

Deciphering angiosperm origins

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Data generated to provide answers to Darwin's 'abominable mystery', i.e. the sudden appearance, and subsequent exponential increase in diversity, of angiosperms in the fossil record are examined. It is observed that as yet we do not have sufficient data either to identify ancestral forms of angiosperms or to fix the time of their origin. In the fossil record first indubitable angiosperms appear only in the Early Cretaceous. Pollen data, however, do suggest that angiospermoid morphology appeared by Late Triassic. The possibility of polyphyletic origin of angiosperms is not ruled out.

Keywords: Angiosperms, ancestral forms, fossil plants, origin.

UNDERSTANDING the origin of angiosperms, the largest group of land plants, has excited the curiosity of botanists and palaeobotanists alike for several decades now. The sudden appearance of angiosperms in the fossil record, followed by an almost exponential increase in their diversity, was an 'abominable mystery' to the famous naturalist Charles Robert Darwin. Tracing the origin of this group of spermatophytes needs identification of ancestral forms (that is, primitive angiosperms or first angiosperms) as well as direct ancestors of angiosperms (that is, the group which evolved into primitive angiosperms). In a way it involves recognition of transitional form(s), those that could be taken (or mistaken) for early angiosperms and ancestral group with equal felicity. Unfortunately, satisfactory answers have eluded us so far, though there have been umpteen hypotheses and theories based on pure intuition, speculations, assumptions, presumptions, philosophical deductions, plant fossils, morphological cladistics, molecular sequencing, etc.¹⁻¹³. Almost all gymnospermous groups have been under the scanner, one time or the other, as potential repository of seeds of angiospermy¹⁴⁻²⁰. Even ferns have been considered²¹. Opinions also differ about the nature of primitive flowering plants. Several 'theories' have been propounded. The Euanthial theory^{22,23} proposed that the primitive angiosperm was a small tree or woody shrub with large complex flowers, such as those of magnolias. According to the Palaeoherb theory²⁴, the primitive angiosperm was a small herb or a weed-like plant with small, uncomplicated flowers and rapid lifecycles as in extant Hamamelidiaceae and Piperales. Still another hypothesis postulates that *Amborella* and Nymphaeales (water lilies) are genetically the most primitive angiosperms, and are therefore a basal angiosperm group⁸. It is interesting to note here that impression of a leaf resembling that of extant water lily, *Nuphar polysepala* has been documented from an Early Jurassic dinosaur tracksite in Utah²⁵. With the recovery of mummified and charcoalified, well-preserved angiosperm flowers

through bulk maceration of Late Jurassic and Early Cretaceous samples, there has been renewed interest in early forms of angiosperms, their affinities and their bearing on the unsolved mystery of angiosperm origins.

Why did the angiosperms happen and how; through natural hybridization over a long period of time or through recurring saltations, or through both? We may never be able to decipher what provided the genetic material required for angiospermization. Even the question when and from whom the angiosperms originated may not find an answer till the starting point of angiospermy is first identified or defined. That is to say, we need to know the characters or features that can be used to distinguish a plant as an angiosperm. There are several such characters, but sometimes these transgress taxonomic groups. Two morphological features that substantially demarcate angiosperms are: (i) ovules enclosed in a carpel, and (ii) stamens with two pairs of pollen sacs²⁶. But where do we look for angiospermy in a fossil plant? Does it reside in the leaf, wood, reproductive organ(s), ovule, or in the pollen, or collectively and simultaneously in all these? Preconceptions based on living taxa cloud our judgement. There are at least three schools of thought. One school accepts leaf and pollen morphology as sufficient evidence for the presence of fossil angiosperms^{27,28}. The second school places more emphasis on the continuity of the pollen record^{29,30}. The third school would accept nothing less than the reproductive structures as definite evidence for the presence of angiosperms²⁶. Analysis of the fossil record strongly suggests that various organs within a clade may have evolved at different rates^{31,32}. This naturally raises the question whether all plant organs acquired angiospermy simultaneously, or whether this process happened in stages³³. It has been suggested that the three most fundamental characteristics of the angiosperms, namely, carpel, flower and double fertilization evolved over a period of 100 Ma, beginning with the carpel, followed by double fertilization, and lastly appearance of the flower¹². Probably, there was much experimentation in ancestral clades before origination of angiospermic characters took place. Angiospermization may have embraced

