REVIEW ARTICLE

THE CRADLE OF THE FLOWERING PLANTS

Vijai Malik*

Department of Botany, CCS University, Meerut
Email: gathwalajai@gmail.com

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Abstracts: Angiosperms (Magnoliophyta or Anthophyta), Cycads (Cycadophyta), Conifers (Coniferophyta), Gnetophytes or Gnetales (Gnetophyta) and Ginkgo (Ginkgophyta) are the five major lineages of the extant seed plant. Of these Angiosperms are the most species rich and include more than 13000 genera and 300000 species. The Conifers are second largest group of seed plants with ca. 70 genera and 600 species. The cycads include ca. 9 genera and 129 species. Gnetales include only 3 genera (*Gnetum, Ephedra* and *Welwitschia*) with 90 species. There is single species of *Ginkgo biloba*. Caytoniales, Bennettiales, *Pentoxylon,* Corystosperms and Glossopterids, are the extinct lineages of seed plants. These have been proposed as putative relative and possible progenitors of the Angiosperms (Soltis et al., 2005).

Keywords: Angiosperms, Cradle, Flowering plants, Seed

INTRODUCTION

The first seed plant appeared near the end of devonian (ca. 370 Mya). The Angiosperms are the dominant land plants which have long fossils records going back to earliest cretaceous (ca. 135 Mya). Their fossils increase in abundance as we move through the cretaceous. This group possibly originated during the Jurassic, more than 140Mya. It appears from fossils record (which includes leaves, wood, pollen, flowers & fruit) that angiosperms underwent a major radiation starting in the early cretaceous (Friis et al., 2011). Fossilized pollen documents the presence of the eudicots at the early cretaceous. Major Angiosperm lineages can be recognized in fossils remains by the mid-cretaceous (e.g. water lilies, Chloranthaceae, Magnoliales, Laurales, Monocots and Eudicots were presents). The oldest unequivocal fossils are pollen grain from about 140 Mya. The placement of water lilies near the base of Angiosperms and their early appearance in the fossils records (Friis et al., 2011) should be taken to mean that the first flowering plant were aquatic; instead many of their characteristics can be interpreted as specialization that evolve within this one lineage. Indeed, the likely most basal branch of the angiosperm tree leads to the single living species *Amborella trichopoda* known as first fruit plant. This shrub, endemic to the forest understory of the tropical island of New Caledonia, is thus the probable sister of all ~300 000 other living angiosperms. Recent evidence has shown that *Archaefructus* is one of the earliest and extinct aquatic genus of flowering plants discovered from China. *Archaefructus* includes three described species *viz. Archaefructus liaoningensis* (Sun et al., 1998), *Archaefructus sinensis* (Sun et al., 2002), and *Archaefructus eoflora (Ji et al., 2004).* Sun et al., (2002) called *Archaefructus* as first flower due to its early age although its position and relationship is a matter of controversy.

Which part of the globe constitutes South-east Asia and land of living fossils?

South-east Asia includes the South-eastern part of the Asiatic continent (Burma, Thialand, Indo-China and Malaya) and the Malayan archipelago (Dobby, 1950). In the West, Dobby draws the Northern boundary of South-East Asia north of tropic of cancer including within it upper Burma; for phytogeographical reasons we include also Assam and tropical Southern China.

South-East Asia and the adjoining parts of North East India, East Asia and Melanesia (i.e. region which include four independent countries of Vanuatu, the Solomon Islands, Fiji, and Papua New Guinea as well as French special collectively of New Caledonia and the Indonesian region of Western New Giunea) is a land of living fossils.

What is the cradle of the flowering plants?

According to Takhtajan (1969) *Cradle of Flowering Plants is a region in which flowering plants experienced a long period of evolution during which the principal families and many genera were differentiated. This region may be their centre of origin probably not very far from their birth place.* Takhtajan was of the opinion that angiosperms arose under environmental stress, probably as a result of adaptation to moderate seasonal drought on rocky mountain slopes, in an area with monsoon climate.

