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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.

Key words: Phyllanthaceae, early Eocene, Rajasthan, Palaeogeography, biogeographic distribution, climate change.

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: Brideliaceae, Phyllanthoideae, Poranthereae and Wielandieae and (b) Antidesmatoideae including six tribes: Scepae, 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, 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 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 meager 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. 2C). 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), maximum width 6.3 cm near the middle portion; apex missing; base seemingly acute; margin entire; texture chartaceous; venation pinnate, eucamptodromous to brochidodromous; primary vein stout; slightly curved; secondary veins 6–7 pairs visible, regular, 0.7–2.0 cm apart, alternate, angle of divergence narrow to moderate acute (40–65°), smoothly curving upwards towards the margin and joining superadjacent secondaries either directly or through percurrent tertiaries; tertiary veins percurrent to irregular reticulate, percurrent tertiaries opposite, sinuous, angle of divergence RR-RA, alternate to opposite, exmedial tertiary veins forming loops at the margin; quaternary veins alternate, irregular; areolation and additional fine features not preserved.

3.2 Fossil comparisons

The characteristic morphological features such as elliptic shape, eucamptodromous to brochidodromous venation, 6 to 7 pairs of secondary veins curving upwards towards the

margin and joining superadjacent secondary veins and reticulate to percurrent tertiaries indicate its proximity to the families Annonaceae and Phyllanthaceae.

After a detailed comparison with various genera of both the families available at the FRI herbarium, it was been found that several genera of the Annonaceae viz., *Anaxagorea* Steven Rechard Hill, *Artabotrys* Robert Brown, *Polyalthia* Blume and *Uvaria* L. show some similarities with the present fossil. *Anaxagorea* can be distinguished from our fossil in having a narrow elliptic shape, mainly brochidodromous venation and secondaries departing the midvein at a more acute angle. *Artabotrys* was found to be different in having intersecondary veins, mainly percurrent tertiaries and festooned brochidodromous venation. *Polyalthia* differs in having intersecondary veins, while *Uvaria* has a narrow elliptic shape and mainly reticulate tertiaries. Of the various genera within the family Phyllanthaceae, three, namely *Antidesma* L., *Aporosa* Blume and *Sauropus* Blume resemble the fossil closely. *Antidesma* differs in having narrow elliptic shape, and possessing mainly brochidodromous venation with secondaries at a more acute angle, while *Sauropus* can be differentiated because of its narrow elliptic shape. Only the genus *Aporosa* was closely similar to the fossil and subsequently a detailed comparison was made with the following species: *A. bourdillonii* Stapf, *A. cardiosperma* (Gaertner) Merrill, *A. fusiformis* Thwaites, *A. latifolia* Thwaites, *A. octandra* (Buchanan-Hamilton ex D.Don) Albert Roy Vickery, *A. villosa* Baillon and *A. acuminata* (<http://www.kew.org/herbcat>). In *A. cardiosperma* and *A. octandra* the distance between two secondaries is less than that in the fossil species. *A. bourdillonii*, *A. fusiformis* and *A. latifolia* are different in having oblong, orbiculate to suborbiculate and wide elliptic shape, respectively. *A. villosa* can be distinguished in possessing

predominantly percurrent tertiaries but *A. acuminata* Thwaites (FRI herbarium sheet no 5058) was found to be identical to the fossil in almost all the morphological features (Plate I, 2; Plate II 2, 4). A table showing comparison between extant and fossil species of *Aporosa* has been provided as supplementary data.

4. Discussion

4.1 Origin and diversification of *Aporosa* in deep time

The position of the Indian plate changed markedly during the Jurassic and Cretaceous as it broke apart sequentially from Gondwana, East Gondwana, Madagascar and finally from the Seychelles Islands (Chatterjee and Scotese, 1999). The northward drift of India to lower latitudes initially must have originated with only a high latitude Gondwanan biota 'on board', but subsequently either new taxa evolved in situ or were exchanged with adjacent landmasses. Thus India had the potential to be a biotic ferry for Gondwana elements and/or as a bridge for dispersal (Briggs, 2003) and a detailed study of Indian fossil taxa is of considerable biogeographic and evolutionary interest

