

THE LIFE CYCLE OF A HETEROSPOROUS PTERIDOPHYTE.

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The Heterosporous Pteridophytes represent the highest stage of development in the second or intermediate series of plants. The term heterosporous is applied to plants in which there are two kinds of nonsexual spores, large and small, called respectively megaspores and microspores. This peculiar spore condition is also present in the seed plants. The megaspore always gives rise to a female individual and the microspore to a male. In the lower Pteridophytes there is only one kind of nonsexual spores and they are, therefore, called homosporous. The Homosporous Pteridophytes should be kept distinct from the Heterosporous, since the development of heterospory represents one of the advancing waves of evolution which brought about profound changes in the character of the vegetation of the earth. The elimination of chance environment in the development of unisexual individuals by predetermining the sex in the spore and the reduction in the size of the gametophytes appear to have been necessary conditions in the evolution of the seed plants.

The living species of Heterosporous Pteridophytes fall into six genera, the remnants of former extensive and dominant groups. The total number of species is about 635, somewhat more than the living Gymnosperms which constitute the next higher subkingdom. Because of their position as the lowest of heterosporous plants a thorough knowledge of their morphology and life history is necessary to a proper understanding of the structures and processes found in the Gymnosperms and Angiosperms. Nevertheless, much of their life history is still obscure and various statements rest on conjecture or imperfectly established facts.

The living Heterosporous Pteridophytes are small herbaceous perennials or rarely annual plants, usually not more than a few inches high. They are quite insignificant when compared with their ancient relatives some of which developed into great trees. The six living genera are named as follows: *Azolla*, *Salvinia*, *Marsilea*, *Pilularia*, *Isoetes*, and *Selaginella*. *Selaginella* is, however, a very complex genus. *Azolla* and *Salvinia* are small floating plants; *Marsilea* and *Pilularia* are creeping geophilous forms usually in wet places; *Isoetes*, known popularly as quillwort, grows in wet or swampy ground and has a short, upright, usually simple rhizome with grass-like leaves; *Selaginella* has very small leaves on branching herbaceous stems which grow either horizontal or erect in wet ground or sometimes in dry places subject to periodical moisture. These plants are usually placed in the classes and orders of the Homosporous Pteridophytes, but since they represent a very important advance in the plant kingdom.

a stage or step taken in several independent lines and by all the higher groups, it seems best to put them together in a sub-kingdom of their own.

The relationship of some of the included fossil forms is still imperfectly understood on account of the absence of properly preserved sporangia. The following orders are usually recognized:

1, Calamariales; 2, Sphenophyllales; 3, Salviniales; 4, Marsileales; 5, Isoetales; 6, Lepidophytales; 7, Selaginellales. The first, second, and sixth orders named above are entirely fossil. These seven orders fall naturally into five classes which may be designated as follows: Calamariæ, Sphenophylleæ, Hydropterides or water ferns including the Salviniales and Marsileales, Isoeteæ or quillworts, and Selaginelleæ, including the Selaginellales and the fossil Lepidodendrids Sigillarids and other genera belonging to the sixth order.

The Hydropterides are the only plants among the Heterosporous Pteridophytes that are leptosporangiate. In this respect they are similar to some of the homosporous ferns. The resemblance, however, does not extend much farther and it is not probable that they are a branch from the homosporous leptosporangiate ferns. The fossil record indicates that the water ferns are much the older group. It might be stated that the term leptosporangiate refers to the origin of the sporangium which in these plants originates from an epidermal cell instead of from hypodermal tissue as in all other higher plants. The Selaginellas are probably descended from the primitive Lycopods but the quillworts show no evident relationship to any known homosporous forms.

Heterosporous Pteridophytes appear in the first known land flora, but these forms were not primitive types; for the primitive floras have either not been discovered or else have left no fossil trace of their existence. There is some evidence that members of this sub-kingdom were present in the Ordovician period; but however that may be they are definitely found in the Silurian and became very important in the Devonian. They culminated in the Carboniferous, which from a botanical point of view might be called the age of Heterosporous Pteridophytes. The coal swamps were full of great tree forms belonging to the genera, *Lepidodendron*, *Sigillaria*, *Calamites*, and others. These plants formed the larger part of the material preserved as coal and were therefore of great economic importance for the future welfare of man. They declined during the Permian and very few appear to have survived the great disturbance known in American geology as the Appalachian revolution. These plants were essentially moisture-loving and when the great changes occurred which mark the transition from the Paleozoic to the Mesozoic they seem to

have been unable to adapt themselves to the new condition of things. The next higher subkingdom, the Gymnosperms, became the dominant group of plants.

