



Paleobotany and theories of angiosperms ancestors

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Abstract

This article is a review of works done concerning the origin of angiosperms and how it diversified and dominate the Earth suddenly. The old postulated theories have been discussed and reasons of the angiosperm origin have been mentioned. Molecular evidences and relatives to the angiosperms are clarified. Finally my opinion and suggestions of the origin of the angiosperms mentioned.

Keywords: angiosperms, botany, evolution, paleobotany

Introduction

Angiosperms are the seed dominant group of plants on the Earth. This group has more than 300, 000 species with great morphological diversity (Eames, 1961) ^[18]. This group of plants astonished the botanists and many questions put to understand how these species dominated the land. All the plants belong to this group have common characters, but the most important of which is the flowers with closed carpels enclosed the seeds. These plants appeared suddenly during the mid-Cretaceous and diversified quickly and dominate the Earth. This made the paleontologists started their searches to know how this group emerged. Their works depended mainly on the geological time scales. Paleontologists tried to find any foot prints to explain how the present taxa evolved and how they adapt with the environmental changes happened through the geological time to still exist. In this concern many opinions and theories have been announced to explain how the first taxa of angiosperms evolved. These opinions have been put to explain the sudden appearance of the angiosperm during the middle Cretaceous period. These studies relied mainly in the fossil records founded in the deep layers of the Earth's crust. The fossil record provides some logical important data in answering many questions such as when and where early angiosperms emerged, why flowering plants dominate, and from what group or groups of plants they evolved. Also researchers postulated how the present taxa adapt the land environment. These studies, which known as paleophytology, concentrated on tracing the fossil plant or animal to give clues to understand how these creatures evolved and to understand the previous climate and environment and the gradual adaptation of these plants to the major climate changes happened. From the recorded fossils paleobotanists suggested that the earliest Angiospermous plants are known from the Early Cretaceous Epoch, this timing depends on the presence of pollen grains like those of angiospermous plants discovered in 2013 in Switzerland dates to the Middle Triassic, suggesting that angiosperms may have evolved much earlier than previously thought (Hochuli and Feist-Burkhardt, 2013) ^[26]. Thomas (1936), depending on the fossil records, considered that the origin of angiosperm is a clue and it is great problem to understand plant evolution. Andrews (1963) ^[2] tried to correlate between the two major groups of

plants, gymnosperms and angiosperms. He thought that an extinct group of gymnosperms may be the first step in the emergence of the angiosperms. Hickey and Doyle (1977) used the fossil pollen grains as indicators to trace the line of evolution and diversification of angiospermous plants. They gave some characters of the primitive angiosperms pollen grains such as monosulcate columellate exine and the leaves with small simple pinnately reticulate. Doyle (2012), basing on molecular data, put another character in tracing the origin of angiosperms and said that the first angiosperms were woody plants with pinnately veined leaves beside monosulcate collumellate pollen grains. He proposed that all the angiosperms have monophyletic origin.

From the last century till now, no convinced opinion revealed how this group of plants dominated the Earth suddenly and researches are still ongoing to remove the veil from the puzzle of quick evolution of angiosperms which Darwin called abominable mystery ((Darwin and Seward 1903). These explorations relayed mainly on studying the micro-fossils, especially those of the pollen grains and leaf remains or prints.

Angiosperms

Angiosperms, a group of plants characterized by many features, the most obvious one is the flower (flowering plants). Mostly it appeared more than 130 million years ago and today dominates the Earth, with great variations in morphological, anatomical, chemical, cytological and palynological characters beside the variations in ecological, life forms and habitats. According to the first fossils of flowers and pollen grains noticed dated to the early Cretaceous period in great quantity, made the researchers thought that it is probable that angiosperms actually arose more than that time. Returning to the fossil records of vascular and non-vascular plants which found in the early Devonian-age rocks, the prediction of the first appearance of Angiosperms before that time came to mind (Van der Kooi and Ollerton. 2020) ^[43]. Basing on the conception that ferns, lycopods, horsetails, and early gymnosperms became prominent and dominant during the Carboniferous period i.e. the Mesozoic era, the prediction that the first flowering plants appeared before from the Jurassic period to early in the Cretaceous period (phylum Anthophyta) arose. The

