Chapter 9

Phylogeny of Angiosperms

Angiosperms form the most dominant group of plants with at least 253,300 species (Thorne, 2007), a number much greater than all other groups of plants combined together. Not only in numbers, angiosperms are also found in a far greater range of habitats than any other group of land plants. The phylogeny of angiosperms has, however, been a much-debated subject, largely because of very poor records of the earliest angiosperms. These earliest angiosperms probably lived in habitats that were not best suited for fossilization. Before trying to evaluate the phylogeny, it would be useful to have an understanding of the major terms and concepts concerning phylogeny in general, and with respect to angiosperms in particular.

ORIGIN OF ANGIOSPERMS

The origin and early evolution of angiosperms are enigmas that have intrigued botanists for well over a century. They constituted an '**abominable mystery**' to Darwin. The mystery is slowly being 'sleuthed' and at the present pace of Sherlock Holms' research, it may be no more mysterious within the next two decades than for any other major group. With the exception of conifer forest and moss-lichen tundra, angiosperms dominate all major terrestrial vegetation zones, account for the majority of primary production on land, and exhibit bewildering morphological diversity. Unfortunately, much less is known about the origin and early evolution of angiosperms, resulting in a number of different views regarding their ancestors, the earliest forms and course of evolution. The origin of angiosperms may be conveniently discussed under the following considerations.

What are Angiosperms?

Angiosperms form a distinct group of seed plants sharing a unique combination of characters. These important characters include carpels enclosing the ovules, pollen grains germinating on the stigma, sieve tubes with companion cells, double fertilization resulting in triploid endosperm, and highly reduced male and female gametophytes. The angiosperms also have vessels. The pollen grains of angiosperms are also unique in having non-laminate endexine and ectexine differentiated into a foot-layer, columellar layer and tectum (tectum absent in Amborellaceae). The angiosperm flower typically is a hermaphrodite structure with carpels surrounded by stamens and the latter by petals and sepals, since insect pollination prevails. Arbuscular mycorrhizae are

Table 9.1 Geological time scale.

Time	Era	Period	Epoch	Stage
m years (mya)				
0.01	Cenozoic	Quaternary	Holocene	
2.5			Pleistocene	
7		Tertiary	Pliocene	
26			Miocene	
38			Oligocene	
54			Eocene	
65			Palaeocene	
74	Mesozoic	Cretaceous	Upper	Maestrichtian
83				Campanian
87				Santonian
89				Coniacian
90				Turonian
97				Cenomanian
112			Lower	Albian
125				Aptian
132				Barremian
135				Hauterivian
141				Valanginian
146				Berriasian
		Jurassic	Upper	
			Middle	
208			Lower	
		Triassic	Upper	
			Middle	
235			Lower	
280	Palaeozoic	Permian		
345		Carboniferous		
395		Devonian		
430		Silurian		
500		Ordovician		
570		Cambrian		
2400	Precambrian	Algonkian		
4500		Archaean		

also unique to angiosperms (except Amborellaceae, Nymphaeales and Austrobaileyales). The vessel elements of angiosperms typically possess scalariform perforations.

There may be individual exceptions to most of these characters. Vessels are absent in some angiosperms (Winteraceae) while some gymnosperms have vessels (Gnetales). The flowers are unisexual without perianth in several Amentiferae, which also exhibit anemophily. In spite of these and other exceptions, this combination of characters is unique to angiosperms and not found in any other group of seed plants.

What is the age of Angiosperms?

The time of origin of angiosperms is a matter of considerable debate. For many years, the earliest well-documented angiosperm fossil was considered to be the form-genus *Clavitopollenites* described (Couper, 1958) from Barremian and Aptian strata of Early Cretaceous (Table 9.1) of southern England (132 to 112 mya-million years), a monosulcate pollen with distinctly sculptured exine, resembling the pollen of the extant genus *Ascarina*. Brenner and Bickoff (1992) recorded similar but inaperturate pollen grains from the Valanginian (ca 135 mya) of the Helez formation of Israel, now considered to be the oldest record of angiosperm fossils (Taylor and Hickey, 1996). Also found in Late Hauterivian (Brenner, 1996) of Israel (ca 132 mya) were Pre-*Afropollis* (mostly inaperturate, few weakly monosulcate), *Clavitopollenites* (weakly monosulcate to inaperturate), and *Liliacidites* (monosulcate, sexine similar to monocots). From Late Barremian have been recorded *Afropollis* and *Brenneripollis* (both lacking columellae) and *Tricolpites* (the first appearance of tricolpate pollen grains)

The number and diversity of angiosperm fossils increased suddenly and by the end of the Early Cretaceous (ca 100 mya) period major groups of angiosperms, including herbaceous Magnoliidae, Magnoliales, Laurales, Winteroids and Liliopsida were well represented. In Late Cretaceous, at least 50 per cent of the species in the fossil flora were angiosperms. By the end of the Cretaceous, many extant angiosperm families had appeared. They subsequently increased exponentially and constituted the most dominant land flora, continuing up to the present.

The trail in the reverse direction is incomplete and confusing. Many claims of angiosperm records before the Cretaceous were made but largely rejected. Erdtman (1948) described *Eucommiidites* as a tricolpate dicotyledonous pollen grain from the Jurassic. This, however, had bilateral symmetry instead of the radial symmetry of angiosperms (Hughes, 1961) and granular exine with gymnospermous laminated endexine (Doyle et al., 1975). This pollen grain was also discovered in the micropyle of seeds of the female cone of uncertain but clearly gymnospermous affinities (Brenner, 1963). Several other fossil pollens from the Jurassic age attributed to Nymphaeaceae ultimately turned out to be gymnosperms.

In the last few years Sun et al., (1998, 2002) have described fossils of *Archaefructus* from Upper Cretaceous (nearly 124 mya) of China, with clearly defined spirally arranged conduplicate carpels enclosing ovules, a feature not reported in earlier angiosperms. The fruit is a follicle. This is considered to be the oldest record of angiosperm flower.

Several vegetative structures from the Triassic were also attributed to angiosperms. Brown (1956) described *Sanmiguilea* leaves from the Late Triassic of Colorado and suggested affinity with Palmae. A better understanding of the plant was made by Cornet (1986, 1989), who regarded it as a presumed primitive angiosperm with features of monocots and dicots. Although its angiosperm venation was refuted by Hickey and Doyle (1977), Cornet (1989) established its angiosperm venation and associated reproductive structures. Our knowledge of this controversial taxon, however, is far from clear.

Marcouia leaves (earlier described as *Ctenis neuropteroides* by Daugherty, 1941) are recorded from the Upper Triassic of Arizona and New Mexico. Its angiosperm affinities are not clear.

Harris (1932) described *Furcula* from the Upper Triassic of Greenland as bifurcate leaf with dichotomous venation. Although it seems to approach dicots in venation and cuticular structure, it has several non-angiospermous characters including bifurcating midrib and blade, higher vein orders with relatively acute angles of origin (Hickey and Doyle, 1977).

Cornet (1993) has described *Pannaulika*, a dicot-like leaf form from Late Triassic from the Virginia-North Carolina border. It was considered to be a three-lobed palmately veined leaf. The associated reproductive structures were attributed to angiosperms but it is not certain that any of the reproductive structures were produced by the plant that bore *Pannaulika*. Taylor and Hickey (1996), however, do not accept its angiosperm affinities, largely on the basis of the venation pattern, which resembles more that of ferns. Much more information is needed before the Triassic record of angiosperms can be established.

Cornet (1996) described *Welwitschia* like fossil as *Archaestrobilus cupulanthus* from the Late Triassic of Texas. The plant had similarly constructed male and female spikes, each possessing hundreds of spirally arranged macrocupules. The fossil has revived renewed interest in gnetopsids.

Given the inconclusive pre-Cretaceous record of angiosperms, it is largely believed that angiosperms arose in the Late Jurassic or very Early Cretaceous (Taylor, 1981) nearly 130 to 135 mya ago (Jones and Luchsinger, 1986).

Melville (1983), who strongly advocated his gonophyll theory, believed that angiosperms arose nearly 240 mya ago in the Permian and took nearly 140 mya before they spread widely in Cretaceous. The Glossopteridae which gave rise to angiosperms met with a disaster in the Triassic and disappeared, this disaster slowing down the progress of angiosperms slow until the Cretaceous when their curve entered an exponential phase. This idea has, however, found little favour.

There has been increasing realization in recent years (Troitsky et al., 1991; Doyle and Donoghue, 1993; and Crane et al., 1995) to distinguish two dates—one in the Triassic when the **stem angiosperms** ('angiophytes' sensu Doyle and Donoghue, 1993 or 'proangiosperms' sensu Troitsky et al., 1991) separated from sister groups (Gnetales, Bennettitales and Pentoxylales) and the second in the Late Jurassic when the crown group of angiosperms (crown angiophytes) split into extant subgroups (Figure 9.1).

Molecular Dating

There have been a number of attempts to estimate the time of divergence of angiosperms (node B in Figure 9.1) by applying a molecular clock to nucleotide sequence data. The results mostly pointing to much earlier origin of angiosperms have, however, been contradictory. The first detailed attempt was made by Martin et al., (1989) using nine angiosperm sequences from *gapC*, the nuclear gene encoding GADPH (cytosolic glyceraldehydes-3-phosphate dehydrogenase). The observed number of nonsynonymous substitutions between each pair of species (K_a) was compared to estimated rates of K_a (substitutions per site per year) inferred from known divergence times (e.g. plants-animals, plants-yeast, mammal-chicken, human-rat). The results implied separation of monocots and dicots at 319 + 35 mya, a dicot radiation at 276 + 33 mya, and cereal grass divergence at 103 + 22 mya. The results were questioned by several authors, since the study used a single gene. Wolfe et al., (1989) attempted to date the monocot-dicot split using a large number of genes in chloroplast genome and using a three-tiered approach. They suggested Late Triassic (200 mya) as the likely estimate of monocot-dicot split. Martin et al., (1993) provided new data to support Carboniferous origin (~300 Mya) of angiosperms. They used both *rbcL* and *gapC* sequences for this study. Sytsma and Baum (1996) conclude that the results strongly caution using the molecular clock for dating unless extensive sampling of taxa and genes with quite different molecular evolution is completed. Thus, the resolution of angiosperm phylogeny may have to wait for a more complete molecular data and its proper appraisal.

What is the place of their origin?

It was earlier believed that angiosperms arose in the Arctic region (Seward, 1931), with subsequent southwards migration. Axelrod (1970) suggested that flowering plants evolved in mild uplands (**upland theory**) at low latitudes. Smith (1970) located the general area of South-East Asia, adjacent to Malaysia as the site where angiosperms evolved when Gondwana and Laurasia were undergoing initial fragmentation. Stebbins (1974) suggested that their origin occurred in exposed habitats in areas of seasonal drought. Takhtajan (1966, 1980), who believed in the neotenous origin of angiosperms, suggested that angiosperms arose under environmental stress, probably as a result of adaptation to moderate seasonal draught on rocky mountain slopes in areas with monsoon climate.

Retallack and Dilcher (1981) believed that the earliest angiosperms were probably woody, small-leaved plants occurring in the Rift valley system adjoining Africa and South America. Some of these angiosperms adapted to the coastal environments and became widespread following changing sea levels during the Early Cretaceous.

Although agreeing with the role of environmental stress, many authors in recent years (Hickey and Doyle, 1977; Upchurch and Wolfe, 1987; Hickey and Taylor, 1992) have suggested that early angiosperms lived along stream- and lake-margins (**lowland theory**). Later, they appeared in more stable backswamp and channel sites, and lastly, on river terraces. Taylor and Hickey (1996) suggested that ancestral angiosperms were

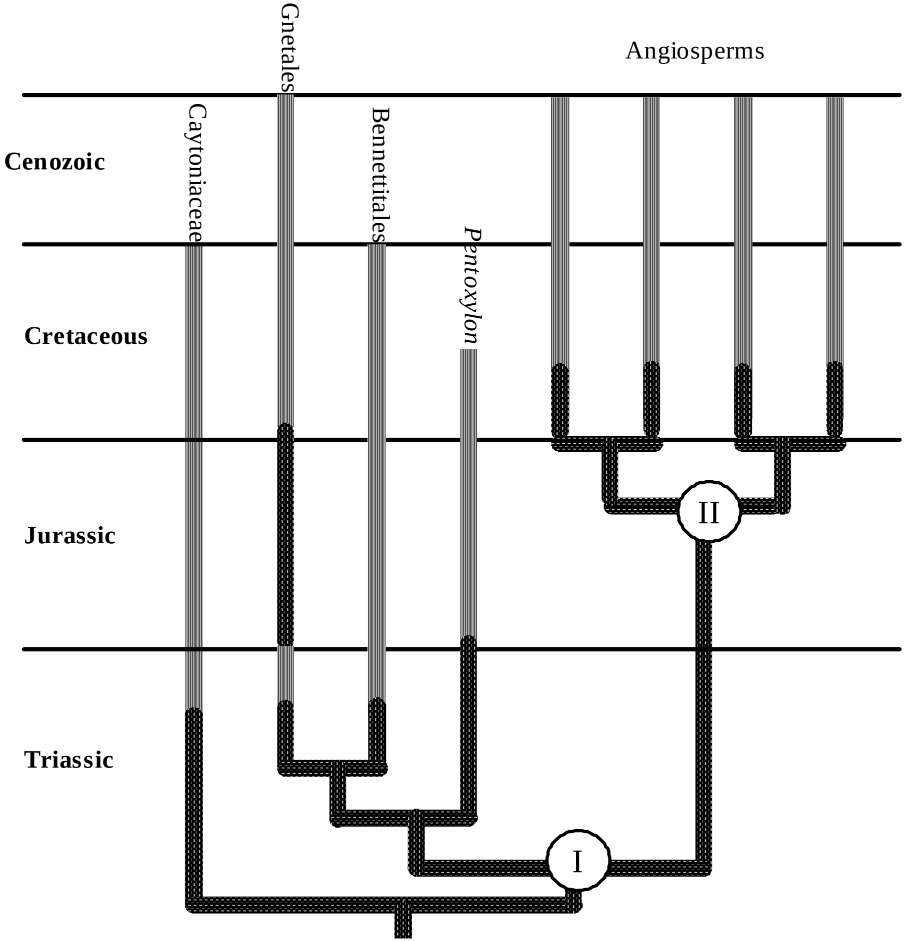

Figure 9.1 Phylogenetic tree of anthophytes (angiosperm lineage and sister groups). Point (I) marks when angiosperm lineage separated from sister groups in the Late Triassic, and (II) marks the splitting of crown angiosperms into extant subgroups in the Late Jurassic. Dotted line represents conclusions for which fossil record is not available (diagram based on Doyle and Donoghue, 1993).

perennial rhizomatous herbs and evolved along rivers and streams on sites of relatively high disturbance with moderate amounts of alluviation. These sites would have been characterized by high nutrient levels and frequent loss of plant cover due to periodic disturbances.