In tracing out the life cycle, *Selaginella kraussiana* will be taken as a representative with incidental references to other types. There is, of course, a well-marked alternation of generations, the gametophyte and the sporophyte, and each generation usually leads an independent existence for at least a part of its life. The conspicuous plant is the sporophyte or nonsexual generation. It consists of a more or less dorsiventral leafy shoot

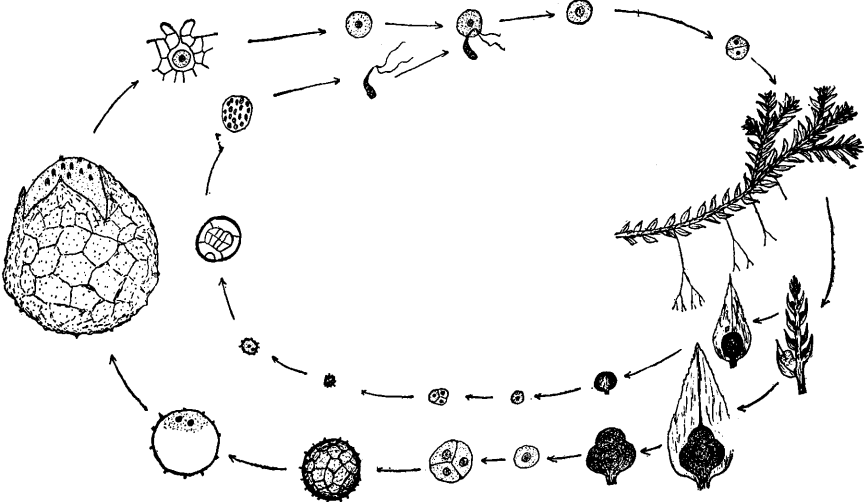


Fig. 1. Diagram of Life Cycle of *Selaginella*.

from the lower side of which dichotomously branched roots grow out. The roots strike ground usually after growing an inch or more in length. In this plant there is no increase in thickness of the stem but some Heterosporous Pteridophytes do grow considerably in thickness by the development of the general tissue but not by a true cambium layer. The vascular bundles are concentric with the xylem in the centre. The stem usually has two bundles side by side each contained in a tubular cavity or air space and connected with the walls of the cavity by means of numerous slender filaments. Other types have a different stem structure.

After attaining a considerable size the sporophyte begins to reproduce by developing cones or primitive flowers at the ends of some branches. The cones are bisporangiate, having two sets of sporophylls which are but slightly differentiated from the ordinary foliage leaves. The two kinds of spore-bearing leaves are

called megasporophylls and microsporophylls. There are numerous microsporophylls in each cone but usually only one megasporophyll which is the lowest one of the set. The microsporophyll has a single microsporangium on the upper side in the axil and the megasporophyll also produces but one megasporangium in the same position. In some of the other classes the two kinds of sporangia may be on the same leaf or leaf segment, which may be closed up like the ovulary of a carpel. The microsporangium and megasporangium produce the nonsexual spores, the microspores and the megaspores. The spores are produced in the following manner: In the microsporangium there are a number of cells called microsporocytes which become free in the cavity by the dissolution of their walls. Each microsporocyte divides twice giving rise to four cells. These cells develop into the microspores. During the first division of the microsporocyte the chromosomes of its nucleus are reduced so that the nuclei of the spores have only one-half as many chromosomes as were present in the nuclei of the sporophyte or nonsexual plant. The megasporangium also contains a number of megasporocytes which divide in the same way as the microsporocytes and form a spore tetrad. During the first of the two divisions the chromosomes are also reduced from the $2x$ number to x . The chromosomes are small bodies which appear in the nucleus during division and are probably special bearers of hereditary tendencies. These reduction divisions of the sporocytes are of great importance in the life cycle of the plant because of the profound changes which take place in the chromosomes. Only four megaspores develop and they become so large that the megasporangium bulges out and becomes somewhat four-lobed. In *Marsilea* only one megaspore develops in each megasporangium. The difference in size between microspore and megaspore in *Selaginella kraussiana* is very great. The ratio in volume in the mature condition is often more than 1 : 2000. The small spore having only a limited amount of cytoplasm and very little room for food material, always produces a male gametophyte when it germinates; while the megaspore always produces a female gametophyte. The determination of the sex is apparently not primarily an inherited character but depends on the environment during the early stages of embryonic development. Thus as stated above, the Heterosporous Pteridophytes by producing a difference of environment in the spore are able to keep the two sexes distinct. Since there are no hermaphrodite individuals there is no possibility of self-fertilization. This is true for all plants which have developed heterospory. The ripe sporangia open by vertical slits and the spores are thus discharged. In *Azolla* the microspores are imbedded in a foamy mass of substance called a massula on which peculiar anchor-like appendages are developed. In *Marsilea* the

sporocarp or modified leaflet containing the sporangia, after being soaked for some time in water, opens in a very peculiar way by the protrusion of a gelatinous ring containing the sori. This process represents an extreme specialization and adaptation to a semi-aquatic life.