progress and diversification of the angiosperms carried out quickly and became the world's dominant plants. Angiosperms quickly adapted to the Earth environment and inhabit all the different habitats. These diversity within the angiosperms taxa made the taxonomists thought that it originated from a common ancestor and developed quickly in different evolutionary lines. Accordingly many theories about the origin and ancestors of the angiosperms have been postulated, most of these theories tried to understand how the carpels formed to enclose the seeds. In this issue, we will go briefly of the most effective theories.

Theories of the ancestors of the angiosperms

There are many theories postulating the first group of plants which were previous ancestor to the angiosperms. All the theories tried to explain how the megasporophyll closed to enclose the ovules. These theories depend on personal thoughts and imaginations and lack reliable fossil evidences. The origin of angiosperms, till now, is unclear and none of these theories and trials gave real clue to understand how this group of plants erupts. Scientists have attempted to search for possible ancestors of angiosperms through phylogenetic analysis based on fossil, morphological, and molecular data. In these efforts, they concentrated mainly on how the archegonia transformed into carpel containing the ovules. All these postulations can be divided into two groups based on the carpel homologies. The 1st. group known as the Phyllosporous origin, in which the carpel is a foliar homolog called "megasporophyll" and closed gradually forming the carpel. The 2nd. Group the "stachyosporous origin" suggested that the carpels originated from the integration of both the ovular axis and foliar appendage, both together modified giving the closed carpel. Other important postulations have been mentioned to know the group of plants which is ancestor to the Angiosperms such as 1. The Isoetes–Monocotyledon theory 2. The Pteridosperm theory 3. The Coniferales-Amentiferae theory 4. The Gnetales-Angiosperm theory 5. Anthostrobilus (Bennettitalean) theory 6. Neo-Pseudanthial theory 7. The Caytonialean theory 8. The Stachyosporous-Phyllosporae theory beside others. All these theories relied on the fossil records and personal thoughts that the Angiosperms must be a developmental stage of the Gymnosperms. Briefly, we will go through each theory and think about its concept.

1. Isoetes-Monocotyledon theory

Campbell and his associates believed that the angiosperms ancestors are any one of the gymnospermous orders; Isoetales, Lycopodiales, Ferns or any Pteridophyta groups. They considered that the great resemblances between the monocotyledons and Pteridophytes are proof to enforce their theory. They predicted that herbaceous pro angiosperm ancestor appeared first as intermediate between Pteridophytes and monocotyledons and gradually they developed giving rise to the monocotyledons. Campbell (1928)^[10] predicted that the Isoetes may be the taxa which developed giving rise to the monocotyledons. He relayed on the possessing of Isoetes to two types of spores and grows in aquatic environment beside the resemblance of the Isoetes embryo to the angiosperms. This theory has been rejected later on and considered as fantastic theory for lacking any fossil evidences. In fact Linnaeus (1775), before Campbell, has the same thoughts about the Isoetes and

described it as seed plant with linear leaves resembling the aquatic monocots.

Campbell (1928)^[10] was under doubt of his theory for lacking fossil proves and said that in spite of the great resemblance between the Isoetes and some monocotyledons, but evidences are still needed to understand the relations between them especially the origin of flowers from Isoetes sporophylls.

This theory is not acceptable, especially after the opinion of considering the monocotyledons are more advanced than the dicotyledons and the woody trees considered primitive than herbs. Meanwhile the separation between the Lycopodiales and Equisetales for being from different phylogenetic lineage supports the weak relation between them and the monocotyledons.

