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Antiquity and migratory paths of angiosperms in India

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ABSTRACT

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In India the earliest angiospermous plants are known in the form of pollen/fruit or ?flower from the Lower Cretaceous (Aptian) of Rajmahal flora. Unfortunately, the Lower and Middle Cretaceous records of angiosperms from India are very poor as compared to those in other continents. The definite records of angiosperms started appearing from the Lameta flora considered as Maastrichtian in age. During the Upper Maastrichtian-Danian they became the most dominant element of the flora. An influx of Southeast Asian elements could only be noticed in the beginning of the Neogene. During upheaval of the Himalayas, temperate angiosperms which were growing luxuriantly in the nearby areas of Tibet and Southwest China, invaded the Himalayan part of India under the prevailing favourable conditions.

Key-words—Fossil records, Cretaceous, Tertiary, Flowering plants, Palaeogeography, Palaeoclimate.

भारत में आवृतबीजियों के पुरावशेष एवं प्रवासी पथ

आर.सी. मेहरोत्रा

सारांश

भारत में सबसे पहली आवृतैकबीजी वनस्पतियाँ राजमहल वनस्पति-जात के निम्न क्रिटेशस (एप्टियन) से पराग/फल या ? पुष्प के रुप में ज्ञात हैं। दुर्भाग्यवश, भारत से प्राप्त आवृतबीजी के निम्न एवं मध्य क्रिटेशस अभिलेख अन्य महाद्वीपों की तुलना में अत्यंत अल्प हैं। लमेटा वनस्पतिजात से आवृतबीजियों के निश्चित अभिलेख मिलने शुरु हुए जिन्हें काल के रुप में मास्ट्रीच्टियन माना जाता है। ऊपरी मास्ट्रीच्टियन-डेनियन के दौरान ये पेड़-पौधों के सर्व प्रमुख तत्व बन गए। नियोजीन के प्रारंभ में दक्षिणपूर्वी एशियाई तत्वों का एक अंतर्वाह ही अवलोकित किया जा सका। हिमालय के प्रोत्थान के दौरान शीतोष्ण आवृतबीजी जो तिब्बत एवं दक्षिण-पश्चिम चीन के नजदीकी क्षेत्रों में प्रचुर मात्रा में उग रहे थे, ने प्रबल अनुकूल स्थितियों के अंतर्गत क्षेत्र आवासित कर दिया।

संकेत-शब्द—जीवाश्म अभिलेख, क्रिटेशस, टर्शियरी, पुष्पीय पेड़-पौधे, पुराभूगोल, पुराजलवायु।

INTRODUCTION

MOST of the herbivorous animals, including humans depend heavily on angiosperms or flowering plants for food and many other useful products. Their utility to man has created interest in their origin, evolution and migration. It is very difficult to define an angiosperm, however, complete encloser of the ovules in a carpel is considered as one of the most important characters for its identification. The other diagnostic features are reticulate venation of leaf, woods with vessels, double fertilization, presence of companion cells in the phloem, tectate-columellate pollen with non-laminated endexine and presence of stamens and carpels on the same floral axis.

A few decades ago, the origin of the angiosperms was thought to be a mystery but in the recent years attempts have been made by various workers (Dilcher, 2001; Doyle, 2002) to solve the problem after combining the fossil data with new molecular information. Though there are several records of Precretaceous angiosperms based on the reticulate venation

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of leaves (Harris, 1932; Cornet, 1986, 1992), woods having vessels (Kräusel, 1928), fruits/seeds and flower like structures (Wieland, 1929; Cornet, 1986, 1992), along with columellate – tectate pollen grains (Rouse, 1959; Cornet & Traverse, 1975; Cornet, 1989; Hochuli & Feist-Burkhardt, 2004), none of them shows definite characters of angiosperms and are, therefore, discarded.

At present the oldest and definite angiosperm records are known in the form of reticulate monosulcate pollen grains known from the Valanginian or Hauterivian of Israel and Italy (Doyle, 2002, p. 174). The earliest definite angiospermous flower named *Archaefructus* Sun *et al*. is known from the Lower Cretaceous (Barremian-Aptian) sediments of Yixian Formation, Liaoning, northeast China (Sun *et al*., 1998). Its two species, namely, *A. liaoningensis* Sun *et al.* and *A. sinensis* Sun *et al*. are complete plants from roots to fertile shoots (Sun *et al*., 2002). These are probably submerged aquatic plants because of their dissected leaves and being found in a lake deposit. The reproductive axes of these plants lack petals and sepals but bear stamens in pairs below conduplicate carpels (Sun *et al.*, 2002).