Are Angiosperms monophyletic or polyphyletic?

Engler (1892) considered angiosperms to be polyphyletic, monocotyledons and dicotyledons having evolved separately. Considerable diversity of angiosperms in the Early Cretaceous and the extant angiosperms led several authors, including Meeuse (1963) and Krassilov (1977) to develop models for polyphyletic origin of angiosperms. This view is largely supported by considerable diversity in the early angiosperm fossils.

Most recent authors, including Hutchinson (1959,1973), Cronquist (1981, 1988), Thorne (1983, 1992, 2000, 2007), Dahlgren (1980, 1989), Takhtajan (1987, 1997), Judd et al. (2002, 2008), Bremer et al. (APG II, 2003), and Stevens (APweb, 2008) believe in the monophyletic origin of angiosperms, monocotyledons having evolved from primitive dicotyledons. This view is supported by a unique combination of characters such as closed carpels, sieve tubes, companion cells, four microsporangia, triploid endosperm, 8-nucleate embryo sac and reduced gametophytes. Sporne (1974), on the basis of statistical studies, also concluded that it is highly improbable that such a unique combination of characters could have arisen more than once, independently from gymnosperm ancestors.

It is interesting to note that Melville (1983) considered angiosperms to be monophyletic but the explanation that he offers clubs him with the proponents of polyphyletic origin. He believes that angiosperms arose from several different genera of Glossopteridae. According to him, the species is not always to be considered as the ancestor for determining a monophyletic nature. A species from another species is monophyletic, as is a genus from a genus, a family from a family. The principle, according to him, is that to be monophyletic, a taxon of any rank must be derived solely from another taxon of the same rank. Glossopteridae and Angiospermidae belong to the same rank subclass. Both taxa consist of minor lineages that may be likened to a rope with many strands, a situation called **pachyphyletic**. This explanation, however, conforms to the concept of minimum monophyly and does not satisfy the rule of strict monophyly, which is now, the accepted criterion for monophyly.

What are the possible ancestors?

Ancestry of angiosperms is perhaps one of the most controversial and vigorously debated topics. In the absence of direct fossil evidence, almost all groups of fossil and living gymnosperms have been considered as possible ancestors by one authority or the other. Some authors even suggested the **Isoetes origin** of monocotyledons because the plant has a superficial resemblance with onion, albeit with no trace of seed habit. The various theories have revolved around two basic theories, viz., the **Euanthial theory** and the **Pseudanthial theory** of angiosperm origin. Some other theories projecting herbaceous ancestry for the angiosperms have also recently received attention, making the question of ancestry of angiosperms rather more ambiguous:

Euanthial Theory

Also known as **Anthostrobilus theory,** Euanthial theory was first proposed by Arber and Parkins (1907). According to this theory, the angiosperm flower is interpreted as being derived from an unbranched bisexual strobilus bearing spirally arranged ovulate and pollen organs, similar to the hermaphrodite reproductive structures of some extinct bennettitalean gymnosperms. The carpel is thus regarded as a modified megasporophyll (**phyllosporous** origin of carpel).

The bisexual flower of Magnoliales has been considered to have evolved from such a structure. Also agreeing with this general principle, various authors have tried to identify different gymnosperm groups as possible angiosperm ancestors:

Cycadeoidales (Bennettitales)

The group, now better known as Cycadeoidales, appeared in the Triassic and disappeared in the Cretaceous. Their potential as angiosperm ancestors was largely built upon the studies of Wieland (1906, 1916). Lemesle (1946) considered the group to be ancestral to angiosperms, primarily because of the hermaphrodite nature of *Cycadeoidea*, which had an elongated receptacle with perianth-like bracts, a whorl of pollen-bearing microsporophylls surrounding the ovuliferous region having numerous ovules and interseminal scales packed together. There were, however, signs of abscission at the base of the male structure, which would have shed, exposing the ovular region.

The plant was believed to look like cycads with a short compact trunk and a crown of pinnate compound leaves (Figure 9.2-A). It was earlier suggested that the microsporophylls opened at maturity but the subsequent studies of Crepet (1974) showed that microsporophylls were pinnate, and distal tips of pinnae were fused, the opening of the

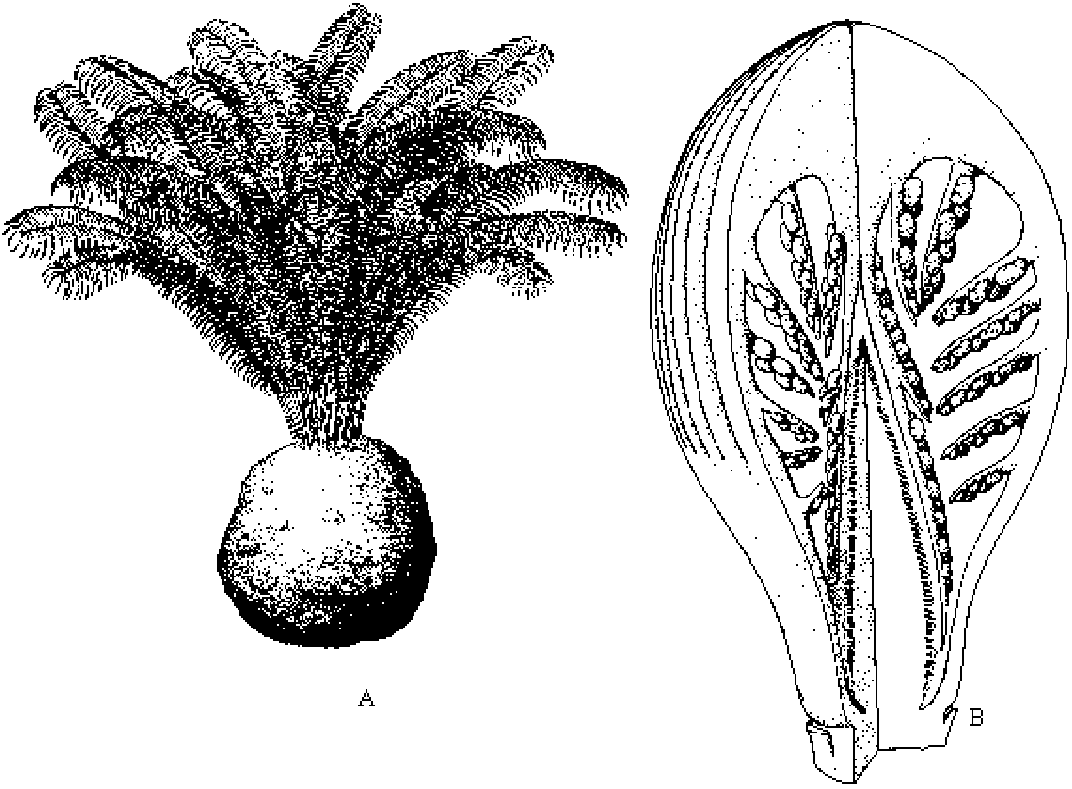

Figure 9.2 *Cycadeoidea.* **A:** Suggested reconstruction of plant with a compact trunk and numerous pinnate leaves. **B:** Suggested reconstruction of the cone cut open to show the arrangement of microsporangia. Ovulate receptacle is in the centre (A, after Delevoryas, 1971; B, after Crepet, 1974).

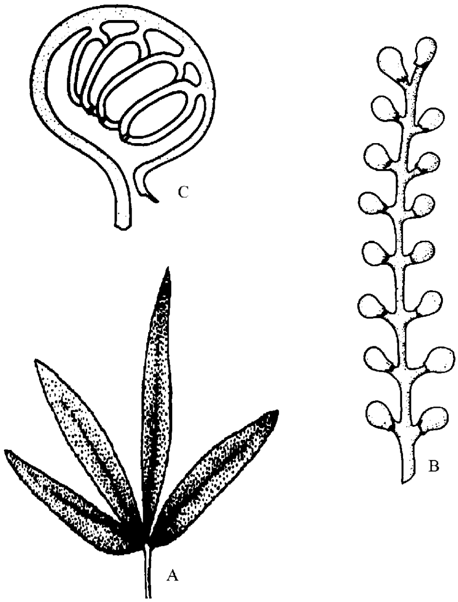

Figure 9.3 Caytoniaceae. **A:** Palmately compound leaf of *Sagenopteris phillipsi.* **B:** *Caytonia nathorstii* with two rows of cupules. **C:** Reconstruction of cupule of *Caytonia sewardii.* (B and C from Dilcher, 1979; C, from Stewart and Rothwell, 1993).

region was not structurally possible, and they later disintegrated internally (Figure 9.2-B). The ovules were terminal in contrast to their position in carpels of angiosperms.

Caytoniaceae

Opinion has strongly inclined in the recent years towards the probability that angiosperms arose from **Pteridosperms** or **seed ferns,** often placed in the order Lyginopteridales but more commonly under Caytoniales. Caytoniaceae was described from the Jurassic of Cayton Bay in Yorkshire by Thomas, and subsequently from Greenland, England and Canada. The group appeared in the Late Triassic and disappeared towards the end of the Cretaceous.

The leaves (*Sagenopteris*) were borne on twigs and not the trunk. These had two pairs of leaflets (rarely 3 to six leaflets) and were net veined. Male structures (*Caytonanthus*) had rachis with branching pinnae, each with a synangium of four microsporangia. The seed-bearing structure (*Caytonia*) had rachis with two rows of stalked cupules (Figure 9.3-B). Each cupule contained several ovules borne in such a way that the cupule is recurved, with a lip like projection (often called stigmatic surface) near the point of attachment (Figure 9.3-C).

The discovery of pollen grains within the ovules was thought to suggest their true gymnosperm position, however, rather than being angiosperm ancestors. Krassilov (1977) and Doyle (1978) regarded the cupule as homologous to the carpel, whereas Gaussen (1946) and Stebbins (1974) considered it the outer integument of the ovule. Cladistic studies of Doyle and Donoghue (1987) support the caytoniales-angiosperm lineage. Thorne (1996) agreed that angiosperms probably evolved during the Late Jurassic from some group of seed ferns.

Cycadales

Sporne (1971) suggested possible links between Cycadales and angiosperms in the palm-like habit of Cycadales, the ovules being borne on leaf-like microsporophylls, trends in the reduction of sporophyll blade as seen in various species of *Cycas*. Although it may be difficult to assume Cycadales as ancestral to angiosperms, the fact that they have been derived from pteridosperms, and yet resemble angiosperms further supports the origin of angiosperms from pteridosperms.

Pseudanthium Theory

Commonly associated with the Englerian School, the theory was first proposed by Wettstein (1907), who postulated that angiosperms were derived from the Gnetopsida, represented by *Ephedra*, *Gnetum* and *Welwitschia* (formerly all placed in the same order Gnetales).

The group shows more angiosperm characteristics than any other group of living or fossil gymnosperms. These include the presence of vessels, reticulate dicot-like leaves

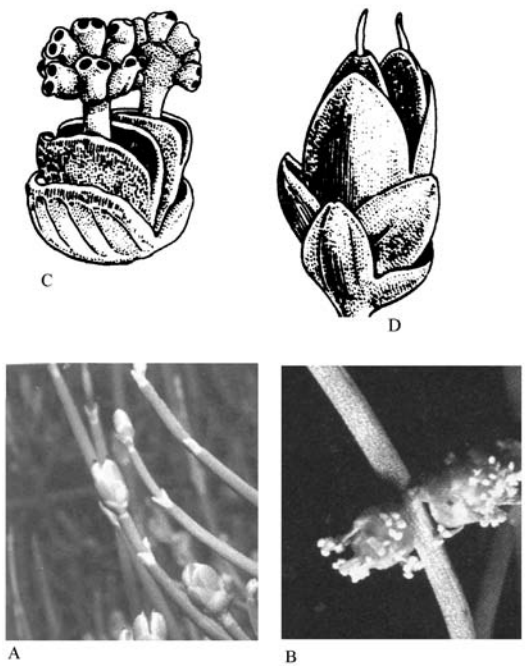

Figure 9.4 *Ephedra.* **A:** A small portion of plant with opposite scale-like leaves. **B:** Male strobili on a branch. **C:** A male strobilus with series of opposite bracts, apical bract subtending male stalk with several microsporangia. **D:** Female strobilus with series of whorled bracts, uppermost closely clasping ovules.