2. Pteridosperm theory

Many earlier phylogenists accepted the idea of that the angiosperms emerged from the modification of any seed plants like Ferns. They considered that the leaves carrying the seeds are the first step in the carpel formation. This postulation accepted by many authors such as Andrews and Kern (1947)^[11], Arnold (1947), Thomas (1957) and Cronquist (1968)^[12]. This theory is known as Cycadofilicales or seed ferns theory. It considered the similarity between both the fern and Cycad leaves and stems with some monocotyledons leaves and stems are proves to be the ancestors of the Angiosperm. In fact fossils of the Pteridosperms were abundant from the Upper Devonian to Permian of Paleozoic Age. These plants are often monoecious, and unisexual i.e. bear two types of spores, micro- and megasporophylls on the same individual. These sexual organs are not arranged in definite strobili like most the Pteridophytes. Features of stem, leaf and seed, made them logic to be considered as the probable beginner of Bennettiales, the pre- ancestors of the Angiosperm. Many fossil evidences and interpretations discussed the possibility of Cycadales, Bennettiales or any other gymnosperms to be the ancestor of Angiosperms. Therefore, emphasis was given to the Pteridosperms as the possible first step in developing the angiosperms. This theory has been accepted by many phytologists in spite of missing connecting fossil records between the Pteridosperms and angiosperms. They started to correlate the structure of the Pteridosperms with those of the Angiosperm. They explained the double fertilization occurs within the angiosperms with (3n) nucleus endosperm as a result of the reduction of female gametophyte and the flowers as modified gymnosperms cones. Melville (1962) mentioned that the reproductive branch of Glossopteridales (Pteridosperm) is somewhat comparable with the present-day angiosperm Dichapetalum. Cronquist (1968)^[12] tried to solve and interpret the mystery of missing connecting fossils by saying that evolution and development can be jumped and not necessary to be in the same line. The seed ferns (Pteridosperms), which considered as the pre-Angiosperm taxa had seed-bearing cupules and specialized organs that produced pollen. Many plant taxonomists believe that the seed-bearing cupules in some groups of seed ferns could have evolved giving rise the carpels of flowers.

3. The Coniferales-Amentiferae theory

Very early, in the Mesozoic era, the gymnosperms were the dominant flora during the Age of Dinosaurs. During this period

the Angiosperms flowers have been first recorded as fossils which made the scientists turned their thinking to the probability of being the conifers as the first ancestors to the Angiosperms.

This theory was first proposed by Engler (1887 and 1894) and Rendle (1903, 1930). They proposed that the ancestors of the Angiosperms may be any taxon of the higher gymnosperms like Conifers, Cordaite or any higher groups of gymnosperms. They predict that these groups modified to give the primitive Amentiferae group (Casuarinaceae, Fagaceae, Salicaceae ...etc). They considered order Amentiferae the most primitive angiosperm group. They relayed on their postulation to the resemblance of the simple naked flowers and tamens by the conifer strobili. They proved their theory by the Araucaria and Agathis gymnosperms as they have covered seeds as well. The way of fertilization in gymnosperms similar, in great extent to that in Angiosperms, as the pollen grains fall on the megasporophyll and only the pollen tube enter to reach the ovule through the micropyle (Doyle, 1994).

This theory faced with many objections since the Amentiferae flowers, now considered from the most advanced group and developed as a result of reductions. Recent taxonomical studies considered the reduction in the organs found in the Amentiferae as more specialized and the unisexual flowers as more advanced than the bisexual ones. In fact this theory did not gain proper rooting and subjected to many arguments.

