COURSE-III: PTERIDOLOGY, GYMNOSPERMS AND PALAEOBOTANY (BSCBO-103)

BLOCK-I- PTERIDOPHYTES

Telome theory & Stelar System

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Introduction

The discovery of a group of earliest known land plants with simple organization of the sporophyte (rootless, dichotomously branched, single terminal sporangium, protostele vascular cylinder) from the upper Silurian and middle Devonian deposits has been of great importance in the understanding of the structure and phylogeny of vascular plants.

A number of theories on land plant evolution exists of which the **Telome theory** of Walter Zimmermann (1930, and later elaborated on 1952) is the most comprehensive.

This theory is based on fossil record and synthesizes the major steps in the evolution of vascular plants.

According to this theory, all vascular plants evolved either directly or indirectly from a simple leafless Rhynia type ancestral form made up of sterile and fertile axes (the telomes).

Evolutionary modification of its parts produce more advanced vascular plants with roots, stems, leaves, protected sporangia and more complex vascular systems.

Zimmermann defines the telome as the single-nerved extreme portion (at base or apex) of the plant body from the tip to the next point of branching.

The following two types of telomes have been recognized on the basis of their function:

- **Vegetative or sterile telomes**: without sporangia also called phylloids.

- **Fertile telomes:** bear terminal sporangia.

The telome grow and divides dichotomously, the new segments become new telomes and older segment below are **mesomes**.

Following evolutionary development telomes may be grouped together in various ways to form more complex bodies **Telome Truss** or **Syntelome.**

(i) Phylloid Truss- Only sterile telomes
(ii) Fertile Truss- Only Fertile telomes

Origin of Telomes and Primitive land plants

According to the Telome theory the early land plants originated from the green algae which lived in tidal zone of the Cambrian and Silurian sea coasts.

The plant body of those algal ancestors was undifferentiated branched thallus (primitive telome).

According to Zimmermann these primitive telomes were formed from the unicellular stage by the following five elementary processes:

(i) Interconnection of cells

(ii) Differentiation of meristem

(iii) Rotation of cell axis

(iv) Shifting of chief phases in alternation of generation

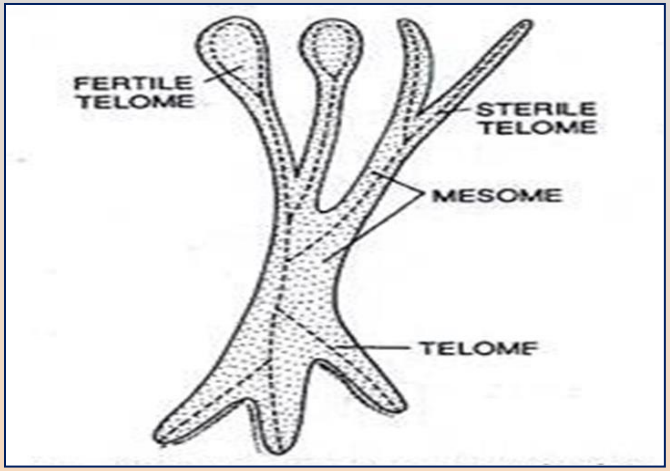
(v) Differentiation of various permanent tissues

The Primitive Land Plant

The telome theory visualizes the Psilophytales of the upper Silurian and lower and middle Devonian deposits (*Zosterophyllum*, *Rhynia*, *Horneophyton and Psilophyton* etc) as representing the sporophyte of the ancient vascular plants.

The sporophyte was relatively undifferentiated (no distinction between leaf and stem) and consisted of single-veined (protostele) telomes which may be sterile and fertile.

The aerial portion developed stomata and the basal portion, hairs or rhizoids. The fertile telome produced terminal sporangia.



Hypothetical diagramme of a primitive land plant

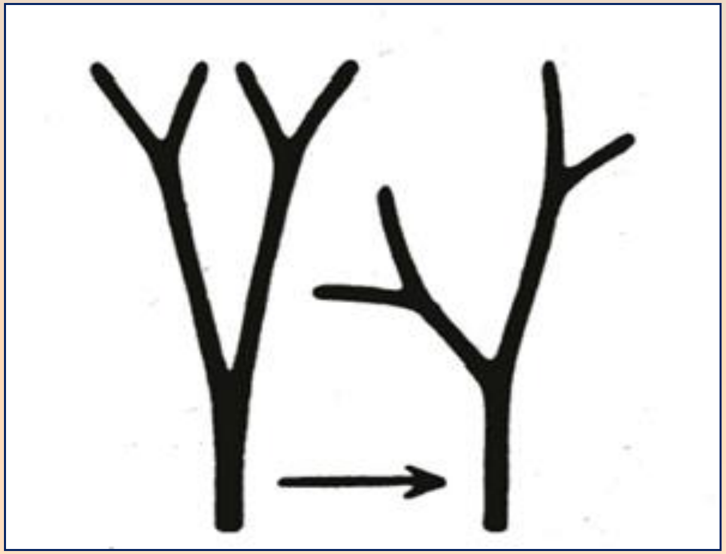
Evolution of Higher Land Plants

From the primitive syntelome of the early land plants the sporophytes of higher land plant evolved by certain organogenetic processes called "**elementary processes**" each following its own trends. Zimmerman suggested that the these elementary processes were responsible for the development of higher vascular plants from the early vascular cryptogams.

Process of Telome Theory

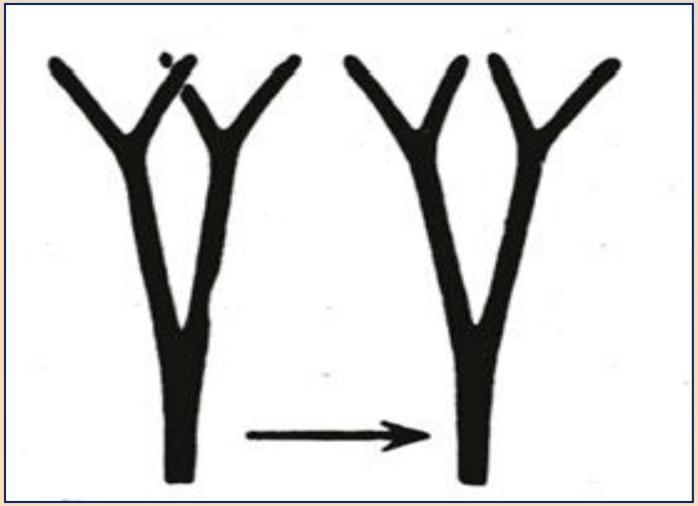
Overtopping:

- One of the two dichotomizing branches becomes stronger and erect becoming the axis while other remained overtopped as short lateral branch.
- It leads to the formation of an axis with lateral appendages, the leaves, e.g. open-veined pinnately compound type of fern leaf.
- Overtopping mesomes form the rachis and the overtopped mesomes constitute the leaflets.



