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1

Introduction to angiosperms

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Although the angiosperms, or flowering plants, are the most recently evolved major group of plants (Figure 1.3), they now occupy a dominant position in the world's vegetation. With the total number of extant species thought to be in the range 240 000 to 300 000, they exceed the combined diversity of algae, bryophytes, pteridophytes and gymnosperms (Sporne, 1974; Prance, 1977). With the exception of conifer forest and moss-lichen tundra, angiosperms dominate all of the major terrestrial vegetation zones, account for the majority of terrestrial primary production, and exhibit a bewildering morphological diversity. They range in habit from minute free-floating aquatics to herbs, epiphytes, lianes, shrubs and large forest trees. Although most are autotrophs, some are parasites or saprophytes, and angiosperms are the only group of vascular plants successfully to have colonized marine habitats that are otherwise only occupied by algae.

What makes an angiosperm?

Angiosperms are distinguished from other seed plants, and united as a group, by several features related to their unique reproductive system. These are carpels enclosing the ovules, pollen-tube growth through the sporophytic carpel tissue, double fertilization resulting in the formation of a triploid endosperm, and the highly reduced male and female gametophytes (Sporne, 1974; Crane, 1985; Doyle & Donoghue, this volume, Chapter 2). However, several other characters that occur in most angiosperms are not universally present within the group, and some characteristic features of angiosperms also occur sporadically in gymnosperms. Together with the enormous diversity of flowering

plants, the relative paucity of strict defining characters makes the group much more difficult to circumscribe than might appear at first sight. Even the characteristic angiosperm flower exhibits great variation in structure that defies unambiguous definition.

Vegetative features

The angiosperms exhibit an extreme range in habit including herbaceous forms not commonly encountered in other seed plants, and lianes otherwise known only in the Gnetales. In vegetative features, angiosperms are unique in that the conducting tissues of the phloem possess companion cells that are derived from the same mother cell as the sieve elements. Most angiosperms also possess vessel elements in the xylem, but the phylogenetic interpretation of this character is complicated by the existence of several angiosperms that lack vessels (e.g. Winteraceae) and the occurrence of vessels in some gymnosperms (Gnetales). The vessels of angiosperms typically have scalariform, reticulate or simple perforation plates (Figures 1.1(a) to (c)), probably derived from tracheids with scalariform bordered pits, and ontogenetic studies indicate an evolutionary trend from elongated narrow vessels with tapering ends and scalariform perforation plates (Figure 1.1(a)) to short and wide vessels with simple perforation plates (Figure 1.1(c)). In the Gnetales the perforation plates are apparently mostly derived from circular bordered pits of typical gymnospermous nature (Bailey, 1944; Martens, 1971), but scalariform perforation plates have also been described from the Gnetales (Muhammad & Sattler, 1982). Whether the vessels of Gnetales and angiosperms have a common origin in a shared ancestor has therefore been the subject of much controversy. The vesselless condition in the angiosperms is most common within magnoliid angiosperms and associated with other vegetative and reproductive features that are generally considered to be primitive, but whether the lack of vessels in these taxa should be regarded as the primitive state or as a result of secondary loss remains unclear (Takhtajan, 1969; Young, 1981).

A further typical vegetative characteristic of the angiosperms is the presence of broad leaves, with the vascular bundles forming a reticulate branching pattern with a hierarchical system of successively thinner veins that often have free endings (Figure 1.1(d) to (e)). In the monocotyledons, the main veins are commonly parallel and the leaf differentiated into blade and sheath, while in the dicotyledons the main veins are usually pinnate or palmate (Figure 1.1(d)) and the leaf differentiated into a petiole and blade. Broad leaves, reticulate venation and the