The origin of Phyllanthaceae is assumed to have been in the tropics of the Old World during the Cretaceous, as a number of primitive taxa of the subfamily Phyllanthoideae are found in Africa/Madagascar and only subsequently appeared in America and the Malay archipelago (Webster, 1994, 2014). The genus *Aporosa* was thought to have originated during the same period on a fragmented island of gondwanic affinity that later accreted to the Sundaland (Southeastern Asia) (Schot, 1998). The present finding from the early Eocene of the Indian subcontinent helps us to better understand the evolution of the genus and therefore we propose two different dispersal scenarios and time frames for the migration of the genus from India to Southeast Asia.

According to the Out-of-India hypothesis some Asian biotic elements had an ancient Gondwanan origin and arrived in Asia by rafting on the Indian plate (McKenna, 1973). As far as the relative position of the Indian subcontinent with respect to Eurasia during the Eocene is concerned, two hypotheses were proposed by Ali and Aitchison (2008) based on the motion paths of the Indian subcontinent given by Acton (1999) and Schettino and Scotese (2005). According to the first hypothesis, India remained isolated until the final contact with Eurasia (Fig. 4B). This hypothesis is now discarded because recent measurements of the timing of initial collision took place at around 56 Ma, or just before the Paleocene–Eocene Thermal Maximum (PETM) (Qinghai et al., 2012). Nevertheless the consensus view is that collision occurred around 55–50 Ma (Garzanti et al., 1987; Searle et al., 1997; Zhu et al., 2005; Green et al., 2008; Najman et al., 2010). The second hypothesis of Ali and Aitchison (2008) suggests a close proximity of India with Southeast Asia since the early Paleogene before the final Indian-Eurasian collision, possibly trailing along Sumatra, the Malay Peninsula, with Myanmar Myanmar (Figure 4A) trailing alongside India and acting as island bridge. Recently, White and Lister (2012) also suggested several acceleration and deceleration scenarios of the Indian plate during its northward progression between 100 Ma and the present.

The isolation of the Indian subcontinent during its northward journey might be responsible for the development of many new lineages and the origin of a few taxa (Morley, 2000; Srivastava and Mehrotra, 2013). This isolation presupposes that *Aporosa* originated on the Indian subcontinent (after the breakup from the other Gondwanaland continents) as the fossil comes from the Paleogene of India and its modern equivalent is also endemic to south India. After the origin, the genus might have migrated to Eurasia in

the Paleogene when, or just before, India made initial contact with Asia (Ali and Aitchison, 2008). This proximity was also proposed by Klaus et al. (2010) who reconstructed the biogeographic distribution of Asian fresh water crab family Gacarcinacidae

The paleontological evidence described from various horizons (Late Cretaceous to early Paleocene) also suggested biotic exchange between India and Eurasia during this time (Prasad et al., 1986; Sahni et al., 1987; Prasad et al., 1994; Prasad and Rage, 1995; Briggs, 2003). After being dispersed to Eurasia during the latest Eocene, the genus underwent significant diversification in the middle Miocene when climate became warmer and moister (Morley, 2000) and further migrated to New Guinea in the later part of Neogene after the mid-Miocene collision between the Australian and Sunda plates (Morley, 1998).

The second possible dispersal scenario could be in beginning of the Neogene when the collision and complete suturing of the Indian plate to the Eurasian plate facilitated the migration of various elements from India to Eurasia via northeastern India (Fig. 1) (Chatterjee and Scotese, 1999; Srivastava and Mehrotra, 2010). Many faunal and floral elements migrated from India to Southeast Asia and vice-versa during this time. One of the best examples is the family Malvaceae. Two genera of this family, namely *Pterospermum* Schreb. and *Sterculia* L. are supposed to have migrated from Eurasia to India and from India to Eurasia, respectively, following the land connections (Srivastava et al., 2012). Recently, a migration pathway from India to Eurasia followed by *Alphonsea* Hook. f. et Thomson of the family Annonaceae, has been proposed (Srivastava and Mehrotra, 2013). This genus was suggested to have originated in the Indian subcontinent

and migrated to the Asian mainland after the complete suturing towards the end of the Oligocene. In the same way, after its origin, *Aporosa* might have followed the same tract and migrated from India to Eurasia in the Neogene (Fig. 1). The genus may have then diversified and further migrated to New Guinea as suggested by Schot (1998). In northwestern India increasingly arid conditions led to the extinction of *Aporosa* there and the genus only survived in the more humid Western Ghats (south India). Many plant taxa found in western India during the early Paleogene are now found only in the Western Ghats due to the moister climate prevailing there.