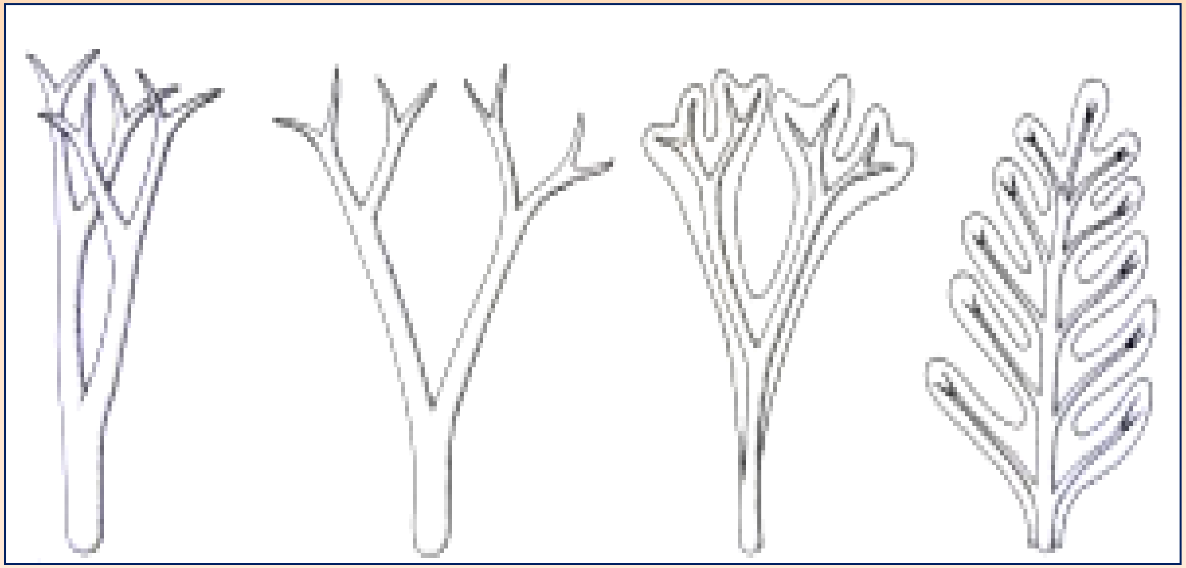
Planation:

- Rearrangement of telomes and mesomes from a three dimensional pattern to a single plane.
- Branching in more than one plane (cruciate dichotomy) is replaced by a dichotomy in a single plane (fan shaped dichotomy).
- By this process an organ of radial symmetry gives rise to one of bilateral symmetry.
- Plantation concerns mainly the evolution of the leaf.



Syngenesis (fusion or webbing):

- Fusion of the telome or telome trusses by the development of connecting tissue (as in the foot of duck) is called syngenesis or webbing.
- Telomes and mesomes connect by the formation of parenchymatous tissue between them (parenchymatous webbing) sometimes accompanied by the fusion of their stele.



Syngenesis is a very important elementary process because it explains the origin and evolution of both the leaf and stele of the stem.

It leads to the formation of:

(i) Foliar appendages with open dichotomous venation. In this case the sterile telomes (Phylloids) become united only by the development of parenchymatous webbing

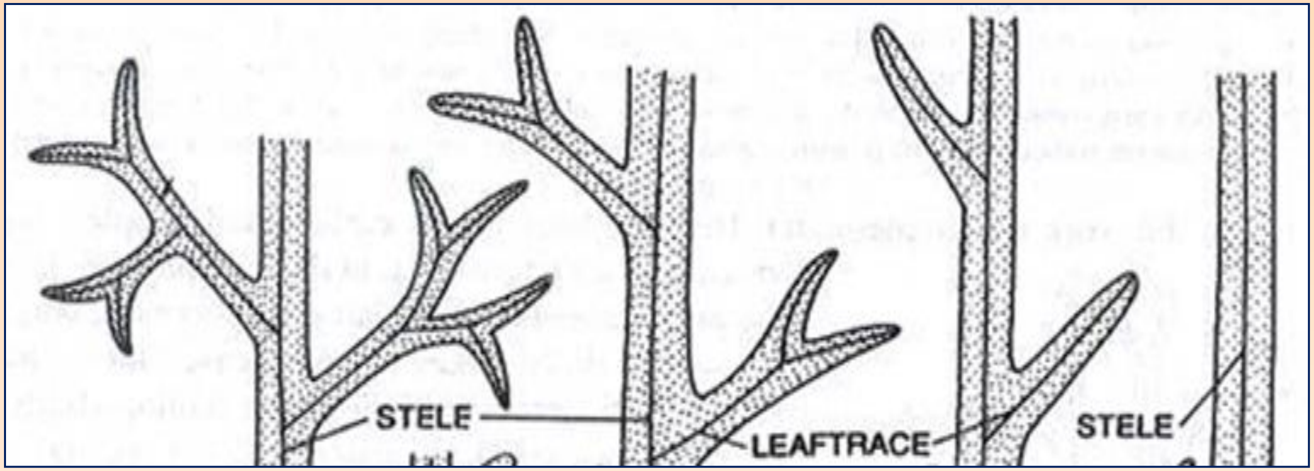
(ii) Pinnately veined leaf: Parenchymatous webbing was accompanied by over-topping.

(iii) Leaf with reticulate venation: if fusion of steles or vascular bundles also occurred.

(iv) Parenchymatous webbing led to the polystelic condition (in an open form) as in many species of *Selaginella*.