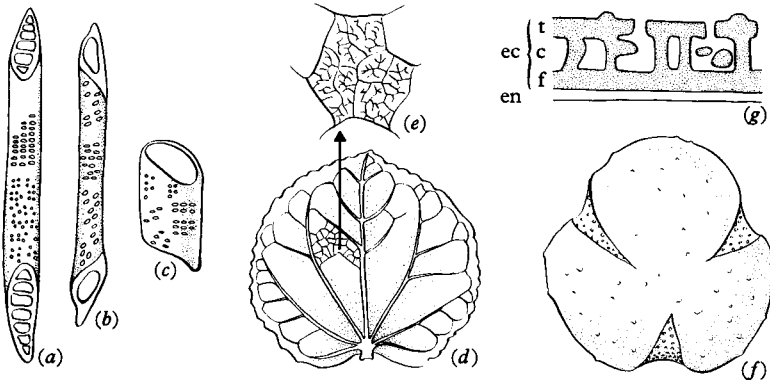


Figure 1.1. Characteristic features of angiosperms. (a) Vessel element with scalariform perforation plates. (b)–(c) Vessel elements with simple perforation plates. (d) Dicotyledonous leaf with palmate primary venation. (e) Detail of venation pattern. (f) Tricolpate pollen grain. (g) Section of pollen wall showing thin endexine (en), and footlayer (f), columellar layer (c) and tectum (t) of ectexine (ec).

presence of a petiole are not exclusive angiosperm features, although in extant non-angiospermous plants this combination is only present in the gymnospermous genus *Gnetum* (Gnetales).

Chemical characteristics of the angiosperms include the presence in many taxa of alkaloids derived from aromatic amino acids and hydrolyzable tannins (Swain, 1976). In contrast, in non-angiosperms the occurrence of alkaloids as secondary metabolites is less common. Alkaloids of angiosperms are also different from those of gymnosperms, and gymnosperm tannins are condensed and non-hydrolyzable (Swain, 1976).

Pollen features

An apparently unique pollen characteristic of the angiosperms is the differentiation of the pollen wall into a non-laminate endexine, with the ectexine differentiated into a foot-layer, columellar layer and tectum (Figure 1.1(g)) (Muller, 1970; Walker & Doyle, 1975). Within the dicotyledons, members of the subclasses Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae and Asteridae are characterized by pollen with three or more apertures that are typically positioned equatorially (Figure 1.1 (f)). However, in the monocotyledons and dicotyledons of the subclass Magnoliidae, the pollen typically has a single distal furrow (monosulcate) and in this feature resembles the pollen grains of some gymnosperms included in the Cycadales, Bennettitales, Gnetales,

Ginkgoales and other groups. The male gametophyte of angiosperms consists of only three cells, compared with the more extensive four-, five- and six-celled male gametophytes of gymnosperms, and the female gametophyte is similarly reduced. In angiosperms the female gametophyte consists typically of only 8 to 16 cells, and no archegonia are differentiated. Although archegonia are also lacking in *Gnetum* and *Welwitschia* (Gnetales), the female gametophyte in these and all other gymnosperms is much more extensive than in angiosperms.

Floral features

To a large extent the diversity of angiosperm floral structure is a reflection of the sophisticated breeding systems that have evolved within the group, and apparently promote gene exchange by outcrossing. The angiosperm flower is typically hermaphroditic (bisexual), with carpels (female parts) and stamens (male parts) aggregated in the same flower, with the former borne above the latter. Outcrossing in hermaphroditic flowers is usually achieved by insects that transfer pollen from the stamens of one flower to the stigma of another. In such typical entomophilous flowers, the reproductive organs are surrounded by a perianth of sterile appendages that are differentiated into an outer group of sepals and an inner group of petals that form the calyx and corolla, respectively (Figure 1.2(a)). The sepals are usually green and typically serve to protect the flower during its development, while the petals are generally colored, frequently function as a visual attractant and are often involved in the production of nectar or odors. These basic floral parts may be free or united both between themselves and to each other. The symmetry of flowers varies from radial (actinomorphic) to bilateral (zygomorphic) and may reflect specialization for pollination by various groups of insects (Proctor & Yeo, 1973; Faegri & van der Pijl, 1979). Other features typical of insect-pollinated flowers include the presence of nectar-producing tissue, ovaries with many ovules, and sticky pollen grains. In contrast, wind-pollinated (anemophilous) flowering plants typically have flowers protruding from the foliage (or formed earlier than the leaves) with a perianth that is inconspicuous or absent (Figure 1.2(b)–(d)). Large quantities of dry, more or less smooth pollen grains are produced typically, and the ovaries usually have one or a few ovules. Other characteristic features of many anemophilous plants are well-exposed reproductive organs aggregated into pendulous catkins, expanded feathery or papillose stigmatic surfaces, and the absence of scent and

