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## Accepted Manuscript

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**First occurrence of mastixioid (Cornaceae) fossil in India and its biogeographic implications**

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## Abstract

Mastixioids in the family Cornaceae, are presently native only in limited areas of Asia, they have rich fossil fruit record in Cenozoic sediments of Europe and North America, but unfortunately none have been reported from Cenozoic sediments of India and Asia until now. Here, we report the occurrence of leaf remains (both impression and compression) along with carbonised fruits, resembling morphologically and anatomically those of the extant endemic species *Mastixia arborea* C.B. Clarke. Our materials were recovered from the middle Miocene to early Pleistocene Siwalik sediments exposed around West Kameng and Papumpare districts in Arunachal Pradesh, eastern Himalaya. These new fossil materials confirm the existence of *Mastixia* in the Miocene-Pleistocene Siwalik forests in India. At present the modern analogue does not grow in the eastern Himalaya and is endemic to the tropical evergreen forests of the Western Ghats, situated at the same palaeolatitude as the fossil locality. Extinction from the entire eastern Himalaya and probable movement of this taxon to the Western Ghats is likely due to climate change in the area, related to the Himalayan Orogeny during Miocene-Pleistocene times. The disappearance of *Mastixia* from this area may be related to the gradual intensification of rainfall seasonality since the late Miocene. The recovery of this species and our earlier-described evergreen taxa from the same Siwalik time (Miocene-Pleistocene), suggest the existence of tropical, warm and humid climatic conditions during the period of deposition. The leaf and fruit remains are here described as new species, namely *Mastixia asiatica* Khan, Bera M et Bera S, sp. nov. and *Mastixia siwalika* Khan, Bera M et Bera S, sp. nov. respectively. This report documents the first fossil record of *Mastixia* leaf remains using both macro and micromorphological

characters. We also review the historical phytogeography, and highlight the phytogeographic implication of, the mastixioids.

**Keywords:** *Mastixia arborea*; macrofossils; Mio-Pleistocene; palaeogeography; palaeoclimate; Arunachal Pradesh.

## 1. Introduction

The mastixioids, a group of angiosperms usually allied to the Cornaceae, are today represented by two modern genera of evergreen trees, *Mastixia* Blume and *Diplopanax* Handel-Mazzetti (Matthew, 1976, 1977; Eyde, 1988; Eyde and Xiang, 1990; Fan and Xiang, 2003). Most of the taxonomic treatments of the 20<sup>th</sup> century have included this group of mastixioids as the subfamily Mastixioideae within the family Cornaceae or dog woods (Harms, 1898; Wangerin, 1910; Matthew, 1976, 1977; Takhtajan, 1980; Eyde, 1988; Stockey et al. 1998). Less commonly this group was treated as a separate family Mastixiaceae in the order Cornales (Takhtajan, 1987; Mai, 1993). Molecular (*rbcL*) data have indicated a close relationship between the mastixioids and the genera *Davidia* Baillon, *Camptotheca* Decaisne and *Nyssa* L. (Xiang et al., 1993; Fan and Xiang, 2003). The adjacent out-group to the clade containing *Mastixia*, *Diplopanax*, *Camptotheca*, *Davidia* and *Nyssa* is the clade containing *Cornus* L., *Alangium* Lamarck, *Curtisia* Ait. and the hydrangeoids (Fan and Xiang, 2003). Murrell (1993) regards *Cornus* as the closest outgroup to *Mastixia* and also considers *Diplopanax* as a subgenus of *Mastixia*, most closely related to the section *Manglesia* of the genus *Mastixia* on the basis of morphological data. Among the characters that these two taxa such as *Mastixia* and *Diplopanax* have in common is the ‘swollen septum’ in the fruits. We suggest that more

needs to be done on the fruit anatomy of this section of the genus *Mastixia* so that closer comparisons can be made.

Mastixioids are presently native only in restricted areas of Southeast Asia (Tiffney and Haggard, 1996). *Mastixia* is a genus comprised of about 19 species of resinous, evergreen trees up to 40 m tall, and its range extends from India through Southeast Asia and New Guinea to the Solomon Islands (Matthew, 1976). This genus usually occurs in primary forests, often with *Dipterocarps*, or in mossy forests and in secondary forests. It occurs from low altitude to 1800 m, in valleys, on slopes or ridges, but generally in moist habitats such as water-logged places, river banks, etc. (Matthew, 1976). *Mastixia arborea*, the nearest modern counterpart of the fossil specimens described here, is an evergreen tree up to 21 m tall and is endemic to the tropical moist evergreen forests of the Western Ghats (Brandis, 1971; Matthew, 1976).

Although mastixioids are not distributed in Europe and North America now, their fossil records are especially rich in these two continents, mainly represented by permineralized fruit remains. They have excellent fossil records from the uppermost Cretaceous to late Miocene of Europe (Chandler, 1926, 1961, 1962; Reid and Chandler, 1933; Kirchheimer, 1934, 1935, 1936a,b, 1938a,b, 1940, 1941, 1943a,b, 1957; Mai, 1964; Palamarev and Petkova, 1966; Mai, 1970; Czecczott and Skirgiello, 1975a,b; Holý, 1977; Mai and Walther, 1978; Gregor, 1978, 1990; Velitzelos and Gregor, 1982; Holý, 1984; Knobloch and Mai, 1986; Mai, 1987; Mai and Walther, 1991; Mai, 1993, 1995, 2001; Czaja, 2003; Ševčík et al., 2007; Martinetto, 2011; Holý et al., 2012) and Eocene sediments of North America (Potbury, 1935; Scott, 1954; MacGinitie, 1969; Wolfe, 1977; Wehr, 1995; Manchester, 1994; Tiffney and Haggard, 1996; Stockey et al., 1998). Most of these

fossils have been assigned to a variable number of morphogenera (Mai, 1993; ICBN: McNeill et al., 2006) and only a small number have been assigned to the two living genera *Mastixia* and *Diplopanax*.

Unlike Europe and North America, to-date no fossil of the mastixioids has been reported from India and Southeast Asia, even though these regions show moderate species richness of the group today (Brandis, 1971; Matthew, 1976, 1977). This lack of fossil evidence limits understanding of the diversification and evolution of the group in India and Southeast Asia. Here, we report *Mastixia* (Cornaceae, Mastixioideae) fossil foliage and fruit remains from the Mio-Pleistocene of Arunachal Pradesh, India. They constitute the first recognition of this genus in South Asia. Although *Mastixia* has frequently been reported from the Cenozoic sediments of Europe (Kirchheimer, 1935; Mai, 1970, 1995; Holý, 1975) and North America (Manchester, 1994; Tiffney and Haggard, 1996) based on isolated fruit remains, corroborative data from both foliage and reproductive structures occurring together has been lacking. This study confirms the presence of this genus in the Neogene of India based on combined evidence from complete leaves, and fruit remains.

The aims of this study are to (1) review the fossil history of mastixioids and provide an improved understanding of the evolutionary and biogeographic history of the group, (2) perform detailed morphological and anatomical examinations of *Mastixia* fossil leaf remains for the first time, and discuss the palaeobiogeographic and palaeoclimatic implications of this new fossil finding, and (3) discuss the possible causes of disappearance of this taxon from the present day vegetation of the entire eastern Himalaya and explain for its endemism.

## 2. Geological setting, materials, and methods

### 2.1. Geological setting

The fossil specimens (leaf impressions and compressions, carbonised fruit remains) of *Mastixia* were recovered during fieldwork undertaken for megafossil sampling in 2008-2010 from road cut sections through the lower part of the Siwalik strata exposed along the Pinjoli road in West Kameng district ( 27.50706 °N, 92.64259 °E) and the upper part of the Siwalik strata exposed along the Itanagar-Banderdewa road in Papumpare district ( 27.06589 °N, 93.64561 °E) of Arunachal Pradesh (situated between 26°27'52" and 29°29'54" N and 91°29'50" and 97°24'56" E), eastern Himalaya (Figs. 1, 2). The lower part of the Siwalik sediments is assigned to the Dafla Formation, while the upper part is assigned to the Kimin Formation (Kumar, 1997).

#### 2.1.1. Age of the fossil material

The Dafla Formation is considered as being middle to late Miocene in age and the Kimin Formation as late Pliocene to early Pleistocene in age. In Arunachal sub-Himalaya the lower, middle and the upper Siwalik are separated from each other by reverse faults and the three units are stacked in a reverse stratigraphic order (Table 1; Joshi et al., 2003). The Siwalik Group is mainly characterised by sandstones along with lenses and streaks of coal and lignite, siltstone, clays and pebble beds. Magnetostratigraphic data suggests that the Siwalik Formation of Arunachal Pradesh was deposited between 13 and 2.5 Ma (Chirouze et al. 2012). The transition between the lower and middle Siwaliks is dated at about 10.5 Ma and the middle to upper Siwaliks transition is dated at 2.6 Ma (Chirouze et al. 2012).