The regions in which climatic factors have greatly promoted the diversification of modern flora are the Cape region of South Africa, the Ethiopian highlands, parts of the Indian Peninsula, South-central Mexico, Northern Venezuela, the coast of Equador and the Northern provinces of Argentina.

Takhtajan (1969) in his book "**Flowering plants, origin and dispersal**" described the Cradle of the Flowering Plants under following headings-

1. The tropical origin of flowering plants
2. Cradle of the flowering plants may be between Assam and Fiji
3. Centre of origin or Centre of Survival

*Corresponding Author

1. The Tropical origin of Flowering plants

Some authors consider Cradle of Flowering Plants in high latitude and favor an Arctic or Antarctic origin whereas other favors Cradle of Flowering Plants in the lower latitude of tropics or subtropics. The most widely supported hypothesis suggested by Heer (1868) is Northern polar origin of Angiosperms. According to this hypothesis the Angiosperms originated in the polar region of the Holarctic (The Holarctic is the name for the biogeographic realm. It encompasses all the nontropical parts of Europe and Asia, Africa north of the Sahara, and North America south to the Mexican desert region. This vast region is often subdivided into the Palaearctic (Old World) and Nearctic (New World) subregions) and from here these spread in successive waves across the whole earth. This hypothesis was strongly supported by Saporta (1877), Hooker (1879), Asa Gray, Adolf Engler, Berry, Chaney, and many other palaeobotanist and phytogeographers. Similar view on evolution and expansion of various animal groups have been expressed by Zoogeographer e.g. Mathew in book "Climate and Evolution" (1915, 1939) maintained that the North temperate zone was the chief centre of evolution of terrestrial vertebrates.

Evidence

Polar or generally northern origin of Angiosperms is supported by presence of many genera common to both flora of Eastern Asia and Atlantic states of North America.

Criticism

It is now quite clear that climatic conditions in the Arctic has always been unfavourable for the development of any rich and varied vegetation. According to Edward (1955) the Arctic and Antarctic with their long winters of comparative darkness are most unlikely places for the development of new groups. Croizat (1952) also strongly criticized the idea of Northern origin of Angiosperms. The North Polar Region is particularly poor in fossil records of the cretaceous and tertiary floras. Evidence also indicates that there have never been a tropical warm climate in the Polar Regions and the atmospheric conditions of extremely low temperature and prolonged darkness certainly do not favor development of tropical forests.

The fossil evidence suggests that angiosperms did not establish in the Arctic until the late Cretaceous, since angiosperm fossils from the early Cretaceous (144 million year) are found only at low latitudes i.e. 45^0 N and 45^0 S (Takhtajan, 1969). On the other hand, the Arctic may have been an important site for some level of floral evolution in the late Cretaceous i.e. 95.5-65 million year ago. In both Northern and Southern hemisphere, Angiosperms reached the higher latitude only at the end of the early cretaceous (144 million year, in the Albian), and in these latitudes they did not replace the relict Jurassic type of vegetation until the beginning of the late cretaceous. Thus, Takhtajan was of the opinion that Arctic or Antarctic origin of Angiosperms must be rejected.

During the past century an accepted view was that the flowering plants had originated in all regions of North Hemisphere, from Arctic to Tropic. Seward (1926, 1933) considered this on the basis of fossils discovered of leaves and inflorescence of *Artocarpus* from Lower Cretaceous in Greenland in Arctic. He believed that during that period the climate of this region was warm. On the other hand Krassilov (1982) and Vakhrameev (1978 and 1991) suggested that Atlantic coasts, central Asia and Mongolia are the fountain head of flowering plants. But many scientists are of the opinion that the flowering plants originated in tropical regions and spread towards polar areas during course of rapid diversification. According to this view the area which has largest number of primitive extant angiosperms can be possible cradle home and also center of diversity, where there are large number of species that will be the center of origin.

Stebbin (1974) suggested that tropical rain forest is the asylum into which freshly produced flowering plants somehow migrated and have since been preserved in more or less unchanged.

Another view regarding cradle home of flowering plants is from Schuster (1972), Axelarod (1959, 1970) and Brenner (1996) who believed it is Gondwanaland.

