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BOTANY

PHANEROGAMS & PALEOBOTANY

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INDEX

PHANEROGAMS & PALEOBOTANY

Chapter 1: Pteridophytes

Module 1: General Characteristics of Pteridophytes 1
Module 2: Stelar Evolution 12
Module 3: Sporophyte Evolution 21
Module 4: Heterospory & Seed Habit 30
Module 5: Alternation of Generation 36
Module 6: Comparative Study of Major Groups 43
Module 7: Economic Importance of Pteridophytes 103

Chapter 2: Gymnosperm

Module 1: General Characteristics of Gymnosperm 106
Module 2: Classification of Gymnosperm 131
Module 3: Origin & Evolution of Gymnosperm 134
Module 4: Comparative Study of Major Goups 147
Module 5: Economic Importance of Gymnosperm 167

Chapter 3: Palebotany

Module 1: Concept of Paleobotany 170
Module 2: Contribution of Bribal Sahni 182
Module 3: Technique for Paleobotanical Studies 185
Module 4: Fossil Records 192
Module 5: Fossil Plants 206

SYLLABUS

Pteridophytes:

Classification of Pteridophytes (Reimer, 1954). Stelar evolution. Telome theory. Sorus – Origin, types, and sporangial development. Heterospory and seed habit – Alternation of generations. Apogamy, Apospory, and parthenogenesis in Pteridophytes. Comparative morphology, anatomy, reproduction, and evolutionary studies of the following groups: Psilopsida, Lycopsida, Sphenopsida, and Pteropsida. Economic importance of Pteridophytes

Gymnosperms:

General character, classification of gymnosperms (Sporne, 1974). Origin and Evolution of gymnosperms. Comparative study of vegetative, anatomical, and reproductive characteristics of Cycadales, Ginkgoales, Coniferales, Gnetales. Economic importance of gymnosperms.

Paleobotany:

Concept of Paleobotany: Geological time scale. Contributions of Birbal Sahni, Technique for paleobotanical studies. Fossilization process, Types of fossils, the fossil records: systematic reconstruction and nomenclature of fossil plants, Determination of Age of Fossils, Fossil Pteridophytes: Rhynia, Sphenophyllum, Lepidocarpon, Botryopteris. Fossil Gymnosperms: Williamsonia and Cordaites.

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Module 1

General Characteristics of Pteridophytes

The word cryptogams is a synthesis of two Greek terms ***kruptos*** meaning **'hidden'** and ***gamos*** meaning **'wedded'**. This single term encompasses all plants that reproduce by means of spores and, do not produce seeds. The algae, fungi, bryophytes and pteridophytes are all cryptogams. The pteridophyta are treated as vascular cryptogams as they have a well developed conducting system. They form the subject-matter of this book. The lower cryptogams (algae, fungi and bryophyta) have no conducting system. The term pteridophyta also has a Greek origin. ***Pteron*** means a "feather" and the name was originally given to this group because of their pinnate or feather- like fronds. Vascular cryptogams are, therefore, an assemblage of seedless vascular plants that have successfully invaded the land and reproduce by means of spores.

The Pteridophytes formed a dominant part of earth's vegetation in the historic past (Two hundred eighty to two hundred thirty million years ago). In the present-day flora, excluding the non-vascular plants, they rank only next to the spermatophytes. Although they have been largely replaced by the spermatophytes in the modern-day flora, yet they occupy an important and a crucial central position in the evolutionary history of the plant kingdom. No doubt lesser in number, the pteridophytes lend a distinct charm and physiognomy to the landscape. The elegant tree ferns of the warm humid forests of eastern Himalayas, Pachmahri and Nilgiri hills, the epiphytic ferns and the hanging club-mosses of the tropical forests attract ones attention. The lithophytic and terrestrial forms that grow in comparatively larger numbers are also a source of great attraction because of their beautiful foliage. Some of them (about a dozen species) grow in water and form a luxuriant hydrophytic component of the lakes (*Salvinia*), ponds and pools (*Azolla, Marsilea*). In India about five hundred species of fern allies have been reported. Dixit (1984) has raised the number to one thousand.

The Pteridophyta have a long fossil history. Their first traces were recognised in the Silurian period of the late Paleozoic age (about 400 million years ago). They flourished well during Devonian, Mississippian and Pensylvanian periods of the late Paleozoic. Late Paleozoic can easily be regarded as the "**Age of Pteridophyta**." The tree ferns, giant horsetails and arborescent lycopods dominated the swampy landscapes of those ancient ages. The present-day lycopods (*Lycopodium, Isoetes, Selaginella, Phylloglossum*) and Sphenopsids (*Equisetales*) are the mere relicts of the mighty lycopsid and sphenopsid group which once boasted of 120-foot *Lepidodendron*, *Sigillaria*, and the colossal *Calamites*. Only the present-day ferns have somehow managed to conserve the former stature, diversity and glory of their ancestors. *Psilotum* and *Tmesipteris*, our two surviving remnants of *Psilopsids* retain the primitive features of the first land plants.

Surange (1966) has given a detailed and a comprehensive account of the Indian fossil pteridophytes. He described one fossil from Psilophyta, seven from Lycopodiophyta, twelve from Arthrophyta, and sixty-six from Pterophyta. He also observed the Indian Paleozoic and Mesozoic pteridophytes which are similar to those found in other parts of the southern hemisphere. A number of fossil ferns have been described from the Rajmahal hills in Bihar. Bose and Sah (1967) and Sharma (1969, 1971, 1972, 1973) have explored these hills and described as many as eighteen species of ferns and one of *Selaginellites* from Brindaban and Dhokuti areas. Suthar and Sharma (1986) presented a complete restoration of *Solenostelopteris jurassica* of Schizaeaceae from the jurassic flora of Rajmahal hills. They described the anatomical details of different organs. Sharma, Suthar and Bohra (1986) have given a detailed account of the work done on Indian fossil pteridophytes (Lycopods, Sphenopsids and ferns). They have pointed that pteridophytes occur throughout the Gondwana system but more frequently during Mesozoic era and the ferns make the major bulk of the assemblage. The Sphenopsida played an important role in the constitution of Glossopteris flora during the Palaeozoic whereas the Lycopods never played any significant role in the constitution of Indian fossil flora.

Largest Fern on Earth

The King Fern (*Angiopteris evecta*) holds the record for the longest fern fronds in the world! Its gigantic fronds can grow up to **25 feet (7.6 meters) long**, making it look like a prehistoric giant among ferns. Found in tropical rainforests, it thrives in warm, humid environments. The thick, fleshy base of its fronds stores water, helping it survive dry conditions.

1.1 Sporophyte

The vascular cryptogams possess an **independent sporophyte** with a vascular system. It exhibits a great variation in form, size and structure. All the living pteridophytes are nearly herbaceous except a few woody tree ferns. They may be dorsiventral or radial in symmetry and have dichotomously or laterally branched stems that bear microphyllous or megaphyllous leaves. The roots are generally adventitious, the primary embryonic root being short lived.

The stem, root and the leaves grow by means of a single, two-sided or three-sided apical cell or by a plurality of such apical initials. A distinct apical meristem has been reported in a number of Lycophyta (*Lycopodium, Isoetes*). Bhambie and Puri (1985) recognised three different configurations of shoot apical meristems as : (i) a single conspicuous pyramidal apical cell and its nearby derivatives, (ii) a group of conspicuous pyramidal or cubical apical initials surrounded by smaller cells and (iii) a lump of meristematic tissue having a central zone and capped by an outer layer. In roots, four kinds of apical organisations have been recognised: (i) a single conspicuous pyramidal cell, (ii) a gradation from one to several cubical cells, (iii) a group of inconspicuous initials and (iv) four tiers of initials. Bir, S. S. and Randhawa (1984, 1987) studied the apical organisation in rhizome, root and leaf of twelve different ferns belonging to different groups and pointed out that a single apical cell always occupies the tip of each growing organ. This single apical cell is replaced by a group of initial cells when the shoot apex becomes sufficiently grown up and well developed. They supported the classical concept of a single apical cell in ferns. The vasculature of the sporophyte may be a simple protostele, medullated protostele (siphonostele), dictyostele, or a polycyclic stelar organisation. Vessels are also present in some members (Selaginella, Equisetum). Loyal and Singh (1978) recorded the presence of vessels in about a dozen species of *Marsilea*. They also recorded the presence of branched vessel members in the root-rhizome-petiole juncture in *M. rajasthanensis*. Presence of vessels has now been reported in a number of ferns such as *Actiniopteris radiata*, *Pteris vittata*, *Nephrolepis cordifolia* and *Helminthostachys zeylanica*. Agshe (1968) reported the presence of sieve tubes in *Equisetum giganteum* and *E. arvense*. Loyal and Maheshwari (1979) noted the presence of well defined sieve plates with a number of pores in the sieve elements of rhizome and petiole of *Marsilea minuta*. The pteridophytes normally possess only **sieve cells** in the phloem and the presence of sieve tubes is considered to be an advanced feature. Secondary growth is absent in majority of the living representatives, *Isoetes* being an exception. Khandewal and Goswami (1977) reported the occurrence of periderm and cork cambium in the roots and rhizomes of *Botrychium, Helminthostachys* and *Ophioglossum*. The sporophyte produces spores that may be **homosporous** (Lycopodium, Dryopteris) or **heterosporous** (*Selaginella, Stylites, Isoetes, Salvinia, Azolla, Pilularia, Regnellidium, Marsilea*). The spores are produced in special structures called the **sporangia** that are invariably subtended by leaf-like appendages called the sporophylls. The sporangia and the sporophylls may be scattered throughout the vegetative axis or may be restricted to a particular area. They are in many cases compacted to form distinct spore producing regions called the **cones** or the **strobili** (*Selaginella, Equisetum*). The sporangia, in some cases, may be produced within specialised structures called the **sporocarps** (*Marsilea, Salvinia, Azolla*). Distinct segregation of vegetative and reproductive shoots and leaves has also been reported in some vascular cryptogams (*Equisetum arvense, Pellaea atropurpurea, Matteuccia struthiopteris*). The development of sporangia may be eusporangiate or lepto-sporangiate. The spores are haploid and germinate to give rise to the gametophyte generation, which also leads an independent existence.

1.2 Gametophyte

It is quite independent from the sporophyte and may be autophytic or saprophytic or partly autophytic and partly saprophytic. It is markedly dissimilar from the sporophyte. The homosporous pteridophytes generally have monoecious prothalli. They may be protandrous or protogynous (*Equisetum*). Dioecious prothalli have also been reported in Equisetum and some ferns (*Pteris, Pteridium, Schizea*). The prothalli in homosporous forms are either green, simple or branched and aerial structures; or they may be subterranean, colourless, tuberous and saprophytic (*Lycopodium*). Mehra and Asha (1986) have recognised seven types of mature prothalli in the pteridophytes as: (i) Cordate prothalli with a distinct cushion and two equal wings, (ii) Unequal cordate prothalli with two wings of different sizes and distinct central cushion, (iii) Lop sided prothalli with only one wing and with a cushion on lateral portion, (iv) Strap-shaped and unbranched prothalli, (v) Strap-shaped and branched prothalli, (vi) Filamentous and much branched prothalli, (vii) Subterranean, brown and mycorrhizic prothalli. The gametophytes are greatly reduced in the heterosporous vascular cryptogams (*Selaginella, Isoetes, Stylites, Marsilea, Salvinia, Azolla, Regenellidium, Pilularia*).

The sex organs may be embedded or projecting. They resemble the bryophytes in general plan of structure. The archegonia have invariably four longitudinal rows of neck cells whose height varies from two to six cells. The neck canal cells vary from one (*Selaginella* and *Equisetum*) to 14 in number (*Lycopodium*). The antheridial development may be Eusporangiate or Leptosporangiate. The antheridia have a single layered jacket enclosing a variable number of spermatozoids. They may have short stalks or may be sessile. The number of cells in a jacket also varies from 3 to many. The gametophytes are **exosporic** in homosporous forms and **endosporic** in heterosporous forms. The zygote develops into an embryo within the archegonial venter and is surrounded and nourished by the prothallial tissue. The development of the embryo may be **endoscopic**, **exoscopic** or **lateral.**

1.3 Habitat of Pteridophytes

Pteridophytes-the **first land vascular plants**, are represented by about 10,000 species distributed throughout the world, both in tropical and temperate climates. Most of the members of this group are terrestrial in nature, prefer to grow in cool and shady places, however aquatic and xerophytic habitat is not uncommon for pteridophytes. A short description of habitat of pteridophytes can be discussed as follows:

a) Terrestrial habitat

Members right from fossil pteridophytes (*Rhynia sp.*) to most advanced pteridophytes (*Pteridium*) grow in terrestrial habitats. Among Psilophyta, terrestrial species are represented by *P.*

nudum, Osmunda sp., Ophioglossum sp. etc. Lycopods growing in such habits are *L. clavatum, L.cernuum, L lucidum, L. reflexum, L.annotinum*. Plants of Lycopodium are either creepers (*L. cernuum*), climbers (*L. volubile*) or mostly epiphytic in nature (*L. phlegmaria, L.carinatum*). Most of the common species of Selaginella (*S. chrysocaulos, S. kraussiana, S. selagiuoides*), *Isoetes* (*I. coromandelina*) are terrestrial. Similar habitat is preferred by *Equisetum* sps, though its species *E. debile* can grow in hydrophytic, mesophytic as well as in xerophytic habitats. *E. palustris* prefers swampy habitats. *E. arvense* grow in open grasslands, railway embankments and exposed sandy and dry places.

Most of the ferns are terrestrial in nature, mostly grow in hilly regions (*Dryopteris, Pteris, Pteridium, Adiantum* etc.) preferring moist and shady environment.

b) Aquatic Pteridophytes

Most of the members of family Marsileaceae and Salviniaceae grow in aquatic and semi- aquatic habitats. Plants of these groups are commonly known as aquatic ferns. Few examples of aquatic pteridophytes are *M. minuta, M. quadrifolia, Salvinia natans, S. auriculata, Azolla filiculoides, A. microphylla* and *A. mexicana*. Two species of Isoetes eg. *Isoetes englemanni* and *I. Japonica* are semi-aquatic pteridophytes. *I. panchananii*, a very common plant of Pachmarhi is also considered as plant of amphibious habitat.

c) Xerophytic Pteridophytes

Most of the xerophytic plants are reported from the genus *Selaginella*. Some common Indian xerophytic species of Selaginella are *S. wightii* and *S. repanda*. *S. lepidophylla* is another xerophytic plant. *Marsilea condensata* and *M. rajasthanesis* are xerophytic pteridophytes as well.

1.4 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 **Spematophyta.** 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.

Classification proposed by Reimers (1954) and Followed by Sporne (1996)

Reimers (1954) in Engler's ***Syllabus der Pflanzen familien*** classified Pteridophytes or the seedless vascular plants as follows: -

PTERIDOPHYTA

Class: - A. **PSILOPHYTOPSIDA**
Order **Psilophytales** (fossil)
Class: - B. **PSILOTOPSIDA**
Order **Psilotales**
Class: - C. **LYCOPSIDA**
Orders 1.**Protolepedodendrales**(f)
2. **Lepidodendrales** (fossil)
3. **Lycopodiales**
4. **Selaginellales**
5. **Isoetales**

Class: - D. **SPHENOPSIDA**
Orders 1. **Hyeniales** (fossil)
2. **Sphenophyllales** (fossil)
3. **Calamitales** (fossil)
4. **Equisetales**

Class: - E. **PTEROPSIDA**
Sub-class 1. **Primofilices** (fossil)
Orders 1. **Cladoxylates** (fossil)
2. **Coenopteridales**
Sub-class 2. **Eusporangiatae**
Orders 1. **Marattiales**
2. **Ophioglossales**.
Sub-class 3. **Osmundidae**
Order 1. **Osmundales**

Sub-class 4. **Leptosporangiatae**
Orders 1. **Filicales**
2. **Marsileales**
3. **Salviniales**

Class A: Psilophytopsida (Primitive Vascular Plants)

Psilophytopsida is considered the most primitive group of vascular plants, representing an early stage in plant evolution. These plants first appeared in the Silurian and Devonian periods and were characterized by simple morphology. Unlike modern plants, they lacked true leaves and roots, instead possessing a dichotomously branching stem with vascular tissue. The sporangia, which produced spores for reproduction, were borne directly on the stem. Because they lacked leaves and roots, these plants absorbed water and nutrients directly through their stem. This class played a crucial role in the transition from non-vascular to vascular plants.

Order: Psilophytales

This order includes the earliest vascular plants, which are now mostly extinct. These plants had primitive conducting tissues and relied on spores for reproduction. Their simple body structure made them highly dependent on external moisture for growth and development. Examples: *Rhynia* – A well-studied fossil genus that had a simple, leafless body and terminal sporangia. *Asteroxylon* – A fossil plant that represents an early stage in the evolution of vascular tissues.

Class B: Psilotopsida (Whisk Ferns and Relatives)

Psilotopsida is a small but significant group of modern pteridophytes that retain some of the primitive characteristics of early vascular plants. These plants are unique in that they lack true roots and possess a simple, dichotomously branching stem, much like the extinct Psilophytopsida. However, they differ from the latter in having enations (small scale-like structures) instead of true leaves. Their sporangia are located on the stem, often in groups of three, which is a defining feature of this class.

Order: Psilotales

This order contains modern whisk ferns, which are primarily found in tropical and subtropical regions. These plants are epiphytic (growing on other plants) or terrestrial and rely on mycorrhizal fungi for nutrient absorption due to their lack of true roots. Their reproduction is spore-based, with gametophytes developing underground in symbiosis with fungi. Example: *Psilotum* – A modern representative of primitive vascular plants, found in warm and humid regions.

Class C: Lycopsida (Club Mosses and Their Relatives)

Lycopsida, commonly known as club mosses and their relatives, includes some of the most ancient vascular plants that have survived into the modern era. These plants are characterized by microphylls—small, scale-like leaves with a single vein. Unlike Psilophytopsida and Psilotopsida, Lycopsida have true roots, stems, and leaves. The sporophyte generation is dominant, and they reproduce via spores produced in cone-like structures called strobili. Some members of this group, such as *Lepidodendron*, grew into large tree-like forms in the Carboniferous period and contributed to coal formation.

Order: Protolepidodendrales – The Early Lycophytes (Extinct Order)

Protolepidodendrales is an extinct group of primitive lycophytes that existed during the Devonian and early Carboniferous periods. These plants were small and exhibited features transitional between early vascular plants and more advanced lycophytes. Unlike modern Lycopodiales, these plants had a rudimentary vascular system and limited structural differentiation. Their significance lies in their evolutionary position as ancestors of later, more developed lycophyte orders.

