ORIGIN OF ANGIOSPERMS

The earliest fossils of flowering plants are dispersed pollen grains from the earliest Cretaceous period, approximately 140 million years ago. The earliest flowers occur slightly later in the fossil record, about 130 million years ago. These early flowering plant fossils can largely be grouped with recognizable, extant groups. The details of angiosperm evolution are not clear. One problem is that many angiosperm features, such as a reduced male gametophyte, reduced female gametophyte, and double fertilization with triploid endosperm, are microscopic and cytological and are not preserved in the fossil record.

Ancestors of Angiosperms

The identity of the ancestors of the flowering plants is a most difficult problem which is as yet far from being solved. Several groups of plants have been considered as ancestral stock for angiosperms.

Bennettilean ancestry

Bennettitales have been proposed as possible ancestors of angiosperms, based on resemblance in structure between the strobili of the Mesozoic genus *Cycadeodea* and the flower of *Magnolia*. But this resemblance is wholly superficial, moreover Bennettitalean seed differs from that of the primitive angiosperms in being exalbuminous, the embryo itself filling almost all the seed cavity, and nutritive tissue being entirely absent or very scanty. Though the Bennettitales was rejected as the ancestors of the angiosperms, it is quite possible that they are connected through common ancestry like seed-ferns.

Gnetalean ancestry

This theory was proposed by Wettstein (1901) and supported by Markgraf (1930) and Fagerlind (1947). The Gnetales resemble angiosperms in many respects. Both of them have two cotyledons, unlike all other Gymnosperms have vessels in their secondary wood, two integuments and net veined leaves. But investigations (Thompson, 1918) have shown that the vessels of *Welwitschia, Ephedra* and *Gnetum* originated in an entirely different way from those of Angiosperms.

Coniferalean Ancestry of Amentiferae

This theory has been proposed by Eichler (1875), Engler (1882, 1892), Engler and Prantl

(1924), Rendle (1904, 1930), Hagerup (1934, 1936) and Doyle (1945). These authors have pointed out the resemblances of angiosperms to conifers and considered that coniferales might have given rise to primitive group of angiosperms known as Amentiferae. The inflorescence of the amentifers like Casuarinaceae, Salicaceae and Fagaceae with their simple and naked flowers were compared with those of conifers. This theory is not acceptable because the amentiferae group is now considered as an advanced group of angiosperms.

Pteridospermean Ancestry

Pteridosperms (Seed ferns) were considered as ancestors of Angiosperms by Long (1966). Features like reticulate venation, monopodial branching, presence of cambium, presence of microsporophylls and megasporophylls on the same plant. Origin of sepals from leaves and petals from sepals and stamens, development of triploid endosperm as extreme reduction of female gametophyte, similarities of seed structure and existence of one or several ovules subtended by a cupule together with information provided by *Glossopteris* reproductive structures are enough to bring seed ferns (Pteridosperms) closest to Angiosperms.

But Pteridosperm ancestry of angiosperms is not completely acceptable because of two serious objections. The scalariform xylem elements never occur in Pteridosperms while they are common in angiosperms. No satisfactory explanation is given for cupule as an equivalent of carpellary wall in case of multiovulate cupules.

Pentoxtlalean theory

Pentoxylales have many similarities with *Pandanus*. These include: erect habit, dioecious nature, tuft of leaves, axillary inflorescence, peduncle with tracheids and spiral thickening and bordered pitting, two layered seed coat of which the inner one is usually tanniferous, seeds enclosed in a fleshy layer sarcotesta, endospermic seeds and minute embryo. Based on these similarities, Meeuse (1961) considered Pentoxylales as ancestors of Angiosperms. In spite of resemblances, authors like Pant and Kidwai (1971) hold that they could equally be the result of parallel evolution.

Caytonialean Ancestry

Caytonialean ancestry of Angiosperms was proposed by Thomas (1925, 1936) and supported by Stebbins (1974). Caytoniales are fossil plants of middle Jurassic period. Caytoniales had angiosperm-like anthers produced in groups or single on branching

pinnate structures, which may be described as sporophylls. Such structures are comparable with the branched stamens found in such plants as *Ricinus, Hypericum* and *Calothamnus*. Caytoniales are characterized by a curved cup-like structure called cupule, in which the ovules are enclosed. Proponents of Caytoniales as the ancestors of angiosperms point to the almost sealed cupule as suggestive of the way a carpel might have evolved. The caytoniales also exhibited leaves with a reticulate venation. Caytoniales, however, are now shown to have relationships with Pteridosperms and they are now classified as Mesozoic remnants of that group.

Durian Theory of Origin of Angiosperms

Durio zibethinus, a member of Bombacaceae from Burmese and Malayan forests was considered by Corner (1949), as a surviving model of primitive angiosperms. It is a cauliflorous tree and bears large, coloured, loculicidal spiny capsules with fleshy arillate seeds. According to this theory the primitive angiosperms are mesophytic, tropical in distribution, with cycad like tree habit, compound leaves, probably monocarpic and producing a large terminal cluster of arillate follicles. The theory has been criticized by a number of morphologists including Pijl (1952), Parkin (1953), Metcalfe (1954) and Eames (1961).

Herbaceous Origin Hypothesis

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. Using the oldest, most complete fossil angiosperm on record, David Dilcher announced the discovery of a new basal angiosperm family of aquatic plant, Archaefructaceae. 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 carpels helically arranged.

Archaefructus was submerged plant with thin stems that 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. 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.

Video 2

Conclusion

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.

Origin of Monocotyledons

Monocotyledons evolved from dicots and are monophyletic. 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). 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 most primitive Monocotyledons. The slide shows origin of monocots according to APGIII classifications, here also monocots are shown to have originated from primitive dicot ancestor before modern dicot groups arose.

References

Singh, (2012). *Plant Systematics:* Theory and Practice Oxford & IBH Pvt. Ltd., New Delhi. 3rdedition.

Simpson, (2006). *Plant Systematics.* Elsevier Academic Press, USA.

T. Pullaiah, *Angiosperms: Origin And Evolution*, Sri Krishnadevaraya University

Angiosperm Phylogeny Group (2009), "An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III", *Botanical Journal of the Linnean Society* 161 (2): 105–121.