According to Axelarod (1959, 1970) the tropical upland of Gondawanaland with seasonal draught in the early Mesozoic world would have been the best place of flowering plants.

Schuster (1972) considered that because of the presence of luxuriant primitive flora in south east Australia, allowing Lausarian derived flora intermingled with Gondwana flora the cradle of home is Gondwanaland.

Since polar hypothesis for the origin of angiosperms does not explain adequately the present distribution of plants, so many workers turned to seek the cradle of their nativity in the lower latitudes- the tropical and subtropical regions. In this way many authors like Hallier, Diels, Bailey, Axelrod, Thorne etc. came out in the favor of tropical origin of Angiosperms.

Aquatic origin of Angiosperms

After the discovery of *Archaefructus* and *Hyrcantha* from northeastern China Sun et al., (2002) and Dilcher et al., (2007) suggested the possibility of aquatic origin of angiosperms because *Archaefructus* looks like some aquatic extant angiosperms e.g. Alismataceae, Cabombaceae and Nymphaeales. Terada et al., (2005) has suggested that *Archaefructus* may have two aquatic habitats, one in medium shallow water such as that of *A. sinensis*, as its larger size suggests, and the other probably very near the lake bank in very shallow water as the smaller size of *A. liaoningensis* might suggest.

2. Cradle of Flowering Plants may be between Assam and Fiji

According to Hallier (1912) the birth place of Angiosperms is in the basin of Pacific Ocean on the hypothetical continent of Pacifica. He considered that ancestors of Angiosperms might probably be found in places like Andes (from Maxico to Patagonia), the Hawaiian Island, New Caledonia and New Zealand. But recent geological investigations do not support it. According to Bailey (1949) the present floras of Northern Australia, New Guinea, New Caledonia, Fiji and the adjacent areas northward to Southern China provides the largest number of missing links in the chain of Angiosperm phylogeny. According to Axelrod (1959) Angiosperms also appeared to have invaded Northeast Asia gradually from the south during the early Cretaceous i.e. 144 mya. Golenkin (1927) suggested the southern part of the Angara continent (with Oceania) as the possible place of origin of the angiosperms, but unfortunately gave no reasons for the suggestion.

This is very striking that many primitive families which are restricted geographically are found on the islands and borders of the Pacific Ocean. Such primitive families concentrated about the pacific basin are *Magnoliaceae, Degeneriaceae, Himantandracae, Eupomatiaceae, Winteraceae, Austrobaileyacae, Amborellaceae, Gomortegaceae, Lactoridaceae, Calycanthaceae, Trochodendraceae, Tetracentraceae, Lardizabalaceae, etc*. But in number of primitive forms the Eastern part of the pacific basin is clearly inferior to the western part which includes a wide area from Assam, China and Japan to Australia, New Zealand, New Caledonia and the Isles of Fiji (Takhtajan, 1969).

According to Takhtajan (1969) Cradle of Flowering Plants must be sought in Eastern and South-eastern Asia, Australia and Melanesia. Geographical distribution of primitive Angiosperms like Magnoliales shows that it was this part of the world which had been (if not the birth place) the original center of widespread cretaceous expansion of flowering plants.

Most probably 'cradle of the angiosperms' was situated in South-East Asia (including Burma, Thailand, Indo-China, and Malaysia) where greater concentration of primitive Angiosperms families (e.g. Magnoliaceae and Winteraceae fig. 1 & 2) are found (Takhtajan (1969). Thus this area or area near to it was the cradle of Angiosperms. Takhtajan (1969) has suggested that the 'cradle of the angiosperms' occurs somewhere between Assam and Fiji. But it cannot be said with exactly where between Assam and Fiji the area was in which the Angiosperms first developed.

