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Introduction to angiosperms

The phylogenetic diversification and ecological radiation of angiosperms (flowering plants) that took place in the Early Cretaceous, between about 135 and 65 million years ago, was one of the major biotic upheavals in the history of life. It had dramatic consequences for the composition and subsequent evolution of terrestrial ecosystems. Ancient Mesozoic vegetation, which was dominated by ferns, conifers, ginkgos and cycads, as well as Bennettitales and other groups of extinct seed plants, was eventually almost entirely replaced by more modern ecosystems dominated by angiosperms. Since the Early Cretaceous, high diversification rates have generated more than 350 000 extant angiosperm species. Today there are more living species of angiosperms than all other groups of land plants combined.

In their rise to ecological dominance angiosperms have exhibited extraordinary developmental and evolutionary plasticity. This has resulted in overwhelming morphological diversity and a great variety of adaptive types. Angiosperms are far more diverse in vegetative form and in the structure of their reproductive organs than any other group of land plants.

In growth habit angiosperms range from minute free-floating aquatics less than 1 mm long (*Wolffia*) and moss-like plants of fast-flowing water (Podostemaceae), to herbs, epiphytes, lianas, shrubs and tall trees. The massive *Eucalyptus* trees of Tasmania reach heights of more than 100 m. In floral morphology the structural diversity of angiosperms ranges from the minute staminate flowers of *Hedyosmum*, which comprise only a single stamen, to the giant blossoms of *Rafflesia*, up to 90 cm in diameter, or to the slender flowers of *Aristolochia* that may be up to 1 m long (Endress, 1994b).

Structural diversity is matched by ecological diversity: angiosperms occupy an astonishing range of habitats from deserts to freshwater swamps, and from tropical rain forests to the Antarctic Peninsula. Except for boreal conifer forests and moss-lichen tundra, angiosperms dominate the vegetation of all the major terrestrial biomes. They are also the only group of land plants that have reinvaded the

marine habitat (e.g. *Zostera*). As a result of their ecological dominance angiosperms account for the majority of terrestrial primary productivity, play a significant role in major geochemical cycles and influence atmospheric composition and climate. They comprise the autotrophic foundation on which almost all terrestrial ecosystems are built.

The diversity of angiosperms also includes great variety in physiology and biochemistry. Most angiosperms are autotrophs, but there are also diverse parasites and saprophytes. Some angiosperms supplement their intake of nitrogen through trapping and digesting animals. A much larger number are involved in elaborate symbiotic associations with a wide range of fungi and bacteria. Several groups of angiosperms have evolved modifications to the basic processes of photosynthesis, which confer significant ecological advantages in arid or hot environments. Angiosperms also produce a bewildering variety of biochemical compounds, many of which appear to be important in interactions with other organisms ranging from fungi to vertebrates. As food, as a source of raw materials, and as key participants in global ecological systems, angiosperms are fundamental to human life and survival.

1.1 PHYLOGENETIC POSITION OF ANGIOSPERMS

1.1.1 Anthophytes and alternative patterns

For almost 150 years, attempts to understand the origin and diversification of flowering plants were hindered by uncertain relationships among the vast array of extant angiosperms, as well as the apparently insuperable morphological 'gap' between angiosperms and other seed plants (gymnosperms). More generally, progress in studying the patterns and larger-scale processes of biological evolution was retarded by the absence of an appropriate methodological framework in which to develop, and choose among, competing phylogenetic hypotheses. As a result, it was difficult to evaluate the great variety of ideas that

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had been published on angiosperm origins, and that had implicated almost all groups of fossil and living gymnosperms as potential angiosperm ancestors (Crane, 1985a). The role of the plant fossil record in contributing to an understanding of angiosperm origins and early evolution was also uncertain. Some authors assumed that palaeobotanical data were either unavailable or uninformative as a source of useful information bearing on angiosperm evolution (e.g. Stebbins, 1974); others argued that only the fossil record could provide reliable data for interpreting angiosperm evolution (e.g. Hughes, 1976, 1994).

Over the past few decades the development of phylogenetic systematics (cladistics) has stimulated intense discussion of the philosophical and methodological bases for reconstructing phylogenetic patterns. Many of the crucial theoretical and other issues that formerly blocked progress in phylogenetics have now been wholly or partly resolved, clearing the way for new research that has made rapid progress. The development of computer software for powerful numerical cladistic analyses of large complex datasets, as well as techniques for rapidly amplifying and sequencing nucleic acids, have also reactivated interest in phylogenetic reconstruction as a key component of modern evolutionary biology and as one of the central goals of contemporary plant systematics. In the process, the nature of what the palaeobotanical record can, and cannot, contribute to studies of angiosperm evolution has been clarified (Crane *et al.*, 2004).

The diversity of land plants can be viewed as a nested set of four major groups: land plants (embryophytes), vascular plants (tracheophytes), seed plants (spermatophytes) and flowering plants (angiosperms) (Figure 1.1). In this context, and in cladistic terms, resolving the question of angiosperm origin requires recognising and defining the major groups of seed plants, determining their phylogenetic interrelationships, and thus establishing the group with which flowering plants share a most recent common ancestor.