Order: Lycopodiales – The Modern Club Mosses

Lycopodiales, commonly referred to as **club mosses**, are small, herbaceous plants that resemble mosses but differ significantly due to their vascular tissues. They are among the few surviving members of an ancient lineage that once included tree-sized relatives. These plants are mostly **homosporous**, producing a single type of spore that develops into a bisexual gametophyte. The sporangia (spore-producing structures) are found on **sporophylls**, which can be scattered among normal leaves or clustered in specialized spore cones (**strobili**). Lycopodiales are typically found in moist, shady environments, particularly in tropical and temperate forests. Examples: *Lycopodium* – A common genus of club mosses, widely distributed in forests. It has creeping stems and small leaves that produce spores. Historically, the spores of *Lycopodium* were used as a source of flash powder due to their flammable nature. *Phylloglossum* – A rare and unique genus with limited distribution, often considered a primitive relative of *Lycopodium*.

Order: Lepidodendrales – The Giant Fossil Club Mosses (Extinct Order)

Lepidodendrales were large, tree-like lycophytes that dominated the forests of the Carboniferous period. Some species grew up to **40 meters (130 feet) tall** and had massive trunks with scaly bark, which left distinct fossil impressions. Unlike modern lycophytes, these plants had secondary growth, meaning they could thicken their stems, similar to modern trees. These plants were **heterosporous**, producing both microspores and megaspores. Their reproductive structures were massive cone-like strobili, which contained spores that were dispersed by wind. The decay of Lepidodendrales over millions of years contributed significantly to the formation of coal deposits, making them an essential part of Earth's geological history. Examples: *Lepidodendron* – A well-known fossil genus with distinct, diamond-shaped leaf scars on its bark. It played a key role in the Carboniferous forests. *Lepidocarpon* – A fossil genus closely related to *Lepidodendron*, known for its unique reproductive structures that resemble early seeds.

Order: Selaginellales – The Spike Mosses (Living Relatives of Lycopodiales)

Selaginellales, commonly known as **spike mosses**, are a group of **heterosporous** lycophytes that exhibit a remarkable ability to survive in extreme conditions. Unlike Lycopodiales, which are mostly homosporous, Selaginellales produce both **microspores** (male) and **megaspores** (female), which is considered a significant evolutionary advancement towards seed plants. One of the most fascinating features of *Selaginella* species is their ability to undergo **desiccation tolerance**. Some species, particularly *Selaginella lepidophylla* (resurrection plant), can survive extreme drought by curling up into a dormant state and then reviving upon rehydration. Example: *Selaginella* – The only living genus in this order, comprising over 700 species. These plants are commonly found in tropical and subtropical forests. Some species exhibit a creeping habit, while others grow in desert conditions.

Order: Isoetales – The Quillworts (Aquatic Lycophytes)

Isoetales is a unique order that includes **aquatic and semi-aquatic** lycophytes commonly known as **quillworts**. These plants have a distinctive corm-like stem that remains buried in the soil, while their long, grass-like leaves emerge above the surface. This group represents one of the most highly adapted lycophyte lineages, with the ability to thrive in wetland and submerged conditions. Unlike Lycopodiales, which are homosporous, Isoetales are heterosporous, producing separate male (microspores) and female (megaspores) gametes. They have a unique method of carbon fixation, known as **Crassulacean Acid Metabolism (CAM photosynthesis)**, which allows them to survive in oxygen-poor aquatic environments. Example: *Isoetes* – The only living genus in this order, with species found in freshwater habitats. Some species, like *Isoetes lacustris*, grow in lakes, while others inhabit marshy areas.

Class D: Sphenopsida (Horsetails and Their Relatives)

Sphenopsida, also known as **Equisetopsida**, is a group of vascular plants that are characterized by their jointed stems, ribbed structures, and whorled leaves**.** These plants are one of the oldest surviving plant groups, dating back to the Devonian period. During the Carboniferous period, they were highly diverse and included large tree-like plants that contributed significantly to coal formation. However, today, the group is represented by only one living genus, **Equisetum** (commonly known as horsetails).

Sphenopsids possess distinctive morphological features that set them apart from other pteridophytes. Their stems are hollow, jointed, and ridged, often impregnated with silica, which makes them rough to the touch. Because of this, *Equisetum* species were historically used as scouring tools for cleaning metal, earning them the nickname **"scouring rushes."** The leaves of sphenopsids are arranged in whorls around the stem and are typically small and scale-like. This reduction in leaf size is an adaptation that minimizes water loss, allowing these plants to survive in a variety of habitats, including marshes, riverbanks, and disturbed areas.

Order: Hyeniales – The Primitive Sphenophytes (Extinct Order)

Hyeniales is an extinct order of early sphenopsids that existed during the Devonian and Carboniferous periods. These plants are considered to be among the earliest members of the Sphenopsida lineage, but due to limited fossil evidence, their evolutionary relationships remain uncertain. They are believed to possess a relatively simple vascular system and reproductive structures compared to later sphenopsids.

Order: Sphenophyllales – The Wedge-Leaved Plants (Extinct Order)

Sphenophyllales is an extinct order of small, climbing plants that had **wedge-shaped leaves** arranged in whorls around the stem. These plants were structurally different from modern horsetails, but they shared some key characteristics, such as jointed stems and spore-based reproduction. Some paleobotanists believe that Sphenophyllales may have been **ancestral to modern Equisetales**, while others classify them as a separate evolutionary lineage. Example: *Sphenophyllum* – A fossil genus that had climbing or scrambling stems with delicate, wedge-shaped leaves. It is considered an important transitional form in the evolution of sphenopsids.

Order: Calamitales – The Giant Horsetails (Extinct Order)

During the Carboniferous era, the order Calamitales flourished and consisted of horsetails that resembled trees. These plants could reach **heights of up to 30 meters (100 feet)** and had thick, woody stems with deep-seated roots that allowed them to grow in swampy environments. Their reproductive structures were similar to those of modern horsetails, producing spores in **cone-like strobili**. The stems of Calamitales were segmented and bore whorled branches, making them structurally similar to modern *Equisetum*. However, unlike their modern relatives, Calamitales exhibited **secondary growth**, meaning their stems could increase in diameter, much like trees. This allowed them to form vast swamp forests that contributed to **coal formation**. Examples: *Calamites* – A well-known fossil genus of tree-like horsetails that was widespread during the Carboniferous period. It played a significant role in forming the coal deposits that we use today. *Calamostachys* – A fossil genus that represents the reproductive structures (strobili) of *Calamites*. These cone-like structures contained spores that contributed to the plant's reproduction.

Order: Equisetales – The Modern Horsetails (Surviving Order)

Equisetales is the **only surviving order** of Sphenopsida, represented by the single living genus **Equisetum**. Unlike their extinct relatives, modern horsetails are much smaller, typically growing between **20 cm and 2 meters tall**. They are commonly found in **moist environments**, such as riverbanks, marshes, and disturbed areas. Modern horsetails have **hollow, ribbed stems** with a high silica content, making them rough and resistant to herbivory. Their roots are well-developed, and they spread via **rhizomes**, allowing them to form dense colonies. Equisetales are **homosporous**, producing a single type of spore that develops into a bisexual gametophyte. The spores are equipped with **elaters**, which help in spore dispersal by reacting to humidity changes. Example: *Equisetum* – The only surviving genus of horsetails, with around 15 species. Some of the well-known species include: *Equisetum arvense* (field horsetail) – A common species with medicinal properties. *Equisetum hyemale* (scouring rush) – Used historically for cleaning due to its high silica content. *Equisetum giganteum* – The largest living horsetail, capable of growing up to **5 meters (16 feet) tall**.

Class E: Pteropsida

Pteropsida is the **largest and most diverse class** of Pteridophytes, encompassing **true ferns and their extinct relatives**. This group represents an advanced stage of vascular plant evolution, featuring **megaphylls**, which are large, highly divided leaves with a complex venation pattern. Unlike the small, scale-like microphylls found in Lycopsida and Sphenopsida, the broad and intricate leaves of ferns play a crucial role in photosynthesis and reproduction. Ferns exhibit a **distinct alternation of generations**, where the **sporophyte** is the dominant phase, and the **gametophyte** is reduced but free-living. The sporophytes produce spores in **sporangia**, which are often clustered into groups called **sori**, found on the underside of fronds. These spores germinate to form the **prothallus**, a small, heart-shaped gametophyte that supports sexual reproduction. Unlike seed plants, ferns rely on **water for fertilization**, as their sperm must swim to the egg for fertilization to occur.

Pteropsida includes both **extinct and modern fern groups**, ranging from ancient, tree-like forms that dominated Carboniferous forests to delicate, floating aquatic species. Their adaptability has allowed them to thrive in diverse habitats, from tropical rainforests to deserts and freshwater ecosystems.

Sub-class 1: Primofilices – The Earliest Ferns (Extinct Group)

Primofilices is a group of **early ferns** that first appeared in the **Devonian period**. These ferns had relatively simple vascular structures compared to modern ferns, and they served as an important evolutionary link between primitive vascular plants and the more complex ferns of later periods. These early ferns played a key role in colonizing land and developing specialized leaf structures that later ferns refined.

Order: Cladoxylales – Extinct Fern-like Plants

Cladoxylales is an extinct order of ferns that existed during the **Devonian and Carboniferous periods**. Unlike modern ferns, these plants had **complex branching systems**, with a unique vascular arrangement that allowed for greater structural support. Some Cladoxylales grew into **tree-like forms**, resembling the large lycophytes (*Lepidodendron*) of the same era. Examples: *Boryopteris* – A fossil genus that displayed early fern-like characteristics with intricate branching. *Zygopteris* – Another fossil genus that had a mix of features seen in both ferns and seed plants, showing an intermediate evolutionary stage

Order: Coenopteridales – A Diverse Order of Extinct Ferns

Coenopteridales is an extinct order of **highly diverse ferns**, which flourished during the **Carboniferous and Permian periods**. Some members of this group were **tree-like**, while others were small and creeping. These ferns had **complex vascular structures** and showed early adaptations for survival in different environments. Some species even displayed features resembling those of early seed plants, suggesting a possible evolutionary connection.

Sub-class 2: Eusporangiatae – Thick-Walled Spore-Producing Ferns

The ferns in Eusporangiatae are unique because they produce **thick-walled sporangia** that develop from **multiple initial cells**. This method of sporangium development differentiates them from the more advanced leptosporangiate ferns, which develop from a single cell. Eusporangiatae ferns are generally **large and tropical**, with simple but robust structures. Example: *Ophioglossum* – Known as the adder's tongue fern, this genus includes ferns with simple, unbranched fronds. They have an unusual reproductive cycle, producing spores in spike-like structures rather than sori.

Order: Marattiales – Large, Ancient Tropical Ferns

Marattiales is an ancient order of **large ferns** that have existed since the **Carboniferous period**. These ferns are characterized by their **thick, fleshy stems**, large fronds, and eusporangiate reproduction. They are mostly restricted to **tropical environments** and have retained many primitive characteristics from their early ancestors.

Order: Ophioglossales – A Unique Group of Primitive Ferns

Ophioglossales includes **primitive ferns** that are distinct from other fern groups due to their **simple, undivided fronds** and underground rhizomes. These ferns are often found in tropical and subtropical regions, where they thrive in humid environments. Example: *Angiopteris* – A large, primitive fern known for its enormous fronds and thick rhizomes. It is commonly found in tropical rainforests.

Order: Osmundales – Primitive Ferns with Fossil Records

Osmundales is a group of **ancient, primitive ferns** with an extensive **fossil record** dating back to the **Triassic period**. These ferns are sometimes called **“royal ferns”** and are considered to be an evolutionary link between eusporangiate and leptosporangiate ferns. Their vascular structures are **well-preserved in fossils**, making them an important subject of study in paleobotany. Example: *Osmunda* – A living genus that includes **large, long-lived ferns** found in wetlands and moist forests.

Sub-class 4: Leptosporangiate Ferns

Leptosporangiate ferns represent the largest and most advanced group of ferns. Unlike eusporangiate ferns, their sporangia develop from **a single initial cell** and have thin walls, which allow for efficient spore dispersal. This group includes true ferns, water ferns, and floating ferns**,** which are widely distributed across various habitats.

Order: Filicales – The True Ferns

Filicales, also known as **true ferns**, make up the majority of modern ferns. They are characterized by their highly divided fronds**,** sori on the underside of leaves, and a wide range of habitats, from tropical rainforests to temperate woodlands. Examples: *Hymenophyllum* – A group of **filmy ferns** with delicate, translucent fronds that require high humidity. *Adiantum* – Known as maidenhair ferns, these plants have distinctive fan-shaped leaves and are often cultivated as ornamental plants.

Order: Marsileales – Water Ferns

Marsileales includes **aquatic ferns** that have **clover-like leaves** and produce spores in hardened structures called **sporocarps**. These ferns are well adapted to wetland environments and are often found in rice fields and marshes. Example: *Marsilea* – A genus of **water ferns** that resembles clover and grows in shallow freshwater habitats.

Order: Salviniales – Floating Ferns

Salviniales consists of small, free-floating ferns that are commonly found in ponds, lakes, and slow-moving water bodies. These ferns are **heterosporous**, meaning they produce two types of spores (microspores and megaspores), a feature that links them to the evolution of seed plants. Examples: *Salvinia* – A floating fern that forms dense mats on water surfaces, often used for wastewater treatment and preventing mosquito breeding. *Azolla* – A nitrogen-fixing aquatic fern that is used in rice paddies to improve soil fertility.

EXAM POINTS

MEMORY TIP

"Playful Penguins Love Singing Every Pleasant Song Over Oval Lakes, Mountains, and Streams"

Each capitalized letter corresponds to the **major classes and orders** in the classification.

Breaking it Down Correctly:

Class A: PSILOPHYTOPSIDA

- **P**layful → **Psilophytales** (Fossil)

Class B: PSILOTOPSIDA

- **P**enguins → **Psilotales**

Class C: LYCOPSIDA

- **L**ove → **Lycopsida**
  - **P**lease → Protolepidodendrales (Fossil)
  - **L**et → Lepidodendrales (Fossil)
  - **L**izards → Lycopodiales
  - **S**ing → Selaginellales
  - **I**ntensely → Isoetales

Class D: SPHENOPSIDA

- **S**inging → **Sphenopsida**
  - **H**appy → Hyeniales (Fossil)
  - **S**ongs → Sphenophyllales (Fossil)
  - **C**heer → Calamitales (Fossil)
  - **E**xcitedly → Equisetales

Class E: PTEROPSIDA

- **E**very → **Pteropsida**

Sub-class 1: Primofilices (Fossil)

- **P**leasant → Primofilices
  - **C**harming → Cladoxylates (Fossil)
  - **C**olors → Coenopteridales

Sub-class 2: Eusporangiatae

- **O**ver → Eusporangiatae
  - **M**ountains → Marattiales
  - **O**rganized → Ophioglossales

Sub-class 3: Osmundidae

- **O**val → Osmundidae
  - **O**ceans → Osmundales

Sub-class 4: Leptosporangiatae

- **L**akes → Leptosporangiatae
  - **F**low → Filicales
  - **M**aking → Marsileales
  - **S**plashes → Salviniales

Virtual Resources

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Pterido Traits

1. **What makes Pteridophytes evolutionarily significant?**
A. First seed plants
B. Transition to vascular plants
C. Dominance in dry climates
D. Development of flowers

2. Which fossil Pteridophyte contributed to coal formation?
A. Psilotum B. Lepidodendron
C. Equisetum D. Marsilea

3. What distinguishes Selaginella from Lycopodium?
A. Homospory
B. Heterospory
C. Absence of roots
D. Dominant gametophyte

4. Why are vessels in Selaginella significant?
A. Primitive trait B. Advanced feature
C. Aquatic adaptation D. Secondary growth

5. What makes leptosporangiate ferns advanced?
A. Single-cell sporangia
B. Thick-walled sporangia
C. Absence of spores
D. Dominant gametophyte

6. Why did Pteridophytes decline in modern flora?
A. Lack of spores
B. Competition from Spermatophytes
C. Inability to photosynthesize
D. Absence of vascular tissue

7. What is the significance of heterospory?
A. Asexual reproduction
B. Step toward seeds
C. Reduced water dependence
D. Larger sporophytes

8. How does Equisetum differ from Psilotum?
A. Jointed stems B. True roots
C. Heterospory D. Seed production

9. Why are sieve tubes in Marsilea significant?
A. Primitive trait B. Advanced feature
C. Xerophytic adaptation D. Secondary growth

10. What role did Pteridophytes play in the Carboniferous?
A. Dominant swamp flora
B. First land colonizers
C. Primary aquatic producers
D. First flowering plants

11. Which Pteridophyte is xerophytic?
A. Salvinia B. Marsilea
C. Selaginella lepidophylla D. Equisetum

12. What is unique about Isoetes?
A. Secondary growth B. Homospory
C. Dominant gametophyte D. Absence of roots

13. Which class includes Psilotum?
A. Lycopsida B. Sphenopsida
C. Psilotopsida D. Pteropsida

14. What characterizes Sphenopsida?
A. Microphylls
B. Jointed stems
C. Megaphylls
D. Eusporangiate sporangia

15. Which group is heterosporous?
A. Lycopodium B. Selaginella
C. Equisetum D. Psilotum

16. What is the ploidy of Pteridophyte spores?
A. Diploid B. Triploid
C. Haploid D. Polyploid

17. Which fossil is associated with Rajmahal Hills?
A. Solenostelopteris B. Lepidodendron
C. Calamites D. Psilotum

18. What is the significance of Calamites?
A. First seed plants
B. Giant Carboniferous horsetails
C. Earliest non-vascular plants
D. Modern ferns

19. Which Pteridophyte is aquatic?
A. Selaginella B. Marsilea
C. Lycopodium D. Equisetum

20. What is the main feature of Eusporangiate ferns?
A. Single-cell sporangia
B. Thick-walled sporangia
C. Absence of spores
D. Dominant gametophyte

Answers

1-B,2-B,3-B,4-B,5-A,6-B,7-B,8-A,9-B,10-A,11-C,12-A,13-C,14-B,15-B,16-C,17-A,18-B,19-B,20-B

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Module 2

Stelar Evolution

2.1 Stele

Sachs (1875) formed an idea that the vascular system of the plant body is a continuous system. The idea was introduced with a greater emphasis by Van Tiegham and Douliot in 1886. They proposed and developed the **Stelar theory** according to which the root and the stem are fundamentally similar in gross anatomy, because in both the cortex encloses the central part of the axis. The central part or the core of the axis is called the stele. So, a stele (Greek word meaning column) is the core of the axis which includes the vascular system, the interfascicular portion, the pith (if present) and some surrounding portions of the fundamental tissue in the vicinity of vascular bundles (pericycle). This concept of the stele as proposed by Van Tiegham and Douliot was widely accepted by the plant morphologists and plant anatomists. The term stele is restricted only to the primary vascular tissue.