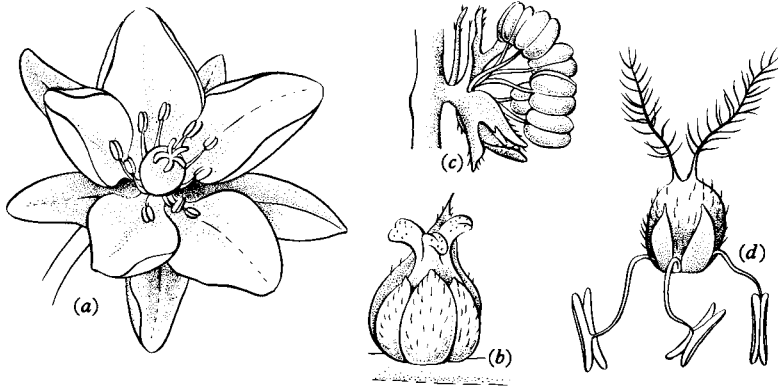


Figure 1.2. Floral features in angiosperms. (a) Entomophilous, hermaphroditic flower of a dicotyledon with showy perianth. (b)–(c) Anemophilous, unisexual flowers of an oak with reduced perianth: (b) female (pistillate) flower; (c) male (staminate) flower. (d) Anemophilous, hermaphroditic flower of a grass with feathery stigmas.

nectar production. These characters prevail in both dicotyledonous (Figure 1.2(b)–(c)) and monocotyledonous plants (Figure 1.2(d)).

Self-fertilization in hermaphroditic flowers may be kept at a low level by various incompatibility systems or by differences in the timing of maturation of stamens and ovaries. In protogynous flowers, the stigmas are receptive to pollination before the stamens mature and release their pollen, while in protandrous flowers, the pollen grains are released before the stigmas become receptive and are often only viable for a short period.

Although most angiosperm flowers are hermaphroditic, separation of the sexes into staminate (male) and pistillate (female) flowers occurs in some groups and this is a further means by which self-fertilization is apparently reduced. The pistillate and staminate flowers may be borne on the same individual (monoecious) or on separate plants (dioecious). Dioecious plants are most common in tropical areas and are generally pollinated by insects. Frequently they exhibit modifications for insect attraction comparable to those of hermaphroditic entomophilous flowers, but in dioecious plants the flowers are generally smaller than those of related hermaphroditic taxa (Bawa & Opler, 1975; Bawa, 1980). Monoecious angiosperms are most common in temperate regions and are less frequent at lower latitudes (Whitehead, 1983). They are typically wind pollinated, with simple flowers. Typical anemophilous

features occur in many trees of temperate regions but are also shared by the grasses, which provide a good example of hermaphroditic anemophilous flowers (Figure 1.2(*d*)). The flowers of most grasses appear to be particularly well adapted to wind pollination in possessing versatile, exserted anthers and an expanded feathery stigma (Figure 1.2(*d*)).