Since the early 1980s (Hill and Crane, 1982; Crane, 1985a) a series of cladistic analyses using parsimony have been conducted to investigate the phylogenetic position of angiosperms among living and fossil seed plants based on syntheses of mainly morphological data (Doyle and Donoghue, 1986, 1992, 1993; Loconte and Stevenson, 1990; Nixon *et al.*, 1994; Rothwell and Serbet, 1994). All of these studies identify angiosperms as a strongly supported clade, and indeed as one of the most strongly supported monophyletic groups in the plant kingdom. Cladistic studies

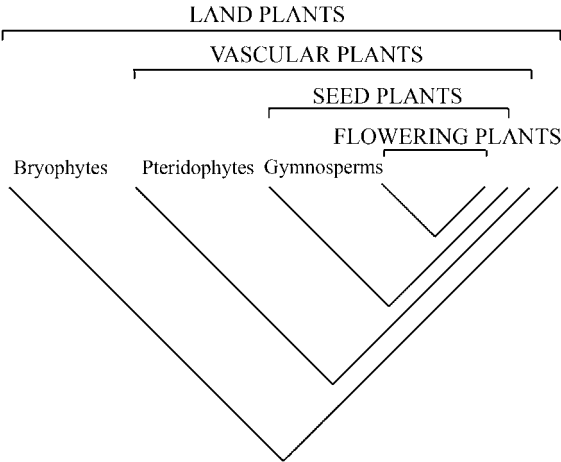


Figure 1.1 Cladistic relationships among land plants (embryophytes) showing the nested positions of three monophyletic groups: vascular plants (tracheophytes), seed plants (spermatophytes) and flowering plants (angiosperms). Under this interpretation bryophytes, pteridophytes and gymnosperms are defined by exclusion (paraphyletic). For example, gymnosperms are those seed plants that are not angiosperms. Adapted from Crane (1985a).

that include a significant representation of extinct seed plants also recognise that the seed ferns (Pteridospermales) as traditionally defined constitute a highly unnatural assemblage of seed plants of diverse relationships (Crane, 1985a). Most studies also confirm the Gnetales as a monophyletic group (but see Nixon *et al.*, 1994).

Morphology-based phylogenetic analyses of extant land plants have generally placed the Gnetales as the closest living relatives to angiosperms (Figure 1.2), and analyses incorporating extinct plants show that among fossils the Bennettitales are also closely related (Figure 1.3), supporting earlier hypotheses of angiosperm and seed plant relationships (Bessey, 1897, 1915; Hallier, 1901; Arber and Parkin, 1907). The angiosperms, Gnetales and Bennettitales, sometimes together with the extinct *Pentoxylon* plant, form a monophyletic group, usually referred to as the anthophytes (e.g. Doyle and Donoghue, 1986), in recognition of their shared possession of flower-like reproductive structures (Figure 1.3). An area of disagreement among these cladistic analyses based on morphological data concerns the resolution of relationships among anthophytes (Figure 1.3). This disagreement arises mainly as a result of uncertainties over the homologies among seed plant reproductive structures, including angiosperm flowers.

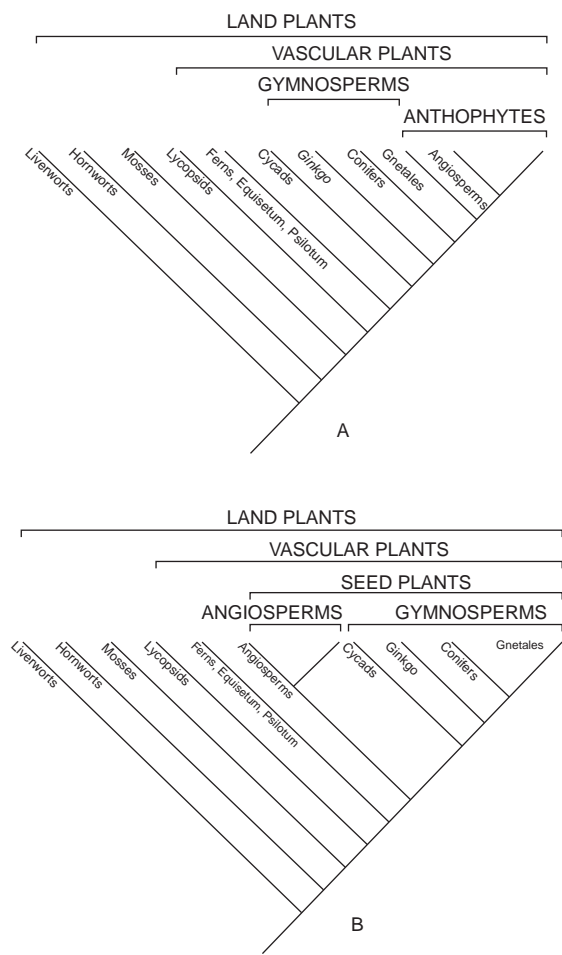


Figure 1.2 Alternative cladistic relationships among extant land plants. (A) Cladogram showing angiosperms nested among other seed plants and forming a monophyletic group with Gnetales (anthophyte clade); under this hypothesis extant gymnosperms are paraphyletic. (B) Cladogram showing angiosperms as sister group to all other seed plants; under this hypothesis extant gymnosperms are monophyletic. (A) and (B) synthesised from several sources.

The relationships of anthophytes to other seed plants are also uncertain. In several analyses anthophytes are nested among two or more of the so-called Mesozoic seed fern groups (Glossopteridales, Caytoniales, Corystospermales, Peltaspermales), often with Caytoniales as the sister taxon to the anthophytes (e.g. Crane, 1985a; Doyle and Donoghue, 1986, 1993). Again, many of the difficulties behind these different interpretations arise from ongoing uncertainties about how key fossil taxa should be compared

with angiosperms and also with each other. These difficulties are further exacerbated by imperfect knowledge of important extant and extinct plants. There is still much more work to be done to develop a more satisfactory comparative dataset on which future integrated cladistic analyses of living and fossil seed plants can be based.

Recent analyses based on morphological data give phylogenetic patterns very similar to those from 25 years ago (Doyle, 2006; Hilton and Bateman, 2006; Friis *et al.*, 2007), but so far this consistency has not translated into broad confidence in the results. A particular difficulty is that recent analyses based on molecular data support alternative interpretations of relationships among extant seed plants. Some of these analyses suggest that angiosperms are the sister group to a clade comprising all other extant seed plants (cycads, *Ginkgo*, conifers, Gnetales) (Figure 1.2), which would make all living gymnosperms (but not necessarily all fossil and living gymnosperms) monophyletic. Other analyses are especially radical in supporting the inclusion of Gnetales within conifers (Hansen *et al.*, 1999; Qiu *et al.*, 1999; Bowe *et al.*, 2000; Chaw *et al.*, 2000; Burleigh and Mathews, 2004). Conifers, as they are traditionally defined, would therefore be paraphyletic. Still other analyses indicate monophyly for conifers with Gnetales as sister to conifers (Burleigh and Mathews, 2004), or suggest that angiosperms and cycads may be sister taxa (Mathews, 2010). Taken together current molecular data do not appear to be sufficient for the unambiguous identification of relationships among extant seed plants (Rydin *et al.*, 2002; Friis *et al.*, 2009a; Mathews, 2010). Recent phylogenetic analyses that bear on the question of angiosperm origin, including those relevant for ideas about the age of angiosperms are reviewed in more detail in Chapter 6.

