ANGIOSPERMS: THE FLOWERING PLANTS

Angiosperms (flowering plants) are seed plants that developed in the early to mid-Cretaceous period about 125 million years ago. They are believed to be derived from a "gymnosperm" ancestor. Some analyses of morphological and molecular data support the view that the angiosperms are allied to the gnetopsids and to an extinct group known as the Bennettitales or cycadeoids. These groups have reproductive structures that can be interpreted as flowers. These early flower-bearing plants likely were derived from seed fern groups identified as caytonids or glossopterids. As the dominant plants on the earth's surface today, angiosperms number well over 200,000 species. They exhibit a wide array of habits, from perennial to annual, and woody to herbaceous and occur in essentially all terrestrial habitats as well as in some aquatic ones. The habitat in which the earliest angiosperms evolved is unknown. Was it a dry upland site, or a moist tropical rainforest, or a coastal area with a mild climate? As yet, there is no conclusive evidence.

The reproductive structures of angiosperms are formed in specialized and often showy organs called flowers. In contrast to gymnosperms that produce seeds exposed in cones, angiosperms form seeds in an enclosed structure, the ripened ovary or fruit located in the center of the flower. The derivation of angiosperm means seed in a box or case and is from the Greek words *angio* meaning box, case, or vessel and *sperm* meaning seed.

The life cycle of angiosperms shows a dominant sporophyte and reduced gametophytes (for angiosperm life cycle, see: http://zygote.swarthmore.edu/phyto1.html). The intricacies of the life cycle depend on meiosis and fertilization occurring in the flower and the retention of the female gametophyte in the flower (on the sporophyte). The outer parts of a flower are sepals and petals, which serve to protect the inner sex organs and, in some cases, to attract pollinators. The inner floral parts are the sex organs, stamens (male) and carpels (female). Generally, the stamens consist of a filament or stalk supporting an anther, while the carpels consist of a stigma, style, and ovary. Meiosis occurs in two places in the flower: in the anther sacs of stamens and in the ovules found within the ovary (the basal part of the carpel).

In the anthers, numerous pollen mother cells undergo meiosis and the four haploid nuclei produced from each meiotic division typically divide by mitosis and develop into pollen grains (male gametophytes). Within each pollen grain, there is a tube nucleus that promotes pollen tube growth through a style (the middle part of the carpel) and a generative nucleus that divides to produce two sperm. Once pollen grains are mature and dehisced from the anther, they can be transported by air, animal, or water to a receptive stigma (the uppermost part of the carpel). **Pollination refers to the transfer of pollen to a stigma**.

In the carpel, one or more ovules are attached to a placenta in the ovary. An ovule consists of a megasporangium, is surrounded by one or two integuments, and develops eventually into a seed. Inside the ovule, a megaspore mother cell divides by meiosis to produce four haploid nuclei (megaspores); three of these disintegrate, leaving one functional megaspore that divides by mitosis to produce an embryo sac. The embryo sac constitutes the female gametophyte and contains four to eight nuclei, of which one is the egg nucleus and two or more are endosperm nuclei.

In order for a pollen grain to germinate on a receptive stigma, the pollen and stigma must be genetically compatible. If a compatible pollen grain lands on a stigma, it will germinate by forming a pollen tube through one of the thinner parts of the pollen wall, in a pore or groove area. The pollen tube will grow through the style and into the ovary of a flower, where it eventually will penetrate an ovule and release two sperm nuclei into the embryo sac. **Double fertilization** then occurs. Within the embryo sac, one sperm combines with the egg nucleus to form a zygote and the second sperm combines with two other nuclei, called polar or endosperm nuclei, to form a fertilized endosperm nucleus that divides mitotically to form endosperm (the nutritive tissue of angiosperm seeds). A wall is formed around these tissues and a seed is produced.

The angiosperms are considered to be monophyletic, or derived from a common ancestor, because they have ovaries, triploid endosperm, and ovules covered by two integuments. Early angiosperms are considered to have had bitegmic ovules (with two integuments), although unitegmic ovules (with one integument) occur in several families and can be secondarily derived from bitegmic ones by fusion of the two integuments or by abortion of one of the two integuments. The inner integument is homologous with the single integument of "gymnosperms" and the outer integument likely developed from the infolding of a pinnately compound ovule-bearing leaf to form a pinnate axis bearing cupules as in *Caytonia*. Double fertilization is another character shared by all the angiosperms, but it also occurs in *Ephedra* (Gnetales), where no endosperm is formed. Flowers are another character found throughout the angiosperms, but similar structures are found in phylogenetically allied groups, such as the Gnetales and extinct cycadeoids. **In contrast to gymnosperms where the vascular system only has tracheids, both tracheids and vessels occur as water-conducting cells in most angiosperms**. If there had been multiple origins for angiosperms, one would not expect to find all of these critical features throughout the group.