(*Gnetum*), male flower with perianth and bracts, strong gametophyte reduction, and fusion of the second male gametophyte with the ventral canal nucleus. *Ephedra* resembles *Casuarina* in habit. Wettstein homologized the compound strobili of Gnetales with the inflorescences of wind-pollinated Amentiferae, and regarded the showy insect pollinated bisexual flowers of *Magnolia* as **pseudanthia** derived by aggregation of unisexual units, the carpel thus representing a modified branch (**Stachyosporous** origin of carpel).

A number of features, however, refute this theory: different origin of vessels (Bailey, 1944) in angiosperms (from tracheids with scalariform pitting) and Gnetosids (from tracheids with circular pitting), several vesselless living angiosperms (cf. Winteraceae). Amentiferae are now regarded as advanced due to floral reduction. Tricolpate pollen grains also represent an advanced condition. More importantly, Gnetopsida is a very young group.

But this theory has been strongly supported by Young (1981), who challenged the view that first angiosperms were vesselless

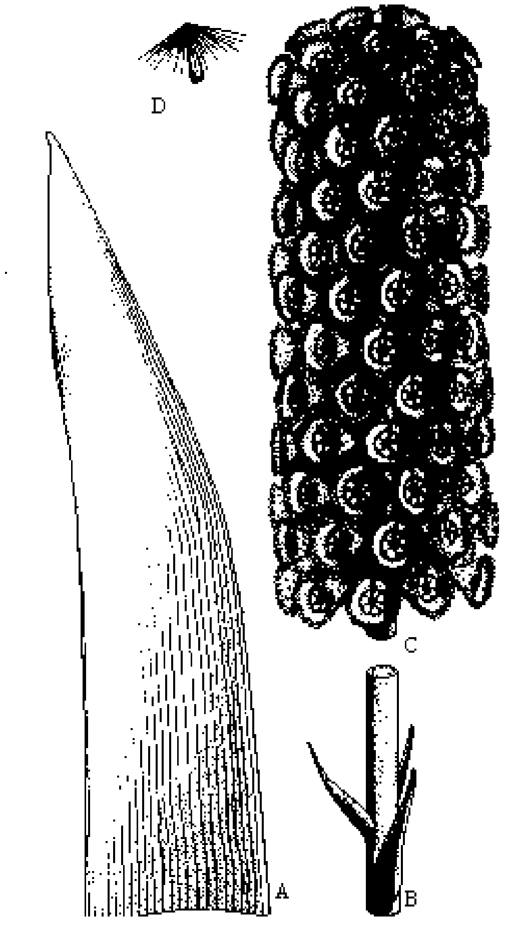

Figure 9.5 Resconstruction of *Archaestrobilus cupulanthus* and isolated organs. **A:** Associated leaf of *Pelourdea poleoensis*. **B:** Associated sterile lower part of strobilus. **C:** Female strobilus with numerous spirally arranged macrocupules. **D:** Dispersed seed. (After Cornet, 1996).

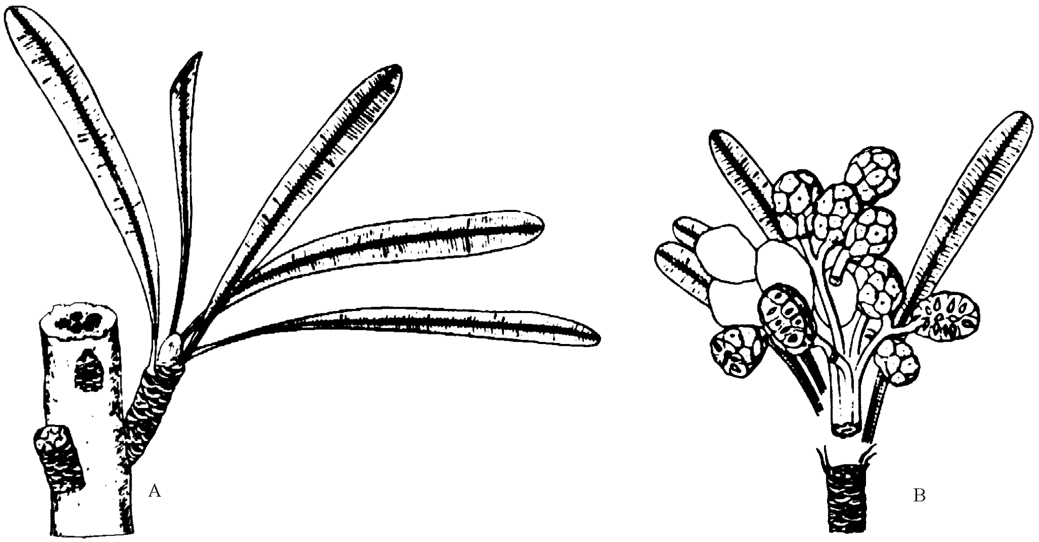

Figure 9.6 Pentoxylales. **A:** Suggested reconstruction of *Pentoxylon sahnii* with strap-shaped leaves. **B:** Suggested reconstruction of seed cones (From Sahni, 1948).

and assumed that vessels were lost in several early lines. Muhammad and Sattler (1982) found scalariform perforations in vessel-elements of *Gnetum*, suggesting that angiosperms may be derived from Gnetales after all. Carlquist (1996), however, concludes that this claim from *Gnetum* does not hold when large samples are examined.

The basal group of angiosperms according to this theory included amentiferous-hamamelid orders Casuarinales, Fagales, Myricales and Juglandales. It is significant to note that Wettstein (1907) also included in this basal group, Chloranthaceae and Piperaceae, which have been inviting considerable attention in recent years.

The importance of Gnetopsids in angiosperm phylogeny has been further strengthened by the discovery of *Welwitschia* like fossil described by Cornet (1996) as *Archaestrobilus cupulanthus* from the Late Triassic of Texas (Figure 9.5). The plant had similarly constructed male and female spikes, each possessing hundreds of spirally arranged macrocupules. Male spikes were borne in clusters of three, whereas female spikes occurred singly. Each female macrocupule had an axially curled (tubular) bract-like organ with a narrow shaft and expanded funnel shaped apex. The macrocupules contained an ovule (or seed) surrounded by sterile scales. Three to four very small bracts were present attached near the base and surrounding the macrocupule.

Each male macrocupule contained filament like appendages instead of sterile scales within. Outside, the macrocupule was crowded with numerous bivalved microsporophylls, each with four pollen sacs attached to an inflated stalk. On the outside of the female macrocupule were present gland-like structures resembling the stalks bearing pollen sacs on the male macrocupule. This suggests an origin from a bisexual macrocupule. The pollen grains are radially symmetrical and monosulcate. The plant is regarded as a gnetophyte more primitive than extant Gnetales.

Ephedra is generally considered to be the most primitive of the three living genera of gnetopsids. Cornet believes that *Archaestrobilus* possessed characters that may be plesiomorphic even for *Ephedra*, such

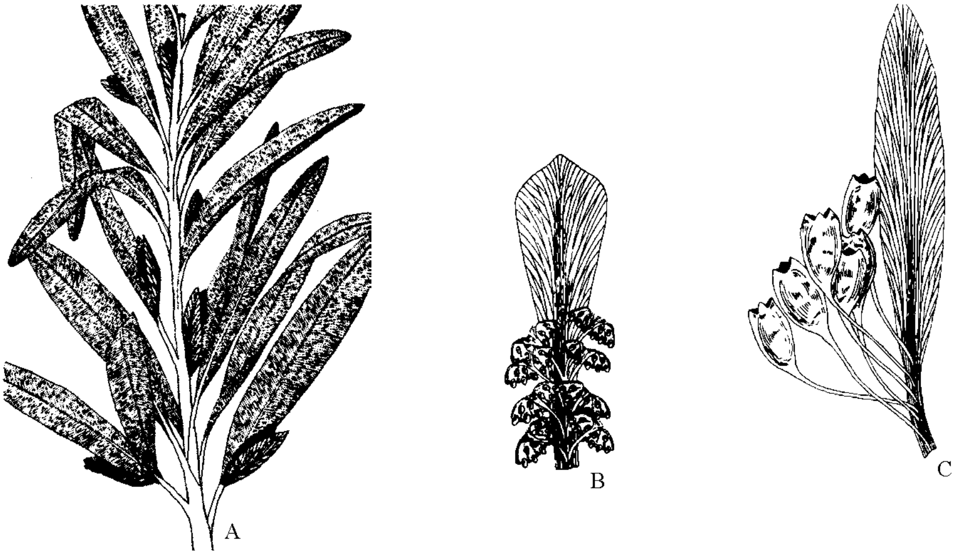

Figure 9.7 Glossopteridae. **A:** *Dictypteridium feistmantelii* (*Glossopteris tenuinervis*) vegetative branch. **B:** Fertile branch (Gonophyll) of *Lidgettonia mucronata* **C:** Fertile branch of *Denkania indica* with cupules. (A: from Chandra and Surange, 1976; B and C from Surange and Chandra, 1975)

as radial symmetry of floral parts which are spirally arranged and not opposite. He believes that Bennettitales, Gnetales, Pentoxylales and angiosperms had a common ancestry sometimes before Late Triassic. Gnetales are relatives of angiosperms and Bennettitales that underwent drastic floral reduction and aggregation in response to wind pollination.

Taylor and Hickey (1996) have presented a hypothesis for the derivation of the flower of Chloranthaceae from the inflorescence unit (anthion) of gnetopsids, with considerable reduction in the reproductive parts.

Anthocorm Theory

This theory is a modified version of the pseudanthial theory and was proposed by Neumayer (1924) and strongly advocated by Meeuse (1963, 1972). According to this theory, the angiosperm flower ('functional reproductive unit') has several separate origins (i.e. angiosperms are polyphyletic). In most Magnoliidae and their dicotyledonous derivatives, they are modified pluriaxial systems (**holanthocorms**) that originated from the gnetopsids via the Piperales, whereas the modification of an originally uniaxial system (**gonoclad** or **anthoid**) gave rise to flowers of Chloranthaceae. Meeuse (1963) postulated a separate origin of monocotyledons from the fossil order Pentoxylales through the monocot order Pandanales.

Pentoxylales (Figure 9.6) were described from the Jurassic of India and New Zealand. The stem (*Pentoxylon*) had five conducting strands. The pollen-bearing organ (*Sahnia*) was pinnate: free above and fused into a cup below. The seed-bearing structure was similar to a mulberry with about 20 sessile seeds, each having an outer fleshy sarcotesta and the inner hard sclerotesta. The sarcotesta was considered homologous to the cupule of seed ferns. The carpel of angiosperms was regarded as a composite structure being an

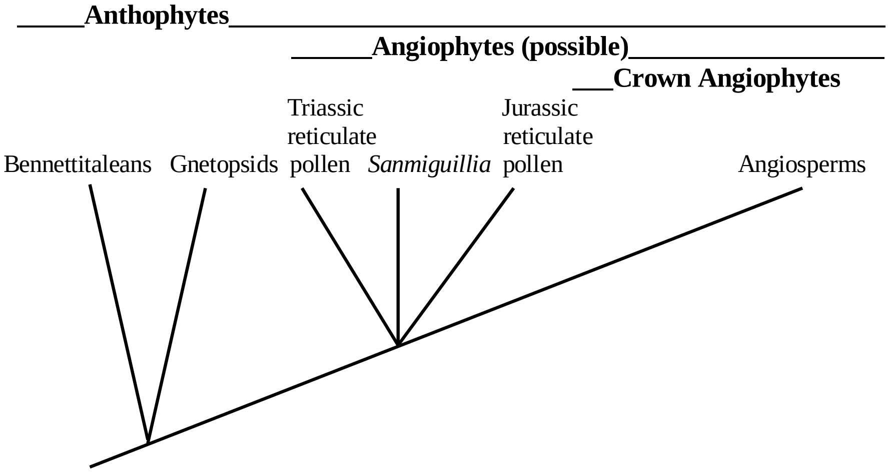

Figure 9.8 A consensus phylogeny of Anthophytes proposed by Taylor and Hickey (1996). Note that *Pentoxylon* has been excluded from sister groups (now only Bennettitaleans and Gnetopsids) of angiophytes.

ovule-bearing branch fused with a supporting bract. It is interesting, however, to note that Taylor and Hickey (1996) no longer include *Pentoxylon* as a member of **Anthophytes**, which include angiosperm lineage and its sister groups Bennettitales and gnetopsids (see Figure 9.12). According to them, *Pentoxylon* lacks key anthophyte characteristics such as distal, medial and proximal positioning of female, male and sterile organs on the reproductive axis, as well as the enclosure of ovules by bract-derived organs.

Gonophyll Theory

The **Gonophyll theory** was developed by Melville, (1962, 1963, 1983) largely on the basis of a study of the venation pattern. He derived angiosperms from Glossopteridae, which formed important elements in the flora of Gondwanaland. He further derived angiosperm flower from **gonophyll,** a fertile branching axis adnate to a leaf. In simple Glossopterids *Scutum* and *Ottokaria,* the fertile branch consisted of a bivalved scale (having two wings) called the **scutella** with terminal ovules on dichotomous groups of branches. Folding of the scutella along the cluster of its ovules forms the angiosperm condition, an indication of this closure being found in the Permian fossil *Breytenia.* In *Lidgettonia,* the fertile branch consists of four to eight disc-like bearing several seeds. In *Denkania,* described from Raniganj , India, about six seed-bearing **cupules** are attached to long stalks borne from the midrib of fertile scale.