1.1.2 Relationships among living angiosperms

Another factor that has contributed to uncertainties about phylogenetic patterns among major groups of seed plants has been the question of how best to represent the enormous diversity of angiosperms in higher-level analyses. Until recently this problem has been further compounded by the very poor resolution of phylogenetic relationships near the base of the angiosperm clade.

In the 1980s important initial progress was made in the development of the phylogenetic framework for angiosperm evolution by overturning the traditional view that angiosperms comprise two distinct lineages; dicotyledons (dicots) and monocotyledons (monocots). Early cladistic

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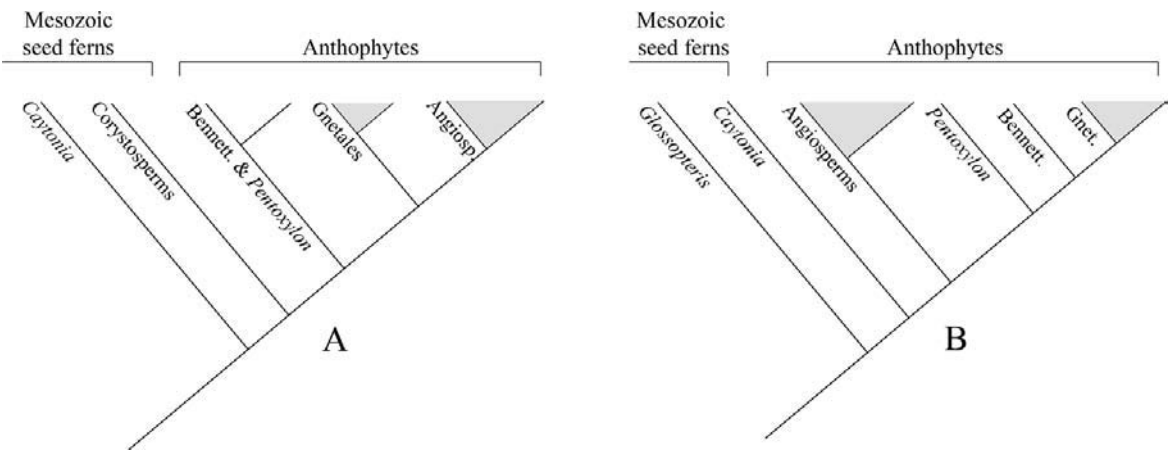


Figure 1.3 Alternative cladistic relationships among anthophytes. (A) Cladogram showing angiosperms nested among other anthophytes. (B) Cladogram showing angiosperms as sister group

to all other anthophytes. (A) adapted from Crane (1985a); (B) adapted from Doyle and Donoghue (1992). For other models of relationships, see Chapter 6.

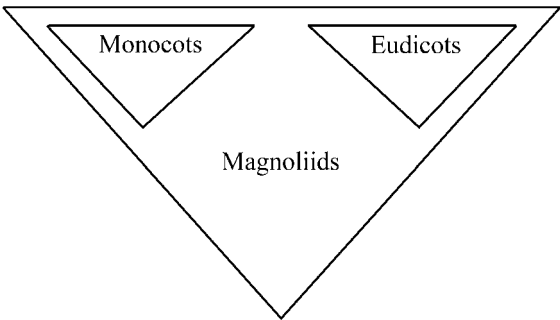


Figure 1.4 Cladistic relationship of the two major groups of angiosperms (monocots and eudicots), both monophyletic, whereas magnoliids *sensu lato* are paraphyletic, in effect the residue of angiosperms after monocots and eudicots have been removed. Magnoliids include the ANITA lineages, Chloranthaceae, *Ceratophyllum* and eumagnoliids (see Figure 1.5).

assessments based on morphological and molecular data identified a paraphyletic basal grade of dicots (broadly equivalent to subclass Magnoliidae of previous classifications such as that of Takhtajan, 1980) in which two major monophyletic groups, monocotyledons (monocots) and eudicotyledons (eudicots), were embedded (Figure 1.4). Eudicots (Chapters 12–15) are defined morphologically by the presence of triaperturate pollen (Donoghue and Doyle, 1989a, 1989b). Such pollen contrasts with the fundamentally monoaperturate pollen of magnoliids, monocots and some gymnosperms. Monocots (Chapter 11) are also strongly supported as a monophyletic group based on

molecular data (Chase *et al.*, 2000), the single cotyledon and other features (Herendeen and Crane, 1995).

Although extant magnoliids account for only about 3% of living angiosperm species they are very diverse in habit, vegetative form and floral structure and biology (Chapter 10). Variation in the number and arrangement of floral parts is especially extreme (Endress, 1994b). Large, multipartite and bisexual flowers, small, simple and frequently unisexual forms, and a variety of other kinds of flowers, are widespread at this level of angiosperm evolution. Until recently, comparative studies of extant magnoliids had been impeded by poor knowledge of many of the key groups. However, as a result of recent detailed morphological and anatomical research these plants are now sufficiently well understood to incorporate into phylogenetic studies in a meaningful way (e.g. Endress, 1987, 1990; Endress and Hufford, 1989; Igersheim and Endress, 1997).

