Diversity of Seed Plants and their Systematics

Gymnosperms I

Evolution of Seed Habit

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One of the most important events in higher vascular plant evolution is the evolution of **Seed Habit**, which is definitely an advance over the **Pteridophytes**. The origin and subsequent evolution of seed habit is well documented in the fossil record, beginning in the Late **Devonian** where the first seeds are found. To attain this outstanding achievement many important steps were involved in the evolution of reproductive system that finally led up to the seed habit. Three prerequisites were essential: (i) protection of the gametophytes and the young developing sporophytes from drying and injury (ii) provision of nourishment for their proper development and (iii) freedom from external water required during fertilization for transference of gametes. All these conditions have been achieved in the seed of gymnosperms and angiosperms where the three successive generations are represented by the parent sporophyte as integument and nucellus, the gametophyte as endosperm and the daughter sporophyte as embryo.

Seeds or ovules are characterized by the presence of a central mass of sporophytic tissue, the **nucellus**. The nucellus is almost entirely enclosed in one or two sterile **sporophytic coats** or **integuments** except for a small opening called as the **micropyle**. Normally the **nucellus** consists of a single **functional megaspore** which is **permanently retained** and **germinates in situ** to produce a cellular **female gametophyte** inside the megaspore and serves as **food source** for developing **embryo** in gymnosperms (see Fig. 1A). In angiosperms the **food storage** function of **megagametophyte** is taken over by **triploid endosperm**. The seed or ovule is shed after fertilization and in many cases after the **zygote** has divided in situ to produce an **embryo sporophyte**.

![Figures showing longitudinal section of Pinar ovule. Megagametophyte (m), archegonial (a); integument (i); nucelus (n); pollen-tube (pseud). B, longitudinal section of Lepidocarpon with well preserved megagametophyte and embryo.](image)

*(Diagram A, reproduced from Stewart, 1987; B, reproduced from Taylor & Taylor, 1993)*
The ovule or seed was earlier defined by Hofmeister (1851) as an **integumented**, indehiscent **megasporangium** where the **nucellus** is homologous to the **megasporangial wall** of a **heterosporous pteridophyte**. In support of his view he cited the example of some fossil pteridophytes, e.g. **Lepidocarpon** and **Miadesmia** which had **megasporangia enclosed** inside **megasporophyll** that **functioned** like the **integument** and which had a **single functional megaspore** that showed **in situ** germination (see Figs. 1B, 3C, D). Such "seed plants", certainly indicated one of the ways in which **seed habit** was attained. Many botanists regard the origin of seed habit as a process that began with **homospory**, was followed by stages of **heterospory** and terminated in a structure called **ovule** or **seed**.

Figure 2  A. Diagram, transverse section megasporophyll of **Lepidocaropsis lanceolatus**. B. **L. semialata** with lateral lamina partially investing the sporangium. (A, B redrawn from Abbot, 1963.) C. **Lepidocarpon lomaxi**. diagram transverse section of megasporophyll. "Micropyle" (m); nucellus (n); integument (i); megagametophyte (mg). D. Diagram, longitudinal section of a gymnosperm ovule.

(All figures reproduced from Stewart, 1987)
**Figure 3.** A. Reconstruction of Permian Selaginella harrisiina and its parts, leaf with ligule (l); microsporophyll (mi); megasporophyll (me). B. Longitudinal section through cone of Selaginella showing mega- and microsporangia (me) and (mi) and ligule (l). C. Longitudinal section of Miadesmia membranacea, showing megasporophyll and megasporangium. D. Miadesmia sp. L.S. of megasporophyll, megasporangium and ligule (l) from Carboniferous. (Figures A,B & D reproduced from Stewart, 1987; Figure C reprinted from Taylor & Taylor, 1995)