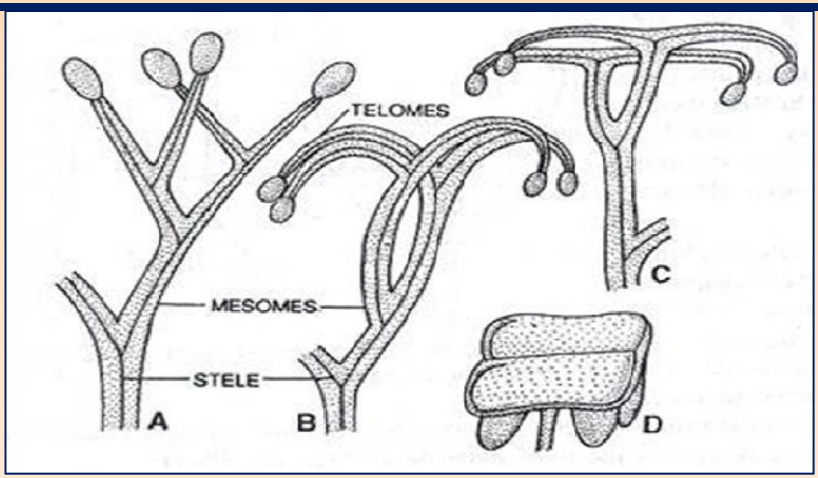
Reduction:

- Activity of terminal meristem of each telome suppressed resulting into much shorter branches
- It involved the transformation of a syntelome into a single needle-like leaf (conifers).
- According to Zimmermann the microphyllous leaves of Lycopsida and Sphenopsida were evolved by the reduction of telome trusses.

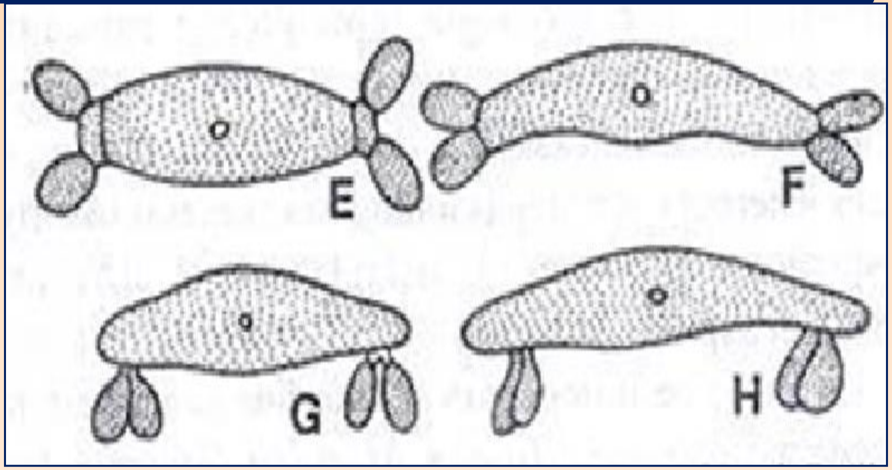


Curvation: The fertile Telomes become curved or bend downwards. Wilson (1953) recognized two separate sub-processes.

- **Recurvation:** When telomes bent down inwards, it is called Recurvation. During this process, the fertile telomes (sporangiophores) were reflexed and sporangia became inverted.
- **Incurvation:** This process accounts for the shifting of sporangia from terminal position to the ventral surface of the leaf in ferns.



Steps in the process of Recurvation



Steps in the process of Incurvation

Merits

- It provides an interpretation of origin and evolution of sporophytes of land plants.
- Structure of the sporophytes of the most primitive known land plants is defined.
- It interprets the morphological features of the lower vascular plant such as the nature of the aerial portion of the plant body of the family Ophioglossaceae and coenopterid ferns.
- This theory emphasises on the fact that the plant body is an axis with a descending portion, the root and an aerial portion, the shoot whose appendages are modified parts of the stem.
- According to Eames, though the theory is built upon structure in the lowest known vascular plants, higher plant can also be interpreted in this way.
- It also connects the fossil and living plants by their phylogenetical relations.

Demerits

•According to Thomas (1950), the telome theory does not explain the whorled or spiral arrangement of sporangia, which is observed in some ancient and primitive plants.

•Application of the telome theory to the origin of Lycopsida has been greatly criticised. Andrews (1960) supports this theory to some extent so far as Sphenopsida and Pteropsida are concerned, but for Lycopsida, he is not in agreement with Zimmermann.

•According to Bower (1946), this theory does not explain how a telome-like characterized body has been developed. It has been taken for granted by Zimmermann (1930) that a telome type body is 'ready-made'.

Stewart (1964) also criticised the telome theory because it does not explain the derivation of the dictyostelic condition.

Many other plants of greater complexity, than *Rhynia* fossils have been discovered e., *Zosterophyllum, Baragnnathia* (Leclercq, 1954) Lyon and Heuber (1964), Heuber and Banks (1967) and Lyon (1964) observed *lateral sporangia* on short vascularised stalks in *Psilophyton* and *Asteroxylon* instead of usual *terminal sporangia*.

This theory has received little attention by angiosperm morphologists. Its application to stamens, venation pattern of leaves and carpels have been critised from time to time.

STELAR EVOLUTION

The stele (=Greek word meaning **pillar** or column) is defined as a central vascular cylinder, with or without pith. Endodermis is the boundary between cortex and stele. The central cylinder or core of vascular tissue, consisting of xylem, phloem, pericycle and sometimes mudullary rays and pith, is technically called the stele.

The concept of the stele as the fundamental unit of vascular system was put forward by Van Tieghem and Douliot (1886) who proposed and developed Stelar theory.

The stele of stem was connected with that of leaf by a vascular connection known as leaf trace.

