seed ferns", an artificial assemblage of a number of early gymnosperm groups) and the Cordaitales. These continued to dominate throughout the period, but during late Carboniferous, several other groups such as Cycadophyta (cycads), Callistophytales (another group of "seed ferns"), and the Voltziales (related to and sometimes included under the conifers) also appeared.

The fronds of some Carboniferous ferns were almost identical with those of living species. Probably many species were epiphytic. Fossil ferns and "seed ferns" included *Pecopteris*, *Cyclopteris*, *Neuropteris*, *Alethopteris* and *Sphenopteris* etc.

**6-Permian Flora:** About the middle of the Permian there was a major transition in vegetation. The swamp-loving lycopod trees of the Carboniferous were replaced by the more advanced conifers, which were better adapted to the changing climatic conditions. The Permian period saw the radiation of many important conifer groups, including the ancestors of many present day families. The *Ginkgo* and Cycads also appeared during this period.

## B - Mesozoic Flora

The **Mesozoic Era** lasted more than 180 million years. During this time, many modern forms of plants, invertebrates, and fishes evolved. For most of this period, the climate worldwide was warm and tropical, and shallow seas covered low-lying landmasses.

**1-Triassic Flora:** On land, the dominant plants included the lycophytes, cycads, ginkgophyta (represented in modern times by *Ginkgo biloba*) and glossopterids. The spermatophytes, or seed plants came to dominate the terrestrial flora: in the northern hemisphere. *Dicroidium* (a seed fern) was the dominant southern hemisphere tree during the early Triassic period.

**2-Jurassic Flora:** The arid, continental conditions characteristic of the Triassic steadily eased during the Jurassic period, especially at higher latitudes. The warm and humid climate allowed lush forests to cover much of the land. Conifers dominated the flora, as during the Triassic this was the most diverse group and constituted the majority of large trees. Exact conifer families that flourished during the Jurassic included the Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae and Taxodiaceae.

The extinct Mesozoic conifer family Cheirolepidiaceae dominated low latitude vegetation, as did the shrubby Bennettitales. Cycads were also common, as were *Ginkgo* and tree ferns in the forest. Smaller ferns were probably the dominant undergrowth. Caytoniaceae seed ferns were another group of important plants during this time and are thought to have been shrubs to small-sized tree. *Ginkgo* like plants were particularly common in the mid to high northern latitudes.

**3-Cretaceous Flora:** Angiosperms spread during this period, although they did not dominate till the end of this period. Their evolution was aided by the appearance of bees. Evolution of angiosperms and insects are a good example of co-evolution. The first representative of many modern trees, including figs, palms and magnolias, appeared in the Cretaceous. At the same time some earlier Mesozoic gymnosperms like Conifers continued to thrive, although other taxa like Bennettitales faded out before the end of this period.

**C -Coenozoic Flora:** The Coenozoic is the age of savannas. At 35 million years ago, grasses evolved from the angiosperms. Plant domestication began with the cultivation of Neolithic founder crops. This process of food production, coupled later with the domestication of animals caused a massive increase in human population that has continued to the present. At the same time, Sahara was green with rivers, lakes, cattle, crocodiles and monsoons.

The major events in geological time history can be summarized as follow:

The first primitive algae and fungi like aquatic plants started to evolve during Proterozoic era (1600 million years ago). The first marine alga evolved during Cambrian period of the



Palaeozoic era. During the Silurian period of Paleozoic era (i.e. between 395 to 430 million years ago) the first definite evidence of the land plants were found but algae was dominant during this period. Evolution of bryophytes also started during Silurian period.

During Pennsylvanian and Missisipian period the earth was covered by the very luxuriant forests which were formed by lycopods, horsetails, seeded ferns and later on with primitive gymnosperms. These periods were most important because most of the coal mines belonged to this period. The dense forests have got submerged in those times which resulted to the present days coal mines.

Pteridophytes started to evolve during Silurian period and dominated during Devonian-Carboniferous periods. During these periods the first forest started to appear and land plants fully established. During Devonian Period, the first gymnosperms also started to evolve.

Angiosperm started to appear during Mesozoic era and gymnosperm started to disappear. Majority of the Cycads disappeared and only a few forms have been left to the present day. In Triassic and Jurassic period of Mesozoic era gymnosperms dominated the earth. During this period cycads and conifers were very common and dicotyledons started to increase. During cretaceous period the first monocotyledons appeared and gymnosperms started to decline.

The Cenozoic era is divided into two periods: tertiary and quaternary. It started after Rocky Mountain revolution. During the Oligocene epoch of the tertiary period, most of the land part was covered by the forests and monocots started to appear.

