STELAR SYSTEM AND ITS EVOLUTION

10.1 WHAT ARE STELE AND STELLAR THEORY?

The central cylinder or core of vascular tissue, consisting of xylem, phloem, pericycle and sometimes medullary rays and pith, is technically called stele. Van Tieghem and Douliot (1886) developed "*Stellar Theory*". They used the term *stele* in collective sense and mentioned that the stele is not only made up of xylem and phloem, but the tissue like pericycle, vascular rays and pith are also associated with it. According to them the cortex and the stele are the fundamental parts of a shoot and both these parts are separated from each other by the endodermis. According to stellar theory, primarily there is no fundamental difference in the gross anatomy of stem and roots, because in both of them a stele is surrounded by the cortex is present.

Although stele is real entity and present universally in all axes of the plants, I n higher vascular plants like ferns, gymnosperms and angiosperms the leaf traces are large and it plays an important role in the vascular system of the axis.

Foster and Gifford (1959) have mentioned that the most debated and controversial aspect of "stellar theory is the nature of the anatomical boundaries which separate the cortex from the stele". According to Van Tieghem and Douliot (1886) the endodermis represents the inner boundary of the cortex. The cells of the endodermal layer have the characteristic casparian strip strips. But in the stems of many seed plants, the characteristic endodermal layer is not present. Some have mentioned that in such cases the pericycle serves as separating layer between the stele and the cortex.

10.2 TYPES OF STELES

Jeffrey (1868) interpreted the stellar theory from the phylogenetic point of view. Based on stellar theory various types of vascular cylinders can be recognised in the roots and stems. Most of the workers recognised two main types of stellar organisations (Jeffrey, 1898; Esau, 1953; Smith, 1955; Foster and Giffor, 1959) i.e., Protostele and siphonostele.

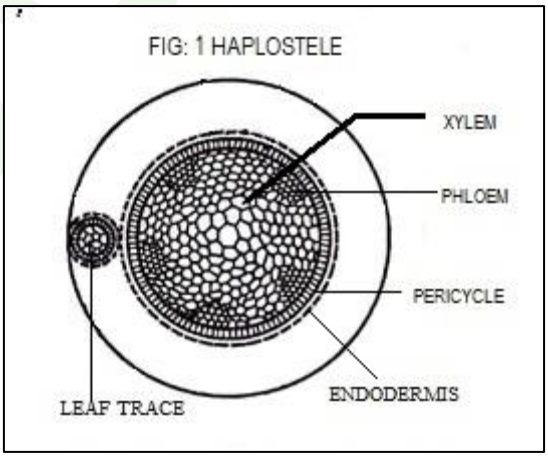
10.2.1 PROTOSTELE

A stele in which the vascular cylinder consists of a solid core of xylem surrounded by phloem, pericycle and endodermis is called protostele (Jeffrey, 1898). According to Jeffrey (1898), the protostele is primitive type of stele in vascular plants. There is no pith in protostele. In most of the pteridophytes, the stem remains protostelic at sporeling stage.

Brebner (1902), Worsdell (1902), Zimmermann (1930 and others have categorised the protosteles into following types:

10.2.1.1 HAPLOSTELE

The protostele with a smooth core of xylem surrounded by a uniform layer of phloem is called haplostele **(Fig. 1)** (Smith, 1955 and Berbner, 1902). It has been observed in fossil genera like *Rhynia, Horneophyton* and living genera like *Selaginella chrysocaulos, S. kraussiana, S. selaginoides, S. willdenowi, Gleichenia dichotoma, Lygodium* and *Cheiropleuria.*



10.2.1.2 ACTINOSTELE

It is a protostele having a xylem core with radiating ribs. In this case the xylem core is star shaped or stellate. Brebner (1902) named such a protostele as actinostele **(Fig. 2).** In actinostele the phloem is not present in a continuous manner but in the form

of separate groups which alternate with the distant ends of the star shaped xylem, eg. *Asteroxylon, Psilotum, Lycopodium serratum* and *Sphenophyllum*.

