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Occurrence of *Shorea* Roxburgh ex C. F. Gaertner (Dipterocarpaceae) in the Neogene Siwalik forests of eastern Himalaya and its biogeography during the Cenozoic of Southeast Asia

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Abstract

We report the occurrence of two leaf impressions and one leaf compression along with one winged fruit and two fruiting calyx lobes, resembling those of *Shorea* Roxburgh ex C. F. Gaertner, in the lower Siwalik (Dafla Formation, middle to upper Miocene), middle Siwalik (Subansiri Formation, Pliocene) and upper Siwalik (Kimin Formation, upper Pliocene to lower Pleistocene) sediments exposed in Arunachal Pradesh, eastern Himalaya. We determine their taxonomic positions based on morphological comparison with similar extant and fossil specimens and discuss their phytogeographic and paleoclimatic implications in terms of the distribution and habitat of fossil and modern populations. The Miocene winged fruit is recognized as *Shorea pinjoliensis* Khan, Spicer RA et Bera, sp. nov. while the Pliocene and Plio-Pleistocene fruiting calyx lobes are recognized as *S. bhalukpongensis* Khan, Spicer RA et Bera, sp. nov. and *S. chandernagarensis* Khan, Spicer RA et Bera, sp. nov. respectively. Based on leaf architecture the Miocene, Pliocene and Plio-Pleistocene leaves are recognized as *S. mioobtusa* Khan, Spicer RA et Bera, sp. nov., *S. pliotumbaggina* Khan, Spicer RA et Bera, sp. nov. and *S. nepalensis* Konomatsu et Awasthi respectively. The discovery of members of *Shorea* indicates that they had arrived in a tropical, warm and humid eastern Himalaya by the Mio-Pleistocene. Present and earlier records of *Shorea* suggest that this genus was a common forest element during Neogene (Miocene time) as well as in the Siwalik forests including Arunachal sub-Himalaya. In this paper, we also review in detail the biogeographic history and suggest possible migration routes of the genus.

Key words: *Shorea*; Miocene-Pleistocene; phytogeography; paleoclimate; Arunachal Pradesh.

1. Introduction

Dipterocarpaceae Blume is one of the main timber-producing families in the tropical rain forests of Southeast Asia and forms a high proportion of the emergent and main canopy strata of the forest (Manokaran et al., 1992). The highest species diversity of dipterocarps is known in evergreen rainforests in Peninsular Malaysia, Sumatra and Borneo (Ashton, 1982; Symington, 1943; Whitten et al., 1987). In particular, Borneo is the main centre of dipterocarp diversity with the highest number of endemic species (155 species). They are one of the 17 families that are widely disjunct among the Africa-Eurasian (-Pacific) regions (Symington, 1943; Radford et al., 1974). Extant Dipterocarpaceae possess the following combination of morphological features: leaf simple, alternate, margin entire or sinuate; venation pinnate; fruit usually nutlike with persistent, variously accrescent calyx of which 2–5 sepals are usually enlarged into wing-like lobes, sepals either free at base or fused at base, forming a cup or tube enclosing the fruit (Ashton, 1982; Li et al., 2000).

The family Dipterocarpaceae *sensu stricto* is homogeneous for only Asian plants while the Dipterocarpaceae *sensu lato* include three subfamilies: Dipterocarpoideae (13 genera, c. 470 spp.) in tropical Asia (from Seychelles, Sri Lanka and India northeastwards to southern China and the Batan Islands, and southeastwards to New Guinea and D'Entrecasteaux Island); monotypic Pakaraimoideae (one genus, one species) is confined to Guyana in South America; and Monotoideae (3 genera, c. 40 spp.) occurs in Africa and South America (Ashton, 1982; Maury-Lechon and Curtet, 1998). Although the phylogenetic placement of Dipterocarpaceae within angiosperms has been problematic, a recent molecular phylogenetic analysis suggests that this family should be assigned to the order Malvales and that Sarcolaenaceae is the sister group to the Dipterocarpaceae (Maury-Lechon and Curtet, 1998; Dayanandan et al., 1999; APG, 2003).