A debatable question is the nature of the stele, or the vascular cylinder in the filicophyta (ferns) and the seed plants. In these plants the large leaf traces seem to play a prominent role in determining the vascular organisation of the stem. Wardlaw and Wetmore (1951) and also Wardlaw (1946) consider these large leaf traces in the megaphyllous vascular plants as distinct units of the structure and regard the stele or the vascular cylinder of the stem as a composite structure. According to them the stem stele is made up of both foliar (leaf) and cauline (stem) vascular elements. The ratio between the two types of elements constituting the stem stele no doubt varies with plants. Wetmore (1953), however, regards that in some ferns the entire vascular organisation of the stem is foliar in nature. It has no doubt been shown (Wardlaw, 1944) that in *Dryopteris dilatata* "the incipient vascular tissue originates in continuity with the active meristems of shoots, buds, leaves and roots." The distinguishing vascular strand of the young leaf primordium, at the shoot apex, becomes united with the complete vascular cylinder of the stem. There are no leaf gaps at this stage. But lower down, i.e. as we proceed towards the mature parts of the stem, small leaf gaps begin to appear at the points of insertion of the leaf trace on the stele of the stem. These small leaf gaps enlarge in size with the enlargement of leaf trace bundles. Since the leaves are arranged in close spirals on the mature stem, the stele of the stem becomes broken by the overlapping **leaf gaps** and appears dissected. These observations indicate that there is a close relationship between the stelar organisation of the stem and the enlargement of the leaves. The formation of the leaf gaps has been explained by Wardlaw (1968) in his own words: "An anatomical analysis also shows that in growing leaf bases, there is a very considerable tangential enlargement, due chiefly to an increase in the volume of the cortical and medullary parenchyma. Concomitant with these developments, the leaf trace which is initially a crescentic mass in cross section, is pulled apart into four or five separate strands, with parenchyma in between. In brief the distribution of growth in the leaf base is such that the initially crescentic vascular trace is disrupted by being subject to tensile stress. The cylindrical, still undifferentiated stele of the shoot is also affected by this tensile stress and hence the formation of the leaf gaps."

It is evident from the above description that changes in the stelar organisation of the shoot are brought about by the appearance of leaf traces and leaf gaps. Wardlaw suggested that these changes can be stopped by defoliation of the shoot apices. He (1944, 1949) conducted experiments on certain ferns (*Dryopteris dilatata, D. filix-mas, Angiopteris evecta, Onoclea sensibilis*, species of *Osmunda* and *Todea*) by removing the young leaf primordia at the apices of the shoots. He obtained the desired results with *Dryopteris dilatata* and *D. filixmas*. In both these cases the young leaf primordia were removed from the shoot apices. Normally the stems show a dictyostelic condition. Under experimental conditions, i.e., when leaf primordia were removed the stem in that region showed solenostelic stelar organisation. Even protostelic condition was also obtained by such experiments. These experiments show that the stelar organisation of the stem in the filicophyta is dependent, to a greater degree on the presence or absence of leaves.

In the microphyllous vascular cryptogams (*Selaginella, Lycopodium, Isoetes*) the leaf traces do not leave any leaf gaps in the stem stele, which therefore remains undisturbed. In these cases the vascular system of the leaf has no bearing on the stem stele.

Creeping Stele

In creeping pteridophytes like ***Nephrolepis*** (sword fern), the stele adapts to horizontal growth, allowing the plant to spread across the forest floor. This adaptation helps the fern colonize new areas and compete for resources.

2.2 Types of steles

Easu (1953) and Smith (1955) recognise two principal types of stelar organisation among the vascular plants. These are: (A) **the Protostele**, and (B) **Siphonostele**.

A. The Protostele

It is simplest and the primitive type of stele. In this case the vascular cylinder consists of the solid core of xylem surrounded by phloem, pericycle, and endodermis. There is no pith. The name protostele was suggested by Jeffrey (1897,1899, 1902) and is regarded as a fundamental stelar type of the vascular plants from which the other type originated in the course of evolution. Brebner (1902) classified the protostele into two: -

(i) Haplostele:

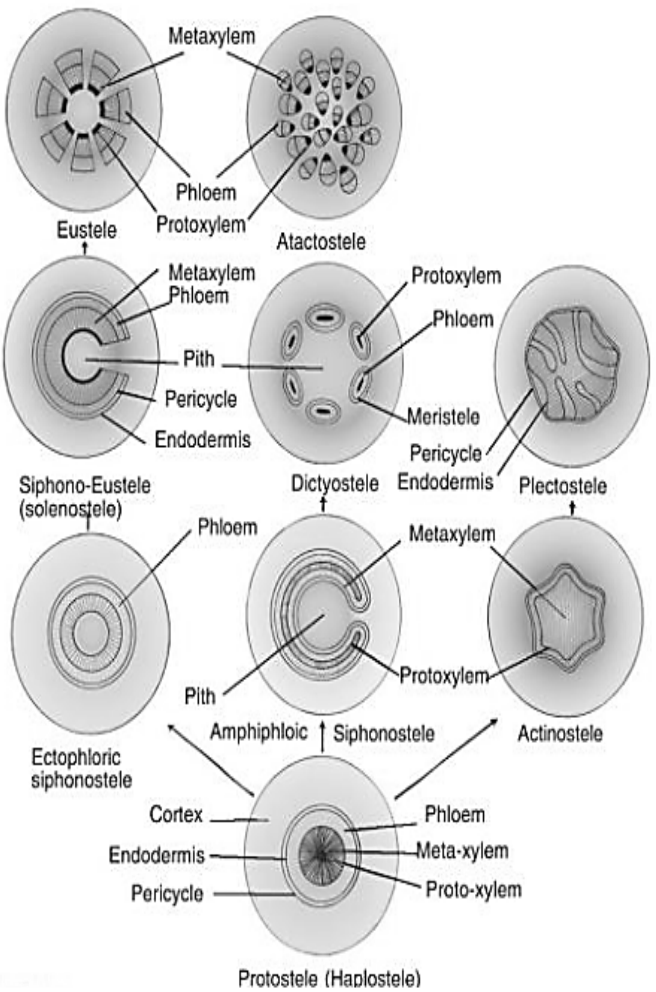
In this type of protostele the central core of xylem is smooth and is surrounded by a uniform layer of phloem. It was found in the extinct psilophytales like *Rhynia* and *Horneophyton*. In the living genera it is characteristic of many species of *Selaginella*, e.g., *S. chrysocaulos, S. kraussiana*, etc. In *S. chrysocaulos* the ribbon-shaped haplostele has two protoxylem groups, i.e., it is diarch and exarch. In *S. kraussiana* there are two haplosteles. Such a condition is called **distelic** as compared to **monostelic** condition in *S. chrysocaulos*. In *S. willdenovii* the condition is tristelic or even tetrastelic because in this case there are three or four haplosteles. In *S. selaginoides* the monostelic haplostele has metaxylem surrounding completely the protoxylem. This condition of xylem is called **mesarch**. Some ferns like *Gleichenia dichotoma, Cheiropleuria* and *Lygodium* have stems that maintain protostelic condition throughout the life of the plant. In the former case the xylem is composed of tracheids mixed with parenchyma cells.

(ii) Actinostele:

In this case the xylem core is stellate or starshaped as in *Lycopodium serratum* and in the upper portions of the stem in *Selaginella selaginoides*. It also occurs in **Psilotum.** The extinct psilophyte named **Asteroxylon** also possessed a star-shaped actinostele. In *Lycopodium volubile* and *L. clavatum* the xylem occurs in the form of parallel plates alternating with phloem plates. Such an actinostele has been named as **plectostele** by Zimmermann (1930, 1938). In *L. cernuum* the actinostele consists of irregular groups of xylem embedded in mass of phloem. Such actinostele is called **mixed protostele**.

Climbing Stele

In climbing pteridophytes like ***Lygodium*** (climbing fern), the stele adapts to support vertical growth. Its flexible, elongated structure allows fronds to twine around supports, helping the fern climb trees and access sunlight in dense forests.



Various types of stelar organisation in the vascular plants

Hymenophyllaceae Protostele Variation

A very interesting sequence of variation in the protostele is illustrated by members of the family Hymenophyllaceae. These can be listed as below:

1. In Trichomanes scandens the xylem forms a central core with a little parenchyma in the centre. The protoxylem forms peripheral groups (exarch).

2. In *Hymenophyllum dilatatum* and *H. demissum* the metaxylem forms a ring around the central parenchyma in which lie embedded a few protoxylem tracheids.

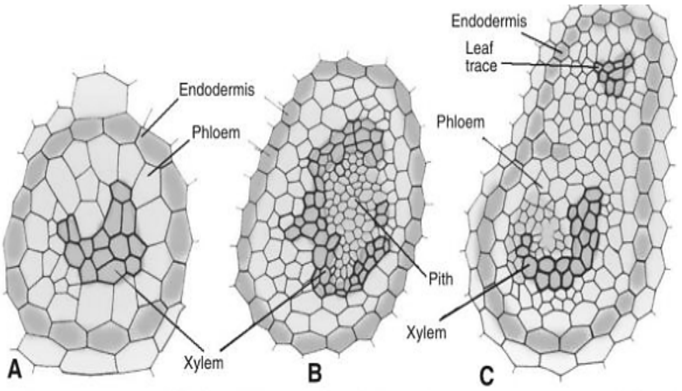
3. In *H. scabrum* the metaxylem ring is interrupted by parenchyma gap thus forming two arcs. The protoxylem lies embedded in the central parenchyma.

4. In *Trichomanes muscoides* the lower xylem arc and phloem are absent thus making a collateral bundle.

B. The Siphonostele

(a) Origin

Medullated protostele is called siphonostele. It is characteristic of the filicophyta. During the development of siphonostele the central core of xylem is replaced by parenchymatous cells so that a definite pith surrounded by xylem appears in the centre. Series of transverse sections cut from the base upwards of rhizomes of certain ferns (*Aneimia, Schizaea*) clearly reveal the development of siphonostele. In *Aneimia phyllitidis* (Bower 1923) the stele at the base of the rhizome is a typical protostele. The leaf traces given out at this stage do not disturb the protostele and also do not interrupt the endodermis. Higher up the sections reveal the presence of a central pith enclosed completely by a ring of tracheids. In this case the whole vascular system is surrounded by endodermis during the development of pith. Similar developmental studies in *Schizaea*, and in the sporelings of *Botrychium, Helminthostachys, Osmunda* and *Gleichenia pectinata*, reveal that the vascular cylinder is completely surrounded by endodermis during the development of pith. Gewirtz and Fahn (1960) conducted similar studies on developmental anatomy of *Ophioglossum lusitanicum*. These observations support the view that the pith is **intraxylary** or **intrastelar** in origin. Boodle (1901), Gwynne Vaughan (1908), Bower (1911), Petry (1914), Thompson (1920), and Gewirtz and Fahn (1960) support this theory of intrastelar origin of pith. Presence of isolated tracheids in the pith in *Botrychium virginianum*, B. *lunaria, B. ternatum* and *Osmunda regails* support the intrastelar origin of pith.



Jeffrey (1897, 1899, 1902, 1917) put forth his view that the pith is extrastelar in origin. He believed that pith originated as a result of invasion of the parenchymatous cells of the cortex into the stele. He assumed that this occurred through leaf and branch gaps. He used the presence of inner endodermis between the pith and the vascular tissue as a proof of extrastelar origin of pith. According to him endodermis penetrated inwards together with the parenchyma of the cortex. This argument has been challenged by certain observations on *Selaginella* and *Pteridium*. In both these genera the endodermis has been proved to be stelar in origin. In *Pteridium aquilinum* Chang (1927) observed that endodermis pericycle and protophloem arise from a common layer of procambial cells.

(b) Types of Siphonostele

The siphonostele is further classified into two types according to the positions of the phloem and the xylem. These are: (i) ectophloic siphonostele, and (ii) amphiphloic siphonostele.

In the **ectophloic siphonostele** the pith is surrounded by a xylem strand, which in turn is surrounded by phloem, pericycle and endodermis. So, in this case phloem is present only external to the xylem. This type of siphonostele is found in some ferns like *Osmunda, Schizaea* and in some dicotyledonous angiosperms like *Phlox, Lindenbergia, Nicotiana* and *Salix*.

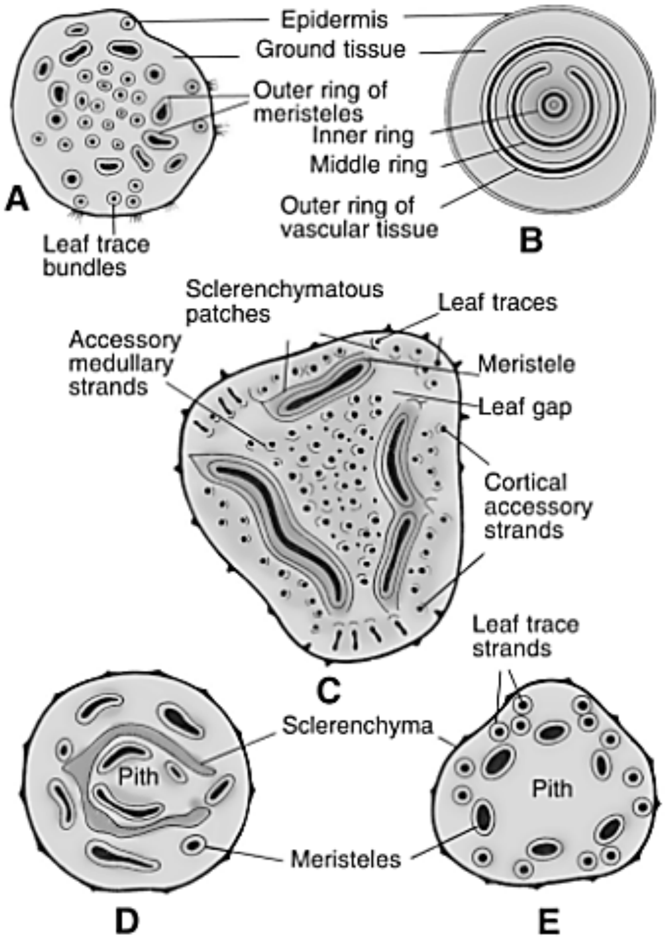
In the **amphiphloic siphonostele** the pith is surrounded by inner endodermis, inner pericycle, inner phloem, xylem, outer phloem, outer pericycle and outer endodermis. It is found commonly among the fern, e.g., *Adiantum, Marsilea, Dipteris, Platyzoma* etc. So, in amphiphloic siphonostele the phloem surrounds the xylem internally as well as externally.

In *Todea hymenophylloides* the inner endodermis appears as a discontinuous sheath. There is no internal phloem.

Both the ectophloic and amphiphloic siphonosteles may occur in the form of a continuous cylinder of vascular tissue. In these cases the leaf traces do not leave leaf gaps and therefore the continuity of the stele is uninterrupted as in some species of *Selaginella*. Such a siphonostele is termed by Jeffrey (1910) as *Cladosiphonic siphonostele*. In the filicophya the siphonostele may be perforated by smaller or larger leaf gaps. Such a perforated siphonostele is named by Jeffrey as Phyllosiphonic. Both these types can be distinguished among ectophloic and amphiphloic siphonosteles. Appearance of leaf gaps in the siphonostele (Phyllosiphonic) leads to a number of modifications.

If the stem or the rhizome bears leaves at distance the leaf gaps also appear at a considerable distance form each other. At such places the stele is interrupted and appears horseshoe-shaped. The leaf trace appears as a small crescentic bundle. e.g., *Adiantum pedatum*. The leaf gap closes at a higher level and the stele again becomes complete and circular. So the stele is perforated at places corresponding to the origin of leaf traces and is complete in between. Such a siphonostele is called **solenostele**. The solenostele may be ectophloic or amphiphloic depending upon the type of siphonostele from which it is derived.

In a number of species of *Dryopteris, Pteris, Pellaea rotundifolia* and a number of other filicophyta, the rhizome is short and the leaves overlap each other. This leads to the overlapping of leaf gaps in the stele so that the lower part of one leaf gap is parallel with the upper part of another gap. Such an arrangement of the leaf gaps results in the formation of a cylindrical network of interconnected vascular strands. A cross-section of such a stele reveals the presence of separate vascular bundles separated by parenchymatous patches. Each such vascular bundle is of concentric type and consists of a central core of xylem surrounded by phloem, pericycle and endodermis. Individually these bundles are called the **meristeles**. Anatomically the meristeles are amphicribral bundles with exarch, mesarch or endarch, xylem. Such a siphonostele is termed as s dictyostele. It is derived from the amphiphloic siphonostele



Stelar types in ferns
A. Polycyclic dictyostele in *Platycerium aethiopicum*; B. Polycyclic stele in *Matonia pectinata*; C. Dictyostele in *Cyathea imrayana*; D. T.S. rhizome of *Pteridium aquilinum* showing dicyclic dictyostele; E. T.S. rhizome of *Dryopteris chrysocoma* showing dictyostele.

Appearance of overlapping leaf gaps in an ectophloic siphonostele results in the splitting of such a stele into separate collateral vascular bundles. Such a modification of ectophloic siphonostele is called **eustele** and is characteristic of seed plants. Like the dictyostele the vascular strands in the eustele are also interconnected. In some cases, the vascular strands are scattered and such a stele is called **atactostele** (Nast, 1944; Esan 1953). It is found in the monocotyledons. Sometimes the vascular bundles in the eustele are bicollateral (cucur-bitaceae, solanaceae), i.e., phloem is present on either side of the xylem (externally as well as internally). Such a condition is believed to be a 'secondary specialisation.' It should not be regarded as a relic of the primitive structure found in the filicophyta.

Sometimes the stele is not interrupted solely by leaf gaps, but some interruptions appear as a result of secondary reductions of the vascular tissue and form interfascicular parenchyma termed as medullary rays. Such parenchymatous interruptions are called **perforations**.

In some filicophyta e.g., *Matonia, Pteridium, Pteris vittata* and *Marattia*, two or more concentric cylinders of vascular tissue are present. Such a stele is called **polycyclic stele**. In *Pteridium aquilinum* there are two concentric circles of vascular tissue. The outer circle is composed of a number of meristeles, i.e., it is dictyostelic. The inner circle consists of only two meristeles. Two patches of sclerenchyma of the ground tissue are present between the two circles of meristeles. Polycylic stele in *Pteris elata* var. *karsteniana* consists of larger number of meristeles in the inner ring than in the outer ring. In this case there are no sclerenchyma patches. There are three concentric rings of vascular tissue in *Matonia pectinata*. Each ring has a typical solenostelic structure. Four concentric cylinders of vascular tissue have been recorded in Pteris podophylla (Bower, 1923). All the four are siphonostelic in nature. In *Platycerium* aethiopicum there are four or more irregular concentric circles of meristeles.

The anatomical study of the stems in dendroid *Cyatheaceae* reveals a still more complex vasculature. Transverse section through the stem of *Cyathea imrayana* reveals the presence of broad meristeles that are enclosed within broad plates of sclerenchyma. The leaf traces arise as number of strands that run obliquely through the cortex. Each leaf trace arises from the lower margin of each leaf gap. In addition to this vasculature a number of other vascular strands are present in the pith and the cortex. Each one of them is surrounded by endodermis and is often accompanied by a sclerenchymatous band. These cortical and medullary strands may anastomose freely and end blindly during their course downwards. These vascular strands are considered to be the **accessory strands** that have originated in the pith or the cortex without any connection with the general vascular system.