### *2.1.2. Sedimentary context*

The lower part of the Siwalik consists of indurated, medium to fine-grained, well sorted, bluish-grey sandstone and bluish-grey, greenish-grey, nodular silty shale (Fig. 2, a). The rocks are in general compacted, indurated, sheared and slickenslided. The upper part of the Siwalik includes alternating layers of soft grey to orange-coloured, loosely packed very coarse to fine grained, grey sandstones, silty-clay and gravelly beds and interbeds of pebbly conglomerate. The sandstones are pebbly in places and are intercalated with claystones and shales (Fig. 2, b). Overall this sedimentary package represents a mozaic of fluvial floodplain environments with the carrying capacity of the rivers increasing in energy over time due to ongoing uplift of the proximal southern flank of the Himalaya.

## **2.2. Materials and methods**

Fossil leaves and fruit remains were collected from the field, carefully exposed in the laboratory, and investigated through comparison of architectural characters with extant specimens. The fossils (Plates I, 1; II, 1; III, 1, 3, 4) were recovered by cleaving large chunks of the massive fossiliferous mudstone with the aid of heavy sledge hammers. Macroscopic images of fossil and relevant extant specimens were photographed using a digital camera (Canon Power Shot A720IS) (Plates I, 1, 2; II, 1-6; III, 1-6). Line-drawings of the fossil specimens including holotype specimens were created using CorelDraw X6 software (Fig. 3). The photographs showing structural details of fossil leaves and their nearest living relatives were taken using an incident light compound microscope (Stemi SV 11, Zeiss) and SEM (S-440, Leica Leo, Cambridge, UK). For comparative purposes, the fossil leaves and fruit remains were examined alongside

herbarium specimens of *Mastixia* and related genera kept at the Central National Herbarium (CAL), Sibpur, Howrah, and also with fresh modern leaves and fruits collected from the forests surrounding the area of the fossil localities. Fossil dimensions were measured directly as well as with the aid of Adobe Photoshop (Adobe, San Jose, CA, USA) software. Plates of fossil and extant specimens were prepared with Adobe Photoshop. For descriptions of leaf and fruit morphology, we followed the terms of Ellis et al., (2009) and Martinetto (2011), respectively.

In order to isolate leaf cuticles the conventional method for cuticle maceration (using Schulze's solution) was applied (Kerp and Krings, 1999). To recover and make visible microscopic features, i.e. stomata and epidermal cells, cuticles of fossil leaves were treated with HCL (10%), HF (40%), dilute HNO<sub>3</sub> (50%), KOH (2-5%) and cuticles of herbarium specimens with dilute HNO<sub>3</sub> (50%) and KOH (2-5%). Cuticles of modern species were stained with safranin for 10 minutes, washed with distilled water and air-dried. Finally, fossil and modern cuticles were washed in polyvinyl alcohol, dried and mounted with DPX (Distrene, Plasticiser, Xylene) and photographed using a transmitted light compound microscope with a camera attachment (Zeiss Axioskop 40). The terminology for cuticular anatomy follows Dilcher (1974). Author citation of a new plant fossil species is mainly after Punt (1994). Stomatal index (SI) is calculated using the formula suggested by Salisbury (1927). The fossil leaf specimens (Holotype CUH/PPL/P/84; Paratype CUH/PPL/IB7/93), fruit remains (Holotype CUH/PPL/IB7/93/f<sub>1</sub>; Paratype CUH/PPL/IB7/93/f<sub>2</sub>) and modern specimens and slides are deposited in the Herbarium and Museum (CUH), Department of Botany, University of Calcutta.

### 2.3. Floristic components in the sediments

Besides leaves and fruits of *Mastixia*, the sediments yielded abundant plant megafossils of many other angiosperm taxa such as *Calophyllum* (Khan et al., 2017), *Dipterocarpus* (Khan et al., 2011), *Elaeocarpus* (Bera et al., 2004), *Shorea* (Khan et al., 2016), as well as gymnosperms such as *Pinus* (Khan and Bera, 2017) and pteridophytes such as *Cyathea* (Bera et al., 2014), and remains attributable to the Thelypteridaceae (Khan et al., 2007). We also processed sediment from the type specimens of *Mastixia arborea* in search of corresponding pollen. Although the samples yielded tricolporate dipterocarpaceous, and elaeocarpaceous pollen, no *Mastixia* grains were observed.

## 3. Results

### 3.1. Systematics of the Miocene-Pleistocene leaf remains

Order: Cornales Link

Family: Cornaceae Dumort.

Sub-Family: Mastixioideae Harms

Genus: *Mastixia* Blumea

Species: *Mastixia asiatica* Khan, Bera M et Bera S, sp. nov. (Plate I, 1, 3; Plate II, 1; Fig. 3, a)

Holotype: CUH/PPL/P/84 (Plate I, 1)

Paratype: CUH/PPL/IB7/93 (Plate II, 1)

Type locality: Road cuttings along the East of Pinjoli area of West Kameng district (CUH/PPL/P/84); Road cuttings along the Itanagar-Bandardewa road in Papumpare district (CUH/PPL/IB7/93).

Type horizon: Lower part of the Siwalik sediments (Dafla Formation, middle to late Miocene; CUH/PPL/P/84); Upper part of the Siwalik succession of sediments (Kimin Formation: late Pliocene to early Pleistocene; CUH/PPL/IB7/93).

Etymology: The specific epithet “*asiatica*” means of Asia and refers to status of the species as the first fossil record of *Mastixia* in Asia.

Repository: The Museum of Palaeobotany-Palynology, Department of Botany, University of Calcutta.

Specific diagnosis: Lamina elliptic; entire margin; acuminate apex and acute base; venation eucamptodromous; secondary veins alternate, curved upwards towards margin, bifurcating towards the margin, acute angle of divergence; hypostomatic leaf; straight and curved anticlinal walls on both ad- and abaxial surfaces; stomatal apparatus paracytic.

Description:

Macromorphology: leaf simple; preserved lamina well-preserved, complete, elliptic to wide elliptic, symmetrical; preserved length 6.8-7 cm, width at broadest point 3.2-4 cm; base acute (Plates I, 1; II, 1); apex acuminate (Plates I, 1; II, 1); margin entire; texture coriaceous; petiole seemingly thick, normal; venation pinnate, simple, eucamptodromous; primary vein single, distinct, moderately stout, thick in the basal half and gradually thinning upward, terminating at the apex, almost straight to slightly curved from the base; secondary veins prominent, 7-9 pairs visible, 0.3 cm to 1 cm apart, mostly alternate, some sub-opposite at the basal region, angle of divergence acute ( $55^{\circ}$  to  $75^{\circ}$ ), lowest pair more acute than middle, about  $80^{\circ}$  (broad acute) in apical part, unbranched, some secondary veins bifurcating towards the margin (Plate I, 1, 3; II, 1), gradually and uniformly curving

upwards and running parallel to each other, moderately thick reaching up to the margin; tertiary veins not clearly seen due to thick cuticle.

Micromorphology: The leaf is hypostomatic; adaxial cuticle of lamina undifferentiated into costal and intercostal areas; epidermal cells usually elongated, irregular, tetragonal, pentagonal or hexagonal, 10-30  $\mu\text{m}$  long and 11-31  $\mu\text{m}$  wide; anticlinal walls of adaxial cuticle straight and curved and 4  $\mu\text{m}$  wide; abaxial cuticle of lamina also undifferentiated into costal and intercostal areas; the abaxial cuticle presenting numerous stomata (Plate I, 5), epidermal cells similar to those on the adaxial surface tetragonal, pentagonal or hexagonal, arranged irregularly, 11-34  $\mu\text{m}$  long and 10-31  $\mu\text{m}$  wide; anticlinal cell walls both straight and curved and 2.6  $\mu\text{m}$  wide (Plate 5, 7, 9); most stomata oval in shape, oriented and distributed irregularly (Plate I, 5, 7), 56-67  $\mu\text{m}$  long and 28-32  $\mu\text{m}$  wide; stomatal apparatus paracytic with one lateral specialised neighbouring cell or subsidiary cell per guard cell (Plate I, 5, 7, 9); guard cells superficial, elongated, 56-65  $\mu\text{m}$  long and 8-14  $\mu\text{m}$  wide; subsidiary cells 64-71  $\mu\text{m}$  long and 19-36  $\mu\text{m}$  wide; stomatal index varying from 18 to 27.

Comparison: The diagnostic features of the present fossil leaves (broad-elliptical shape, acute base, acuminate tip, entire margin, eucamptodromous venation, alternate secondary veins, some with bifurcating nature towards the margin) collectively suggest that the fossil leaf remains described here shows the closest affinity with extant leaves of *Mastixia Blumea* of the family Cornaceae (Plates I, 2, 4; II, 2; Fig. 3, b).