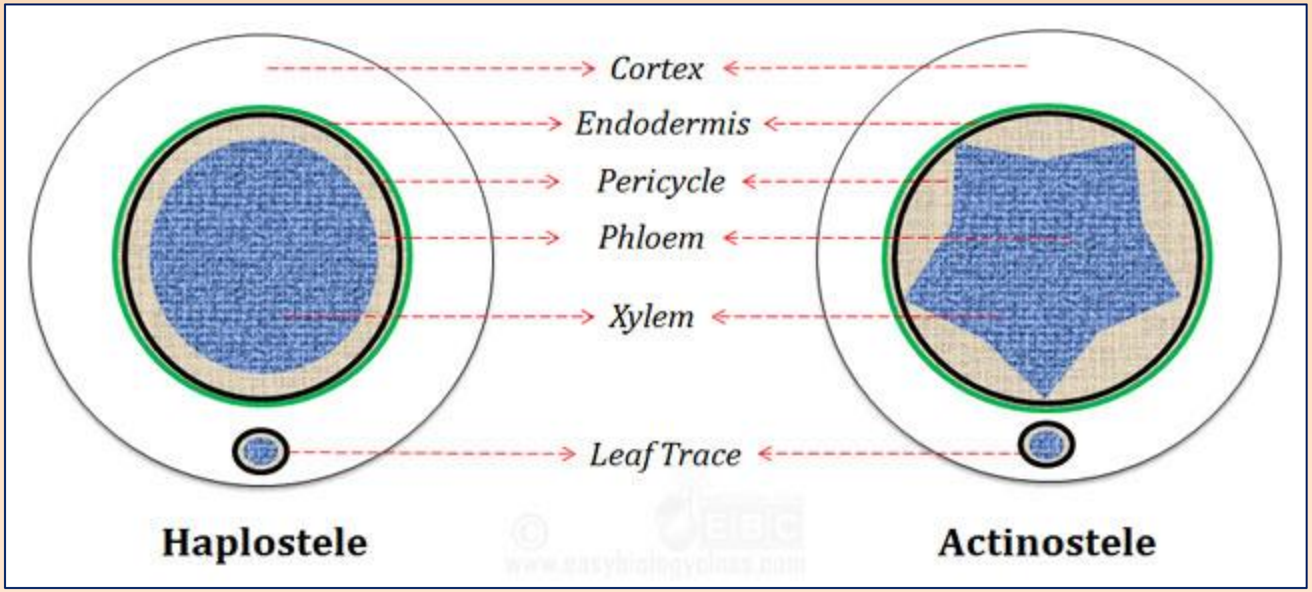
Types of stele in Pteridophytes

The stele in pteridophytes can be differentiated into two major groups.

1. **Protostele:** It is the most simplest and primitive type of stele. In protostele, the vascular bundle is a concentric solid mass and the central core of xylem is surrounded by a layer of phloem and finally surrounded by a layer of pericycle. The protostele exists in following forms:

a) **Haplostele:** This is the most primitive type of stele. In this the xylem forms a solid, smooth and spherical central core which is surrounded by a continuous concentric layer of phloem e.g. *Lygodium, Selaginella.*

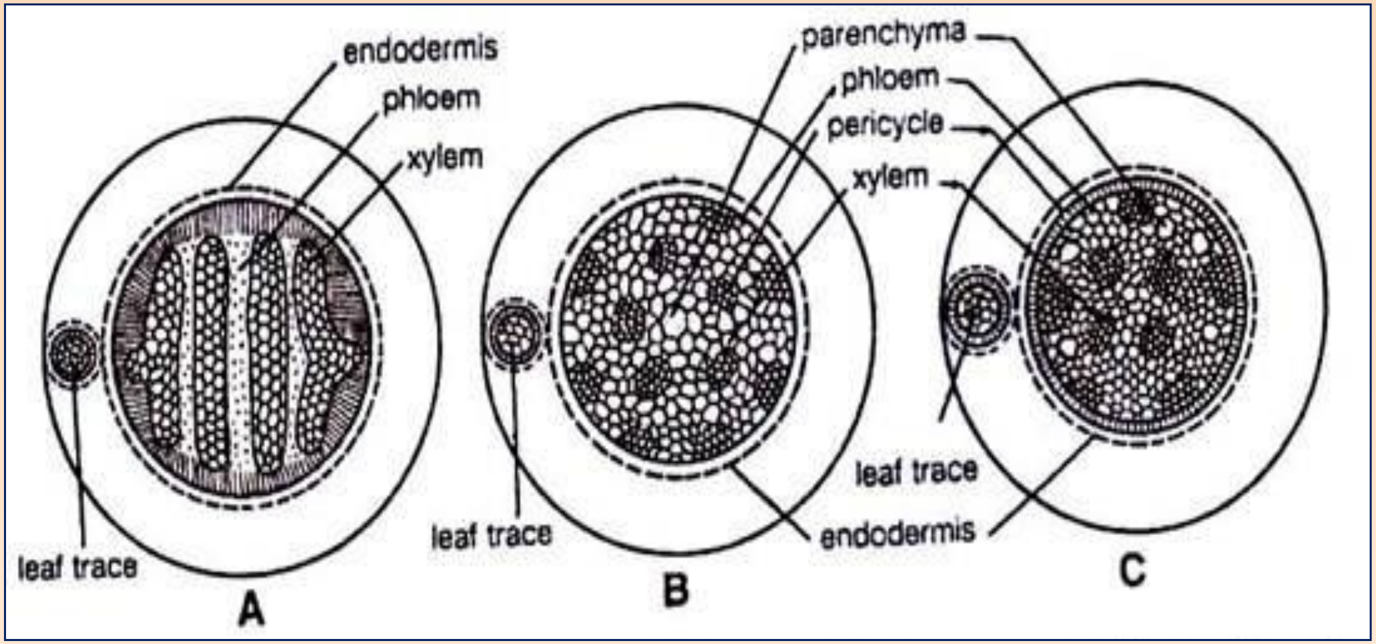
b) Actinostele: This is the modification of the haplostele and somewhat more advanced in having the central xylem core with radiating ribs and phloem is not concentric but present in between the radiating ribs of xylem e.g. *Psilotum*. The protoxylem is present at the tips of radiating arms.



c) Plectostele: In the stem of some species of *Lycopodium* the solid core of xylem gets broken in a number of plate-like lobes, more or less lying parallel to one another. The phloem alternates with xylem plates e.g. *Lycopodium volubile.* This specialized form of protostele is termed as plectostele.

d) Mixed protostele: In this type, masses of xylem and phloem are uniformly distributed. Scattered groups of xylem are embedded in the ground tissue of phloem e.g. *Lycopodium cernnum.*

e) Protostele with mixed pith: In the centre there is parenchyma cells associated alongwith the tracheids e.g. *Lepidodendron*. It may be derived from the transformation of the tracheids into parenchyma and may be first step in formation of pith. Such type of protostele is termed as mixed-protostele.