The leaves of *Glossopteris* (Figure 9.7) are lanceolate, with distinct reticulate venation. In *Glossopteris,* the fertile region is cone-like with a transition from leaves to fertile scales, spirally arranged and conforming to the **anthostrobilus**. In *Mudgea,* there is a suggestion of **anthofasciculi**, i.e. leafy structures with two fertile branches, one male and the other female, forming the angiosperm flowers as found in *Ranunculus* and *Acacia.*

Melville believed that angiosperms arose 240 mya ago in the Permian and took around 140 mya before they spread widely in the Cretaceous. It is pertinent to point out, as explained earlier, that although he considered

Figure 9.9 Dr D. L. Dilcher palaeobotanist with the Florida Museum of Natural History at the University of Florida, who has pioneered research on Angiosperm fossils with specimen (above left) and reconstruction (above right) of recently described (Sun, Dilcher et al., 2002) *Archaefructus sinensis*, believed to be the oldest angiosperm fossil nearly 124 mya old.

angiosperms to be monophyletic, his justification puts him among the proponents of the polyphyletic origin of angiosperms.

Herbaceous Origin Hypothesis

The herbaceous origin hypothesis resembles the Pseudanthial theory but the ancestral plant is considered to be a perennial rhizomatous herb instead of a tree. The term **paleoherb** was first used by Donoghue and Doyle (1989) for a group of derivative (not ancestral) forms of Magnoliidae having anomocytic stomata, two whorls of perianth and trimerous flowers, including Lactoridaceae Aristolochiaceae, Cabombaceae, Piperales, Nymphaeaceae and monocots.

According to this hypothesis, ancestral angiosperms were small herbaceous plants with a rhizomatous to scrambling perennial habit. They had simple leaves that were reticulately veined and had a primary venation pattern that would have been indifferently pinnate to palmate, whereas the secondary veins branched dichotomously. The vegetative anatomy included sieve-tube elements and elongate tracheary elements with both circular-bordered and scalariform pitting and oblique end walls. The flowers occurred in cymose to racemose inflorescences. The small monosulcate pollen had perforate to reticulate sculpturing. Carpels were free, ascidiate (ovules attached proximally to the closure) with one or two orthotropous, bitegmic, crassinucellate ovule and dicotyledonous embryo. The aforesaid authors cite extreme rarity of fossil angiosperm wood and abundance of leaf impressions in early fossils.

Consensus is emerging from recent phylogenetic studies that gnetopsids represent the closest living relatives of angiosperms, whereas the closest fossil group is the Bennettitales. Angiosperm lineage, together with these two groups, constitutes **Anthophytes**. The group is believed to have split in the Late Triassic, the angiosperm lineage continuing as **Angiophytes** up to the Late Jurassic when it further split into **stem Angiophytes** (the early extinct angiosperms) and **crown Angiophytes** constituting the extant groups of angiosperms (Figure 9.8).

Krassilov, who believed in the polyphyletic origin of angiosperms, identified three Jurassic groups as proangiosperms: Caytoniales, Zcekanowskiales and Dirhopalostachyaceae. Pollen germinating on the lip, according to him, would be rather disappointing because these plants would then be classified as angiosperms and excluded from discussion of their ancestors. He evolved the Laurales-Rosales series from Caytoniales. Zcekanowskiales had bivalved capsules provided with stigmatic bands and showed links with monocots. Dirhopalostachyaceae had paired ovules exposed on shield-like lateral appendages and probably evolved in Hamamelidales.

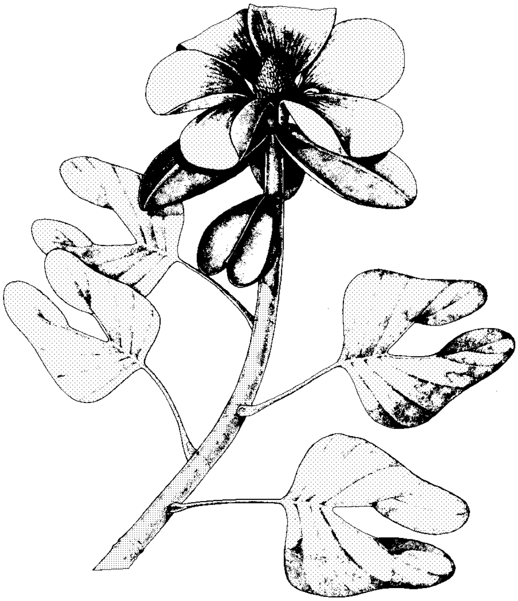

Figure 9.10 Reconstruction of leafy branch with flower of *Archaeanthus linnenbergeri* from middle Cretaceous. (After Dilcher and Crane, 1984.)

Using the oldest, most complete fossil angiosperm on record, David Dilcher (Figure 9.9), a palaeobotanist with the Florida Museum of Natural History at the University of Florida, recently announced the discovery of a new basal angiosperm family of aquatic plant, Archaefructaceae. It was published in the journal *Science* with coauthors Ge Sun of the Research Center of Palaeontology at Jilin University, Qiang Ji of the Geological Institute of the Chinese Academy of Geosciences at Beijing and three others (Sun et al., 2002). The family is based on a single genus *Archaefructus* with two species, *Archaefructus sinensis* and *Archaefructus lianogensis*. These were probably aquatics herbs and living at least 124 mya. *Archaefructus* has perfect flowers rather unlike those of extant angiosperms— there is no perianth, the receptacle is very elongated, and the stamens are paired. The fruits are small follicles formed from conduplicate carpels helically arranged. Adaxial elongate stigmatic crests are conspicuous on each carpel. Earlier to this, Dilcher and Crane (1984) had described *Archaeanthus linnenbergeri* (Figure 9.10) from uppermost Albian/mid-cenomanian (approx 110 mya) of middle Cretaceous as a primitive flowering plant with simple bilobed leaves, terminal flower with numerous free carpels producing follicle fruit.

Archaefructus was about 50 cm high, rooted in the lake bottom and was partially supported by the water. Thin stems reached to the water's surface. Pollen and seed organs extended above the water. The leaves were possibly submerged. Seeds probably dispersed on the water and floated towards the shore where they germinated in shallower areas, he added. This is considered to be the oldest record of an angiosperm flower. It is placed in a distinct family Archaefructaceae, probably sister to all extant angiosperms. According to Stevens (2005), It is unclear as to how it relates to extant angiosperms and its flowers are perhaps better interpreted as inflorescences (Zhou et al. 2003; Ji et al. 2004; Crepet et al. 2004).

Transitional-Combinational Theory

J. Stuessy (2004) published a **transitional-combinational theory** for the origin of angiosperms, initiating renewed interest in angiosperms and also serving to explain several recent divergent viewpoints and findings. The theory suggests that the angiosperms evolved slowly from the seed ferns in the Jurassic. Carpel was the first to develop, followed by the double fertilization and then the development of flower. These three fundamental transitions may have taken more than 100 million years to complete. The theory is proposed in view of the difficulty in finding ancestors for angiosperms, yet also considering their sudden appearance and explosive evolutionary success. The extant angiosperms did not appear until Early Cretaceous when the final combination of all three important angiosperm features occurred, as presented by fossil record. This combination provided the opportunity for explosive evolutionary diversification, especially in response to selection from insect pollinators, as also the accompanying modifications in compatibility and breeding systems. The theory attempts to explain discrepancy between fossil and molecular phylogenetic data, latter suggesting pre-Cretaceous origin of angiosperms when DNA (and protein) sequences showed first changes accompanying carpel evolution, much earlier than final combination of all the three angiosperm features. The theory also suggests that barring extinct seed ferns, from which the carpel arose, other gymnosperms had no direct phylogenetic connections to modern angiosperms.

Stuessy suggests that meaningful morphological cladistic analyses should focus on ties between pteridosperms and angiosperms directly, and not include rest of the gymnosperms. He believes that new biology of pollination and breeding systems that favoured outcrossing and developed angiosperm pollen, took place only after the

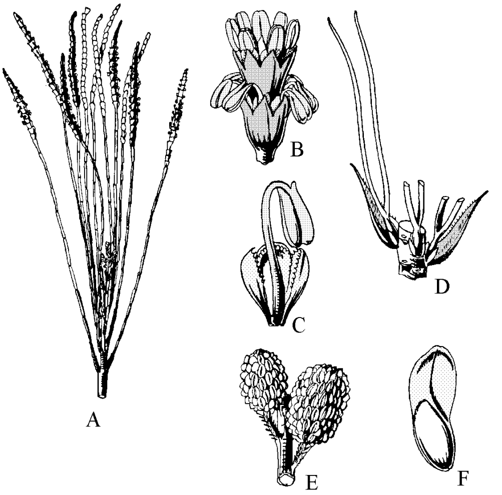

Figure 9.11 Casuarinaceae. *Casuarina suberba.* **A:** Branch with male inflorescences; **B:** Portion of male inflorescence; **C:** Male flower with single stamen; **D:** Part of female inflorescence showing 3 flowers; **E:** Fruits; **F:** Seed with broad wing.

flower had developed, explaining the absence of angiosperm pollen record prior to 130 mya.

Origin of monocotyledons

It was originally believed (Engler, 1892) that monocotyledons arose before dicotyledons and are polyphyletic (Meeuse, 1963). It is now largely believed that monocotyledons evolved from dicots monophyletically. According to Bailey (1944) and Cheadle (1953), vessels had independent origin and specialization in monocots and dicots, and thus monocots arose from vesselless dicots. Cronquist did not agree with the independent origin of vessels in two groups. He considered monocots to have an aquatic origin from ancestors resembling modern Nymphaeales. This was strongly refuted, however, by studies of vessels done by Kosakai, Mosely and Cheadle (1970). They considered it difficult to believe that putatively primitive Alismataceae evolved advanced vessels in an aquatic environment yet gave rise to terrestrial monocots with more primitive vessel elements in the metaxylem of roots. They thus favoured the origin of Alismataceae from terrestrial forms.

According to Hutchinson (1973), monocots arose from Ranales along two lines, one (Ranunculoideae) giving rise to Alismatales and other (Helleboroideae) giving rise to Butomales. Takhtajan (1980, 1987) proposed a common origin for Nymphaeales and Alismatales from a hypothetical terrestrial herbaceous group of Magnoliidae. Dahlgren et al., (1985) believed that monocots appeared in the Early Cretaceous some 110 mya ago when the ancestors of Magnoliiflorae must have already acquired some of the present attributes of that group but were less differentiated; some other dicotyledonous groups had already branched off from the ancestral stock. Thorne (1996) believes that monocotyledons appear to be very early offshoot of the most primitive dicotyledons. In their *rbcL* sequence studies, Chase et al., (1993) and Qiu et al. (1993) found the monocots to be monophyletic and derived from within monosulcate Magnoliidae. *Acorus*, Melanthiaceae, and *Butomus* are regarded to be the least specialized Monocotyledons.

BASAL LIVING ANGIOSPERMS

Angiosperms are now increasingly believed to have evolved in very Late Jurassic or very Early Cretaceous. The course of evolution within the group is being thoroughly examined with newer tools of research.

There was general agreement for nearly a century that the early angiosperms were woody shrubs or small trees (herbaceous habit being derived), with simple evergreen entire and pinnately veined leaves with stipules. Concerning the most primitive living angiosperms, there have been two opposing points of view: **Englerian school** (Considering Amentiferae, particularly Casuarinaceae to be the most primitive dicots) and the **Besseyan school** (Bisexual

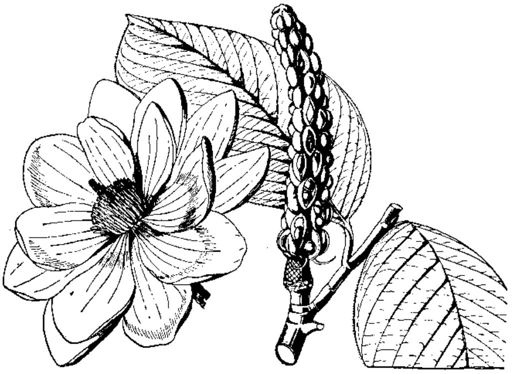

Figure 9.12 Flower and a twig of *Magnolia campbellii* with elongated fruiting axis (reproduced with permission from Oxford University Press).

flowers of Magnoliales to be the most primitive). During the last few years the **paleoherbs** are emerging as the strong contenders. The candidate basal groups are discussed below:

Casuarinaceae

According to the **Englerian School**—the view now largely rejected— Amentiferae with reduced unisexual flowers in catkins (or aments) constitute the most primitive living angiosperms. Engler, as well as Rendle (1892) and Wettstein (1935) considered Casuarinaceae (Figure 9.11) to be the most primitive dicot family, and the one derived from Ephedraceae. It is now agreed that Casuarinaceae and the other members of Amentiferae have advanced tricolpate pollen grains, wood anatomy is relatively advanced and the simplicity of flowers is due to reduction rather than primitiveness. They have also secondarily achieved wind pollination. Other advanced features include trilacunar nodes, cyclic stamens, syncarpous pistil with axile placentation.

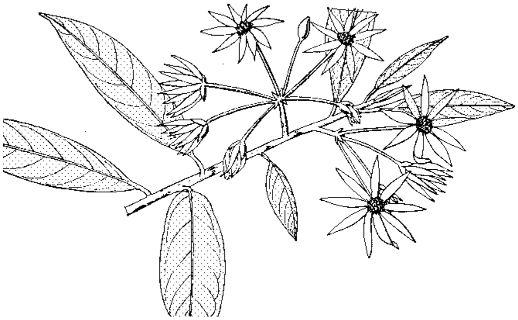

Figure 9.13 Winteraceae Flowering twig of *Drimys winteri*.

Magnoliids

The alternative **Besseyan School** (**Ranalian School**) considers the Ranalian complex (including Magnoliales), having bisexual flowers with free, equal, spirally arranged floral parts, representative of the most primitive angiosperms.