The early angiosperm fossils help to confirm morphological specialization at specific times in the geological record. The early fossils consist of leaves, stems, pollen, and sometimes flowers. Typically, these parts occur as isolated fragments. The fossils often are recognizable to family and sometimes to genus. The early fossils of angiosperm leaves usually are simple and with entire margins and pinnate venation. The more complex leaf types, with compound leaves and lobed and serrated margins, appear later in the fossil record. Fossilized stems of flowering plants have vascular tissue made up of tracheids or tracheids and vessels. Wood consisting only of tracheids has been considered to be ancestral by some authors, but recent phylogenetic analyses indicate that such wood structure may have been secondarily derived in angiosperms by the loss of vessel elements. Early angiosperm pollen has one sulcus or groove and is described as **monosulcate**. The more complex pollen types have three or more grooves or pores (e.g., **tricolpate**, **triporate**, **polycolpate**). The earliest known fossil flowers have separate petals, and several to many spirally arranged carpels with superior ovaries. Fused carpels or compound gynoecia represent a derived condition. Leaflike or **conduplicate** carpels with an ovary and a stigmatic crest are among the earliest types of fossilized carpels.

Fossil information may only occasionally be used, along with that gained from developmental studies of living organisms, to establish ancestral and derived traits of particular characters. One of the best examples is provided by pollen. Since monosulcate is the first recognizable pollen type known in the angiosperms, it represents an ancestral or **plesiomorphic** state of pollen. Three or more grooves or pores on pollen indicate a derived or **apomorphic** state. With the support of the fossil record, a trend representing a transitional series of states of one basic character can be established. In pollen, the trend showing evolutionary development and specialization is monosulcate pollen to tricolpate or polycolpate pollen.

Families with several ancestral or plesiomorphic characters typically are placed at the base of classification systems, whereas families that usually have few ancestral characters and many derived or apomorphic characters generally represent the end points of branches of the phylogenetic tree. The following trends of character states (ancestral to derived) of both vegetative and reproductive characters have traditionally been used in to construct angiosperm classifications. These trends are only general tendencies, since the polarity or determination of what is ancestral and what is derived has to be determined in each particular group under study.

ANCESTRAL OR PLESIOMORPHIC	→	**DERIVED OR APOMORPHIC**
autotrophic (nutritionally independent)	→	**parasitic or mycotrophic**
woody habit	→	**herbaceous** habit
leaves simple, with pinnate venation and entire margins	→	**leaves with varying features**
manyness (>20) of floral parts	→	**fewness** of parts
separate parts	→	**fused** parts
spirally arranged floral parts	→	**cyclic or definite whorls** of parts
actinomorphic (radial) symmetry	→	**zygomorphic** (bilateral) symmetry
undifferentiated perianth	→	**differentiated perianth** (sepals and petals)
polypetaly (separate petals)	→	**sympetaly** (fused petals)
leaflike (laminar) stamen	→	**stamen differentiated to form filament and anther**
monosulcate pollen	→	**tricolpate, triporate, or polycolpate pollen**
conduplicate carpel (ovary and stigmatic crest)	→	**carpel with stigma, style, and ovary**
superior ovary	→	**inferior ovary**
apocarpy	→	**syncarpy**
simple fruit formed from a single carpel	→	**compound fruit** formed from fused carpels or a compound gynoecium

The angiosperms are usually classified in two major groups, the dicotyledons and the monocotyledons. **Cotyledon** refers to a seed leaf, or the first leaf evident upon seed germination. In dicotyledons, two seed leaves are formed, and in monocotyledons, one seed leaf is formed. The two groups differ in other important vegetative and reproductive characters (see Table, Comparison of Dicotyledons and Monocotyledons). Several features of monocotyledons are considered to be derived or apomorphic. These include the solitary cotyledon, absence of a vascular cambium, dissected stele ('scattered' arrangement of vascular bundles in the stem), adventitious root system, sheathing leaf bases, and herbaceous habit. These unifying features of the monocotyledons serve to substantiate that the group is monophyletic. Recent phylogenetic analyses indicate that the dicotyledons are ancestral to monocots and therefore are paraphyletic.