4.2 Palaeoclimatic implications

Fossil records help in understanding the relationships between evolution, extinction and climate change. The Paleogene witnessed marked changes in global climate and apparently plants underwent profound evolutionary and biogeographic changes at the Paleocene-Eocene boundary (Givnish and Renner, 2004). The modern counterpart of our fossil (i.e. *Aporosa acuminata*) is endemic to the Western Ghats and Sri Lanka and is a characteristic component of the evergreen forests in these areas. Following the long established approach of reconstructing past environments based on those of the Nearest Living Relative (NLR), we infer the presence of equatorial rain forests in Rajasthan at the time of deposition. *Aporosa* was the essential component of these forests that also experienced widespread expansion under the climatic optimum in the Paleogene (Morley, 2000). This is further supported by the earlier described evergreen and coastal elements from Rajasthan (Lakhanpal and Bose, 1951; Shukla et al., 2012; Shukla and Mehrotra, 2014) and a foliar physiognomic analysis (Shukla et al., 2014) based on two different horizons from the Gurha lignite mine that revealed that the

annual average relative humidity was around 80% and suggest a growing season precipitation of $1.8 \text{ m} \pm 0.9 \text{ m}$. The high uncertainties are a function of water not being limiting to growth in such a moist regime.

The paleoequatorial position (Fig. 2 B) of the Indian subcontinent in the early Eocene (~50 Ma) at $< 10^\circ \text{ N}$ (Molnar and Stock, 2009) favoured the growth of wide spread Indian rain forests during the Paleogene and these forests are now restricted to a small area in south India, in the form of Western Ghats (Prasad et al., 2009). Further, the recovered palynoassemblage from the early Eocene lignite mines of Rajasthan shows close taxonomic compositional similarity with the modern vegetation of Western Ghats, further indicating existence of tropical rain forests in western India in the past (Prasad et al., 2009).

As the Indian plate shifted from the equator to higher northern latitudes, the position of Gurha lignite mine moved away from the influence of the Intertropical Convergence Zone (ITCZ) and so became drier. At almost 30° N the fossil site is right where the dry descending air of the Hadley cell would normally produce desert conditions. The extent of greater India to the north of the Gurha depositional site is unclear (Wang et al., 2014), but the depositional site was near the western coastline as evidenced by mapped marine deposits associated with coeval lignites nearby in Gujarat (Sahni et al., 2004). This position of the Indian subcontinent supported a moist regime and resulted into thick vegetation cover during the early Eocene time.

As the Indian plate moved further north and collided with the Asian plate, it caused a change in the land and sea distribution and contributed further uplift to an already elevated Tibet (Kutzbach et al., 1989; Molnar et al., 1993; An et al., 2001;

Zachos et al., 2001; Spicer et al., 2003) and subsequently built the Himalaya (Wang et al., 2014). The cumulative effects of all these changes are thought to be responsible for the evolution and intensification of the monsoon system in the Neogene (Ruddiman and Kutzbach, 1989; An et al., 2001; Zheng et al., 2004, Boos and Kuang, 2010) and so caused massive changes in the biota, not only of India, but across Asia. By itself the tracking the existence of genera such as *Aporosa* through their fossil occurrences often leads to multiple hypotheses regarding causes of range change, but taken together with other such studies should eventually result in a clearer understanding of the evolution of Asia biotic/climate system and even help constrain palaeogeographic reconstructions.

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Legends for the figures and plates:

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).

