RETHINKING THE ANGIOSPERM FOUNDATION

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INTRODUCTION

About 250,000 species of angiosperms (flowering plants) form much of the land vegetation of the world. They are more abundant than any other kind of land plant and extremely important for humans (and other animals) in many ways. One special angiosperm feature is endosperm, the tissue in seeds, often starchy, which provides nutriment to embryos and developing seedlings when seeds germinate. Endosperm from grains provides us with our daily bread, rice, pasta, oatmeal, cornmeal, beer and whisky. N.B. In the seeds of species from some angiosperm families, food is stored not in endosperm, but in embryo, cotyledons, or some other tissues, but that is another story.

Mid 20th Century Views on Angiosperm Phylogeny

Back in the 1950s, when I learnt many "facts" of botanical life, the angiosperms were regarded as a very distinct monophyletic group (descended from one common ancestor) and so they still may be. Unique features, particularly their flowers, and seeds enclosed within ovaries, set them apart from the other extant seed plants, the gymnosperms (pines, cypresses, yews, junipers, podocarps, kauris, ginkgos, cycads, gnetum etc.), which are polyphyletic (derived from a variety of ancestors). There was general agreement among academic botanists that angiosperms consisted of two main branches:

1. the dicotyledons, usually having two seed leaves, more or less reticulate leaf venation, and flowers usually with four, five or more sepals, petals and stamens (there are a few exceptions to all these rules); and

2. the monocotyledons, with a single seed leaf, (often highly specialised), usually parallel leaf venation and sepals, petals and stamens in threes, or multiples of three. Dicotyledons in the above sense occur in a ratio of about three to every one monocotyledon species.

A commonly held view (cf. Pool 1941; Robbins, Weir and Stocking 1957) was that certain "primitive" dicotyledon groups, the Magnoliaceae and Ranunculaceae and related families, with numerous, simple, unfused carpels and other flower parts, spirally arranged on an axis, were the nearest to the basic stock from which the angiosperms had evolved. The monocots, as well as the "advanced" dicots were considered to have evolved as separate branches from the "primitive", dicot stock. However, the actual ancestors of the angiosperms were unknown. At the time the oldest known angiosperm fossils were from mid Cretaceous sediments (about 80 million years old); the group must have originated earlier. A simplified version of an hypothetical phylogenetic "tree" for the families of angiosperms, from the 1940s, is shown in Fig. 1; there were other, alternative, models for the detailed phylogenetic pathways in the group, also.

Flowers, Carpels, Fruit, Ovules, Seeds and Endosperm

Angiosperm flowers, as opposed to the more simply-organised cone-like reproductive structures of gymnosperms, are relatively elaborate, with sepals, petals, stamens and gynoecium (one or more carpels). A carpel is a single ovary, plus associated parts, the stigma which receives pollen, and the style down which the pollen tubes extend. One or more ovules are surrounded by the carpel wall which forms the ovary (hence angiosperm - angion = a vessel; sperma = seed). In a multicarpellate flower the carpels may be free, or more or less fused to one another and to other flower parts. The ovary, when carpels are fused, is a composite organ which may or may not show clear signs of the numbers of carpels present. When the ovules are fertilised and develop into seeds the ovary walls expand and develop into the fruit which contains them.

A Mid - 20th Century Model for Relationships and Implied Phylogeny of Angiosperms (simplified and using modern names for each family) (after Pool, 1941)