Magnoliaceae

Bessey (1915), Hutchinson (1959, 1973), Takhtajan (1966, 1969) and Cronquist (1968) all believed that large solitary flower of *Magnolia* (Figure 9.12) ('**Magnolia the primitive theory**') with an elongated floral axis bearing numerous spirally arranged stamens and carpels, is the most primitive living representative. The stamens of *Magnolia* and other closely related genera are laminar, perianth undifferentiated, and pollen grains monosulcate and boat-shaped. In the subsequent works, however, Takhtajan agreed that the flower of Magnolia is more advanced than those found in Winteraceae and Degeneriaceae.

Winteraceae

After several decades of *Magnolia* being considered as the most primitive living angiosperm, the view was challenged by Gottsberger (1974) and Thorne (1976), who considered the most primitive flowers to have been middle sized, with fewer stamens and carpels, and grouped in lateral clusters as in the family Winteraceae, to which such primitive genera as *Drimys* (Figure 9.13) have been assigned. This view is supported by the occurrence of similar stamens and carpels, absence of vessels, morphology similar to pteridosperms, high chromosome number suggesting a long evolutionary history, and less specialized beetle pollination of *Drimys* compared to *Magnolia*.

Takhtajan (1980, 1987) later acknowledged that moderate sized flowers of *Degeneria* and Winteraceae are primitive, and the large flowers of *Magnolia* and Nymphaeaceae are of secondary origin. However, he considered Degeneriaceae to be the most primitive family of living angiosperms. Cronquist (1981, 1988) also discarded *Magnolia* while considering Winteraceae to be the most primitive.

Degeneriaceae

Takhtajan, who was earlier a strong supporter of *Magnolia* as the most primitive living angiosperm, has abandoned this view in favour of Degeneriaceae and Winteraceae to be the basal angiosperm families, but has maintained since 1980 to regard Degeneriaceae as the most primitive.

Degeneriaceae (Figure 9.14) may be recognized by their spiral, entire, exstipulate leaves and large, axillary flowers with many tepals and a single carpel. Vessel elements have scalariform perforations. Leaves are spirally arranged and pollen boat-shaped. The most significant plesiomorphic features include stigma running the entire length of the carpel, laminar stamens with three veins, the fruit a follicle and embryo with 3 to 4 cotyledons.

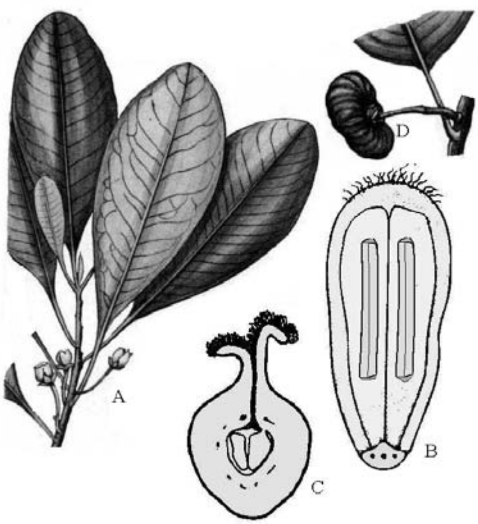

Figure 9.14 Degeneriaceae. *Degeneria vitiensis*. **A:** Branch with flowers; **B:** Stamen; **C:** Transverse section of carpel; **D:** Fruit.

Calycanthaceae

Suggestions have also come projecting Calycanthaceae (Loconte and Stevenson, 1991) as basic angiosperms with a series of vegetative and reproductive angiosperm plesiomorphies such as shrub habit, unilacunar two-trace nodes, vessels with scalariform perforations, sieve-tube elements with starch inclusions, opposite leaves, strobilar flowers, leaf-like bracteopetals, poorly differentiated numerous spirally arranged tepals, and few ovulate carpels. Food bodies terminating the stamen connectives indicate beetle pollination.

The family (Figure 9.15) is regarded as the most basal family of Laurales. It is interesting to note that genus *Idiospermum* (which was recognized as new genus based on *Calycanthus australiensis* by S. T. Blake in 1972) was considered as the most primitive flowering plant by these authors. Endress (1983) had described 'In all respects, *Ideospermum* gives the impression of a strange living fossil'.

Paleoherbs

The last decade of the twentieth century has seen the strong development of an alternative **herbaceous origin hypothesis** for angiosperms (Taylor and Hickey, 1996) originally developed as paleoherb hypothesis. The most primitive angiosperms are considered to be rhizomatous or scrambling perennial herbs with simple net-veined leaves, flowers in racemose or cymose inflorescences,

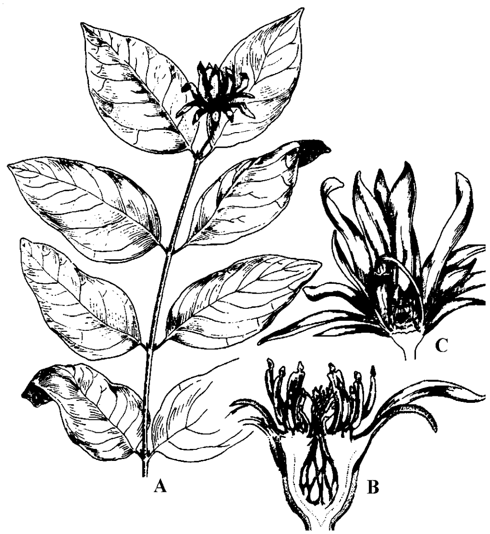

Figure 9.15 Calycanthaceae. *Calycanthus occidentalis.* **A:** Flowering twig with solitary terminal flower. **B:** L. S. of flower showing free carpels. **C:** Flower with some tepals and stamens removed.

with free carpels containing one or two ovules. A number of families are included in the group. Thorne (2000) had placed all of them under Magnoliales, along with Magnoliaceae and Winteraceae. In his later revision (2003), however, placed Amborellaceae and Chloranthaceae (together with Trimeniaceae and Austrobaileyaceae) under Chloranthales, the first order of Magnoliidae (and accordingly angiosperms), the families arranged in that order. Subsequently (2006, 2007) he separated them under distinct subclass Chloranthidae, at the begining of angiosperms. The family Ceratophyllaceae is placed after the monocot families, towards the beginning of Ranunculidae. The placement of Amborellaceae at the beginning of angiosperms is found in the classification schemes of Judd et al. (2003), APG II (2003) and APweb (Stevens, 2003). The position of the other two families is, however, not settled. Judd. et al. and APweb consider both Chloranthaceae (towards the end of basal families before Magnoliid complex) and Ceratophyllaceae (towards the end of Magnoliid complex) as having uncertain position. APG II, like Thorne places Amborellaceae and Chloranthaceae at the beginning of angiosperms (but as unplaced families), whereas family Ceratophyllaceae is placed before Magnoliids.

Chloranthaceae

Taylor and Hickey (1996) consider Chloranthaceae (Figure 9.16) the basic angiosperm family. The family shows several plesiomorphic characters such as flowers in an inflorescence, plants dioecious, carpels solitary, placentation apical, and fruit drupaceous with small seeds. The family is the oldest in the fossil record, the fossil genus *Clavitopollenites* being assigned to Chloranthaceae and closer to the genus *Ascarina*. The stems of *Sarcandra* are primitively vesselless, but Carlquist (1996) has reported vessels in this genus. The family is considered to be earliest to record wind pollination in angiosperms.

The plants are mostly herbaceous, some species being shrubs. The flowers are highly reduced, subtended by a bract and without any perianth, and arranged in decussate

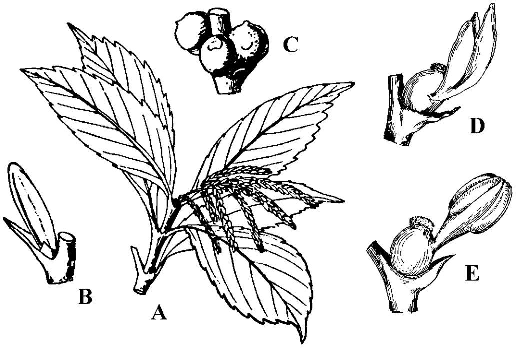

Figure 9.16 Chloranthaceae. **A:** *Ascarina lanceolata*, flowering branch. **B:** A male flower **C:** fruit **D:** Bisexual flower of *Chloranthus henryi* with bract, three stamens and pistil with tufted stigma. **E:** Bisexual flower of *Sarcandra glabra.*

pairs. The flowers are unisexual in *Ascarina*, *Hedyosmum* and *Ascarinopsis* but bisexual in *Chloranthus* and *Sarcandra*. Stamens vary in number from 1 to 5. The carpel lacks style, and single orthotropous ovule is bitegmic.

Taylor and Hickey believe in the origin of Chloranthaceae from gnetopsids, hypothesizing that the ovule and the bract subtending the floral unit in Chloranthaceae are homologous with one of the terminal ovules and proanthophyll subtending the anthion (inflorescence unit) of gnetopsids. Chloranthaceae has undergone considerable reduction in its number of parts as well as general level of elaborateness.

They also believed that the outer integument of the angiosperm bitegmic ovule has ring-like origin and is homologous with the ovular bracts that form the second integument in the gnetopsids.

Ceratophyllaceae

Chase et al., (1993) on the basis of *rbcL* had expressed the view that Ceratophyllaceae represents the basal angiosperm family. The family has fossil record extending back to the Early Cretaceous. Cladistic studies by Sytsma and Baum (1996) based on molecular data support the placement of *Ceratophyllum* (Figure 9.17) at the base of angiosperms, but the authors cautioned that resolution of basal angiosperm relationships may have to await both the collection of additional molecular and morphological data as well as further theoretical advances in phylogenetic systematics. Hickey and Taylor (1996) felt that aquatic plant with highly reduced vegetative body and pollen wall, tenuinucellate, unitegmic ovules is a poor candidate for the basal-most position. Thorne (1996) believed the family is highly specialized and its relationships are highly obscured. Other specialized features include lack of roots, dissected leaves, reduced vasculature and the lack of stomata.

Loconte (1996) carried out cladistic analysis of the above taxa proposed by different authors as most basal angiosperms. He included 69 taxa in the study scoring 151 apomorphic character-states. Parsimony analysis using PAUP resulted in 10 trees at 590 steps. Calycanthaceae appeared as first branch. Magnoliaceae, Winteraceae and Chloranthaceae hypotheses appeared two steps longer, whereas Ceratophyllaceae and Casuarinaceae hypotheses appeared six steps longer.

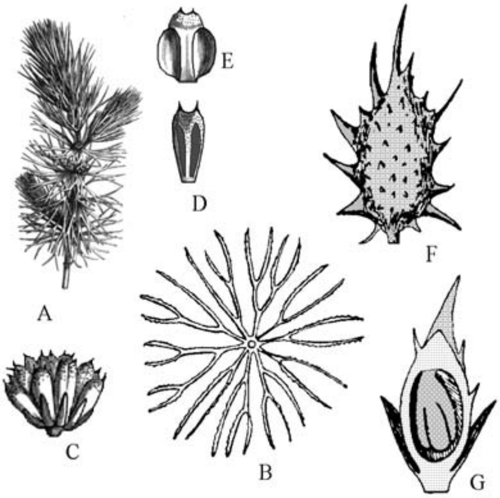

Figure 9.17. Ceratophyllaceae. *Ceratophyllum submersum*. **A:** A portion of plant; **B:** Whorl of leaves at node; **C:** Male flower; **D:** Young stamen; **E:** Dehiscing stamen; **F:** Fruit; **G:** Longitudinal section of fruit with pendulous seed.

Other families that are considered belonging to paleoherbs and share plesiomorphic features include Saururaceae, Piperaceae, Aristolochiaceae, Barclyaceae, Cabombaceae and Nymphaeaceae. They share characters of herbaceous habit, tectate-columellate monosulcate pollen, apocarpous gynoecia, and simple floral units.

Amborellaceae

The family Amborellaceae has attracted considerable interest in the recent years, being unique in angiosperms in lacking pollen tectum and being inaperturate to lacerate. Amborellaceae (Figure 9.18) are

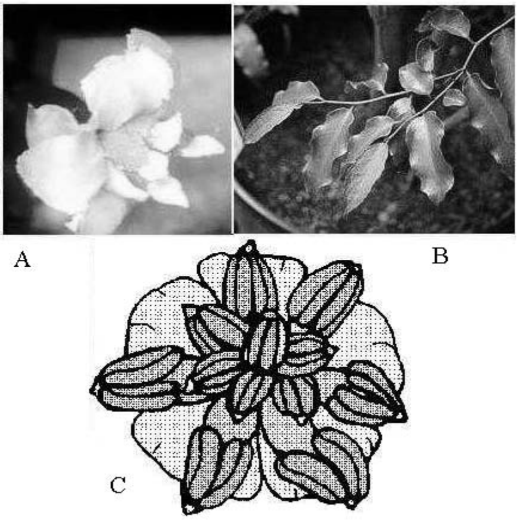

Figure 9.18 Amborellaceae. *Amborella trichopoda*. **A:** Fully opened female flower; **B:** Close up of a branch; **C:** Male flower. (photo B, courtesy University of California, Santa Cruz; A, photo courtesy Missouri Botanical Garden).

shrubs without vessels, with unilacunar nodes, 2-ranked, exstipulate leaves; the margins are both serrate and rather undulate. The plant is dioecious and the flowers are small in cymes, with an undifferentiated perianth of spirally arranged 5-8 tepals. The staminate flowers have 10-25 stamens, sessile anthers and pollen with granulate ektexine. The carpellate flowers have 1-2 staminodes and 5-6 whorled incompletely closed carpels that develop into drupelets with pock-marked stones and pockets of almost resinous substances.

Relationships at the base of the angiosperm lineage are being clarified. Amborellaceae are most likely to be sister to other angiosperms, Nymphaeaceae sister to the rest, then Austrobaileyales.