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several groups simultaneously³⁴, such as Caytoniales, Czekanowskiales, Dirhopalostachyaceae, etc. or may have been confined to just one group¹², i.e. the Jurassic seed-ferns. Origin of the angiosperms may not have been a single event. It may even remain a matter of controversy and debate because, unless the first angiosperm was the product of a violent mutation in the parent group, there would have been a long-drawn list of transitionals. Some researchers believe that the number of features shared by the angiosperms strongly negate the hypotheses of polyphyletic origin of angiosperms³⁵, whereas others provide data supporting polyphyletic origin^{36,37}. So, the effort to draw a boundary between an angiosperm and a proangiosperm would be as difficult and as controversial as drawing the Permian–Triassic or any other geological system boundary. In spite of all these odds, efforts continue in this direction, which have been reviewed and compiled from time to time.

Evidence on record conclusively proves the existence of indubitable crown-group angiosperms by the Aptian^{38,39}. Indubitable angiosperm pollen have been reported from Valanginian–Hauterivian³⁰. It is generally believed that evidence for the existence of pre-Cretaceous angiosperms is not conclusive. Does the absence of angiosperm fossils in older strata suggest that angiosperms originated during Early Cretaceous? The answer would be a categorical no, because the absence of data does not record an event. Pre-Cretaceous angiosperms may have inhabited dry uplands⁴⁰, which were unlikely sites for fossilization and preservation. So, how far back in time can we trace putative angiosperm ancestors? Phylogenetic trees based on molecular studies⁴¹ place the origin of angiosperms in the Early Jurassic or even earlier. Dispersed pollen with angiosperm-like morphologies have been reported from the Middle Triassic (242–227 Ma BP) in the Arctic Realm⁴². Though these pollen show superficial similarity with Early Cretaceous magnoliid or monocot pollen, evidence is not unequivocal because a well-developed foot-layer has not been observed. Palaeobotanical evidences available so far suggest that angiosperm-like morphologies may have originated in the Triassic⁴³. Molecular data even suggest that monocotyledon clade separated from dicotyledon clade in the Early Carboniferous⁴⁴.

Sanmiguelia lewisii, a much researched plant of Late Triassic that inhabited the semiaquatic environment, had leaves that were similar to angiosperm leaves; but it is not accepted as an example of early angiosperms as the leaf did not have a definite midrib and no putative angiosperm pollen had been found associated with it. Now that monosulcate, tectate–granulate pollen, believed to be primitive angiosperm pollen, have been recovered from associated pollen organ *Synangispadix tidweli*⁴⁵, does it make *S. lewisii* more likely an ancient angiosperm? Not yet, because *Synangispadix* is supposedly comparable with ginkgopsid strobili and the exine of the pollen is glabrous, similar to the pollen exine of the bennettitales and ginkgoales, and not granulate like that of magnoliid pollen⁴⁶.

Further, *Sanmiguelia* is far too back in time! Some molecular biologists⁴⁷, however, do accept *Sanmiguelia* as an angiosperm ancestor. Leaves of *Furcula granulifera*, also of the Late Triassic, too had angiospermoid venation, but its forked midrib and bifurcated lamina have been declared as purely gymnospermous characters. It has been remarked that if only the undivided type of leaf were known, and if it were a Tertiary fossil, *Furcula* would unquestionably be regarded as an angiosperm on the basis of venation alone⁴⁸. Though the presence of forked midrib and bifurcate lamina has recently been observed in abnormal leaves of cultivated *Eucalyptus* and *Ixora* (S. M. Singh, unpublished), the fact remains that *Furcula* too has so far been not found in association with putative angiosperm pollen. There are sympathizers, who believe that these Late Triassic plants should not be summarily dismissed as angiospermids solely because of their age; there however is a caveat that a great deal of additional data are needed before such affinities can be fully substantiated⁴⁹.

