

INTRODUCTION TO SEED PLANTS

Any understanding of the origin and morphology of the seed requires us to revisit the concept of heterospory (also see p. 103 in Simpson's *Plant Systematics* for diagram).

Heterospory = production of two different types of spores (in two different types of sporangia): (1) megaspores (developing into female gametophytes = megagametophytes) and (2) microspores (developing into male gametophytes = microgametophytes). Sperm and egg are produced by different types of gametophytes in heterosporous plants.

Each of the two principal free-sporing lineages of vascular plants (lycophytes and ferns, that is) have both homosporous and heterosporous taxa, with heterospory being independently derived from homosporous in both groups. In heterosporous lycophytes and heterosporous ferns (as in homosporous lycophytes and ferns), the spore is the unit of dispersal and is released from the sporangium of the parent sporophyte prior to spore germination.

From now on, we will be studying heterosporous plants that produce **only one functional megaspore and retain it within the megasporangium -- the seed plants**. All of the seed plants are heterosporous; the transition to heterospory from homosporous happened before all characteristics of the seed evolved.

[See p. 102, 104, and 105 of Simpson's *Plant Systematics* for diagrams that illustrate the following points]

General points about evolution of seed:

1) Maternal protection and care by the sporophyte for the megagametophyte was taken to a new level in the seed plants; not only is the only functional megaspore retained in the megasporangium (of the sporophyte) but also the megagametophyte that germinates from that megaspore develops inside the megasporangium. Further, the zygote resulting from fertilization of the egg (produced by the megagametophyte), by sperm delivered via a pollen tube, develops up to the point of being an embryo inside the same confines of the immature seed (=ovule).

2) Seed plants also evolved a reproductive biology that no longer required free-standing water for sperm transport. In fact, in seed plants the gametophyte generation (both mega- and micro-gametophytes) develops without direct need for (or contact with) soil moisture at all (moisture is provided to the gametophytes via the connection to the parent sporophyte).

Innovations of seed plants:

1) Heterospory: seen in various woody "progymnosperm" taxa (e.g., Archeopteris) from Paleozoic that are evidently ancestors of true seed plants but lack true seeds.

2) Evolution of pollination

Pollination brings together the microgametophyte and megagametophyte without water or soil contact (water pollination evolved much later). Evolution of pollination involved reduction of the microgametophyte to a few-celled state, still contained within the microspore wall at the time of its dispersal from the microsporangium (probably by wind in earliest seed plants). Pollination required evolution of a pollen chamber in the megasporangium to receive pollen. After reaching the pollen chamber of megasporangium, the immature microgametophyte (= pollen grain) germinates and grows down into the megasporangium and ultimately releases sperm in the vicinity of the egg. The mature microgametophyte is merely a pollen tube.

- 3) Evolution of indehiscent megasporangium w/ one functional megaspore (one gametophyte develops inside megasporangium). Indehiscent = not opening at maturity.
- 4) Origin of seed abscission (that is, release of the seed from the plant). Seed abscission represents dispersal of the remains of the megasporangium, remains of the megagametophyte, and the embryo. Unlike in heterosporous lycophytes and ferns, which release their megaspores from the megasporangium, seed plants delay dispersal until the next generation of sporophyte is produced from the megagametophyte that germinated from the megaspore.
- 5) Evolution of integument = tissue surrounding the megasporangium that develops into the seed coat (after pollination, the integument seals off summit of megasporangium at least somewhat in earliest true seed plants).

Ovules and seeds

The immature seed = ovule (not to be confused with ovary -- the structure in flowering plants that contains the ovules). In its earliest stages of development (prior to pollination), an ovule is merely a megasporangium surrounded by integument. Later, the ovule includes the megaspore, and subsequently the megagametophyte, and finally the embryo. At maturity the mature seed contains 3 generations of tissue: (1) the (diploid) integument and megasporangial remains of the sporophyte that bore it, (2) the (haploid) megagametophyte remains inside, and, inside that, (3) the (diploid) embryo (which will germinate to become a new sporophyte). The ovule and resulting seed contain (and protect) all stages of the life cycle, even the earliest stages of growth of the sporophyte (embryo) and the post-germination microgametophyte (pollen tube).

Evolutionary evidence of seeds (Rothwell & Scheckler 1988):

First fossils in the upper Devonian (ca. 350 Ma), before diversification of modern lineages of seed plants.

Evidence from **uniformity of structure of early seed plants** that the living seed plants constitute a **monophyletic group**.

Ecological considerations

Evolution of seed improved the ability to colonize unexploited or ephemeral habitats

- 1) Independence from soil moisture for gametophyte growth and reproduction (wind dispersal of immature microgametophyte (=pollen grain)).

- 2) Excellent dispersibility of sporophyte (embryo): Early seed plants produced large numbers of small, readily dispersible seeds (later, innovations of fleshy, edible seed coat or wings further enhanced dispersability).
- 3) Rapid growth (resources in seeds allowed head-start at vulnerable stage in early life of sporophyte -- when root system must become established quickly).
- 4) Shoots (stems, leaves) resistant to desiccation and extensive root systems -- not directly related to seed evolution, but these features are seen in earliest seed plants and would have promoted life in drier habitats.
- 5) Dormancy -- in some seeds, tissues surrounding embryo allow for persistence in dormant state until environmental conditions permit growth.