EVOLUTIONARY TRENDS

Although there has been some recent controversy regarding the habit of the most primitive living angiosperms being woody or herbaceous, the general features of primitive angiosperms are largely settled. They have simple alternate exstipulate leaves, which are entire and petiolate with poorly organized reticulate venation and with unilacunar, two-trace nodes. The vessels are absent or tracheid-like. Flowers are bisexual, radially symmetrical with spirally arranged floral parts. Stamens are broad, undifferentiated with marginal microsporangia. Carpels are broad with large number of ovules, stigma along the margin and not completely sealed, ovules bitegmic, crassinucellate. Fruits are follicular.

Coevolution with Animals

Studies on comparative morphology, pollination biology and biochemistry have clearly elucidated the role of animals in the evolution of angiosperms. It is suggested that Animal kingdom and Plant kingdom, particularly the Angiosperms have undergone a process of co-evolution, wherein the evolution of one has influenced the other. This has proceeded in various ways.

Pollination

Early seed plants, the gymnosperms were wind pollinated with sticky sap exuding from micropyles trapping the pollen. Early insects, the beetles were probably attracted to this sap and pollen by chance. The better pollination and increased seed set encouraged the selection towards showy flowers more attractive to insects, edible flower parts, protein rich pollen, nectaries and bisexual flowers so that same insect visit can both deposit the pollen and pick up for visit to another flower. Increased visits by insects posed danger to the exposed seeds, resulting in selection towards protection of seeds in closed carpel, a major step towards the evolution of angiosperms. Increased protection of seeds encouraged smaller seeds in increased numbers and shorter life cycle to overcome drought conditions. Complete closure of carpel was accompanied by the differentiation of stigmatic region for receiving pollen, and the distinct style to keep the stigma within the reach of insects. To suite to the floral mechanisms the early beetles were slowly replaced by higher insects such as moths, butterflies, bees, wasps and flies, coinciding with the floral diversification of angiosperms.

Beetle pollinated flowers are typically dull or white with fruity odours, edible petals and heavily protected seeds. Bee pollinated flowers are brightly coloured (blue or yellow but not red) with honey guides and with lot of pollen and nectar. Butterfly pollinated flowers are red, blue or yellow. Moth pollinated flowers mostly open at night and have heavy fragrance to attract moths. Moth and Butterfly pollinated flowers generally have long corolla tubes with nectaries at the base. Bird pollinated flowers are bright red or yellow, produce large amount of nectar, with little or no fragrance. Bat pollinated flowers are dull coloured, open at night and have fruity odour.

Biochemical coevolution

Plants and their insect predators are believed to have undergone adaptive radiation in stepwise manner, with the plant groups evolving new and highly effective chemical defenses against herbivores and the latter continually evolving means of overcoming these defenses. Mustard oils of Brassicaceae are toxic for many animals, yet they attract other herbivores such as cabbage worm which uses the mustard oils to locate the cabbage plant for laying its eggs. The chemical hypericin in genus *Hypericum* repels almost all herbivores but the beetle genus *Chrysolina* can detoxify hypericin and use it to locate the plant.

The evolution of new chemical defense of plant has resulted in plants often acquiring the growth hormones found in insect larvae. Proper levels of juvenile hormone in insect larvae are essential for the hatching of insect larvae into normal sexual adults. Several species of plants such as *Ageratum* contain hormone **juvabione**, similar to the juvenile hormone of insects. Such plants if ingested by the insect larvae elevate the level of hormone, resulting in their development into abnormal asexual adults. The larvae as such, learn to avoid such plants.

Some plant products help insects against predators. Monarch butterfly, for example, ingests cardiac glucoside from milkweed *Asclepias.* Such butterflies if ingested by blue jays make latter violently sick. Blue jays learn to recognize the toxic brightly coloured monarch butterflies. The milkweed, thus helps to protect monarch butterfly from blue jay.

Basic evolutionary trends

Evolution within Angiosperms has proceeded along different lines in different groups. Numerous trends in the evolution of angiosperms have been recognized from comparative studies of extant and fossil plants. The general processes involved in attaining diversity of angiosperms are underlined below.

Fusion

During the course of evolution in angiosperms, fusion of different parts has led to floral complexity. Fusion of like parts has led to the development of gamosepaly, gamopetaly, synandry and syncarpy in various families of angiosperms. Stamens have shown fusion to different degrees: fusion of filaments only (monadelphous condition in Malvaceae), fusion of anthers only (syngenesious condition found in Asteraceae) or complete fusion (synandry as in *Cucurbita*). Carpels may similarly be fused only by ovaries (Synovarious: Caryophyllaceae), only by styles (synstylous: Apocynaceae) or complete fusion of both ovaries and styles (Synstylovarious: Solanaceae, Primulaceae). Fusion of unlike parts has resulted in an epipetalous condition (fusion of petals and stamens), formation of gynostegium (the fusion of stamens and gynoecium: Asclepiadaceae) and formation of an inferior ovary (fusion of calyx with ovary: Apiaceae, Myrtaceae, etc.).

Reduction

Relatively simple flowers of many families have primarily been the result of reduction. The loss of either stamens or carpels has resulted in unisexual flowers. The loss of one perianth whorl has resulted in monochlamydeous forms, and their total absence in achlamydeous forms. There has also been individual reduction in the number of perianth parts, number of stamens and carpels. Within the ovary different genera have shown reduction in the number of ovules to ultimately one, as seen in the transformation of follicle into achene within the family Ranunculaceae. There has also been reduction in the size of flowers, manifested in diverse families such as Asteraceae and Poaceae. Reduction in the size of seeds has been extreme in Orchidaceae. Male flower of *Euphorbia* presents a single stamen, there being no perianth or any trace of a pistillode, only a joint indicates the position of thalamus and the demarcation between the pedicel and the filament.

Change in Symmetry

From simple radially symmetrical actinomorphic flowers in primitive flowers developed zygomorphic flowers in various families to suit insect pollination. The size of corolla tube and orientation of corolla lobes changed according to the mouthparts of the pollinating insects, with striking specialization achieved in the turn-pipe mechanism of *Salvia* flowers, and female wasp like flowers of orchid *Ophrys*.

Elaboration

This compensating mechanism has been found in several families. In Asteraceae and Poaceae, the reduction in the size of flowers has been compensated by an increase in the number of flowers in the inflorescence. Similarly, reduction in the number of ovules has been accompanied by an increase in the size of ovule and ultimately seed, as seen in *Juglans* and *Aesculus*.

Remoration

The term was suggested by Melville (1983) to refer to evolutionary retrogression found in angiosperms and their fossil relatives. The fertile shoots of angiosperms, according to him, show venation pattern changes progressively from vegetative leaves through successive older evolutionary stages in bracts and sepals, and the most ancient in petals. The innermost parts in a bud as such represent the most primitive evolutionary condition, and the outermost the most recent condition.

There has been some shift in the understanding of angiosperm phylogeny to support the stachyosporous origin of angiosperm carpel (Taylor and Kirchner, 1996). With the acceptance of such a viewpoint, the reproductive axis with many flowers, few carpels per flower and few ovules per carpel are ancestral. Evolution proceeded along two directions from this: one with few flowers, each of which had many carpels and few ovules and the other with few flowers, each containing few carpels and many ovules. The evolutionary trends in angiosperms are thus often complicated and frequent reversal of trends may be encountered, as for example the secondary loss of vessels in some members.

Xylem evolution

Xylem tissue of angiosperms largely consists of dead tracheids and vessels, supporting fibers and living ray cells. Tracheids are elongate, imperforate water conducting cells found in almost all lower vascular plants, gymnosperms and angiosperms. Vessels are perforate elements largely restricted to angiosperms, although also found in extant gnetopsids, some species of *Equisetum*, *Selaginella*, *Marsilea* and *Pteridium*. The presence of vessels in gnetopsids, the closest relatives of angiosperms, had given rise to the speculation that the latter arose from former. The studies of Bailey and associates, however, showed that the vessels in the two groups arose independently. In gnetopsids,

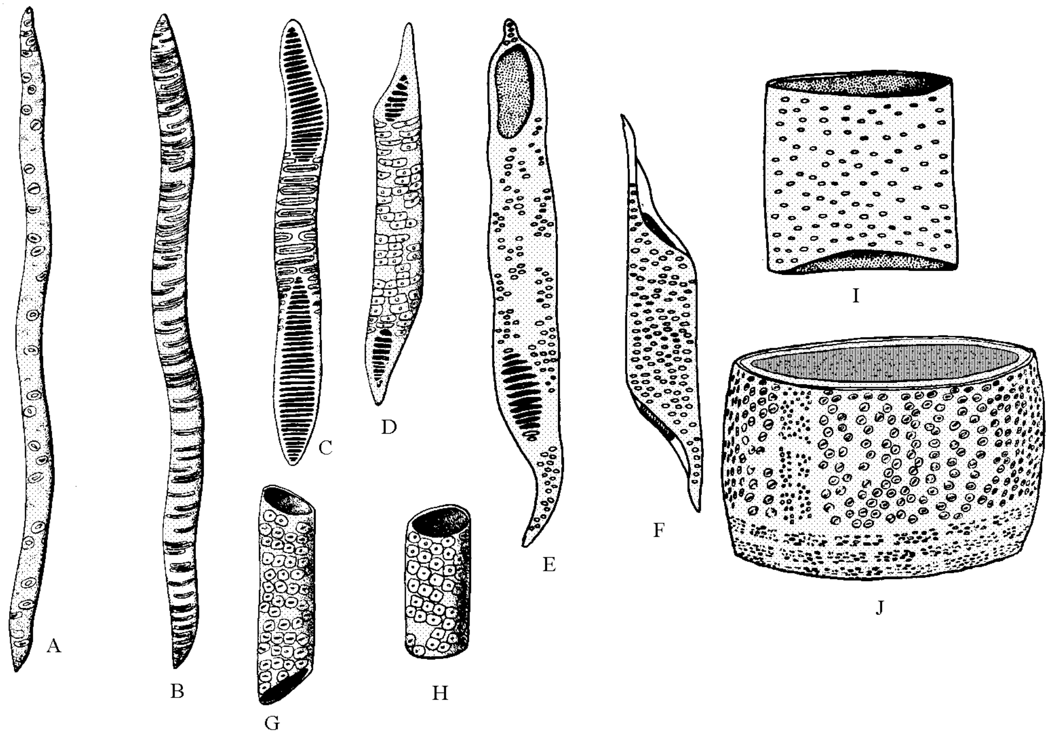

Figure 9.19 Presumed evolutionary transformation of gymnosperm tracheid with circular pitting (**A**) to angiosperm tracheid with scalariform pitting (**B**), further to vessel-element with oblique perforation plate with numerous scaraliform bars (**C**). Further shortening and broadening of vessel-element, perforation plate becoming more and more horizontal and reduction in the number of bars in the perforation plate ultimately led to shortest, broad vessel element with transverse simple perforation plate. Vessel-element **E** shows one scalariform and one simple perforation plate. Note conspicuous tails, a reminder of tracheids in vessel-elements **D, E** and **F** with still oblique perforation plates. **J** represents the vessel-element of *Quercus alba*, being more broader than long and with a simple large perforation.

they developed from tracheids with circular pitting and in angiosperms from tracheids with scalariform pitting. It is also pointed out by Carlquist (1996) that circular pitting in the vessels of gnetopsids, as also the gymnosperm tracheids in general, is different from angiosperms in having pits with torus and pit margo with pores much larger than those of angiosperms. Although some angiosperms do have pit membrane with torus, the pit margo is always absent.

Because all fossil and almost all extant gymnosperms possess tracheids with circular-bordered pitting, it has led to the conclusion that the tracheid is the most primitive type of tracheary element in the angiosperms. As tracheids have given rise to vessel elements, the most primitive type of vessels have long narrow vessel elements with tapering ends. The tracheids in angiosperms have scalariform pitting, and as such it is assumed that these tracheids arose from tracheids of gymnsperms with circular pitting. In the transformation of tracheids with scalariform pitting to vessel elements with scalariform pitting, the earliest elements had perforation plates with numerous scalariform bars. During further evolution of vessels, elements became smaller and broader, and perforation plates more horizontal. There has been an accompanied reduction in the number of scalariform bars, resulting in shortest broadest vessel elements with simple perforation plate and transverse end wall (Figure 9.19) in most advanced forms. Hamamelididae were once regarded to be primitive due to their simple floral structure, but have advanced vessel elements and thus considered advanced over Magnoliidae with primitive elongated narrow vessel elements. This is supported by studies on floral anatomy and palynology.

Carlquist (1996), based on a survey of wood anatomy, has identified a number of distinct evolutionary trends in angiosperms. The cambial initials have shortened, the ratio of length accompanying fibers to vessel elements (F/V ratio) has shown an increase from 1.00 in primitive dicotyledons to about 4.00 in the most specialized woods, and angular outline of vessels changed to circular outline together with widening of their diameter. There was also a progressive reduction in the number of scalariform bars, ultimately resulting in simple perforation, facilitating an easier flow of water. The lateral walls showed a shift from scalariform to the opposite circular pits and finally to alternate circular pits, so as to provide better mechanical strength. Imperforate tracheids have shown a shift to fibre-tracheids to finally libriform fibres. Shortening of fusiform initials is correlated with storeying of woods. It is interesting to note that cladistic studies have shown that present-day vessel-less angiosperms do not form a single clade and are distributed in diverse groups such as Hamamelidales (*Trochodendron* and *Tetracentron*), Magnoliales (Amborellaceae, Winteraceae), and Laurales (*Sarcandra*: Vessels have been, however, reported in root secondary xylem by Carlquist, 1987 and in stem metaxylem by Takahashi, 1988). This led Carlquist to conclude that vessels have originated numerous times in dicotyledons.