Because of the breaking of the xylem mass into different forms, the actinosteles shows following variations:

I. **PLECTOSTELE:** In plectostele the xylem gets broken into a number of parallel plates. Such xylem plates alternate with the phloem plates (Zimmermann, 1930). E.g *Lycopodium clavatum* and *L. volubile.*

II. **MIXED PROTOSTELE:** In this type the xylem groups are uniformly scattered in the ground mass of the phloem. Such actinostele is called mixed protostele. E.g. *Lycopodium cernuum.*

III. **MIXED PROTOSTELE WITH PITH**: Sometimes, thin parenchyma cells remain associated with the xylem in mixed protostele. E.g. In genera like *Hymenophyllum demissum, H. dilatatum, Lepidodendron intermedium* and *L. selaginoides* the centre of the protostele is occupied by the parenchyma cells among the tracheids. Such parenchyma cells represent the mixed pith and such type of stele is called **mixed protostele with pith**.

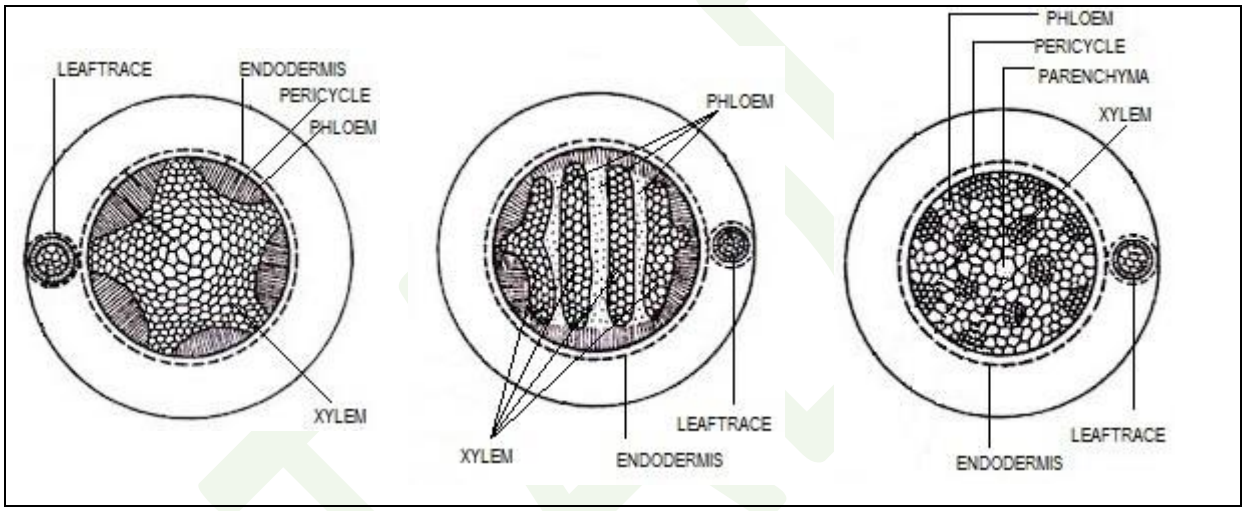


Fig. 2A: ACTINOSTELE Fig. 2B: PLECTOSTELE Fig. 2C: MIXED PROTOSTELE

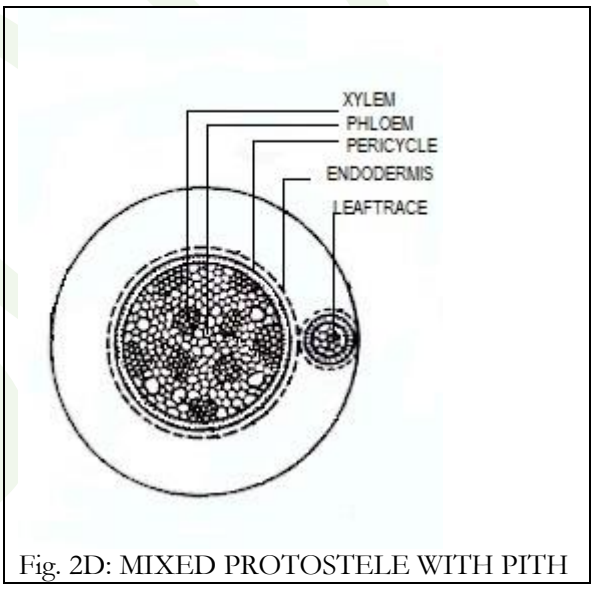


Fig. 2D: MIXED PROTOSTELE WITH PITH

10.2.2 SIPHONOSTELE: A medullated protostele is called siphonostele.

10.2.2.1 ORIGIN OF SIPHONOSTELE

It is a well-accepted phenomenon that a stele having a tubular vascular region and a central parenchymatous region was evolved from a protostele (Jeffrey, 1898). In a siphonostele the centrally placed xylem core is replaced by parenchymatous cells called pith. The pith is surrounded by xylem in the siphonostele. Different stages of changing of a protostele into siphonostele can be observed if transverse sections at different levels (from base upwards) are observed in genera like *Anemia phyllitidis, Botrydium, Gleichenia, Helminthostachys. Osmunda and Schizaea.*