The recognition of magnoliids as a paraphyletic group simplifies and focuses attempts to precisely root the angiosperm tree, which is essential for clarifying both the patterns and processes of morphological evolution within the group. Extensive sampling of magnoliids for phylogenetic analyses based on molecular data has achieved good coverage of extant diversity at this level and has begun to produce consistent resolution of relationships (Figure 1.5). These analyses identify Amborellaceae, Nymphaeales and Austrobaileyales (including Austrobaileyaceae, Schisandraceae, Trimeniaceae) as the earliest diverging lineages at the base of the angiosperm phylogenetic tree (Qiu *et al.*,

1999, 2000; Soltis *et al.*, 1999, 2002; APGII, 2003; APGIII, 2009). This basal grade of angiosperms has been referred to as the ANITA grade; from *Amborella*, Nymphaeaceae, *Illicium* (Schisandraceae), Trimeniaceae and Austrobaileyaceae (Qiu *et al.*, 1999). The remaining magnoliids, except for Chloranthaceae and *Ceratophyllum*, form a monophyletic group composed of Magnoliales, Laurales, Piperales and Canellales (APGIII, 2009). This clade was termed eumagnoliids by Soltis *et al.* (2000b) and magnoliids by the APGII (2003). In this book, to avoid confusion, and to maintain the broader conventional use of the informal term magnoliid, we refer to the basal grade of angiosperms as the ANITA grade and to the Magnoliales, Laurales, Piperales and Canellales clade as eumagnoliids. The phylogenetic framework of angiosperm evolution that has been established based on molecular phylogenetics is briefly reviewed in Chapter 7.

1.1.3 Origin of the angiosperm flower

Pre-cladistic hypotheses of flowering plant phylogeny were inextricably linked to concepts of the primitive angiosperm flower. They can be divided broadly into two contrasting sets of ideas: the Euanthial Theory, also known as the Ralian Theory (Bessey, 1894, 1896, 1897, 1915; Hallier, 1900, 1901, 1902, 1912; Arber and Parkin, 1907), and the Pseudanthial Theory (Wettstein, 1907).

Under the Euanthial Theory the angiosperm flower is interpreted as a simple, bisexual, uniaxial system bearing spirally arranged lateral leaf-like appendages (bracts and sporophylls) potentially homologous with the strobilus of the Cycadales or Bennettitales (Chapter 6). According to the Euanthial Theory the insect-pollinated flowers of Magnoliaceae and related families are most similar to the angiosperm floral archetype, which would have had numerous helically arranged parts. More simple flowers, for example, those of Piperales, or wind-pollinated trees such as Betulaceae, Juglandaceae and Myricaceae, are considered to be derived from the basic *Magnolia*-type by simplification, reduction and fusion of parts.

Under the Pseudanthial Theory the angiosperm flower is interpreted as a compound, pluriaxial (multiaxial) structure potentially homologous to the cone of conifers or Gnetales (Chapter 6). According to this interpretation the angiosperm flower is composed fundamentally of a primary axis bearing secondary axes, with both orders of branching bearing lateral appendages. According to the classical Pseudanthial Theory the wind-pollinated flowers of angiosperms such as the

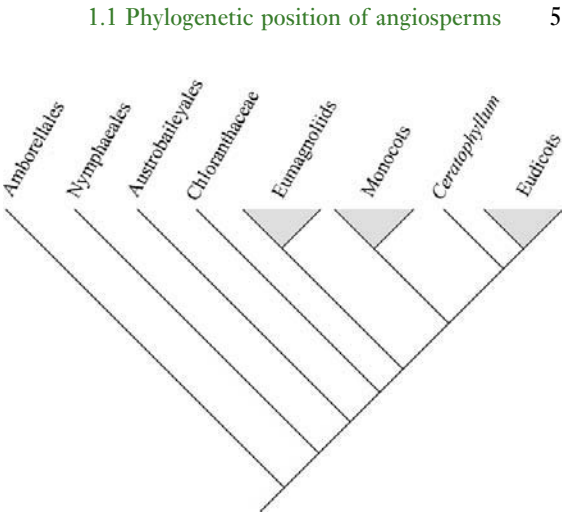


Figure 1.5 Cladistic relationships among major groups of angiosperms. Note the position of monocots, eudicots and eumagnoliids nested among ANITA grade plants (*Amborella*, Nymphaeales, and Austrobaileyales) and other magnoliids (Chloranthaceae and *Ceratophyllum*).

Piperales, as well as those of the Betulaceae, Juglandaceae and Myricaceae, are most similar to the angiosperm floral archetype. In these plants the flowers are typically small, simple, unisexual and aggregated on elongated inflorescence axes. The gynoecium is unilocular and contains a single orthotropous or anatropous ovule. Large, bisexual, insect-pollinated flowers, such as those of *Magnolia* and its allies, are considered derived. They are interpreted as pseudanthia formed by the aggregation of unisexual floral units.

With the recognition that Betulaceae, Juglandaceae and Myricaceae occupy a relatively derived position within the angiosperm clade, many authors in the 1980s implicitly accepted the Euanthial Theory. However, since then the situation has become more complicated. Many early fossils, and several of the earliest diverging angiosperm lineages (e.g. Amborellaceae, Trimeniaceae, Hydatellaceae, Chloranthaceae), have flowers that are very simple. It seems unlikely that they can be accounted for simply by pervasive patterns of reduction from larger flowers with more numerous parts. A comprehensive theory of the origin and early evolution of angiosperm flowers, which accounts for all the relevant variation is yet to emerge. Identifying the likely basic condition for floral features in angiosperms, and establishing their homology with reproductive structures of other seed plants, will require integration of a fully resolved pattern of relationships at the magnoliid grade with significantly improved information on early angiosperm fossils and their close relatives among other seed plants.

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1.2 CHARACTERISTIC FEATURES OF ANGIOSPERMS

There is currently no support from phylogenetic analyses based on morphological or molecular data for angiosperm polyphyly. The extraordinary diversity of angiosperms, and especially the bewildering variety among their flowers, has sometimes led to the suggestion that they are polyphyletic. However, a clear suite of characters (autapomorphies) unites angiosperms as a well-defined monophyletic group and distinguishes them from other seed plants. Several other potential defining features are not universally present in the group, for example vessel elements with scalariform or simple perforation plates (section 1.2.1), and tectate columellate pollen (section 1.2.2). Full resolution of relationships at the magnoliid grade based on both morphological and molecular data, and also including fossils, will be necessary to clarify the precise pattern of evolution of these features. Other characteristic angiosperm features, such as broad leaves with reticulate, open venation, or ovules with more than one envelope surrounding the nucellus, also occur in non-angiospermous plants.