Croizat (1952) emphasized the importance of Malesia as a centre of phytogeographical connections. According to him Malesia is one of the most important phytogeographic zones of the world and from its boundaries all five continents can easily be reached. Thus it is valuable evidence in support of the hypothesis that cradle of Angiosperms was situated somewhere between Assam and Fiji, most probably in the area corresponding to what is now South-east Asia. From South-east Asia, Angiosperms spread over the entire Northern hemisphere. Temperate and subtropical elements were able to reach North America very early by way of North Pacific track across the Bering-Aleutian area. From South-East Asia Angiosperms could well have colonized also the territories of Southern hemisphere. A serious flaw in the South-east Asian center of origin theory, acknowledged by Takhtajan (1969**)** himself, is the lack of fossil evidence. Hughes (1994) has argued directly for the primacy of the fossil record to reveal events of the past.

Komarov (1908) gave a general conclusion which is true for phylogenetic series of higher taxa like genera, families and orders. It states that the geographical distributions of plants must be based primarily on the distributions of series, not on those of isolated species, because these there are a much greater element of uncertainty and chance for species. Study of such series can give not only a picture of their evolution in time, but also the direction of their movement in space. Thus, when analyses of a sufficiently large number of phylogenetic series all produce similar results then, our conclusions for the centre of origin and centre of dispersal true. The more closely they agree, the more certain the correctness of our conclusions. We should not conclude the birth place of angiosperms on the basis of existing geographical distributions of taxa which consist of only distinct isolated representatives. Besides, we should conclude the birth place of angiosperms if distinct taxa form well marked phylogenetic series.

Thus, Takhtajan (1969) has stated that it is impossible to ignore the fact that the primitive members of many groups of angiosperms, especially of the more primitive groups, themselves clearly tend to occur in south-east Asia and the neighboring regions of the western Pacific Ocean basin. In the area between Assam and Fiji grow not just isolated primitive types, but whole groups of closely interrelated genera and even families.

Distribution of some primitive families (Takhtajan, 1969):

The species of Magnoliaceae are concentrated in greater number in east and South East Asia. In America its species are very poor, whereas in Africa they are completely absent. All the 12 genera of this family are found in East and South East Asia and most primitive genera and species are confined to that region. Of the 12 genera of the family only three are found in America viz. *Magnolia, Talauma,* and *Liriodendron*. Certainly the Magnoliaceae came to America from Asia probably by two routes, a northern and a southern. The northern route was taken by *Magnolia* and *Liriodendron*. The southern

route was taken by *Talauma*. The most primitive species of *Magnolia* and *Talauma* are found in Asia including all the main stages of evolutionary development of *Magnolia* with species like *M. griffthii* and *M. pterocarpa* and *M stellata*. The section *Maingola* of genus *Magnolia* is most primitive and is found in Assam and Upper Burma and through Indo-China to the Malayan archipelago with species like *M. griffthii* (Assam and Upper Burma), *M. paeliana* and *M. guatavii* (Assam), *M. annamensis* (Annam), *M. maingayi* (Malayan peninsula and Sarawak), *M. aequinoctialis* (Sumatra) and *M. macklotii* (Sumatra and Java). *Manglietia*, a South Eastern genus is very close to *Magnolia* and also in some respects it is more primitive than *Magnolia*. *Manglietia* is found from the Eastern Himalayas, Assam and South China through Thialand and Indo-China to Java with most primitive species of this genus in continental part of South-East Asia (Fig-1).

The family Winteraceae are rival in its primitiveness with Magnoliaceae. The largest and most primitive genus *Drimys* of this family is found in Philippines, Borneo, Celebes, Amboina, New Guinea, Eastern Australia, Tasmania, Juan Fernandez, and America from Mexico to Cape Horn. Next primitive genus of this family is *Bubbia* whose species are mostly found in old world i.e. New Guinea, Queensland, Lord Howe Island, New Caledonia, and Madagascar (Fig-2.).

The Degenariaceae are endemic to Fiji and Himantandraceae occur in North East Australia, New Guinea, and the Mollucas.

