Pliocene *Albizia* (Fabaceae) from Jharkhand, eastern India: reappraisal of its biogeography during Cenozoic in Southeast Asia

How to cite:

Hazra, Taposhi; Hazra, Manoshi; Spicer, Robert A.; Spicer, Teresa E.V.; Mahato, Sumana; Bera, Subir; Kumar, Sanchita and Khan, Mahasin Ali (2021). Pliocene Albizia (Fabaceae) from Jharkhand, eastern India: reappraisal of its biogeography during Cenozoic in Southeast Asia. Palaeoworld (Early Access).

For guidance on citations see FAQs.

© 2021 Elsevier B.V. and Nanjing Institute of Geology and Palaeontology, CAS

https://creativecommons.org/licenses/by-nc-nd/4.0/

Version: Accepted Manuscript

Link(s) to article on publisher’s website:
http://dx.doi.org/doi:10.1016/j.palwor.2021.03.004

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online’s data policy on reuse of materials please consult the policies page.

oro.open.ac.uk
Pliocene *Albizia* (Fabaceae) from Jharkhand, eastern India: reappraisal of its biogeography during Cenozoic in Southeast Asia

Taposhi Hazra, Manoshi Hazra, Robert A. Spicer, Teresa E.V. Spicer, Sumana Mahato, Subir Bera, Sanchita Kumar, Mahasin Ali Khan

PII: S1871-174X(21)00026-3
DOI: https://doi.org/10.1016/j.palwor.2021.03.004
Reference: PALWOR 629

To appear in: *Palaeoworld*

Received Date: 16 September 2020
Revised Date: 24 February 2021
Accepted Date: 17 March 2021

Please cite this article as: T. Hazra, M. Hazra, R.A. Spicer, T.E.V. Spicer, S. Mahato, S. Bera, S. Kumar, M.A. Khan, Pliocene *Albizia* (Fabaceae) from Jharkhand, eastern India: reappraisal of its biogeography during Cenozoic in Southeast Asia, *Palaeoworld* (2021), doi: https://doi.org/10.1016/j.palwor.2021.03.004

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2021 Elsevier B.V. and Nanjing Institute of Geology and Palaeontology, CAS.
Pliocene Albizia (Fabaceae) from Jharkhand, eastern India: reappraisal of its biogeography during Cenozoic in Southeast Asia

Taposhi Hazra, Manoshi Hazra, Robert A. Spicer, Teresa E.V. Spicer, Sumana Mahato, Subir Bera, Sanchita Kumar, Mahasin Ali Khan

Abstract

Albizia, a diverse tree genus, occupies monsoonal warm, humid rain forests in tropical and subtropical regions. We recovered a well-preserved compound fossil leaf and two fossil fruits of Albizia (Fabaceae) from the latest Neogene (Rajdanda Formation: Pliocene) sediments of Jharkhand of Chotanagpur Plateau, eastern India. On the basis of the architectural features of the fossil leaf, a new species is established as A. mahuadanrensis Hazra, Hazra and Khan, n. sp., characterised by a bipinnate, compound leaf having a rachis bearing opposite, asymmetrically ovate to sub-rhomboeid leaflets, pulvinus on leaflet petiolule and brochiodromous secondary veins. Based on both morphological and anatomical characters of the fossil fruits, A. palaeoprocera Hazra, Hazra and Khan, n. sp. is erected, characterised by flattened to broadly linear shaped, wingless fruits; ovate-elliptic shaped seed chambers having ellipsoidal seeds in one series; irregularly polygonal to rectangular epidermal cells with oblique end walls and randomly oriented, scattered, paracytic stomata. Analysis of Albizia fossil occurrences indicates that the legume taxon was common in Neogene
forests of India and elsewhere. The present-day distribution of the closely affiliated modern species of the fossil taxa indicates a warm and humid tropical environment during the time of deposition. We also review the biogeographic history of Albizia in India and other Asian countries.

**Keywords:** Albizia; biogeography; eastern India; fossil leaf and fruits; paleoclimate; Pliocene

1. Introduction

Fabaceae, today the third largest angiosperm family, comprises 19,500 species and 770 modern genera with worldwide distribution, encompassing a broad range of life forms ranging from tiny alpine ephemerals to huge tropical rainforest canopy trees (LPWG et al., 2013; Ma et al., 2017). This family has a long fossil history, with diverse and abundant records from Cenozoic sediments (Herendeen, 1992; Tao et al., 2000; Srivastava and Mehrotra, 2010; Ma et al., 2017). Relatively few legume megafossils have been studied in India (Bhattacharyya, 1985; Awasthi and Mehrotra, 1995; Prasad et al., 2004; Guleria et al., 2005).