Stelar System: A. Plectostele B. Mixed protostele C. Mixed protostele with pith

2. Siphonostele: Medullated protostele is called siphonostele. It is characteristic of Filicophyta. This is the modification of protostele. During the development the siphonostele the central core of xylem is replaced by parenchymatous cells so that definite pith surrounded by xylem appears in the centre.

On the basis of branch and leaf gaps Jeffrey (1910), distinguished two types of siphonosteles, **cladosiphonic siphonosteles** (leaf gaps not found) and **phyllosiphonic siphonosteles** (leaf and branch gaps are present).

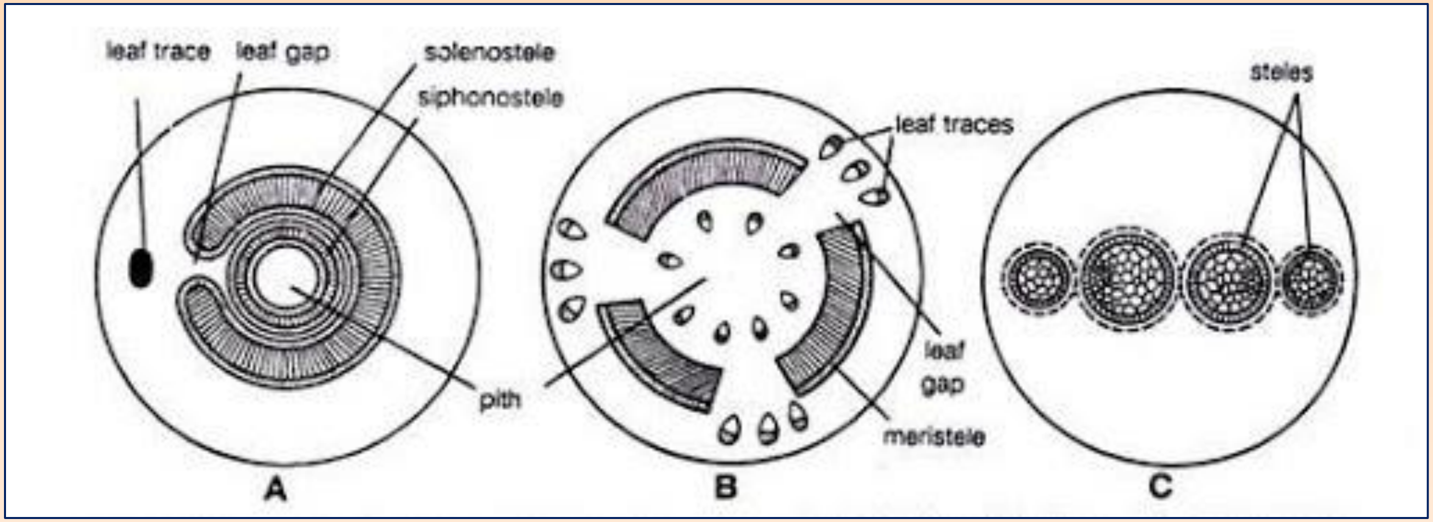
Origin of pith in siphonostele

There is a general acceptance that siphonostele is evolved from a protostele. Two theories have been proposed to explain the origin of pith.

Intrastelar origin of pith: According to this view, pith has originated as a result of transformation of tracheary elements of the central xylem core into parenchyma. Thus, the pith is totally intra –stelar. This view is supported by Boodle (1901), Gwynne–Vaughani (1908), Bower (1911). E.g., *Osmunda regalis*, *Botrychium ternatum* where tracheids are scattered throughout the pith (mixed pith).

Extrastelar origin of pith: This hypothesis was supported By Jeffrey (1902, 1910 and 1917).

According to this view, protostele has transformed into siphonostele due to migration of cortical cells into stelar axis. Openings such as leaf and branch gaps, probably provided passage for invasion of parenchyma. This view derives support from amphiphloic siphonostele that has two endodermal layers; one delimits the stele from the cortex and the other from the pith. Since endodermis is a structure peculiar to cortex, the pith is considered as cortical in origin.