In order to compare and find the nearest specific affinity of the present fossil leaf remains, several modern species of *Mastixia* were examined (Table 2). Among them, the Miocene-Pleistocene leaf remains resemble *Mastixia arborea* C.B. Clarke, *M. tetrandra*

(Wight ex Thw.) C.B. Clarke, *M. pentandra* Blume *M. trichotoma* Blume and *M. tetrapetala* Merr. in lamina morphology and venation course (Plates I, 2; II, 2-6). *M. pentandra*, *M. tetrandra*, and *M. trichotoma* differs from our recovered fossil leaves in having attenuate to caudate leaf apices (Plate II, 3, 4, 5). However, *M. tetrandra* differs in having more acute secondary veins (Plate II, 4). In *M. pentandra*, the secondary veins are relatively more widely spaced than in the fossil specimens. The characteristics of the apex and base are also different. In this modern taxon the apex is caudate and the base is acuminate, in contrast to the acuminate apex and acute base in the present fossil specimens (Plate II, 2, 3). The Mio-Pleistocene leaf remains differ from *M. tetrapetala* in having an acute base as compared to the cuneate base in *M. tetrapetala* (Plate II, 6). The curvature of secondaries is also dissimilar (Plate II, 6). The leaves of modern *Mastixia arborea* show a closer similarity to the fossil leaf remains in size, shape (wide elliptic), nature of the apex (acuminate), nature of the base (acute) and venation pattern (eucamptodromous venation, acute angle of divergence with a specific curvature and bifurcation of alternate secondary veins) (Plates I, 1-4; II, 1, 2).

To verify the identification of our fossil specimens based on the above-mentioned macromorphological features we also examined the cuticular micromorphological characters of both fossil (Plate I, 5, 7, 9) and modern leaves (Plate I, 6, 8, 10) of *Mastixia arborea*, and observed that both modern and fossil specimens show similar epidermal features. So, based on the combination of both macromorphology (size, shape, apex, base and nature of secondary veins) and micromorphological epidermal features (irregularly arranged tetragonal to hexagonal epidermal cells on both ab- and adaxial cuticle, straight-curved anticlinal cell walls, paracytic type stomata, size, shape, orientation and

distribution of stomata), our leaf specimens are assigned to the genus *Mastixia* and we regard *Mastixia arborea* as a possible modern relative.

No fossil leaves resembling *Mastixia* have been described previously from either India or even Asia. Therefore, being different from extant taxa, these Mio-Pleistocene leaf remains have been described under a new specific name. Because the fossil specimens resembles *Mastixia* and are recorded from Asia for the first time, they are described here as a new species, *Mastixia asiatica* Khan, Bera M et Bera S, sp. nov.

### **3.2. Systematics of the Plio-Pleistocene fruit remains**

Species: *Mastixia siwalika* Khan, Bera M et Bera S, sp. nov. (Plate III, 1, 3, 4; Fig. 3, c, d)

Holotype: CUH/PPL/IB7/f/61 (Plate III, 1)

Paratypes: CUH/PPL/IB7/f/62 (Plate III, 3); CUH/PPL/IB7/f/63 (Plate III, 4)

Type Locality: Road cuttings along the Itanagar-Bandardeva road in Papumpare district.

Type horizon: Upper part of the Siwalik succession of sediments (Kimin Formation: late Pliocene to early Pleistocene).

Etymology: The Latin epithet 'siwalika' is chosen in reference to the Siwalik deposits from where carbonised fruit remains were recovered.

Repository: The Museum of Palaeobotany-Palynology, Department of Botany, University of Calcutta.

Specific diagnosis: Cylindric-ovoid; 2.1-2.2 X 1 cm; endocarp gently ribbed, with prominent furrows; unilocular, U-shaped locule in cross section.

Description: Carbonised endocarps cylindrical-ovoid in shape; 2.1- 2.2 cm in length and maximum breadth 1 cm; the external surface of the endocarp rough with the typical longitudinal striations and outgrowths, thick walled and gently ribbed, with prominent furrows, some furrows discontinuous (Plate III, 1, 3, 4; Fig. 3, c); more or less round apex and pointed base; 1-loculed, single-seeded, endocarp; germination valve extending from nearly the apex to the base of the endocarp not clearly visible externally; resin ducts absent; the locule U-shaped in cross section with arms that almost parallel one another (Plate III, 4; Fig. 3, d), the arms of the 'U' also mark the position of dehiscence of the fruit.

Comparison: Mastixioids (Cornaceae, Mastixioideae) fruits can be distinguished easily in the fossil record by locules that are U-shaped in cross section, an infold of the endocarp into this locule; ribs, furrows that are prominent on the endocarp's surface; and an elliptical germination valve that extends from nearly the apex to the base of the endocarp (Mai, 1993). It is clear from the above list of characters that our Plio-Pleistocene fossils represent fruits of this group of angiosperms. The Arunachal fruit remains share characters with both of the extant genera of the family Cornaceae, namely *Mastixia* and *Diplopanax* (Table 3). Both genera have one locule per fruit and U-shaped locules in cross section. *Diplopanax* differs in the external ornamentation of the endocarp surface. The external surface of the endocarp of *Diplopanax* is relatively smooth and lacks the typical longitudinal striations and outgrowths characteristic of mastixioids. It also differs from our material in the presence of resin ducts in endocarp and the lack of ribs and furrows on the surface of the endocarp. A ribbed and furrowed endocarp is a unique characteristic of *Mastixia* fruits. So, we have included the Plio-Pleistocene fossils in the



genus *Mastixia*. All of the available characters for the fruits have led us to conclude that this is the most reasonable assessment given the material currently available. Other than fruit size, we cannot find any significant characters to preclude an assignment of the Arunachal fruit remains to the modern genus *Mastixia*. Among the species of extant *Mastixia*, the Plio-Pleistocene fruit remains resemble with the fruits of the extant species *M. arborea*, *M. tetrandra*, *M. pentandra* in external morphology (Plate III, 2, 5, 6). In *M. tetrandra* and *M. pentandra*, the shape of endocarps is more cylindrical than in the fossil specimens. However, *M. tetrandra* and *M. pentandra* differ in having more pointed bases (Plate III, 5, 6). The Mio-Pleistocene fruit remains also differ from the aforesaid modern taxa in having more prominent striations (furrows) on the endocarp's external surface. Our Siwalik fruit remains show the close resemblance to the fruits of the extant species *M. arborea* in shape (cylindrical-ovoid), size, apex (more or less round), base (pointed) and external surface ornamentation of the endocarps (endocarps with the typical longitudinal striations including gentle ribs and prominent furrows) (Plate III, 1, 2, 3). The thick walled, unilocular and gently ribbed endocarps with longitudinal furrows; U-shaped locules in the endocarp's cross section affords comparison to a limited number of fossil taxa so-far described in Europe and North America, thus providing new material for the palaeobiogeographic history of the mastixioids. Our fossil fruits differ from the earlier fossil records of *Mastixia*, *Diplopanax* and *Eomastixia* in having different sizes, shapes, thicknesses and sculptures of the unilocular endocarps (Table 3). The fossil species *Diplopanax eydei* Stockey et al. differs from our fossil specimens in the presence of resin ducts in endocarp and the absence of ribs and furrows on the surface of the endocarp. The infold structure of endocarp is also different. In *Diplopanax eydei* infold of

endocarp is broad and shallow, in contrast to the U-shaped infold with parallel arms in the present fossil specimens. However, *Mastixa rattazzii* Martinetto, *Mastixa eydei* Tiffney and Haggard, and *M. oregonensis* (Scott) Tiffney and Haggard differ in having strongly ribbed endocarp. The fossil morphogenus *Eomastixia* Chandler differs from present fossil specimens in the presence of resin ducts in endocarp. On the basis of such differences, our Plio-Pleistocene fruit remains have been described as a new species. As our fossil specimens establish the first ever record of *Mastixia arborea* fruit remains and are recovered from the Siwalik sediments of Arunachal sub-Himalaya, we propose a new species, *Mastixia siwalika* Khan, Bera M et Bera S, sp. nov.

## 4. Discussion

### 4.1. Biogeographic implications

Mastixioids (Cornaceae, Mastixioideae) fruits are mainly reported from the Cenozoic i.e. in both Paleogene (mostly Oligocene in age) and Neogene (Miocene in age) sediments of Europe (Martinetto, 2011) (Fig. 4, a). However, fossil mastixioid fruits first appear in Central Europe in Upper Cretaceous sediments (Knobloch and Mai, 1986), probably suggesting a European origin of the group. Following that they are found in the Eocene sediments of England (Chandler, 1926, 1961, 1962; Reid and Chandler, 1933); Oligocene sediments of Germany (Mai and Walther, 1978, 1991), Czech Republic (Holý, 1984), Bulgaria (Palamarev and Petkova, 1966), and Italy (Martinetto, 2011) as well as in Miocene sediments of Germany (e.g. Kirchheimer, 1957; Mai, 1964, 1970, 1993, 1995, 2001; Czaja, 2003), Poland (Czeczott and Skirgiello, 1975a, b), southwestern France (Gregor, 1990), Mediterranean area (Greece) (Velitzelos and Gregor, 1982) and the

Czech Republic (Holý, 1977; Ševčík et al., 2007; Holý et al., 2012). In contrast to Europe, North America has revealed a much lower diversity of mastixioids in its geological past (Potbury, 1935; Scott, 1954; MacGinitie, 1969; Wolfe, 1977; Wehr, 1995; Manchester, 1994; Tiffney and Haggard, 1996; Stockey et al., 1998). They are reported from the Paleogene (Eocene) sediments. The oldest known fossil record is dated to the middle Eocene (Manchester, 1994), implying that mastixioids probably first appeared in North America no later than the mid Eocene.