4. Gnetales-Angiosperm theory

Another studies of fossil evidence showed that groups of Cycad-like gymnosperms known as Bennettitales and Gnetales (Ephedra, Welwetschia and Gnetum) found in the fossil records long time ago are closely related to Angiosperms. These studies depend on the similarity between the strobili or cones of the Gnetales with the Angiospermous flowers, seeds have two cotyledons, unisexual inflorescence, reticulate leaf venation and the resemblance between the xylem in both groups. This theory first postulated by Richard von Wettstein (1901) and approved by Markgraf (1936)^[29] and Fagerlind (1947a)^[21] and they proposed that it might be common origin of the two groups. The great resemblance in the fertilization between the Gnetales and Angiosperms, made this postulation under consideration. In fact Gnetales precede double fertilization in which two sperms are delivered to the vicinity of the egg, and both sperm nuclei fuse with nuclei from the female parent. In each group, one product is the zygote while in flowering plants; the second sperm typically fuses with two other nuclei, resulting in a triploid nucleus that develops into the endosperm. In Gnetum and Ephedra, the second fusion nuclei are diploid and begin to develop as an extra embryo.

5. Anthostrobilus (Bennettitalean and euanthial) theory

This theory first proposed by Arber and Parkins (1907). This theory suggests that the flowers may originated from bisexual strobilus bearing spirally arranged ovulate and pollen grains leave similar to that in the Bennettitales. Thus, it considered the carpel resulted from a modified megasporophyll (Phyllosporous origin) that closed including the seeds. They considered the bisexual flower of the Magnoliales to be derived from the modification of this structure. The resemblance between the Cycadeoideae, and the Magnolia flower in the arrangement of bract and stamens as well as the cone shape and the Magnolia receptacle made this

postulation acceptable at that time. On the other hand, they found great dissimilarities in stem anatomy, micro- and megasporophylls, seed and micropylar position between the Cycadeoideae and the Angiosperms which made this theory unacceptable afterwards. Arber and Parkins (1907) mentioned that the two groups may have originated from a the same ancestor of seed ferns and diversified in the early history long time ago, while Takhtajan (1980) said that the Magnolophyta is monophyletic and most probable derived from Bennettitales.

6. Neo-pseudanthial

This theory suggests that the carpels in angiosperms rose from an integration between gymnosperms cone axis and megasporophylls (Nixon *et al.*, 1994; 15 Hickey and Taylor, 1996). It stated that the flowers originate from unisexual structures similar to Ephedra. Frolich and Parker (2000) considered the last two theories (Anthophyte and Neo-Pseudanthial) acceptable and can be sisters to Angiosperms or originated from two different parallel ancestors i.e. paraphyletic. They considered Gnetales more closely related to gymnosperms than Angiosperms. The external similarity of Bennettitales with Angiosperms can also be explained in terms of common ancestry of both these groups. Takhtajan (1969) stated that the "angiosperms arose from some very old group of gymnosperms, which must have had primitive secondary xylem of scalariform tracheids at least in the early wood, and primitive bisexual strobili. He continued that the strobili must have been of a type that could have diverged to give rise to the primitive Bennettitalean strobilus and the primitive Angiosperm flower". Furthermore, the primitive Angiosperm like Magnolia lacks vessels in secondary woods closely resembles seed ferns. Thus, Takhtajan found that the most probable origin of Angiosperms could be a Pteridospermous ancestry.

7. Caytonealyan theory

The Caytonealyan theory first proposed by Thomas (1925 & 1936) based on fossil records from the middle Jurassic period. He found that some members of the Caytoniales fossils have anthers arose singly or in branched manners like those in some Angiospermous groups like *Calothamus*, *Hypericum* and *Ricinus communis* flowers. This similarity in the structure of the anthers made Thomas thought that it might be the ancestor of the angiosperms. In fact the Caytoniales shows affinity to the seed ferns more than that of the Angiosperms, especially in the morphology of the ovary-like structure of the Caytoniales which cannot be considered as precursor of the Angiosperm carpels. Stebbins (1974)^[36] gave another explanation to the cupules of the Caytoniales, which are stalked, dehiscent and multi ovulate, to be homologous to the Angiosperms anatropous, funiculated ovules. He considered this resemblance is enough to consider the Caytoniales as the ancestor of the Angiosperm.