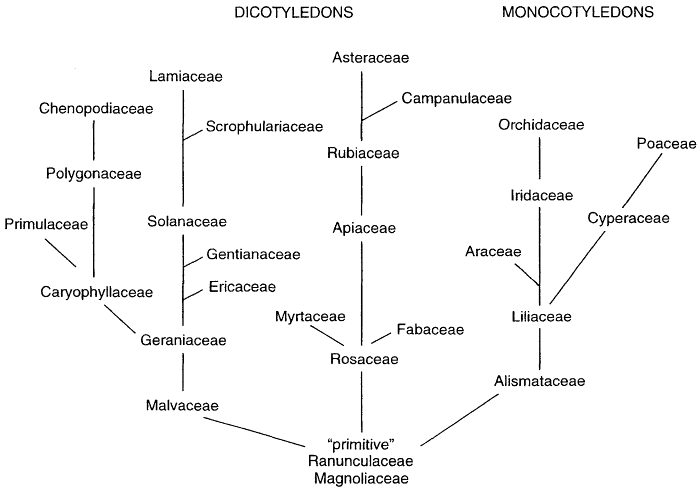

Fig. 1. Angiosperm phylogeny: a mid-20th Century view

Table 1. Families considered to be near the base of the Angiosperm lineages †

		Kinds of Plants	No. of Genera	No. of Species	Distribution Range	N.Z. Indigenous Representatives
A.	**"Basal" Angiosperms**					
	Amborellaceae	S	1	1	New Caledonia	-
	Illiciaceae	T, S	1	42	E.-S.E. Asia, Malesia, S.E. USA, Mexico, Caribbean	-
	Schisandraceae	V	2	49	E.-S.E. Asia, Malesia, S.E. USA	-
	Trimeniaceae	T, S, V	2	6	Malesia, E. Australia, New Caledonia, Fiji, New Guinea, Samoa, Marquesas	-
	Austrobaileyaceae	V	1	1	N.E. Australia	-
	Cabombaceae	Ha	2	6	E. Africa, S. Asia, Japan, E. Australia, N. America, C. America, Caribbean, S. America	-
	Nymphaeaceae	Ha	6	67	Widespread Tropics - Cool Temperate	-
B.	**"Primitive" Monocot Angiosperms**					
	Acoraceae	Ha	1	2	Widespread N. Temperate, India, Malesia, New Guinea	-
	Alismataceae	Ha	14	100	Widespread, Tropics, Temperate	-
C.	**"Magnoliid" Angiosperms**					
	Magnoliaceae	T, S	7	182	E.-S.E. Asia, Malesia, New Guinea, E. U.S.A., Mexico, Caribbean, N.E. S. America	-
	Winteraceae	T, S	8	90	Madagascar, Malesia, E. Australia, Tasmania, New Caledonia, Solomons, Mexico, S. S. America, Juan Fernandez	*Pseudowintera*
	Degeneriaceae	T	1	2	Fiji	-
	Chloranthaceae	T, S, H	4	75	Madagascar, E.-S.E. Asia-Malesia, New Caledonia, Fiji, Marquesas, Mexico, Caribbean, E. S. America	*Ascarina*
	Aristolochiaceae	S, V, H	7	400	Widespread Tropics - Temperate	-
	Monimiaceae	T, S,	23	165	Widespread Tropics - Warm Temperate	*Hedycarya*
	Atherospermataceae	T	7	14	New Guinea, E. Australia, Tasmania, New Caledonia, W.S. America	*Laurelia*
	Lauraceae	T, S, Vp	50	3000	Widespread Tropics - Warm Temperate	*Beilschmiedia* *Litsea* *Cassytha*
	Piperaceae	T, S, V	5	3000	Widespread Tropics - Warm Temperate	*Macropiper* *Peperomia*

<and about 12 other families> T-trees, S-shrubs, V-vines, H-Herbs, a-aquatic, p-parasitic

† Make comparisons in this Table with information in Mabberley 1991 and Thorne 2000

Each seed is surrounded by an integument (coat), and contains an embryo and endosperm, (which comprises much of the volume of the seeds of many species). The first stage in the inception of endosperm occurs in the embryo sac of an ovule when two haploid polar nuclei join to form a diploid fusion cell (haploid - with one set of chromosomes; diploid, with two, in this case both originating from the female parental tissue). Then, after pollination of the flower, a pollen tube grows down the style and into the ovule adjacent to the embryo sac. Two haploid sperm (male) nuclei are released from the pollen tube tip. One fuses with the egg nucleus to initiate the biparental, diploid zygote, which develops into the embryo. The other joins with the fusion cell, initiating the biparental, triploid endosperm tissue (triploid - with three sets of chromosomes).

Refined Phylogenetic Hypotheses Later in the 20th Century

Since the 1950s angiosperm relationships have been examined extensively through detailed anatomical and developmental studies and by cytologic, chemo- and molecular taxonomic methods and cladistic analysis. Views on the broad patterns of relationships within the group have been much refined since the 1970s (cf. Fig. 2) (Heywood 1978; Thorne 2000). Again, there are alternative versions.

