EVOLUTIONARY TRENDS IN ANGIOSPERMS

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 inclosed 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 thedifferentiation 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 instepwise 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 inbracts 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,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 tracheidsarose 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 generais 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 morenprimitive families the connective is produced above into an appendage which disappears progressively in more advanced families. Broad laminar filament, merging with the rest of m 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 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 oyle (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 inValanginian 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 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.

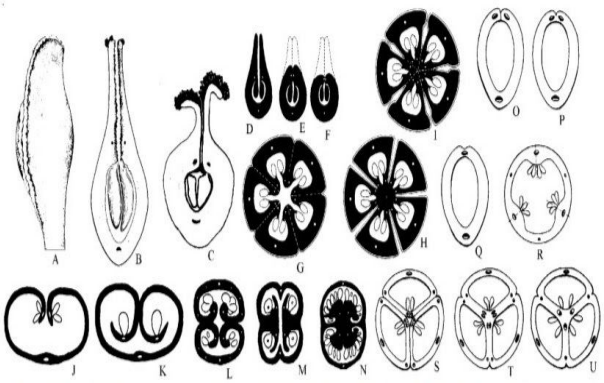

Figure 9.22 Phyllosporous concept of carpel evolution. **A-I**, conduplicate closure; **J-N**, involute closure; **O-U**, closer along margins. **A:** Carpel of *Drimys piperita* with long stigmatic crest; **B:** Transverse section of same showing partially closed margins; **C:** Transverse section of 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).

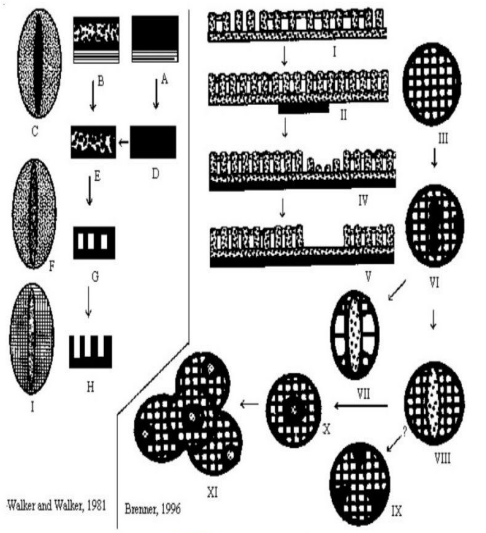

Figure 9.21 Two different models for evolution of exine and pollen grains in Angiosperms. Walker and Walker, 1984 (on left). **A:** Exine of ancestral gymnosperm with homogenous sexine and laminated nexine; **B:** Same but sexine with granular infratectal layer; **C:** Pollen grain of same, boat shaped 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).

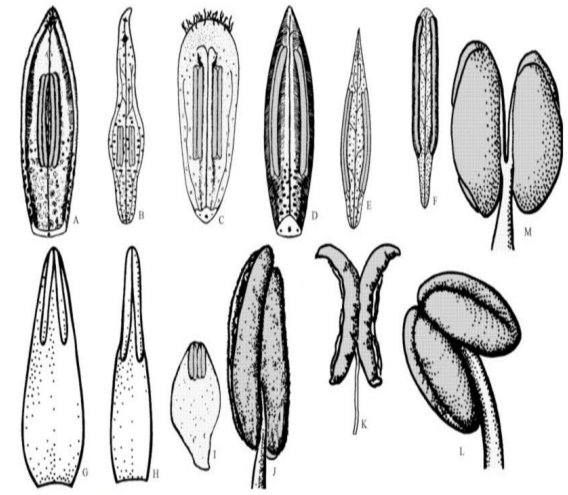

Figure 9.20 Evolution of stamen in angiosperms. **A-D:** Primitive laminar stamens without clear distinction of anthers and filaments; **A:** *Austrobaileya scandens* with adaxial pollen sacs (microsporangia); **B:** *Himantandra baccata* with abaxial pollen sacs; **C:** *Degeneria vitiensis* with abaxial 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.

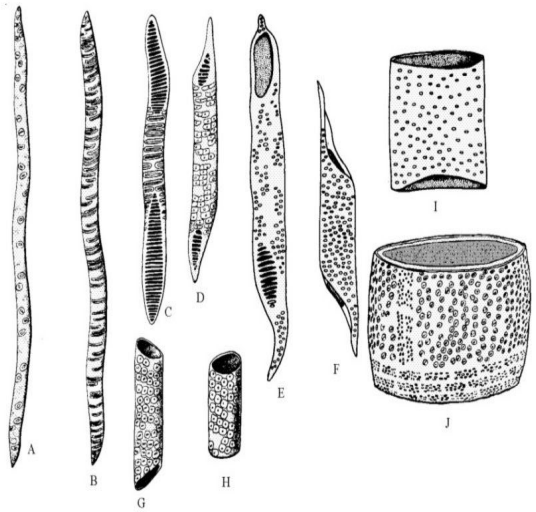

Figure 9.19 Presumed evolutionary transformation of gymnosperm tracheid with circular pitting (**A**) to angiosperm tracheid with scalariform pitting (**B**), further to vessel-element with oblique perforation plate with numerous scalariform bars (**C**). Further shortening and broadening of vessel-element, 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.