8. Stachyosporo-Phyllosporae theory

This theory combining the two lines of proposing how the carpels originate, Stachyosporo and Phyllosporae. It was first proposed by Sahn (1920)^[13] on the basis of supposing differences in ovule position borne on stem (Stachyosporo) or on leaves (Phyllosporae), and it was later approved, redefined and expanded by Lam (1948)^[27]. According to this theory most of the Angiospermous dicotyledons; Archchlamedeae and Sympetalae;

were thought to have ovules enclosed in foliar carpels while the Monochlamydeae Dicotyledons and most of the Monocotyledons were considered to have mega sporangia protected by sterile organs. This theory was rejected and considered unacceptable by Eames (1961) ^[18], according to studies in comparative morphology and anatomy.

9. Durian theory

Scientists started to think about the ecological and environmental conditions which led to the emergence of the Angiosperms. This postulation first proposed by Corner (1949) on the basis of ecology, phytogeography and morphological features of Angiosperms. Corner suggested that the primitive Angiosperms must be originated as mesophytic, tropical Cycad-like tree with compound leaves, with monocarpic ovary and follicle fruits. He supposed that members of the Bombacaceae may be from the primitive Angiosperms. He thought that the primitive Angiosperms must be originated in humid habitats and gradually habituated the terrestrial ones. This theory has been criticized and rejected later by many authors like Eames (1961) ^[18].

According to the geographic origin of angiosperms, where and when exactly the first record of the Angiosperm fossils, a subject still under investigation and not known till now. Some botanists believe that angiosperms first developed in the Northern Hemisphere; others look at the Southern Hemisphere. At that time, all of the world's major landmasses were grouped into a supercontinent called Pangaea. The southern part of this continent is referred to as Gondwana land, and the northern part is called Laurasia. Based on the belief that the first emergence of angiosperms was in wet habitats; what is known about late Cretaceous Angiosperms and their habitats; some scientists suggest that the westernmost, semiarid regions of Gondwana land may be the place where Angiosperms first evolved. The super continent; Pangaea; separated to the new configurations with new climatic regimes and new habitats resulting to the emergence of some primitive Angiosperms.

10. Herbaceous origin hypothesis

Taylor and Hickey (1996) put the main characters of the primitive Angiosperms. They predicted that the primitive members of Angiosperms may be small herbaceous plants with a rhizomatous to scrambling perennial habit. They may have simple morphological and anatomical characters such as simple leaves that with reticulate pinnate to palmate venation, whereas the secondary veins branched dichotomously. The vegetative anatomy included sieve-tube and elongate tracheary elements with both circular-bordered and scalariform pitting and oblique end walls. The flowers arise in inflorescences and not solitary. Pollen grains small in size with monosulcate aperture and perforated to reticulate exine sculpturing. Carpels mostly 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 records, Dilcher (1974) announced the discovery of a new basal Angiosperm family of aquatic plant, Archaeofractaceae. These were probably aquatic herbs and living at the ancient history. Archaeofractus has special characters such as perfect flowers rather unlike those of extant Angiosperms. Cronquist (1968) ^[12], Takhtajan (1969), Stebbins (1974) ^[36] and Doyle suggested many

scenarios to interpret how this group of plants succeeded and dominated the Earth. They correlated the evolution of the Angiosperms with the pollinators and insect evolutions.

Axelrod (1952) ^[9] suggested that the Angiosperms were existed in the early pre-Jurassic period. This opinion gained great acceptance between the paleobotanists as it was supported by fossil evidences. In fact fossils of pollen grains and flowers resemble those of Angiosperms were found in great percentage during the Jurassic time. In the same time they did not accept that the pre Angiosperms was from the gymnosperms because there are many of the gymnosperms have more advanced and complex structures than the Angiosperms.