**Table-11.1: GEOLOGICAL TIME SCALE**

EON	ERA	PERIOD	EPOCH	DURATION (MILLION YEARS AGO)	GEOLOGICAL CONDITION	TYPE VEGETATION	OF
<b>PHENEROZOIC</b>	COENOZOIC	Quaternary	Recent	0.001	End of last ice age, climate warmer	Decline of woody plants, rise of herbaceous ones	
			Pleistocene	1	Repeated glaciations, four ice ages	Great extinction of species	
		Tertiary	Pliocene	13	Continued rise of mountains of western north America, volcanic activity	Decline of forests, spread of grasslands flowering plants (monocotyledons)	
			Miocene	25	Sierra and Cascade mountains formed; volcanic activity in north west U.S., climate cooler		
			Oligocene	36	Lands lower, climate warmer	Maximum spread of forests; rise of monocotyledons	
			Eocene	58	Mountains eroded; no continental seas; climate warmer		
			Paleocene	63			

Rocky Mountain revolution (Little destruction of fossils)					
MESOZOIC	Cretaceous		135	Andes, Alps, Himalayas, Rockies formed late; earlier, inland seas and swamps; chalk, shale deposited	First monocotyledons; first oak and maple forests; gymnosperms declined
	Jurassic		181	Continents fairly high; shallow seas over some of Europe and western U.S.	Increase of dicotyledons; Cycads and conifers are common
	Triassic		230	Continents exposed; wide spread desert conditions; many land deposits	Gymnosperms dominant, declining towards end extinction of seed ferns
Appalachian revolution (Some loss of fossils)					
PALEOZOIC	Permian		280	Continents rose; Appalachian formed; increasing glaciations and aridity	Decline of lycopods and horsetails
	Carboniferous	Pennsylvanian	320	Land at first low; great coal swamps	Great forest of seed fern and gymnosperm
		Mississippian	345	Climate warm and humid at first, cooler later and land rose	Lycopods and horsetails dominant; gymnosperms increasingly widespread
	Devonian		405	Smaller inland seas; land	First forest; land plants

				higher; more arid; glaciation	well established; first gymnosperm
		Silurian	425	Extensive continental seas; lowlands increasingly arid as land rose	First definite evidence of land plant; algae dominant
		Ordovician	500		Land plants probably first appeared; marine algae abundant
		Cambrian	600	Lands low; mild climate; earliest rocks with abundant fossils	Marine algae
<b>PRECAMBRIAN</b>	Second great revolution (Considerable loss of fossils)				
	PROTEROZOIC		1600	Great sedimentation; volcanic activity later; extensive erosion repeated glaciation	Primitive aquatic plants- algae, fungi
	First great revolution (Considerable loss of fossils)				
	ARCHEOZOIC		3600	Great volcanic activity; some sedimentary deposition; extensive erosion	No recognizable fossils

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## ***11.5 IMPORTANCE OF PALAEOBOTANICAL RESEARCH***

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### **11.5.1 What Is Paleobotany**

Palaeobotany is the branch of botany which focuses on the study of plant fossils. It is the branch of palaeontology which deals with the identification of the plant remains from geological contexts. This study helps in the biological construction of the plant environments and its evolutionary history. Stenbery (1761-1838) is known as the father of Palaeobotany. The most ancient plant fossils were microscopic algae that lived more than one billion years ago during Precambrian times. The first tree may have been *Wattieza*, fossils of which have been found in New York in 2007 which belonged to Middle Devonian (about 385 million years ago). Prior to this discovery, *Archaeopteris* was known as earliest tree. Both of these reproduced by spores rather than seeds and are considered to be links between ferns and the gymnosperms.

### **11.5.2 Importance of Palaeobotany**

As a branch of botany, palaeobotany is important because the fossil record helped to understand the long process of plant evolution. Since the 1940, fossil evidences had helped to explain the origin of major classes of organisms, such as algae and fungi. This knowledge of sequential occurrence of different plant groups is used to develop an understanding of environmental relationship among different plant groups. Researchers now also have evidences for the origin of the earliest vascular plants and the formation of reproductive structures, such as cones of gymnosperms and flowers of angiosperms. The location of fossils is also used for determining the climate of the past.

The climate of the world had changed continuously as continents have shifted over the earth's surface. For example, the location of coal deposits (which are the remains of giant lycophyte trees) in what is now Pennsylvania indicates the warmer climate that must have existed then. Palaeobotanical study also helped in the study of the nature of communities of fossil plants and animal species of that time. Sometimes paleobotanical study can be used for the discovery of underground reserves of fossil fuels.