*Albizia* Durazzini is an ecologically and economically important taxon represented by more than 120–140 species in tropical and subtropical regions of Asia, Africa and Madagascar, America, and Australia (Gunn, 1984; Lewis, 2005). It grows at elevations from sea-level to 1500 m in a variety of climatic zones where annual rainfall ranges from 600 mm to 2500 mm, yet survives in areas in low (300 mm annually) and irregular rainfall (Lowry et al., 1994), and in temperature as high as 49°C and down to −5°C. In India, this genus has eighteen extant species (Sanjappa, 1992) with some threatened taxa (*A. sikaramensis*, *A. thompsonii* in Tamil Nadu, Andhra Pradesh, Bihar and Orissa; *A. arunachalensis* in Arunachal Pradesh).

The fossil record of *Albizia* is limited in Indian Cenozoic and most fossils are leaflet and wood remains (Prakash, 1975; Antal and Awasthi, 1993; Awasthi and Mehrotra, 1995; Mehrotra et al., 1999) (Table S1). To date, no authentic fossil fruit of *Albizia* has been reported. Therefore, the occurrence of well-preserved *Albizia* fruits and compound leaf from the same sedimentary beds of Chotanagpur Plateau is significant.
Here, we report the compound leaf and fruit fossils of *Albizia* from the latest Neogene (Pliocene) sediments of eastern India, with a discussion on the historical phytogeography of *Albizia* and its adaptation to different climatic conditions during Cenozoic.

2. Geological setting

*Albizia* leaf and fruit fossils were collected from the latest Neogene sediments (Rajdanda Formation: Pliocene; Prakash et al., 1987) of Mahuadanr valley (23.3965°N, 84.1066°E) in Jharkhand, exposed along the left bank of Birha river for about a length of 2.6 km and a width of 1.5 km (Fig. 1). The lithology in the studied section includes mostly shale (arenaceous and clayey) and sandstone (Fig. 2). ‘Papery shales’ with millimetre scale laminations commonly occur here. Yellowish brown sandstones containing carbonised wood remains are interbedded with the shale layers; sandstones mostly pinch out and sporadically become lenses. The highly fossiliferous unit bearing fossil leaves, fruit remains, fossil fishes, remains of bird etc. occur within the upper 0.5 m of the studied unit. We recovered a large number of well-preserved fossil leaf impressions and compressions affiliated with modern tropical angiosperm taxa, namely, *Albizia, Cassia, Ficus, Ziziphus, Terminalia, Lagerstroemia, Semecarpus, Psidium, Gardenia, Mitragyna, Hylodesmum, Desmodium, Mangifera* etc. (Hazra et al., 2020). The occurrence of pyrite within the fossiliferous shale layer indicates a reducing (euxinic) environment during deposition (Bajpai et al., 2001). Various workers (Prakash et al., 1987; Srivastava and Bande, 1992; Srivastava et al., 1992; Singh and Prasad, 2007, 2008, 2009a, 2009b, 2010; Singh and Chauhan, 2008) suggested ‘late Tertiary’ (Pliocene) age of the Rajdanda Formation. Prakash et al. (1987) assigned a Pliocene age to these sedimentary deposits based on the presence of fossil *Sindora* wood, an index fossil of Pliocene age (Guleria, 1992). The district resource map as published by the Geological Survey of India of Palamau, Jharkhand, also assigns a Pliocene age to the Rajdanda Formation (Fig. 1A).

3. Material and methods

One well-preserved fossil leaf impression with six leaflets and two fruits of *Albizia* were collected, by Taposh Hazra and Manoshi Hazra (19/05/2019), from the Rajdanda Formation (Pliocene) near Mahuadanr (23.3965°N, 84.1066°E; 353 m
a.s.l.), Jharkhand, eastern India (Fig. 1). They require little preparation before photography, but details of fruits and margins of leaflets are not exposed in the initial fracture and are revealed by careful removal of overlying matrix using fine needles, scalpels and brushes. Macroscopic images of fossils and relevant extant specimens were photographed using a digital camera (Canon Power Shot A720IS). The photographs of holotype specimens were drawn using CorelDraw 19, so as to precisely detail the venation pattern. In order to isolate fruit cuticles, the conventional method for cuticle maceration (using Schulze’s solution) was applied (Kerp and Krings, 1999). To visualize microscopic features, such as stomata and epidermal cells, cuticles of fossil and modern fruits were treated with HCL (10%), HF (40%), dilute HNO3 (50%) and KOH (2–5%). Photographs showing structural details of fossil fruits, leaflets and relevant modern specimens were taken using an incident light compound microscope (Stemi SV 11, Zeiss), and a transmitted light compound microscope with a photographic attachment (Zeiss Axioskop 40).

