Stelar Types & Its Evolution in Pteridophytes

Stele is the central cylinder or core of vascular tissue in higher plants and Pteridophytes. It consists of xylem, phloem, pericycle and medullary rays and pith if present.

The term stele has been derived from a Greek word meaning rod or column. Van Tieghem and Douliot (1886) introduced this term and put forward the stelar theory. The theory suggests that the cortex and the stele are the two fundamental parts of a shoot system. Both these components (stele and cortex) separated by endodermis.

Tieghem and Duoliot recognized only three types of steles. They also thought that the monostelic shoot were rare in comparison of polystelic shoots.

But now it is an established fact that most shoots are monostelic and polystelic condition rarely occurs. The stele of the stem remains connected with that of leaf by a vascular connection known as the leaf supply.

There are several types of stele found in pteridophytes which are:

1. Protostele
2. Siphonostele
3. Solenostele
4. Dictyostele
5. Polycyclic stele
6. Eustele
7. Polystele

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1. Protostele

Jeffrey (1898), for the first time pointed out the stelar theory from the point of view of the phylogeny. According to him, the primitive type of stele is protostele.

In protostele, the vascular tissue is a solid mass and the central core of the xylem is completely surrounded by the strand of phloem. This is the most primitive and simplest type of stele.

- Pith is absent in protostele i.e. it is non-medullated.
- Majority of the pteridophytes show protostelic conditions in their rhizome, stem or roots.

There are five forms of protostele

1. Haplostele
2. Actinostele
3. Plectostele
4. Mixed Protostele
5. Mixed Protostele with pith

(a) Haplostele

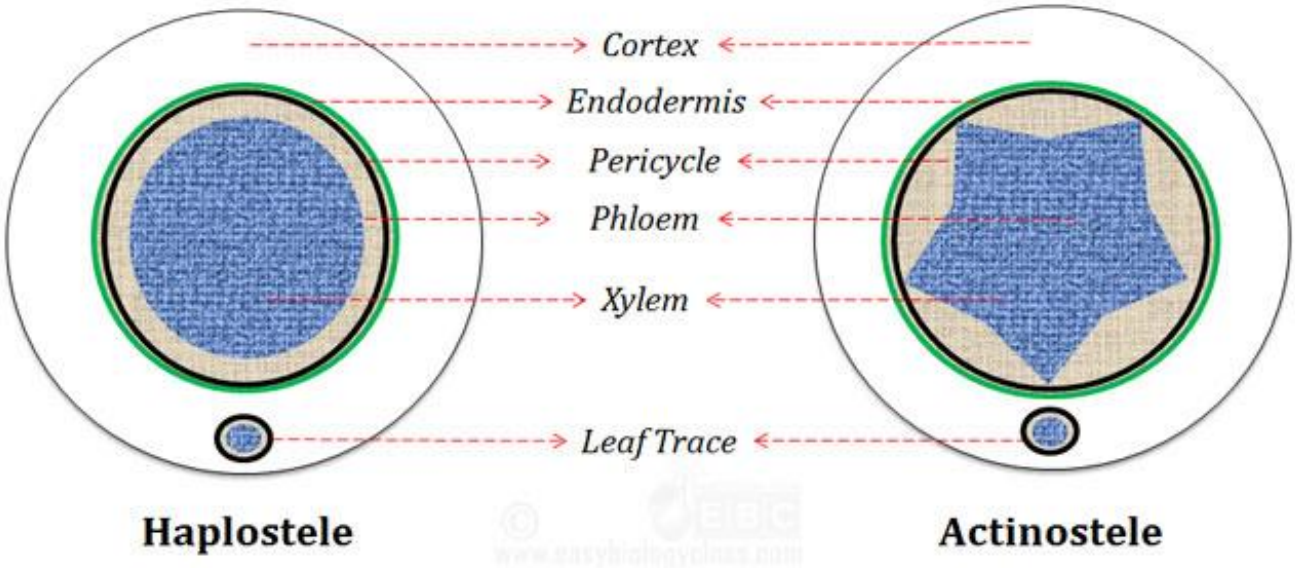
This is the most primitive type of protostele. Here the central solid smooth core of xylem remains surrounded by uniform layers of phloem (e.g., in Selaginella spp., Gleichenia, Lycopodium).