1.2.1 Vegetative features

Vascular system. Two principal types of stem vascular system are present in angiosperms. In most dicots the stems have longitudinal strands of primary vascular tissue arranged in a ring around the central pith to form a eustele. This is the basic condition in most seed plants. In most woody seed plants, including most dicots, a cambium, which produces secondary xylem to the inside and secondary phloem to the outside, develops between the primary xylem and the primary phloem and extends between the bundles to form a continuous cylinder producing secondary tissue. However, in herbaceous dicots cambial development is often partially or completely suppressed. In monocots, and in a few dicots, vascular bundles are scattered throughout the stem to form an atactostele. A cambial zone may develop in each bundle early in its development, but all trace of it is usually lost at maturity (Sporne, 1974). Monocots do not produce typical wood (secondary xylem), but in some groups (e.g. many palms) a different form of secondary growth occurs in which a zone of dividing cells (primary thickening meristem) develops in the parenchyma tissue beneath the apical meristem. In other monocots, a zone of dividing cells forms a thickening ring that produces new parenchyma as well as secondary

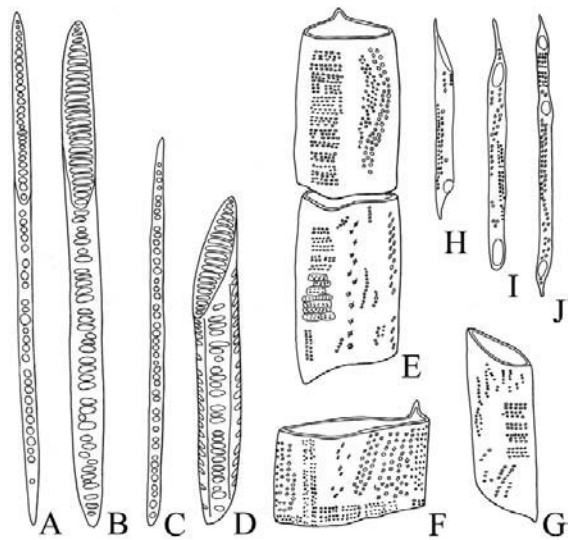


Figure 1.6 Tracheids and vessels of angiosperms. (A, B) Tracheids from a vessel-less angiosperm showing circular pits (A) and scalariform pits (B). (C) Tracheid from a vessel-bearing angiosperm showing circular pits. (D) Vessel element with scalariform perforation plate. (E–G) Wide vessel elements with simple perforation plates: note two continuous vessel elements in (E). (H–J) Narrow vessel elements with simple perforation plates. (A–D) redrawn from Carlquist (1988); (E–J) redrawn from Esau (1977).

bundles. In the context of seed plants as a whole it is clear that in monocots the capacity to produce typical secondary tissues has been lost, apparently in an irreversible way. The cellular structure of angiosperm vascular tissue is significantly modified compared with that in other seed plants. In the phloem, a unique feature of angiosperms, seen in both dicots and monocots, is that the companion cells accompanying the sieve tubes are typically derived developmentally from the same initial cell as the sieve elements. In the xylem, a characteristic modification seen in almost all angiosperms is the presence of vessels composed of vessel elements (Figure 1.6), which are connected by scalariform or simple perforation plates to form long tubes. In some highly specialised groups (e.g. certain Cactaceae and aquatic plants) secondary loss of vessels has clearly occurred. However, there are also vessel-less taxa among the ANITA grade angiosperms (Amborellaceae) and eumagnoliids (Winteraceae), as well as among the earliest diverging groups of eudicots (Trochodendraceae). In these cases it is more difficult to decide whether the lack of vessels is plesiomorphic or reflects secondary loss. The absence of vessels in

1.2 Characteristic features of angiosperms 7

Amborella is especially interesting given its position as the sister group to all other angiosperms in phylogenetic analyses based on molecular data.

Arguments based on parsimony analyses of basal angiosperms (prior to the recognition of the ANITA grade) suggest that vessels in angiosperms originated only once, and that the vessel-less condition is secondary (Donoghue and Doyle, 1989b). However, based on functional considerations, Carlquist (1996a) argued that vessels originated several times, and there is also the complication that the distinction between tracheids and vessel elements is not always straightforward based on light microscope studies alone (Carlquist and Schneider, 2002). Whichever interpretation is correct, it is clear that vessel elements evolved from tracheids. Vessel elements differ from tracheids in having perforated end walls (perforation plates) and are also generally wider in diameter. Among angiosperms, ontogenetic and phylogenetic studies indicate a broad evolutionary trend from long narrow vessel elements with long oblique scalariform perforation plates to short, broad elements with transverse, simple perforation plates. The changes associated with this general trend occurred repeatedly within many separate lineages (Carlquist, 1996a).

In non-angiosperm seed plants, vessels are known with certainty only in the Gnetales. Vessels in the Gnetales differ from those of angiosperms in having foraminate perforation plates with circular perforations, and thus the phylogenetic significance of this character as a link to angiosperms, where scalariform perforation plates are thought to be basic, is uncertain (Muhammad and Sattler, 1982; Carlquist, 1996b). On the whole, differences in vessel element and tracheid characters support an independent origin of the vessels in the two groups. In particular, vessels of Gnetales often have pits with a thick central torus, suspended by margo strands; a feature that is unknown in the angiosperms (Carlquist, 1996b). Vessel-element-like cells have been observed in Permian wood from China of possible gigantopteridalean affinity (Li *et al.*, 1996) and have also been reported from the leaf bundles of a bennettitalean plant (Krassilov, 1984). The significance of these discoveries remains uncertain.