4. Systematic description

For comparative analysis, specimens of extant *Albizia* species were examined critically and photographed from the collections of the Central National Herbarium (CAL), Sibpur, Howrah, India. We also critically examined the digital herbarium catalogue, Kew, UK (https://apps.kew.org/herbcat/navigator.do). Our fossil leaf descriptions follow with the standard terminologies for architectural description of dicotyledonous leaves (Hickey, 1973; Ellis et al., 2009). Morphological descriptions of fossil fruits are based on the terminology of Gunn (1984) and EBFC (1988, 1993, 1994, 1995). The terms used by Dilcher (1974) and Wang and Tao (1991) are used for cuticular features. Author citation of a new plant fossil species is mainly after Punt (1994). The fossil specimens including leaf holotype (SKBUH/PPL/JH/81), fruit holotype SKBUH/PPL/JH/F1A), paratype (SKBUH/PPL/JH/F1B) and respective slides (SKBUH/PPL/JH/F1A/SL1, SKBUH/PPL/JH/F1A/SL2, SKBUH/PPL/JH/F1A/SL3) are housed in the Museum of the Palaeobotany and Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University (SKBUH), Purulia.

4.1. Systematic description of fossil leaf
Order Fabales Bromhead
Family Leguminosae Jussieu
Genus *Albizia* Durrazini

*Albizia mahuadanrensis* Hazra, Hazra and Khan, n. sp.
(Figs. 3A, B, 4A, C, 5D, 10A)

**Etymology:** The new species is named after Mahuadanr, the locality where the fossil leaf specimen was collected.

**Holotype:** SKBUH/PPL/JH/81 (Fig. 3A, B).

**Type locality:** Mahuadanr (23.3965°N, 84.1066°E; 353 m a.s.l.), Latehar district, Jharkhand, eastern India.

**Diagnosis:** Leaf compound, bipinnate, pinnae paripinnate; rachis stout bearing opposite, asymmetrically ovate to sub-rhomboid leaflets, leaflets base asymmetrical; apex rounded or sub-truncate; pulvinus present on leaflet petiolule; secondary veins brochiodromous, with prominent loops towards the margin; intersecondaries present; tertiary veins mostly percurrent and looping to adjacent to tertiary veins; quaternary veins prominent and alternate.

**Description:** Leaf compound, bipinnate, pinnae paripinnate; rachis prominent, stout and glabrous, preserved length 7.6 cm and width 0.26 cm, rachis bears opposite leaflets; each leaflet 3–4 cm long, flat and concave with raised margins; asymmetrically ovate to sub-rhomboid in shape; length 2.9–3.8 cm, width 1.2–1.5 cm, asymmetrical at the base, apex round to or sub-truncate, entire margin; leaflet petiolule short, stout and 0.2–0.5 cm in length; pulvinus present on the petiolule of the leaflet; primary vein prominent, moderate and slightly curved towards the apex of the leaflet; venation pinnate; secondary veins slender, irregularly spaced, showing moderate acute angle of divergence, brochiodromous, arching, forming loops several times towards the margin; intersecondary veins present; tertiary veins fine, more likely percurrent, large number of tertiary veins branching from the secondary veins and looping to adjacent tertiary veins; quaternary veins prominent, alternate and right angle to adjacent tertiary veins.

**Comparison:** For comparison with species of *Albizia*, we studied the herbarium sheets of twenty available species of this genus and found that four species of *Albizia*
namely, *A. lucidior* (Steudel) Nielsen, *A. retusa* Bentham, *A. lebbek* (Linnaeus) Bentham and *A. procera* (Roxburgh) Bentham are morphologically similar to the new species (Table 1). *Albizia lucidior* differs in having sessile and linear leaflets, while the new species possesses well-developed petiolules in sub-rhomboidal to ovate leaflets. *Albizia retusa* differs in having a broadly cuneate base, a rounded apex and an obovate shape of the leaflets. *Albizia lebbek* is distinguished by shape (obliquely oblong) and the nature of the apex (obtuse) and base (one half cuneate, the other half round) of the leaflets. The size, shape, nature of the apex, the base and venation pattern of leaflets of the new species suggest a close affinity with modern leaflets of *A. procera* leaf (Central National Herbarium, sheet No. 28516) (Figs. 3C, 4B, D; Table 1).