- Named by Brebner in 1902.
- Usually present in fossil genera like Rhynia and Horneophyton.

(b) Actinostele

This is the modification of the haplostele and somewhat more advanced in having the central xylem core with radiating ribs or arms (e.g., in Psilotum spp., Asteroxylon, Lycopodium serratum).

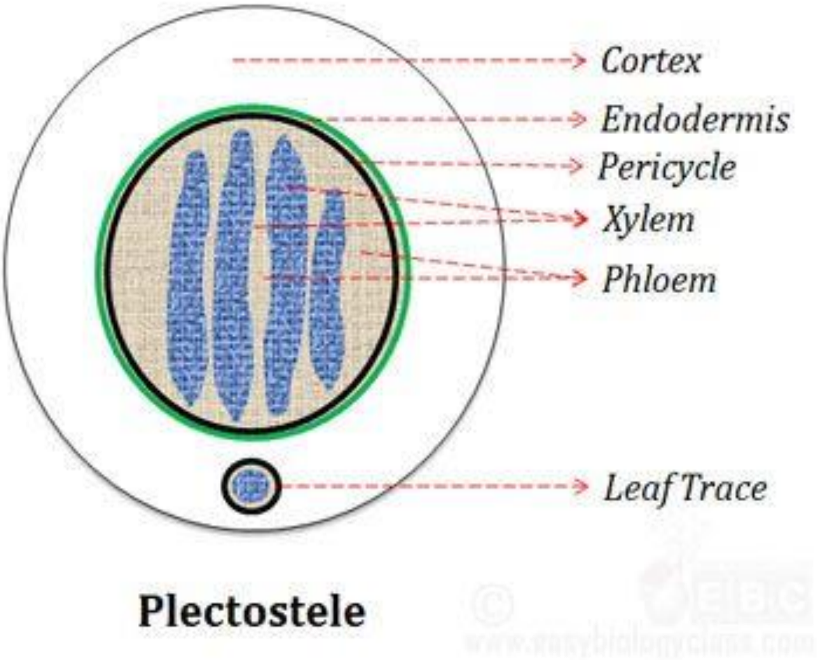
- Xylem is star shaped or stellat, hence the name.
- The phloem is not present in continuous manner.
- Phloem occurs as separate patches between arms of the xylem.
- Named by Brebner in 1902.



(c) Plectostele

This is the most advanced type of protostele. Here the central core of xylem is divided into number of plates arranged parallel to each other. The phloem alternates the xylem (e.g., in Lycopodium clavatum).

- Named by Zimmerman in 1930.



(d) Mixed protostele
Xylem is divided into several units or groups. Each xylem units are scatteredly arranged inside the ground mass of phloem. Example: Lycopodium cernuum.

