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Paleobotany and Theories of Angiosperms Ancestors

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Research Article

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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 evidence 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). This group of plants astonished the botanists and many questions were put to understand how these species dominated the land. Through the geological time scales, fossils played a key stone in discovering the evolutionary lines in the steps of development in all living creatures. Paleontologists tried to find any foot prints to explain how the present lives exist. For a large, well-represented, and widely distributed plant group as the angiosperms, many opinions have been announced to explain how it 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 found in the deep layers of the Earth`s crust. The fossil record provides important data to answer 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 how the present taxa adapt to the land environment. These studies, which are 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. From the recorded fossils paleobotanists suggested that the earliest angiospermous plants are known from the Early Cretaceous Epoch (about 145 million to 100.5 million years ago), pollen grains like those of angiosperm discovered in 2013 in Switzerland dates, suggesting that angiosperms may have evolved, previously thought Thomas (1936) considered that the origin of angiosperm is a clue and it considers great problem to understand plant evolution. Andrews (1963) 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 They said that the oldest angiosperm may have monosulcate columellate pollen grains with small simple pinnately reticulate leaves. 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 monosulcatecollumellate pollen grains. He proposed that all the monophyletic origin.

From 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 Darwin called an abominable mystery ((Darwin and Seward 1903). These explorations relayed mainly on studying the micro-fossils, especially 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 a variety of species, life forms, and habitats. Fossils of flowers and pollen grains noticed dated period, it is probable that angiosperms actually arose more than that time. Fossil records of vascular and non-vascular plants have been found in the early Devonian-age rocks, as mentioned by Van der Kooi and Ollerton (2020). Ferns, lycopods, horsetails, and early gymnosperms became prominent during the Carboniferous period. The gymnosperms were the dominant flora during the Age of Dinosaurs i.e. the Mesozoic era. It is predicted that the first flowering plants appeared before from the Jurassic period to early in the Cretaceous period (phylum Anthophyta). The progress of the angiosperms was

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carried out quickly and became the world's dominant plants.Angiosperms quickly adapted to the Earth's environment and inhabit all the different habitats. It has different sizes, life forms, morphology, and internal structures besides the variability in the flowers, seeds, fruits, and pollen grains. This 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 ancestors have been postulated. 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 group of plants which were the previous ancestor to the angiosperms. These theories are speculative and depend on personal thoughts and lack reliable fossil evidence. till now, is unclear and all the trials to understand of plants erupts are under investigation and research works. Scientists have attempted to search for possible ancestors of angiosperms through phylogenetic analysis data. In these efforts, concentrated on how the archegonia become a carpel containing the ovules. These postulations can be divided into two groups based on the carpel homologies. The 1st. group is 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 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 Stachyospory-Phyllospermae theory beside others. Briefly, we will go through each theory and think about its concept.

1-Isoetes-Monocotyledon theory

Campbell and his associates believed that gymnospermousorders; Isoetales, Lycopodiales, Ferns, or any Pteridophyta groups. They relayed on this theory on the great resemblances between the monocotyledons and Pteridophytes. They thought herbaceous pro angiosperm ancestor appeared first and gradually they developed and dominate the Earth. Campbell (1928) mentioned that the Isoetes may have a possible relationship with the monocotyledons relaying on the possessing of Isoetes to two types of spores and grows in aquatic environment besides the resemblance of the Isoetes embryo to the angiosperms. This theory, later on, was considered a fantastic theory for lacking fossil evidence. In fact, Linnaeus (1775), before Campbell, described the Isoetes as seed plants with linear leaves resembling the aquatic monocots. Campbell (1928) was under doubt of his theory for lacking proves and said that in spite of the great resemblance between the Isoetes and some monocotyledons, but evidence are still needed to understand the relations between them especially the origin of flowers from Isoetes sporophylls.

This theory is not acceptable, especially after 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. This postulation accepted by many authors such as Andrews and Kern (1947), Arnold (1947), Thomas (1957), and Cronquist (1968). This theory is known as Cycadofilicales or seed ferns theory. It relayed on the similarity between the fern and Cycad leaves and stems with some monocotyledons leaves and stems.