It had often been held that vessels arose first in the secondary xylem and later in the metaxylem, and that specialization has gradually advanced from the secondary to primary xylem. Carlquist pointed out that scalariform pitting is widespread in the metaxylem of vascular plants and if primitive angiosperms were herbs, in accord with paleoherb hypothesis, metaxylem would be expected to have scalariform pitting of tracheary elements. The development of woody habit—if featured paedomorphosis—would extend scalariform patterns in secondary xylem.

Stamen Evolution

The most primitive type of Stamen in angiosperms represented in genera like *Degeneria*, *Austrobaileya*, *Himantandra* and *Magnolia* (Figure 9. 20) and other primitive genera is laminar, 3-veined leaf-like organ without any clear cut distinction of fertile and sterile parts. The pollen sacs (sporangia) are borne near the centre either on the abaxial (dorsal) side (*Degeneria*, Annonaceae and Himatandraceae) or on adaxial (ventral) side (*Austrobaileya* and *Magnolia*). Semilaminar stamens occur in some other primitive families like Nymphaeaceae, Ceratophyllaceae and Eupomatiaceae. In further specialization of stamen, there has been reduction of sterile tissues and retraction of marginal areas. The proximal part became filament and distal part the anther. The midvein region formed the connective, and distal part the appendage, as seen in several genera.

In primitive families, connective forms a major part of anther. In more advanced families, the connective is highly reduced (Acanthaceae, Plantaginaceae) or may be almost absent. In some families such as Betulaceae, the connective as well as the upper part of filament may become divided and two anther lobes get separated. In more primitive families the connective is produced above into an appendage which

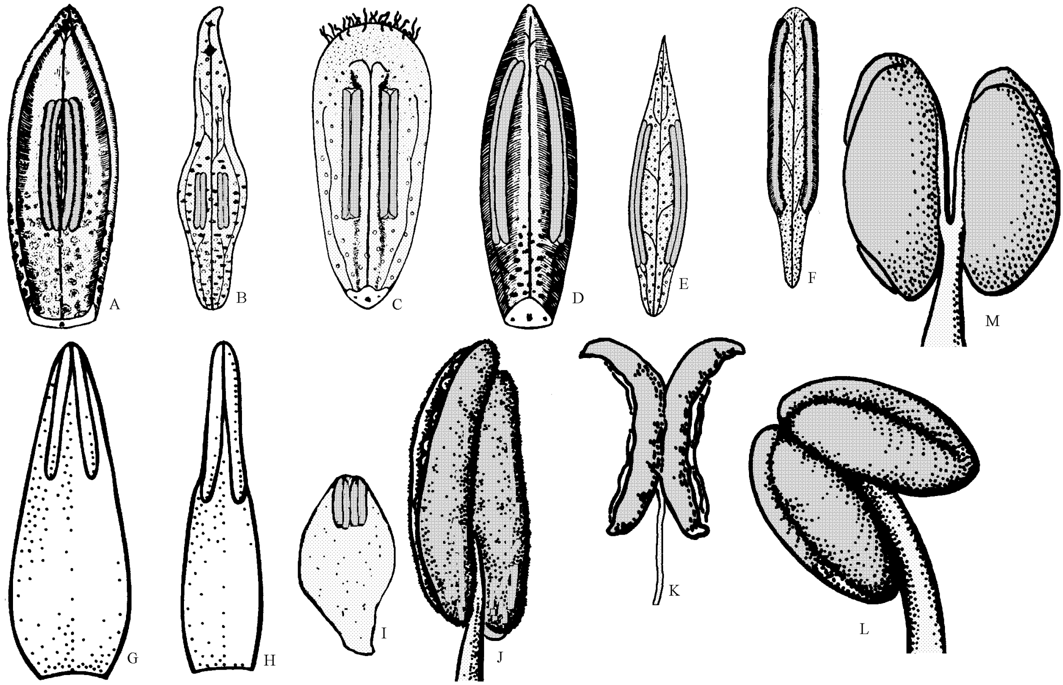

Figure 9.20 Evolution of stamen in angiosperms. **A-D:** Primitive laminar stamens without clear distinction of anthers and filaments; **A:** *Austrobaileya scandens* with adaxial pollen sacs (microsporangia); **B:** *Himantandra baccata* with abaxial pollen sacs; **C:** *Degeneria vitiensis* with abaxial pollen sacs; **D:** *Magnolia maingayi* with adaxial pollen sacs; **E:** Laminar stamen of *Magnolia nitida* with marginal pollen sacs and prolonged sterile appendage; **F:** Semilaminar stamen of *Michelia fuscata* with marginal pollen sacs and narrowed filament; **G:** Outer semilaminar stamen of *Nymphaea odorata* with petaloid filament and narrow anthers; **H:** inner stamen with narrower filament and differentiated anther region; **I:** Stamen of *Illicium parviflorum* with reduced anther region and broad filaments; **J:** Stamen of *Opuntia pusilla* with well differentiated anthers and filament; **K:** Stamen of *Poa pratensis* with reduced connective and thread-like filament; **L:** Stamen of *Penstemon canescens* with well-defined filament and large anthers with distinct anther lobes but reduced connective; **M:** Stamen of *Betula nigra* with divided connective and filament.

disappears progressively in more advanced families.

Broad laminar filament, merging with the rest of stamen represents the most primitive state. It becomes narrower and finally terete in advanced families. The stamens with well marked narrow filament may have basal, dorsal or versatile attachment with anthers. Basifixed condition is the most primitive, versatile the most advanced often commonly seen in grasses and Amaryllidaceae.

It is generally agreed that primitive stamen was laminar, with two pairs of sporangia, borne on adaxial or abaxial side, because both situations are met in primitive families. During the course of evolution, the stamen became more slender, its laminar form slowly disappearing, and sporangia occupying marginal position. The transformation of broad laminar to narrow stamens is clearly depicted in *Nymphaea* from outer to inner stamens and in different species of the genus.

A typical anther of angiosperms is bithecous with two anther lobes with the two anther sacs in each, finally merging into one. The anther with a single anther lobe, as in Malvaceae, has a single final sac (theca) and as such monothecous. The monothecous anthers of Malvaceae and some other families result from splitting of stamens, thus separating the two anther lobes. In others, like *Salix*, there may be a partial connation of two stamens resulting in apparent dichotomy. Anatomical evidence

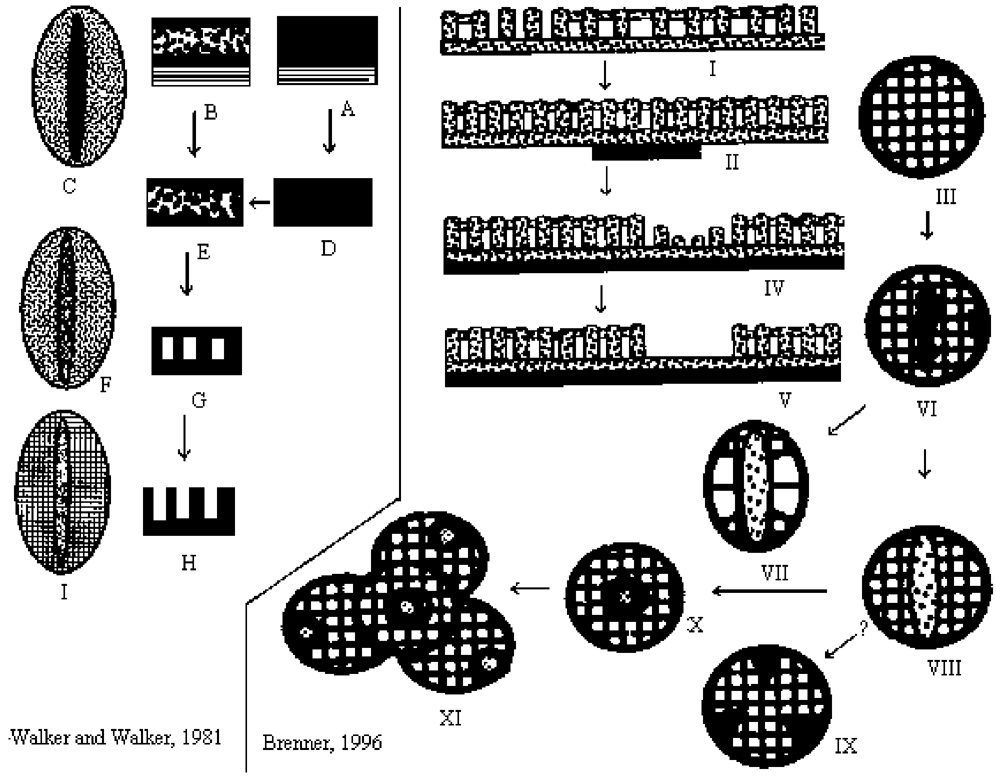

Figure 9.21 Two different models for evolution of exine and pollen grains in Angiosperms. Walker and Walker, 1984 (on left). **A:** Exine of ancestral gymnosperm with homogenous sexine and laminated nexine; **B:** Same but sexine with granular infratectal layer; **C:** Pollen grain of same, boat shaped and monosulcate; **D:** Exine of most primitive angiosperm with smooth sexine and disappearance of laminated nexine; **E:** Same but with homogenous sexine; **F:** Monosulcate pollen of same; **G:** Exine with development of tectum, infratectal layer and homogenous nexine; **H:** Same but with loss of tectum.: **I:** Monosulcate pollen grain with intectate exine. Brenner, 1996 (on right). **I:** Exine of early angiosperm, tectate-columellate and without aperture; **II:** Exine with initiation of endexine (shaded solid black); **III**. Nonaperturate early pollen with circular outline; **IV:** Exine with complete endexine layer and initiation of sulcus; **V:** Exine with developed sulcus; **VI**: Monosulcate pollen of basal angiosperms; **VII:** Monosulcate boat-shaped pollen of Magnoliids and monocots; **VIII:** Circular monosulcate pollen of dicots; **IX:** Tricolpate pollen of Eudicots which might have developed from monosulcate or inaperturate forms; **X:** Uniporate pollen; **XI:** Uniporate pollen of Winteraceae in tetrads. (Modified from Brenner, 1996).

shows two independent vascular supplies derived from opposite sides of the receptacle, as opposed to families where splitting of stamens occurs.

Pollen grain evolution

A large number of families in monocots and several primitive dicots of the magnoliid complex bear monosulcate pollen grains, a condition generally considered to be the primitive one in angiosperms. Walker and Doyle (1975) and Walker and Walker (1984) suggested that the primitive angiosperm pollen grain is large- to medium-sized, boat-shaped, smooth-walled, with homogenous or granular infratectal layer, the tectum being absent (pollen atectate) and endexine (a layer unique to angiosperms, being absent in gymnosperms) either missing or poorly developed under the apertural area. This type of pollen is found among extant angiosperms in Annonaceae, Degeneriaceae and Magnoliaceae. The prototype of this was gymnosperm pollen which was monosulcate, large, boat-shaped with laminated nexine, homogenous sexine or with granular infratectal layer (Figure 9.21), a pollen type common in Bennettitales, Gnetopsids (excluding *Gnetum*) and *Pentoxylon*. In evolution of angiosperm pollen from this, the laminated nexine disappeared, nexine became granular to tectate with columella and reticulate surface to those with intectate collumellae.

Brenner and Bickoff (1992) recorded globose inaperturate pollen grains from the Valanginian (ca 135 mya) of the Helez formation of Israel, now considered to be the oldest record of angiosperm fossils. These pollen grains resemble those of *Gnetum* in general shape and lack of aperture, and also found in Chloranthaceae, Piperaceae, and Saururaceae, which are gaining increased attention as basal angiosperm families. This led Brenner (1996) to postulate a new model for the evolution of angiosperm pollen. The earliest pollen in angiosperms, developed in Valanginian or earlier from stock that also gave rise to *Gnetum*, had small pollen, circular in outline, tectate columellate, and without aperture. A possible intine thickening was accompanied by developments of endexine layer above intine in Hauterivian. The next step involved evolution of sulcus and divergence of monocot and dicot pollen types from basic dicot stock. In Barremian diversification of monosulcate pollen grains occurred with migration to different geographical regions. In Lower Aptian tricolpate pollen evolved from either monosulcate or inaperturate forms in northern Gondwana, resulting in evolution of eudicots.

It is suggested by Brenner that the formation of sulcus during Early Cretaceous may have been an adaptation that was a more effective way of releasing recognition proteins involved in pollen-tube development while the later development of tricolpate condition in the Aptian would be a further extension of this process.

The formation of endexine before aperture development may reflect the development of intine thickening, which is related to sulcus development. In extant angiosperms, the intine beneath the aperture stores recognition proteins.

Carpel evolution

Carpel is a structure unique to angiosperms enclosing and protecting ovules. The evolution of carpel probably played a major role in diversity and success of angiosperms as it not only protected seeds from predators, but also carried associated benefits. These included seed dissemination via the evolution of numerous dispersal mechanisms, effective fertilization by transport of pollen grains to the stigma and growth of a pollen tube, promotion of outbreeding by insect pollinators through the evolution of special structural mechanisms and through the developments of intraspecific and interspecific incompatibilty.

It is more common in recent years to differentiate three types of carpels, a terminology developed by Taylor (1991). **Ascidiate** carpels have ovules attached proximally to the closure, **plicate** ones have ovules attached along margins of the closure and **ascoplicate** carpels are intermediate between the two.

The nature of carpel in angiosperms has been the subject of considerable discussion. The dominant view supported by Bailey and Swamy (1951), Cronquist (1988), Takhtajan (1997) and several others considers carpel as homologous to megasporophyll, appropriately named as **phyllosporous** origin of carpel (Lam, 1961). Others believe that carpel consists of a subtending bract with placenta representing a shoot with distally placed ovules, concept named as **stachyosporous** origin (Pankow, 1962; Sattler and Lacroix, 1988).