Regarding the origin of siphonostele from protostele two views have been put forwarded, i.e., i) interstellar origin of pith and ii) extrastellar origin of pith.

(i) **INTERSTELLAR ORIGIN OF PITH:** According this view the centrally placed or innermost vascular tissue changes into parenchymatous cells which behaves as pith. The interstellar origin of pith is evidenced by the study of fossil ferns (Bower, 1923) and this view is supported by scientists like Boodle (1901), Gwynne Vaughan (1903, 1914), Petry (1914), Gewirtz and Fahn (1960).

(ii) **EXTRASTELLAR ORIGIN OF PITH:** This view was supported by Jeffrey (1902). According this view, the pith originated as a result of the invasion of cortical parenchymatous cells into the stele. This invasion occurs through the leaf gaps and branch gaps. Therefore, according to Jeffrey (1902) the pith and cortex are the homologous structure. Chang (1927), while working on *Pteridium aquilinum,* has criticized this extrastellar origin of pith theory of Jeffrey.

A third opinion has been put forward by Eames (1936) and Eames and MacDaniels (1947). According to these workers the pith is extrastellar in origin in some pteridophytes e.g. *Lycopodium* whereas it is extrastellar in origin in others e.g. higher ferns.

b) TYPES OF SIPHONOSTELE

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

1. **ECTOPHLOIC SIPHONOSTELE**: In this case the phloem is restricted only to the external side of the xylem. The pith is central in position. The phloem is externally surrounded by the pericycle and endodermis. A leaf trace is also visible. E.g. *Osmunda, Schizaea, etc.*
2. **AMPHIPHLOIC SIPHONOSTELE:** In this case, the phloem is present on both the external and internal side of the xylem. The pith is present in the centre. Eg. Rhizome of *Marsilea.* In this case xylem on its inner side remains surrounded by inner phloem, the inner pericycle, inner endodermis and centrally placed pith. On the outer side of the xylem are present the outer phloem, the outer pericycle, and the outer endodermis. E.g. *Adiantum, Dipteris.*

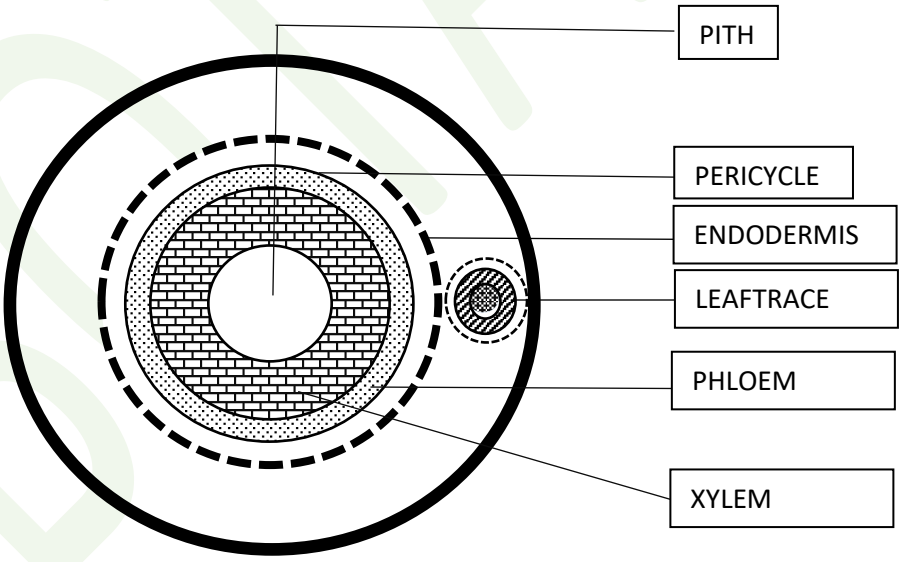


Fig. 3A ECTOPHLOIC SIPHONOSTELE

c) OTHER MODIFICATION OF SIPHONOSTELE:

1. CLADOSIPHONIC SIPHONOSTELE: A siphonostele which has no leaf gap is called **cladosiphonic siphonostele. E.g.** *Selaginella.*

2. PHYLLOSIPHONIC SIPHONOSTELE: It is a siphonostele which remains perforated by smaller or larger leaf gaps e.g. *Fillicophyta.*

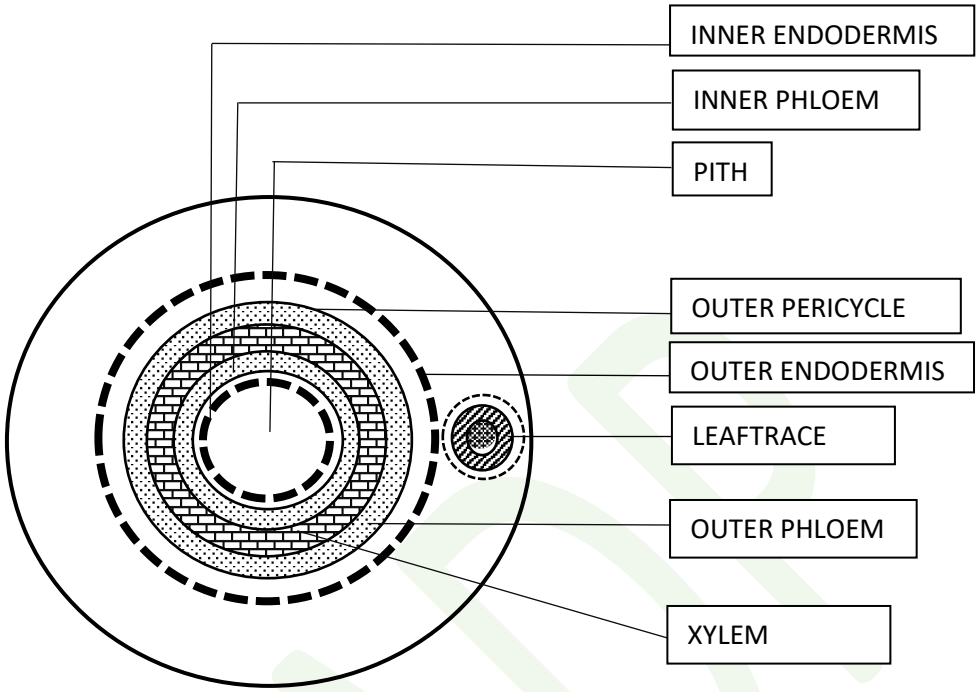


Fig. 3B AMPHIPHLOIC SIPHONOSTELE

3. SOLENOSTELE: If the siphonostele is perforated at a places corresponding to the origin of the leaf trace, such a condition is known as solenostele. It may be of following three types:

(i) ECTOPHLOIC SOLENOSTELE: This is a solenostele derived from ectophloic siphonostele. So, in the case the phloem is present only on the outer side.

(ii) AMPHIPHLOIC SOLENOSTELE: This is a solenostele derived from amphiphloic siphonostele, i.e, phloem is present on both the sides of xylem, e.g. *Adiantum pedatum*.

(iii) DICTYOSTELE: This is a type of solenostele which is broken into a network of separate vascular strands, mainly because of the crowded leaf gaps (Brebner, 1902). Each separate vascular strand is known as meristele, e.g. *Ophioglossum lusitanicum, Pteris, Adiantum capillaris-veneris, Dryopteris chrysocoma, D. rigidia* and *D. filix-max*.

In ferns and other members, the formation of dictyostele is because of the rhizome being short and thus overlapping of leaves takes place. It happens because of the overlapping of leaves takes place. It happens because of the overlapping of the leaf gaps in the stele. The whole stele appears as a network of interconnected vascular strands.

4. **EUSTELE:** If the stele is split into distinct collateral vascular bundles, it is called eustele. It is a modification of the ectophloic siphonostele. The splitting takes place because of the overlapping leaf gaps.
5. **ATACTOSTELE:** Differing from the eustelic condition, the vascular strands in some cases are scattered. Such a stele has been named as atacostele by Esau (1953). It occurs in monocotyledons.