Fig. 2. Location and geological section where *Aporosa eocenicus* Shukla et al., sp. nov. was collected. A: Map showing the fossil locality. B: Map showing the early Eocene location of the Gurha Mine, Rajasthan, India relative to Asia based on Molnar and Stock (2009). The position (red star) of northwestern India shows the rate of India's northward migration through time as well as its rotation in an anticlockwise direction. Uncertainties (95%) are indicated by ellipses. C: Generalized litholog showing the fossiliferous horizon.

Fig. 3. Line diagram of the fossil leaf.

Fig. 4. Relative position of the Indian plate with respect to the Eurasian plate during the middle Eocene (Klaus et al., 2010). (A) Motion path of the Indian subcontinent as

proposed by Acton (1999). (B) Motion path of the Indian subcontinent as proposed by Schettino and Scotese (2005).

PLATE I

Aporosa leaves.

1. Fossil leaf of *Aporosa eocenicus* Shukla et al., sp. nov. showing shape size and venation pattern.
2. Modern leaf of *Aporosa acuminata* showing similar shape, size and venation pattern as in the fossil.

PLATE II.

Aporosa leaves.

1. An enlarged portion of the fossil leaf showing eucamptodromous venation (red arrows).
2. An enlarged portion of the modern leaf showing similar kind of venation pattern (red arrows).
3. The fossil leaf showing brochiododrmous venation (yellow arrows), exmedial tertiary vein forming loop (green arrow) and irregular reticulate (blue arrows) and percurrent tertiary veins (red arrows).
4. The modern leaf showing similar venation pattern (yellow arrows), exmedial tertiary vein forming loop (green arrow) and irregular reticulate (blue arrows) and percurrent tertiary veins (red arrows).