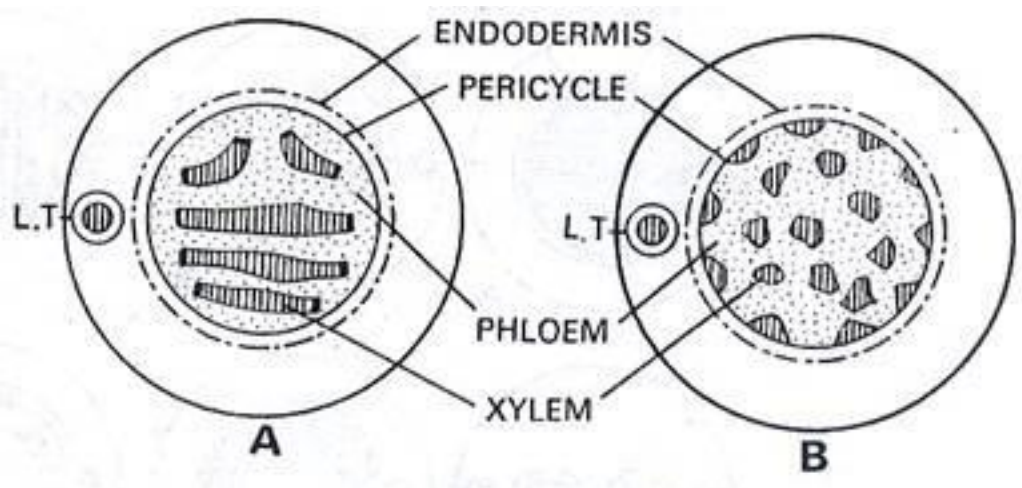


Fig. 32.3. Stelar system in ferns. A, plectostele; B, mixed

(e) Mixed protostele with pith
Here the xylem elements (i.e., tracheids) are mixed with the small patches of parenchymatous cells of the pith. This type is found in primitive fossils and living ferns. They are treated to be the transitional types in between true protosteles on the one hand and siphonosteles on the other (e.g., in Hymenophyllum demissum, Lepidodendron selaginoides etc.).

2. Siphonostele

This is the modification of protostele. A stele in which the protostele is medullated or with pith at the centre is known as siphonostele. Such stele contains a tubular vascular region and a parenchymatous central region i.e the central core of pith is surrounded by the xylem.

- It is advanced than protostele.

Origin of siphonostele

There are different views among the scientists regarding the origin of siphonostele. But they all agreed that, the siphonostele is originated from protostele by formation of pith in the center. Here, the centrally placed xylem core is replaced with parenchymatous pith.

Different stages of changing protostele to siphonostele can be observed in the T.S at different levels in Gleichenia, Osmunda and Anemia.

There are two views regarding the origin of pith in the siphonostele.

Jeffrey's theory

According to this theory, the pith is formed as a result of the invasion of cortical parenchymatous cells into the stele. The invasion of pith occurs through the leaf gap or branch gap.

Thus pith and cortex are homogeneous structures according to this theory.

This theory is not accepted by most of the authors since in many pteridophytes there is stele without leaf gaps but having siphonostele.

Boodle's theory

According to the theory proposed by Boodle (1901), and Gwynne Vaughan, the siphonostele has been evolved from the protostele by a transformation of the inner vascular tissue into parenchyma.

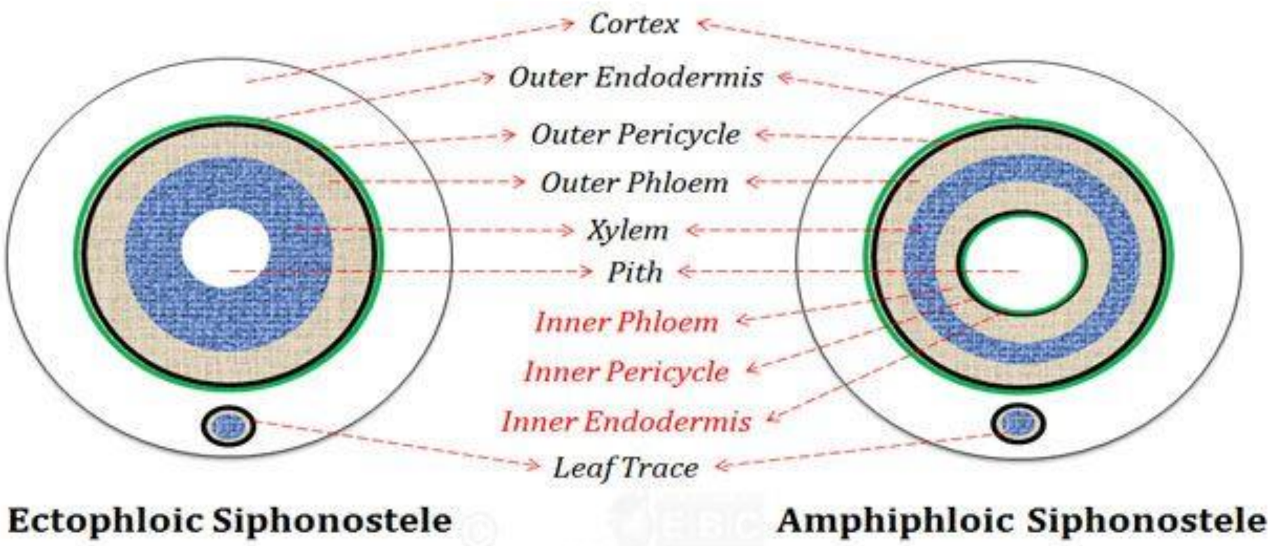
A siphonostele may be of the following types

(a) Ectophloic

In this type of siphonostele, the pith is surrounded by concentric xylem cylinder and next to xylem the concentric phloem cylinder.