In fact fossils of the Peteridosperms were abundant from the Upper Devonian to Permian of Paleozoic Age. These plants are often monoecious, but bear two types of spores, micro-and megasporophylls on the same individual which are not arranged in definite strobili like most the Peteridophytes. Features of stem, leaf, and seed, made their logic to be considered as the probable beginner of Bennettitales. Many pieces of evidence and interpretations discussed the possibility of Cycadales, Bennettitales, or any other gymnosperms to be the ancestor of angiosperms. Therefore, emphasis was given to Pteridosperms as possible first step in developing the angiosperms. Fossil abundance and examinations made most of phylogenists accept this theory at that time, in spite of missing connecting fossil records between the Pteridosperms and angiosperms. They explained the double fertilization occurs within the angiosperms with (3n) nucleus endosperms the flowers as modified gymnosperms cones. Melville (1962) mentioned The reproductiv branc of the Glossopteridales (Pteridosperm) is some what comparable the present-day angiosperms Dichapetalum. Cronquist (1968) sought to unravel the mystery of missing link fossils, and stated that "morphologically, it is the long way from known seeds fern to the angiosperm, but each of differences could logical be bridgeds in cours evolution." Seed fern dating back millions of years from angiosperms. Grasses (Pteridosperms) had seed-bearing cupules and specialized pollen-producing organs.Many plant taxonomists believe that the seed-bearing cupules in some groups of seed ferns may have evolved into carpets of flowers.

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3-The Coniferales-Amentiferae theory

Very early the gymnosperms were dominant flora during the Age of Dinosaurs in the Mesozoic era. 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 ancestors of angiosperms may be any 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 similar, ingreat extent to that in angiosperms, as the pollen grains fall on the megasporophyll and only enters to reach the ovule (Doyle, 1994).

This theory faced with many objections since the Amentiferae flowers, now considered from the 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 was subjected to many arguments.

4-Gnetales-Angiosperm theory

Another study of fossil evidence showed that groups of Cycad-like gymnosperms known as Bennettiltales and Gnetales (Ephedra, Welwetschia, and Gnetum) found in the fossil records a 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 was first postulated by Richard von Wettstein (1901) and approved by Markgraf (1936) and Fagerlind (1947a) and they proposed that it may be the common origin of the two groups. The great resemblance in the fertilization between the Gnetales and Angiosperms, made this postulation under consideration. In factGnetales precede double fertilization in which The two sperm are transmitted to the periphery 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 the other two nuclei, resulting in a triploid nucleus that develops into the endosperm for the seed. In Gnetum and Ephedra, the second fusion product is diploid and begins to develop as an extra embryo.

5-Anthostrobilus (Bennettitalean and euanthial) theory

This theory was first proposed by Arber and Parkins (1907). This theory the flowers may originate from bisexual strobilus bearing spirally arranged to ovulate and pollen grains leave like that in the Bennettitales. Thus the carpel resulted from a modified megasporophyll (Phyllosporous origin). The bisexual flower of the Magnolialesis considered to be derived from this structure. The resemblance between the Cycadeoideae and the Magnolia bract and stamens the cone shape and the Magnolia receptacle made this postulation acceptable. On the other hand, they found great dissimilarities in stem anatomy, micro-and mega-sporophylls, seed, and micropylar position between the Cycadeoideae and the angiosperms which made this theory unacceptable. Arber and Parkins (1907) mentioned that the two groups may have originated from the same ancestor of seed ferns and diversified in the early history a long time ago, while Takhtajan (1980) said that the Magnolophyta is monophyletic and most probable derived from Bennettitales.

6-Neo-pseudanthial

This theory carpels in angiosperms raised from integration between gymnosperms megasporophylls 15 Hickey and Taylor, 1996). It states that the flowers originate from unisexual structures similar to Ephedra. Frolich and Parker (2000) considered the last two theories (Anthophyte and Neo-Pseudanthial) sister to angiopsperms or originated from two different parallel ancestors i.e. paraphyletic to them. They considered Gnetales more closely related to gymnosperms than angiosperms. The external similarity of Bennettitales with angiosperms can also be explained in terms of the common ancestor of these two groups in Pteridosperms. Takhtajan (1969) noted that "angiosperms arose from a very ancient group of gymnosperms which, at least in early wood, must have had primitive secondary scalariform tracheid xylem and primitive bisexual strobili." He maintained that strobili must have been a species that could have split off to give rise to the primitive Bennettitalean strobilus and the primitive angiosperm flower". Also, primitive angiosperm such as Magnolia lack vessels in secondary trees that closely resemble seed ferns. Thus, angiosperms may have evolved from a Pteridosperm ancestor.

7-Caytonealyan theory

The Caytonealyan theory was first proposed by 1936) records period. He found that some members of the Caytoniales fossils have anthers that 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 show affinity to the seed ferns more, especially in Caytoniales which cannot be considered a precursor carpels. Stebbins (1974) gave another explanation to the cupules of the Caytoniales, which are stalked, dehiscent and multi ovulate, to be homologous to the angiosperms anatropous, funiculate ovules.