Latest Ideas About Angiosperm Phylogeny

Recently, as a result of DNA sequencing studies of a wide range of taxa (cf. Friedman and Floyd 2001) it has been proposed that there is a "basal" group of angiosperm genera and families, rather different from those which, in the mid 20th Century, were thought to be the most primitive (Fig. 3, Table 1). The view now is that three main lineages diverged, in sequence, from ancestors that resembled the modern members of the "basal" angiosperms. These offshoots were: the monocots; the group of families which includes the Magnoliaceae; the "advanced" dicots (sometimes called "eudicots"). The "eudicots" may have diverged directly from "basal" angiosperm-like ancestors, or from ancestors like some of the magnoliids. Since their origins various specialisations have evolved in members of these three lineages, while the plants in the lineages of "basal" angiosperms have remained unspecialised. Among "primitive" features retained by them are: small flowers; spirally arranged, numerous free floral parts; lack of distinction between sepals and petals; intergrades between stamens and petals; carpels with an opening into the inner cavity which is closed by the secretion of a gummy material on the inner carpel surface. Carpel closure (which occurs at the time between pollination and fertilisation) is achieved in more advanced angiosperms by fusion of the peripheral parts of the inner carpel surface, or by a combination of gum secretion and fusion. In one "basal" angiosperm family, Illiceaceae, there is fusion of the carpel opening.

Williams and Friedman (2002) indicated that the double fertilisation which gives rise both to a diploid embryo and the initial triploid endosperm cell (supposedly a character common to all angiosperms) does not occur in several of the "basal" angiosperms (Fig. 3). In them, the endosperm is diploid and derived entirely from the female parent. However at least one of the "basal" angiosperms, *Amborella,* probably has triploid endosperm. It is possible that the triploid endosperm phenomenon evolved more than once. Another, less likely, possibility is that diploid endosperm is a secondary development (i.e., all angiosperm ancestors really did have triploid endosperm).

A Simplified Late 20th Century Model of Degrees of Specialisation of Angiosperm Families (evolutionary connections are implied, but indefinite). (after Heywood 1978; Thorne 2000)

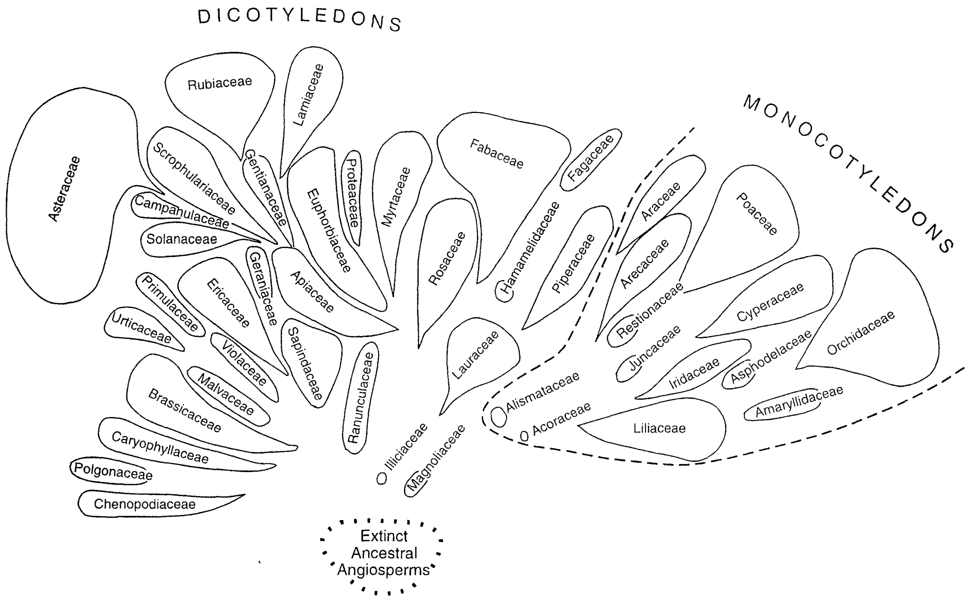

Fig. 2 Angiosperm phylogeny: a late-20th Century view

In the mid 20th Century the most primitive monocots were thought to be the Alismataceae and related families. In some respects their floral features are like those of the "eudicot" family Ranunculaceae (Fig. 1). However, according to one recent DNA study the most primitive living monocots are the Acoraceae (Table 1). Another study places Acoraceae and Alismataceae together as "primitive" monocots.

Some members of the "basal" angiosperm waterlily families Nymphaeaceae and Cabombaceae have a range of features like "eudicots" (whorled flower parts; fusion of floral parts, including carpels; inferior ovaries (i.e., lying below the insertion of the calyx, corolla and stamens). They also have some monocot-like features (sepals and petals in multiples of three). As well as the DNA affinities with other "basal" angiosperms, many waterlily species have free carpels and numerous stamens, which may grade into petals. Though there are vessels in the xylem, they are primitive in form, like those of Illiciaceae and Chloranthaceae.