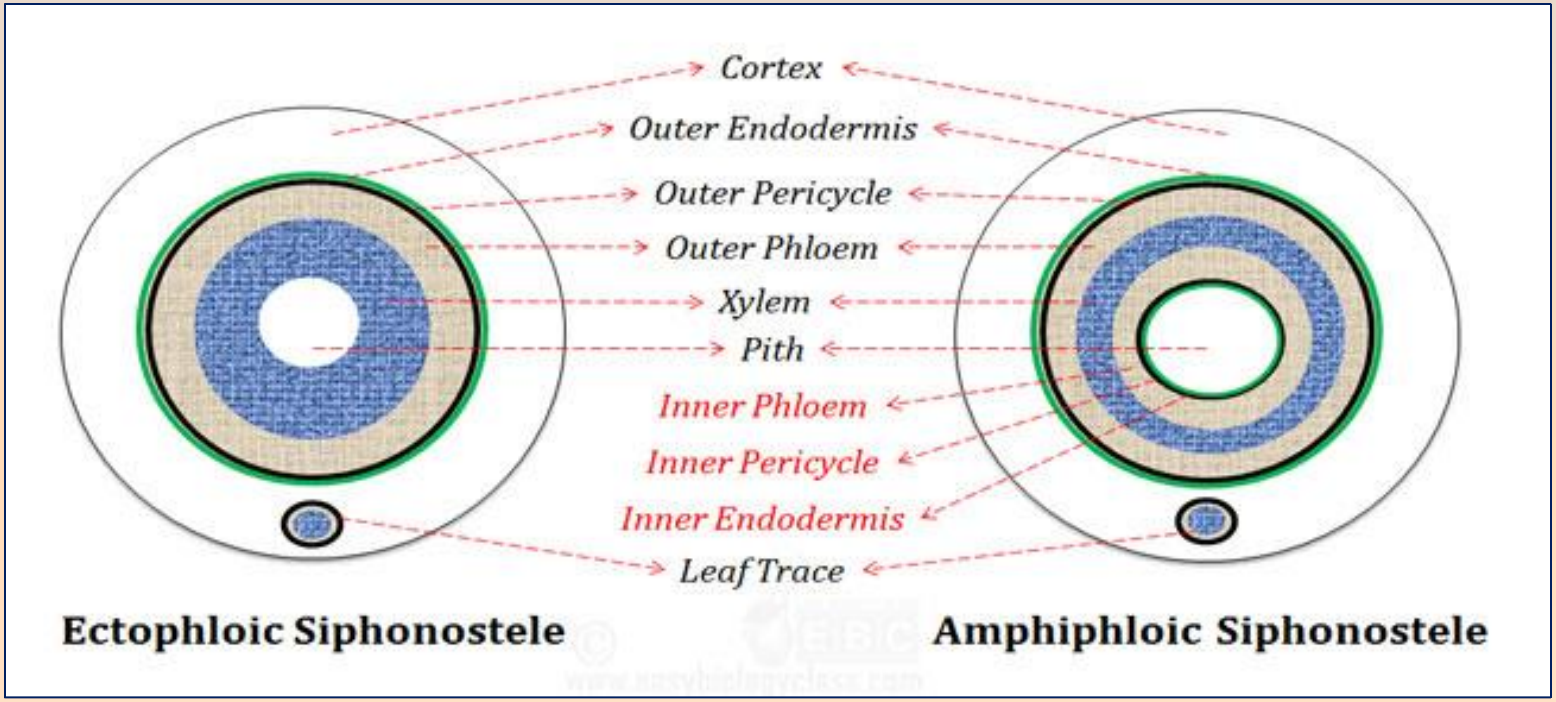


Stelar seytem: A. Polycyclic solenostele, B. Polycyclic dictyostele, C. Polystele

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

(a) Ectophloic siphonostele: The pith is surrounded by concentric xylem cylinder and next to xylem the concentric phloem cylinder. It means the phloem is restricted only on the external sides of the xylem. (e.g. *Osmunda* and *Schizea*). The pith is central in position. The phloem is externally surrounded by pericycle and endodermis.

(b) Amphiphloic siphonostele: The pith is surrounded by the vascular tissue. The concentric inner phloem cylinder surrounds the central pith. Next is the concentric xylem cylinder which is immediately surrounded by outer phloem cylinder. It means phloem is present **both sides** of xylem. (e.g., *Marsilea* rhizome).



Cortex
Outer Endodermis
Outer Pericycle
Outer Phloem
Xylem
Pith
Inner Phloem
Inner Pericycle
Inner Endodermis
Leaf Trace
Ectophloic Siphonostele
Amphiphloic Siphonostele

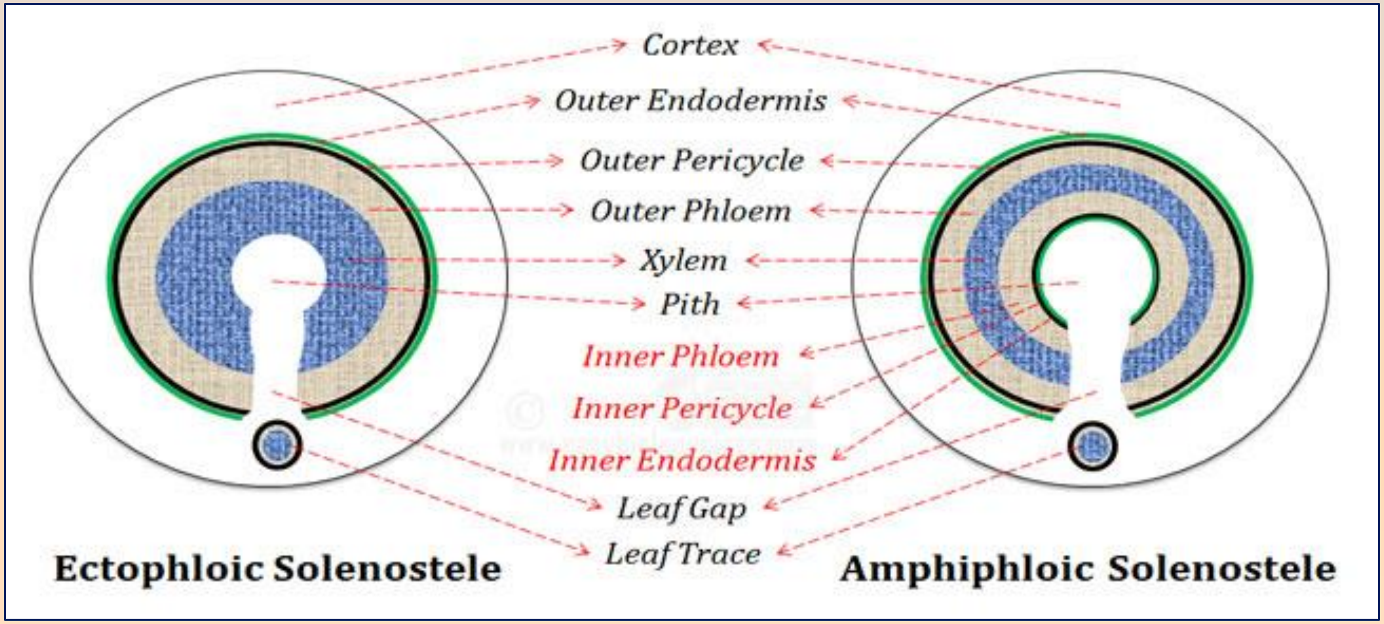
Other modification of Siphonostele

3. Solenostele

If the siphonostele perphorated at the place or places to the origin of the leaf trace, such a condition is known as Solenostele.

Ectophloic solenostele: This type of solenostele derived from the ectophloic siphonostele. So, here the phloem is present only side of xylem.

Amphiphloic solenostele: This type of solenostele derived from the amphiphloic siphonostele. So in this case the phloem is present on both the sides of the xylem.