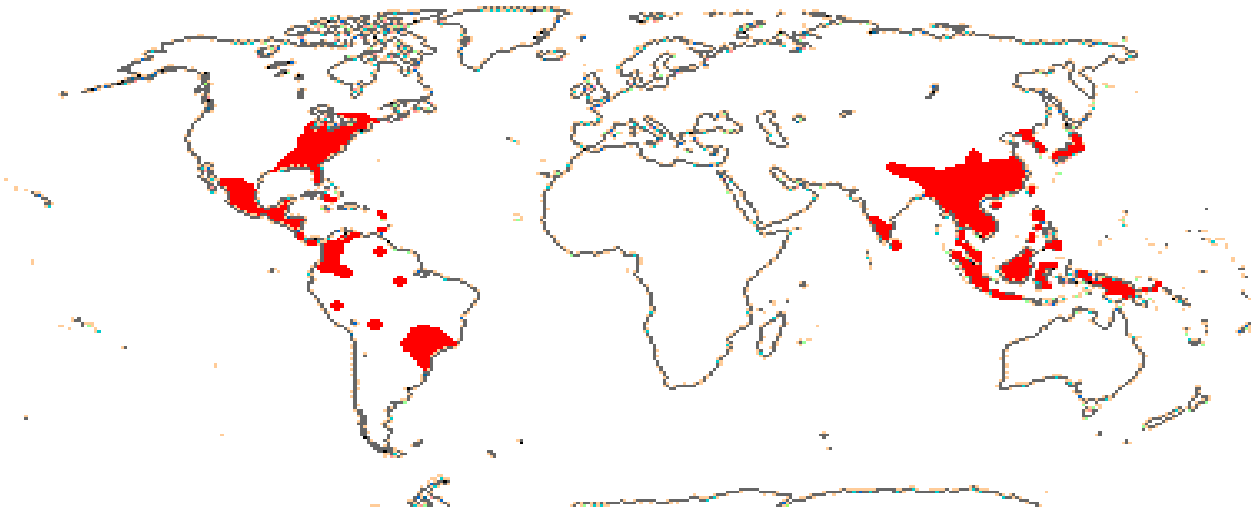

Fig-1. Distribution of Magnoliaceae in world

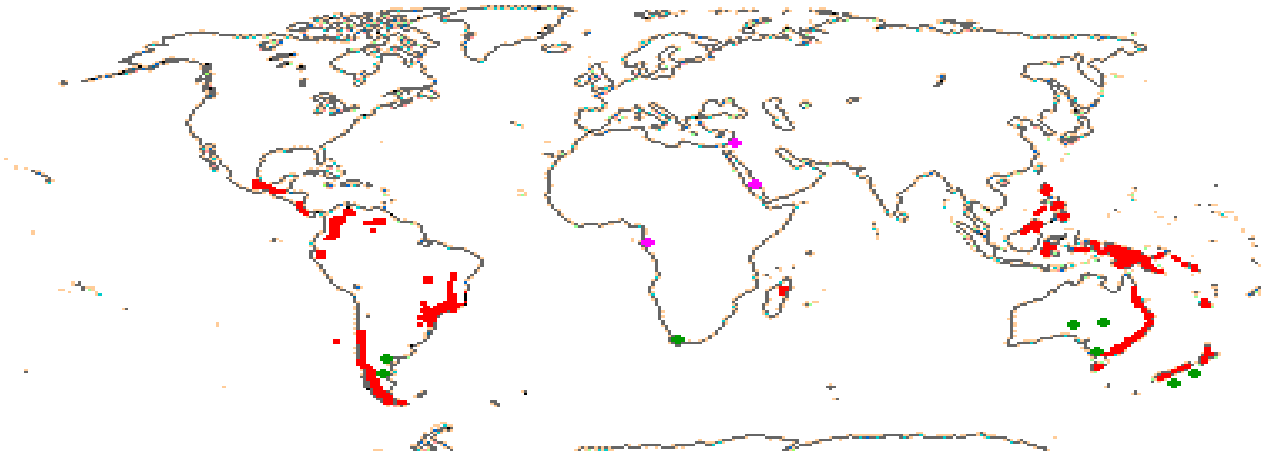

Fig-2. Distribution of Winteraceae in world

Fig-3. Distribution of Amborellaceae in world

North-east India as cradle of Flowering plants

The flora of India represents taxa of different countries like Afghanistan, Bhutan, Bangladesh, China, Nepal, Pakistan, Myanmar, Malaysia, Indonesia, Thailand and some European countries like Africa, America, and Australia etc. Himalayan region of India is supposed to be much younger than Deccan Peninsula and North East India, as it harbors most of the advanced families. Assam, North East India, Deccan Peninsula etc are the older phytogeographical regions of India and the age of these regions is more or less identical in age with Sri Lanka, South West China and Malaya Peninsula. North-East India shows its floristic relationship with Myanmar, South West China and Malaya Peninsula. It has the richest reservoir of plant diversity in India and forms part of one of the 'biodiversity hotspots' of the world. Takhtajan (1969) has suggested North Eastern region of India as the true "cradle of flowering plants" because

1. Primitive plant families such as Magnoliaceae, Lauraceae, Hamamelidaceae, Degeneriaceae, Tetracentraceae and Lardizabalaceae are well represented here.
2. This region is regarded as the place of origin of progenitors of many cultivated crops.
3. North-east India is richest in biological diversity at community level, at the species level, and in endemics.
4. North-east India is recognized as refugium of flowering plants with higher evolutionary activities and active center of speciation.

India is considered as a sanctuary of primitive flowering plants. North-eastern region of India (Assam & Arunachal Pradesh) contain more than 130 primitive Angiosperms like *Altingia excelsa, Aspidocarya uvifera, Betula alnoides, Decaisnea insignis, Euptelea pleiosperma, Exbucklandia populnea, Haematocarpus validus, Holboellia latifolia* var. *angustifolia, Houttuynia cordata, Magnolia caveana, M. griffithii, M. hodgsonii, M. pterocarpa, Pycnarrhena pleniflora, Tetracentron sinense* and species of *Camellia, Magnolia, Michelia, Rhododedron*, orchids and several wild and economic plants. This suggests that perhaps in this region evolutionary development of Angiosperms have taken place. Primitive 9 families with their genera in India (Rao, 1997) are given in the following table-1.