According to the palaeogeographic distribution of the group, it seems that mastixioids originated from Europe during the Late Cretaceous, and arrived in North America during early Eocene time. As for many other seed plants this was most possibly through the North Atlantic Land Bridge (NALB) (Fig. 4b). At that time, the NALB was a corridor for the floristic exchanges between the two continents (Tiffney and Manchester, 2001). The earlier records also suggest that they were common forest elements growing in both Europe and North America during the Eocene.

Fossil mastixioids are common in Eocene sediments of the middle latitudes in Europe, while in the Oligocene they were found in southern Europe i.e. Italy (Martinetto, 2011). This suggests a southward retreat of the group's distribution in this continent from the Eocene to Oligocene, probably in response to the global cooling initiated during the Eocene–Oligocene transition (Tiffney 1985; Graham 1999; Xiang and Soltis 2001; Zachos et al., 2008). The group even reached more southern latitudes in the Miocene (Fig.4a). Our late Miocene-Pleistocene Asia occurrence of *Mastixia* is among the southernmost fossil records of the genus (Fig. 2a, b). This is in agreement with the

inferred historical southward retreat of the mastixioid group, which is also consistent with its modern distribution pattern (Fig. 2a).

Fossil records also indicate that Europe, where several known fossil species of the mastixioids have been reported, may have been a centre for mastixioid evolution and considerable diversification in the past. The numerous occurrences of mastixioids, which are well-known thermophilous plants, have been conventionally used to show that the early–middle Cenozoic climate in Europe was warmer than today (Mai, 1995). However, another important climatic requirement of mastixioids is high humidity. This may be consistent with the warm and humid climate throughout the European Cenozoic (Mosbrugger et al., 2005). In Europe, the mastixioids remained prevalent during the Miocene. Based on the lack of fossil occurrences in the continent after the Miocene, the group likely disappeared from Europe by that time. The disappearance of mastixioids from Europe might be related to the cooling in the late Neogene (Manchester 1987; Ehlers et al., 2011). However, extinction of the mastixioids in North America after the Eocene might be related to the cooling initiated during in the Eocene–Oligocene transition and drying due to the uplift of Rocky Mountains (Graham 1993; Retallack et al., 2004; Mix et al., 2011; Fan et al. 2014).

It is interesting to note that mastixioids do not occur in Europe and North America at present, and they are now confined to the tropical evergreen forests of some limited areas of India and neighbouring Southeast Asia (Tiffney and Haggard, 1996). All fossil mastixioids occurred outside their modern geographic limits, until now. Despite flourishing in the modern era, convincing records of mastixioids from the Indian and Southeast Asian Cenozoic have historically been lacking (Bande, 1992; Mehrotra, 2003).

The newly discovered fossil materials confirm the existence of *Mastixia* (Mastixioideae) in the eastern Himalaya during Miocene-Pleistocene time, but the modern analogue, *Mastixia arborea*, is not present in today's flora of the eastern Himalaya (Brandis, 1971; Hazra et al., 1996). *Mastixia arborea* is now endemic only to the tropical evergreen forests of the Western Ghats (south India), situated at the same latitudes as the fossil locality at the time of deposition (Fig. 4c). The occurrence of the present fossils in the Arunachal foothill, eastern Himalaya may suggest that during the Mio-Pleistocene, they were growing in an area having climatic conditions similar to those prevailing in the Western Ghats at present. This hypothesis is consistent with quantitative climatic parameters (relative humidity, RH 80.79%; warm month mean temperature, WMMT 27.8–28.3 °C;  $\pm 3.3$  °C growing season precipitation, GSP 174–242 cm  $\pm 92$  cm during the Mio-Pleistocene time in Arunachal Pradesh; RH 81%; WMMT 28–30.3 °C, GSP 183–330 cm at present in Western Ghats) (Srivastava and Mehrotra, 2013; Khan et al., 2014a). Drastic environmental changes play an important role in the alteration and diversification of floral distribution patterns during Neogene times (Huggett, 2004). Some taxa adapted to the changed climatic conditions and continued to flourish, while others either suffered regional extinction or migrated to areas with suitable tropical littoral and swampy conditions. The climate during the late Cenozoic changed dramatically due to the rapid uplift of the high Himalaya (Chatterjee and Scotese, 1999; Ding et al., 2017), the onset and development of the Northern Hemisphere ice sheet (Zachos et al., 2001, 2008), closure of the Tethys and loss of littoral environments along the Himalayan front (Lakhanpal, 1970) and modifications of monsoonal circulation (Molnar, 1993; Ding et al., 2017). Among these factors, the modern Asian monsoon system locally amplified the

seasonality of precipitation (Su et al., 2013a; Tang et al., 2013, 2015). Under these circumstances regional extinction of plants cannot be ruled out. For example, *Cedrus* disappeared from southwestern China due to the strong Asian winter monsoon during the Quaternary (Su et al., 2013b). *Mastixia arborea* may have also experienced the same fate. Significant changes in the climate (during the Pleistocene time mean annual temperature, MAT 25.38 °C; mean annual precipitation, MAP 1898 mm; warm month mean temperature, WMMT 28.05 °C; cold month mean temperature, CMMT 20.86 °C; present day MAT 29.5 °C; MAP 3000-5000 mm; WMMT ±30–35 °C; CMMT 9.8-12°C) and latitude (from approx. 8°–15°N to 27°17'20"N) after Pleistocene in Arunachal Himalayas might be the two possible reasons for the extinction of *Mastixia arborea* from present day vegetation not only of Arunachal Pradesh but also of the entire northeast India. This taxon is now confined to the tropical evergreen forests of the Western Ghats. This is consistent with the climatic variables in the fossil and modern locality of the taxon (MAT 29.5 °C; MAP 3000-5000 mm; WMMT ±30–35 °C; CMMT 9.8-12°C in Arunachal Pradesh; MAT 27.1–27.8 °C; MAP 1839-3291 mm; WMMT 28–30.3 °C, CMMT 26.7–28.2°C in Western Ghats) (Hazra et al., 1996; Srivastava and Mehrotra, 2013; Dhar and Nandargi, 2014).

We speculate that *Mastixia* also disappeared from the present day flora of the entire eastern Himalaya most probably because of the gradual amplification of MSI (monsoon index) from the Miocene to the present. The MSI for the eastern Himalayan Lower Siwalik flora (mid Miocene) is 42.6 while that of the modern is 60.3 (Khan et al., 2014a). It appears then that in mid Miocene times the monsoon in the area was weaker than now. The higher the MSI is the greater the difference in precipitation between the wet and dry

seasons. The ratios of the precipitation during the three consecutive wettest months (3WET) to the three consecutive driest months (3DRY) for eastern Himalaya are  $>4.9:1$  which is much weaker than the present day where the ratio for that region is over 120:1 (Khan et al., 2014a).

#### 4.2. Palaeoclimatic significance

The Nearest Living Relative (NLR) method is a powerful approach to obtain qualitative and quantitative palaeoclimatic (or palaeoenvironmental) information based on the assumption of the similarity of a fossil taxon or assemblage to its nearest living relative in morphological characters, although it has some limitations and its accuracy and consistency depend on geological age, identification of taxa and taphonomy (Mosbrugger, 2009).

Our fossil material provides unequivocal evidence that *Mastixia* trees occurred in Arunachal Pradesh, eastern Himalaya during the Mio-Pleistocene time when the Dafla Formation (= lower part of the Siwalik) and Kimin Formation (= upper part of the Siwalik) were deposited. It is worth mentioning that other tropical evergreen trees, such as *Gynocardia odorata* (Achariaceae); *Calophyllum inophyllum*, *C. polyanthum* (Calophyllaceae); *Shorea assamica* (Dipterocarpaceae); *Canarium bengalense* (Burseraceae); *Dysoxylum procerum*, *D. costulatum* (Meliaceae); *Dracontomelum mangiferum* (Anacardiaceae); *Acacia catechuoides*, *Pongamia pinnata*, *Millettia pachycarpa*, *Mastertia assamica* (Fabaceae); *Combretum chinense* (Combretaceae); *Cinnamomum bejolghota*, *Actinodaphne obovata*, *A. angustifolia* (Lauraceae); *Croton caudatus*, *Macaranga denticulata* (Euphorbiaceae); *Quercus lamellosa*, *Q.*

*semicarpifolia* (Fagaceae) and *Knema glaucescens* (Myristaceae) are also recorded from the Dafla and Kimin Formations of Siwalik sediments of Arunachal Pradesh, eastern Himalaya during Mio-Pleistocene time (Khan and Bera 2007; Khan and Bera, 2010, 2014a,b; Khan et al., 2011, 2014a,b, 2015, 2017). The recovery of *Mastixia*, a genus considered to be an indicator for wet evergreen rainforests (Matthew, 1976), and our earlier-described evergreen taxa, collectively suggest the existence of tropical, wet, evergreen rainforests in Arunachal Pradesh during the middle Miocene to early Pleistocene time. However, at present a tropical semi evergreen forest cover is found in the area of investigation (Hazra et al., 1996). Evergreen elements indicate the prevalence of a tropical, warm, humid climate during the deposition of the sediments in contrast to the present day relatively overall drier climate of the area. This clearly shows that there has been a substantial change in the precipitation regime of this region since the middle Miocene. Ongoing Himalayan uplift may have been responsible for this change. Extant *Mastixia arborea*, similar to our fossil specimens, is an important component of moist evergreen forests in association with *Calophyllum* and *Elaeocarpus* (Matthew, 1976). This observation can be extended back through the period of Siwalik sedimentation because *Mastixia* co-occurs with *Calophyllum* and *Elaeocarpus* found in upper Siwalik strata (late Pliocene to early Pleistocene) of the eastern Himalaya (Bera et al., 2004; Khan et al., 2017).