Ashton (1982) divided the Asian dipterocarps (subfamily Dipterocarpoideae), the most species-rich subfamily, into the two tribes Dipterocarpeae and Shoreae based on many differences in details of the fruit calyx and wood anatomy. This subfamily comprises 12 genera in Asia and one genus endemic to the Seychelles with around 470 species, and at least 100 intraspecific entities. Tribes are also distinguished based on the basic chromosome number where x=11 for tribe Dipterocarpeae and x=7 for tribe Shoreae (Jong and Kaur, 1979, Somego, 1978). The tribe Shoreae (or imbricate-Shoreae group) consists of *Dryobalanops, Hopea, Neobalanocarpus, Parashorea, Shorea* with imbricate fruit sepals, grouped vessels, resin canals in tangential bands, and a basic chromosome number of x=7. The tribe Shoreae is richer in species than Dipterocarpeae due to species richness in the genera *Shorea* and *Hopea*. *Shorea* Roxb., which we study here, is the dominant emergent tree genus in tropical Asia (Ashton, 1982).

Shorea is the largest and economically most important genus of Dipterocarpaceae, encompassing about 196 species in 11 sections, of which 163 species are distributed in Malaysia, mostly in Indonesia, and in particular on Sumatra and Borneo (Kalimantan). *Shorea* is also distributed in Ceylon, India, Myanmar, Thailand, Srilanka, China, and Malacca (Ashton, 1982; Peel et al., 2007). In India, two species are endemic in southern India, one in Assam and one in the well known sal forests in northern and central India (Singh and Kushwaha, 2005 ; Raju et al., 2011).

Dipterocarps are known in Paleogene and Neogene fossil floras of Southeast Asia and Africa, but these occurrences are principally represented by fossil woods with fewer leaves and pollen (Bancroft, 1935; Gregory et al., 2009). Fossil leaves of *Shorea* are mainly reported from the Neogene of India (Bande and Srivastava, 1990; Antal and Awasthi, 1993; Prasad, 1994; Antal and Prasad, 1997, 1996; Prasad et al., 2004; Joshi and Mehrotra, 2007; Khan et al., 2015), Neogene of Nepal (Konomatsu and Awasthi, 1999; Prasad et al., 1999, Prasad and

Pandey, 2008), Palaeogene of China (Feng et. al., 2013) and reliable fossil woods are well documented in the Neogene and Quaternary of Asia (Awasthi and Srivastava, 1992; Prakash et al., 1994; Awasthi and Mehrotra, 1997; Srivastava and Saxena, 1998; Mehrotra et. al., 1999; Bera and Banerjee, 2001; Shar et al., 2007; Gregory et al., 2009). Convincing reproductive remains are rare, and to date, only four authenticated winged fruits of *Shorea* have been reported. Two have been recovered from Miocene sediments of India (Khan and Bera, 2010; Shukla et al., 2012), one from the late Eocene of South China (Feng et al., 2013) and one from the Miocene of Southeast China (Shi et al., 2014). From this point of view, the occurrence of reproductive remains along with leaf remains of *Shorea* from one location i.e. Mio-Pleistocene Siwalik sediments of Arunachal Pradesh is very remarkable.

In this mauscript, we (1) report for the first time, and describe, six specimens of three *Shorea* species (*S. obtusa*; *S. tumbuggaia* and *Shorea leprosula*) based on a winged fruit, fruit wings and associated leaves collected from the Mio-Pleistocene Siwalik sediments of Arunachal sub-Himalaya (Fig. 1); (2) review in detail the historical phytogeography of *Shorea* and highlight the phytogeographic implication of this occurrence; and (3) discuss the physiological tolerance of members of *Shorea* to climate and their evolution in the Siwalik forests of Arunachal Pradesh, eastern Himalaya from the middle Miocene to lower Pleistocene.

