Review of Palaeobotany and Palynology 166 (2011) 63–68

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Research papers

Eocene out-of-India dispersal of Asian dipterocarps

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ARTICLE INFO

Article history:
Received 16 February 2011
Received in revised form 11 April 2011
Accepted 9 May 2011
Available online 23 May 2011

Keywords:
Early Eocene
Dipterocarpaceae
Biogeography
Resin chemistry
Palynology

ABSTRACT

The Dipterocarpaceae, a well known and economically important family of trees of the tropical rain forests of Asia, comprise over 470 species. These angiosperm trees contribute to 30% of the total area in typical lowland evergreen forests in Southeast Asia. Despite their remarkable diversity and regional ecological dominance, the origins and phytogeographical evolution of the family are poorly understood. The earliest dipterocarp fossils recorded in SE Asia come from Oligocene (34–23 Ma) sediments of Borneo. Here, we report an occurrence of Asian dipterocarps from approximately 53 Ma old sediments from western India based on fossil resin chemistry and palynological data. An important implication of our finding is that Asian dipterocarps must have originated in Gondwana and dispersed from India into Asia once the land connection between the Indian and Asian plate was well established during the middle Eocene (49–41 Ma). Moreover, the present study supports the hypothesis which suggests that many angiosperms did not originate in the SE Asian region, but dispersed into the area from western Gondwanaland.

1. Introduction

The Dipterocarpaceae comprise large trees that dominate the canopy of lowland equatorial forests. They typically contribute to 30% of the total area in lowland evergreen forests in Southeast Asia (Aiba and Kitayama 1999) and play a dominant role in Asian rain forest ecology (Ashton 1982, 1988). There is no equivalent elsewhere in the tropics of a single, highly diverse, family dominating large-tree forests over such large areas (Corlett 2007). The Dipterocarpaceae comprise three subfamilies: the Dipterocarpoideae in Asia, the Pakaraimoideae in South America and the Monotoideae in Africa. There are approximately 520 species in 17 genera amongst which the Asian dipterocarps include 470 species alone. This family is well known as one of the major sources of valuable commercial hardwood timber while its resins and leaves contribute significantly to the rural economies of SE Asia. Two opposing hypotheses have been proposed to explain the origin of the Asian dipterocarps. Some hypothesize that the family originated in Southeast Asia, most probably from West Malaysia in the late Mesozoic (Lakhanpal 1970; Sasaki 2006) and migrated into India during the late Cenozoic Era. The occurrence of bicadinanes diagnostic of Dipterocarpaceae resins in late Cenozoic fluvio-deltaic oils from across SE Asia represented a further connection with this age (Stout 1995). Others suggest that Dipterocarpaceae have a Gondwanan origin and reached Asia by rafting on the Indian plate (Ashton 1982; Ashton and Gunatilleke 1987; Dayanandan et al. 1999; Ducousso et al. 2004). Here, we report the occurrence of Dipterocarpaceae from more than 53 Ma old sediments from India based on fossil resin chemistry and palynological data. Our findings suggest that Asian dipterocarps migrated from India into Asia as the land connection between the Indian and the Asian plate was established at *ca.* 50 Ma ago (Scotese et al. 1988; Rowley 1996).

2. Sample and methods

2.1. Samples

Fossil resins, lignite and carbonaceous shale samples were collected from the Vastan lignite mine (21°25′47″ N: 73°07′30″ E) Cambay Basin, western India (Fig. 1). The rock strata are referred to as the Cambay Formation. The studied section is 30 m thick and is composed of shale, clay, calcareous clay and lignite beds. The sediments of the lower half of the Vastan lignite mine section were deposited in estuarine to lagoonal environments whereas the upper half was deposited under shallow marine conditions (Sahni et al. 2006). Fossil pollen having affinities with those of the modern Dipterocarpaceae family have been recorded from the lower part of

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doi:10.1016/j.revpalbo.2011.05.002