EARLIEST (LOWER CRETACEOUS) RECORDS FROM INDIA

The Lower Cretaceous records of angiosperms in India are unfortunately very poor. The earliest reports are from the Rajmahal Hills, Jharkhand, the age of which is considered as Lower Cretaceous (Aptian; Tiwari & Tripathi, 1995; Banerji, 2000). First of all Sahni (1932) described *Homoxylon rajmahalense* Sahni from there and considered its affinities with vessel less members of Magnoliales. Gupta (1934), Hsü and Bose (1952) and Bose and Sah (1954) have renamed it as *Sahnioxylon rajmahalense* Bose & Sah showing its affinities with Bennettitales. Later on, Vishnu-Mittre (1956) described a pollen grain, *Sporojuglandoidites jurassicus* Vishnu Mittre, from there. The surface of the grain shows number of pores in the exine and was compared with juglandoid grains. Potonié (1960) raised doubt over its pollen grain character after examining its only specimen. In the last decade Tiwari and Tripathi (1995) reported angiospermous pollen, *Retimonocolpites* Pierce and *Clavatipollenites* Couper, from the same sediments. As far as records of megaremains are concerned, Sharma (1997) described an early angiosperm fructification which resembles *Lesqueria* Crane & Dilcher and *Archaeanthus* Dilcher & Crane known from the Middle Cretaceous of U.S.A. (Crane & Dicher, 1984; Dilcher & Crane, 1984). Subsequently, Banerji (2000) described an angiospermous fruit and a questionable flower from the same beds. The fruit, *Sonajoricarpon rajmahalensis* Banerji, is a follicle or pod with many seeds and resembles the fruit of *Butea frondosa* of Fabaceae. As the family Fabaceae is quite ‘advanced’ and the study is based on a solitary specimen, the authoress has provisionally placed it under the form genus *Sonajoricarpon* Banerji. The flower like structure was described without assigning any name to it due to its poor preservation. These are the only reports of angiospermous fossils from the Rajmahal flora which is otherwise very rich and dominated by pteridophytes and gymnosperms.

MIDDLE-LATE CRETACEOUS RECORDS FROM INDIA

It is very significant to note that there is not even a single record of megafossil from the Middle Cretaceous sediments of India though by this time rich angiospermous assemblages are known from similar deposits of Europe, N. America, S. America and Australia (Mehrotra, 2003). It is usually accepted by botanists that once angiosperms evolved, they superseded the other groups of seed plants (gymnosperms). If they evolved in India during the Lower Cretaceous, they must have been dominant in the Middle to early Late Cretaceous flora. But definite angiospermous records started appearing from the Lameta flora of Nand-Dongargaon area which is Maastrichtian in age (Mohabey *et al*., 1993). According to Raju and Mishra (1996), the absence of angiosperms in India after the Albian and before the Maastrichtian could be due to marine deposits which are usually devoid of plant fossils.

The Lameta flora which is otherwise dominated by algal forms, includes one palm leaf and two dicot woods belonging to Lecythidaceae and Sapindaceae (Kar *et al*., 2004). Angiosperms can be seen as the most dominant element (about 68%) in the Deccan Intertrappean flora which is considered as Upper Maastrichtian-Danian in age. The reason of their sudden abundance could be due to the link of India with Africa via Greater Somalia during the Campanion-early Maastrichtian (Chatterjee & Scotese, 1999; Mehrotra, 2003), however, the hypothesis needs more evidences to corroborate. The flora is represented by all the possible plant parts, viz. woods, leaves, fruits, seeds, roots, petioles, peduncles, infructescences and flowers, etc. They are equally represented by both monocotyledonous and dicotyledonous taxa. The monocots are dominated by palms though Pandanaceae, Cyclanthaceae, Araceae, Xyridaceae, Smilacaceae, Musaceae, Zingiberaceae, Cannaceae, etc. are also known. Palm woods occur profusely in the field but are difficult to be assigned to their natural genera. However, some of the taxa that have been identified, are: *Areca*, *Borassus*, *Cocos*, *Hyphaene*, *Nypa*, *Arenga*, *Chrysalidocarpus*, *Livistona*, *Licuala*, etc. (Bande *et al*., 1988; Mehrotra, 2003). The dicotyledonous forms are very rich and mostly occur in the form of woods. The important and reliably identified genera are *Dracontomelum* and *Lannea* of Anacardiaceae, *Leea* of Ampelidaceae, *Polyalthia* of Annonaceae, *Aristolochia* of Aristolochiaceae, *Bursera* and *Canarium* of Burseraceae, *Lophopetalum* of Celastraceae, *Garcinia* of Clusiaceae, *Terminalia* of Combretaceae, *Tetrameles* of Datiscaceae, *Diospyros-Maba* of Ebenaceae, *Elaeocarpus-Echinocarpus* of Elaeocarpaceae, *Mallotus* and *Phyllanthus* of Euphorbiaceae, *Homalium* and *Hydnocarpus* of Flacourtiaceae, *Gomphandra-Stemonurus* of Icacinaceae, *Barringtonia* of Lecythidaceae, *Lagerstroemia* of Lythraceae, *Heynea, Turraeanthus* and *Walsura* of Meliaceae, *Artocarpus* of Moraceae, *Melaleuca-Callistemon, Eucalyptus, Syzygium* and *Tristania* of Myrtaceae, *Zizyphus* of Rhamnaceae, *Atalantia-Limonia* of Rutaceae, *Nephelium* (*sensu lato*) of Sapindaceae, *Ailanthus* and *Simarouba* of Simaroubaceae, *Sonneratia* of Sonneratiaceae, *Dombeya* and *Sterculia* of Sterculiaceae, *Grewia* of Tiliaceae, *Trapa* of Trapaceae and *Gmelina* of Verbenaceae (Bande *et al*., 1988; Mehrotra, 2003).