Sporne (1962) uses a different nomenclature for the stelar organisation in the vascular cryptogams. He regards the ectophloic siphonostele as **medullated protostele**. The term **solenostele** has been used for amphiphloic siphonostele and such siphonosteles that are perforated by leaf gaps at considerable distances. Sporne has not used the term siphonostele for the pteridophytes. The term **dicytostele** is used when leaf gaps overlap and the solenostele is much dissected. So according to Sporne the steles are of the following types: (i) protostele; (ii) medullated protostele; (iii) solenostele; (iv) dictyostele; and (v) polycyclic stele.

Carbon Age

During the Carboniferous period (360–300 million years ago), giant pteridophytes like *Lepidodendron* and *Calamites* dominated the landscape. Their massive steles supported tree-like structures, and when these plants died, they formed the coal deposits we use today. So, every time you see coal, think of pteridophytes!

2.3 Evolution of the Stelar System

The consensus of opinion now favours Jeffrey's belief (1898) that protostele is the primitive type of stele. It is considered to be a fundamental stelar organisation that was present in the earliest vascular plants and is now retained by some living vascular cyptogams like *Psilotum, Tmesipteris, Selaginella, Lycopodium, Gleichenia*, etc. The primitive vascular plants like the extinct psilophytales also possessed protostelic vascular organisation e.g., *Rhynia, Horneophyton, Asteroxylon*. Presence of exclusively protostelic stems in the earliest vascular plants and their retention in some of living vascular cryptogams lends a strong support to Jeffrey's view that protostele is phylogenetically a primitive type of vasculature. In its simplest form the protostele is **haplostelic**. During further elaboration the central core of xylem became irregular and assumed an almost star-like shape (*Asteroxylon*, some species of *Selaginella* and *Lycopodium*). Such a modification of protostele was termed as **actinostele** by *Brebner*. As a result of further elaboration, the xylem splits up into a number of parallel plates alternating with phloem. Such a modification was called **plectostele** by Zimmermann (1930). It is found in some species of *Lycopodium*. Haplostele to actinostele and then to plectostele is considered to be one line of evolution of the protostele (Zimmermann, 1930). It can be regarded as a **Lycopsid line of evolution**.

Another very important evolutionary change that occurred in the protostele was the appearance of the central pith. This step led to many important changes in the protostelic organisation and gave rise, on further elaboration, to complicated stelar types. The origin of pith has been explained variously by various authors. Two theories have been put forth to accord for its origin. These are the **intrastelar theory** and the **extrastelar** or **invasion theory**. Appearance of pith led to the conversion of the protostele into a new type of stele called the **siphonostele**. Elaboration of siphonostele also followed two courses of evolution:

(a) The appearance of pith resulted in the formation of a stele consisting of a central pith surrounded by a complete ring of xylem, which in turn was surrounded by a complete ring of outer phloem, pericycle and endodermis. Such a stele was designated **as ectophloic siphonostele** (medullated protostele). In its simplest form such a siphonostele is uninterrupted by leaf gaps and is also called **Cladosiphonic**. In the megaphyllous vascular plants the complete and uninterrupted cylinder of ectophloic siphonostele becomes interrupted by the appearance of leaf gaps. It is now called **phyllosiphonic**. In case the leaves do not overlap the stele is interrupted only at considerable distances (nodes) by one leaf gap. In between the two gaps the vascular cylinder remains complete. Such a stele is also called solenostele or **siphono-eustele** (Zimmermann, 1930, 1938). In case the leaves on the stem overlap the leaf gaps also overlap and lead to the formation of a much dissected stelar organisation. It is made up of a number of separate and collateral vascular bundles. This condition is called **eustele** and is met with in the seed plants. In case the vascular bundles are scattered, as in monocotyledons, the stele is termed as **atactostele**.

(b) During another line of evolution, the medullation of the protostele was followed by the appearance of phloem on either side of the xylem and likewise internal pericycle and endodermis also appeared. As a result, the siphonostele consisted of a central pith surrounded by internal endodermis, internal pericycle, internal phloem, xylem, external phloem, external pericycle and external endodermis. Such a siphonostele is called **amphiphloic siphonostele** (*Marsilea, Adiantum*). It may be **cladosiphonic** or **phyllosiphonic**. The phyllosiphonic amphiphloic siphonostele with only one leaf gap at the node is called **amphiphloic solenostele**. In case the lea gaps over-lap the resultant stele is called the **dictyostele**. Dictyostele is very common in the filicophyta. In many eusporangiate and leptosoporangiate ferns the dictyostelic stems are protostelic at their bases. One such example is afforded by *Ophioglossum lusitanicum* (Gewirtz and Fahn, 1960). Recent experimental studies (Wardlaw, 1944, 1968) also reveal that dictyostelic condition can be changed to solonostelic or even protostelic condition by removing the young leaf primordia from shoot apices (*Dryopteris dilatata*). All these observations prove that protostele is the basic or the fundamental stelar type from which the complicated steles or vascular systems arose by elaboration.

Polycyclic condition exhibited by some ferns like *Marattia, Matonia, Pterdium, Cyathea*, etc., also originated from the protostelic condition by further elaboration. This is borne out by the fact that in *Matonia pectinata* there is a regular transition from protostelic condition to solenostele and then to a polycyclic condition. The stem is protostelic at the base, then becomes solenostelic and ultimately polycyclic. (Three concentric circles of siphonosteles). This developmental phenomenon is termed as recapitulation. Occurrence of such a developmental phenomenon lends further support to Jeffery's view that protostele is a primitive condition.

A number of workers have presented a different interpretation of the evolution of stelar system in the seed plants. They believe that the leaf gaps of the seed plants (Gymnosperms and Angiosperms) are not morphologically equivalent to those of ferns. Namboodri and Beck (1968) and Beck (1970) have put forth an explanation that the **eustele** in gymnosperms is not derived from filicean type of **siphonostele** nor are there any filicean type of leaf gaps. These authors studied the stelar organisation in primitive gymnosperms like *Calamopitys foerstei* and *Lygenopteris oldhamia* and found that the eustele in these originated direct from the **protostele** through longitudinal dissection, without any intervening siphonostelic stage. Such a mode of organisation of the primary vasculature in the woody angiosperms that are now living has been studied by Dormer (1945, 1946, 1954); Devadas (1970), Devadas and Beck (1971, 1972), Sporne (1958) and Slade (1971). According to their view filicean leaf gaps are absent in the eustele of primitive gymnosperms like *Lygenopteris*. It has now been held that angiosperms originated from the Pteridosperms (Takhtajan, 1969; Delevoryas, 1962; Beck, 1962, 1970), and if this view is correct then there are no fern type leaf gaps in the angiosperms also. Such a view has been supported by Sporne (1958) and Slade (1971). So according to this interpretation the eustele originated directly from the protostele without the intervention of Siphonostele.

Namboodri and Beck (1968) have put forth a new concept that parenchymatous areas may arise in the stele without having any connection with the leaf gaps. Such a conclusion is based on detailed study of the primary vasculature in gymnosperms and angiosperms (Slade, 1971) and is against Jeffery's leaf gap concept for ferns.

The above view supports another new interpretation that the primary vasculature of the stem is Cauline and not foliar. The protostele is clearly axial, not a foliar structure. "That this is true be- comes very apparent when one considers that the ancestral psilophytes from which the protostelic progymnosperms must have evolved were leafless" (Devadas and Beck, 1972).

Usually, primary vasculature of stem is considered to be foliar in nature (Esau, 1965 b; Philipson and Balfour, 1963; O'Neil, 1961; Nast 1944); but the above view of its cauline nature is at variance with this.

2.3.1 Leaf Traces and Leaf Gaps

A leaf trace is that part of the vascular cylinder that extends between the leaf base and the point where it merges with the vascular system of the stem. The number of the leaf traces associated with one leaf or may be more than one. So, leaf traces connect the vascular system of the leaf with that of the stem.

In ferns and the seed plants the portion, lying immediately above the point of divergence of leaf trace from the vascular cylinder of the stem, becomes parenchymatous. In parenchymatous region the vascular elements are absent, but this region is limited to only a short distance up, beyond which the vascular tissue is present. These parenchymatous regions in the vascular cylinder are described as **Leaf gaps** or **lacunae**. The vascular plants in which the leaf traces leave leaf gaps are called **megaphyllous**. There are no leaf gaps in the lower vascular plants such as *Selaginella* and *Lycopodium*. In these cases, the leaves are small and their comparatively thin leaf traces do not leave leaf gaps. Such plants are called **microphyllous**.

2.3.2 Branch Traces and Branch Gaps

The branches develop from buds and have vascular connections with the main axis. These vascular connections that connect the vascular system of a branch with that of the stem are called **branch traces**. Similarly, there are branch gaps which are the parenchymatous areas in stem vascular system just above the origin of branch trace. The leaf gaps and the branch gaps are not actually breaks in the continuity of the vascular cylinder because the vascular tissue maintains lateral connection just above and below the gap.

EXAM POINTS

Types of Steles

Stele	Characteristics	Examples
Protostele	Simplest, primitive type. Solid core of **xylem** surrounded by **phloem, pericycle, and endodermis**.	*Rhynia*, *Selaginella*, *Psilotum*
Siphonostele	**Medullated protostele** with a central **pith** surrounded by **vascular tissue**.	*Osmunda*, *Adiantum*
Dictyostele	Highly dissected siphonostele with **overlapping leaf gaps**, forming **separate meristeles**.	*Dryopteris*, *Pteris*
Eustele	Vascular bundles arranged in a **ring**, common in seed plants.	**Dicots** (e.g., *Salix*, *Nicotiana*)
Atactostele	**Scattered vascular bundles**, seen in monocots.	*Zea mays*, *Palm*

Vascular Shift

1. What is the simplest and most primitive type of stele?
A. Siphonostele B. Protostele
C. Dictyostele D. Eustele

2. Which type of stele is characterized by a central pith surrounded by xylem and phloem?
A. Protostele B. Plectostele
C. Actinostele D. Siphonostele

3. In which group of plants is the haplostele commonly found?
A. Ferns B. Selaginella
C. Angiosperms D. Gymnosperms

4. What is the term for a stele with star-shaped xylem?
A. Haplostele B. Solenostele
C. Plectostele D. Actinostele

5. Which stele type is found in Lycopodium with parallel xylem and phloem plates?
A. Haplostele B. Actinostele
C. Plectostele D. Siphonostele

6. What is the term for a siphonostele with phloem on both sides of the xylem?
A. Ectophloic B. Amphiphloic
C. Cladosiphonic D. Phyllosiphonic

7. Which stele type is characterized by overlapping leaf gaps and dissected vascular bundles?
A. Protostele B. Siphonostele
C. Dictyostele D. Eustele

8. What is the term for a stele with scattered vascular bundles, as seen in monocots?
A. Protostele B. Siphonostele
C. Eustele D. Atactostele

9. Which stele type is considered the most advanced in seed plants?
A. Protostele B. Siphonostele
C. Eustele D. Dictyostele

10. What is the term for a stele with concentric rings of vascular tissue?
A. Polycyclic stele B. Solenostele
C. Dictyostele D. Actinostele

11. Which theory suggests that the pith originates from cortical parenchyma invading the stele?
A. Intrastelar theory B. Extrastelar theory
C. Cauline theory D. Foliar theory

12. What is the term for the parenchymatous region above a leaf trace in the stele?
A. Leaf gap B. Branch gap
C. Medullary ray D. Pericycle

13. Which group of plants lacks leaf gaps in their stelar organization?
A. Ferns B. Selaginella
C. Angiosperms D. Gymnosperms

14. What is the term for the vascular connection between a branch and the main axis?
A. Leaf trace B. Pericycle
C. Medullary ray D. Branch trace

15. Which stele type is derived from an amphiphloic siphonostele with overlapping leaf gaps?
A. Protostele B. Solenostele
C. Dictyostele D. Eustele

16. What is the term for a siphonostele with a single leaf gap at each node?
A. Cladosiphonic B. Phyllosiphonic
C. Solenostele D. Dictyostele

17. Which stele type is found in the rhizome of Dryopteris?
A. Protostele B. Siphonostele
C. Dictyostele D. Eustele

18. What is the term for a stele with bicollateral vascular bundles?
A. Eustele B. Siphonostele
C. Protostele D. Atactostele

19. Which stele type is characterized by a central core of xylem without pith?
A. Protostele B. Siphonostele
C. Dictyostele D. Eustele

20. What is the term for the vascular connection between a leaf and the stem?
A. Leaf trace B. Branch trace
C. Medullary ray D. Pericycle

Answers

1-B,2-D,3-B,4-D,5-C,6-B,7-C,8-D,9-C,10-A,11-B,12-A,13-B,14-D,15-C,16-C,17-C,18-A,19-A,20-A

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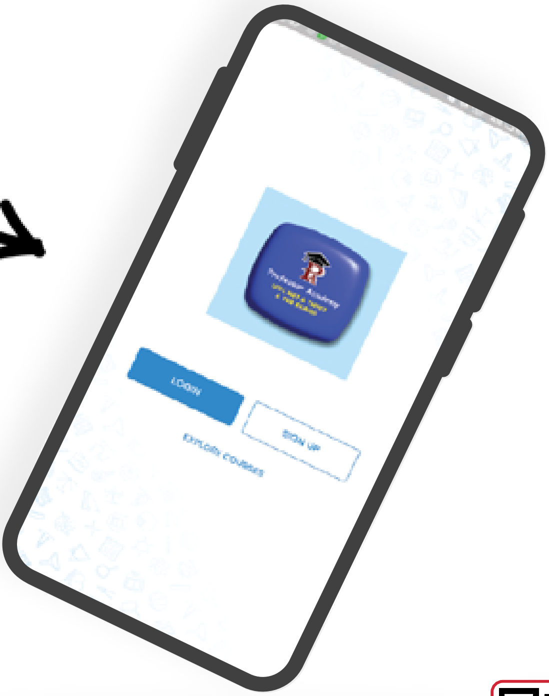

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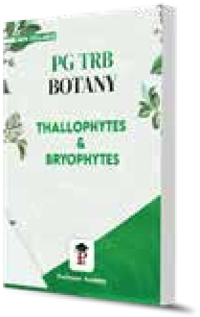

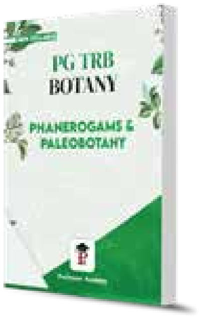

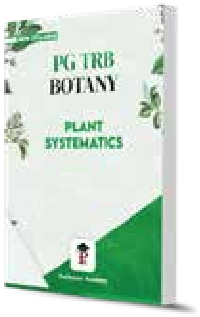

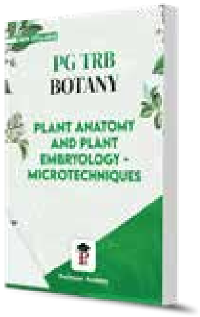

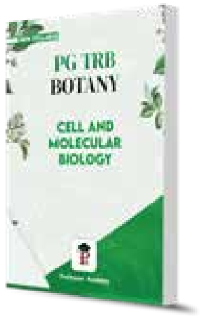

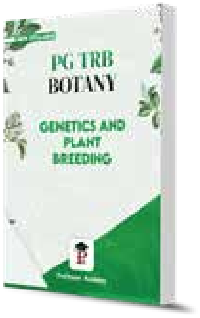

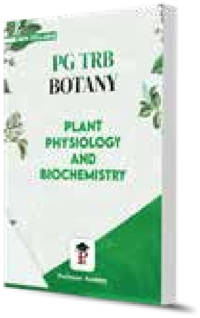

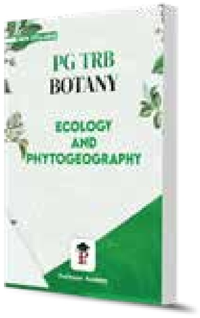

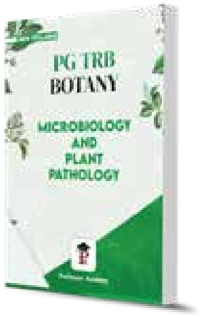

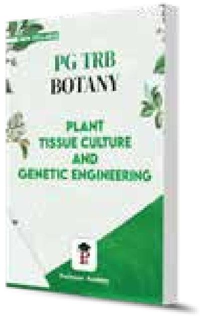

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Module 3

Sporophyte Evolution

According to a general belief the earliest and the primitive sporophyte of the land plants was axial in nature. The leaves and branches were evolved later by a modification of the central stem. These primitive land plants were supposed to have rootless, leafless and dichotomously branched green stems. The vascular system was a simple protostele. Some of the ultimate branches terminated in sporangia. This assumption is supported by the discovery of some simple plants in the upper Silurian and Devonian periods of earth's history (*Rhynia, Horneophyton, Psilophyton, Asteroxylon* and others). Discovery of such plants led may botanists to propose theories explaining the appearance of leaves, branches, root and sporangia on the sporophyte. These theories tend to explain the process of elaboration of the primitive sporophyte into the modern sporophyte possessing roots, leaves and variously disposed sporangia. Of all these theories **Telome theory** of Zimmermann (1930) has attracted great attention and has a large number of supporters.

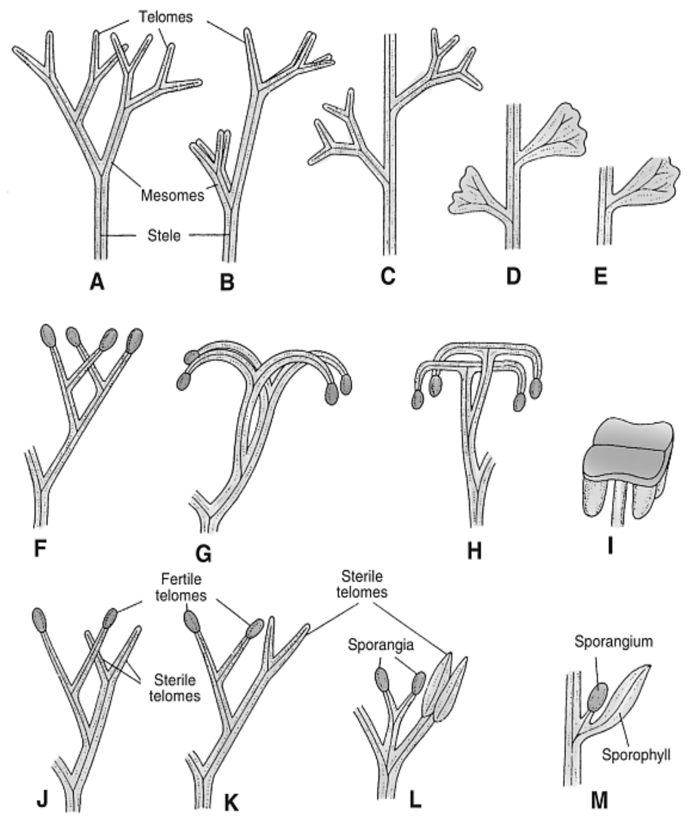
3.1 Telome Theory

This theory was first proposed by **Zimmermann** in 1930 and later elaborated by him in 1938. Zimmermann postulated that all the vascular plants evolved from a very simple, leafless and a dichotomously branched ancestral type like *Rhynia*. Such a plant is made up of sterile and fertile branches. The fertile branches terminated in sporangia. The simple and terminal parts of a dichotomously branched stem were designated as telomes. The telomes meet each other at the point of forking. Portions of the stem below the forking were called mesomes. The telomes were classified as sterile or vegetative telomes also called **phylloids** and **fertile telomes**. The fertile telome consists of a terminal and a stalked sporangium usually traversed by a single vascular strand up to its base. As evolution proceeded there was a change from dichotomous to sympodial branching as a result of the fusion of two or more telomes called the **telome trusses** or **syntelomes**. The fertile telome trusses were called the **sporangial trusses** and sterile telome trusses were called the **phylloid trusses**. Both the types of syntelomes also occurred together to form mixed **telome trusses** or **mixed syntelomes**.