Most angiosperm pollen have columellate–tectate exine and solid, non-laminated nexine (endexine). But so also did the pollen *Classopollis*, characteristic of the extinct conifer family Hirmeriellaceae⁵⁰; the family had no other feature even remotely suggestive of angiospermy. Late Triassic (Norian) records of the pollen *Liliacidites* and *Retimonocolpites* cannot be summarily dismissed⁵¹. The Late Triassic reticulate–columellate pollen of the Crinopolles (crino = lily-like) group are supposed to be reminiscent of *Liliacidites* pollen⁵². Presence of pollen types with reticulate–columellate exine, similar to pollen of some acanthaceous taxa, in the Late Triassic^{27,28,53} further supports the fact that in the pollen at least, angiospermid characters had indeed appeared by the Late Triassic. The suggestion that tricolpate *Eucommiidites*, which extended from Late Triassic into the Late Cretaceous²⁹, may have been an angiospermoid pollen seems to have found some support in the organization of the Cenomanian pollen organ, *Bayeritheca hughesii*. The peltate microsporophylls of this taxon have been equated with the angiosperm stamen and its synangia are supposed to be ancestral to angiosperm pollen sacs⁵⁴. However, this pollen-type has also been observed in the micropyle and pollen chambers of certain gymnospermous ovules, e.g. *Allicospermum retemirum*, *Erdtmanispermum balticum* and *Spermatites pettensis*, and was also produced by other pollen-producing organs, e.g. *Erdtmanitheca texensis* and *Eucommiitheca hirsuta*. These taxa are placed in the order Erdtmanithecales and are believed to have a gnetalean affinity⁵⁵. Comparison of sporangia of *E. hirsuta* with *Arberiella* and *Lithangium* or even *Kendrostrobis*⁵⁵ of the Permian Gondwana flora, however, seems to be a bit stretched. *Arberiella* sporangia have a typical surface topography⁵⁶, which is quite different from that of *Eucommiitheca* sporangia, and are consistently associated with eretmonian male fructifications, *Eretmonia* and *Glossotheca*. Parent fructification of *Lithangium* sporangia is not known, whereas *Kendrostrobis cylindricus* most likely was an sphenophyllalean fructification.

Clavatipollenites is another angiospermoid fossil pollen, which resembles the pollen of extant genus *Ascarina* of the Chloranthaceae⁵⁷. It is not yet known if other organs of the plant that produced this pollen too had angiospermoid characters; primitive chloranthaceous fruits though have been found associated with similar pollen in the Middle Cretaceous of North America. *Clavatipollenites/Retimonocolpites* first appeared in the Upper Berriasian of Spain and became widespread by Barremian, occurring in Australia, China, Europe, central and northwest Africa, North America and Argentina. Records of this genus from the earliest Jurassic need verification.

It thus seems to be reasonably certain that angiospermoid characters did evolve in the leaf and pollen by the Late Triassic, but the presence of an angiosperm or angiosperm-like plant during that period is yet to be substantiated. Molecular evidences for a pre-Cretaceous origin of angiosperms^{44,58,59} also support the view that the angiosperms originated much before their first coherent appearance in the fossil record in the Early Cretaceous.