**Figure 3:** Reconstruction of Permian Selaginella harrisiina and its parts. Note leaf with legume (l), microsporophyll (mi), megasporophyll (me). B. Longitudinal section through cone of Selaginella showing mega- and microsporangia (me) and (mi) and ligule (l). C. Longitudinal section of Miadesmia membranacea, showing megasporophyll and megasporangium and ligule (l), from Carboniferous. (Figures A,B & D, reproduced from Stewart, 1987; Figure C, reproduced from Taylor & Taylor, 1995)
The earliest known vascular plants like *Cooksonia, Rhynia, Horneophyton, Zosterophyllum*, etc. which appeared in Upper Silurian and Lower Devonian were all **homosporous**. By the Middle Devonian some vascular plants like *Protobariophyton* (Petit, 1970) and *Chaleuria* (Andrews et al., 1974) were reported as being **anisosporous** producing large and small spores in the **same sporangium**. In *Chaleuria*, the smaller microspores ranged 30-40 µm in diameter while the megaspores were 60-156 µm in diameter (see Fig. 4C, D.). Such plants were succeeded in the Upper Devonian by plants like *Barinophyton*, where too, the sporangium consisted of a mixture of **small** and **large trilete** spores, the trilete microspores, several thousand in number ranging in size from 33-48.5µm in diameter; the trilete megaspores, about 30 in number, are exceptionally large ranging from 700-900µm in diameter (Brauer, 1980). The **occurrence of two sizes of spores in the same sporangium** seems to be an evolutionary situation in heterospory preceding a later and more definite **distinction** between **microspore** and **megaspore**. Ultrastructure of large and small spores in *Barinophyton* (Taylor and Brauer, 1983) is different, indicating the plant to be **biologically heterosporous**.
Heterospory had evolved in the arborescent lycopod, *Cyclostigma* by Upper Devonian times. In *Cyclostigma*, the cones were bisporangiate with about 24 megaspores per megasporangium.

Another arborescent lycopod *Flemingites (Lepidostrobus) schopfii* from later Carboniferous times was bisporangiate having both micro- and megasporophylls attached compactly in tight spirals to a cone axis (see Fig. 5A). The megasporophylls with megasporangia were present in the lower part of cone and microsporophylls with microsporangia were present on upper part of cone axis, resembling a massive *Selaginella* strobilus in general organization (see Fig. 1A, B). The microspores of *F. schopfii* were 20 to 30 um in diameter and triplete megaspores numbering 12 to 29 persporangium were larger being 700-1250 µm in diameter.

Some cones of lepidodendrids were monosporangiate, producing only megaspores. The most common and highly evolved reproductive structure is that of *Lepidocarpon* (see Figs. 1B, 4A, B), because organization of the sporophylls resembled function of integuments in seed plants. The adaxial sporangia on sporophylls consisted of two lateral laminae and a distal extension. The lateral extensions partially cover the sporangium. Inside the sporangium is one large, functional, trilete megaspore and three aborted spores. Some fossil specimens revealed cellular megagametophytes with well preserved archegonia (see Fig. 1B).

Another isolated lycopod megasporophyll from Carboniferous of Europe, *Miadesmia* has cones containing only megasporophylls. Each megasporangium attached near proximal end of sporophyll is completely enveloped by integument-like lateral laminae except in distal region. The enveloping sporophyll is divided into elongate, tentacle-like extensions. The sporangium contains one large, functional megasore, sometimes also cellular megagametophyte per megasporangium (see Fig. 3C, D).

Besides *Lepidocarpon* and *Miadesmia*, another well known heterosporous form from the Lower Carboniferous, is a fern called *Stauropteris burntslandica* (Surange, 1952) having *Bensonites* type of megasporangium which is unintegumented (see Fig. 5D) but presents a few seed-like features: the megasporangia are shaped like nucelli with a sterile vasculated region below and the megasporangium consists of a single tetrad of four spores out of which only two are functional and two abortive; the plant was shedding the entire megasporangium and in some megasporangia there was a small terminal pore in the sporangial cavity for communication with the exterior and which could serve as an inlet for male element.

The above mentioned fossil forms provide important clues in recording the transition between stages of heterospory and the seed habit.

**Further on than heterospory, towards ovule formation:**

- After the onset of heterospory, a number of evolutionary events took place in the evolution of ovule, eg.
  