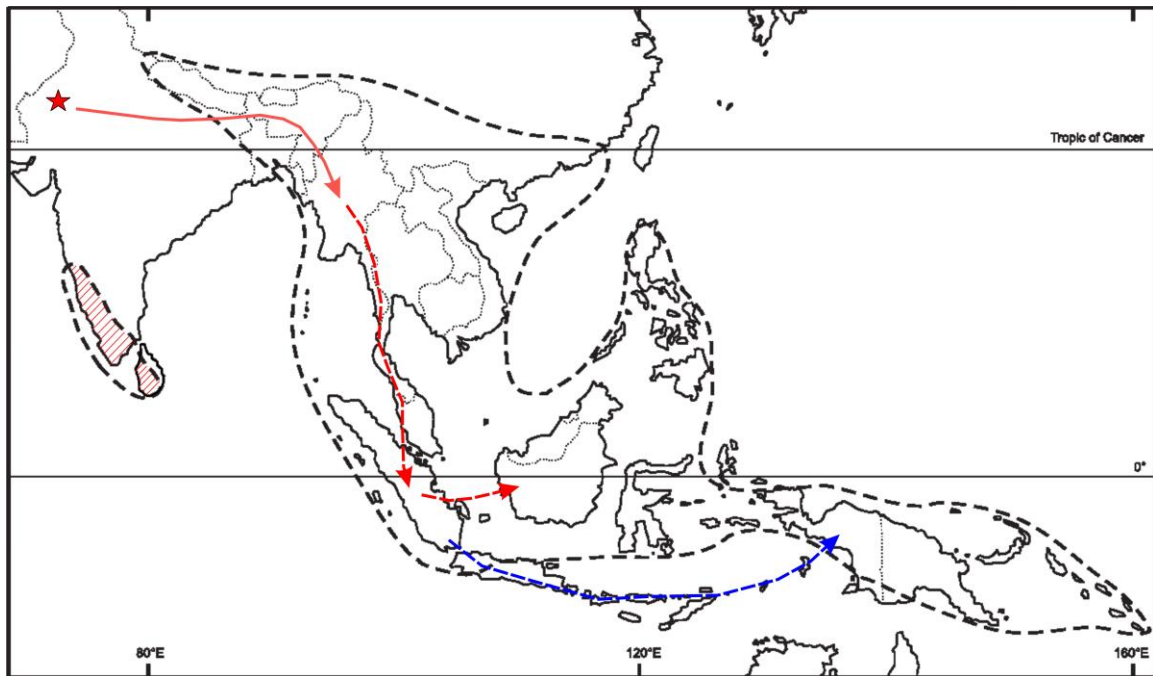


Fig. 1

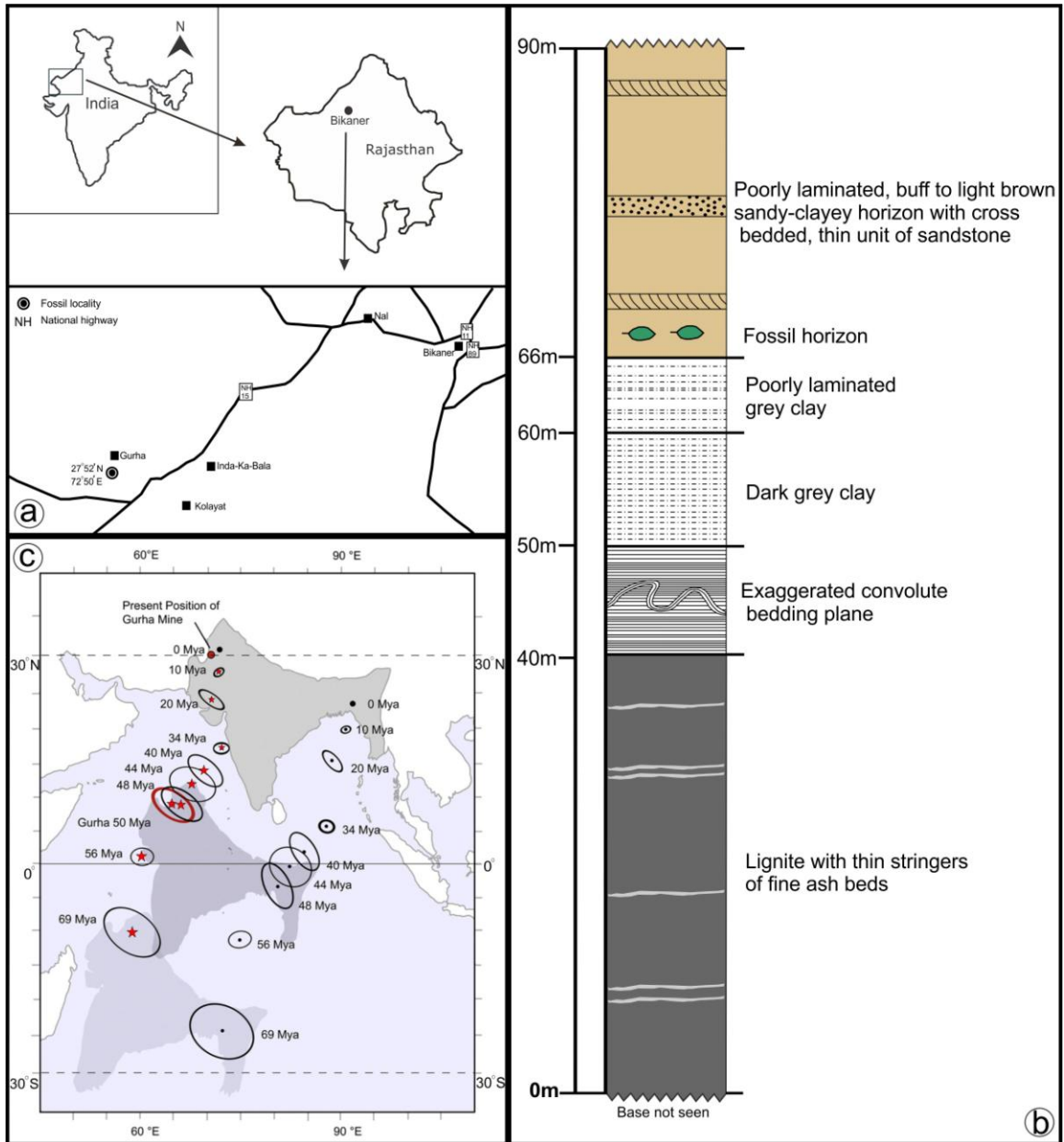


Fig. 2

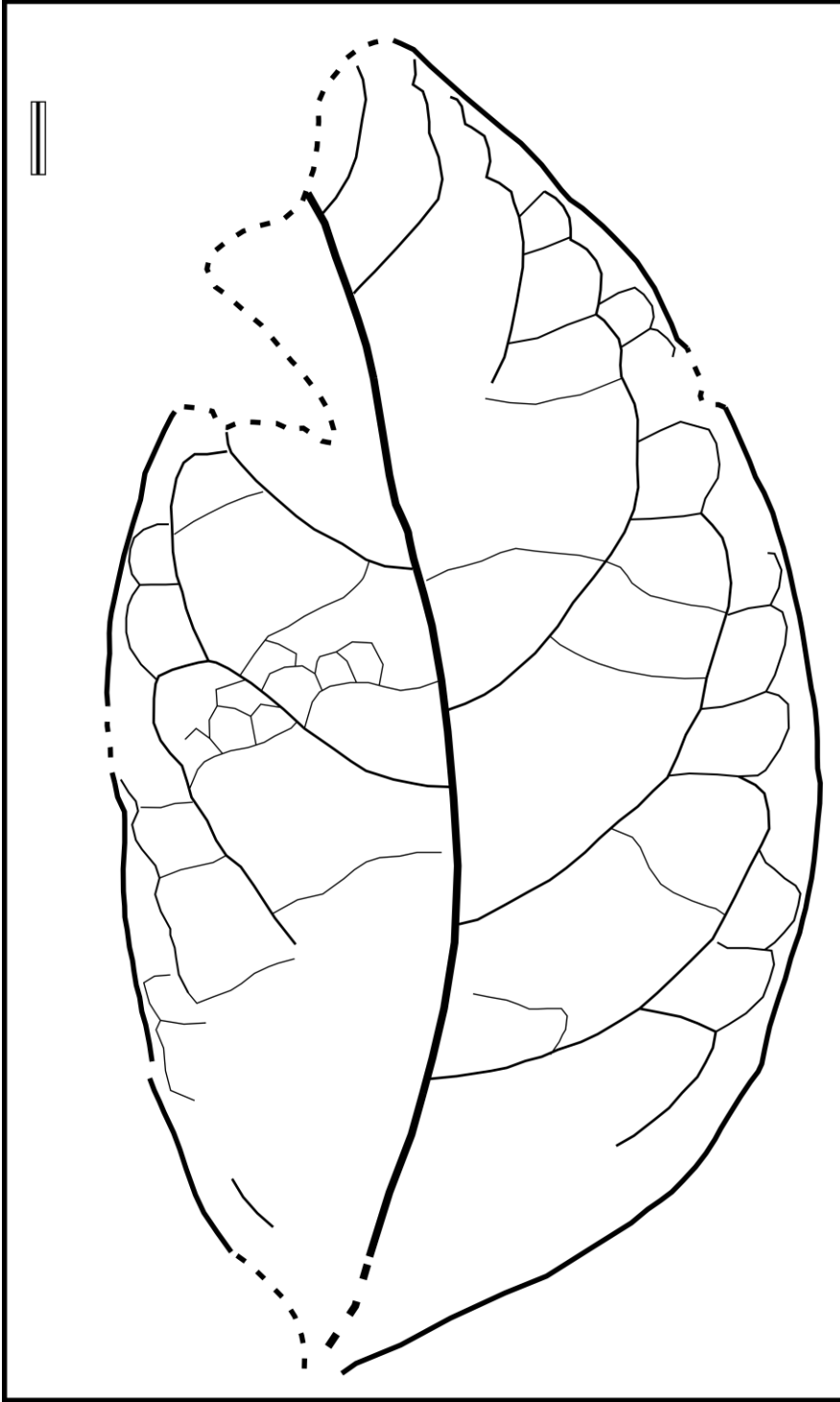


Fig. 3

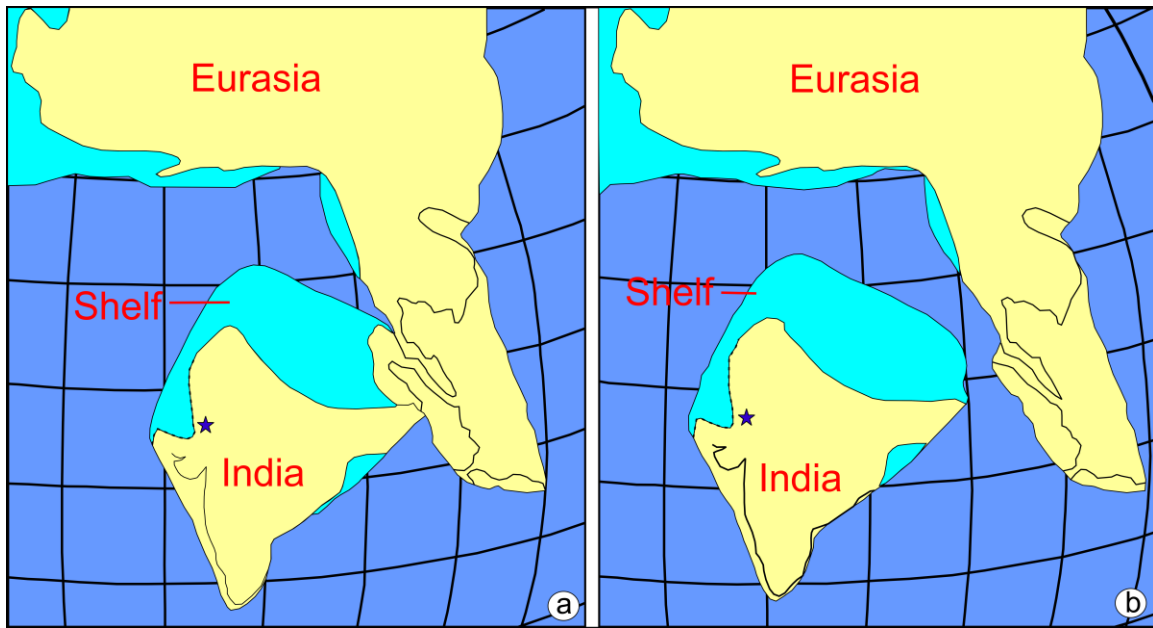