Leaves. Angiosperm leaves show great variety in form, ranging from the minute scale-like leaves of *Casuarina* and the linear leaves of grasses, to the giant peltate floating leaves of *Victoria* (Nymphaeaceae) and the large oblong leaves of *Musa* (Musaceae). Despite this diversity, Hickey (1978) recognised four features typical of most angiosperm leaves: intercalary growth during most of the leaf blade

extension; a hierarchical system of successively thinner veins (usually three or more vein orders); freely ending veinlets; and vein anastomoses between two or more orders of veins to form a reticulate pattern (Figure 1.7). Hickey and Wolfe (1975) also consider stipules as typical of angiosperms although they are not common among monocots.

In monocots the main veins are usually more or less parallel, and the leaf is differentiated into a sheath and a blade. Some monocots (e.g. *Dioscorea*) have distinctly petiolate leaves with an expanded blade and more complex venation. In dicots the main veins are typically arranged in a pinnate or palmate pattern, and the leaf is differentiated into a petiole and a blade. Compound leaves are also common in many groups of dicots. Leaves with reticulate venation, sometimes with freely ending veinlets, occur scattered in non-angiosperm plants, for example in dipteridaceous ferns (Figure 1.8) and the enigmatic Palaeozoic Gigantopteridales (Figure 1.9), but outside angiosperms, among living seed plants, broad, petiolate leaves with several discrete orders of venation, freely ending veinlets, and a reticulate pattern of venation occur only in Gnetales (*Gnetum*, Figure 1.9).

Stomatal anatomy can be used to distinguish different groups among seed plants. Within angiosperms two main stomatal types, as well as more complex variations, have been recognised (Fryns-Claessens and Van Cotthem, 1973). The most common developmental pattern is the mesogenous, or syndetocheilic, type, in which guard cells and their adjacent cells are formed from the same epidermal initial cell. Cells adjacent to the guard cells may be undifferentiated, but typically they are readily distinguished from the surrounding epidermal cells as two subsidiary cells that are parallel to the guard cells. The perigenous, or haplocheilic, pattern of stomatal development consists of guard cells and adjacent cells (undifferentiated or differentiated into subsidiary cells) that are formed from different epidermal initials. This developmental pattern is widely distributed among monocots (Tomlinson, 1974).

Among non-angiosperm seed plants, mesogenous stomata (inferred from the arrangement of the subsidiary cells parallel to the guard cells: paracytic) are known in extant Gnetales (*Gnetum*, *Welwitschia*), and also in the extinct Bennettitales and Erdtmanithecales. This is one of the features that has been used to define the angiosperm clade (Chapter 5). Stomatal characters have not contributed substantially to establishing large-scale phylogenetic patterns among angiosperms, but have proved useful in systematically more restricted studies (e.g. Baranova, 1972).

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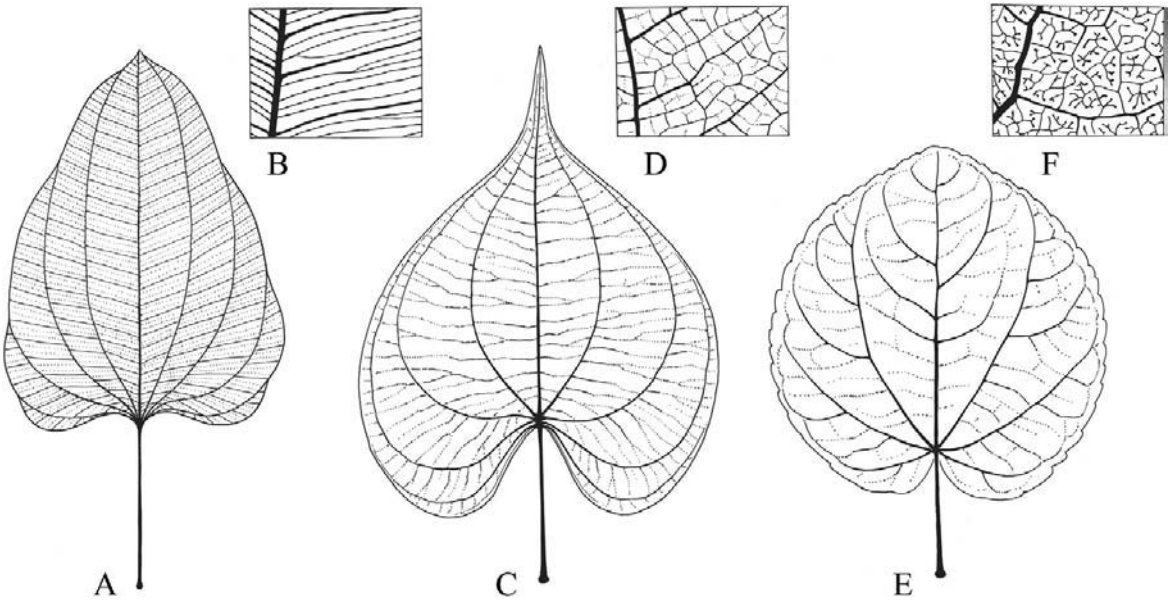


Figure 1.7 Leaves in angiosperms. (A, B) Leaf (A) and detail of venation (B) in *Stemona cochinchinensis* (Stemonaceae, monocot). (C, D) Leaf (C) and detail of venation (D) in *Dioscorea hemsleyi*

(Dioscoreaceae, monocot). (E, F) Leaf (E) and detail of venation (F) in *Cercidiphyllum japonicum* (Cercidiphyllaceae, eudicot). Based on herbarium specimens in the Swedish Museum of Natural History.

Stomatal details have also been widely used in studies of fossil angiosperm leaves, especially in comparing fossil leaves with those of living plants (e.g. Dilcher, 1974).

1.2.2 Reproductive features

Angiospermy. Most of the unique defining characters of angiosperms are related to their characteristic and complex reproductive system. The most important feature, which has also given its name to the group, is angiospermy: the enclosure of the ovules in carpels. Endress and Igersheim (2000a) showed that in many angiosperms at the ANITA grade, which now appear to be the earliest diverging lineages in the group, carpal closure is achieved solely by secretion and not by postgenital fusion of the carpal wall itself. They also showed that a combination of secretion and postgenital fusion in the closure of the carpels is common among other early diverging angiosperm lineages.