Cortex
Outer Endodermis
Outer Pericycle
Outer Phloem
Xylem
Pith
Inner Phloem
Inner Pericycle
Inner Endodermis
Leaf Gap
Leaf Trace
Ectophloic Solenostele
Amphiphloic Solenostele

4. Dictyostele

In the more advanced siphonosteles of Pteropsida, the successive gaps may overlap each other.

Brebner (1902) called the siphonosteles with overlapping gaps as dictyosteles. So, in this case the solenostele broken into a network of separate vascular strands, due to crowded leaf gaps.

In such cases each separate vascular strand is known as meristele. Each meristele is of protostelic type. The dictyostele is a ring of many meristeles.

5. Eustele

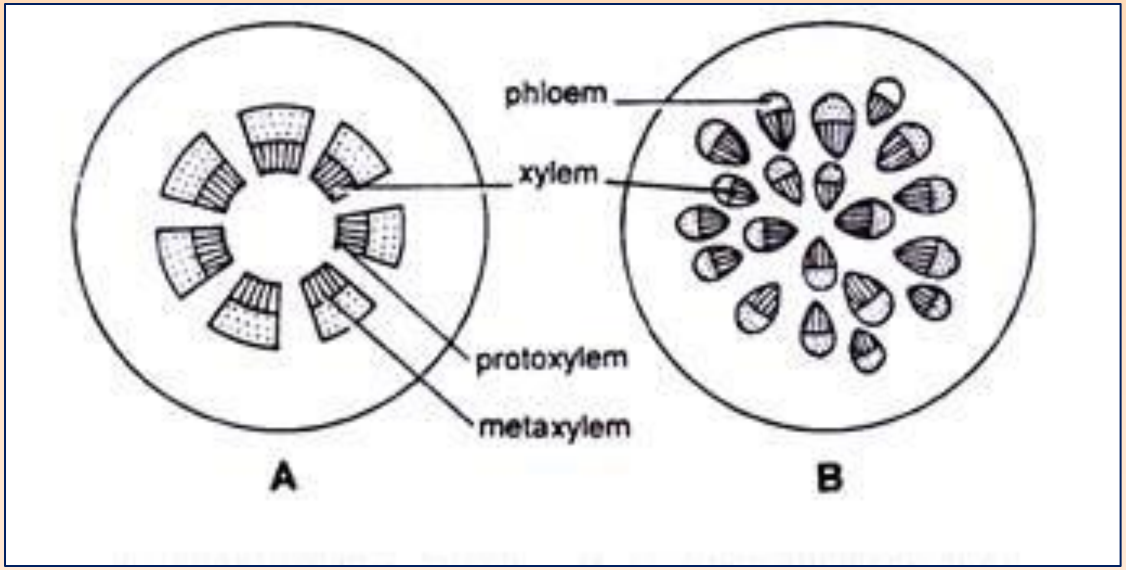
According to Brebner (1902), there is one more modification of the siphonostele known as eustele.

Here the stele is split into distinct collateral vascular bundles. So the vascular system consists of a ring of collateral or bicollateral vascular bundles situated on the periphery of the pith.

In such steles, the inter-fascicular areas and the leaf gaps are not distinguished from each other very clearly. The example of this type is *Equisetum*.

6. Atactostele

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



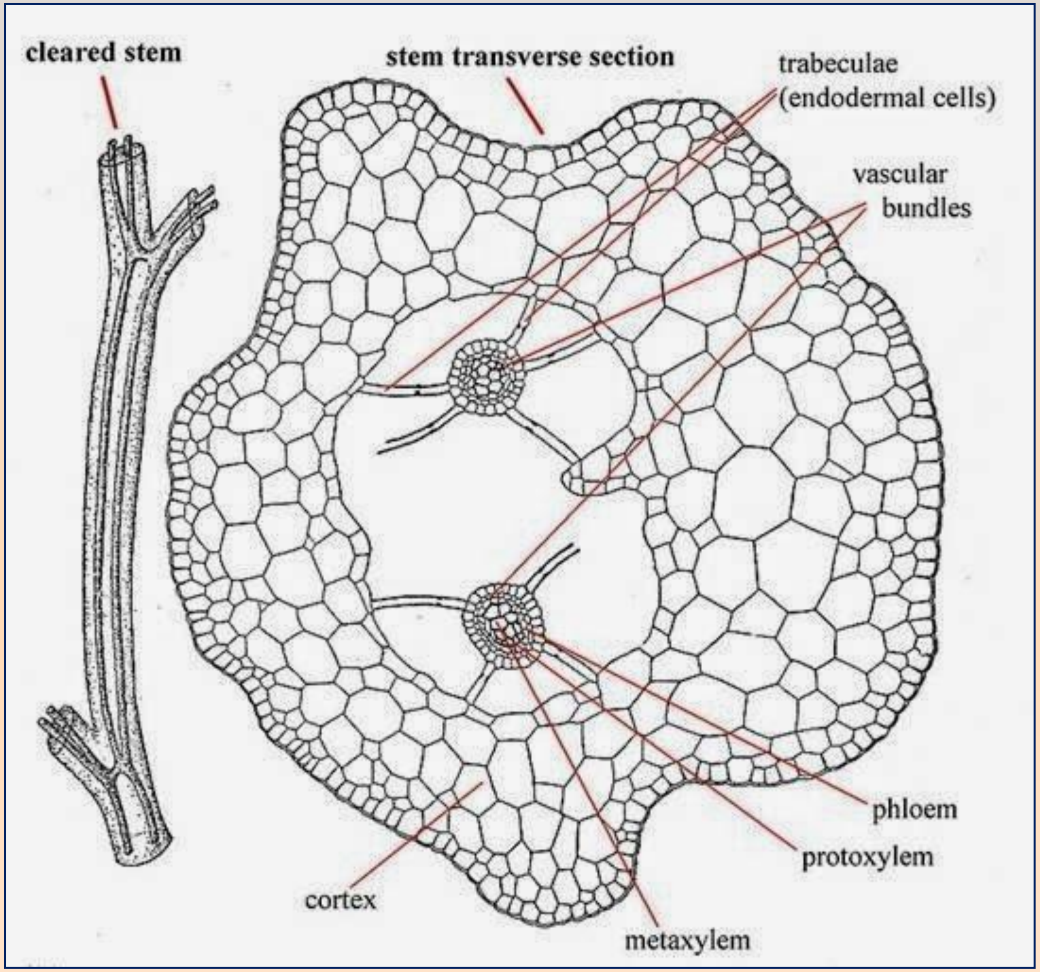
A. Eustele, B. Atactostele

7. Polycylic Stele

When the vascular tissue present in the form of two or more concentric cylinders, such a stele is called polycyclic stele. A typical polycyclic stele possesses two or more concentric rings of vascular tissue. This may be a solenostele or a dictyostele. Two concentric rings of vascular tissue are found in *Pteridium aquilinum* and three in *Matonia pectinata.*