Fossil leaflet specimens having affinity with *Albizia* have been reported from Cenozoic sediments of India, China, and Japan (Tables 2 and S1; Fig. 5), which differ from the new species in leaflet architecture and venation pattern. Guo (2011) and Li et al. (2017) reported *A. scalpelliformis* from the Miocene sediments of China as having an affinity to modern *A. julibrissin*. In *A. scalpelliformis*, the base is lobate and the apex is obtuse, in contrast to the asymmetrical base and round to sub-truncate apex of our Pliocene leaflets. Recently, Ito et al. (2017) described *A. kalkora* from Pleistocene sediments of Japan, which differs in having three secondary veins diverging at the side of the leaflet closest to the leaf base and in having obtuse apex. Chen et al. (1983) reported *Albizia* leaflet fossils bearing a close resemblance in leaflet architecture to modern species *A. corniculata* (Loureiro) and *A. odoratissima* (Linnaeus) Bentham from the late Eocene sediments of China, which differ in having an elliptic to obliquely ovate, asymmetrical leaflet with camptodromous venation pattern. Guo and Zhang (2002) reported an *Albizia* species having similarity with living species *A. odoratissima* from the Oligocene Sanhe Formation of Jilin, China, represented by a subrhombic, asymmetrical leaflet with camptodromous venation. Our new Pliocene species is characterized by ovate to sub-rhomboidal, asymmetrical leaflets with brochiodromous venation pattern.

4.2. Systematic description of fossil fruits

*Albizia palaeoprocera* Hazra, Hazra and Khan, n. sp.

(Figs. 6A, C, 7A, C, E, 8A–D, 9F, 10B)
**Etymology:** New species name “*palaeoprocera*” is derived by adding the prefix “*palaeo*” to the modern comparable specific epithet “*procera*”.

**Holotype:** SKBUH/PPL/JH/F1A (Figs. 6A, 8A–D).

**Paratype:** SKBUH/PPL/JH/F1B (Fig. 6C).

**Type locality:** Mahuadanr (23.3965°N, 84.1066°E; 353 m a.s.l.), Latehar district, Jharkhand, eastern India.

**Diagnosis:** Fruits flattened and broadly linear in shape; closely spaced primary veins in fruit valve arising from sutures, divided several times and anastomosing to form a fine reticulum; sutures distinct, thickened and wingless; 11 ovate-elliptic shaped seed chambers; ellipsoidal seeds in one series and not overlapping; epidermal cells irregularly polygonal to rectangular with oblique end walls, straight arched anticlinal walls and smooth periclinal walls; stomata randomly oriented, scattered, stoma mostly paracytic.

**Description:**

**Macromorphology:** Both compressed and impressed fruit specimens straight, flattened with coriaceous to a sub-ligneous epicarp, broadly linear in shape with parallel sides; fruits 26–28 cm long and 2–3 cm wide; stipe is not preserved; both ends well-preserved, apex shape more or less round to acute, base acute; each valve with numerous, closely spaced primary veins arising from both dorsal and ventral sutures, valves strongly curved and horizontally extending to the central portion of the fruit; most of the primary veins thin and not consistent across the width of the fruit; some prominent primary veins fused near the sutures, divided several times and anastomising to form a fine reticulum like structure; sutures distinct, thickened and easily recognisable, sutures without wing-like structure; seed chambers throughout the recovered compressed holotype fruit specimen are 11 in number, each 7.5–12 mm in length and 4.5–6.5 mm in width and ovate to elliptic in shape, five seed chambers are visible in our impression fruit specimen; seeds ellipsoidal, arranged in a single series and not overlapping, 5.3–6.8 mm in diameter and oriented perpendicularly along the fruit length.

**Micromorphology:** Epidermal cells of the compressed fruit specimen 15–41 µm long and about 13–21 µm wide, irregularly polygonal to rectangular with oblique end walls; anticlinal walls straight arched and periclinal walls smooth (Fig. 8A–D);
stomata almost elongated, irregularly distributed and randomly oriented, 10–17 µm long and 11–15 µm wide, stomatal apparati mostly paracytic (Fig. 8A), with one lateral specialised neighbouring cell or subsidiary cell per guard cell, few cyclocytic stomata also found (Fig. 8D); guard cells superficial, not sunken, elongated, 9–14 µm long and 2–4 µm wide.