(b) Amphiphloic

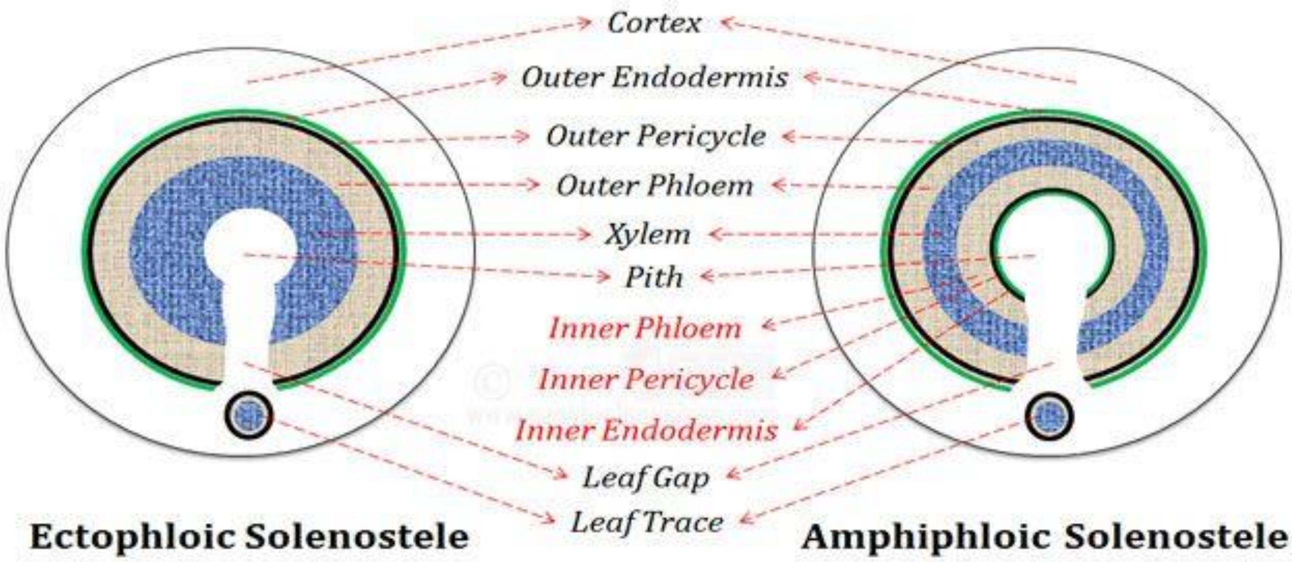
In this type of siphonostele the pith is surrounded by the vascular tissue. The concentric inner phloem cylinaer surrounds the central pith. Next to the inner phloem is the concentric xylem cylinder which is immediately surrounded by outer phloem cylinder (e.g., in Marsilea rhizome).



3. Solenostele

In solenostele, pith is found with one leaf gap. It may be ectophloic or amphiphloic solenostele.

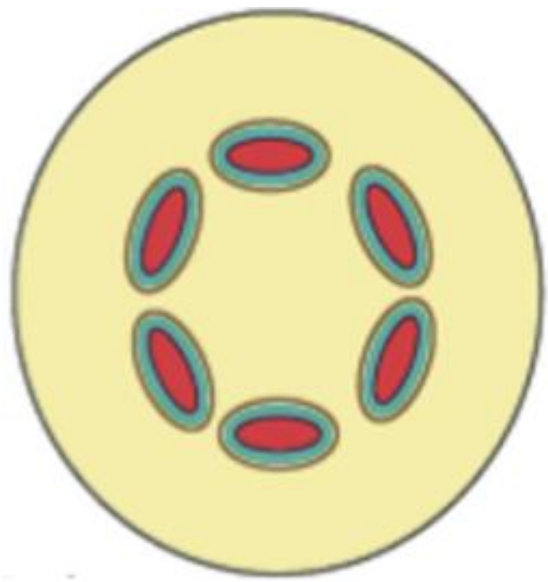
(a) Ectophloic: Xylem is surrounded by only on the outer side by phloem. E.g. in Osmunda.
(b) Amphiphloic: In center, pith is found. Xylem is surrounded on both sides by phloem. E.g. Marsilea rhizome.