Table 1.

Name of Family	Name of Genera
Magnoliaceae	*Magnolia, Manglictia, Michelia, Pachylarnax, Paramichelia, Talauma,*
Tetracentraceae	*Tetracentron*
Illiciaceae	*Illicium*
Eupteliaceae	*Euptelea*
Annonaceae	*Alphonsea, Annona, Artabortys, Cyathocalyx, Desmos, Fissitigma, Friesodielsia, Goniothalamus, Melodorum, Miliusua, Mitrephora, Orophea, Polyalthia, Trivalvaria, Unona, Uvaria*
Myristicaceae	*Horsfieldia, Knema, Myristica*
Schizandraceae	*Kadsura heteroclita*
Lauraceae	*Actinodaphne, Alseodaphne, Beilschmiedia, Cinnamomum, Cryptocarya, Dehaasia, Endiandra, Lindera, Litsea, Machilus. Neocinnamomum, Persea,*

	Phoebe
Chloranthaceae	*Chloranthus elatior*

According to Hutchinson (1969) *Magnolia pterocarpa* of North-East India is perhaps the most ancient species of living Angiosperms. But according to recent view *Amborella trichopoda* is the first fruit plant.

Recent View

Eastern Asian origin of Angiosperms

Archaefructus is one of the earliest and extinct aquatic genus of flowering plants. It was discovered from China in the past decade. It had very primitive floristic characters of ancient angiosperms. It was found in western Liaoning and its neighboring areas in the East Asia at northern middle latitudes. Thus, logically the place of origin (or one of the places) with the earliest diversification of ancient angiosperms was western Liaoning in East Asia. On this basis Sun (1998) and Sun et al. (2002) proposed the hypothesis of "Eastern Asian Origin of Angiosperms". According to this hypothesis the ancient angiosperms might first occur at the middle latitudes of East Asia, covering the territory of western Liaoning, Mid-Eastern Monglolia, Russian Baikalia and Far-East (Fig-4). This region probably contained some difficult paleoenvironmental challenges under which plants might live, such as volcanic activity, arid or semiarid climates, often isolating plant populations during pre-Cretaceous time (Sun et al., 1998, 2002).

