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Aporosa Blume from the paleoequatorial rainforest of Bikaner, India: Its evolution and diversification in deep time

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ABSTRACT

The Gondwanan origin, northward migration and subsequent collision with Asia means that the Indian subcontinent is of particular interest regarding the origin and dispersal of numerous plants and animal species. With this in mind, we describe a fossil leaf of *Aporosa* Blume (Phyllanthaceae) from the Paleogene of the Indian subcontinent and discuss its evolution and diversification with respect to the moving Indian plate and its connection with Southeast Asia since the early Cenozoic. At present, *Aporosa* Blume is confined to Southeast Asia with a few species in India and New Guinea. It is represented by six endemic species growing in the evergreen forests of India and Sri Lanka, including *Aporosa acuminata* Thwaites, which is morphologically close to the here described fossil from Bikaner, Rajasthan, India. From the age of the fossil and the distribution of its modern comparable form, it is assumed that *Aporosa* originated on the Indian subcontinent and then was distributed to Southeast Asia, supporting the 'Out of India' hypothesis. Diversification of the genus might have taken place either in the Paleogene or Neogene. Our fossil leaf material also indicates the existence of palaeoequatorial (<10° N) tropical rain forests in western India during the Paleogene in contrast to dry and desertic climate occurring today.

1. Introduction

The Phyllanthaceae is a morphologically diverse family of about 2000 species, belonging to the order Malpighiales. The family is common in the tropics, but many constituents also occur in the southern temperate zone. This family has been separated from Euphorbiaceae sensu lato (s.l.), along with some other families (Pandaceae, Picrodendraceae and Putranjivaceae) on the basis of molecular data (Savolainen et al., 2000; Wurdack et al., 2004; Samuel et al., 2005; Kathriarachchi et al., 2006; APG, 2009). The Phyllanthaceae is further divided into two subfamilies (a) Phyllanthoideae sensu stricto (s. s.) covering four tribes: Bridelieae, Phyllanthoideae, Poranthereae and Wielandieae and (b) Antidesmatoideae including six tribes: Scepeae, Antidesmateae, Bischofieae, Uapaceae, Jablonskieae and Spondiantheae. The family is known from the late Cretaceous onwards from Canada, France and India in the form of wood, pollen and fruits (Muller, 1981; Prakash et al., 1986; Nambudiri and Binda, 1989; Gruas-Cavagnetto and Köhler, 1992; Mai, 1996).

The genus *Aporosa* Blume (subfamily Antidesmatoideae) consists of about 80 species of small trees distributed in the tropical rain forests of Southeast Asia. Six endemic species occur in the remnant forests of south India and Sri Lanka, while others are found in Assam, Bangladesh, Myanmar, Sikkim, the Malay Archipelago and the Solomon Islands (Fig. 1). A phylogenetic study of *Aporosa* based on its modern distribution was undertaken by Schot (1998), who recognized three monophyletic and five paraphyletic groups. The monophyletic groups are: Frutescens, Benthamiana and Octandra. The species of the first two groups occur on Sundaland, in the Malay Peninsula, Sumatra, West Java and Kalimantan, while some species reach the Philippines and Sulawesi. The Octandra group is mainly found on the mainland of Asia with six endemic species in south India and Sri Lanka and two species in west Malaysia. The paraphyletic groups occur in Sundaland and New Guinea. Schot (1998) suggested constant interbreeding between the species of Sundaland, India and New Guinea as evidenced by their phylogenetic patterns because many of the New Guinean species are geographically intermingled among their Sundaland and Asian relatives. A hypothesis to account for the origin and evolution of *Aporosa* was proposed by Schot (1998) on the basis of its present biogeographical distribution. However, because fossils are the best tool to reconstruct the origin and biogeographic history of any extant taxon over geological time, we describe a leaf fossil with features comparable to those found in leaves of the extant genus *Aporosa*, summarize its biogeographic distribution in deep time and discuss changes in its distribution in relation to the drastic

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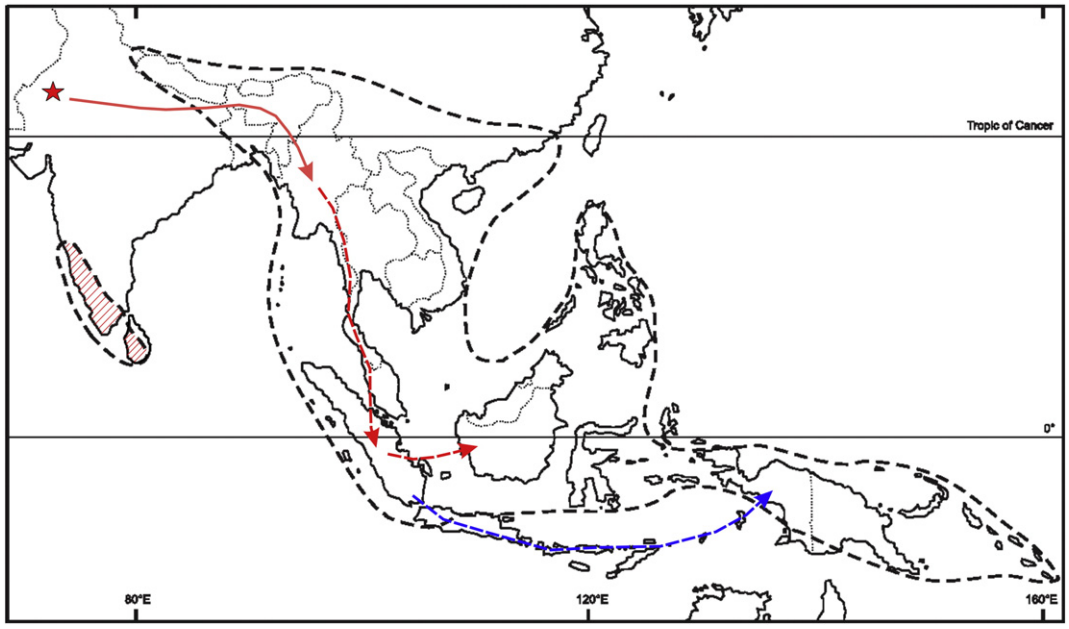