4. Dictyostele

Solenostele that is broken into a network of separate vascular strands are called dictyostele. This breaking up of stelar core is due to the presence of large number of leaf gaps.

Each such separate vascular strands is called meristele. Each meristele is of protostelic type. The dictyostele with many meristeles looks like a cylindrical meshwork.



Examples: Pteris, Adiantum capillus-veneris.

5. Polycylic Stele

This type of stelar organization is the most complex one amongst all vascular cryptogams (pteridophytes). Such type of steles are always siphonostelic in structure.

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.

(a) Polycyclic solenostele

(b) Polycyclic dictyostele

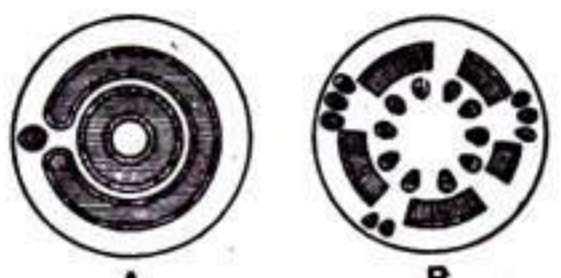
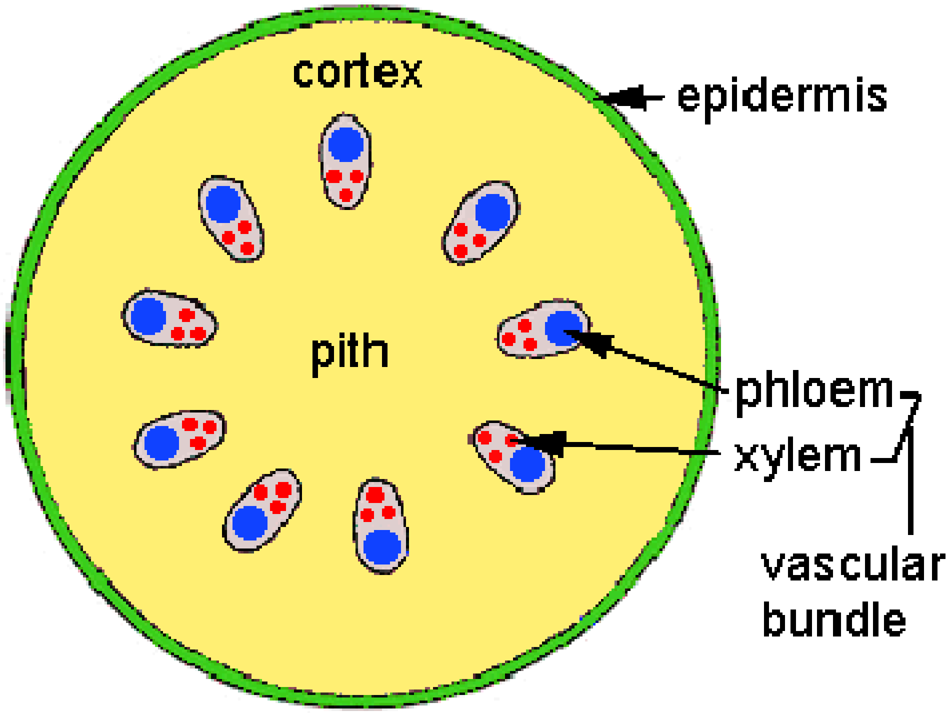


FIG. 581. Polycyclic stele—types (diagrammatic. sectional views). A. Polycyclic solenestele. B. Polycyclic dictyostele.

6. Eustele

According to Brebner (1902), there is one more modification of the siphonostele known as eustele. Here the vascular system consists of a ring of collateral or bicollateral vascular bundles situated on the periphery of the pith. The example of this type is internode of Equisetum.