For the quantitative reconstruction of palaeoclimate, we undertook CLAMP (Climate Leaf Analysis Multivariate Program) analysis on the fossil flora of Arunachal sub-Himalaya (Khan et al., 2014a). CLAMP analysis suggests a MAT (mean annual temperature)  $23.6\text{--}25.3\text{ }^{\circ}\text{C} \pm 2.8\text{ }^{\circ}\text{C}$ ; a CMMT (cold month mean temperature)  $16.9\text{--}21.2$



°C  $\pm$  4 °C, a WMMT (warm month mean temperature) of 27.8–28.3 °C  $\pm$  3.3 °C and a weak monsoonal climate with GSP (growing season precipitation) of 174–242 cm  $\pm$  92 cm during the Miocene-Pleistocene (Khan et al., 2014a). The available Mio-Pleistocene leaves of *Mastixia* were similar in size and shape to those of today, apparently reflecting mesic conditions. Other foliar physiognomic characters of the fossil leaves such as the presence of an acuminate 'drip tip', the base morphology, an entire margin, and venation pattern are also in conformity with our interpretation of warm and wet climatic conditions in Arunachal sub-Himalaya during Siwalik sedimentation.

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### **Captions of Table, Text-figures and Plates**

Table 1. Generalised lithotectonic succession in Arunachal Pradesh (after Joshi et al., 2003).

Table 2. Comparative morphological chart of the available modern leaves among species of *Mastixia* of Cornaceae.

Table 3. Main diagnostic characters of *M. siwalika* and other comparable modern and fossil mastixioid fruits (modified after Tiffney and Haggard, 1996; Stockey et al., 1998 and Martinetto, 2011)

Fig. 1. Map of Arunachal Pradesh showing the sites of the fossil localities.

Fig. 2. Geological map of Arunachal foothills (modified after Singh and Tripathi, 1990), the leaf symbol indicates the position of the fossil localities. (a) Lithological column for part of the exposed road-section along Pinjoli road near culvert no. 48/1 in West Kameng district (lower part of the Siwalik strata); (b) Lithological column for part of the exposed road-section along the Itanagar-Bandardewa road in Papumpare district (upper part of the Siwalik strata).

Fig. 3. (a) Line drawing of fossil leaf of *Mastixia asiatica* Khan, Bera M et Bera S, sp. nov. showing shape, size, acuminate apex (black arrow), acute base (green arrow), primary vein (red arrow), secondary veins (blue arrows) and bifurcated nature of secondary veins near the margin (indicated by pink arrow) (Holotype: CUH/PPL/P/84); (b) Line drawing of modern leaf of *Mastixia arborea* C.B. Clarke showing similar shape, size, apex (black arrow), base (green arrow), primary vein (red arrow), secondary veins (blue arrows) and bifurcation of secondary veins (indicated by pink arrow); (c) Line drawing of a carbonised endocarp of *Mastixia siwalika* Khan, Bera M et Bera S, sp. nov. showing characteristic furrows (red arrows) (Holotype: CUH/PPL/IB7/f/61); (d) Line

drawing of a imperfect cross-section of endocarp showing U-shaped locule (marked by blue arrow) (Paratype: CUH/PPL/IB7/f/63) (Scale Bar = 1 cm).

Fig.4. (a) Map showing present day distribution, earlier and present fossil localities of mastixioids (Cornaceae, Mastixioideae); (b) Map showing fossil localities and possible migratory path (indicated by red arrows) of mastixioids; (c) Map showing modern distribution and fossil locality of studied taxon of *Mastixia arborea*.

Plate I. *Mastixia asiatica* and *Mastixia arborea* leaves. (1) *Mastixia asiatica* Khan, Bera M et Bera S, sp. nov. showing acuminate apex (black arrow), acute base (yellow arrow), primary vein (red arrow) and secondary veins (blue arrow) with its bifurcation nature (pink arrow) (Holotype: CUH/PPL/P/84); (2) *Mastixia arborea* C.B. Clarke showing similar apex (black arrow), base (yellow arrow), primary vein (red arrow) and secondary veins (blue arrow) with its bifurcation nature (pink arrow); (3) Enlarged view of Fig. 1; (4) Enlarged view of Fig. 2 (Scale bar = 1 cm); (5), (7) *Mastixia asiatica* - Abaxial cuticle, paracytic type stomata (black arrow), anticlinal cell walls (blue arrow) (Scale bar = 10  $\mu\text{m}$ ); (6), (8) *Mastixia arborea* - Abaxial cuticle, paracytic type stomata (black arrow), anticlinal cell walls (blue arrow) (Scale bar = 10  $\mu\text{m}$ ); (9) *Mastixia asiatica* - SEM of the stomatal complex (Scale bar = 10  $\mu\text{m}$ ); (10) *Mastixia arborea* - Details of stomatal complex (Scale bar = 10  $\mu\text{m}$ ).

Plate II. *Mastixia* leaves. (1) Another fossil leaf of *Mastixia asiatica* Khan, Bera M et Bera sp. nov. showing shape, size, apex, base, primary vein (red arrow) and secondary veins (blue arrow) with its bifurcated nature towards the margin (pink arrow) (Paratype: CUH/PPL/IB7/93); (2) Another modern leaf of *Mastixia arborea* C.B. Clarke showing similar shape, size, apex, base, primary vein (red arrow) and secondary veins (blue

arrow) with its bifurcated nature (pink arrow); (3) Modern leaf of *M. pentandra* Blume; (4) Modern leaf of *M. tetrandra* (Wight ex Thw.) C.B. Clarke; (5) Modern leaf of *M. trichotoma* Blume; (6) Modern leaf of *M. tetrapetala* Merr. (Scale bar = 1 cm).

Plate III. *Mastixia* fruits. (1) Endocarp of *Mastixia siwalika* Khan, Bera M et Bera S, sp. nov. showing apex (black arrow), base (red arrow) and gentle ribs and prominent furrows (white arrows) on the surface (Holotype: CUH/PPL/IB7/f/61); (2) Modern fruit of *Mastixia arborea* C.B. Clarke showing similar apex (black arrow), base (red arrow) and surface striations (white arrows); (3) Another carbonised endocarp of *Mastixia siwalika* showing gentle ribs and prominent furrows (white arrows) (Paratype: CUH/PPL/IB7/f/61) (4) *Mastixia siwalika* - Endocarp's imperfect cross-section showing a U-shaped locule (pink arrow) (Paratype: CUH/PPL/IB7/f/63) (5) Modern fruit of *M. tetrandra* (Wight ex Thw.) C.B. Clarke; (6) Modern fruit of *M. pentandra* Blume (Scale bar = 1 cm).