2. Geological background

The Himalayan foothill zone (also known as the sub-Himalayan zone) is where the Siwalik Group outcrops (Acharya, 1994). 'Siwalik' sediments make up a thick (~7000 m) succession of Neogene freshwater coarsely bedded sandstone, siltstone, clay and conglomeratic molassic deposits exposed along the length of the Himalayan foothills from the Potwar Plateau in the west to the Brahmaputra River in the east (Bora and Shukla, 2005; Parkash et al., 1980). They

accumulated close to sea level in a long but narrow foredeep to the south of the rising Himalaya. During the latest phase of the rise of the Himalaya, in Pleistocene to recent times, these 'Siwalik' sediments were uplifted, folded and faulted to form a continuous mountain range of relatively low height ranging from 1000 - 1200 m a.m.s.l., some 2400 km in length and 20 - 25 km in width. From west to east along their length the Siwaliks have been divided into seven sectors: Jammu, Himachal Pradesh, Uttar Pradesh, Nepal, Darjeeling-Sikkim, Bhutan, and Arunachal Pradesh (Ranga Rao, 1983). The Arunachal Pradesh sector is the focus of the work presented here.

In Arunachal Pradesh the Siwalik Group occurs as a linear belt all along the foothills from the border with Bhutan in the west to Roing in the Dibang valley in the east where it ends against the Roing Fault (Kumar, 1997; Anand-Prakash and Singh, 2000). Its northern limit is defined by the MBF (Main Boundary Fault) separating it from the pre-Tertiary succession, while in the south the Brahmaputra Alluvium of the Brahmaputra Plain defines its boundary. Along the Himalayan foothills of Arunachal Pradesh the Siwalik sediments are sub-divided into lower Siwalik (Dafla Formation, middle to upper Miocene), middle Siwalik (Subansiri Formation, Pliocene) and upper Siwalik (Kimin Formation, upper Pliocene to lower Pleistocene) exposed in reverse stratigraphic order (Joshi et al., 2003) (Table 1). Recently, on the basis of magnetostratigraphic data, Chirouze et al. (2012) proposed that the Siwalik Group of Arunachal Pradesh was deposited between 13 and 2.5 Ma. 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.

A generalized description of the lower, middle and upper Siwaliks (Fig. 2) is as follows: The lower part of the Siwalik (Dafla Formation, middle to upper Miocene) consists of indurated, medium to fine-grained, well sorted, bluish-grey sandstone and bluish-grey, greenish-grey, nodular silty shale (Fig. 2, c). The rocks are in general compacted, indurated, sheared and

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slickenslided. The middle Siwalik (Pliocene; Subansiri Formation) rocks are generally poorly indurated, medium to coarse grained, salt and pepper textured multi-storied sandstones, with grey shale intercalations, siltstones and conglomerates (Fig. 2, b). In comparison to the lower Siwalik, the rocks are more friable and loose. The upper part of the Siwalik Group (Kimin Formation, upper Pliocene to early Pleistocene) is mainly represented by loosely packed very coarse to fine grained, friable, grey sandstones which are highly limonitised in places. The sandstones are pebbly in places and are intercalated with claystones and shales (Fig. 2, a).

3. Materials and Methods

The fossil leaf impressions and compressions, winged fruits and fruiting calyx studied here were collected from the Siwalik (middle Miocene-lower Pleistocene) sediments of Pinjoli road area ca.18 km east of Bhalukpong (near culvert no. 48/1), Bhalukpong-Tawang road area (opposite to Jangchip chorten) in the West Kameng district and Chnder Nagar-Gohpur road near Itanagar in the Papumpare district of Arunachal Pradesh (situated between $26^°27'52''$ and $29^°29'54''$ N and $91^°29'50''$ and $97^°24'56''$ E), India (Fig. 1). Most specimens required little or no preparation before photography, but details of calyx lobes and leaf margins not exposed in the initial fracture were revealed by careful removal of overlying matrix using needles. Macroscopic images of fossil and relevant extant specimens were photographed using a digital camera (Canon Power Shot A720IS) (Plates I, 1-5; II, 1-7; III, 1-5; IV, 1-6; V, 1-6). Line drawings of holotype specimens (those venation pattern is rather unclear) are given (Fig. 3, a, c, e, f). In order to isolate leaf cuticles the conventional method (Schulze's solution method) for cuticle maceration was applied (Kerp and Krings, 1999). Monographs showing structural details of fossil leaves, winged fruits and calyx lobes and their nearest living relatives 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).