**Comparison:** By examining herbarium specimens of all available species of *Albizia*, we found that *A. julibrissin* Durazzini, *A. kalkora* (Roxburgh), *A. odoratissima* (Linnaeus) Bentham, *A. retusa* Bentham, *A. thompsonii* Brandis, *A. lebbeck* (Linnaeus) Bentham, *A. amara* (Roxburgh) Boivin, *A. chinensis* (Osbeck) and *A. procera* (Roxburgh) Bentham were similar to our new species (Table 3). However, our new species is distinguished by being flattened, broadly linear in shape and 26–28 cm long, while the fruits of *A. retusa* are oblong in shape and smaller in size (12–14 cm). *Albizia julibrissin, A. chinensis* and *A. thompsonii* are distinguished by having long tapered fruit apex. The fruits of *A. odoratissima* bear oblong to orbicular seeds (2.5–3.7 cm wide), whereas new species bears ellipsoidal seeds (5.3–6.8 mm in diameter). *Albizia kalkora* differs in having slightly constricted margins between adjacent seed-bearing chambers and ovate to elliptical seeds. *Albizia amara* is distinguished from our Pliocene new species by its fruits size (10–24 cm long) and seed shape (ovate-orbicular). *Albizia lebbeck* is distinguished by fruit shape (flat, oblong and turgid above the seeded region) and the nature of the fruit apex and base (obtuse). The fruits of modern *A. procera* (Central National Herbarium, sheet No. 28516) show a closer similarity to our fossil fruit remains in size, shape, nature of the apex, base and seed chambers (Figs. 6, 7), as well as in cuticular micromorphological characters (Fig. 8A–D) of irregularly arranged tetragonal to hexagonal epidermal cells, straight-curved anticlinal cell walls, smooth periclinal walls and randomly oriented paracytic type of stomata. Therefore, based on the combination of both macromorphology (fruit architecture) and micromorphological epidermal features, we regard *A. procera* as the most closely related extant species to the new species.

Fossil fruit species of *Albizia* reported from Cenozoic sediments of India and elsewhere (Table S1) are compared with our Pliocene new species to show that our new fruit species differs from them in size, shape, apex, base features and the nature of the seed chambers (Table 4; Fig. 9).
5. Discussion

5.1. Paleobiogeographic implications (Fig. 11)

*Albizia* is a genus of subtropical and tropical trees in Asia, Africa, Madagascar, America, and Australia (Gunn, 1984, 1991; Doyle and Luckow, 2003; Kirkbride et al., 2003; Lavin et al., 2005) (Fig. 11). *Albizia* fossils, particularly the reproductive structures, are important for reconstructing paleoclimate, and evolutionary and biogeographic history of the genus.

The earliest reliable macrofossil record of *Albizia* is from the late Eocene Relu Formation of China (Chen et al., 1983); post-Eocene *Albizia* fossils have been reported from China (Hu and Chaney, 1940; WGCPC, 1978; Cao and Cui, 1989; Tao et al., 2000; Guo and Zhang, 2002; Guo, 2011; Li et al., 2017; Ma et al., 2017) and India (Prakash, 1975; Antal and Awasthi, 1993; Awasthi and Mehrotra, 1995; Mehrotra et al., 1999). Oligocene *Albizia* fossils have been reported from only China (Guo and Zhang, 2002; Ma et al., 2017).

Most fossil records for this legume genus in both India and China are from Miocene sediments (Table S1). As the seasonal, monsoonal climate of the early Miocene became warmer and moister associated with the rise of the Himalaya (Molnar et al., 1993; Morley, 2000; Farnsworth et al., 2019), and the Indian and Eurasian plates firmly sutured, plant migration between India and the main land Asia took place freely, according to available megafossil records (Jacques et al., 2015), when *Albizia* drastically expanded its geographic distribution, species diversity and abundance, becoming an important component of the Miocene forests of India-China region.

According to the fossil record, it seems likely that *Albizia* first originated in China during Eocene and subsequently migrated to the India and other Asian countries (Korea and Japan) during the Neogene. The significant diversification of *Albizia* took place during the Miocene in China due to the prevalence of a warm and humid climate (Sun and Wang, 2005). Transoceanic dispersal or long-distance dispersal (LDD) might have taken place during the Plio-Pleistocene (Cronin et al., 1994) and *Albizia*, being mostly salinity tolerant, might have reached Japan during this period, where Plio-Pleistocene *Albizia* fossils have been reported (Onoe, 1971; Hase, 1988; Ito et al., 2017).
5.2. Paleoclimatic interpretations