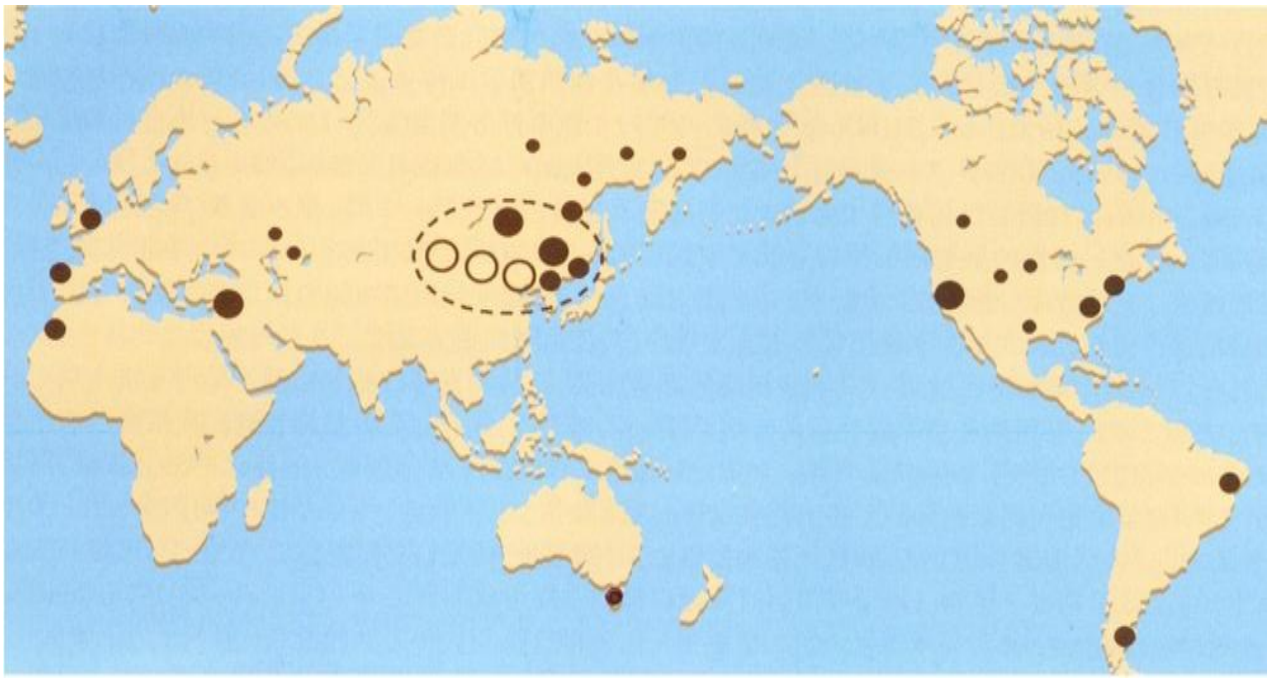

Fig-4: Sketch of a suggested center of origin of angiosperms in the world (redrawn from Sun et al., 2001, 2002)

Centre of Origin or Centre of Survival

Takhtajan considers south-east Asia (including Burma, Thailand, Indo-China, and Malaysia) to be the most likely region where angiosperms originated, since this is the region where the highest abundance of primitive angiosperms occurs at present.

Descendants of the first angiosperms may have dispersed far from their point of origin (Takhtajan, 1987). So current distribution of Angiosperms may not necessarily be similar to those of the past. In a phylogenetic series, "the most advanced members are farther from the centre of origin" (Takhtajan, 1987). Thus, it is not necessary that all primitive Angiosperms concentrated in South-East Asia. They are also found outside South-east Asia. Primitive forms are not only found within the area of their origin of taxa but they are also found outside it. Taxa may have been completely disappeared from the area of their origin, but they may be persisted and found far away from the area of their origin. Amborellales are now only found New Caledonia, which emerged from ocean ca. 37 million years ago. *Amborella* must have lived elsewhere for a long time before it dispersed to New Caledonia and became extinct in its original area of occurrence (Christenhusz, et al., 2017). Thus, on the basis of present distribution of living angiosperms it can be concluded that the islands and peninsulas of South-East Asia is mere a refugium or centre of survival, of primitive angiosperms and it is not the cradle and initial distribution centre of angiosperms.