In *Selaginella kraussiana* the spores germinate sometime before they are discharged. The microspore has divided into two cells and the female gametophyte has developed to a considerable extent. This is a very interesting condition, since it represents one stage toward the development of seed plants in which the spores are not discharged and the gametophytes are completely parasitic in the sporangia. In some *Selaginellas* the cones with the sporangia and spores are shed.

The gametophytes are very small especially the male. The vegetative part of the male thallus is represented practically by a single cell. The remaining cells developed inside of the spore wall represent the antheridium or spermary. In some of the *Heterosporous Pteridophytes* the antheridium breaks through the microspore wall, in others the spermatozoids escape through the break in the wall, no part of the male thallus protruding. The cells of the antheridium are differentiated into peripheral or wall cells and two masses of central cells from which the spermatozoids are developed. The spermatozoids are very small and have two flagella. In the quillworts and water-ferns the spermatozoids are multiciliate. Externally the male gametophytes of most *Heterosporous Pteridophytes* look very much like the pollen-grains of the seed plants with which they are homologous.

The female gametophyte projects somewhat beyond the megaspore wall. It begins its development by free cell formation and later a layer of cells is formed in one side of the spore. This breaks through the spore wall and a number of archegonia or ovaries are produced, but the greater part of the spore cavity is filled with irregular vegetative cells. The female thallus is destitute of chlorophyll and is dependent upon the food laid up in the spore. In *Marsilea* the female gametophyte is much more reduced having only a single archegonium whose neck projects from one end of the megaspore. In its older stages the female gametophyte may develop some chlorophyll. Each archegonium as usual contains a single oosphere or egg which has been formed by the division of a mother cell. The sister cell of the egg, called the ventral canal cell, always dissolves. This small female gametophyte is homologous with the so-called "embryosac" of the seed plants.

While the gametophytes are lying on damp ground, and when covered with water, fertilization is accomplished. In some *Selaginellas*, however, fertilization occurs while the megaspores containing the female gametophytes are still in the megasporan-

gium. The spermatozoids swim through the water and enter the necks of the archegonia. So far the Selaginellas are still dependent on an aquatic condition. When a spermatozoid reaches the egg its nucleus unites with the egg nucleus and as a result there is a double amount of chromation in the fertilized egg. When the oospore germinates its nucleus produces twice as many chromosomes as were present in the cells of the parent gametophytes. This conjugation or fertilization stage, therefore, represents the second profound change in the life cycle of the plant and is just opposite in its results to the reduction division.

The oospore is the first cell of the sporophyte generation. It is not discharged but begins to divide by a transverse wall. The outer cell develops into a suspensor while the inner gives rise to the embryo proper. In other classes the embryogeny is quite different and there seems to be much difference in the embryogeny of different Selaginellas. In the water ferns the development of the embryo is much the same as in the homosporous ferns.

The embryo is pushed down into the centre of the mass of food cells in the lower part of the female gametophyte by the rapid growth of the suspensor. It develops a foot, root, and stem tip with two small leaves called cotyledons. The foot occupies the cavity of the megaspore and takes up the food stored there. The root grows out, passes down into the ground, and begins to take up water with dissolved mineral salts. The stem with the cotyledons grows upward, develops chlorophyll, and thus begins the manufacture of food. The embryo changes gradually from a phagophyte, nourished entirely by the female parent, to a holophyte, manufacturing its own food from the simple compounds taken from the earth and air. It also passes gradually from the enclosed condition to the external world, there being no such sudden change as the embryo undergoes during the sprouting of a seed.

The little embryo sporophyte, having established relationships with the moist soil, air, and sunlight, continues to develop into a mature plant while the female gametophyte, its mother, dies. The gametophytes are short lived and are so reduced in body that their life consists mainly in accomplishing the important process of fertilization and in assisting the sporophyte to get a proper start during its early and helpless, juvenile stage.