Where did the angiosperms appear first? They could not have appeared simultaneously at distant locations (*Archaeofructus* in late Late Jurassic or Barremian⁶⁰ of China and angiospermoid pollen in Late Jurassic of France⁶¹), unless a polyphyletic origin induced by some global catastrophe is assumed. No evidence is forthcoming from the fossil record, and parsimony analyses, based on morphological characters, strongly negate the idea of polyphyletic origin of angiosperms²⁶. One would assume that angiosperms originated in the regions where *Sanmiguelia* or *Furcula* flourished, if these were angiospermoid plants at all. But there is a rider. It is generally accepted that the angiosperms are basically a tropical group and hence the 'cradle of angiosperms' could have been located only in a tropical region, for example, somewhere between Assam and Fiji⁶². In-depth analysis of modern distribution of primitive families of angiosperms, such as Degeneriaceae, Winteraceae, Amborellaceae and Monimiaceae has suggested that they may have originated on the Australian Plate of the Gondwana Supercontinent⁶³. There, however, is a suggestive lack of evidence in the fossil floras of the region. The other possible location is South East Asia, including South China¹⁰. Another question that needs to be answered satisfactorily is whether the first angiosperms evolved in higher altitudes⁶⁴, gradually entering the lowland due to climatic shifts⁶⁵, or they inhabited tidal flats of coastal regions¹⁸, or was the environment irrelevant to angiosperm evolution, which may have coincided with evolution of resident insect communities⁶⁶.

Which plant group was ancestral to the angiosperms? Currently, the consensus seems to support the view that it was one of the gymnosperms. Which one? The wood of archaic angiosperms have large tracheids, scalariform pitting and multiseriate xylem rays. The perforations of the vessel members of angiosperms apparently resulted due to dissolution of the pit-membranes of scalariform bordered pits. That means, all such plants which have pycnoxylic wood

are to be left out of consideration as these have small tracheids, bordered pits and narrow xylem rays. These include the conifers, cordaites, taxads, ginkgos, gnetales and glossopterids. Even otherwise the cordaites and glossopterids disappeared by earliest Triassic, too far back in time to be on comfort level with the earliest presumed appearance of the angiospermoid characters, which did not appear for another 15–20 Ma at least. The glossopterids had no presence in Euramerica, the land of *Sanmiguelia* and *Furcula*. *Mexiglossa* from the Middle Jurassic of Mexico⁶⁷, had *Glossopteris*-like morphology but no other details, such as information about wood, cuticle or fertile organs are known.

Like the angiosperms, *Gnetum* and *Welwitschia* too lack archegonia, the only gymnosperms that do so. *Gnetum gnemon* has net-veined leaves similar to those of *Coffea arabica* and its vessels do show scalariform pitting similar to that in the angiosperms. It is, however, to be remembered that the gnetalean *Ephedra* is the only gymnosperm, living or fossil, that shares double-fertilization with the angiosperms. The product of second fertilization in *Ephedra*, however, is additional embryos and not a triploid endosperm as in angiosperms⁶⁸. This is taken as a proof that the gnetales are closely related to the angiosperms; may be they had a common immediate ancestral group. In fact, morphological cladistic analyses group angiosperms along with Bennettitales and Gnetales in a lineage named as anthophytes²⁰. No indubitable gnetaleans older than the enigmatic *Sanmiguelia*, however, are known (except for ephedroid pollen recorded from the Middle–Late Permian^{69–71}), which leaves them out of consideration in spite of the fact that they have vessels in the secondary xylem and double integument in the ovules. The presence of vessels and net-venation in the gnetales could also be due to parallelism rather than indicate a direct relationship with the angiosperms. The vessels of angiosperms, as also those of *Selaginella*, *Equisetum*, *Pteridium* and Gnetales, seem to have originated within the groups, rather than being inherited. It is also a fact that by the time true gnetaleans become identifiable in the fossil record, wood with vessels had already appeared. Molecular studies also suggest that the Gnetales are comparatively close to conifers than to angiosperms^{58,72}. Though the origin of second integument of angiosperm ovule is not fully understood yet, the outer integument of the gnetalean ovule is believed to be ontogenetically different from the outer integument of the angiosperm ovule⁶³. Double fertilization, vessels and leaf morphology may have appeared independently in gnetophytes and angiosperms⁷². The answer to when, why and how the angiosperm family Podostemaceae lost double fertilization may have some bearing on this aspect⁷³. The similarities of Gnetales with the angiosperms may be due to convergence⁷⁴. These data thus confirm morphology-based observations that Gnetales were related to coniferophytes^{2,75}.