Zimmermann postulated that the primitive vascular cryptogams originated from the green algae. The unicellular green algae divided in all planes to form a parenchymatous thallus. Later meristematic tissues developed and erect radially constructed branches came into existence. It was followed by the appearance of distinct alternating generations. The sporophyte branched dichotomously and possessed a central conducting strand. Such algal ancestors, according to Zimmermann, led to the evolution of early vascular plants of the upper Silurian and Devonian periods. They possessed heteromorphic alternation of generations and their sporophytes were simple and dichotomously branched. Some of the branches terminated in sporangia. They possessed no leaves and had no roots. The vascular system was a simple protostele. The aerial and simple stems possessed stomata. The function of roots was performed by hair or rhizoids. These sporophytes had subterranean portions called the **rhizomes**.

Enation Theory of Microphyll Origin

Bower's Enation Theory (1935) suggests that microphyllous leaves evolved from superficial outgrowths (enations) of the stem, which later developed a vascular supply, progressing from Psilophyton to Drepanophycus.



Telome concept of Zimmermann

A. Illustrates hypothesis of telomes and mesomes; B. Overtopping; C. Planation; D-E. Webbing and syngenesis; F-I. Illustrate the origin of the sporangiophores of Sphenophyta by recurvation and fusion and flattening of the telcomes and mesomes; J-M. Illustrating the origin of Lycophyta.

These early land plants evolved into the higher vascular cryptogams along three independent lines of evolution. These were the Lycopsid, Sphenopsid and Pteropsid trends of evolution. During the course of this evolution certain elementary processes of progressive differentiation took place in the sporophytes. These can be listed as: (i) Overtopping (ii) Plantion, (iii) Webbing or syngenesis, (iv) reduction, and (v) recurvation. All these elementary processes of organogenesis were believed to have occurred in varying degrees in the different taxonomic groups.

3.1.1 Overtopping

The equally dichotomising axes developed unequal dichotomy. This resulted in the formation of short and long branches. The short branches appeared as lateral shoots. This led to the development of a sympodial axis which ultimately changed to a monopodial axis with lateral branches. These lateral branches metamorphosed into leaves.

3.1.2 Planation

The equal dichotomies were originally in more than one plane. They were arranged in planes successively at right angles. During the process of planation, the dichotomies became arranged in a single plane. It is an important process that led to the evolution of the leaf.

3.1.3 Syngenesis or Webbing:

As the name indicates the adjacent telomes and mesomes were connected with each other by the development of a parenchymatous tissue between them. This is also called parenchymatous webbing. During this process the steles of the concerned telomes also fused. Syngenesis was considered to be of two types by Zimmermann: -

(a) Foliar syngenesis

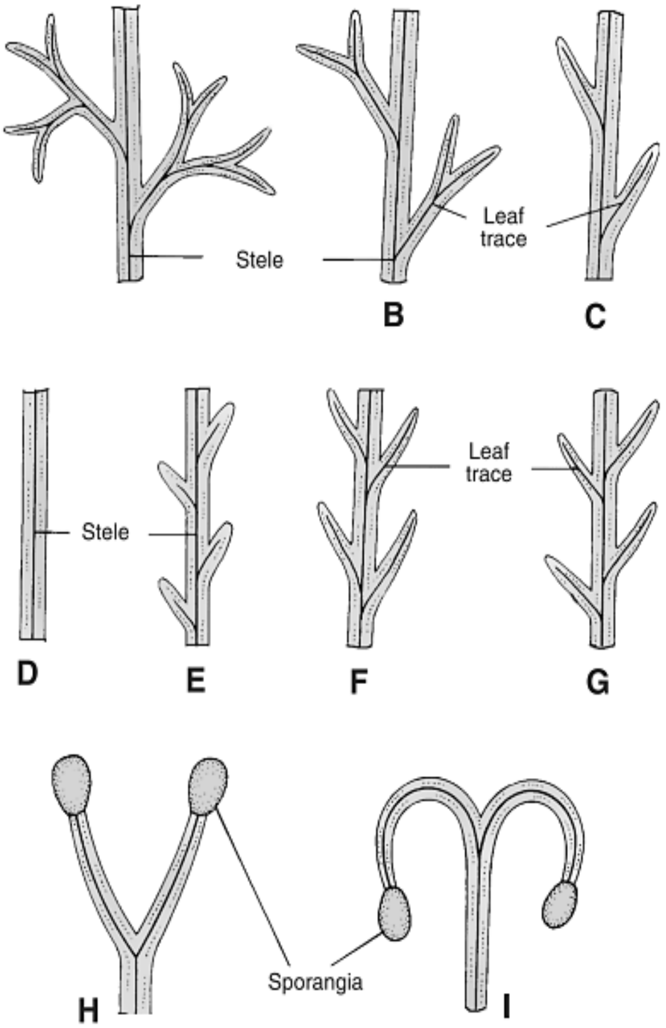
During this process there is coalescence or fusion of apical meristems of the telomes. When these meristems fuse to form a marginal meristem, a lamina with veins develops. The activity of these meristems leads to the formation of parenchymatous webs between the telomes. Such developments resulted in the formation of lateral foliar appendages. In case foliar syngenesis is accompanied by overtopping, the leaves with pinnate venation are formed. Sometimes foliar syngenesis is accompanied by fusion of the vascular strands. This results in the development of **netveined** leaves or leaves with reticulate venation. Overtopping, planation and foliar webbing brought about the evolution of a megaphyllous leaf.

(b) Axial syngenesis

Zimmermann visualised that during this process there was absorption of a number of branches into a single stout axis. The fusing branches had protosteles and their fusion led to the appearance of a complex stelar organisation. In case the shoots united by the formation of parenchymatous webs the resulting stelar organisation was a polystelic condition. In case during axial syngenesis the steles anastomosed in different manners, the resultant stelar organisation was of diverse types, e.g., siphonostele, eustele, solenostele.

3.1.4 Reduction

It is supposed to have brought about the evolution of simple and unbranched microphyllous leaves of the lycopods (*Lycopodium, Selaginella, Isoetes*). It was brought about by the reduction of the syntelome to a single needle-like lateral appendage.



A-C. Illustrating reduction of syntelomes to single needle like lateral appendages (C); D-G. Illustrating origin of microphylls;H-I. Recurvation

3.1.5 Recurving

During this process the fertile telomes were supposed to become reflexed. As a result, the sporangium assumes an inverted position. Zimmermann called this process as **incurvation**. Wilson (1953) recognised two processes –

(a) Recurvation: During this process the sporangia bent downwards as in Sphenophyta.

(b) Incurvation: This led to the shifting of the sporangia to the ventral surfaces of the foliar appendages thus bringing about a condition found in the ferns.

Wardlaw (1952), however, pointed out that all these changes can be embraced within one term, which he calls as **recurvation**. While discussing the above listed five elementary processes of organogenesis as postulated by Zimmermann, it becomes evident that microphyllous leaves originated as a result of the process of **reduction**. The megaphyllous leaves of ferns (Filicophyta) originated as a result of combined processes of overtopping, planation and foliar syngenesis.

3.2 Merits of the Telome Theory

It is an outcome of a master mind that has portrayed, in a skilful manner the origin and evolution of the sporophytes of land plants. Zimmermann has based his theory mostly on account of his comparative study of the fossil as well as living genera of the vascular plants. Many of his assumptions are correct and based on exact phyletic relationships between the various groups of plants both living and extinct. His five 'elementary processes' of planation, overtopping, syngenesis, reduction and recurvation give us a unified concept of the manner in which evolution might have proceeded in the land plants. These processes explain in a simple and lucidway as to how the primitive land plants led to the evolution of both the simple and the complex land plants of today. It explains in a nice manner that the entire sporophyte is an axis that has an underground portion called the root and an aerial part called the shoot. The appendages of shoot that is the sporophylls, sporangia and sterile leaves are nothing but modified parts of the stem. While building up his theory Zimmermann has taken into consideration the morphological aspects of the various groups of extinct and living groups of plants.

3.3 Demerits of the Telome Theory

This theory is open to criticism in its application to the origin of Lycophyta (Lycopsida). The origin of microphyllous leaves of the Lycophyta by reduction of telome trusses is not exemplified by any living or extinct vascular plant. Andrews (1960) has expressed his views on the Telome theory in the following words. "Zimmermann's scheme for the pteropsids or at least some pteropsids, has much supporting evidence; his concept for the articulates may be valid, but we are only on the verge of understanding the origin of this group; his content for the lycopsids is, so far as I am aware, purely hypothetical."

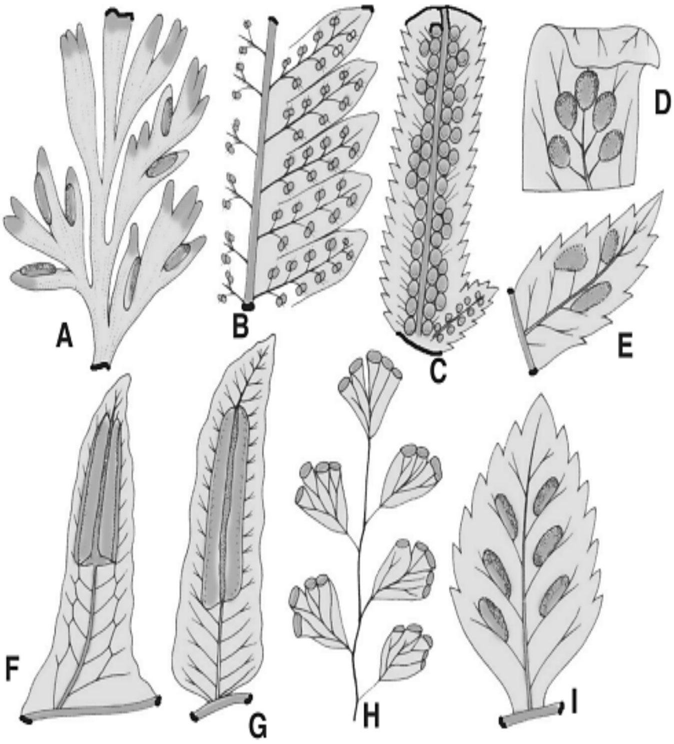
3.4 Spore Producing Members

The spores are produced within specialised structures called the **sporangia**. The sporangia, in most of the living filicophyta, occur in small or large groups called the **sori** (singular = sorus). The sori are variously arranged on the margins or ventral surfaces of leaves or leaflets. Such leaves are called the **sporophylls**.

The leaves, in most of the filicophyta, serve a dual purpose of photosynthesis and reproduction. In the common ferns like *Adiantum*, *Pteris* and *Dryopteris* and leaf or leaflet can bear sori on its under surface. There is no distinction between fertile and sterile leaves. There are, however, some ferns which exhibit segregation of photosynthetic and reproductive function. The genus *Osmunda* affords a good example of cases where a few pinnae or leaflets of a leaf are set aside for bearing sporangia whereas the others are sterile and photosynthetic. *Osmunda regalis* has a pinnate compound leaf in which the upper or distal pinnae are fertile whereas the lower or proximal pinnae are sterile. In *Osmunda claytonniana* and *O. javanica* certain pinnae, anywhere along the leaf have smaller size and bear sporangia. These examples illustrate restriction of sporangiferous area in the same leaf. In *O. cinnamomea* the leaves are dimorphic, i.e., there are two types of leaves. There are: (i) sterile leaves that have well developed leaf blades and appear late in season, and (ii) fertile leaves that lack lamina and appear earlier in season. Other examples of this type are *Matteuccia struthiopteris* and *Blechnum spicant* in which the rhizome bears : (i) sterile leaves that are large and broadly expanded and (ii) fertile leaves or sporophylls that are attenuated and have reduced lamina. These two types of leaves occur in distinct alternating zones. In *Pellaea altropurpurea* the sterile leaves have oval pinnae and fertile fronds have narrow and elongated pinnae.

3.4.1 Sorus

The term sorus has a Greek origin. It actually means a heap or a group. The group of sporangia is, therefore, called a **sorus**. A sorus may have from two to many sporangia. The sorus may be protected by a revolute margin or by a special outgrowth called the **indusium** or it may be unprotected and naked. Besides the sporangia, the sorus also includes the **receptacle** or the **placenta** on which the sporangia arise. The indusium if present may also be regarded as a part of the sorus.



Fern Sori

***A. Asplenium; B. Polystichum; C. Dryopteris; D. Mattecucia struthiopteris; E. Aethyrium filix-foemina; F. Blechnum occidentale; G. Lomaria spicant; H. Adiantum; I. Asplenium lanceolatum*.**

There are some ferns in which the sporangia are naked (without indusium) and occur scattered along the veinlets. They do not form sori, e.g., *Leptopteris hymenophylloides.* In *Todea barbara* the sporangia are densely scattered and are not covered by an indusium. The sori in this case are ill defined. The sporangia in both these cases are superficial. In the living genera of the Marattiales the superficial sporangia are arranged in definite sori. In *Christensenia* the sori are naked, circular and are irregularly arranged between the lateral veins. In *Marattia, Angiopteris, Danaea*, etc., the sori are elongated and are situated below the lateral veins. Among the polyopoidaceae the sori are naked in Polypodium and some other genera.

The Ophioglossales are a group of interesting ferns in which the sporangia are marginal in position and are borne on fertile spikes that arise on ventral surface of a sterile lobe. The leaf, in the ophioglossales, consists of a petiole which bears a simple or a dissected sterile lamina from whose ventral surface arises a simple or a branched fertile spike. The fertile spike in *Ophioglossum* bears sporangia arranged in two rows. The sporangia are embedded and fused together. The spike terminates in a small sterile process. Every sporangium is supplied with a vascular trace. The fertile spike in *Helminthostachys* bears groups of sporangiophores arranged in many rows. Each sporangiophore bears groups of sporangia and a few green scale-like lobes at the tip. The spike in *Botrychium* is branched once, twice or many times. Each branch bears two rows of marginal sporangia. The sporangia in *Osmunda, Davallia, Trichomanes* and many other ferns are also marginal in position. In *Osmunda* the fertile pinnae are bladeless, i.e., have either reduced or no lamina. In *Schizaeaceae* the sporangia occur isolated and are protected by a false indusium. They originate from initials that arise marginally, but get displaced to ventral side during development.

In *Glecheniaceae* the sporangia form distinct sori on the ventral surface of the leaves. The sori are seated at the vein ends or rarely along the middle of the vein. The sori are covered only by hair and scales. There are no indusial flaps. The sorus consists of a single circle of sporangia.

In *Hymenophyllaceae* the sori are marginal and are characteristic in that the vein supplying the receptacle grows through it (by the activity of a basal meristem) and forms a long thin bristle, e.g., *Trichomanes*. The sorus is protected by a cup-shaped indusium. The indusium is bilipped in *Hymenophyllum*.

The indusium in *Dicksoniaceae* consists of two flaps that form box-like structure in *Cibotium baromet*. The sori are marginal in position. The sori in *Mattoniaceae* are ventral in position and are usually arranged in two rows on either side of the mid-rib. Each sorus has 6-9 sporangia around the receptacle. The tissue of the receptacle grows and overarches to form an umbrella-like indusium. The indusial stalk is thick and massive. In *Dipteridaceae* the sori are naked.

In *Cyatheaceae* the ventral sori are arranged on either side of the mib-rib of pinnae and the indusium may be absent (*Alsophila*) or scale-like (*Hemitelia*) or well developed (Cyathea). In *Cyathea medullaris* the young sporangia are covered by hair-like outgrowths that are multicellular. In this species the indusium grows slowly. In *Hemitelia* indusial flap develops along one side of the placenta.

The sori in the *Polypodiaceae* are marginal in origin except for some genera (*Dryopteris, Athyrium, Asplenium*, etc.) where they are found on the ventral surface of the leaflets and are superficial in origin. They are usually seated on the vein endings. In *Pteridoideae* the sori become confluent and appear as a single continuous sorus (*Pteris*). The form and development of the indusium is variable in the various sub-families of the *Polypodiaceae*. The sori are usually covered by two laterally developed indusial flaps. e.g., *Pteridium*. Both these flaps originate from the receptacle (true indusium) as in *Dryopetris*. In *Pteris* and *Adiantum* the sori are protected by the inwardly turned margins of the leaflets. Such a protective device is called **false indusium**. The indusium is reniform in *Dryopteris*; circular in *Polystichum lobatum*, funnel-shaped in *Davallia*; elongated and curved in *Asplenium lanceolatum*, *Lomaria spicant* and *Blechnum occidentale*. In the last named genera the sori become confluent and are covered by a common indusium. In *Lomaria*, the lamina is greatly reduced. In *Athyrium filixfoemina* the indusium is reniform with lacerated margins. In *Matteuccia struthiopteris*, the indusium is cup-shaped with dentate margins and is thin and papery. In this case the leaflet margins become strongly, inrolled and afford additional protection to the sori. The same is the case in *Onoclea*. In *Adiantum* the sporangia develop on the underside of special marginal flaps of lamina that become reflexed and protect the sorus.

In marsileales and the salviniales the sporangia develop in sori that are borne within distinct structure called the sporocarps. The sporocarps in *Marsilea* enclose sori that contain both micro and megasporangia. In Salviniales the smaller sporocarps contain many microsporangia each and the larger ones contain one or more megasporangia per sporocarp.

(A) Origin

The evolution of sori represents a significant adaptation that enhances spore dispersal and ensures reproductive success in various plant and fungal species. In ferns, sori are clusters of sporangia, which are specialized structures that produce and release spores. The development of sori allowed ferns to optimize their reproductive strategy by ensuring a higher concentration of spores in a single location, increasing the likelihood of successful dispersal. Similarly, in fungi, sori-like structures have evolved to enhance spore production and distribution, allowing these organisms to thrive in diverse environments. By clustering spores together, sori provide an efficient mechanism for synchronized spore release, ensuring maximum dispersal potential through wind, water, or other environmental factors.