Endress and Igersheim (2000a) recognise four different types of angiospermy among magnoliids (Figure 1.10): Type 1 carpal closure formed by secretion only, without any postgenital fusion of the carpal wall, as seen in Amborellaceae, some Nymphaeales (e.g. *Cabomba*, *Brasenia*), Trimeniaceae,

Schisandraceae and Austrobaileyaceae at the ANITA grade and also in Chloranthaceae; Type 2 carpal closure formed partly by secretion in the centre and partly by postgenital fusion in the periphery leaving a completely unfused canal up to the stigma, as seen in Schisandraceae, Annonaceae, Myristicaceae and Canellaceae; Type 3 carpal closure formed by postgenital fusion over the entire periphery of the carpal wall with secretion in an inner unfused canal that ends below the stigma, as in many Magnoliaceae; and Type 4 carpal closure by complete postgenital fusion of the carpal combined with a pollen-tube-transmitting tissue, as seen for example in Degeneriaceae, Laurales, and some Winteraceae among magnoliids, as well as in most monocots and eudicots.

The closed carpal protects the developing ovules and in most cases also protects the seeds during their development. Enclosure also excludes the pollen grains from direct contact with the ovule. Instead of germinating inside the micropyle, which is typical of non-angiosperm seed plants, pollen grains germinate on a specialised portion of the carpal: the stigma (Figure 1.11). Pollen tubes then grow from the stigma through the pollen-transmitting tract of the carpal and into the embryo sac within the ovule, where the male gametes are released. Growth of the pollen tube through the sporophytic carpellary

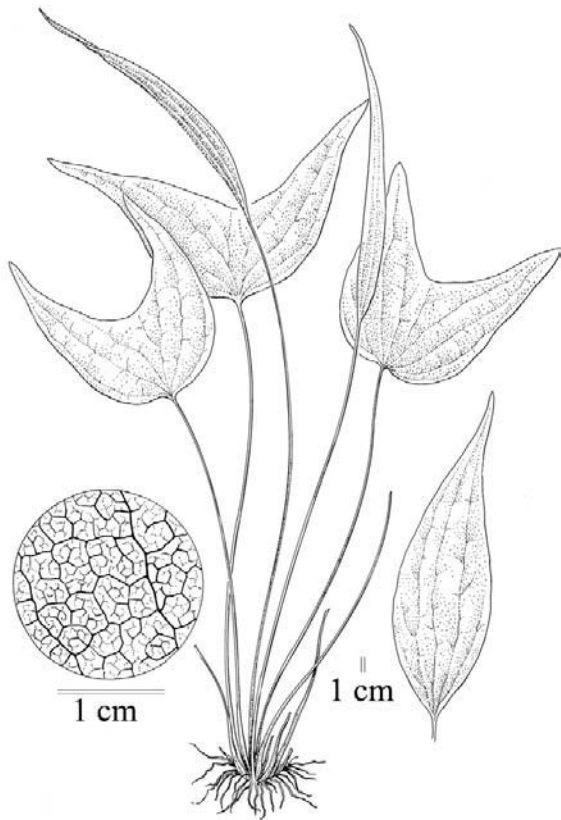


Figure 1.8 *Cheiropleuria bicuspis*, an extant fern (Dipteridaceae) with reticulate venation and freely ending veinlets. Based on herbarium specimens in the Swedish Museum of Natural History.

tissue, or through a secretion from this sporophytic tissue, creates the possibility for sophisticated interactions between gametophytes and sporophytes, and in some cases the growth of pollen with a particular genetic profile (e.g. pollen from the parent plant) may be blocked. Such mechanisms can help to ensure outbreeding, and to the extent that this generates additional variability or facilitates reproductive isolation it may be an important factor in the evolutionary success of angiosperms (Heslop-Harrison, 1983). Male gametophyte competition, expressed by differences in growth rates among the pollen tubes, may also be another advantageous trait made possible by the closed carpel (Mulcahy, 1979). The formation of syncarpous ovaries with a common stigmatic area from which pollen tubes may access ovules in different carpels may further enhance pollen competition (Endress, 1982).

Flowers. The angiosperm flower is formed by female organs (carpels) and male organs (stamens) that are often surrounded by a perianth (Figures 1.12, 1.13). The perianth may be undifferentiated, consisting of parts that are all of one kind (tepals), or it may be differentiated into an outer zone of sepals forming the calyx, and an inner zone of petals forming the corolla. Most angiosperm flowers are bisexual (hermaphroditic) with both carpels and stamens in the same flower. However, unisexual flowers, in which the stamens and carpels are separated into staminate and pistillate flowers, occur in many different angiosperm lineages. In bisexual flowers the stamens always occur below or around the carpels. *Lacandonia* (Triuridaceae) is exceptional in that this pattern is apparently reversed, with stamens occurring in the centre of the flower and surrounded by carpels (but see also Rudall and Bateman, 2010).

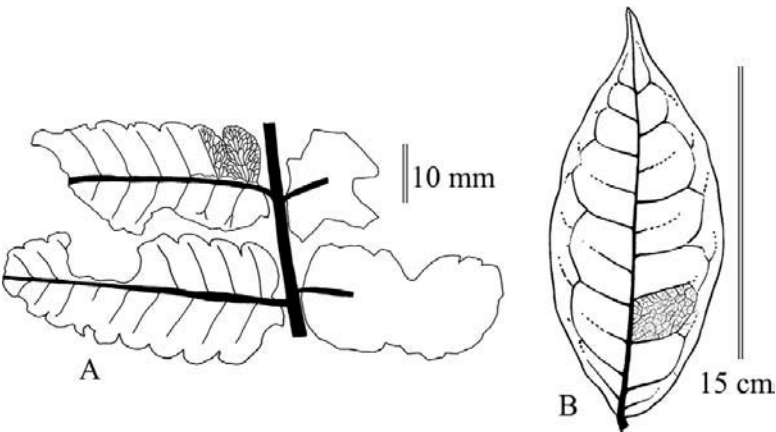


Figure 1.9 (A) Leaf of *Gigantonoclea lagrelii* (Gigantopteridales), a Palaeozoic plant (probable seed plant) with reticulate venation. (B) Leaf of extant *Gnetum gnemon* (Gnetales) with reticulate venation and freely ending veinlets. (A) redrawn from Glasspool *et al.* (2004); (B) based on herbarium specimens in the Swedish Museum of Natural History.

