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Heterospory and Origin of Seed Habit

Heterospory

The production of two kinds of spores differing in structure and function, the smaller one producing the male gametophyte and larger one producing the female gametophyte, is termed heterospory.

For the first time distict heterospory, structural as well as functional, is evident in pteridophytes, but of the several hundred forms in the group, only 9 genera (*Selaginella, Isoetes, Stylites, Marsilea, Pilularia, Regnellidium, Salvinia, Azolla,* and *Platyzoma*) are heterosporous.

Fossil record and heterospory

Palaeontological record shows that the earliest vascular plants were homosporous and probably produced exosporic monoecious gametophytes similar to present-day homosporous forms. Somewhat later in the lowermost strata of Upper Devonian (Frasnian stage), a free-sporing heterosporous condition was attained, in which spores are heterosporous but produce exosporous gametophytes, e.g. *Barinophyton*. Therefore, from a free-sporing homospory evolved the free-sporing heterospory.

Initial steps of heterospory are revealed by *Calamostachys*, a fossil sphenopsida. The genus has homosporous as well as heterosporous forms and the size of surviving spores is related to number of degenerating spores. *C. binneyana* is a homosporous form but in some sporangia the spores are of different sizes and in *C. casheana* adjacent sporangia are presumed to be microsporangia and megasporangia, the latter containing spores three times the diameter of microspores and having smaller, apparently degenerating spores.

The next important step of heterospory– reduction in number of megaspore- is revealed by *Archaeopteris*. The sporangia are of same size and these contain large number of microspores or small number of megaspores.

The number of megaspores in each megasporangium, however, is highly variable. An extensive spore degeneration in megasporangia is shown by *Stauropteris burntislandica*, a heterosporous coenopterid fern. In each tetrad there are two large spores and two small spores, probably degenerated ones. The reduction in megaspore number was greater in *Lepidocarpon* where three spores of each tetrad aborted.

Developmental events and heterospory

In the absence of sex determination process, in heterosporous pteridophytes, the developmental events are the best guide for an understanding of the phenomenon of heterospory. It has been pointed out that differences between microspores and megaspores are not there not only in terms of size and sex-expression but these spores are to be viewed in terms of food reserves, organelles, nuclear shape and wall construction.
A perusal of the forms showing heterospory indicates that the most significant events in the determination process are:

(a) Time of sex determination.
(b) Number of archesporial cells in a sporangium; whether the archesporial cells directly differentiate as sporocytes or divide mitotically thereby increasing the number of sporocytes.
(c) Number of sporocytes initiating and completing meiosis.
(d) Number of spores attaining maturity.

In *Equisetum, Ceratopteris* and *Onocloea*, the spores are all alike but under certain conditions produce heterothallic gametophytes though their development in early stages are similar. Thus segregation of sex can be observed during later stages of gametophytic development, a phenomenon known as 'incipient heterospory' which precedes true heterosporous condition. The female prothalli which are somewhat larger in size become hermaphrodite later if fertilization fails.

In *Selaginella*, the process of sex determination is operative both at premeiotic and postmeiotic stages. The developmental processes of both kinds of sporangia are same up to the formation of sporocytes (spore mother cells) in the genus *Selaginella*. In the micro-sporangium, in most cases all the sporocytes give rise to microspores after reduction division. In the megasporangium, generally only one sporocyte is functional which undergoes reduction division to form megaspores.

In *Isoetes* also not all but a few archesporial cells differentiate into megasporocytes while in the microsporangia most of the archesporial cell take part in the formation of microsporocytes.

In *Marsilea* sex determination starts at post-meiotic period. Development of both the sporangia up to the sporogenesis are identical. In both the sporangia 64 spores are produced. In the microsporangium all the spores survive while in the megasporangium all of them excepting one degenerate.

Now the question may arise why most of the megaspore mother cells degenerate and why most of the megaspores become non-functional. The former takes place due to the following reasons:

1. Loss of RNA stainability as found in some species of *Selaginella*.
2. The non-viable cells may not contain mitochondria or any of the cell organelles and are generally smaller in size than the viable ones.
3. Due to presence of lysosomes which bring about lysis of the cells.

Thus it is evident from the above discussion that the origin of heterospory is not confined to a particular stage but may start either at pre or post-meiotic stage or at both the stages, and is guided by number of factors.