The pteridosperms or seed-ferns, believed to have had all the potential seeds of angiosperm ancestry, could not

have been their direct ancestors; the two were separated by tens of millions of years. Remember, we are looking for immediate ancestor(s) of the angiosperms and not trying to decipher their ancestral lineage. The latter can easily be traced back to the first organism produced on the earth. It thus leaves out only Caytoniaceae as a putative ancestor of the angiosperms. The family was present at the right time, but did it have the right credentials? Its wood is not known. The leaf was palmately compound and the leaflets had reticulate venation, similar to that in some of the glossopterids, which were simple leaves. The ovulate organ *Caytonia* was a pinnately branched axis that bore two rows of small, ovule-containing stalked cupules. The cupules were globose, recurved with an opening close to the pedicel. A lip-like structure projected over the opening. Each cupule produced up to 32 small, orthotropous, platyspermic ovules. The micropyles of the ovules faced the opening of the cupule. It has been suggested that the cupule of *Caytonia* was not homologous with the ovary of angiosperms but the complete megasporophyll was equivalent of an angiosperm carpel. If one of the *caytonias* had leaf-like megasporophyll, and if the cupular wall evolved into the outer integument, the *caytonialean* cupule could have been the evolutionary precursor of an anatropous ovule with the leaf-like megasporophyll transforming into the carpel of archaic angiosperms⁶³. And if the *caytonialean* capsule itself was derived by involution of a glossopterid gonophyll⁷⁶, the ancestry of the angiosperms can be traced back to the glossopterids. However, we know now for sure that the glossopterid fructification was a bifacial foliar and not a strobiloid structure⁷⁷, and the glossopterids and *caytonias* were distant by tens of millions of years. The glossopterid lineage did survive the so-called end-Permian catastrophe or extinction event, but there is no concrete evidence to suggest that this lineage had prolonged beyond Early Triassic. This also negates the observation that *Bernettia phialophora*, consisting of a scale-like sporophyll covered with *Welwitschia*-like microsporangia (with ephedroid pollen) or ovules, suggests glossopterid reproductive organs⁷⁸, and hence links anthophytes (Bennettiales + Gnetales + angiosperms) with glossopterids and *Caytonia*.

The cycadeoids, which cohabited the earth with the *Caytoniales*, have been one of the first candidates recommended as the ancestral group of the angiosperms. Initially it was believed that the cycadeoid reproductive organ was like a bisexual flower⁷⁹. Investigation of new material has suggested that it was a bisporangiate cone in which each microsporophyll was so recurved that its tip reached back to the base. The microsporophylls surrounded a conical, ovule-bearing receptacle⁸⁰. The strobilus may have evolved into the flower^{64,81}, such as that of *Tasmannia piperita* of family Magnoliaceae. Cladistic analyses of morphological characters have suggested that the cycadeoids are closely related to the angiosperms⁶. It has been further suggested that certain 'glossopterid' fructifications from South Africa, for example, *Plumsteadia*,

Lerouxia and *Vannus* could have been ancestral bennettiales⁵¹. How far these suggestions are acceptable is difficult to say, as they have taken into consideration subjective interpretations of the nature of the ovuliferous receptacle and the microsporophylls of the cycadeoids, the additional cutinized layer in the seed of presumed bennettitale *Vardekloeftia*, and the organization of 'glossopterid' fructifications. Some combined morphology/molecular analyses seem to suggest that the bennettiales are a sister group to the cycads and do not belong in the anthophytes⁹.