Taxonomic determination required extensive literature and herbarium searches to compare the Arunachal specimens with other previously identified fossil and extant taxa that share similar morphological features. Extant *Shorea* specimens were examined and photographed in the collections of the Central National Herbarium (CAL), Sibpur, Howrah. In this report, terms used to describe the winged fruits, persistent calyx lobes and leaves are in conformity with the standard terminology for architectural description of dicotyledonous leaves (Hickey, 1973; Leaf Architecture Working Group, 1999). 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). Both the fossil (specimen numbers CUH/PPL/P/83; CUH/PPL/P/f/4; CUH/PPL/B/24; CUH/PPL/B/f/1; CUH/PPL/C/8 and CUH/PPL/C/f/7) and modern specimens and slides are deposited in the Museum of the Department of Botany, University of Calcutta (CUH).

4. Results

4.1. Systematics of the Miocene leaf

Order: Malvales Jussieu ex Berchtold et Presl

Family: Dipterocarpaceae Blume

Subfamily: Dipterocarpoideae Burnett

Tribe: Shoreae Ashton

Genus: *Shorea* Roxburgh ex C. F. Gaertner

Species: *Shorea mioobtusa* Khan, Spicer RA et Bera, sp. nov. (Plate I, 1, 2, 4, 6, 8)

Holotype: CUH/PPL/P/83 (Plate I, 1)

Type Locality: Road cuttings along the East of Pinjoli area of West Kameng district.

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Type horizon: Lower part of the Siwalik sediments (Dafla Formation, middle to upper Miocene).

Etymology: The specific name is derived by adding the prefix 'mio' to the modern comparable specific epithet *obtusa*.

Collectors: Mahasin Ali Khan and Subir Bera.

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

Specific diagnosis: Lamina wide elliptic; entire margin; apex and base obtuse; venation eucamptodromous; secondary veins alternate, curved upwards towards margin, moderate acute angle of divergence; hypostomatic leaf; adaxial and abaxial cuticle with costal and intercostal areas; curved anticlinal walls; stomatal apparati paracytic.

Description: Macromorphology: Leaf simple; preserved lamina complete, symmetrical, wide elliptic; maximum length about 5.7 cm and maximum width about 3.5 cm; apex obtuse (Plate I, 2); base obtuse to rounded; petiole not preserved; margin entire; texture coriaceous; venation pinnate, simple, eucamptodromous; primary vein single, prominent, moderately stout, straight, thick in the basal half and gradually thinning upward, terminating at the apex; secondary veins alternate, fine in thickness and unbranched, 10-11 pairs visible, 0.5-0.6 cm apart, angle of divergence moderate acute (50^0-55^0), the secondary veins start almost straight, then gradually and uniformly curved up, and connected to the adjacent secondaries by tertiary cross veins, but without forming any secondary marginal loops (Plate I, 4); inter-secondary and intra-marginal veins not seen; tertiary veins very faint, percurrent, simple, seemingly relationship with midvein oblique; further venation details not clearly seen due to thick cuticle.