10.2.3 POLYSTELE

Sometimes more than one stele is present in the axis of some pteridophyte like *Selaginella,* such a condition is known as polystele. It is a type which must have been derived from a protostele because each such stele shows a protostelic condition. In *Selaginella kraussiana*, generally, two steles are present but in *Selaginella laevigata* as many as sixteen steles are present in the axis.

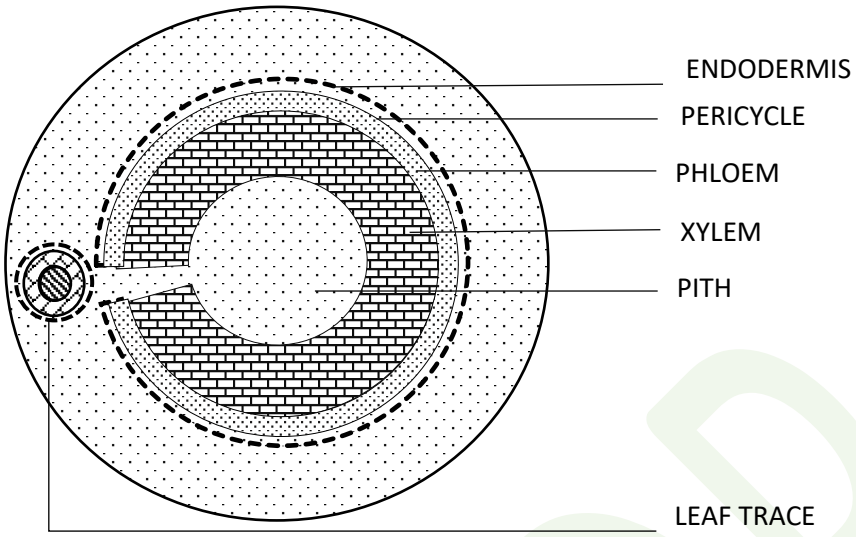


Fig. 4A ECTOPHLOIC SOLENOSTELE