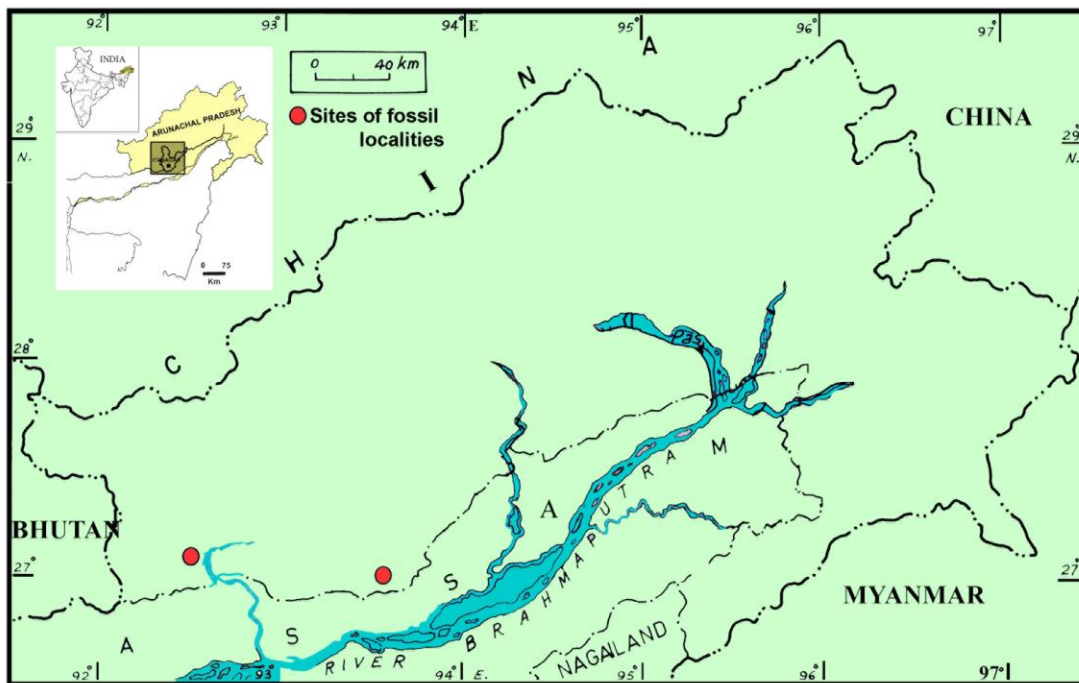


Fig. 1

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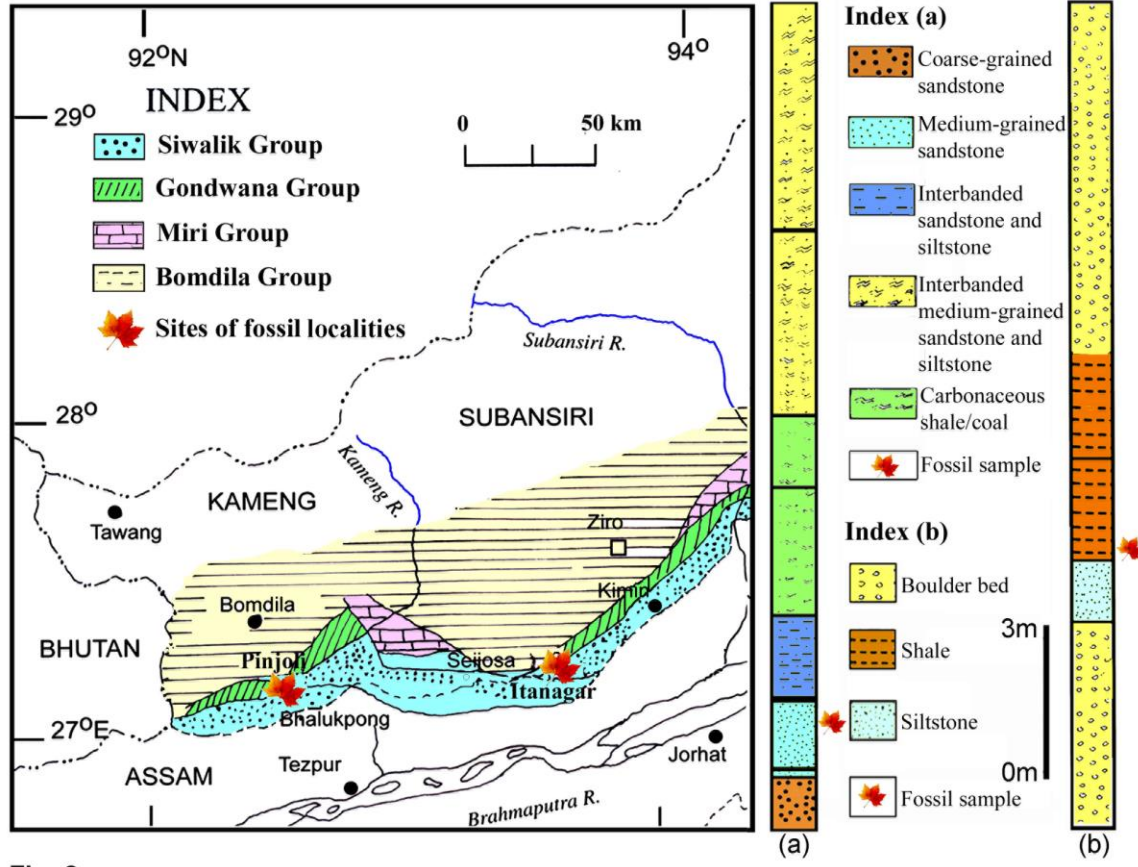