  (a) Reduction in the number of megaspores in the megasporangium from many to single tetrad, like those of *Stauropteris, Lepidocarpon, Miadesmia* etc. that show a single spore tetrad with reduction in the number of fully developed spores to two or usually one proximal megaspore. Undoubted seeds of *Archaeosperma arnoldii* described by Petit and Beck (1968) also contained a trilet functional megaspore and three abortive ones in a tetrahedral tetrad (see Fig. 6E).

  (b) Retention of the single functional and three abortive megaspores in the megasporangium. Additional protection to megaspore is provided by formation of one or more protective coats, the integument that delimited a micropyle. Change from tetrahedral to linear tetrad.

  (c) Germination of micro- and megaspores begins *in situ* (while they are still inside the sporangia and the megasporangia are attached to parent plant).

  (d) Formation of a pollen tube or pollen tube-like structure from endosporic microgametophyte.

  (e) Formation of an endosporic megagametophyte within an indehiscent megasporangium (nucellus) (see Fig. 2C).

  (f) Elaboration of the apex of indehiscent nucellus to form pollen chamber for pollen reception.

  (g) Pollination (replacing transfer of antherozoids through the medium of water as in bryophytes and pteridophytes), where light weight microspores (due to progressive reduction in male gametophytes) are passively carried to the attached megasporangia by pollinating agents like wind or other agencies present in the terrestrial environment.
(h) **Fertilization** is effected by means of a pollen tube (siphonogamy) and is **completed** while the megasporangium is attached to the parent plant, although, in primitive forms, e.g. the Pteridospermales, and the Cordaitales fertilization was completed only after shedding of the seeds.

(i) The female gametophyte is **intraspore** being permanently retained within the megaspore and is totally dependent on parent sporophyte for its nutrition. The megagametophyte is also reduced and can easily tap the supply of nutrients from the surrounding nucellar tissue of parent sporophyte. The **multicellular megagametophyte** has archegonia in the distal end which have no neck canal cells and often the ventral canal cell too is absent. They appear like ovoid cavities which may be partially filled with remains of vesiculate cytoplasm.

(j) **Another important step** in the **evolution** of seed habit is information regarding the **movement** of sperms to archegonia. Studies of Carboniferous ovules or pre-ovules suggest two possible mechanisms:

(i) **enlargement** of megagametophyte resulted in dehiscence of nucellus and megaspore membrane, thereby, directly exposing the archegonia to flagellated sperms or

(ii) **formation** of pollen tube to allow movement of sperms through an indehiscent megasporangium and megaspore membrane to the archegonia.

Some evidence for both mechanisms is present in the Upper Carboniferous suggesting that evolution of ovules with pollen tubes from pre-ovules with dehiscent megasporangia could have occurred in Upper Devonian or Lower Carboniferous.

(k) **Product of fertilization** - the zygote, is divided to form an embryo inside the seed before the seed was shed by the parent plant. Abundant food reserves accumulated in and around the embryo in the endosperm to enable the embryo to tide over the initial period of establishment on the ground.

However, it may be mentioned here that there are very few reports of embryos in fossil seeds although hundred of ovules have been investigated. There could be three possible explanations for the absence of embryos:

(i) Embryo development continued outside the seed; or

(ii) Only a very small percentage of ovules developed embryos; or

(iii) Embryos developed only after seeds had fallen on the ground (as existed in a number of living gymnosperms).

The oldest seed plant known up to date which seems to take one to the beginning of seed evolution is *Elkinsia polymorpha*, a seed-fern described from Late Devonian of West Virginia (Rothwell et al., 1989). The specimens consisted of loose tufts of cupules produced on a cruciateforked branching system (see Fig. 6A, B, C). Cupules were produced in pairs or singly, with each cupule containing 16 sterile branch tips surrounding 4 orthotropous ovules. The ovules were isodiametric, up to 6.5 mm long, and consisted of a 4-5 lobed integument, where the lobes were fused only in the basal region. Distally the integumentary lobes are wide apart. Each lobe of integument was vascularized by a small terete strand. The lobed integument surrounded a cellularized extension of the nucellus that functioned as a pollen receiving mechanism. Each ovule contained a large, presumably functional megaspore as well as small aborted megaspores.