Origin and form of the primitive angiosperms

Hypotheses about the nature of primitive angiosperms may be divided broadly into two opposing theories, developed over the contrasting floral characteristics associated with entomophily and anemophily (Doyle & Donoghue, this volume, Chapter 2). The most widely accepted view is the Euanthial, or Anthostrobilus, Theory (Arber & Parkin, 1907), in which the angiosperm flower is interpreted as being derived from an unbranched bisexual strobilus bearing spirally arranged ovulate and pollen organs, similar to the hermaphroditic reproductive structures of some extinct bennettitalean gymnosperms. The Bennettitales and the angiosperms were linked by those authors by hypothetical transitional hemiangiosperms that bore ovules on the margin of leaf-like structures resembling the megasporophylls of extant *Cycas*. Among living angiosperms, the strobiloid flower of the Magnoliaceae and related families, with numerous, free flower parts, were interpreted as being most similar to the basic archetype (Bessey, 1897, 1915). The flowers of the Magnoliaceae are typically solitary and large, with many spirally arranged carpels, stamens and perianth parts on an elongated axis. They are hermaphroditic, usually pollinated by beetles, and have a showy perianth. The stamens are often more or less laminar, and the gynoecium is apocarpous, with each carpel enclosing several ovules. According to the Euanthial Theory, more simple flowers, including the typical anemophilous forms, are derived from the basic *Magnolia* type, by reduction and fusion of parts.

Over the last two decades the fossil record has reinforced the view that extant Magnoliidae are among the most primitive living angiosperms, but the Euanthial Theory has also received some support, over a much longer period, from comparative studies with extant angiosperms. This interpretation of the angiosperm flower, developed by Bessey and by Arber and Parkin, also forms the basis of most modern phylogenetic classifications of flowering plants (Cronquist, 1968, 1981; Thorne, 1968; Hutchinson, 1969; Takhtajan, 1969, 1980; Walker & Walker, 1984).

The alternative, Pseudanthial Theory (Wettstein, 1907) interprets the

angiosperm flower as being derived from unisexual gymnosperm reproductive structures, perhaps similar to those of the gnetalean gymnosperms. According to this concept, the small, simple, unisexual, anemophilous flowers of some Hamamelididae (Fagales, Casuarinales, Juglandales, Myricales, sometimes collectively termed the Amentiferae) and of the Piperales, retain the largest number of primitive floral characters among living angiosperms. The flowers are typically aggregated on elongated axes, and the gynoecium is unilocular, enclosing a single anatropous or orthotropous, unitegmatic ovule. However, the occurrence in the Amentiferae of occasional, often imperfectly developed, bisexual flowers may suggest that the unisexual condition is secondary. This is also supported by the discovery of small bisexual flowers from the Upper Cretaceous that may have been produced by early primitive members of the Juglandales or Myricales (Friis, 1983). In addition, the fossil pollen record clearly demonstrates that triaperturate, particularly triporate grains, typical of the Amentiferae are not present in the initial radiation of the angiosperms, and are substantially predated in the fossil record by pollen resembling that of extant Magnoliidae (Muller, 1970; Doyle & Hickey, 1976). However, while the primitive status of the Amentiferae has been convincingly refuted, the phylogenetic position of the Piperales, themselves included within the Magnoliidae, remains of considerable interest. In particular, the Chloranthaceae have emerged as an especially critical group. While this family is often considered to be highly derived within the Magnoliidae (Walker & Walker, 1984), this may be in conflict with the abundance of chloranthoid pollen very early in the angiosperm fossil record (Muller, 1981; Walker & Walker, 1984). Furthermore, recent analyses of the relationships between major groups of seed plants have identified both the Gnetales and Bennettitales as gymnosperms that may be equally, and very closely, related to angiosperms (Crane, 1985; Doyle & Donoghue, this volume, Chapter 2).

A major problem in any theory of angiosperm origin is the difficulty of explaining the derivation of the closed angiosperm carpel from the ovuliferous structures in gymnosperms. In both the Bennettitales and Gnetales, the naked ovules are borne directly on an axis, with no evidence of sporophylls or other organs that might contribute to carpel formation. However, in several other groups of Mesozoic gymnosperms the ovules are borne on leaf-like structures, permitting several plausible possibilities for the derivation of the carpel. Attention has centered mainly on the Caytoniales, Corystospermales and Glossopteridales (Andrews, 1963; Stebbins, 1974; Doyle, 1978; Retallack & Dilcher, 1981; Crane, 1985),