TERTIARY RECORDS

During the Tertiary the earliest plant fossil records are known from the Upper Palaeocene-Eocene sediments. In northeast India they are described from the Tura Formation of Garo Hills, Lakadong Sandstone Formation of Khasi Hills and Therria Sandstone Formation of Jaintia Hills, Meghalaya (Mehrotra *et al*., 2005), while in western India they are from the Panandhro and Rajpardi Lignite Mines of Kutch (Lakhanpal *et al*., 1984; Mehrotra, 2003) and Fuller's Earth deposits of Rajasthan (Lakhanpal & Bose, 1951; Kaul, 1951). Among the monocots, *Cocos, Nypa* and *Pandanus* continued from the Deccan Intertrappean flora, while among the dicots *Artocarpus, Atalantia, Garcinia, Grewia, Lagerstroemia, Sonneratia, Syzygium, Terminalia,* etc. continued in the flora. Some new forms, such as, *Bauhinia, Bombax, Calophyllum, Cinnamomum, Ficus, Mangifera, Mesua, Nelumbo, Phoebe, Pterocarpus,* etc. also appeared in the flora which is dominated by dicots. Palms are very few and the definitely identified one is *Nypa* only.

The dicot forms became richer during the Oligocene (Awasthi & Mehrotra, 1995) but the palms are represented by *Nypa* only (Mehrotra *et al*., 2003). The new forms are *Saccopetalum, Kayea, Pterygota, Santiria, Parishia, Entada, Rhizophora, Vernonia, Memecylon, Avicennia, Alstonia, Myristica, Apollonias, Bridelia,* etc.

After the Oligocene, an influx of Southeast Asian elements has been observed in the fossil records as Dipterocarpaceae, a typical Southeast Asian family, could be seen in the fossil records at the beginning of the Neogene (Awasthi, 1992; Guleria, 1992). The other forms, such as, *Gluta* and *Swintonia* of Anacardiaceae, *Sindora, Koompassia, Afzelia-Intsia,* etc. of Fabaceae entered India along with dipterocarps. It proves that the land connections between the Indian and Asian plates were completely established by the end of Oligocene/beginning of Miocene after the collision of the former with the latter at the end of Eocene.

Up to the Palaeogene the flora of India was predominantly tropical as most of the forms found as fossils are growing at present either in northeast India or in the Western Ghats or Myanmar where the climate is tropical with a uniform temperature throughout the year, annual rainfall > 2000 mm and a long rainy season. The wide distribution of the tropical rainforest family Dipterocarpaceae throughout India during the Neogene indicates a more or less uniform tropical moist climate throughout peninsular India during the period (Guleria, 1992).

During the second phase of the upheaval of the Himalayas in the middle Miocene, some small fresh water basins were formed in the Tibetan side in which the Kargil molasse and other Miocene sediments of Ladakh-Karakoram area were laid down. The occurrence of fossil temperate elements of Sino-Japanese origin, such as, *Trachycarpus* and *Prunus,* in the same sediments indicates that the temperate conditions started appearing in the Himalayas during the period. It has been observed that most of the temperate taxa of the Neogene flora of Yunnan and Tibet of China have been found in the Upper Plio-Pleistocene flora of Karewa of Kashmir from where most of the taxa spread westwards and southwards due to the development of favourable climatic conditions (Mehrotra *et al*., 2005).

QUATERNARY RECORDS

The third phase of the upheaval of the Himalayas took place in the Pleistocene due to which the height of Kashmir Himalayas had been uplifted. As a result some of the Chinese taxa disappeared/migrated to those areas in the Himalayas which were altitudinally lower. Nowadays, some of these taxa, such as, *Acer, Betula, Castanopsis, Desmodium, Machilus, Magnolia, Myrica, Quercus, Rhus, Rosa, Sorbus, Symingtonia, Viburnum,* etc. can still be found in the Eastern Himalayas. Thus, the fossil plants from the Karewa of Kashmir and Neogene of China are the major constituents of the present day subtropical/temperate angiospermous elements of India (Mehrotra *et al*., 2005).

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