Micromorphology: Hypostomatic leaf; adaxial cuticle clearly differentiated into costal and intercostal areas; costals about 3-5 cells wide; cells over costal areas are seemingly rectangular to polygonal, arranged end to end in rows along veins, 9-21 μm long and about 8-10 μm wide; epidermal cells over intercostal areas mostly pentagonal to hexagonal, sometimes triangular, arranged irregularly, 13-19 μm long and 15-29 μm wide (Plate I, 6); anticlinal walls mostly curved, sometimes straight in cells of intercostal areas, 2.5 μm wide; periclinal walls smooth; abaxial cuticle differentiated into costal and intercostal areas (Plate I, 6); costals about 3-5 cells wide; cells over costal areas elongate, narrow, seemingly rectangular to polygonal arranged end to end in rows along veins, 15-27 μm long and about 8-14 μm wide; anticlinal walls of costal cells not clear; periclinal walls unspecialised; cells over intercostal areas mostly pentagonal to hexagonal, sometimes triangular, arranged irregularly, 10-18 μm long and 11-28 μm wide; anticlinal walls mostly curved, sometimes straight in cells of intercostal areas 2.7 μm wide; intercostals stomatiferous; stomata almost circular, irregularly distributed and oriented (Plate I, 8), 60-69 μm long and 30-38 μm wide; stomatal apparati paracytic, with one lateral specialised neighbouring cell or subsidiary cell per guard cell; guard cells superficial, elongated, 60-72 μm long and 10-15 μm wide; subsidiary cells 67-71 μm long and 20-23 μm wide; stomatal index varying from 15-28.

Comparison: The clear venation pattern of the Miocene leaf provides convincing evidence for placing it in the Dipterocarpaceae. According to "Field Key to Principal Field Groups" of Ashton (1982), it is clear that the venation pattern of the Miocene leaf occurs in the genera *Neobalanocarpus* Ashton, *Shorea*, and some species of *Hopea* Roxburgh. In the monotypic *Neobalanocarpus* and *Hopea* populations, the lamina apex angle is usually acute, and the apex shape is somewhat acuminate, in contrast to the obtuse and convex apex of the Miocene leaf. Therefore, the fossil leaf described here shows the greatest similarities to *Shorea*.

Among extant *Shorea*, the Miocene leaf resembles *Shorea obtusa*, *Shorea talura*, *Shorea stellata* and *Shorea pauciflora* in lamina morphology and venation course (Plates I, 3, 5; V, 1, 2, 4). However, *S. talura* differs from the Miocene leaf in the presence of intersecondary veins (Plate V, 4). In *S. stellata*, the secondary veins are relatively more wide spaced than in the fossil specimen. Curvature of secondaries is also dissimilar (Plate V, 1). The Miocene leaf differs from *Shorea pauciflora* in having obtuse apex as compared to the acute-acuminate apex in *S. pauciflora* (Plate V, 2). The leaves of *S. obtusa* Wall. show closer similarity to the fossil leaf in size, shape (wide elliptic), nature of apex (obtuse), nature of base (obtuse) and venation pattern (eucamptodromous venation, acute angle of divergence with a specific curvature of alternate secondary veins and percurrent tertiaries) (Plate I, 1-5).

Shorea fossil leaves have been described from the Neogene sediments of India (Bande and Srivastava, 1990; Antal and Awasthi, 1993; Prasad, 1994; Antal and Prasad, 1996, 1997; Konomatsu and Awasthi, 1999; Prasad et al., 2004; Joshi and Mehrotra, 2007; Khan et al., 2015), Neogene sediments of Nepal (Prasad et al., 1999; Prasad and Pandey, 2008; Prasad and Dwivedi, 2008) and Paleogene sediments of China (Feng et al., 2013) (Table 2). The present fossil leaf has been compared with all the known species and found to be different from them in shape, size, apex, base and venation patterns (Table 2). Thus, in being different, the present specimen has been described under a new specific name. As the fossil specimen resembles *S. obtusa* and is recorded from the Miocene sediments, it is being described here as a new species, *S. mioobtusa* Khan et al. sp. nov.

We also examined the cuticular characters of both fossil (Plate I, 6, 8) and modern leaves of *S. obtusa* (Plate I, 7, 9) to verify the identification. Based on the combination of both macromorphology and micromorphological epidermal features (both surface of laminar cuticle clearly differentiated into costal and intercostal areas; pentagonal to hexagonal epidermal cells over intercostal areas of both ab-and adaxial cuticle; curved anticlinal cell

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walls, paracytic type stomata, size, shape, orientation and distribution of stomata) the leaf specimen is assigned to the genus *Shorea* and regarded *S. obtusa* as a possible modern related form.