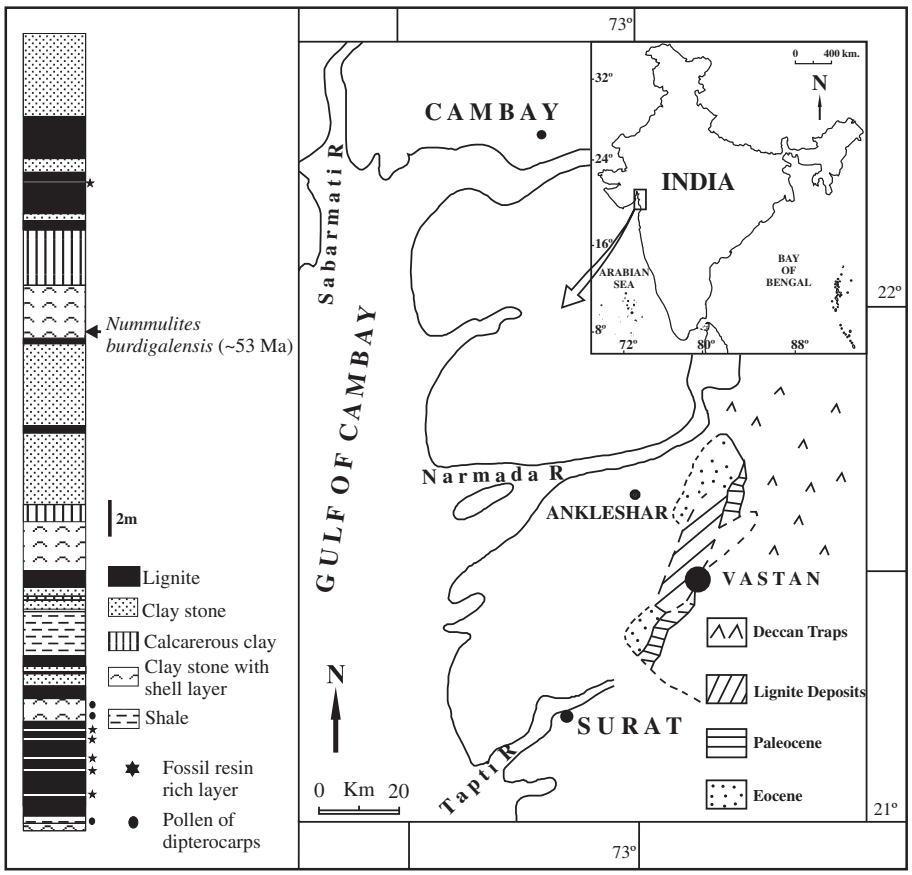

Fig. 1. Location and lithological column of the Vastan lignite mine section showing the position of fossil resin-bearing layers and pollen of dipterocarps.

the sequence. Fossil resins were collected from both the bottom and top lignite seams. The age diagnostic benthic foraminifera *Nummulites burdigalensis burdigalensis* which occurs in the upper half of the Vastan sequence (Fig. 1) indicates an early Cuisian (*ca.* 53 Ma) age of the fossil resin-bearing horizon (Punekar and Saraswati 2010). Dinoflagellate cysts suggest an early Eocene (*ca.* 54–55 Ma) age for the resin-bearing lignites (Garg et al. 2008). Recently, Clementz et al. (2010) reported the second Eocene Thermal Maximum (ETM2; *ca.* 53.7 Ma.) from the middle part of the mine section based on organic carbon $\delta^{13}C$ data which corroborates the biostratigraphic age of the resin-bearing lignite section. We obtained the extant dammar resin from a dipterocarp tree (genus *Shorea robusta*) from a sal forest of West Bengal, eastern India.

2.2. Palynological preparation

Rock samples were thoroughly cleaned with water. Crushed shale samples were kept in 40% HF for 3–4 days. Carbonaceous shale samples were then kept in HNO_3 for 24 h. The macerated samples were washed with water 4–5 times by siphoning and were then sieved with 500 mesh (29 μm). Samples having a calcareous mineralogy were first kept in HCl for 12 h and were then treated with hydrofluoric acid. Lignite samples were kept in HNO_3 for 24–36 h. The samples, when pulverized, were washed 2–3 times with water and were sieved. After removal of minerals, samples were treated with 5–15% solution of potassium hydroxide for 2–5 min and were then washed. Very fine mineral particles remaining in the macerated residue were removed with the help of heavy liquid (zinc chloride). Water-free macerated residue was mixed with a few drops of polyvinyl alcohol and spread uniformly over the cover glass. The cover glass was oven dried for *ca.* 30 min and then mounted in Canada balsam.

2.3. Pyrolysis–GC–MS

Flash pyrolysis was conducted at 600 °C/20 s using a Chemical Data Systems (CDS) analytical Pyroprobe 5150. The pyrolysis chamber was held at 300 °C. GC–MS analysis of the flash pyrolysates was performed using an Agilent 6890 N GC coupled to a Micromass AutoSpec Ultima magnetic sector mass spectrometer. A 60 m × 0.25 mm i.d. × 0.25 μm DB1-MS capillary column was used with a split of 15 mL min^{-1} using helium carrier gas. The GC oven was an initial 40 °C for 2 min, increased at 4 °C min^{-1} to 310 °C and held isothermal for 20 min. Full scan acquisitions were performed over the range *m/z* 50–600 at *ca.* 1 scan s^{-1}. Mass spectral conditions included 70 eV electron energy, 250 °C source temperature and a 300 °C transfer line temperature. Product identifications were based on mass spectral interpretation and correlation to previously published data.

3. Results

We recovered well-preserved macroscopic pieces of fossil resin from 53 Ma old sediments in the Vastan lignite mine (Sahni et al. 2006; Punekar and Saraswati 2010). We previously reported cadinane and bicadinane distributions in a preliminary study of the Vastan resin