Why America, Africa and Madagascar are not cradle for flowering plants?

According to Takhtajan (1969) the extensive region between Assam and Fiji cannot be simply a 'refugium' of ancient Angiosperms, or in other words,

merely a centre of their survival. In fact during the Mesozoic and Cainozoic climatic and general physiographical conditions were no more stable in the area of east and South-east Asia, Australasia, and Melanesia, than in tropical America or even in tropical Africa.

Inspite of that, the extremely rich flora of tropical America is significantly poorer in primitive angiosperms than the flora of the western part of the Pacific basin, and the flora of tropical Africa is almost devoid of them.

It is difficult explain why no members of the Magnoliaceae, Winteraceae, Himantandraceae, Dageneriaceae or any other archaic family have survived in the African flora, if they had existed there previously. Of the family of the Magnoliales, only the Canellaceae and the Annonaceae are represented in Africa. In Madagascar besides Canellaceae and Annonaceae, Winteraceae (*Bubbia perrieri*), and Chloranthaceae (*Ascarinopsis coursii*) as well the endemic family Didymelaceae are also found.

Although primitive Angiosperms are appreciably numerous in America than in Africa and Madagascar, even in America they are still far fewer and, as a rule, more specialized than in East and South-East Asia. The American Members of Magnoliaceae and Winteraceae (appear to be more advanced than those in South-East Asia), for examples, are markedly inferior in number and diversity to those of the Western Pacific (South-East Asia) and are representative of the less primitive forms (Takhtajan, 1969). So America, Africa and Madagascar are not possible sites for the "cradle of the angiosperms".

Several primitive Magnoliales and other living fossils grow in Assam, Upper Burma, Yunnan, Mountain region of Thialand, Loas, and Vietnam, Malesia and Melanesia. If one considers this striking concentration of primitive Angiosperms and has visited some of these lands oneself, one is force to conclusion that this region of the world is a fragment of the ancient area which was first colonized by the Angiosperms. But it has not been proved and it is very likely that the initial center of Angiosperm expansion and their center of origin was situated somewhere in or near this region.

Drawback

The weak point of South-east Asian origin of the Angiosperms is the absence of any direct evidence in the geological records. Paleobotanical studies are not sufficient to locate the birth place and primary centre of the Angiosperms.

Complete authentic remains of Angiosperms are found only from early cretaceous. These remains are very fragmentary and very few. These remains do not tell about the location of the centre from which they initially spread. All the available evidence indicate that Angiosperms spread from low latitude to high latitude and not in opposite direction. The history of the Angiosperm of tertiary period are too fragmentary that it cannot serve as material for phylogenetic and phytogeographical analysis in the same way as living Angiosperms living today.

Epilogue

Darwin in his famous letter to Joseph Hooker in July of 1879 described the Cretaceous diversification and subsequent rapid rise of flowering plants (angiosperms) as an "abominable mystery": how could they have achieved worldwide ecological dominance by early Paleogene times when the oldest angiosperm fossils are only Cretaceous in age?. The father of evolutionary theory could not fathom this rapid diversification and rather invoked the idea that 'there was during long ages a small isolated continent in the Southern hemisphere, which served as the birthplace of the higher plants'. However, recent phylogenetic and palaeobiogeographical analyses have suggested Triassic origin for the stem angiosperms. Takhtajan (1969) concluded that the original center of distribution was situated somewhere between Eastern India and Polynesia. In all probability it was the part of the world that is today South-East Asia. Probably this conclusion is right but it cannot claim to be certain. After the discovery of *Archaefructus* Sui Ge et al. (1998) suggested that the Eastern Chin dawning site or one of the regions of the origin site of flowering plants. She remarked that, progress in the study of dawning process of flower has always been insight and the discovery of *Archaefructus* is only the first step in demystifying the 'abominable mystery' put by Darwin (1859) on the early evolution of flowering plants.

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