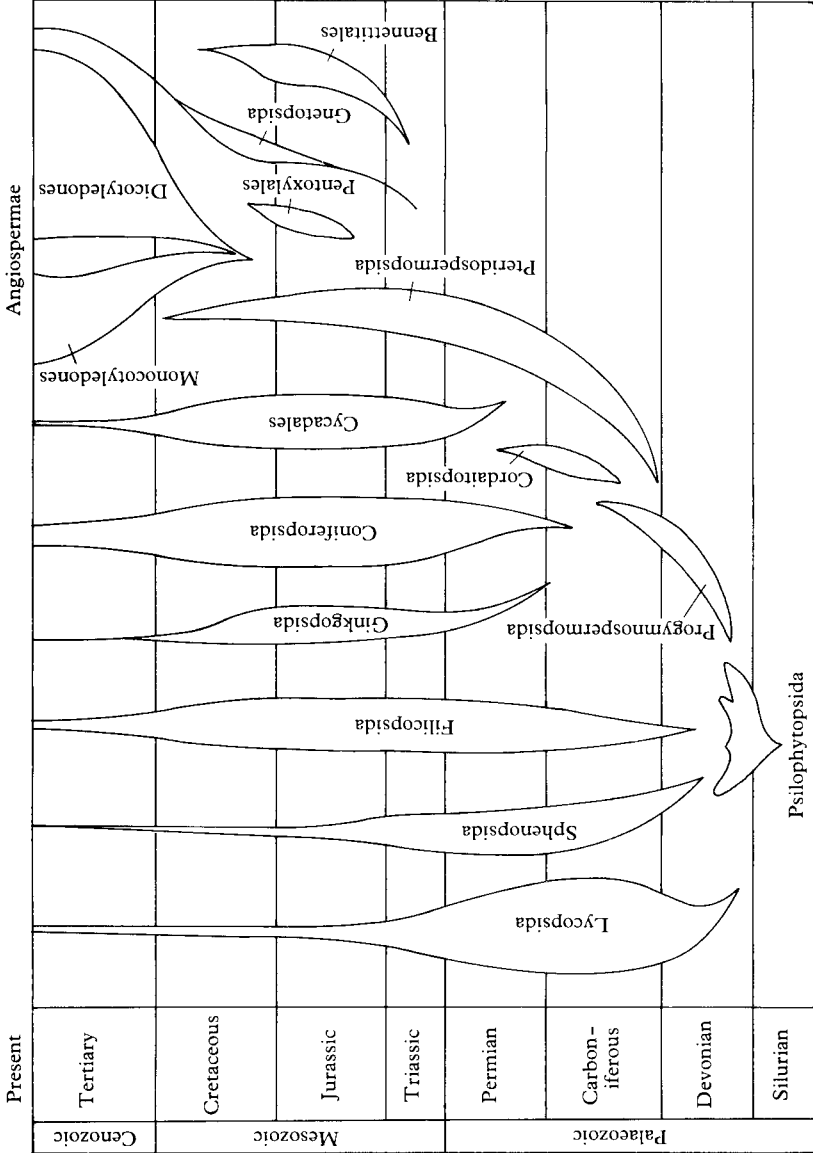


Figure 1.3. Stratigraphic range and generalized phylogenetic position of major groups of land plants.

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all extinct taxa included in a highly heterogeneous group of extinct seed plants, the pteridosperms (seed ferns). The traditional interpretation of the position of angiosperms relative to other vascular plants which incorporates these interpretations of the angiosperm carpel, is summarized in Figure 1.3. The complex issues involved in interpreting the origins and relationships of the angiosperms are discussed in more detail by Doyle and Donoghue in Chapter 2. These authors adopt a numerical cladistic approach in attempting to resolve the relationships between major groups of seed plants, and also consider some of the possible evolutionary processes and ecological factors that may have played an important role in angiosperm origin.