The pentoxylales, which were more or less restricted to the Early Cretaceous and virtually were contemporaries of first identifiable angiosperms, have also been amongst the suitable candidates which have found favour with the cladists. The pollen organ, *Sahnia nipaniensis* has been interpreted to be organized in a flower-like manner⁸². No other organ of the pentoxylales, however, shows a trend towards angiospermy. *Carnoconites*, the ovulate organ of the pentoxylales, has been considered by some cladists as 'ovulate head/receptacle', each ovule supposed to be cupulate, representing a highly reduced megasporophyll that is borne on a stem homologue. Others have interpreted ovulate fructification to be the product of a single sporophyll, and cupulate nature of the ovule to be highly speculative⁸³.

Thus those who believe that we are much closer to the answer on ancestry of angiosperms than we were five decades ago, are being too optimistic. Tracing angiosperm ancestors in the fossil record is proving to be as difficult and as interesting as tracing the lineage of a person from a badly damaged birth register. In fact, we are no better informed about the origin of angiosperms than we were at the beginning of this discussion. Why? Because angiospermy probably did not happen as a one-time event. It gradually evolved over a period of time, different organs probably achieved angiospermy at different times, because huge time intervals are ignored like when theorizing that lyginopterid pteridosperm cupules were forerunners of angiosperm carpel, because too many ifs and buts are involved and, probably also because evolution is being visualized as a docile child not given to tantrums, i.e. as if it follows or has followed some straightjacketed Isaac Asimovean mathematical formula(e).

Cladistic analyses of taxonomic characters and gene sequences, it is claimed, offer a clearly defined, objective and repeatable method for deciphering phylogenetic relationships based on rigorous analysis of empirical evidence. Not all phylogeneticists subscribe to this view. Molecular sequencing is a comparatively new discipline and is still in the process of development and refinement. Though phylogeneticists and cladists both have the same goal, they differ in method, language and philosophy, and hence the results obtained by them are often different. The cladists are also criticized for discarding good taxonomic characters which cannot be fit within the software programs, or are inconsistent with their groups⁸⁴. Cladistic analysis which includes palaeobotanical data further suffers from the inherent weakness of imperfection of information (missing

data) bundled with subjective interpretations of palaeobotanical data. For example, phylogenetic relationship of the glossopterid group of plants will be differently announced depending upon whether the group is scored for a homogeneous or a heterogeneous suite of characters. Interpretations of the *Caytonia* cupule either as homologous with the second integument of angiosperm ovule or as homologous with the angiosperm carpel, will substantially affect phylogenetic hypotheses based on cladistics. Therefore, the so-called support enlisted from shared character analyses favouring Bennettitales and Gnetales as groups most closely related to angiosperms, and probably also to pentoxylales, is suspect. Shared characters can be better understood through analysis of evolutionary trends rather than by numerical analysis³³. Further, if one of the above discussed groups of fossil gymnosperms was ancestral to the angiosperms, an important question regarding whether angiosperm embryo sac could be derived from the gymnosperm archegonium needs to be answered. At the present state of our knowledge, the answer is a categorical no⁸⁵.

To conclude:

1. Angiospermoid morphology apparently appeared by Late Triassic.
 2. Direct ancestor(s) of the angiosperms is(are) yet to be identified.
 3. Basal angiosperms appeared by Late Jurassic (on the basis of pollen data currently available).
 4. Early angiosperms were perhaps herbaceous plants with small flowers; a final word on this issue, however, is not yet available.
 5. Major diversification of angiosperms took place between 130 and 90 Ma BP, simultaneously with diversification of insect pollinators.
 6. Pinales are an unrelated group.
 7. Gnetales seem to be a sister group, and not an ancestral group.
 8. Caytoniaceae is among the suitable candidates; however its pollen was bisaccate and had alveolar exine.
 9. The cycadeoid 'flower' in fact was a strobilus, the microsporophylls of which did not open at all.
 10. Polyphyletic origin also remains a possibility.
 11. The mystery of angiosperm origins still waits for its Monsieur Poirot.
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