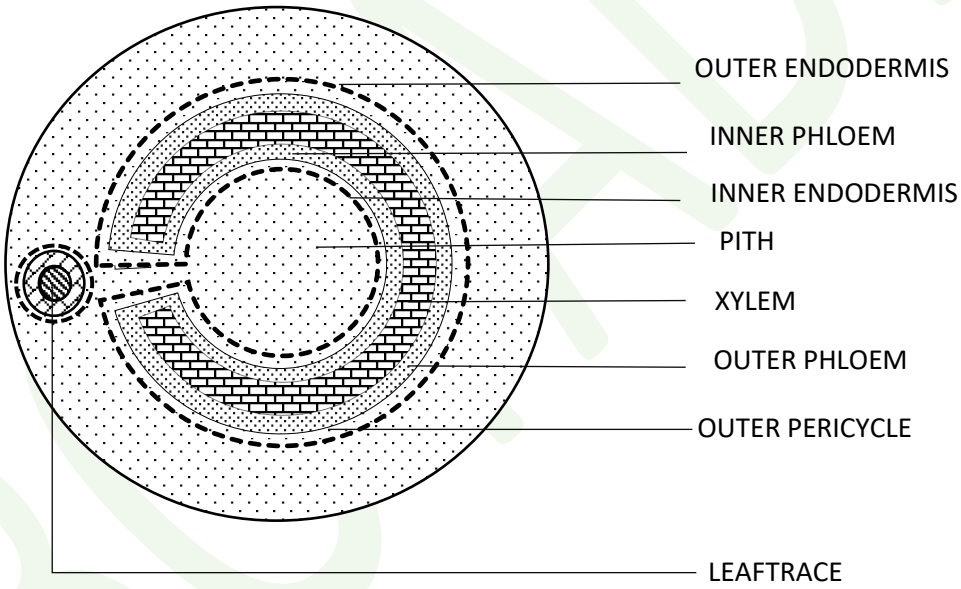


Fig. 4B AMPHIPHLOIC SOLENOSTELE

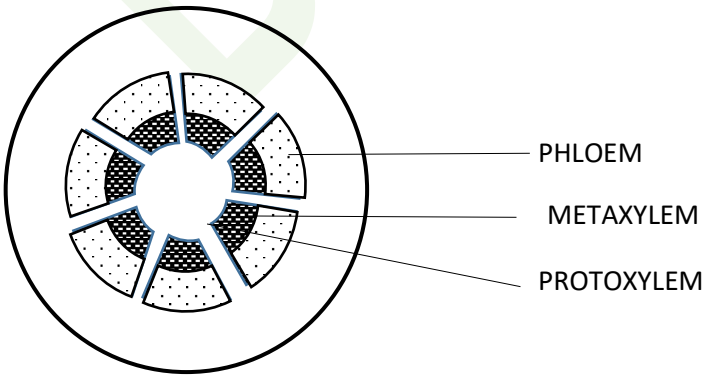


Fig EUSTELE

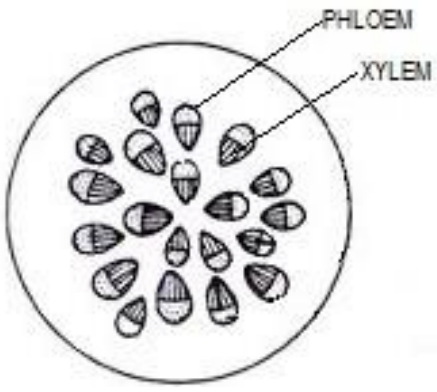


Fig. ATACTOSTELE

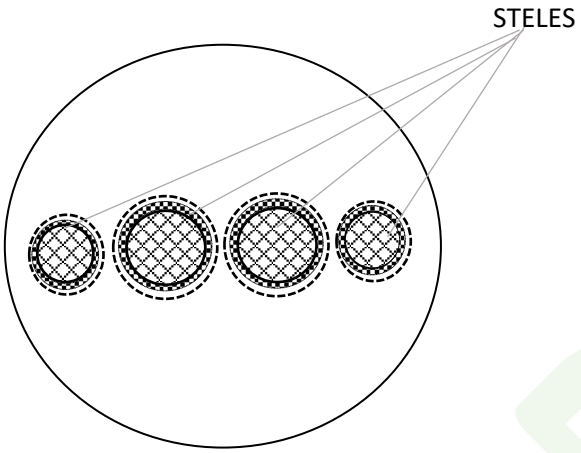


Fig. POLYSTRELE

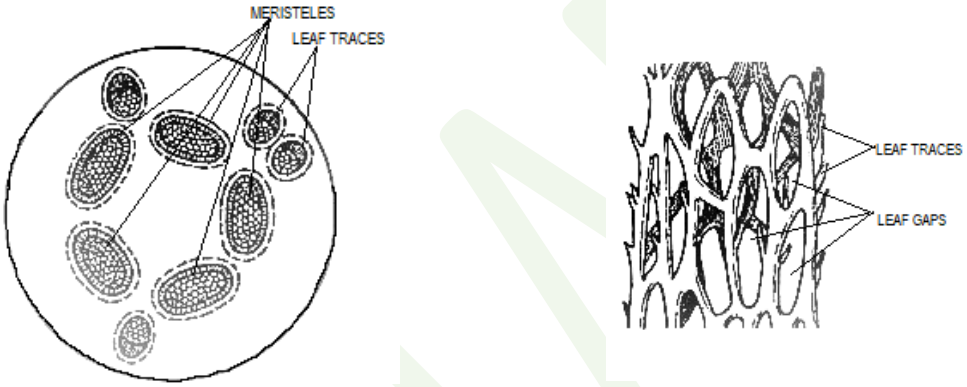


Fig.: Stellar system: A. Dictyostele, B. Vascular skeleton of dictyostele

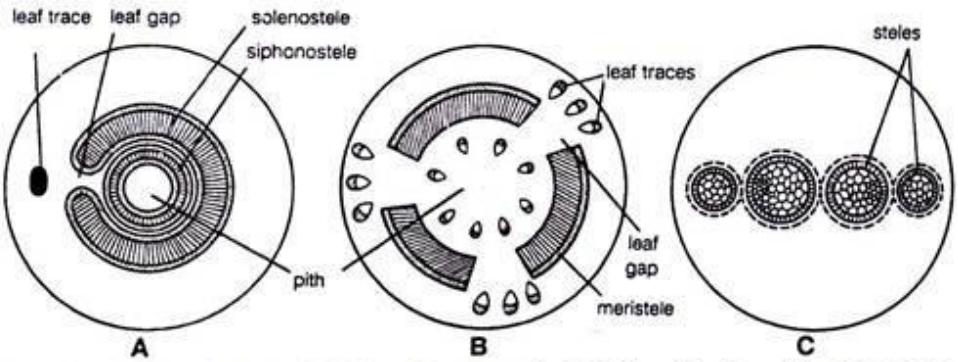


Fig. 6 (A–C). Stelar System : A. Polycyclic solenostele, B. Polycyclic dictyostele, C. Polystele