4.2. Systematics of the Miocene winged fruit

Species: *Shorea pinjoliensis* Khan, Spicer RA et Bera, sp. nov. (Fig. 3, f; Plate II, 1, 2)

Holotype: CUH/PPL/P/f/4 (Fig. 3, f; Plate II, 1)

Type locality: Road-cutting section, East of Pinjoli area of West Kameng district, Arunachal Pradesh.

Type horizon: Lower part of the Siwalik sediments (Dafla Formation, middle to upper Miocene).

Collectors: Mahasin Ali Khan and Subir Bera.

Etymology: The epithet "*pinjoliensis*" recognizes Pinjoli area, the locality where specimen was collected.

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

Specific diagnosis: Fruit body is spherical; calyx lobe elliptic to obovate with entire margin and parallelodromous-like venation; 7-8 longitudinal parallel primary veins arising from base; secondary veins (tertiaries) seemingly percurrent.

Description: One fossil fruit has been collected from the lower Siwalik (Dafla Formation) and is preserved as fruit body with one persistent calyx lobe attached (Fig. 3, f; Plate II, 1, 2); the fruit body is spherical, 0.2 cm long, 0.3 cm wide (Fig. 3, f; Plate II, 1, 2); calyx lobe arises from the base of the fruit body, the lobe is slightly asymmetrical, elliptic to obovate, with the widest part tapering gradually toward the base, 2.6 cm long and 0.7 cm wide, the lobe base is

0.3 cm wide, the lobe apex is broken (Fig. 3, f; Plate II, 1, 2); margin is entire; Seemingly 7-8 longitudinal parallel primary veins preserved, independent of each other originate from the lobe base and radiate towards apex, all the primary veins are fine in thickness on the basal half, gradually thinning even more upward; the admedial five primaries are somewhat thicker than the faint outermost ones; arching secondaries branch from the primary not preserved; Secondary veins (tertiaries) are not clearly preserved, seemingly percurrent; further venation details not seen. Cuticle preparations were unsuccessful because organic material has been greatly weathered.

Comparison: Fruits with wing-like enlarged calyx lobes generally exist in modern genera of the family Dipterocarpaceae, modern genera *Gyrocarpus* Jacq. (Hernandiaceae), *Alberta* E. Meyer (Rubiaceae), and fossil genus *Lagokarpos* McMurran et Manchester of unknown family (McMurran and Manchester, 2010). However, our Miocene winged fruit differs from the *Gyrocarpus Alberta* and *Lagokarpos* in the venation pattern of the calyx lobe (McMurran and Manchester, 2010).

In order to compare and find the nearest generic affinity of the present fossil fruit, several modern genera of Dipterocarpaceae were examined. The fossil specimen shows resemblance to the extant fruits of some genera of this family such as *Shorea*, *Parashorea* and *Hopea*. But, based on the above-mentioned diagnostic features, our Miocene fruit certainly belongs to *Shorea*. On the other hand, Miocene specimen differs from the *Parashorea* and *Hopea* in the venation pattern of the fruiting calyx lobes.

Populations of *Shorea*, the most diversified genus of Dipterocarpaceae, vary remarkably in morphology, but the fruit dimensions and the venation of the enlarged calyx lobes pinpoint a specific determination (Ashton, 1982; Shi and Li, 2010). The unique characteristic of the *Shorea* fruit is the number of primary veins per calyx lobe. The number of primary veins per

calyx lobe of *Shorea* is 5–14 (Shi and Li, 2010). In our Miocene fruit, there are seemingly 7-8 primary veins (Fig. 3, f; Plate II, 1, 2).