An important evolutionary adaptation in ferns is the development of the indusium, a thin membrane that covers and protects the sori. The primary function of the indusium is to safeguard the developing sporangia from environmental damage, such as desiccation, excessive sunlight, and herbivory. Early ferns likely lacked this protective covering, which may have made their reproductive structures more vulnerable to external threats. Over time, species that developed an indusium had a reproductive advantage, as their spores were more likely to mature successfully and be released under favourable conditions. The diversity of indusium structures seen in modern ferns—ranging from flat protective membranes to rolled margins of leaf tissue—demonstrates how different species have evolved unique solutions to the challenges of spore protection and dispersal.

The evolution of sori is an example of **convergent evolution**, where similar reproductive strategies have independently evolved in different groups of organisms. While ferns developed sori for efficient spore dispersal, fungi also evolved similar clustered spore-producing structures to enhance reproduction. Some fungal species, such as rust fungi and smuts, produce sori-like structures that release spores in response to environmental cues, ensuring that they spread effectively and colonize new hosts. Similarly, some red algae also form sori, highlighting the widespread evolutionary success of this reproductive strategy across different biological kingdoms. Despite arising in different evolutionary lineages, the fundamental function of sori remains the same: to optimize the production, protection, and dispersal of reproductive spores.

Fossil evidence suggests that sori-bearing plants have existed for over 350 million years, dating back to the **Carboniferous Period** when ferns and other spore-producing plants dominated Earth's landscapes. Some of the earliest known vascular plants had sporangia arranged in clusters similar to modern sori, indicating that this reproductive strategy was an early evolutionary development. Fossils of ancient ferns, such as Archaeopteris, provide insight into how early sori structures evolved over time. As flowering plants (angiosperms) became more dominant in later geological periods, ferns had to adapt to new environmental conditions, leading to the refinement of sori structures and spore dispersal mechanisms to ensure their continued survival.

(B) Types of sorus

According to the mode of development of sporangia in a sorus Bower (1935) classified the sori in ferns, into the following three types:

i) The simple sorus:

The sporangia in such a sorus develop simultaneously and all of them mature together, e.g., *Ophioglossum* and *Osmunda*.

ii) The Gradate or Basipetal Sorus:

The placentae or the receptacles are long and almost cylindrical. They bear mature or older sporangia at their distal ends and younger sporangia near the proximal or basal part. Such a sorus is found in *Dicksonia, Loxosoma, Trichomanes, Cyathea, Alsophila*, etc.

iii) The Mixed Sorus:

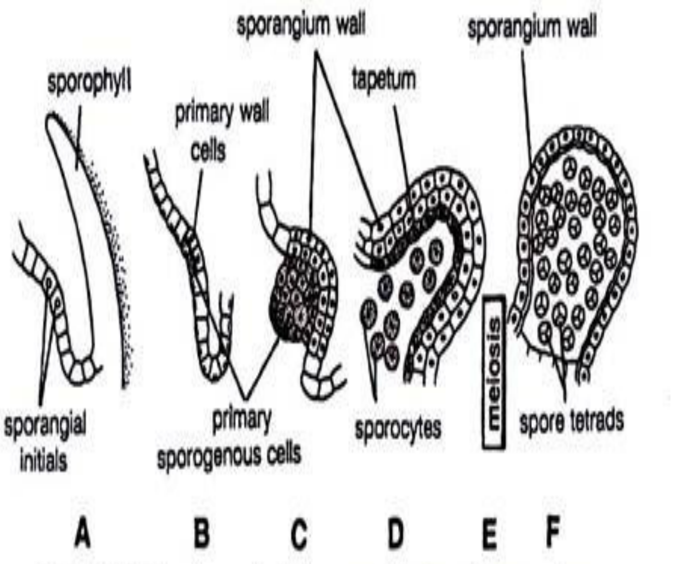
Such a sorus is an aggregation of old and young sporangia that occur mixed and show no regular arrangement in a sorus. The young and old sporangia are indiscriminately mixed. The sporangia usually have long stalks and vertical annulus. The number of spores varies between 12-64. Such a sorus is found in majority of the living ferns, e.g., polypodiaceae (*Adiantum, Pteris, Pteridium, Davallia*, etc.)

(C) Sporangial Development

In pteridophytes, sporangia play a crucial role in reproduction by producing and dispersing spores. The development of sporangia in these plants can be classified into two distinct types based on their origin and mode of development: **eusporangiate** sporangia and **leptosporangiate** sporangia. These two types exhibit differences in their initial formation, cell division patterns, and the number of spores they produce.

i) Eusporangiate Type

The eusporangiate type of sporangium originates from a group of superficial cells, rather than a single cell. These initial cells undergo **periclinal divisions**, forming two distinct layers: an outer layer known as the primary wall layer and an inner layer known as the primary sporogenous cells. As development progresses, the outer wall cells continue dividing, ultimately forming the protective sporangial wall, which consists of multiple layers, providing durability and structural support.



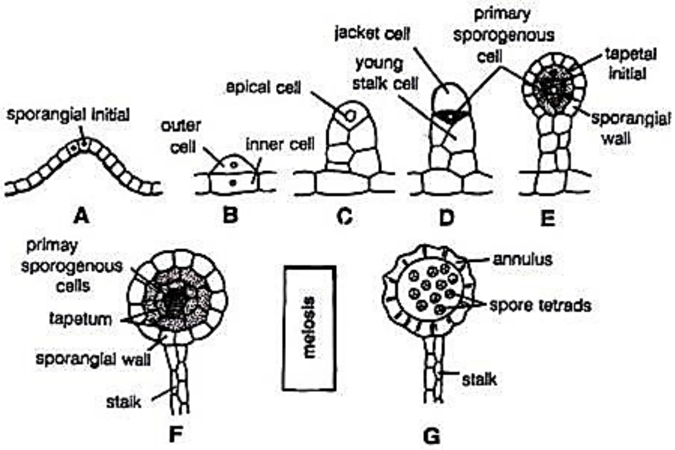
Inside the developing sporangium, the primary sporogenous cells divide further. Some of these cells transform into tapetal initials, while others become sporogenous tissue. The tapetal initials give rise to the tapetum, a specialized nutritive tissue that supports the developing spores. The tapetum forms two layers that contribute to spore wall development and nutrient supply. Meanwhile, the sporogenous cells undergo meiotic division, leading to the formation of haploid spores, which will later disperse and germinate to produce gametophytes.

This type of sporangial development is characteristic of primitive pteridophytes, including *Psilotopsida* (whisk ferns), *Marattiaceae* (giant ferns), and *Ophioglossales* (adder's tongue ferns). Eusporangiate sporangia are relatively large, multilayered, and produce a large number of spores, making them structurally robust and well-adapted for survival in a variety of environments.

ii) Leptosporangiate Type

In contrast to the eusporangiate type, leptosporangiate sporangia develop from a single superficial initial cell rather than a group of cells. The process begins when the initial cell undergoes a transverse division, producing an outer and an inner cell. The inner cell contributes to the formation of the stalk, while the entire sporangium develops from the outer cell.

The outer cell undergoes a series of three successive periclinal divisions, producing a thin, single-layered sporangial wall. Unlike eusporangiate sporangia, the leptosporangiate type produces a relatively small number of spores due to the limited number of sporogenous cells. The sporogenous cells undergo meiotic division, forming haploid spores, which are eventually released for dispersal.



One of the distinctive features of leptosporangiate sporangia is the presence of a specialized annulus, a ring-like structure composed of differentiated cells with thickened walls. The annulus plays a crucial role in spore dispersal by facilitating the opening and dehiscence of the sporangium through mechanical tension. As the sporangium dries, the annulus contracts, leading to a sudden release of spores, enhancing their dispersal efficiency.

Leptosporangiate sporangia are characteristic of more advanced ferns in the Polypodiopsida class, including families such as Polypodiaceae, Dryopteridaceae, and Pteridaceae. These ferns typically produce a large number of small, lightweight spores that are well-adapted for wind dispersal, allowing them to colonize new habitats effectively.

Elementary Processes of Sporophyte Evolution

Process	Description
Overtopping	Unequal **dichotomy** results in a **dominant main axis and lateral short branches** → Formation of **monopodial axis** and **leaves**.
Planation	Initially **dichotomous branches were in different planes** → Later arranged in **one plane**, leading to **flat leaf structures**.
Syngenesis	**Fusion of telomes** to form **complex structures**:
	Foliar Syngenesis → Formation of **leaf lamina with veins**.
	Axial Syngenesis → Fusion of **multiple branches into a single strong axis** (leading to complex **steles**).
Reduction	**Simplification of structures** → Led to **microphyllous leaves** (*Lycopodium, Selaginella*).
Recurving	**Sporangia became reflexed** → Led to **downward-facing sporangia** as seen in **ferns and Sphenophyta**.

Types of Sorus

Type	Characteristics	Examples
Simple Sorus	All sporangia develop simultaneously.	*Ophioglossum*, *Osmunda*
Gradate Sorus	Older sporangia at top, younger at base.	*Cyathea*, *Alsophila*
Mixed Sorus	Random arrangement of young and old sporangia.	*Adiantum*, *Pteris*, *Pteridium*

Ferns to Forests

1. What is the most primitive type of sporophyte in land plants?
A. Leafy sporophyte
B. Axial sporophyte
C. Rooted sporophyte
D. Branched sporophyte

2. Which theory explains the evolution of leaves and branches in vascular plants?
A. Telome theory
B. Enation theory
C. Stelar theory
D. Sporangial theory

3. What are the terminal parts of a dichotomously branched stem called in the Telome theory?
A. Mesomes
B. Telomes
C. Syntelomes
D. Phylloids

4. Which process in the Telome theory leads to the formation of a sympodial axis?
A. Planation
B. Overtopping
C. Webbing
D. Reduction

5. What is the term for the fusion of adjacent telomes and mesomes?
A. Planation
B. Syngenesis
C. Recurvation
D. Reduction

6. Which process in the Telome theory explains the evolution of microphyllous leaves?
A. Overtopping
B. Planation
C. Reduction
D. Recurvation

7. What is the term for the bending of fertile telomes to position sporangia?
A. Overtopping
B. Planation
C. Recurvation
D. Webbing

8. Which group of plants is thought to have evolved from green algae according to Zimmermann?
A. Bryophytes
B. Pteridophytes
C. Gymnosperms
D. Angiosperms

9.What is the term for the arrangement of dichotomies in a single plane?
A. Planation
B. Overtopping
C. Webbing
D. Reduction

10. Which process in the Telome theory leads to the formation of net-veined leaves?
A. Foliar syngenesis
B. Axial syngenesis
C. Reduction
D. Recurvation

11. What is the term for the fusion of vascular strands during axial syngenesis?
A. Protostelic condition
B. Monostelic condition
C. Polystelic condition
D. Siphonostelic condition

12. Which theory suggests that microphylls evolved from superficial outgrowths of the stem?
A. Telome theory
B. Enation theory
C. Stelar theory
D. Sporangial theory

13. What is the term for the protective structure covering a sorus in ferns?
A. Indusium
B. Placenta
C. Annulus
D. Tapetum

14. Which type of sorus has sporangia developing simultaneously?
A. Simple sorus
B. Gradate sorus
C. Mixed sorus
D. Basipetal sorus

15. What is the term for a sorus with sporangia of different ages mixed together?
A. Simple sorus
B. Gradate sorus
C. Mixed sorus
D. Basipetal sorus

16. Which type of sporangium develops from a single superficial initial cell?
A. Eusporangium
B. Leptosporangium
C. Protosporangium
D. Megasporangium

17. What is the term for the nutritive tissue surrounding developing spores?
A. Annulus
B. Tapetum
C. Placenta
D. Indusium

18. Which group of ferns exhibits dimorphic leaves with distinct fertile and sterile forms?
A. Osmunda
B. Adiantum
C. Dryopteris
D. Pteris

19. What is the term for the ring-like structure that aids in sporangium dehiscence?
A. Tapetum
B. Annulus
C. Placenta
D. Indusium

20. Which process in the Telome theory leads to the formation of a monopodial axis?
A. Overtopping
B. Planation
C. Webbing
D. Reduction

Answers
1-B,2-A,3-B,4-B,5-B,6-C,7-C,8-B,9-A,10-A,11-D,12-B,13-A,14-A,15-C,16-B,17-B,18-A,19-B,20-A

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Module **4**

Heterospory & Seed Habit

4.1 Heterospory

`Heterospory is a condition that interprets the production of spores of two different sizes and two different developmental patterns. The two different sizes are the small and the larger spores. The former are called the **microspores** and the latter are termed as **megaspores**. They have differential development patterns because the microspores germinate to produce the male gametophytes or **microgametophytes** that bear male sex organs called the antheridia, and the megaspores germinate to produce the female gametophytes or the that bear archegonia or the female sex organs. The two kinds of spores are produced in two kinds of sporangia. The micro spores in **microsporangia** and the megaspores in **megasporangia**. The microspores are produced in large numbers and are smaller in size as compared to megaspores that are produced in comparatively much smaller number and are large in size. The large size of the megaspores is attributed to the availability of more nutrients. They are few in number per megasporangium and get more nutrition, as compared to many microspores per microsporangium. The reduction in the number of megaspores has been achieved either through reduction in number of spore mother cells, or by the disintegration of developing spores.

The most important aspect of heterospory is that it is an expression of sex determining process of the plant. It has brought about, along with its onset, a phenomenal shift of sex determining capacity from the gametophyte to the sporophyte. In all the homosporous individuals the sex determinants exert their effect in the gametophytes during the formation of the antheridia and the archegonia. In the heterosporous individuals the sex determinants exert their influence during sporogenesis. In *Selaginella*, as we have seen, the stages of development of both the kinds of sporangia, 'are similar up to the formation of spore mother cells. Thereafter the differences start. In the microsporangia all the spore mother cells are functional and produce microspores, whereas in megasporangia only a few or one mother cell is functional. Heterospory has also freed, during the course of evolution, the sporophyte from aquatic habitats, and such an emancipation, has enabled the sporophyte to grow freely under varied environmental conditions. It is, therefore, a significantly evolutionary development during the struggle to conquer land.

Heterospory is the most important evolutionary development in the vascular plants because it has ultimately to lead to seed developments. It is rather a pre-requisite to seed habit. Besides bringing along with it the phenomenon of pollination, it has also resulted in the reduction of the gametophytic tissue, their endosporic nature, precocious germination of the spores, partial and ultimately complete retention of the megasporangium and female gametophyte on the sporophyte, reduction in the number of megaspores to one; reduction in the number of male gametes, and ultimately loss of mobility of the male gametes in angiosperms and organic union between the megaspore and the megasporangium. All these new developments are vital for seed habit. These changes have gradually developed in vascular plants and led to seed habit.

The heterospory can be better discussed if we examine evidences from palaeobotany, from developmental studies and from the experimental results.

(a) Evidence from Palaeobotany

The available fossil record suggests that there was an early and widespread occurrence of heterospory in almost all the major plant groups. A number of heterosporous genera belonging to the Lycopsida, Sphenopsida and Pteropsida were known in the late Devonian and early Carboniferous periods. Some of them exhibit stages where heterospory is not pronounced whereas in others heterospory was well developed and approached the seed condition. These various grades of heterospory in these early land plants advance strong suggestions as to the origin of the heterosporous condition. Williamson and Scott (1894) discovered and described two species of Calamostachys (Sphenopsida) that indicate the initial steps that have led to heterospory. These species are *C. binneyana* and *C. casheana*. The former species is homosporous but in some sporangia there were a few spores of unequal sizes. *C. casheana* showed distinct heterospory as there were microspores and megaspores produced in separate sporangia. The megasporangia contained small and aborted spores. This shows that abortion of spores leads to the differences in size and number. Thoday (1906) described *Sphenophyllum dawsoni* (sphenopsida) which has usually been considered homosporous. Thoday found that some sporangia in this species showed abortion of some spore tetrads and the remaining spores grew larger in size than the spores usual for the species. In *Stauropteris burntislandica*, Chaloner (1958) reported that the megasporangia contained tetrads of megaspores in which two spores were large and two small. This is also a case of reduction in the number of megaspores due to abortion. Scott (1901) reported that in *Lepidocarpon* (Lycopsida) three megaspores out of each tetrad had aborted and only one matured. Ramanujam and Stewart (1969) also reported a *Lepidocarpon* cone from Pennsylvanian of Illinois in which there are 3 abortive megaspores and one functional megaspore. In *Lepidostrobus braidwoodensis*, Arnold (1938) reported that the megasporangia contained only one matured megaspore in addition to a number of aborted spores. In *Miadesmia* the seed like megasporangia contained only one megaspore and there was trace of aborted spores.

These examples give us an idea of the reduction in the number of spores and differences in their sizes but whether it was achieved through abortion of the spores or through reduction in the number of spore mother cells, cannot be determined as there is no information regarding the development of the sporangia and the spores. We have no developmental record to show that these spores produced heterothallic gametophytes. In the absence of such an information, it is not possible to shed light on the importance of the difference in the size of the spores, and whether these spores actually produced two kinds of gametophytes. Baxter (1972) discovered a heterosporous fern from a coal ball from Middle Pennsylvanian of Kansas. He found small pinnules that bear stalked pendant sporangia that appeared like blunt arrowheads in a median longitudinal section. Each sporangium has one megaspore and is attached to the lower surface of the pinnule. A marginal indusium covers the sporangia partially. The megaspore completely fills the sporangium.

(b) Developmental Evidence

The living representative of the major divisions of the vascular cryptogams (*Lycopsida, Sphenopsida, Pterospsida*) include a number of heterosporous genera (*Selaginella, Isoetes, Marsilea, Pilularia, Regnellidium, Salvinia, Azolla* and *Stylites*). They afford us the possibilities of extensive morphological, developmental and comparative studies that can throw much light on the origin of heterosporous condition in the plants. The development of the sporangium in all the living plants follows a common developmental pattern. In all cases archesporium is formed by the lower cell or cells cut off from the sporangial initial or a group of initials. The outer cells differentiate into the jacket initials. The archesporial cells by further division become sporogenous cells or spore mother cells, which undergo reduction division to form the spores. This is the common basic pattern of sporangial development.

Differences are, however, there in the details of development in different groups of plants. These are:

1. Whether the sporangium arises from a single initial or a group of initials.
2. The number of cells making up the primary archesporial tissue.
3. Whether the archesporial cells act directly as spore mother cells or they divide mitotically and then act as sporocytes (spore mother cells).
4. Number of functional sporocytes.
5. Number of spores which mature.
6. Origin of the tapetal layer and its time of disorganisation.

A few of these differences have played a role in the development of heterospory. These comparative and developmental studies illustrate the various pathways that have led to heterospory. The time at which the sex determinants activate and exert their influence to segregate sex seems to play a major role in illustrating the different developmental pathways leading to heterospory.