The occurrence of compound leaf with leaflets and fruits of *Albizia* from Rajdanda Formation (Pliocene) of Jharkhand, eastern India, associated with other fabaceous genera (*Cassia*, *Erythrina*, *Butea*, *Millettia* and *Bauhinia*) from the same locality (Srivastava et al., 1992; Singh and Prasad, 2008), provides significant evidence for the diversity and evolution of Fabaceae during the Neogene. *Albizia*, native to Asia and other regions, is highly diversified in tropical-subtropical forests (Gunn, 1984, 1991; Doyle and Luckow, 2003; Kirkbride et al., 2003; Lavin et al., 2005), indicating warm, humid climates (Chen et al., 1983; Tao et al., 2000; Guo and Zhang, 2002; Guo, 2011; Li et al., 2017; Ma et al., 2017). *Albizia procera*, the most closely related modern taxon of our Pliocene fossil specimens, generally survive under a warm and humid climate with a mean annual temperature (MAT) from 21°C to 32°C and a mean annual precipitation (MAP) 2500 mm (Sivakrishnan and Swamivelmanickam, 2019). We, thus, suggest a warm and humid tropical climate with high rate of precipitation during the Pliocene in the ancient forest of Jharkhand, which is consistent with previous studies (Puri and Mishra, 1982; Srivastava and Bande, 1992; Srivastava et al., 1992; Singh and Prasad, 2007, 2008, 2009a, 2009b, 2010; Singh and Chauhan, 2008) and with quantitative climatic data by CLAMP analysis (Hazra et al., 2020).

Acknowledgments

TH, MH, SM, SK and MAK gratefully acknowledge the Department of Botany, Sidho-Kanho-Birsha University for providing infrastructural facilities to accomplish this work. RAS and TEVS were supported by NERC/NSFC BETR Project NE/P013805/1. SB acknowledges the Centre of Advanced Study (Phase-VII), Department of Botany, University of Calcutta for providing necessary facilities. Thanks are due to the authorities of Central National Herbarium, Sibpur, Howrah for permission to consult the Herbarium. Two anonymous reviewers provided constructive recommendations that improved the manuscript.

References


Figure captions

Fig. 1. (A) Geological map of Mahuadanr and adjoining areas, Latehar District of Jharkhand (part of the district resource map of Palamu district, Bihar (Geological Survey of India)). (B) Map showing the fossiliferous locality near Mahuadanr, Latehar District, Jharkhand.

Fig. 2. Fossiliferous horizon bearing leaf and fruit remains collected for this study.

Fig. 3. (A, B) Fossil leaf A. mahuadanrensis Hazra, Hazra and Khan, n. sp. showing rachis bearing opposite leaflets (holotype: SKBUH/PPL/JH/81). (C) Part of a modern leaf of A. procera showing rachis bearing opposite leaflets. Scale bar = 1 cm.

Fig. 4. Leaflets of A. procera and A. mahuadanrensis. (A) Fossil leaflet of A. mahuadanrensis showing asymmetrical base and round to sub-acute apex, shape, size and venation pattern. (B) Leaflet of A. procera showing same nature of apex and base, similar shape, size and venation pattern. (C) Enlarged portion of the fossil leaflet showing primary vein (blue arrow), secondary vein (black arrow) and its dichotomously branching towards the margin (white arrow) and tertiary vein (yellow
arrow). (D) Enlarged portion of the modern leaflet showing similar primary vein (blue arrow), secondary vein (black arrow) and its dichotomously branching towards the margin (white arrow) and tertiary vein (yellow arrow). Scale bar = 1 cm.

Fig. 5. Fossil Albizia leaflets. (A) Albizia scalpelliformis Li et al., 2017. (B) A. palaeolebbek Antal and Awasthi, 1993. (C) A. kalkora Ito et al., 2017. (D) A. mahuadanrensis Hazra, Hazra and Khan, n. sp. Scale bar = 1 cm.

Fig. 6. Fruits of A. procera and A. palaeoprocera. (A) Compressed fruit of A. palaeoprocera showing the broadly linear shape with well-preserved ends and seed chambers (white arrow) (holotype: SKBUH/PPL/JH/F1A). (B) Fruit of extant A. procera showing similar nature of base, apex, shape and seed chambers (white arrow). (C)Impression fossil fruit of A. palaeoprocera showing the broadly linear shape with well-preserved ends and seed chambers (white arrow) (paratype: SKBUH/PPL/JH/F1B). Scale bar = 1 cm.

Fig. 7. Fruits of A. procera and A. palaeoprocera. (A) Enlarged view of A. palaeoprocera showing the valve venation with primary veins, distinct sutures and seed chambers. (B) An enlarged view of modern fruit of A. procera showing similar valve venation with primary veins and distinct sutures. (C) An enlarged portion of (A) showing seed chamber with distinct sutures (white arrow). (D) An enlarged portion of (B) showing similar shape of seed chamber with distinct sutures (white arrow). (E) Detailed valve venation with primary veins and seed chambers with distinct sutures (white arrows) of A. palaeoprocera. Scale bar = 1 cm.