To date, only four fossil fruits representing *Shorea* have been reported from Paleogene and Neogene sediments of India and China. One reported from the middle to upper Miocene sediments of Arunachal Pradesh, eastern Himalaya (Khan and Bera, 2010), one from early Miocene sediments of Gujarat, western India (Shukla et al., 2012), one from late Eocene of South China (Feng et al., 2013) and one from middle Miocene sediments of Southeast China (Shi et al., 2014). These fossils differ from our Miocene specimen described here in morphological characters (Table 3). Because fruiting calyx lobe architecture within this genus varies greatly, and poor preservation of venation pattern of calyx lobe and cuticle information of the Miocene fruit is unavailable, it is unreasonable to refer it to a particular extant species. As fruit recovered from the Pinjoli area of West Kameng district of Arunachal Pradesh, we propose a new species, *Shorea pinjoliensis* et al. sp. nov.

4.3. Systematics of the Pliocene leaf

Species: *Shorea pliotumbuggaia* Khan, Spicer RA et Bera, sp. nov. (Fig. 3, a; Plate III, 1, 2)

Holotype: CUH/PPL/B/24 (Fig. 3, a; Plate III, 1)

Type locality: Road cuttings along the Bhalukpong area of West Kameng district.

Type horizon: Middle part of the Siwalik sediments (Subansiri Formation, Pliocene).

Etymology: The specific name is derived by adding the prefix 'Plio' to the modern comparable specific epithet *tumbuggaia*.

Collectors: Mahasin Ali Khan and Subir Bera.

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

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Specific diagnosis: Lamina wide elliptic; entire margin; apex mucronate-obtuse and base obtuse; eucamptodromous venation; secondary veins sub-opposite to alternate, curved upwards towards margin, moderate acute angle of divergence.

Macromorphology: Leaf simple; preserved lamina complete, symmetrical, fairly wide elliptic; preserved size 2.5 x 1.7 cm; apex seemingly mucronate-obtuse (Fig. 3, a; Plate III, 2); base obtuse; petiole preserved, 0.2 cm long, slightly bent; margin entire; venation pinnate, simple, eucamptodromous type; primary vein single, stout, almost straight, thick in the basal half and gradually thinning upward, terminating at the apex; secondary veins sub-opposite to alternate, unbranched, seemingly 6-7 pairs visible, 0.3-0.5 cm apart, angle of divergence moderate acute (40^0-45^0), the secondary veins uniformly curved up; inter-secondary and intra-marginal veins not seen; further venation details not clearly seen.

Comparison: The important diagnostic features of the recovered Pliocene fossil leaf indicates it resemblances to the leaves of only three genera, *Neobalanocarpus* Ashton, *Shorea*, and *Hopea* Roxburgh, of the family Dipterocarpaceae. In *Neobalanocarpus* and *Hopea*, the lamina apex is somewhat acuminate, in contrast to the mucronate-obtuse apex of the Pliocene leaf. Therefore, the Pliocene leaf described here shows the greatest similarities to *Shorea*.

Three species of *Shorea* show general similarity with the fossil specimen, *Shorea tumbuggaia* Roxb., *Shorea roxburghii* and *Shorea thorelii* (Plates III, 5; V, 3, 6) and of these the fossil specimen has the closest resemblance to *Shorea tumbuggaia* in size, shape, and venation pattern (Fig. 3, b; Plate III, 5). Leaves of *Shorea roxburghii* and *Shorea thorelii* are larger in size. However, secondary veins are alternate in contrast to the sub-opposite to alternate secondary veins. Moreover, secondary vein angle to the midvein are comparatively more acute than those in the fossil Pliocene leaf. The apex in *Shorea roxburghii* is rounded in contrast to the mucronate-obtuse apex of the fossil specimen. Comparison of the Pliocene fossil leaf with all the earlier described species (Table 2) shows that it is distinct from them

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and a new species is suggested. As the fossil specimen resembles *S. tumbuggaia* and is recorded from the Pliocene sediments, it is being described here as a new species, *S. pliotumbuggaia* Khan et al. sp. nov.