In the homosporous vascular cryptogams, e.g., *Lycopodium, Dryopteris, Pteridium*, etc., the sex determinants exert their influence during the development of the sex organs. In *Equisetum,* Hauke (1963) observed that the gametophytes that are all alike in early stages of development show distinction into two types during further vegetative growth and it is easy to determine which will bear antheridia and which archegonia. In this case the sex determinants exert their influence earlier, i.e., before the formation of sex organs. In these cases, sex determinants exert their influence in the gametophytes, their time, however, differs. In *Selaginella*, which is a heterosporous vascular cryptogam the sex determinants exert their influence during the differentiation of the sporocytes (spore mother cells). In the sporangia destined to develop into megasporangia only one megasporocyte is functional, whereas in the microsporangia all the sporocytes are functional. From this stage onwards there is clear differentiation between the two types of sporangia that will produce two types of spores that in turn develop into male and female gametophytes. The same is the case in *Marsilea* and *Isoetes*. This is a significant drift in the time of activation of sex determinants. It has shifted from the gametophyte to the sporophyte. It is a small shift, but very significant, because it has brought along with it the condition of heterospory in the vascular cryptogams.

In the angiosperms the stamens (microsporophylls) and carpels (megasporophylls) appear quite different at maturity so that we can tell in advance that the stamens will bear microsporangia and the carpels will bear ovules that contain megasporangia. Here sex determinants exert their influence before the maturation of the sporophylls. In many gymnosperms and some angiosperms, the reproductive bodies are borne on special branches which can be identified before they bear the reproductive bodies. This can be ascertained by their position and morphology. In these cases, the sex determination occurs during the vegetative growth of the branch. So, in the seed plants the sex determinants exert their influence much earlier than in the heterosporous pteridophytes.

Incipient Heterospory

Platyzoma microphylla and *Ceratopteris thalictroides* exhibit incipient heterospory, where their sori contain two types of sporangia producing small male and large female spores, with female prothalli capable of delayed antheridia formation if fertilization fails.

(c) Experimental Evidence

Only a few experimental studies have been conducted to approach the problem of origin of heterospory. All these studies were conducted with the basis that differences in spores size are due to abortion of most of the spores, greater abortion leaving greater nutrition for the remaining and functional spores, that grow in size. Shattuck (1910) performed a series of experiments on *Marsilea* and tested the effect of nutrition on spore size. He was able to alter spore size by growing plants under variable conditions of light, temperature and nutrition. He found that in plants growing under favourable circumstances the microsporangia contained a number of aborted microspores. The functional spores enlarged, grew larger in size, and it was found that spore enlargement was proportional to spore abortion. He found that microsporangia showing microspore abortion developed spores that were 16 times larger than their original size. In extreme cases of abortion only a single spore survived and looked like a megaspore and showed all the structural characteristics of a megaspore. Under unfavourable conditions Shattuck (1910) was able to induce the formation of the large number of smaller spores in the megasporangia. He attributed these induced changes in the spore size to be due to change in the nutritional state of the sporangia. It was not possible for him to germinate these altered spores and therefore no conclusive results could be achieved. In the absence of such a conclusion these experimental studies cannot throw any light on the origin of heterospory.

Variations in the nutritional environments of the sporangia may alter the pattern of spore formation, but it appears that it is something else in the cellular controls system that regulates the differentiation of spores into two different sexual entities. It depends upon factors in the genetic system of the cell.

4.2 Heterospory & Seed Habit

Heterospory is considered to be a pre-requisite to seed formation. In addition to heterospory the seed plants show the following characteristics that have led to the formation of the seed.

(i) Reduction in size of the male gametophyte.
(ii) Formation of one megaspore within a megasporangium or the nucellus, as we call it in the seed plants.
(iii) The megasporangium is surrounded by an additional protective coat called the integument.
(iv) The megaspore is never shed and is permanently retained within the megasporangium. Fertilization and formation of embryo takes place in situ.
(v) Histological union between the megaspore and the megasporangium (nucellus). In the seed plants the megaspore is never free from the nucellar cells. They have a complete organic fusion, which is lacking in *Selaginella* and all other cryptogams.

Selaginella, no doubt, illustrates an example of heterosporous vascular cryptogams, that approach seed habit because of the following notable characteristics: -

1. It is heterosporous.
2. The megaspores start germination within the megasporangia and their time of release from the megasporangia varies with species.
3. The number of megaspores in *S. rupestris* and *S. monospora* is reduced to one.
4. In. *S. rupestris* the megaspore is never shed and fertilisation and development of embryo up to the formation of rhizophore, stem and cotyledons takes place while the megaspore is enclosed within the megasporangium, which retains its connection with the parent plant. This condition can be linked to **Vivipary** in some angiosperms.

After considering the above listed points we can, however, reach conclusion that the heterosporous vascular cryptogams like Selaginella and Marsilea fail to develop seeds because :-

1. They have no protective structure like the integuments surrounding their megasporangia.
2. The retention of megaspores permanently within the megasporangia has not become established.
3. Histological union between the megaspore and the megasporangium is absent (Martens,1966)
4. Lack of resting period after the development of embryo.

Similar to the nucellus of *Pinus* and other seed plants, the Selaginella megasporangium contains a megaspore that is equivalent to the embryo sac cell or megaspore of *Pinus*. The endosperm in Pinus is comparable to the female prothallus of *Selaginella*. Both have archegonia with eggs contained in their venters. In *Selaginella* only integuments are absent. The sporangial wall of *Selaginella* is two layered and could act as a protective structure. As a matter of fact the outermost wall of megasporangium in *Selaginella* becomes thick and sufficiently strong at maturity.

Regarding the retention of megaspore within the megasporangium, it has also been achieved by *S. rupestris*. This feature could not become common to all the species because there is no histological union between the megaspore wall and the wall of the megasporangium. In the presence of such a union, the megaspore could never come out of the megasporangium. Such a union if present in *Selaginella*, could also usher in an era of rest for the embryo after its development. In such a case the whole megasporangium could have fallen down from the plant and a megasporangium with contained embryo could easily be regarded as a primitive seed. In case we find a living example of a seed plant in which there are traces of separation of megaspore from the megasporangium we can regard it as a clue to the origin of seed habit. Martens (1966) has worked on these lines and has arrived at a more or less safe conclusion. Weterkeyn and Sloover (1962) conducted fluorescence microscopy on microspores of certain seed plants and megaspores of pteridophyta and found that a deposition of callose is responsible for isolating the spores from tetrads and from sporangial wall. This is called **megaspore mother cell callose** or **megasporocyte callose**. Such a callose formation is absent in the seed plants. They found it to be present in traces in one member of the cycadales (*Encephalartos*). In this case there is a little separation between megaspore and nucellus (megasporangium). Such a traces is lost in other groups of gymnosperms. As for the fossils no membrane analysis of the megasporocytes has been made. It can be presumed that such an isolation mechanism of megaspores from the megasporangia might have been present in the Pteridosperms.

Evidence for Heterospory

(a) Palaeobotanical Evidence

Plant/Fossil	Findings
Calamostachys binneyana	Mostly homosporous, but some sporangia had **unequal spores**.
Calamostachys casheana	Clear **heterospory** with **microspores & megaspores** in different sporangia.
Sphenophyllum dawsoni	**Spore abortion** led to a mix of large & small spores.
Stauropteris burntislandica	**Two large & two small megaspores per tetrad**, showing heterospory.
Lepidocarpon	**One functional megaspore, three aborted megaspores**, closer to seed formation.

(b) Developmental Evidence

Plant	Developmental Characteristics
Selaginella	Sex determinants influence **sporogenesis stage** rather than gametophyte development.
Marsilea	Megasporangia produce **one functional megaspore**, others abort.
Isoetes	**Clear differentiation** in sporangial development, leading to heterospory.
Equisetum	Homosporous, but gametophytes **differentiate into male & female types later**.

Reproductive Leap

1. What is the main evolutionary outcome of heterospory?
A. Seed formation
B. Homospory
C. Increased spore size
D. Reduced gametophytes

2. In heterosporous plants, sex is determined during:
A. Gametophyte formation
B. Sporogenesis
C. Fertilization
D. Spore shedding

3. Which fossil genus shows early heterospory?
A. Lepidocarpon
B. Calamostachys
C. Stauropteris
D. Miadesmia

4. Why are megaspores larger than microspores?
A. Abortion of microspores
B. Increased spore production
C. Fewer spores, more nutrients
D. Smaller sporangia

5. What is absent in Selaginella but present in seed plants?
A. Heterospory
B. Microspores
C. Megasporangia
D. Integuments

6. What is the role of callose in seed plants?
A. Enhances spore production
B. Promotes spore abortion
C. Isolates megaspores
D. Prevents fertilization

7. Which plant exhibits incipient heterospory?
A. Selaginella
B. Platyzoma
C. Equisetum
D. Lycopodium

8. What causes the reduction in megaspore number?
A. Spore abortion
B. Lack of nutrients
C. Increased spore production
D. Homospory

9. What is common between Selaginella and seed plants?
A. Integuments
B. Free-living gametophytes
C. Homospory
D. Megaspore retention

10. What is the key difference between Selaginella and seed plants?
A. Heterospory
B. Histological union of megaspore & megasporangium
C. Microspore production
D. Archegonia formation

11. What is the primary function of microspores in heterosporous plants?
A. Produce female gametophytes
B. Form seeds
C. Produce male gametophytes
D. Develop into megaspores

12. Which of the following is a prerequisite for seed habit?
A. Heterospory
B. Homospory
C. Abortion of spores
D. Increased spore size

13. What is the significance of megaspore retention in seed plants?
A. It allows spore shedding
B. It ensures in situ fertilization
C. It promotes homospory
D. It reduces spore size

14. Which plant group shows a shift in sex determination from gametophyte to sporophyte?
A. Homosporous plants
B. Algae
C. Bryophytes
D. Heterosporous plants

15. What is the primary role of the integument in seed plants?
A. Produce spores
B. Form male gametophytes
C. Protect the megasporangium
D. Promote spore abortion

16. Which fossil plant shows a reduction to one functional megaspore?
A. Calamostachys
B. Lepidocarpon
C. Stauropteris
D. Miadesmia

17. What is the key difference between Selaginella and seed plants regarding megaspores?
A. Selaginella lacks integuments
B. Seed plants shed megaspores
C. Selaginella has no megasporangia
D. Seed plants lack microspores

18. What is the primary evidence for heterospory in fossil plants?
A. Equal-sized spores
B. Abortion of spores
C. Homosporous sporangia
D. Lack of spore mother cells

19. What is the role of the tapetum in sporangial development?
A. Forms the spore wall
B. Provides nutrients to spores
C. Aborts spores
D. Produces microspores

20. Which experimental study linked nutrition to spore size variation?
A. Shattuck (1910)
B. Martens (1966)
C. Thoday (1906)
D. Chaloner (1958)

Answers

1-A,2-B,3-B,4-C,5-D,6-C,7-B,8-A,9-D,10-B,11-C,12-A,13-B,14-D,15-C,16-B,17-A,18-B,19-B,20-C

Module 5

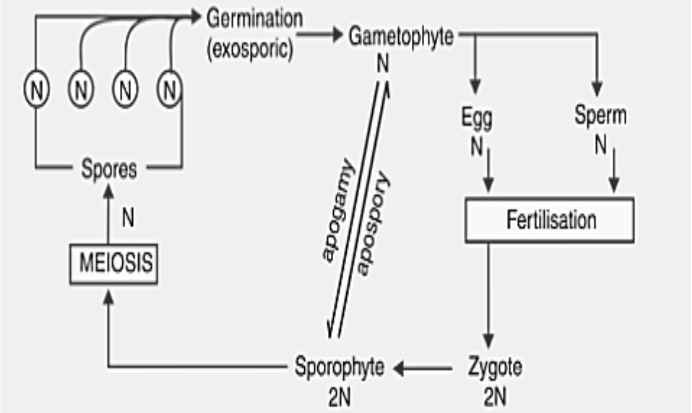
Alternation of Generation

Hofmeister (1851) used this term in plants. He observed that in Mosses and Ferns there are two types of morphologically distinct individuals in the life cycle. Both alternate in a life cycle i.e., there are some events which lead one generation to produce the other and thus cause alternation. The actual phenomenon responsible for bringing about alternation was exposed by the significant discovery of "the periodic Reduction of Chromosomes" by Strasburger (1894). Strasburger discovered the process of **meiosis** in plants. This discovery revealed that the reduction in the number of chromosomes leads to the formation of a new individual in the life cycle. This individual has haploid number of Chromosomes in its nuclei. It bears sex organs and is concerned with sexual reproduction. It was given the name **'gametophyte'** and represented gametophytic generation. The haploid gametes unite (fertilization or syngamy) and establish a diploid nucleus or a **Synkaryon**. Fertilisation establishes a diploid cell or the zygote, which is a pioneer structure of the diploid individual or the sporophyte. It germinates to form the embryo, which in turn develops into the sporophyte individual. This generation is termed the **sporophyte generation**. The sporophyte individual bears sporangia which produce spores as a result of **meiosis**. These spores are haploid and are also known as **meiospores**. The spores are the pioneer structures of the gametophyte generation. They germinate to give rise to the gametophyte individual known as the prothallus in vascular cryptogams.

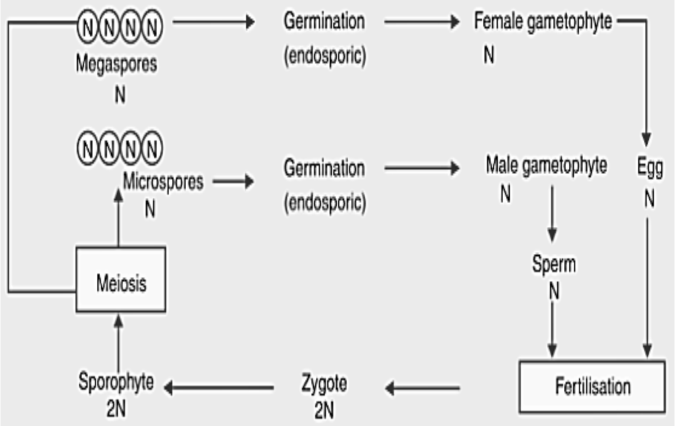
Both the generations can reproduce vegetatively and effect an increase in the number of their individuals. The above events, as displayed by the normal life cycle of a vascular plant, lead us to the following conclusions;

(i) There are two distinct individuals in the life cycle of vascular cryptogams.
(ii) These individuals are produced by the germination of the haploid spores and the diploid zygote.
(iii) The one produced by the spores is the gametophyte plant. To it is attributed the function of sexual reproduction and is haploid.
(iv) The zygote produces the embryo which gives rise to the diploid individual called the sporophyte. It bears haploid spores (or meiospores) after a process called the meiosis.
(v) The two generations alternate with each other in the life cycle.
(vi) Meiosis and syngamy (fertilization) are the two significant stages that switch on the life cycle from one generation to the other.
(vii) The number of chromosomes is halved during meiosis and is doubled during syngamy or fertilisation.

In the vascular plants the sporophyte individual is a complicated, independent and a dominant generation, whereas the gametophyte is comparatively much reduced. The gametophyte in the homosporous forms, though inconspicuous and comparatively short-lived, is independent and may be surface living and green (autophytic) or subterranean and non-green (*Lycopodium*). They are always exosporic and thus are not enclosed by the spore wall. They are also infected by an endophytic or a mycorrhizic fungus in some genera (*Lycopodium, Psilotum* and *Tmesipteris*). The heterosporous land plants, surprisingly enough, display a considerable reduction in their gametophytes. The gametophytes are reduced and **endosporic**. They have, as a rule, separate male and female prothalli. The male prothallus is extremely reduced and represented only by single prothallial cell. The female prothallus, on the contrary, is well developed because it has to nourish the developing embryo. Such a dioecism is unknown in homosporous land plants, but is a regular feature in the heterosporous ferns



Life Cycle of Homosporous Cryptogam



Life Cycle of Heterosporous Cryptogam

The sporophyte in the vascular cryptogams is no doubt independent but it has to depend upon the gametophyte during its earlier stages of development. It achieves its complexity after establishing its independence. The sporophyte, however complex it may be, has never achieved complete independence. The huge and giant sporophytes of the gymnosperms, during their earlier stages of development, are completely at the mercy of the food stored in the gametophyte. This is true even in the case of apogamously formed sporophytes. This food in the homosporous plants is truly gametophytic in origin, but in the heteroporous plants the food is mainly drawn from the sporophyte plant and is only stored in the gametophytic tissue. The angiosperms, on the other extreme, tell a different tale. The food stored in the endosperm is derived from the sporophyte and is stored in a triploid tissue. The morphological complexities of the sporophyte of vascular plants coupled with their elaborate and well organised anatomical set-up equipped with efficient means of dispersal confer upon them the potentialities to live under varied environmental conditions. These capabilities are responsible for their being stamped as efficient land dwellers.

Both the homosporous and heterosporous vascular plants exhibit **heteromorphic** type of alternation of generations because the sporophyte and the gametophyte individuals present marked morphological and anatomical differences. While studying the life cycle of a heterosporous individual a common feature that attracts our attention is the difference in the size of spores. It poses a serious question before us. Why the microspores (smaller in size) give rise to the male gametophyte and the megaspores to the female gametophyte? This question has not been satisfactorily answered. Two possible reasons have no doubt been suggested.

The first suggestion tends to explain the cause of difference in size. The megaspores are larger in size and produce female prothalli. The latter have to lodge the developing embryo sporophyte that requires lot of nourishment. The larger spores have greater nutritional store and can produce a well-developed female prothallus that is capable of hoarding food sufficient for the development of embryo sporophyte. The microspores are smaller in size and thus have little food stored in their protoplasts. They cannot afford to produce massive prothallial tissues. They germinate to develop one or two- celled prothallus that bears a single antheridium. The function of the antheridium is to produce spermatozoids. After their liberation it has nothing to do and, therefore, perishes. This can be the cause of their smaller size. The microspores are produced in large numbers as they are likely to be wasted during dissemination.

The cause of their being unisexual appears to be a contrivance towards cross pollination. The monoecious or bisexual gametophytes of homosporous vascular plants have many chances of self- fertilisation, unless they are submerged under water. The dioecious prothalli have extremely rare chances of self-fertilisation and suffer from a great disadvantage if they grow under terrestrial conditions. Under such circumstances they have little chance of fertilisation because the spermatozoids cannot reach the archegonia. This difficulty is solved to a greater extent by the phenomenon of heterospory. The microspores that need not carry much food are light in weight and smaller in size. They can be easily carried by wind and other agents to the female prothalli. The chances of their wastage are eliminated to a great extent, on account of their large number per microsporangium. Those which fall on the female prothallus have absolutely no difficulty in effecting fertilisation as the spermatozoids have not to travel a long distance and require only a little moisture which is provided by dew drops. Chances of self-fertilisation under these circumstances are rare, and cross-fertilisation is usually affected. This leads to outbreeding and ultimately to variations and rapid evolution. Heterospory has, as a matter of fact, freed the sporophyte from aquatic environments. Such an emancipation from aquatic habitats has conferred on the sporophyte the freedom to grow under varied environmental conditions. Heterospory is, therefore, regarded as a necessary step towards the evolution of seed habit and must be significant development during the struggle to conquer land.