Fig. 4



Plate I

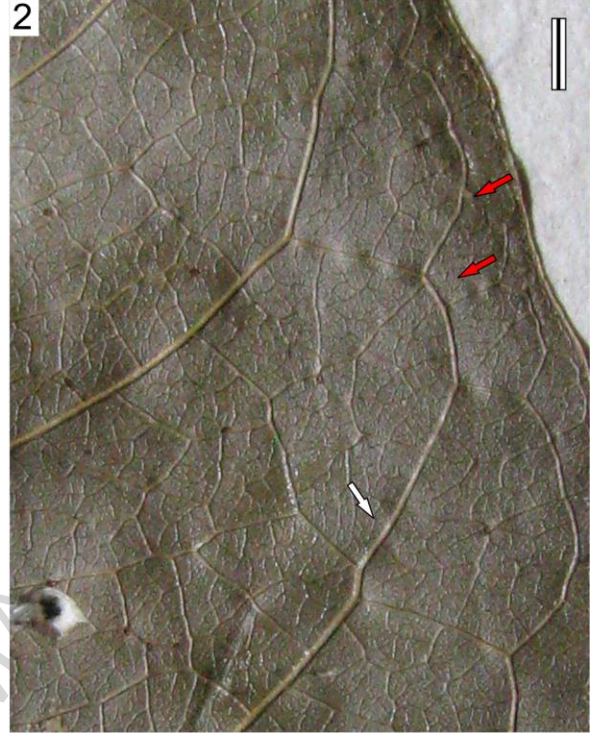


Plate II

Highlights

- The Indian subcontinent is of interest regarding the origin and dispersal of plants
- The fossil leaf is close to *Aporosa acuminata*
- Its presence indicates the existence of tropical rain forests
- Dry and deserts conditions prevail in around the fossil locality today

ACCEPTED MANUSCRIPT