Fig. 8. (A–D) Albizia palaeoprocera cuticle showing irregularly arranged epidermal cells, anticlinal wall (blue arrows), paracytic (white arrows) and cyclocytic type (red arrow) of stomata; (A, B) from slide SKBUH/PPL/JH/F1A/SL1; (C) from slide SKBUH/PPL/JH/F1A/SL2; (D) from slide SKBUH/PPL/JH/F1A/SL3. (E, F) Albizia procera cuticle showing irregularly arranged epidermal cells, anticlinal wall (blue arrow) and paracytic type of stomata (white arrow). Scale bar = 10 µm.
Fig. 9. Fossil Albizia fruits. (A) Albizia scalpelliformis Li et al., 2017. (B) A. cf. kalkora Li et al., 2017. (C) Albizia sp. Li et al., 2017. (D) A. ningmingensis Ma et al., 2017. (E) Leguminosites albizziformis Edwards, 1923. (F) A. palaeoprocera Hazra, Hazra and Khan, n. sp. Scale bar = 1 cm.

Fig. 10. (A) Line drawing of a fossil leaf A. mahuadanrensis showing rachis (red arrow) with shape, size, primary vein (pink arrow), secondary veins (light blue arrow) and their dichotomous branching at some distance from the margin (black arrow), tertiary veins (green arrow) and quaternary veins (blue arrow) of the leaflets. (B) Line drawing of a fossil fruit A. palaeoprocera showing the broadly linear shape with eleven seed chambers. Scale bar = 1 cm.

Fig. 11. Map showing modern distribution and megafossil occurrences of Albizia through geological past.

Abstract

Albizia, a diverse tree genus, occupies monsoonal warm, humid rain forests in tropical and subtropical regions. We recovered a well-preserved compound fossil leaf and two fossil fruits of Albizia (Fabaceae) from the latest Neogene (Rajdanda Formation: Pliocene) sediments of Jharkhand of Chotanagpur Plateau, eastern India. On the basis of the architectural features of the fossil leaf, a new species is established as A. mahuadanrensis Hazra, Hazra and Khan, n. sp., characterised by a bipinnate, compound leaf having a rachis bearing opposite, asymmetrically ovate to sub-rhomboid leaflets, pulvinus on leaflet petiolule and brochiodromous secondary veins. Based on both morphological and anatomical characters of the fossil fruits, A. palaeoprocera Hazra, Hazra and Khan, n. sp. is erected, characterised by flattened to broadly linear shaped, wingless fruits; ovate-elliptic shaped seed chambers having ellipsoidal seeds in one series; irregularly polygonal to rectangular epidermal cells
with oblique end walls and randomly oriented, scattered, paracytic stomata. Analysis of *Albizia* fossil occurrences indicates that the legume taxon was common in Neogene forests of India and elsewhere. The present-day distribution of the closely affiliated modern species of the fossil taxa indicates a warm and humid tropical environment during the time of deposition. We also review the biogeographic history of *Albizia* in India and other Asian countries.

Table 1. Comparative morphological chart of the extant *Albizia* compound leaves with opposite leaflets related with *A. mahuadanrensis* n. sp.

<table>
<thead>
<tr>
<th>Species of Albizia</th>
<th>Petiolule</th>
<th>Apex</th>
<th>Base</th>
<th>Size</th>
<th>Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. lucidior</em></td>
<td>4–5 mm</td>
<td>Acute</td>
<td>Cuneate</td>
<td>7–15 × 3–7 cm</td>
<td>Oblong to linear</td>
</tr>
<tr>
<td><em>A. retusa</em></td>
<td>1–2 mm</td>
<td>Rounded</td>
<td>Broadly cuneate</td>
<td>2–3 × 1–1.7 cm</td>
<td>Ovate-subrhombic to obovate</td>
</tr>
<tr>
<td><em>A. lebbek</em></td>
<td>1–1.5 mm</td>
<td>Obtuse</td>
<td>One half cuneate, another round</td>
<td>2.7–5 × 1–2.5 cm</td>
<td>Obliquely oblong</td>
</tr>
<tr>
<td><em>A. procera</em></td>
<td>2–3 mm</td>
<td>Round or sub-acute to emerginate</td>
<td>Unequal</td>
<td>2.5–5 × 1.8–3 cm</td>
<td>Ovate to subrhombic</td>
</tr>
<tr>
<td><em>A. mahuadanrensis</em></td>
<td>2–5 mm</td>
<td>Round to sub-truncate</td>
<td>Asymmetrical</td>
<td>2.9–3.8 × 1.2–1.5 cm</td>
<td>Asymmetrically ovate to subrhombic</td>
</tr>
</tbody>
</table>

Table 2. Comparative morphological chart of fossil leaflets of *Albizia*.