- It is the modification of ectophloic siphonostele.
- Splitting takes place because of the overlapping leaf gaps.



7. Polystele

More than one stele in the axis of pteridophytes is present known as polystele. It is a type that must have derived from protostele because each such stele shows protostelic condition. In Selaginella kraussiana generally two stele present. But in Selaginella laevigata as many as 16 steles are present.

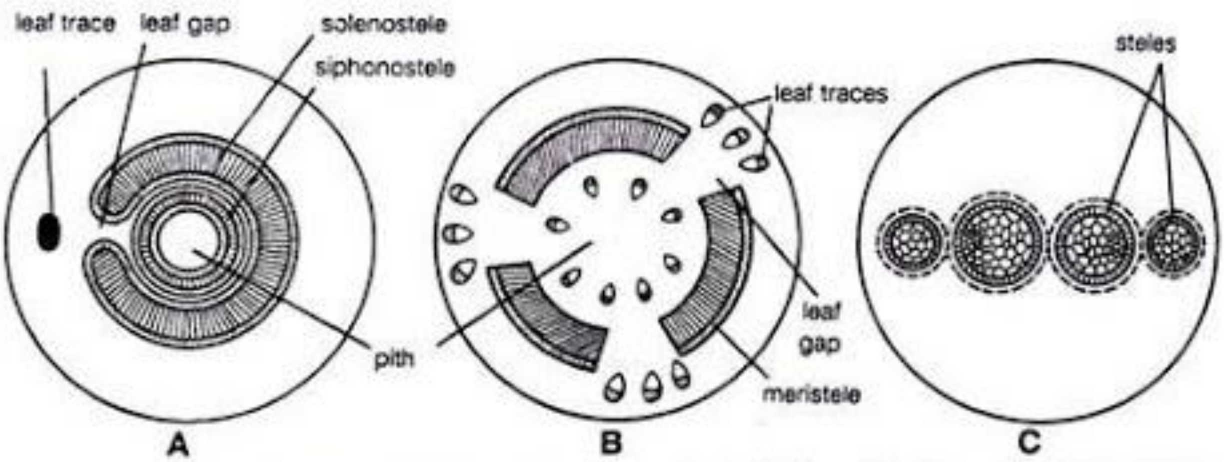


Fig. 6 (A–C). Stelar System : A. Polycyclic solenostele, B. Polycyclic dictyostele, C. Polystele

Other modifications of siphonostele

1. **Cladosiphonostele**: No leaf gaps present. It is the simplest type of siphonostele. And found in several species of Selaginella.
2. **Phyllosiphonic siphonostele**: Siphonostele that remain perforated by smaller or larger leaf gaps caused by leaf traces. Members of Filicophyta.

Heterospory in Pteridophytes:

Most of the Pteridophytes produce one kind of similar spore. Such Peridophytes are known as homosporous and this phenomenon is known as homospory. However, there are some Pteridophytes which produce two different types of spores (differing in size, structure and function).

Such Pteridophytes are known as heterosporous and the phenomenon is known as heterospory. The two types of spores are microspores and megaspores. Microspores are smaller in size and develop into the male gametophyte while the megaspores are large and develop into female gametophyte.

According to Rashid (1976) only 9 genera of Pteridophytes are heterosporous. These are Selaginella, Isoetes, Stylites, Marsilea, Pilularia, Regnellidium, Salvinia, Azoll and Platyzoma.

Origin of Heterospory:

The origin of heterospory can be better discussed on the basis of evidences from paleobotany, developmental and experimental studies.

1. Palaeobotanical evidences:

It has been suggested that heterospory arose due to degeneration of some spores in a few sporangia. As more nutrition becomes available to less number of spores, the surviving spore grow better, hence increase in their size.

Palaeobotanical evidences show that the earlier vascular plants wert all homosporous and the heterosporous condition appeared subsequently in the lowermost upper Devonian. Anumber of heterosporous genera belonging to the Lycopsida, Sphenopsida and Pteropsia were known in the late Devonian and early Carboniferous periods.

During this period important heterosporous genera were Lepidocarpon, Lepidostrobus, Mazocarpon, Plaeuromeia, Sigillariostrobiis (members of Lycopsid) Calamocarpon, Calamostachys, Palaeostachys (members of Sphenosida). Some of these forms even arrived at the seed stage.