Recent molecular data about the origin of angiosperms

By the beginning of this century the DNA sequence revealed new relations between the taxa, especially those of the Angiosperm Phylogeny Group (APG). Accordingly new thinking about the Angiosperms pre-ancestors, and relationships between the taxa have been discovered and new data added. Sokolov and Timonin (2007) ^[35] pointed to the importance of considering the molecular data in investigating the ancestors of Angiosperms and to understand the relations between the different groups. They pointed to the monophyly of all the extant gymnosperms which opposed the ancient Angiosperms. This opinion contradicts all the proposed theories of the Angiosperms ancestors to be from the gymnosperms. They thought that the most acceptable theory about the flower is just the male theory. Doyle (2012) found that the early Angiosperms were woody tree, in spite of the early presence of aquatic and simple flowers groups. He found that the early fossils seed plants have molecular relationships with glossopterids, Bennettitales, and Caytonia; these results are consistent with proposed homologies between the cupule of glossopterids and Caytonia and the Angiosperm bitegmic ovule. Jurassic molecular dates for the Angiosperms depending on the fossil record did not sure if the first Angiosperms were restricted to wet forest understory habitats and did not radiate until the Cretaceous. Doyle theory contradicts the herbaceous origin of the angiosperms. Willis and McElwain (2013) ^[46] postulated that the first emerging of Angiosperms was in Israel the place they first recorded Angiosperms fossil pollen grains beside the two places, Morocco and England. Thus Scutt (2018) ^[34] mentioned that the ANA-Grade Angiosperms (Ambrollela, Nymphaeles and Austrobaileya) may provide clues about morphological, ecological, and molecular characteristics of primitive Angiosperms.

Sara Fields (2021) made a study to investigate the most probable factors lead to the diversification and success of the Angiosperms. She reviewed the different theories postulated in the origin and places of probable emergence of Angiosperms and the environmental factors and interactions with the other plant groups. In fact, the early Angiosperms must be adapted to the Earth environment, with strong leaves, efficient vessels, and strong seed coats to overcome drought and variable temperature. The origin of Angiosperms and their Earth invasion, dominance and diversifications will stay need evidences and more investigations.

My own conclusion

According to the previous theories and hypothesis, Angiosperms may have multi origins. These pre ancestors may be from any

gymnospermous or seed ferns taxa, which exposed to different environmental factors in different regions of the world. For that not all the Angiosperms in the same level of evolution and not all the organs developed parallel to each other. Different evolutionary lines must be postulated with the different proposals of the Angiosperms origin and place of emerging. All these theories, combined with the molecular data and fossil records must put in one basket to understand how this group of plants dominated the Earth and to know how to conserve them. Another way of thinking take us to believe that this group of plants arose suddenly as an adaptation to environmental and climatic disorders happened in the last geological centuries. The origin of the Angiosperms can be any gymnospermous plants, which may differ from place to place according to the environmental stresses at that place. Nair (1975) ^[10] proposed that the Angiosperms may evolved from any group of plants with tricolpate or trilete pollen apertures and different lines of evolutions undergone separately resulting the varieties of Angiospermous taxa.

From the different opinions concerning the primitive and advanced characters, the acceptable one is that the monocotyledons are more advanced than the dicotyledons, and the APG systems (I, II, III & IV) found that most of the taxa have common relationships, in spite of being from different taxonomical category. This can take us to consider that the line of evolution not necessary be in the straightway and evolution depends on multiple conditions. To answer the questions, how and when the Angiosperms evolved? Researchers must put in considerations that not all the taxa can adapt to environmental changes in the same way, and each taxa can survive or die. Also, they have to keep in consideration that the origin of Angiosperm may be other taxa which extinct completely in accordance to the great extinction happened during the previous geological times. The second step is the diversification of the Angiospermous taxa which can be correlated to the evolution of insects and some other pollinators.

Now a day, many Angiospermous taxa cannot adapt with the climatic changes happened and under extinction. This fact takes us to more wide thinking about how the environment and climate can change the type of vegetation, distribution and speciation. Meanwhile, the origin of Angiosperm may be multi origins and each one faced different environmental conditions led to the wide spread of them and dominate the Earth with many different characters.

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