Palynology (the study of pollen) is an important sub-discipline of paleobotany. Palynologists search samples of lake sediment, river sediment, or a bog peat of known age, carefully identifying and counting the microscopic pollens. From the study of fossil pollens, the types of forests or other plant communities that may have occurred in that environment can be inferred.

### **11.5.3 Palaeobotany in India**

The work on the Indian fossil was started by Fiestmental. He was the director general of geological survey of India. He published a monograph of Indian fossil forms. After him Seward and Bencroft made a number of additions.

Prof. Birbal Sahni was a pioneer of paleobotanical study in India. He is also known as father of Indian paleobotany. Prof. Sahni published a number of monographs on Indian fossils. In between 1918 and 1949 Prof. Sahni published a large number of papers dealing with nearly every aspect of fossil botany. The most important Indian fossil he described was of *Williamsonia seawardiana*.

The collection of fossil plants were made from Raniganj coal field in Bengal, place near Nagpur, Reeva state, Kotah state, in some parts of Kashmir near about the Sutlej river, salt range in Punjab (now in Pakistan), and Rajmahal hills( Bihar).From here he got important fossil types as *Homoxylon rajmahalense*, *Rajmahalia paradoxa*, *Williamsonia seawardiana* and form genera of Pentoxylae.

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## 11.6 SUMMARY

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Fossils are evidence of ancient life forms or ancient habitats which have been preserved by natural processes. They were the actual remains of a once living thing, or even traces of past events. Geologists can tell the age of a fossil through a variety of radiometric dating techniques. The breakdown of radioactive isotopes of certain elements, such as carbon, uranium and potassium takes place at a known rate, so the age of a rock or mineral containing these isotopes can be determined.

Perhaps one of the most important functions of fossils from a scientific perspective is that they constitute one line of evidence for understanding evolution. Using information pieced together from fossil evidence, scientists can reconstruct body types of animals that no longer existed now and put together a “Tree of Life” to describe the evolutionary relationships among organisms.

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## 11.7 GLOSSARY

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**Absolute dating:** A means of estimating the age of rocks with some degree of accuracy using measurements of radioactive isotopes.

**Archean:** An eon of geologic time extending from about 3.9 billion years to 2.5 billion years ago.

**Biostratigraphic zone:** Unit of geologic time defined by the presence of one or more fossil species. Interval zones use the range of single species; assemblage zones use the ranges of a group of species, while abundance zones use maximum or minimum abundances instead of just presence and absence data.

**Body fossil:** The remains of an ancient organismlike shells, bones, teeth, and leaves.

**Breccia:** Rock consisting of sharp fragments embedded in clay or sand.

**Calcareous:** Containing or like calcite (calcium carbonate).

**Carborundum:** Any of various abrasives or refractories of silicon carbide, fused alumina, and other materials.

**Cast:** A structure that forms when sediments fill a mold and hardened, forming a replica of the original structure.

**Cenozoic:** The third and current (most recent) geologic era of the Phanerozoic eon, which began 65.5 million years ago and colloquially referred to the "Age of Mammals", angiosperms (flowering plants) and in certain areas conifers the predominant form of plant life.

**Coal swamp:** name given to the vast equatorial tropical forests and swamplands of the late Carboniferous, from which most modern black coal comes from (brown coal in contrast is Tertiary in age). Despite the name, coal swamps did not themselves contain any coal.

**Decay rate:** The rate at which a population of radioactive atoms decays into stable daughter atoms. Rate often expressed in terms of half life of the parent isotope.

**Decay:** The change from one element or isotope to another. Only certain isotopes decay. The rest are said to be stable.

**Eon:** The largest division of geologic time in the geological timescale. Any span of one billion years.

**Epoch:** A division of the geologic time shorter than a period. Epochs are further divided into several ages.

**Era:** A division of the geologic time shorter than an eon and measuring major stages in the evolution of life.

**Fossil record:** the history of life on Earth through geological time, as preserved through fossil remains in sedimentary rock.

**Fossil:** Evidence or trace left in rock of an ancient organism. A fossil may be a bone, shell, leaf impression, footprint, insect in amber, etc.

**Geological time scale:** A system of chronologic measurement relating stratigraphy to time that is used by geologists, paleontologists and other earth scientists to describe the timing and relationships between events that have occurred during the history of the Earth.

**Microfossil:** A fossil so small that it must be studied with the help of a microscope.

**Paleobiogeography:** The branch of paleontology that deals with the geographic distribution of plants and animals in past geologic time, especially with regard to ecology, climate, and evolution.