Fig. 1. Map showing present distribution of *Aporosa* (black dotted line) and *Aporosa acuminata* (shaded part with red colour) and past occurrence of *Aporosa* (marked with star) and its possible migration route from India to Eurasia (red dotted line) and further up to New Guinea (blue dotted line).

change in the climatic conditions of western India (Rajasthan) that have occurred since our fossil material was alive.

To date, a few leaf fossils belonging to *Calophyllum* L. of the Calophyllaceae, *Garcinia* L. and *Mesua* L. of the Clusiaceae (Lakhanpal and Bose, 1951) and a fruit of *Cocos* L. (Arecaceae) are known from the Paleogene succession of Rajasthan (Shukla et al., 2012). Recently, a leaf of *Uvaria* L. of the Annonaceae was described from the same lignite mine where the present fossil was found (Shukla and Mehrotra, 2014). In view of these meagre fossil records, the present finding of *Aporosa* fossil becomes important in terms of biogeographic and climatic interpretation.

2. Geological settings, material and methods

The fossil leaf described here was collected from the Gurha lignite mine, located 22 km NW of Kolayat (Fig. 2a) (27° 52′; N 72° 50′ E), Bikaner, Rajasthan. The lignite of this mine belongs to the Palana Formation which is exposed near Kolayat and Nagaur. The Gurha mine section for the most part represents deposition in a lake (Shukla et al., 2014). The mine exposes grey clays, silty clays, sands, lignites and volcanic ash (Fig. 2b). Observed sedimentation began with a significant influx of volcanic ash that is now altered to clay. The lignite forms more or less uniform deposits containing abundant amber and charcoal particles dispersed throughout. The plant fossils were collected from light to dark, clay bands overlying the lignite. Fossil leaves, flowers and legume fruits were found in abundance around the 70–72 m level. The sedimentary succession has been described in detail by Shukla et al. (2014). The lignite exposed in Rajasthan and Gujarat is considered to be early Eocene in age (Sahni et al., 2004 and references therein). Palynological study of this mine has yielded the following taxa: *Dandotiaspora telonata* Sah et al., *Palmidites plicatus* Singh, *Palmaepollenites eocenicus* (Biswas) Sah et Dutta, *Matanomadhiasulcites matanomadhensis* Kar, *Retitribrevicolporites matanomadhensis* (Venkatachala et Kar) Kar, *Tricolpites reticulates* Cookson ex Couper, *Triorites bellus* Sah et Kar, *Lakiapollis matanomadhensis* Venkatachala et Kar, *Lakiapollis ovatus* Venkatachala et Kar, *Clavaperiporites clavatus* Navale et Misra, *Lanagiopollis rugularis* Morley, *Ratariapollenites* sp., *Tricolporopollis rubra* Dutta et Sah, *Rhoipites kutchensis* Venkatachala et Kar and *Retistephanocolporites* sp. van der Hammen & Wijmstra. (Shukla et al., 2014). The occurrence of most of these taxa confirms an early Eocene age, as they were also recorded from various early Eocene sediments of western India (Kar and Sharma, 2001; Tripathi et al., 2009). Moreover, the Vastan lignite mine, Gujarat considered to be coeval with the Gurha lignite mine (Sahni et al., 2004), and based on dinoflagellate and isotopic studies, is considered to be ~55–52 Ma.

The terminology used in describing the fossil leaf is based on the nomenclature proposed by Dilcher (1974) and Ellis et al. (2009). Necessary permission was obtained from the Director, Forest Research Institute (FRI), Dehradun for the herbarium consultation. The fossil specimen was identified with the help of herbarium sheets of the extant plants available there. The fossil type specimen is housed in the museum of the Birbal Sahni Institute of Paleobotany, Lucknow.

3. Systematic paleobotany

Order Malpighiales
Family Phyllanthaceae
Tribe Antidesmeae
Genus *Aporosa* Blume
Type species: *A. ecocenicus* Shukla et al., sp. nov.
Aporosa ecocenicus Shukla et al., sp. nov.
Holotype: Specimen no. BSIP 40109 (Fig. 3; Plate I, 1; Plate II, 1, 3)
Repository: Birbal Sahni Institute of Palaeobotany.
Type locality: Gurha Lignite Mine, Bikaner, Rajasthan (Fig. 2a).
Stratigraphic horizon: Palana Formation, early Eocene
Etymology: The specific epithet refers to the age of fossil.
Specific diagnosis: Leaf elliptic; margin entire; venation eucamptodromous to brochidodromous; secondary veins 6–7 pairs visible, regular, 0.7–2.0 cm apart, angle of divergence narrow to moderate acute; tertiary veins percurrent to irregular reticulate.

3.1. Description

Leaf nearly complete, simple, symmetrical, mesophyll, elliptic; preserved lamina length 12 cm (estimated lamina length 13.5 cm),