<table>
<thead>
<tr>
<th>Fossil species of Albizia</th>
<th>Modern close relatives</th>
<th>Petiolule</th>
<th>Apex</th>
<th>Base</th>
<th>Size</th>
<th>Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albizia</td>
<td><em>A. julibrissin</em></td>
<td>Not preserved</td>
<td>Obtuse</td>
<td>Truncate</td>
<td>1.2–1.4 × 0.43–</td>
<td></td>
</tr>
<tr>
<td>Species of <em>Albizia</em></td>
<td>Fruit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------------</td>
<td>-------</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>A. julibrissin</strong></td>
<td><strong>Apex</strong></td>
<td><strong>Base</strong></td>
<td><strong>Margin</strong></td>
<td><strong>Size</strong></td>
<td><strong>Shape</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Long tapered</td>
<td>Acute</td>
<td>Parallel</td>
<td>8–20 × 1.5–3 cm</td>
<td>Flat, broadly linear</td>
<td></td>
</tr>
<tr>
<td><strong>A. kalkora</strong></td>
<td>Round</td>
<td>Acute</td>
<td>Parallel or sometimes constricted</td>
<td>8–12 × 2–3 cm</td>
<td>Broadly linear</td>
<td></td>
</tr>
<tr>
<td><strong>A. odoratissima</strong></td>
<td>Rounded to rostrate</td>
<td>Acute</td>
<td>Parallel or sometimes constricted</td>
<td>15–20 × 2.5–3.7 cm</td>
<td>Flat, strap-shaped</td>
<td></td>
</tr>
<tr>
<td><strong>A. retusa</strong></td>
<td>Acute to acuminate</td>
<td>Obtuse</td>
<td>Almost parallel</td>
<td>10–12 × 2–3 cm</td>
<td>Oblong</td>
<td></td>
</tr>
<tr>
<td><strong>A. thompsonii</strong></td>
<td>Long tapered</td>
<td>Acute</td>
<td>Wavy margin</td>
<td>8–12 × 3–4 cm</td>
<td>Strap-shaped</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Comparative morphological chart of the extant *Albizia* fruits related with *A. palaeoprocera* n. sp.
<table>
<thead>
<tr>
<th>Fossil species of Albizia</th>
<th>Modern close relatives</th>
<th>Fruit</th>
<th>Apex</th>
<th>Base</th>
<th>Margin</th>
<th>Size</th>
<th>Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Albizia scalpelliformis</em></td>
<td><em>A. julibrissin</em></td>
<td>Not preserved</td>
<td>Not preserved</td>
<td>Straight margin with irregular constriction near the base</td>
<td>7.4‒12.4 × 1.4‒2.2 cm</td>
<td>Flat to broadly linear</td>
<td></td>
</tr>
<tr>
<td>Li et al.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. cf. kalkora</em> Li et al.</td>
<td><em>A. kalkora</em></td>
<td>Not preserved</td>
<td>Not preserved</td>
<td>Undulated margin with constriction</td>
<td>8.0 × 1.3‒2.3 cm</td>
<td>Flat to broadly linear</td>
<td></td>
</tr>
<tr>
<td>Albizia sp. Li et al.</td>
<td><em>A. chinensis</em></td>
<td>Acuminate</td>
<td>Acuminate</td>
<td>Undulated</td>
<td>5.0 × 0.8‒1.3 cm</td>
<td>Flat to broadly linear</td>
<td></td>
</tr>
<tr>
<td><em>A. ningmingensis</em> Ma et al.</td>
<td><em>A. kalkora</em></td>
<td>Nearly round</td>
<td>Not preserved</td>
<td>Almost parallel</td>
<td>9.6 × 2.0 cm</td>
<td>Flat to broadly linear</td>
<td></td>
</tr>
<tr>
<td>Leguminosites <em>albizziformis</em> Edwards</td>
<td><em>A. lebbek</em></td>
<td>Not preserved</td>
<td>Obtuse</td>
<td>Almost straight with slight constriction</td>
<td>9.0 × 2.5‒3.0 cm</td>
<td>Flat to broadly linear</td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Comparative morphological chart fossil fruits of *Albizia*.
<table>
<thead>
<tr>
<th>A. palaeoprocera</th>
<th>A. procera</th>
<th>Almost round</th>
<th>Almost round</th>
<th>Parallel</th>
<th>26–28 × 2–3 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hazra, Hazra and</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Khan, n. sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Almost round

Parallels

26–28 × 2–3 cm