Timing and pattern of the early angiosperm radiation

A long pre-Cretaceous history of the angiosperms has been postulated by several authors (Axelrod, 1952, 1960, 1970; Takhtajan, 1969; Stebbins, 1974), and although it is possible that the angiosperm lineage may have diverged from closely related gymnosperms very early in the Mesozoic (Crane, 1985; Doyle & Donoghue, this volume, Chapter 2), it is unlikely that the angiosperms were diverse during the Triassic and Jurassic. The available fossil evidence indicates instead that the initial major diversification of angiosperms took place during the late Early Cretaceous, following the first appearance of undoubted angiosperm fossils in the Barremian or slightly earlier in the Hauterivian (Figure 1.3). Palynological data suggest that the angiosperm radiation began at low palaeolatitudes (Brenner, 1976; Hughes, 1976), but, within a relatively short span of time during the mid-Cretaceous (Aptian–Turonian), angiosperms became established world wide as the ecologically dominant terrestrial plant group (see Upchurch & Wolfe, this volume, Chapter 4; Crane, this volume, Chapter 5).

The differentiation of the two major angiospermous groups, the dicotyledons and the monocotyledons, was established very early in angiosperm history. The earliest well-documented angiosperm fossils include dispersed monosulcate pollen grains of the form-genus *Clavati-pollenites*, first described by Couper (1958) from Barremian and Aptian strata of southern England. These grains are believed to be angiospermous on the grounds that their sculptured exine shows a tectate structure (cf. Figure 1.1 (*g*)), coupled with a single distal furrow. *Clavati-pollenites* grains are closely similar to pollen of the extant chloranthaceous genus *Ascarina* (Couper, 1958; Walker & Walker, 1984) and unequivocally

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indicate the early appearance of the Piperales. Other pollen types, leaves and floral structures with chloranthoid characters also occur in Aptian and Albian strata of eastern North America (Upchurch, 1984; Walker & Walker, 1984; Friis, Crane & Pedersen, 1986), and clearly establish the importance of this family in the initial angiosperm radiation. The oldest unequivocal fossils of the Magnoliales so far recorded are pollen grains related to the Winteraceae recorded from Aptian–Albian strata of Israel (Walker, Brenner & Walker, 1983) and leaves with features characteristic of Magnoliales from Aptian–Early Albian strata of eastern North America (Upchurch, 1984). Large magnolialean flowers with numerous free parts of the kind predicted by the classic formulation of the Euanthial Theory are not recorded until the Late Albian and Cenomanian (Dilcher & Crane, 1984; Crane & Dilcher, 1984).

Extant Chloranthaceae include both anemophilous and entomophilous taxa, and comparisons of fossil and Recent material indicate that a differentiation into insect and wind pollination systems was also established in the Early Cretaceous chloranthoid angiosperms (Friis *et al.*, 1986). Low pollen production in many entomophilous plants, combined with the unspecialized morphology of much magnolialean pollen, may explain the apparent paucity of the Magnoliales relative to the Chloranthaceae in the early palynological record of angiosperm diversification.

Triaperturate pollen grains diagnostic of non-magnoliid dicotyledons appear in the latest Barremian or earliest Albian (slightly later than monosulcate chloranthoid pollen) and increased dramatically both in diversity and in abundance during the mid-Cretaceous. The earliest triaperturate grains are small, with microreticulate ornamentation and three equatorial colpi. Albian floral structures with pollen *in situ* indicate that at least some of these are related to probable members of the Hamamelididae and Rosidae, which may have borne platanoid and *Sapindopsis* foliage, respectively (Crane, Friis & Pedersen, 1986). The very small size and microreticulate sculpture of the pollen grains in some of these triaperturate forms suggest entomophily.

Monosulcate pollen of possible monocotyledonous affinity is recorded during the Aptian and Albian (Kemp, 1968; Doyle, 1973; Walker & Walker, 1984). They are elongated in shape and have reticulate sculpture of the exine differentiated into areas with either a coarse or fine network. Similar features occur in extant entomophilous groups, whereas smooth monoporate pollen grains typical of anemophilous monocotyledons are not recorded until the Late Cretaceous (Muller, 1970; Doyle, 1973).