8-Stachyospory-Phyllospermae theory

This theory was first proposed by Sahni (1920) on supposed differences in ovule position borne on the stem (Stachyospory) or on leaves (Phyllospermae), and it was later approved, redefined and expanded by Lam (1948). 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 organs. This theory was however considered unacceptable by Eames (1961), according to studies

9-Durian theory

This postulation, phytogeography, and morphological features of angiosperms. Corner must be originated as mesophytic, tropical Cycad-like tree with compound leaves, with monocarpic ovary and follicle fruits. He supposed that the Bombacaceae may be from criticized and rejected later by many authors like Eames (1961).

According to the geographic it stills a subject under investigation and has not been known till now. Some botanists believe that angiosperms first developed in the Northern Hemisphere; others face the Southern Hemisphere. At that time, all of the world's major landmasses were grouped into a supercontinent called Pangea. The southern part of this continent is called the land of Gondwana, and the northern part is called Laurasia. Based on the belief that the first appearance of angiosperms was in wet habitats; What is known about Late Cretaceous angiosperms their habitats; Some scientists suggest that the westernmost, semi-arid regions of Gondwana territory may be where angiosperms first evolved.. The supercontinent; Pangaea; separated into new configurations with new climatic regimes and new habitats resulting in the emergence of some primitive angiosperms.

10-Herbaceous origin hypothesis

According to this hypothesis, primitive members of angiosperms were small herbaceous plants with a rhizomatous to scrambling perennial habit. They had 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 both circular-bordered and scalariform pitting and oblique end walls. The flowers arise in inflorescences and not solitary. Pollen grains are small in size with a monosulcate aperture and perforated to reticulate exine sculpturing. Carpels are mostly free, ascidiate (ovules attached proximally to the lid) with one or two orthotropic, bitegmic, crassinucellate ovules and dicotyledonous embryos.

Using the oldest, most complete fossil angiosperm records, Dilcher (1974) announced of aquatic plants, Archaefructaceae. These were probably aquatics herbs and living at ancient history. Archaefructus has special characters such as perfect flowers rather unlike those of extant angiosperms—very elongated, and the stamens are paired. The fruits are small follicles formed from carpels helically arranged. Archaefructus was a submerged plant with thin stems that reached the surface of the water. Pollen and seed organs stretched out above the water. The leaves were probably submerged in water. The seeds probably dispersed in the water and swam towards the shore and sprouted in shallower areas. This is considered the oldest record of an angiosperm flower.. It is distinct family Archaefructaceae, probably extant angiosperms

Axelrod (1952) angiosperms existed in the early pre-Jurrassic period. This opinion gained great acceptance between the paleobotanists as evidence. were found in great percentage during the Jurrassic time. In the same time, they did not accept that the pre angiosperms were 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. Accordingly new thinking about the angiosperms pre-ancestors, and relationships between the taxa have been discovered. Sokolov and Timonin (2007) pointed considering the molecular data in investigating the understand the relations between the different groups. They pointed to the monophylly of all the extant gymnosperms which opposed the ancient angiosperms. This opinion contradicts all the proposed theories of the ancestors of the angiosperms to be from the gymnosperms. They most accepted theory about the flower is just the male theory. Doyle (2012) found that the early angiosperms were a 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 consistent with proposed homologies between cupule of glossopterids, Caytonia the angiosperm bitegmic ovules. 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) postulated that the first emerging of angiosperms was in Israel as they recorded the first angiosperms fossil pollen grains in Israel, Morocco and England dates from around 135 MYA. ThusScutt (2018) mentioned that the ANA-Grade angiosperms (Ambrollela, Nymphaeles, and Austrobaileya) may provide clues about morphological, ecological, and molecular characteristics of angiosperms.

Sara Fields (2021) made a study to investigate the most probable factors that lead to the diversification and success of 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 angiosperms their Earth invasion, dominance, diversifications will stay need evidence and more investigations.

Conclusion

According to the previous theories and hypothesis, angiosperms may be originated from any gymnosperm taxa and exposed to different environmental factors in different regions of world. For that, not all the angiosperms in the same level of evolution, and not all the organs developed parallel each other. Different evolutionary lines must be postulated with the different proposals of the origin place of the angiosperms of emerging. All these theories, combined with the molecular data and fossil records must be 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 takes us to believe this group of plants arose suddenly as an adaptation to environmental and climatic disorders that happened in the last geological centuries. The origin of the angiosperms can be any Gymnospermous plants, which may differ from place to place according the environmental stresses at that place.

Now a day, many Angiospermous taxa cannot adapt to the climatic changes that happened and are 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 that led to the widespread of them and dominate the Earth with many different characters.

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