Fig. 2

ACCEP

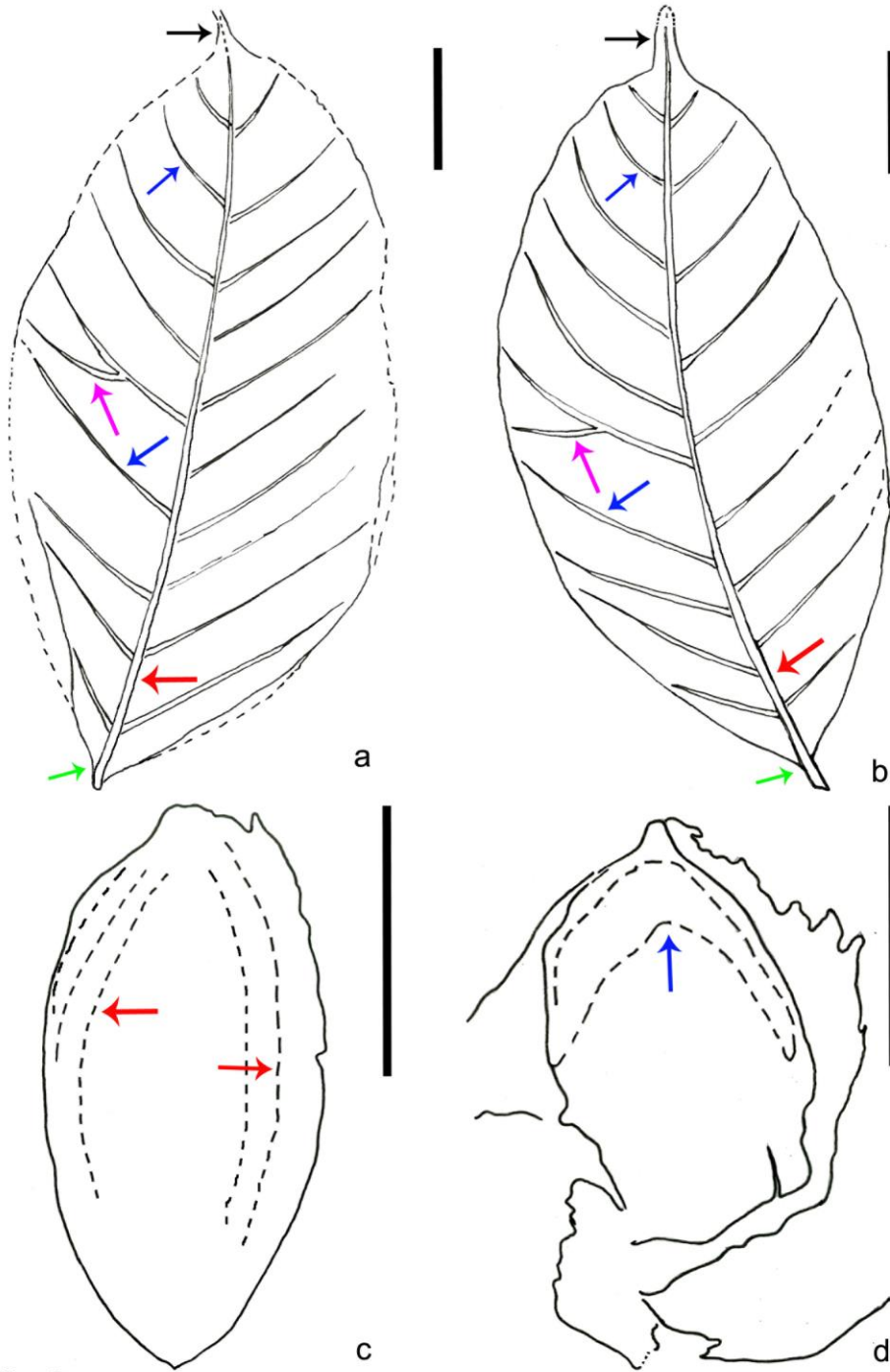


Fig. 3

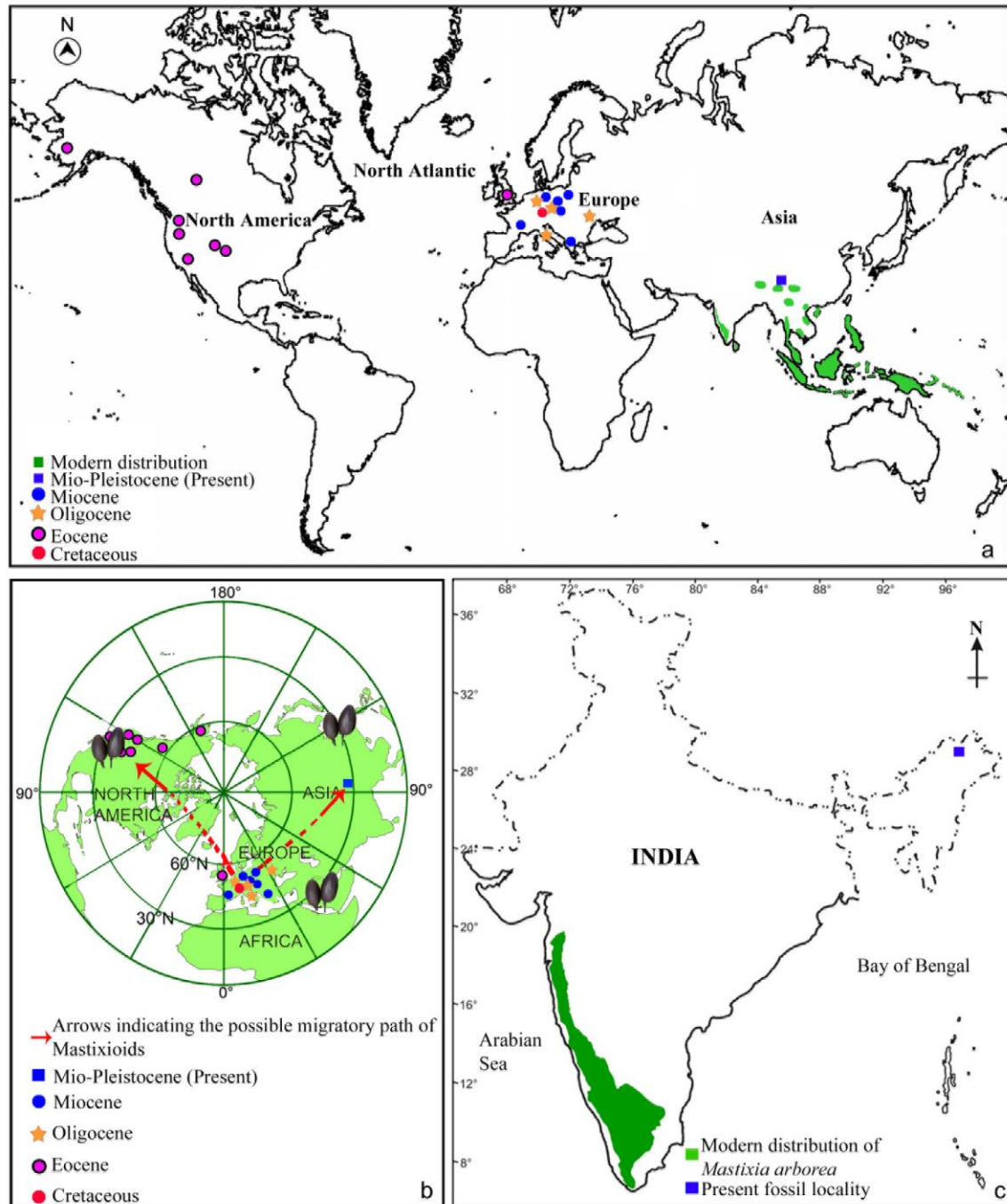


Fig. 4

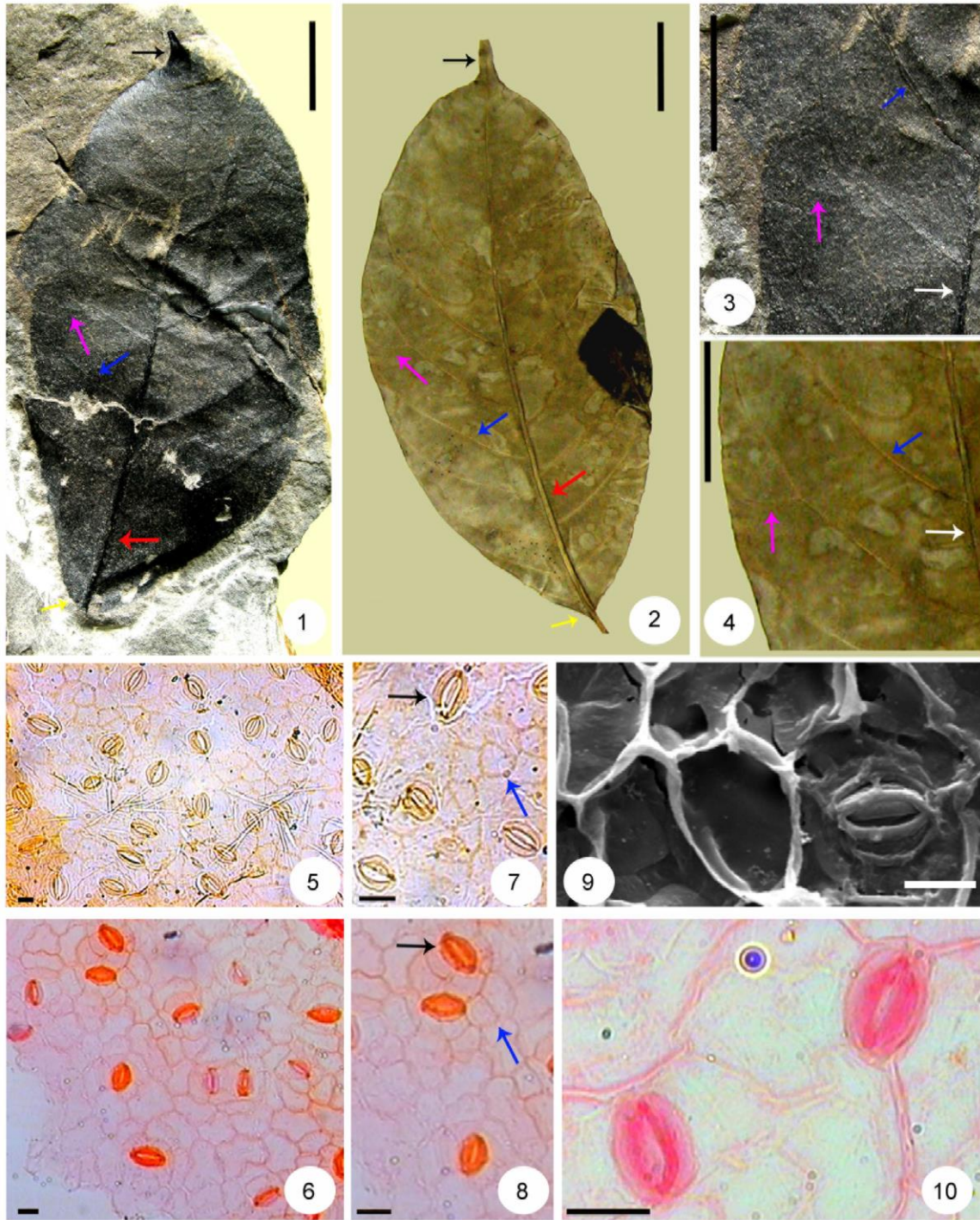


Plate I

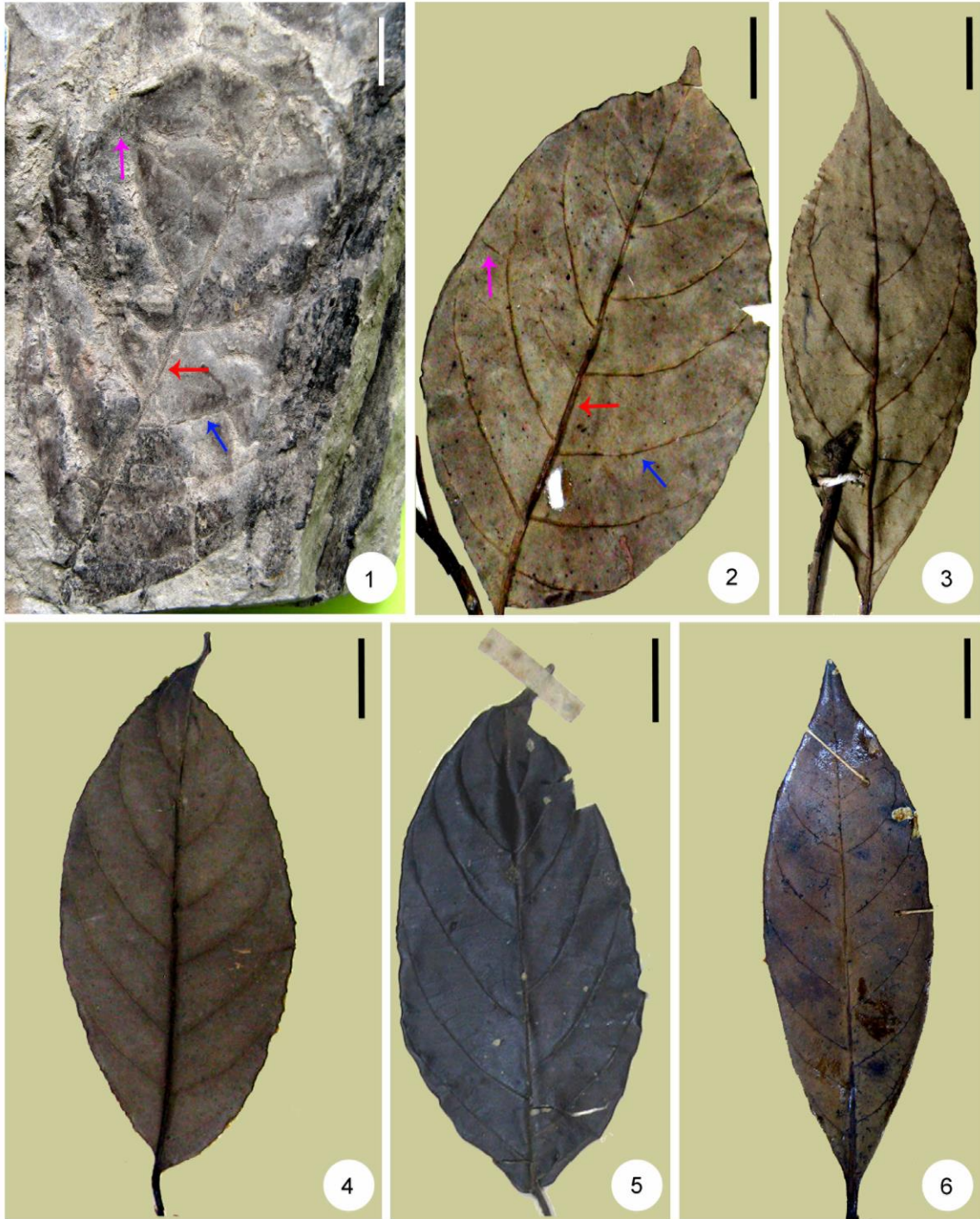


Plate II

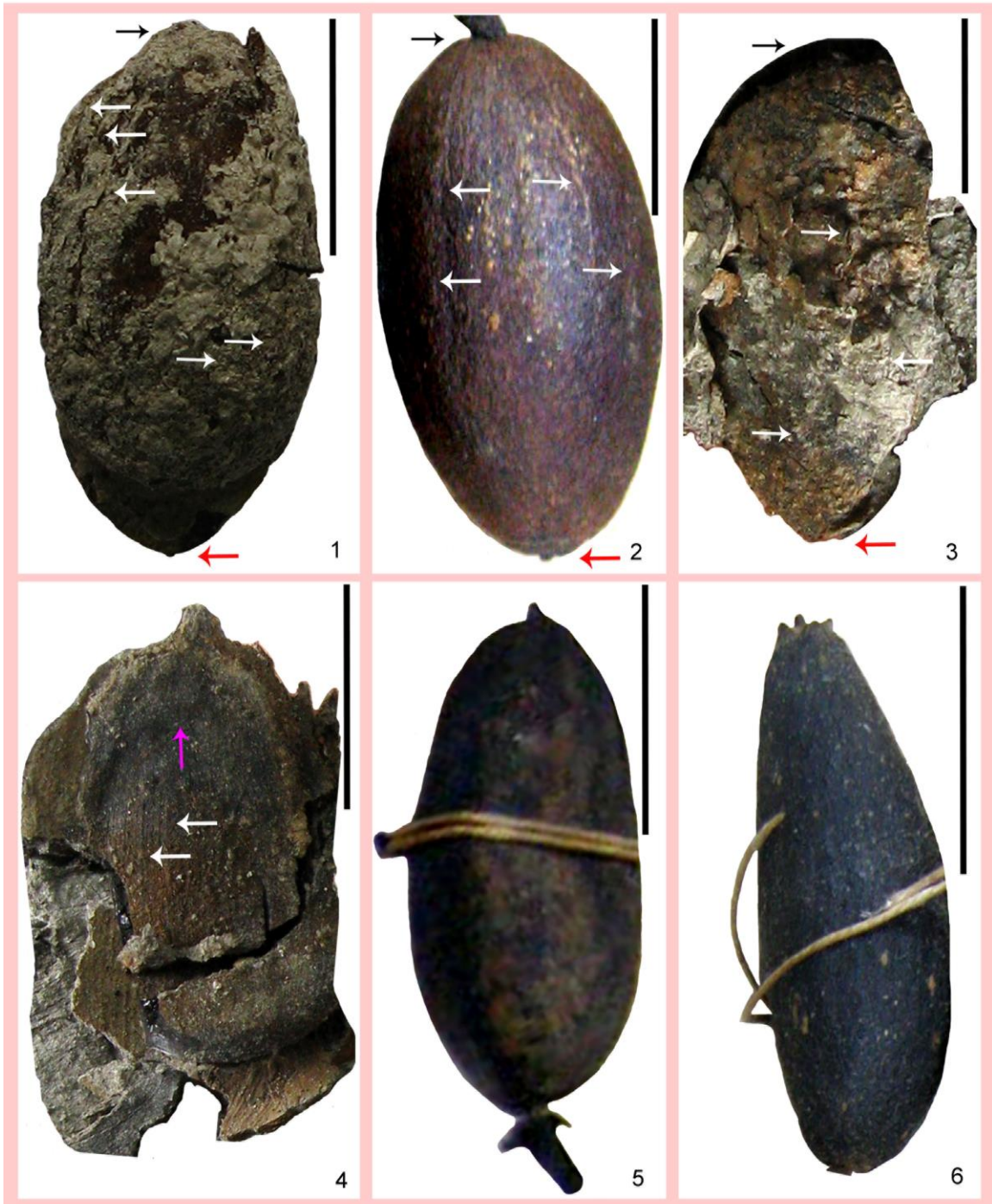


Plate IV

**Table 1**

<b>NORTH</b>		
Gondwana Group		Carbonaceous shale, sandstone and coal
Lower Siwalik (Dafla Formation)	Main Boundary Faults	Well indurated sandstone, shale and siltstone with plant fossils
Middle Siwalik (Subansiri Formation)	Thrust	Weakly indurated sandstone and shale and siltstone with plant fossils
Upper Siwalik (Kimin Formation)	Thrust	Sandstone and claystone/shale with plant fossils fossil wood
Assam Alluvium/ Quaternary deposits	Main Frontal Fault	
<b>SOUTH</b>		



Table 2

Species of <i>Mastixia</i>	Leaf morphological characters									
	Apex	Base	Margin	Size	Shape	Balance	Venation pattern	Angle of divergence of secondary veins	Nature of secondary veins	Tertiary veins
<i>M. arborea</i>	Acuminate	Acute	Entire	Microphyll, Mesophyll	Elliptic to wide elliptic	Symmetrical	Eucamptodromous	Moderate acute	Alternate to sub-opposite; some bifurcating towards the margin	Percurrent
<i>M. tetrandra</i>	Attenuate to caudate	Acute	Entire	Microphyll	Elliptic	Symmetrical-asymetrical	Eucamptodromous	Narrow acute	Alternate to sub-opposite	Percurrent
<i>M. pentandra</i>	Caudate	Acuminate	Entire	Microphyll	Narrow Elliptic	Symmetrical	Eucamptodromous	Wide to moderate acute	Alternate; intersecondary veins present	orthogonal reticulate-percurrent
<i>M. trichotoma</i>	Attenuate to caudate	Acute	Entire	Microphyll	Elliptic	Symmetrical-asymetrical	Eucamptodromous	Narrow acute	Alternate	Percurrent