**Palynology:** The study of pollen, living and fossil.

**Permineralization:** A type of fossilization in which minerals are deposited into the pores of the original hard parts of an organism.

**Sediment:** Number of materials deposited at Earth's surface by physical (such as wind, water, and ice), chemical (precipitation from oceans, lakes, and rivers), or biological agents (organisms, living and dead).

**Stratigraphy:** A branch of geology dealing with the classification, nomenclature, correlation, and interpretation of stratified rocks.

**Trace fossil:** Fossil not of an organism itself but of the traces and impressions it left behind while alive (footprints, burrows, resting traces, etc).

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## ***11.8 SELF ASSESSMENT QUESTIONS***

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### **11.8.1. Multiple Choice Questions:**

1. Birbal Sahni was a renowned:
  - (a) Algologist
  - (b) Paleobotanist
  - (c) Physiologist
  - (d) Bryologist
2. What can fossils tell us about past animals and life?
  - (a) Information about the past environment.
  - (b) Where animals came from
  - (c) What animals from the past looked like
  - (d) All of the above
3. What kind of scientist studies the history of plants and animals?
  - (a) A botanist
  - (b) A geologist
  - (c) A chemist
  - (d) A paleontologist
4. What is amber?
  - (a) Hardened tree sap
  - (b) A hard shell
  - (c) An insect's body
  - (d) Wet, sticky tree sap
5. What does a scientist need to know to figure out the absolute age of a rock?
  - (a) The rate of decay of the rock's half-life
  - (b) The rate of decay for a radioactive element in the rock
  - (c) The half-life of a radioactive element in the rock
  - (d) The rate of decay for all elements in the rock
6. Why doesn't every plant and animal turn into a fossil?
  - (a) Only animals turn into fossils. Plants do not form fossils.
  - (b) It is a very complicated process for animals/plants to turn into fossils.
  - (c) Many animals/plants are destroyed before they can turn into a fossil.
  - (d) Both b and c.
7. The Birbal Sahani Institute of Palaeobotany was established in the year?
  - (a) 1942
  - (b) 1943
  - (c) 1946
  - (d) 1948
8. Fossiliferous area in India to which Prof. Sahni gave special attention was:
  - (a) Rajmahal hills of Bihar and Salt range of Punjab
  - (b) Rajasthan desert
  - (c) Karakoram Hills
  - (d) Shivalik Hills of Northern Himalaya
9. Which division on the geologic time scale is the shortest?
  - (a) Epoch
  - (b) Era
  - (c) Eon
  - (d) Period
10. How old do Paleontologists believe the Earth is?
  - (a) 2.6 billion years old
  - (b) 3.6 billion years old
  - (c) 4.6 billion years old
  - (d) 5.6 million years old
11. Which is the correct order of geologic time?
  - (a) Era > Eon > Period > Epoch
  - (b) Eon > Era > Period > Epoch
  - (c) Epoch > Period > Era > Eon
  - (d) Era > Eon > Epoch > Period
12. What was probably the first organism on Earth?



- (a) Plants (b) Alligators  
(c) Bacteria (d) Fish
13. Which is the most recent era of time: the one that we are currently in is?  
(a) Mesozoic (b) Paleozoic  
(c) Coenozoic (d) Precambrian
14. During which era did flowering plants became common?  
(a) Precambrian (b) Cenozoic  
(c) Mesozoic (d) Paleozoic
15. What is the longest part of Earth's history?  
(a) Precambrian (b) Paleozoic Era  
(c) Mesozoic Era (d) Cenozoic Era
16. During which era were the first land plants formed?  
(a) Precambrian (b) Paleozoic  
(c) Mesozoic (d) Cenozoic

**11.8.1 Answer Key :** 1-(b), 2-(d), 3-(d), 4-(a), 5-(b), 6-(d), 7-(c), 8-(a), 9-(a), 10-(b), 11-(b), 12-(c), 13-(c), 14-(b), 15-(b), 16-(b)

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### ***11.10 SUGGESTED READINGS***

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- [http://www.maropeng.co.za/content/page/the\\_science\\_of\\_studying\\_fossils](http://www.maropeng.co.za/content/page/the_science_of_studying_fossils)

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### ***11.11 TERMINAL QUESTIONS***

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- Q1. Write a brief account on: 1. Paleobotany 2. Fossilization
- Q2. What is geological time scale and how it is useful for study of fossil?
- Q3. What are different techniques used for the study of the fossils?
- Q4. Define radiocarbon dating.