8. Polystele

Some times more than one stele are present in the axis of some pteridophytes. Such a condition is called Polystelics. Such stele shows polystelic condition. Certain species of *Selaginella* have polystelic condition.



Polystelic (distelic) condition in Selaginella Stem

Evolution of the Stelar system

It is now generally clear that the simplest type of stele is protostele.
It is fundamental type for the vascular plants in general and the pteridophyta in general and all the other types of stele have been derived from it in the course of evolutionary specialization. As far as known all pteridophytes in the initial (sporeling) stage start with protostelic stem.

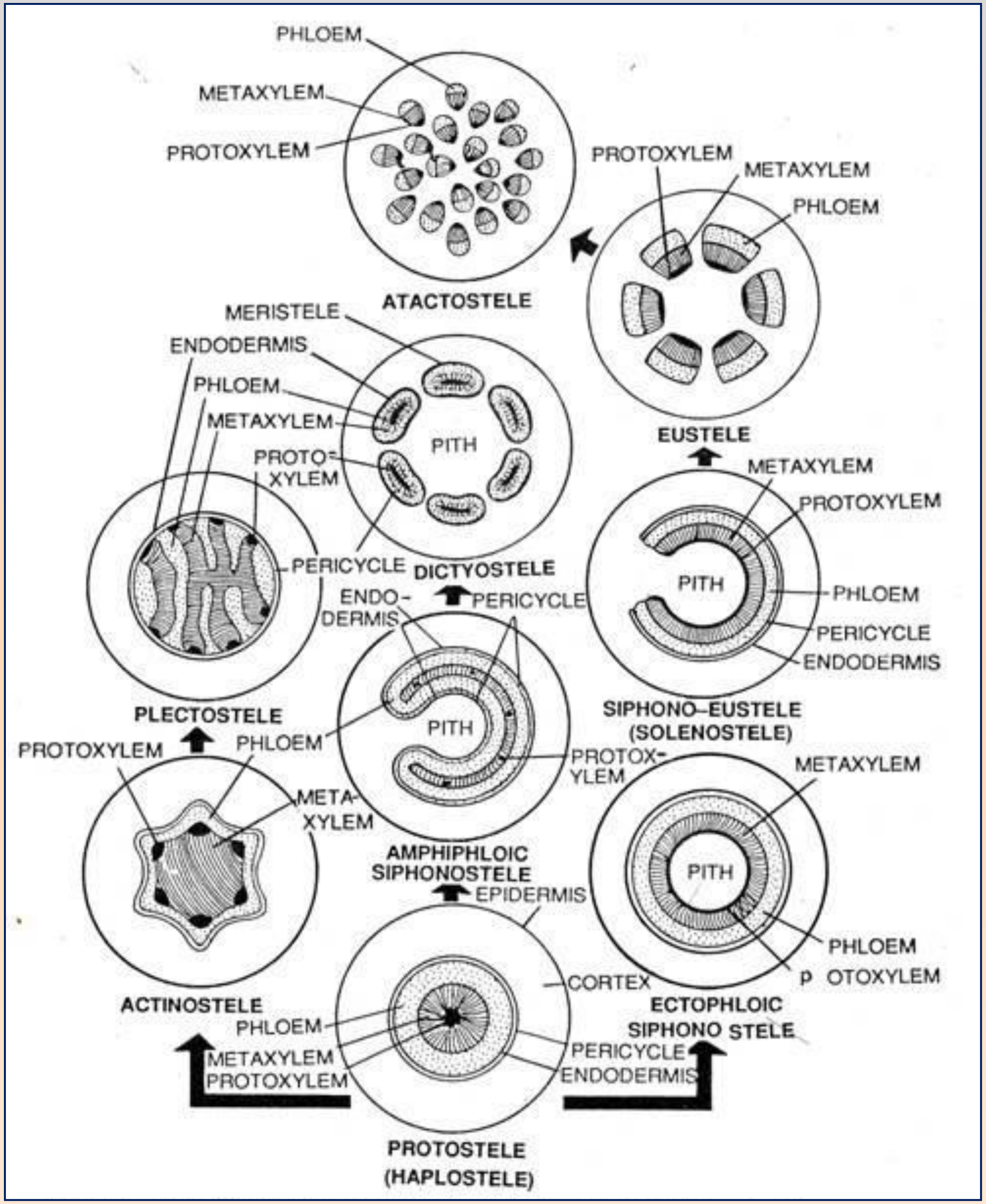
When the shoot grows accompanying an increase in size, there is internal differentiation of the stele. The first step is appearance of parenchyma, scattered in the xylem core and finally a central parenchymatous medulla or pith is developed in the protostele. Such type of stele is called Siphonostele.

The method by which medullation came about in a protostele and formed a siphonostele is a debated question and explained by two hypotheses viz. Extra-stelar and Intra-stelar origin of pith.

In its simplest form the siphonostele has no leaf gaps e.g. *Selaginella* and known as cladosiphonic siphonostele in contrast with phyllosiphonic condition with leaf gaps.

Siphonosteles which are perforated by scattered leaf gaps are known as Solenostele and a siphonostele with more overlapping gaps is known as dissected siphonostele or dictyostele.

The final elaboration of the stellar organization in pteridophytes consists in the development of a number of separate steles. Such a stele is known as Polycyclostele. Another modification of siphonostele is the Eustele in which the vascular system consists of collateral vascular bundles.



Different types of Steles arranged in evolutionary sequence

Thank you