<i>M. tetrapetalata</i>	Acute	Cuneate	Entire	Microphyll	Narrow elliptic	Symmetrical	Eucamptodromous to Brochidromous	Acute	Alternate to sub-opposite; intersecondary veins present	Percurrent

Table 3

Taxa	Diagnostic characters						
	Endocarp surface	Locule number	Resin ducts in endocarp	Infold and septum	Infold number	Lacunae in endocarp wall	Infold external ornamentation
<i>Mastixia</i> , living	Smooth, rough, gently ribbed	One	Absent	Infold U-shaped with arms converging toward the exterior; infold narrow with parallel margins	One septum	Absent	Absent
<i>Diplopanax</i> , living	Smooth	One	Present	Infold U-shaped with parallel arms	One septum	Absent	Absent
<i>Mastixia rattazzii</i> (Italy, Oligocene)	Strongly ribbed	One	Absent	Infold narrow with parallel margins	One septum	Present?	Absent
<i>Mastixia eydei</i> , M.	Strongly ribbed	One	Absent	Infold narrow with	One septum	Absent	Absent

<i>oregonensis</i> (North America, Eocene)				parallel margins			
<i>Eomastixia</i> (Europe, Cretaceous to Miocene)	Rough, gently and strongly ribbed	One, two or more	Present	Infold U-shaped with arms converging toward the exterior	One septum	Absent	Absent
<i>Diplopanax eydei</i> (British Columbia, Eocene)	Smooth	One	Present	Infold broad and shallow	One septum	Absent	Absent
<i>M. siwalika</i> (Arunachal, Plio-Pleistocene)	Rough, gently ribbed	One	Absent	Infold U-shaped with arms that almost parallel one another	One septum	Absent	Absent

## Highlights

- First ever fossil record of mastixioids from India and Southeast Asia
- Diagnoses based on leaf and fruit micro- and macromorphology
- Discusses reasons for endemism and loss of *Mastixia* from entire eastern Himalaya
- Reviews phytogeography and highlights phytogeographic implications for mastixioids
- Tropical, warm and humid climatic conditions suggested at times of deposition