Other ovulating cupules which were almost equally ancient are *Moresnetia zalcsskyi* (Fairon-Demaret & Scheckler, 1986), *Xenotheca devonica* (Rothwell & Scheckler, 1988) and *Hydrasperma tenius* (Long, 1977).

Another ovuliferous structure described from slightly younger Devonian beds was the cupulate seed of *Archaeosperma arnoldii* (Pettitt & Beck, 1968). The fossil consisted of 2 cupules, each surrounding a small shortly pedicellate orthotropous ovule (see Fig. 6 D, E). At the apex of the flask-shaped ovules, the integuments is serrated into a number of lobes that formed a rudimentary micropyle; the lobes are free only for one-fifth of the distance from base of seed to its apex and fused below; the basal portion of integument bore prominent trichomes. The middle and basal part of nucellus are fused with integument. The nucellus contained a megaspore of *Cystosphorites devonicus* type. These megaspores were not formed in a linear tetrad like other seeds but were borne in a tetrahedral tetrad with one large functional trilete megaspore and three abortive ones, at the distal end of a large *Cystosphorites* type of megaspore. The large megaspore is often found as a dispersed spore and is obtained by bulk maceration of surrounding matrix. *Archaeosperma*, undoubtedly, is an example of an ovule which is well along the evolutionary road leading to seed habit.
Besides *Archaeosperma*, other well preserved Devonian seeds indicated effective reception of pollen by modification of distal end of the nucellus to form a hollow pollen-chamber, crowned by a funnel-like tube termed as salpinx of lagenostome.

The earliest seeds had no micropyle since the integumentary lobes were loosely arranged around the apex of nucellus.

Figure 5: A. *Flemingites* (Lepidostrobus) *schoffii* - L.S. cone showing microsporangia (mi) and megasporangia (me). B. Longitudinal section of *Stenopteris burmiallandica* sporangium. B, cellular megagametophyte, MG, in *Flemingites schoffii* megaspora. C, Polar view of *F. schoffii* archegonium showing four neck cells, N.
(All figures reproduced from Taylor & Taylor, 1993)
In the early evolution of seeds two basic types have been identified. Some of them were radially symmetric or rounded in cross section (radiospermic) and others were flattened in one section (platyspermic). The radiospermic seeds are usually attributed to the Peteridosperms and the platyspermic seeds to the Cordaitales.

Related with the evolution of seed habit is also the origin of integument. In lycopsids like *Lepidocarpon* and *Miadesmia*, parts of sporophylls have been modified to form integuments around the megasporangia (see Fig. 2A-D). Several theories about the origin of integument have been cited from time to time, but the most attractive hypothesis is based on the telomic concept (Zimmermann, 1952). This theory envisions a dichotomously
branched axial system bearing terminal sporangia as the evolutionary starting point. According to this theory, there occurred gradual reduction of some of the axes (termed telomes and mesomes by Zimmermann) so that eventually a single sporangium became surrounded by an aggregation of sterile processes. In such a structure, several modifications were necessary to evolve a seed (see Fig. 7A-D).

Chaloner and Pettitt (1987) have attempted to reconstruct a series in evolution of seed habit from a condition where many megaspores are present (e.g. *Archaeopteris*) to a reduction in number of megaspores as seen in *Bothrodendrostrobus* (see Fig. 8G, H) where only four equal sized megaspores occur. The next stage in evolution of seed habit is the condition seen in *Bensonites* where two of the megaspores are larger than the other.
two. However, the case of *Archaeosperma*, only one megaspore of tetrahedral tetrad is large and functional while the three others are greatly reduced in size and non-functional. In the genus *Cardiocarpus* further reduction in size of the three non-functional megaspores of the tetrahedral tetrad is seen. The last stage is the linear tetrad as seen in *Cycas* (and in most present day gymnosperms) where the functional megaspore is much enlarged and the three non-functional megaspores are short lived and degenerate (see Fig. 8A-F).

Thus, seed habit which seems to have evolved in the Upper Devonian era, is represented by the oldest seed-bearing gymnosperm, *Archaeosperma* and presumably cupules bearing two seeds preceded those with only one.
Suggested readings -