5.1 Abnormalities in the Life Cycle

The normal life cycle of a vascular plant has two alternating generations. These are the diploid sporophyte and the haploid gametophyte. Both alternate regularly in the life cycle and this alternation is brought by two significant steps known as the fertilisation and the meiosis. The regular alternation of chromosome number is sometimes impaired by the occurrence of two common phenomena known as **apogamy** and **apospory**.

(a) Apogamy

It was first reported by Farlow (1874) in *Pteris cretica*. Apogamy can be defined as the development of a sporophyte directly from the gametophyte without the intervention of sex organs and gametes. The sporophytes thus formed usually have the same chromosome number as the gametophyte i.e., haploid number for the species. Apogamy occurs in nature and has also been induced under experimental conditions. It is a common and a widespread phenomenon in the ferns. Natural apogamy has been reported in more than 50 species of ferns belonging to 20 genera. In some species of ferns apogamy appears to be a necessity and is a regular process. It is perhaps due to the inherited constitution of the plant. Natural apogamy is commonly known in *Dryopteris, Pteris, Pellaea, Adiantum, Osmunda, Todea, Athyrium, Cheilanthes, Polystichum, Asplenium*, etc. To this list can be added a number of genera and species in which apogamy has been experimentally induced. Cases of parthenogenetic development of the egg into the sporophyte are not included under apogamy, because apogamy is the development of vegetative tissue of the prothallus into the sporophyte. Apart from the ferns apogamy has also been induced in some species of *Lycopodium* and *Equisetum*. It has been estimated that 12 percent of the cytologically investigated homosporous ferns are apogamous.

Regarding the cause of apogamy, several explanations have been put forth. Lang (1898) induced the formation of sporophytic buds, roots, sporangia and tracheids in various fern prothalli by avoiding watering of the prothalli from above. Brown (1923) summarised literature regarding the induction of apogamy by avoiding fertilisation of the egg. Many workers regard failure of normal fertilisation as a cause of apogamous production of sporophytes. Mottier (1931), however, demonstrated that in *Matteuccia struthiopteris* failure of fertilisation does not induce apogamy. Brown (1923) induced apogamy in *Phegopteris polypodioides* by avoiding normal fertilisation. Other conditions favouring apogamy have also been suggested. These are: culture in bright light and at higher temperatures (Nathansohn, 1900); by lowering the vitality of the prothallus by fungal and algal attack: and failure of formation of functional sex organs under various unfavourable nutritional conditions. Willams (1938) suggested that in addition to the environmental factors there must also be some internal factors such as the nature of inherent susceptibility due to abnormal nuclear composition and behaviour, that bring about apogamy.

Ageing of the prothallus has also been regarded as one of the factors influencing apogamous developments on the prothalli of some ferns. Recent work (Whittier and Steeves, 1960) on *Osmunda, Adiantum* and *Pteridium* has shown that apogamy can be induced by growing the prothalli on an agar culture medium rich in glucose. Wetmore and his associates (1963) demonstrated that when prothalli of *Onoclea, Osmunda* and *Todea* are planted erect on a medium containing one per cent sucrose, cylindrical and radially symmetrical growths with vascular strands are produced. De Maggio (1964) induced the formation of sporophytic buds on the prothalli of *Lycopodium obscurum* grown in culture media containing coconut milk and sucrose. These experiments reveal the effect of nutritional factors in inducing apogamy. Loyal and Chopra (1973) induced apogamy in *Regnellidium diphyllum*.

Work during the last 15 or 20 years has revealed that one out of every 15 species of ferns have what is called the "apogamous life cycle" in which both generations have the same chromosome number. The question now arises as to how this apogamous type of life cycle is maintained cytologically. Two methods are known. According to one method, which is rare, both the processes of spore formation and fertilisation are eliminated from the life cycle. The sporophyte or the fern plant produces a prothallus or the gametophyte which arises as a bud from the leaf and develops into a full-fledged prothallus. It is produced from the diploid tissue by mitosis and is, therefore, diploid in constitution. This diploid prothallus does not bear sex organs but instead gives rise to sporophytic buds that develop into diploid sporophytes. Such a method, therefore, involves the occurrence of both apospory and apogamy in the same plant. It is not a common method and has since been reported in *Athyrium filix foemina* var. *clarissiana*, *Dryopteris filix-mass* var. *cristata apospora* (Farmer and Digby, 1907); and in *Trichomanes kraussiana* (Georgevitch, 1910). Sarbadhikari (1939) discovered it in *Osmunda javanica*. It has been induced in *Pteris vittata* by Palta.

The second method which is very common among the ferns involves the formation of spore mother cells that actually double their chromosome number by the fusion of daughter nuclei. During this method the number of spore mother cells is reduced. Normally the sporangia in the leptosporangiate ferns possess 16 diploid spore mother cells, but in apogamous ferns there are only 8 spore mother cells with their nuclei having double the chromosome number (tetraploid). They will undergo meiosis and produce 32 diploid spores. These spores will produce diploid gametophytes. So, the number of chromosomes in both the generations is same. These gametophytes will bear sporophytic buds that will develop into full-fledged diploid sporophytes. Sex organs are usually not produced by such gametophytes and there is thus no fertilisation. Such a method is known to occur in a large number of ferns and is by far the commonest.

In India it has been reported by Mehra (1944) in *Adiantum lunulatum*; and by Mehra and his students (see Mehra, 1961) in thirty species of Himalayan ferns (*Pteris cretica, P. aspercaulis, P. blumeana, P. biaurita ; Dryopteris paleacea, D. fibrillosa, D. odontoloma, D. attrata ; Adiantum caudatum* and others). Mehra (1961) has given a vivid description of the apogamous and aposporous Himalayan ferns and has discussed their bearing on speciation and phyletic relationship among the ferns.

Evans (1965) has reported an interesting case of apogamy in a species of *Polypodium*. In this case he reported the formation of **32 mitospores** in the sporangia. The sporangia have 16 spore mother cells which do not undergo meiosis, but instead divide mitotically into 32 spores. These spores are reniform in shape and occur in diads rather than tetrads. He reported this sequence to occur regularly in all sporangia. The spores germinate readily to form prothalli which bear numerous apogamous sporophytic buds. The prothalli bear stomata but produce no sex organs. Virginia, M. Marzenti (1967) reported apogamy in *Asplenium curtissii* and *A. plenum*. In both the species the spore mother cells do not undergo reduction division and act directly as spores. These spores germinate to produce gametophytes that bear antheridia containing viable sperms, and also bear apogamous sporophytes.

Unique Fern Gametophyte

Gametophyta appalachiana, discovered in North America, is a ribbon-like fern gametophyte reproducing via gemmae, lacking a natural sporophyte. Stokey (1951) induced sporophyte formation apogamously, linking it to Vittariaceae.

(b) Apospory

The phenomenon of apospory was recorded by Druery (1884) in a fern called *Athyrium filixfemina* var. *clarissima*. He observed the development of prothalli from the stalk of the sporangium as well as from the spore case of this fern. Later apospory was noticed in many ferns and some workers induced it under cultural conditions. During this phenomenon gametophytes or prothalli develop from the vegetative tissue of the sporophyte and not from the spores. Such prothalli are diploid i.e., they have the same chromosome number as the sporophyte. Normally the haploid spores germinate and give rise to the haploid gametophyte, but during apospory spores are not required. Apospory thus is the development of gametophytes from the vegetative parts of the sporophyte without the intervention of spores. Bower reported it in two species of Trichomanes in 1885. In this case aposporous gametophytes were produced from soral regions of the leaf and from leaf tips. Later apospory was reported by several authors in many genera and species of ferns. Druery and Neurnberg (1938) and Steil (1939, 1951) reviewed the literature on apospory and apogamy in ferns. Bristow (1962) developed gametophytes from a callus tissue derived from the sporophyte of the fern *Pteris cretica*. This callus developed into gametophytes when grown in media containing only mineral nutrients. De Maggio and Wetmore (1961) isolated zygotes and undeveloped embryos from the archegonia of *Todea barbara* and cultured them. They were able to induce these isolated zygotes to develop into thalloid structures that resembled the gametophytes of this fern. Bell (1959) reviewed many cases of apospory in ferns and was tempted to state that the phenomenon of apospory must be general among ferns. Wetmore and De Maggio (1963) have also reviewed cases of apospory and apogamy among ferns.

Several factors seem to influence the aposporous development of gametophytes from vegetative tissues of the sporophyte:-

1. Briston (1962) demonstrated that mineral nutrition is responsible for the formation of prothalli from callus tissue obtained from the sporophytes of *Pteris cretica*. When he supplied sucrose to such a callus tissue, it developed into a sporophyte.

2. Goebel (1902) and Beyerle (1932) demonstrated that there is a pronounced relation between the stage of development of sporophytic cells (under culture) and the kind of organs regenerated. They observed that in *Ceratopteris thalictroides* aposporous gametophyte developed on decapitated young sporophytes with one or two leaves whereas in older sporophytes only shoot buds developed. Beyerle (1932) observed that in *Davallia canariensis* and in *Nephrolepis biserata* the prothalli develop on leaf tips and shoot buds at the basal and older parts of the leaf.

3. In some ferns e.g., *Drynaria rigidula, Polypodium aureum* and *P. heracleum* the leaves develop prothalli under dim light and sporophytic buds under strong light. Koehler (1920) also demonstrated that in *Platycerium bifurcatium* prothalli develop on leaves grown under dim light whereas the same leaves produce sporophytic buds on exposure to strong light.

4. The work done in Punjab University Botany Laboratories (Mehra and Palta, 1969 to 1973) on tissue culture has revealed interesting results. A few examples are being cited here. They obtained root callus tissue from the roots of a tetraploid *Cyclosorus dentatus* on Knudson's medium +2% sucrose +2, 4-D. The callus was fragile and its cell suspensions were obtained in sterile distilled water. The isolated cells of the callus were then placed on three different media:

A. Knudson's medium basal.
B. Knudson's medium +1% sucrose.
C. Knudson's medium + 2% sucrose.

In A the root cells behaved as spores and germinated to give rise to a prothallus. This shows that under mineral nutrition the callus tissue is induced to form gametophytes because basal Knudson's medium contains only minerals. In B the callus cells gave rise to structures that were partly gametophytes and partly sporophytes. They called such structures as Gameto-sporophytes. In C the callus cells gave rise to the complete sporophytes (regeneration).

Apospory has also been induced in *Pteris vittata* by Palta (1973). Sexually produced normal sporophytes produced gametophytes from the juvenile leaves. These gametophytes bore normal sex organs in Knudson's medium (Km) without sucrose. In this exact species he was able to produce apogamous sporophytes in KM with 2% sucrose. Later this apogamous sporophyte was placed in KM without sucrose. After 3 weeks' time the apical pinnae of the same sporophyte produced aposporous gametophytes. So, with a change in the nutritional set-up of the environments apogamy and apospory can be induced at any time.

In some ferns. e.g., *Actinostachys* and *Schizaea* the sporophytes are very similar but the gametophytes are very different, whereas in majority of the higher ferns the gametophytes are very similar but sporophytes are quite different and dissimilar. It means that a certain set of expressions has evolved in the sporophyte and another in the gametophyte, with a considerable overlap (Bierhorst, 1971). Bierhorst (1971) has further opined that the "degree of overlap or the degree of differential expression of certain genomic segments, has occasionally changed and is of some morphological significance." It has also been noticed that there are close similarities in the developmental, patterns of some sporophytic and gametophytic structures such as antheridia, archegonia, sporangia and the hair or the trichomes. The later stages of development between the anteridia and sporangia of Equisetum are quite similar. In some ferns the establishment of initials of archegonia, antheridia and sporangia is similar. The divisions which establish these initials are on a similar pattern. Similarly, the structure and development of trichomes on the sporophytes and prothalli of certain ferns is very similar. In the words of Bierhorst "these are all subtle expressions of apogamy and differ only in degree from those which drastically upset the life cycle ... "

(c) Parthenogenesis

This may be defined as the phenomenon where the egg develops into embryo without the act of fertilisation. This act is very common in algae, fungi and ferns. According to Farmer and Digby (1907) in homosporous leptosporangiate ferns, apospory was followed by neither apogamy nor fertilisation but by parthenogenesis. There are various species of *Selaginella* where parthenogenesis has been reported. In *S. atroviridis* with unisporangiata strobili the egg develops into embryo without fertilization. This phenomenon has also been observed in S. intermedia and *S. langere* (Hieronymus, 1911). Bruchman (1912, 1919) and Goebel (1915) observed parthenogenesis in a few other species of Selaginella with bisporangiate strobili (*S. anacardia, S. rubicaelis* and *S. helvetica*). In these cases, archegonial neck remains closed and does not permit spermatozoids to enter. The egg, in these species develops directly into embryo. In *Marsilea drummondii* too the megaspores on germination produced diploid megagametophyte (1970 Strasburger), which without fertilization developed into sporophytes.

Generation Flip

1. Who coined "Alternation of Generation"?

A. Druery
B. Strasburger
C. Farlow
D. Hofmeister

2. What switches the life cycle from sporophyte to gametophyte?

A. Meiosis
B. Mitosis
C. Fertilization
D. Spore germination

3. Which generation is dominant in vascular plants?

A. Gametophyte
B. Sporophyte
C. Prothallus
D. Zygote

4. What is the gametophyte's primary role?

A. Sexual reproduction
B. Spore production
C. Nutrient storage
D. Vegetative growth

5. What distinguishes microspores from megaspores?

A. Microspores are larger
B. Megaspores are fewer and nutrient-rich
C. Microspores produce female gametophytes
D. Megaspores are in microsporangia

6. What does meiosis achieve in alternation of generations?

A. Doubles chromosomes
B. Produces diploid spores
C. Reduces chromosomes
D. Forms the zygote

7. What characterizes homosporous plants?

A. Two spore types
B. Dioecious gametophytes
C. Independent gametophytes
D. Endosporic development

8. What is the integument's role in seed plants?

A. Protect megasporangium
B. Produce spores
C. Form male gametophytes
D. Promote spore abortion

9. What is apogamy?

A. Sporophyte from gametophyte without fertilization
B. Gametophyte from sporophyte without spores
C. Egg development without fertilization
D. Spore formation without meiosis

10. What causes apogamy in ferns?

A. Reduced spore size
B. High nutrients
C. Presence of integuments
D. Fertilization failure

11. What is apospory?

A. Gametophyte from spores
B. Gametophyte from vegetative tissue
C. Spores without meiosis
D. Zygotes without fertilization

12. How does parthenogenesis differ from apogamy?

A. Parthenogenesis involves egg development
B. Apogamy involves fertilization
C. Parthenogenesis occurs in algae
D. Apogamy doubles chromosomes

13. What characterizes heterosporous plants?

A. Same-sized spores
B. Homosporous sporangia
C. Dioecious gametophytes
D. No spore mother cells

14. Why are megaspores fewer in heterosporous plants?

A. Increased spore production
B. Spore abortion
C. Lack of nutrients
D. Homospory

15. What defines alternation of generations in vascular plants?

A. Dominant gametophyte
B. Spores without fertilization
C. Absence of meiosis
D. Haploid-diploid alternation

Answers

1-D,2-A,3-B,4-A,5-B,6-C,7-C,8-A,9-A,10-D,11-B,12-A,13-C,14-B,15-D

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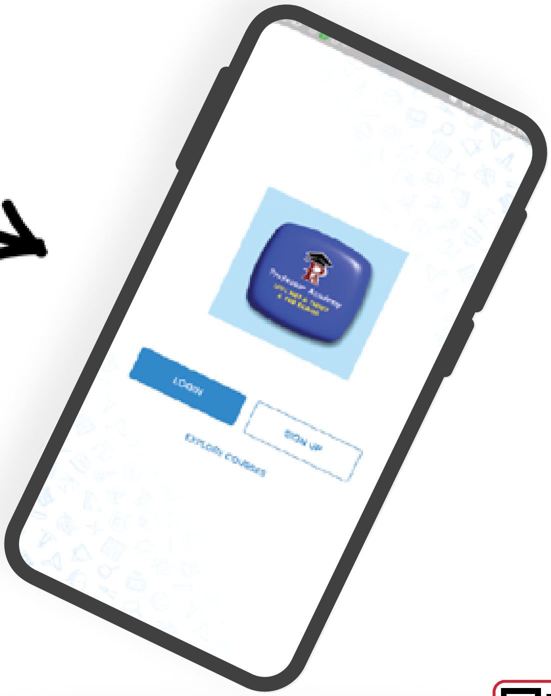

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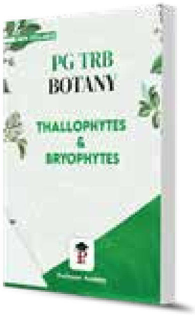

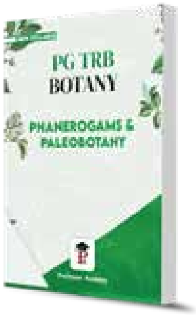

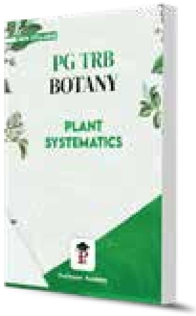

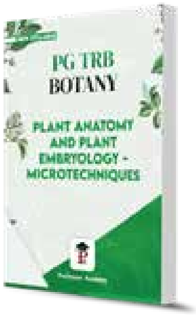

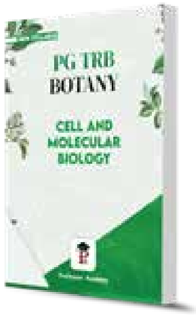

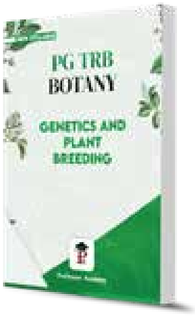

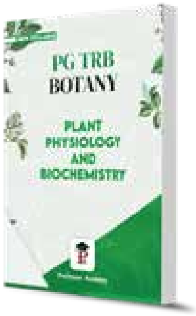

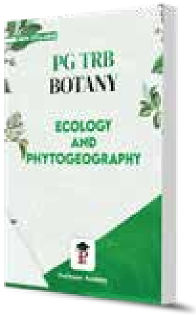

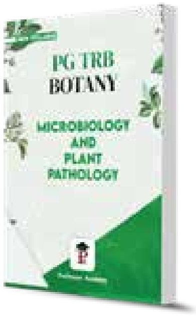

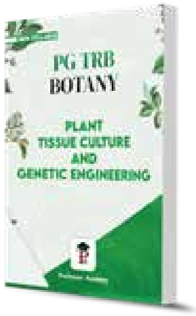

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