Amborella, considered by some to be the most primitive living angiosperm, is without vessels in its xylem, but is anomalous among the "basal" angiosperms in (probably) having triploid endosperm. Among the magnoliid angiosperms some members of Chloranthaceae have carpels like those of "basal" angiosperms and members of Winteraceae lack xylem vessels.

At present no formal terminology has been applied to differentiate the "basal" and magnoliid angiosperms from the "eudicots". The unqualified term "dicotyledon" is clearly not very useful as a means for describing any of the angiosperms now. Drawing conclusions about relative "primitiveness" is tricky, considering the mixtures of characters thought to be relatively primitive or more advanced. No doubt more will be heard about all this in due course.

The Mystery of Angiosperm Origins

In the mid 20th Century there were some tentative suggestions about progenitors of the angiosperms (cf. Pool 1941). Among them were extinct groups of seed plants, the pteridosperms and cycadeioids. Later in the 20th Century the extinct glossopterids and ancestors of the Gnetales (extant species of which are *Gnetum,* and *Ephedra*) were considered as angiosperm precursors. *Gnetum* is a woody gymnosperm with leafy, vaguely flower-like reproductive structures, found in tropical regions including New Guinea. A strong case for the Gnetales link with angiosperms was made in the mid 1990s. The view now, however, based on DNA evidence (cf. Friedman and Floyd 2001) is that gymnosperms, extinct or living, are not closely related to the angiosperms. No totally credible progenitor for the angiosperms is known as yet.

The earliest well-authenticated angiosperm fossils have been found in early Cretaceous rocks, 130 million years old, in the USA and Europe. They include: *Nymphaea*-like plants, with flowers; seeds like those of *Illicium* or *Nymphaea*; pollen like that of *Amborella.* As well fossils of magnoliid angiosperms, Winteraceae, Chloranthaceae and Lauraceae have been recovered from sediments of the same age; the angiosperms were firmly established by this time (cf. Endress 2001), but no fossil monocots older than early upper Cretaceous are known for certain. If the monocots did evolve earlier than the magnoliids they probably were small, soft, herbaceous forms at first (and did not readily become fossilised). It is possible that the earliest

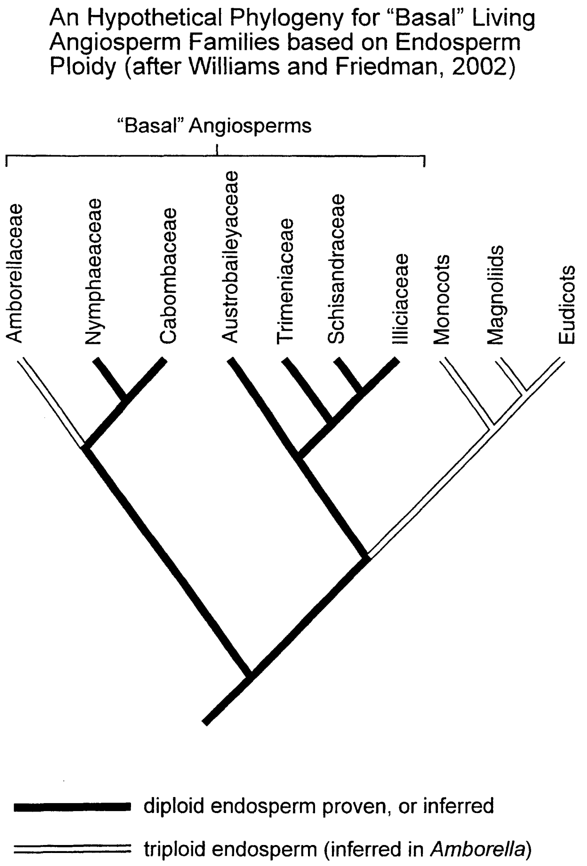

Fig. 3. The phylogeny of the most primitive living angiosperms: a 2002 view

angiosperms originated as early as the late Jurassic (Thorne 2000) or even in the Triassic (Mabberley 1997, p. 39).

Some mysteries remain to be solved before the story of angiosperm origins and early evolutionary radiation can be told with utmost confidence. It is possible that research on New Zealand representatives of the "primitive" angiosperms can provide useful evidence towards the solutions.

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