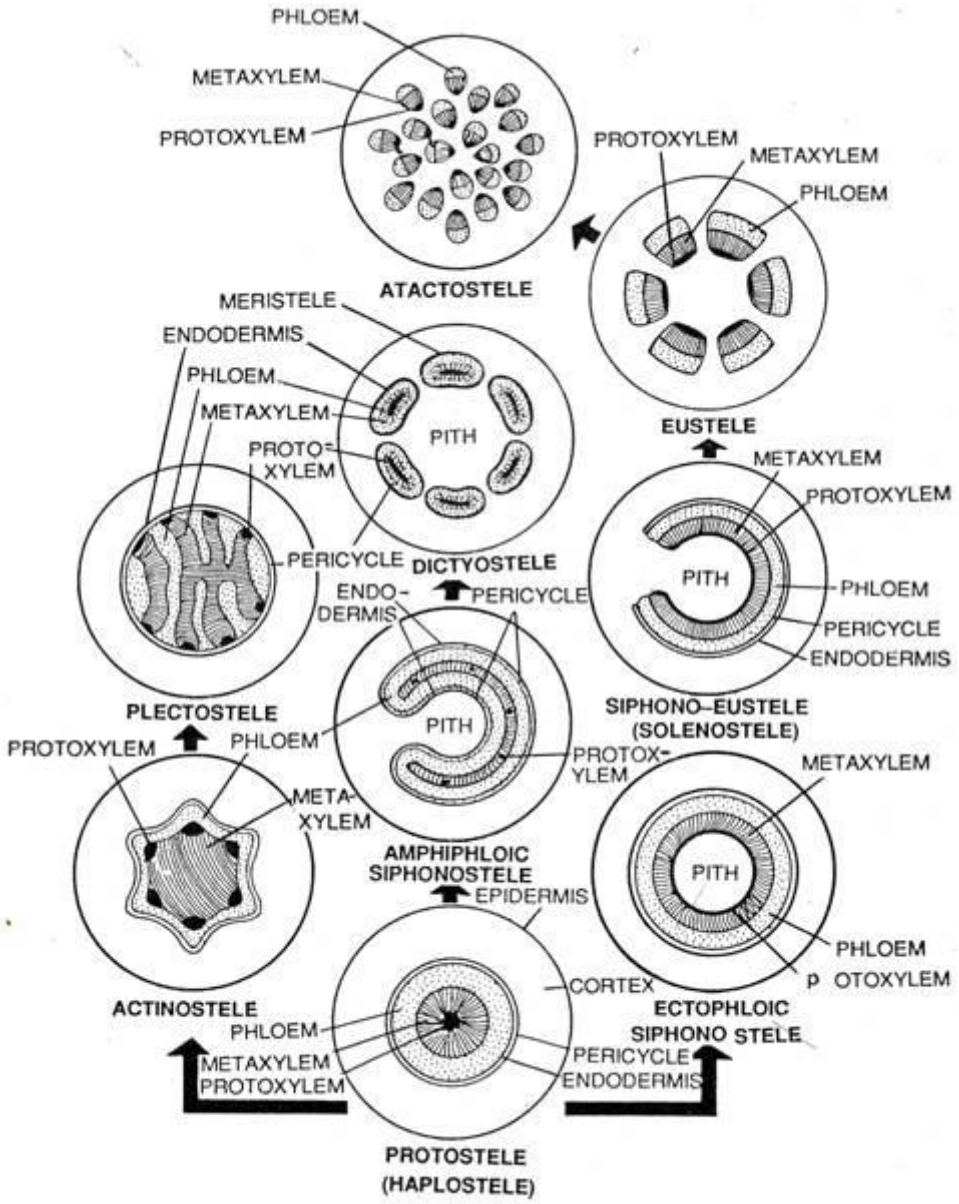


Fig. 37.43. The stelar system. Different types of steles arranged in evoluntionary sequence.