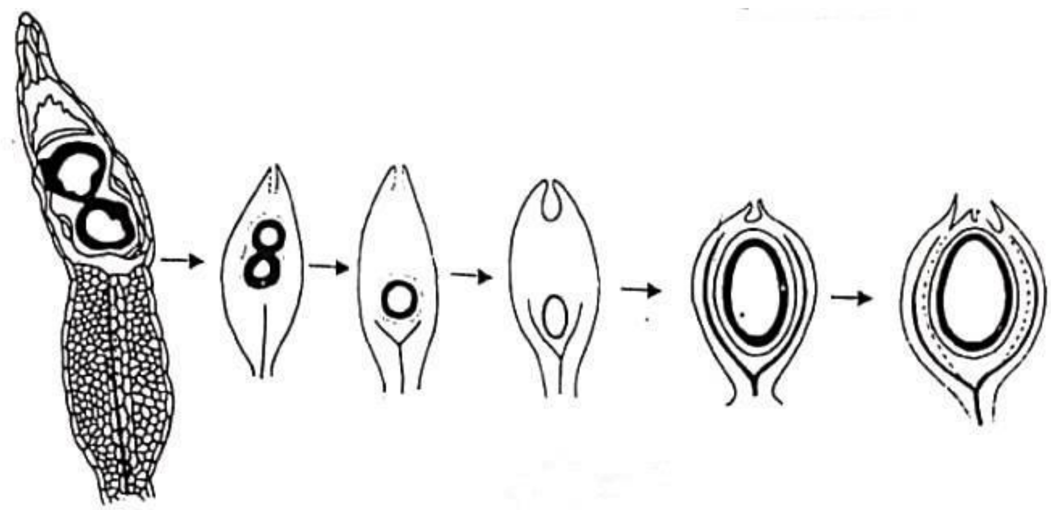
Origin of seeds

Ovule evolution requires the following important steps after heterospory is established.

1. A single megaspore survives and becomes functional and the three others are aborted.
2. This functional megaspore is retained within the megasporangium and no liberation of it is possible due to fusion of the megaspore wall with the tissue of the megasporangium.

3. Formation of a protective covering, the integument, the nucleus remains accessible normally only through the micropyle.
4. Formation of pollen tube is facilitate siphonogamy.
5. Endosporic megagametophyte develops within the indehiscent megasporangium.
6. The nuclear apex prepared itself to receive the pollen.

Stauropteris burntislandica, a uniquely heterosporous fern represents a specialized type of eusporangiate megasporangium. The sporangium is spindle shaped with two functional megaspores as its distal end. The lower part of the sporangium is parenchymatous for storing foods and is supplied with a vascular trace. Andrews (1966) suggested several steps regarding how the said megasporangium turned into a seed.



Origin of a Seed from Vascularized Megasporangium (Andrews)

1. Of the two megaspores one aborts and the other increase in size.
2. The megaspore settles towards the base of the sporangium.
3. A vascular strand splits and extends round the megaspore.
4. The sporangial wall and apex modify and ultimately give rise to a medullosan or a lyginopterid type of seed.

If pteridophytes are considered with respect to seed habit, it becomes evident that in *Selaginella* heterospory has reached very close to the seed habit in the following way.

1. There is reduction in the number of megaspores and finally it has been reduced to one only in *S. rupestris, S. monospora* and *S. sulcata*.
2. The genus exhibits endosporic development of gametophyte although there is shedding of the megagametophyte from the megasporangium but the time at which it sheds varies from species to species.

An extreme condition is noticed in case of *S. rupestris* and *S. apus* where not only the development of megagametophyte but also fertilization followed by development of embryo takes place within the megasporangium while it still remains attached with the strobilus. This phenomenon may be compared with that of viviparous germination, characteristic of a few angiosperms.

Hence among different species, *S. rupestris* and *S. apus* have approached seed habit in possessing the above characters.

3. Another very striking feature approaching seed habit is that in some species of *Selaginella* development of megagametophyte takes place in the left formed by partial opening of the megasporangial wall, a phenomenon known as incipient type of pollination.

However, inspite of the presence of the said characters, *Selaginella* and other heterosporous pteridophytes still escape the appellation of having seed habit due to following deficiencies.

(a) Absence of integument or seed coat surrounding the megasporangium.

Integument like structures which are present in fossil lycopods namely *Lepidocarpon* and *Miadesmia* are essentially the outgrowth of the sporophylls and not a true integument.

(b) Histological union between the megaspore and megasporangium wall is absent. Hence its permanent retention within the megasporangium has not been achieved. The lack of this union is due to the formation of a carbohydrate of callose type, also known as megasporocyte callose and which is not found to occur in the seed plant (Waterkeyn and Sloover, 1962).

(c) Absence of dormant period, the characteristic of a seed.

(d) The fossil members *Lepidocarpon* and *Miadesmia* lack micropylar opening, receptive chamber and siphonogamy, which are also the essential features encountered in seed plants.