Phyllosporous origin

Among the believers of phyllosporous origin, suggest that carpel is a folded leaf with adaxial surfaces (**conduplicate**), or involute abaxial surfaces in contact (**involute**) with many ovules along the margins (or submargins) of closure (Bailey and Swamy, 1951; Eames, 1961). Others suggest that the leaf is fundamentally **peltate** (Baum, 1949; Baum and Leinfellner, 1953), as many carpels have cup-shaped primordia.

The conduplicate view of the origin of carpel was advocated by Bailey and Swamy (1951). In primitive type of carpel, the stigma is represented by a crest extending from

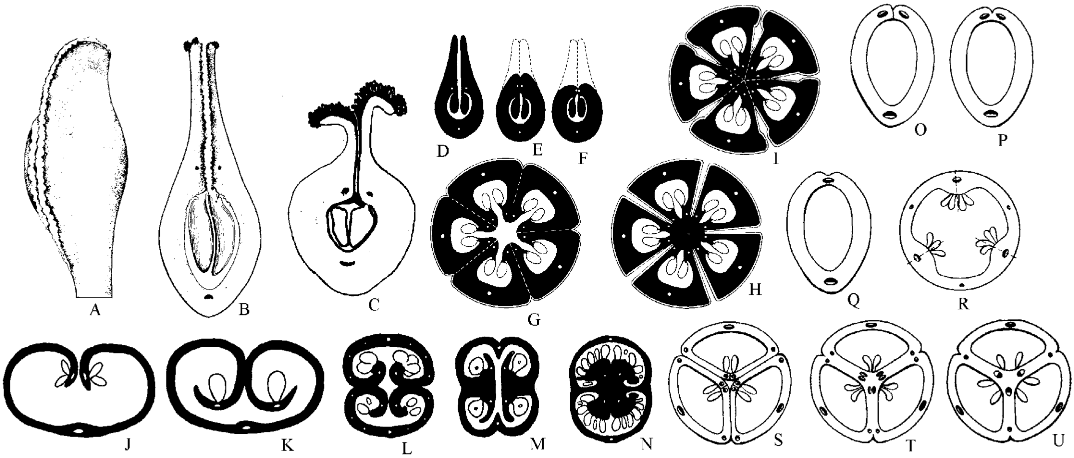

Figure 9.22 Phyllosporous concept of carpel evolution. **A-I**, conduplicate closure; **J-N**, involute closure; **O-U**, closer along margins. **A:** Carpel of *Drimys piperita* with long stigmatic crest; **B:** Transverse section of same showing partially closed margins; **C:** Transverse section of carpel of *Degeneria vitiensis* with flared up margins and conspicuous papillose growth; **D-F:** Stages in conduplicate closing of carpel with disappearance of stigmatic region (broken lines) from the body of carpel and its localization towards the tip, resulting in marginal placentation; **G:** Fusion of adjacent carpels by lateral cohesion of open conduplicate carpels forming parietal placentation; **H:** Fusion by adnation of free margins of conduplicate carpels to the thalamus forming axile placentation; **I:** Fusion by cohesion of ventral surfaces of the carpels formong axile placentation. **J-K:** Involute closing of carpels by meeting of dorsal surfaces of carpels. **M-N:** Examples of fused carpels with involute closure. **L:** *Erythraea centaurium*; **M:** *Isanthus brachiatus*; **N:** *Limnophila heterophylla*. **O-Q:** Closure by fusing margins of carpel with ultimate merging of ventral bundles; **R:** Fusion of margins of adjacent opens carpels with merging of ventral bundles and formation of parietal placentation. **S-U:** Fusion of sides of closed carpels with merging of adjacent lateral bundles and ventral bundles resulting in axile placentation. (**A-H** based on Bailey and Swamy, 1951; **J-N** based on Eames, 1961; **O-U** after Eames and MacDaniels, 1947).

apex to base of carpel (decurrent) as in some species of *Drimys*, *Himantandra* and *Degeneria*. In *Degeneria* and *Butomus*, the double nature of the crest is evident in margins flaring back from the line of contact. In *Degeneria* and *Drimys*, the margins of carpels are incompletely closed by interlocking papillose cells of the stigmatic crest. The carpels have three traces, one dorsal and two ventral, the latter providing vascular supply to ovules. From this type of carpel, the closed carpel of other angiosperms developed by closure of adjacent adaxial surfaces (Figure 9.22 D-F) and concentration of stigmatic margins to the upper part of the carpel, reduction in the number of ovules and their restriction to lower part differentiating as ovary, the middle sterile portion forming the style. The fusion of adjacent carpels in the formation of syncarpous gynoecium may have proceeded along different directions. Lateral cohesion of open conduplicate carpels resulted in unilocular ovary with parietal placentation (Figure 9.22 G). Axile placentation (with number of locules equalling the number of fusing carpels) may have resulted from adnation of free margins to the thalamus (Figure 9.22 H) or cohesion of ventral sutures of carpels (Figure 9.22 I). Different families of angiosperms exhibit different degrees of fusion, some like Caryophyllaceae with free styles and stigmas, others like Solanaceae with complete fusion of ovaries, styles and stigmas. Free central placentation may result from dissolution of septa from ovary with axile placentation (Caryophyllaceae) the placental column being attached to the base and top of the ovary. It may also result from protruding thalamus carrying the placenta from the base of the ovary (Primulaceae). The basal placentation with the number of ovules reduced to basal one may be derived from one (Alismataceae) or more than one carpels (Asteraceae).

Laminar placentation with ovules scattered over the entire inner surface of the ovary wall is considered to be the most primitive type, present in Nymphaeaceae, Cabombaceae, Butomaceae and other relatively primitive families. The ovules in these carpels derive their vascular supply chiefly from a smaller meshwork of the bundles, and rarely from dorsal bundle or ventral bundles. There was consequent reduction in the number of ovules and their restriction to submarginal position with vascular supply coming from ventral bundles. The evidence of this transition is seen in Winteraceae and Degeneriaceae.

Closing of carpels may also result from fusing of incurved margins of carpels. Progressive fusion results in final fusion of adjacent ventral bundles (Figure 9.22 O-P) in follicular carpel. Fusion of margins of adjacent open carpels results in parietal placentation with only ventral bundles ultimately merging, whereas the fusion of sides of closed carpels results in axile placentation with both adjacent lateral bundles as well as ventral bundles merging.

Involute closing of carpels was advocated by Joshi (1947), Puri (1960) and several other workers. In such carpels, the margins of the carpel are involuted and abaxial (and not adaxial surfaces) or margins are in contact. The example of such carpels involved in the formation of syncarpous gynoecium is seen in several genera (Figure 9.22 L-N). Although there have been suggestions that involute types may have evolved from conduplicate types, Eames (1961) considered it highly unlikely, as such a derivation would involve change from contact by adaxial sides to contact by abaxial sides, a major change, far more complicated and circuitous than usually found in evolutionary derivation. He suggested that several independent closure of carpels occurred in different phylogenetic lines.

The theory that the carpel is a **peltate** leaf was strongly advocated by Baum and Leinfellner (1953). The peltate form of carpel is assumed to have arisen by turning upward (ventrally of the basal lobes of the lamina and their fusion, margin to margin, as in the formation of peltate leaves. A transverse meristem, known as **cross zone,** develops where the two marginal meristems meet. As the carpel primordium elongates,

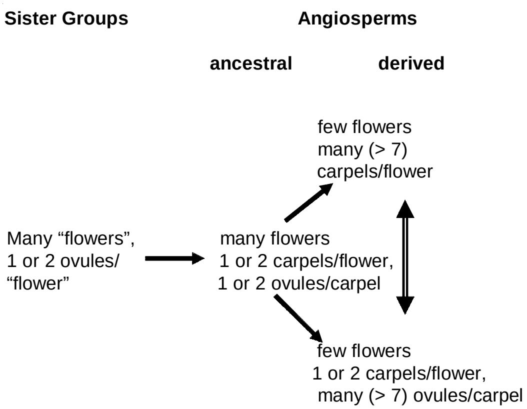

Figure 9.23 Evolution of carpel and floral types in angiosperms based on stachyosporous model proposed by Taylor and Kirchner (1996). Ancestral type is based on suggested homologies between female structures of sister groups.

the cross zone, continuous with the marginal meristems, is said to build up a ventral strip of carpel wall, which, united with the lateral walls, forms a tubular organ. Under this theory, the ovules are borne on the wall formed by the cross zone. Peltate carpels may be **manifest peltate** carpels with well-defined stalks and tubular lamina with well-marked cross zone (*Thalictrum*) or **latent peltate** with short tubular base and cross zone present only in early ontogeny (*Calycanthus*). According to this theory, the achene of *Ranunculus* having a single ovule on latent cross zone is considered to be the first stage in the building of tubular follicle. This theory is reverse of the most commonly held view that the follicle represents a more primitive state, and that the achene of *Ranunculus* is derived.

Stachyosporous origin

The idea was first developed by Hagerup (1934, 1936, 1938) who suggested that conduplicate carpels have two growth areas. The theory was further developed by Lam (1961), Melville (1962, 1983—who proposed a variation of this as **gonophyll theory**) and more recently Taylor (1991) and Taylor and Kirchner (1996). The theory is gaining increased interest with the renewed interest in gnetopsids as close relatives of angiosperms. The theory holds that the carpel envelope represents a bract and placenta homologous with a shoot bearing distally placed ovules. This bract-terminal ovule system is directly homologous to the one found in outgroups including Gnetales, the closest living sister-group. According to this theory, ascidiate carpel with few ovules represents an ancestral stage. It is believed that the origin of plicate (conduplicate) and ascoplicate carpel types would be due to integration of the gynoecial primordia and ovular (placental) growth areas.

Taylor and Kirchner found further evidence for stachyosporous origin from:

1. Ingroup phylogeny based on structural and DNA sequences, *rbcL cpDNA* datasets which place either woody or herbaceous magnoliids as basal clades suggest that ascidiate carpels with 1 or 2 ovules represent ancestral state.
2. Outgroup analysis involving Bennettitales, Gnetales and Cordaitales which suggest that female reproductive structures are compound organs.
3. Morphogenic analysis involving understanding of floral development in *Antirrhinum* and *Arabidopsis* through mutagenic analysis, study of the development of carpel in *Datura* by examining chromosomal chimeras (carpel wall is similar to petals and leaves in development; carpel with two types of primordia, one forming the wall and one with distinct central ridge which develops into septum, placenta and false septum and functions like floral apex), study of carpel development in *Nicotiana* using *Ac*-GUS reporter system using GUS bacterial gene as marker (showing that whereas carpel wall is composed only L1 and L2 layers, the placental region has an additional L3 layer).

Based on new evidence, Taylor and Kirchner concluded that ancestral carpel is ascidiate with marginal stigma and basal to slightly lateral placentation of one or two orthotropous ovules. The evolution of curved ovules and placement of the ovules in other positions was to direct the micropyle away from the stigma or pollen-tube transmission-tissue. They suggested that reproductive axes with many flowers, few carpels per flower, and few ovules per carpel were ancestral (Figure 9.23).

From such an ancestral type developed two types of inflorescences: one with few flowers, each of which had many carpels and few ovules and the other with few flowers each containing few carpels and many ovules.

Gonophyll theory

Melville (1962, 1983) developed his gonophyll theory largely on the basis of studies of vasculature in leaves and floral whorls. This theory is a variation of stachyosporous origin. According to him, the ovary consists of sterile leaves and ovule-bearing branches attached to the petiole of the leaf. Each leaf, together with the fertile branch, is considered a unit and termed as **gonophyll** instead of carpel. This theory has already been discussed under probable ancestors of angiosperms.

Evolution of Inferior ovary

It has been universally agreed that the inferior ovary in angiosperms is a derived state. The nature of origin of this type had two opposing views. Linnaeus, de Candolle and many early botanists believed in the origin of an inferior ovary through adnation of bases of outer floral whorls to the gynoecium, a view known as **appendicular theory** (Candollean theory, concrescence theory). Others believed in the **receptacular theory** (**axial theory**) developed by German school of botanists and supported by Schleide, Eichler, Sachs and others, according to which inferior ovary resulted from invagination of the floral receptacle which surrounds the ovary.

The accumulating anatomical evidence has shown that inferior ovary has evolved a number of times in different groups of angiosperms, in some due to adnation of floral parts and in others due to axial invagination. In certain plants like *Hedera*, separate traces related to different floral organs are found, in others like *Juglans*, different stages of bundle fusion can be found in the inferior ovary. Such plants also have normal orientation of vascular bundles (phloem outside, xylem inside) and evidently, the inferior ovary is appendicular in origin.

An axial invagination of floral receptacle will eventually result in inverted vascular bundles (xylem on outside, phloem inside) in the inner part of inferior ovary, with normal orientation in the outer part. This has been observed in the inferior ovaries of Cactaceae and Santalaceae. In others like *Rosa*, the lower part of the fleshy receptacle has invaginated receptacular tissue whereas the upper portion consists of fused floral parts. The adnation of floral parts above or surrounding the ovary in a large number of plants forms hypanthium, a structure distinct from but often confused with the calyx tube, the latter involving the cohesion of sepals only. The development of inferior ovary has occurred within several families, as genera with superior ovary and those with inferior ovary may be encountered in the same family as seen in Rosaceae, Gesneriaceae, Nymphaeaceae and several others. In Nymphaeaceae, *Nuphar* has superior ovary, *Nymphaea* semi-inferior and *Euryale* superior ovary.