10 Introduction to angiosperms

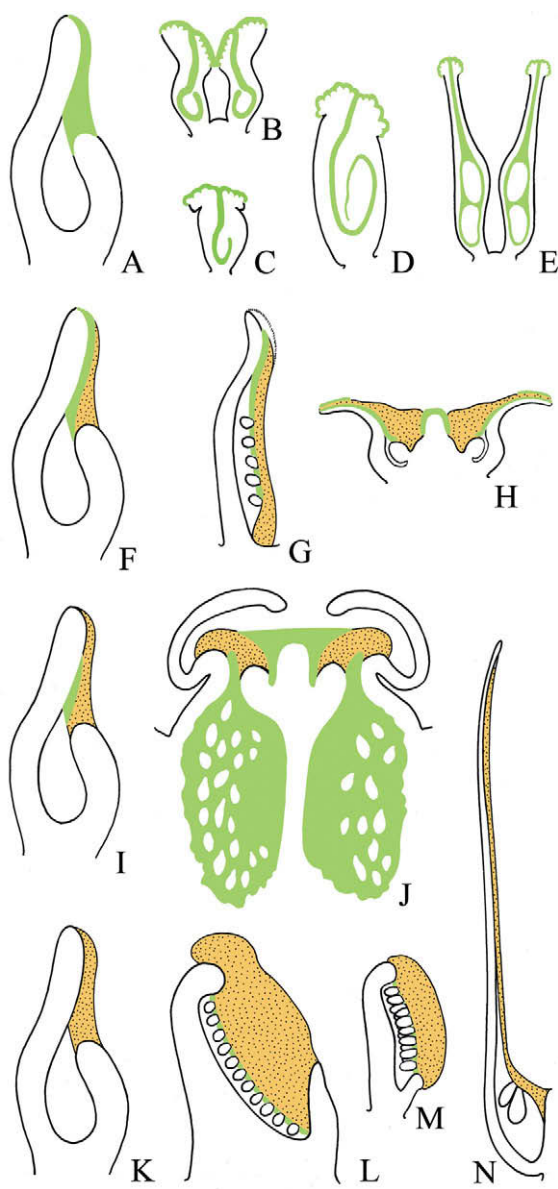


Figure 1.10 The four main types of angiospermy (carpel closure) among magnoliid angiosperms, illustrated in median longitudinal section. (A–E) Angiospermy type 1 closure formed by secretion; schematic section (A) with ovules omitted; *Amborella*, Amborellaceae (B); *Chloranthus*, Chloranthaceae (C); *Trimenia*, Trimeniaceae (D); *Cabomba*, Nymphaeaceae (E). (F–H) Angiospermy type 2 closure formed partly by secretion in a continuous internal canal and partly by postgenital fusion in the periphery; schematic section (F) with ovules omitted; *Asimina*, Annonaceae (G); *Illicium*, Schisandraceae (H). (I, J) Angiospermy

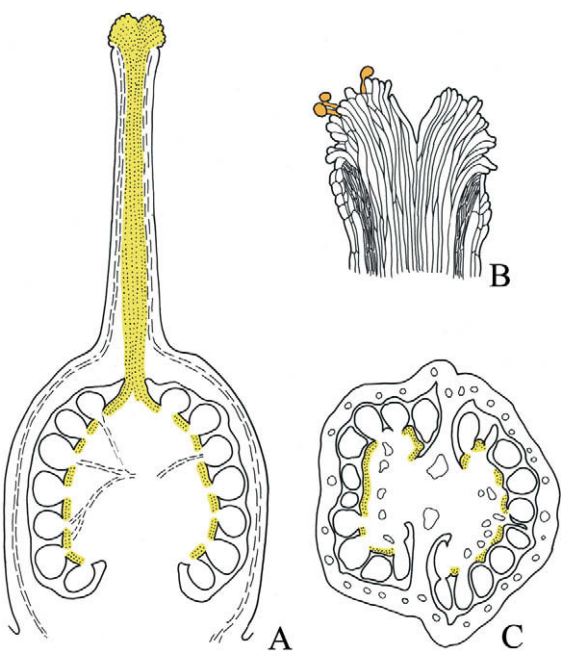


Figure 1.11 Pollen–carpel interactions in angiosperms (*Lycopersicon esculentum*, Solanaceae). (A) Longitudinal section of ovary showing location of pollen-tube-transmitting tissue (yellow stippling) through which the pollen tubes grow *en route* to the ovules. (B) Longitudinal section of apical part of style showing pollen grains on the stigmatic surface, where they germinate and each produces a single pollen tube; pollen grain and pollen tube shown in orange. (C) Transverse section of ovary with two locules, showing location of pollen-tube-transmitting tissue (yellow stippling) adjacent to the locules in which the ovules occur. Redrawn from Endress (1994b).

type 3 closure formed by a combination of types 1 and 2 with fusion in the periphery of the carpel wall and secretion in the inner parts, but without a continuous canal; schematic section (I) with ovules omitted; *Nymphaea*, Nymphaeaceae (J). (K–N) Angiospermy type 4 closure formed entirely by postgenital fusion; schematic section (K) with ovules omitted; *Degeneria*, Degeneriaceae (L); *Tasmannia*, Winteraceae (M); *Liriodendron*, Magnoliaceae (N). Green areas show secretion; orange areas show postgenital fusion. Based on Endress and Igersheim (2000a).