According to Williamson and Scot (1894) two species of Calamostachys form the initial stage that might lead to the heterospory. These species were C. binneyana and C. casheana. In C. binneyana most of the sporangia were with large number of small spores in tetrads but in some sporangia spores were large.

However, in C. casheana two different types of spores-microspores and megaspores were present in different sporangia. Similar type of abortion of spores was also observed in Stauropteris (Chaloner, 1958Lepidocarpon and Calamocarpon).

2. Evidences from Developmental Studies:
In heterosporous Pteridophytes the development of micro and megasporangia follow the same pattern. They have identical organization but for their size. While in megasporangia most of the spore mother cells degenerate but in microsporangia only a few mother cells are disorganize.

The phenomenon of heterospory becomes distinct either before or after meiosis. In Selaginella Isoetes it is distinct before meiosis. In the microsporangium all the sporocytes undergo meiosis and form a large number of microspores. However, in megasporangium, a part of the sporogenous tissue degenerates they provide nutrition to growing sporocytes (megaspores).

In Isoetes there are only 50-300 megaspores in megasporangium. In Selaginella erythropus megasporangium contains only one megaspore which is functional.

In Marsilea, Salvinia and Azolla the phenomenon of heterospory becomes distinct after meiosis. In Marsilea 64 microspores and 64 megaspores are formed after meiosis in microsporangium and megasporangium respectively. In microsporangium all the microspores are functional while in magasporangium one megaspore is functional and rest degenerate.

3. Evidences from Experimental Studies:
Experimental studies on Selaginella (Goebel, 1905) and Marsilea (Shattuck, 1910) suggest that nutritional factors mainly govern the heterospory. Under conditions of low light intensity, the photosynthetic activity of Selaginella was retarted and it produced microsporangia. By sudden lowering of the temperature, the size of the microspores in the sporocarp of Marsilea increases by six times.

Biological Significance of Heterospory:

The phenomenon of heterospory is of great biological significance on account of the following facts:
(i) The development of the female gametophyte starts while the megaspore is still inside the megasporangium.

(ii) Same is true of microspores i.e., they also start germinating into male gametophytes while they are still inside microsporangium.

(iii) The female gametophyte derives its nourishment from the sporophyte i.e., female gametophyte is dependent on sporophyte for its nourishment.

(iv) The dependence of female gametophyte on sporophyte for its nourishment provides better starting point for the development of new embryo than an independent green prothallus which has to manufacture its own food.

Seed Habit in Pteridophytes:

The adoption of heterospory and the retention and germination of a single megaspore within megasporangium to form a female gametophyte, led to the phenomenon of "seed habit", a characteristic feature of the spermatophytes. A seed is that ovule which contains an embryo developed as a result of fertilization.

The origin of seed habit is associated with the following:
(i) Production of two types of spores (heterospory).

(ii) Reduction in the number of megaspores finally to one per megasporangium.

(iii) Retention and germination of the megaspores and fertilization of the egg.

(iv) Continued development of the fertilized egg into the embryo while still in situ.

From the above observations it is concluded that the life history of Selaginella approaches towards seed habit because of the following features:
1. The occurrence of the phenomenon of heterospory.

2. Germination of megaspore inside megasporangium.

3. Retention of megaspore inside megasporangium either till the formation of female gametophyte or even after fertilization.

4. Development of only one megaspore per megasporangium for example, in Selaginella monospora, S. rupestris, S. erythropus etc.

Though Selaginella as well as lower Spermatophytes shows homologies in their structure as follows:
Selaginella:
1. Megasporangium.

2. Megaspore.

3. Female gamestophyte.

4. Archegonium.

5. Egg.

Lower Spermatophytes (Gymnosperms):

1. Nucellus of ovule.

2. Megaspore (Embryosac).

3. Endosperm.

4. Archegonium.

5. Egg.

Even then the seeds are not formed in Selaginella because:

1. Megasporangium is not surrounded by integument.

2. The retention of megaspore permanently inside the megasporangium has not been well established.

3. The embryo immediately gives rise to the sporophyte without undergoing a resting period.