4.4. Systematics of the Pliocene fruiting calyx

Species: *Shorea bhalukpongensis* Khan, Spicer RA et Bera, sp. nov. (Fig. 3, c; Plate III, 1, 3)

Holotype: CUH/PPL/B/f/1 (Fig. 3, c; Plate III, 1)

Type locality: Road cuttings along the Bhalukpong area of West Kameng district.

Type horizon: Middle part of the Siwalik sediments (Subansiri Formation, Pliocene).

Collectors: Mahasin Ali Khan and Subir Bera.

Etymology: The epithet "*bhalukpongensis*" recognizes Bhalukpong area, the locality where fruiting calyx specimen was collected.

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

Specific diagnosis: Calyx lobe elliptic to lanceolate, the lobe apex rounded; entire margin; presence of longitudinal parallel primary veins.

Description: The holotype (CUH/PPL/B/f/1) is a fruiting calyx lobe preserved as a partial impression fossil lacking carbonaceous material (Fig. 3, c; Plate III, 1, 3). The sepal lobe is elliptic to lanceolate, with the widest part through the upper and middle portion, then narrowing slowly toward the base, 1.8 cm long and 0.6 cm wide, length to width (L/W) ratio 2.2/1; lobe base is 0.3 cm wide; the lobe apex is rounded (Fig. 3, c; Plate III, 1, 3); margin is entire; venation pattern is very poorly presrved, longitudinal parallel primary veins preserved, independent of each other, originate from the lobe base and radiate towards apex, among

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primary veins only four are clearly seen, others are very faint and unclear; detailed venation pattern not clearly preserved.

Comparison: Herbarium sheets of the available modern species of the genus *Shorea* such as *S. tumbuggaia*, *S. roxburghii*, *S. stellata*, *S. obtusa*, *S. leprosula* and *S. talura* were critically examined (Fig. 3, c; Plates II, 3-7; III, 4) and it was found that fruiting calyx lobe of only one species *S. tumbuggaia* is very similar to our Pliocene specimen in size, shape and the nature of lobe apex (Fig. 3, c; Plate III, 1, 3, 4). This similarity is consistent with the robust occurrence of leaf remain resembling *S. tumbuggaia* along with it in the same sediments (Plate III, 1). Although the Pliocene fruit wing and leaf were not attached to each other, their close association indicates that they are likely produced by the same species of plant.

The present fossil fruiting calyx lobe has been compared with the earlier reported specimens (Table 3) and it was found that it differs from them in sepal lobe architecture. On the basis of such differences, our Pliocene specimen has been described as a new species. As the calyx lobe was recovered from the Bhalukpong area of West Kameng district of Arunachal Pradesh, we propose a new species, *Shorea bhalukpongensis* Khan et al. sp. nov.

4.5. Systematics of the Plio-Pleistocene leaf

Species: *Shorea nepalensis* Konomatsu et Awasthi, 1999 (Plate IV, 1, 3)

Figured specimen: CUH/PPL/C/8

Collecting location: Road cuttings along the Chander Nagar-Gohpur road in Papumpare district.

Stratigraphic horizon: Upper part of the Siwalik sediments (Kimin Formation, upper Pliocene to lower Pleistocene).

Collectors: Mahasin Ali Khan and Subir Bera.

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

Macromorphology: Leaf simple, preserved specimen almost symmetrical, elliptic; preserved lamina length 8.8 cm and maximum width 4.1 cm; apex and base seemingly acute; margin entire; venation pinnate, simple, eucamptodromous type; primary vein prominent, straight, stout; secondary veins 8-9 pairs visible, angle of divergence acute, moderate ($50^{°}$-$60^{°}$), alternate, 0.4 - 0.8 cm apart, uniformly curving upward, unbranched; both inter-secondary and intramarginal veins absent; tertiary veins seemingly percurrent, mostly simple and relationship with midvein oblique; further detailed venation are not discernible.

Comparison: The elliptic shape, entire margin, eucamptodromous venation, acute angle of divergence with a specific curvature of alternate secondary veins and percurrent tertiaries are the most important architectural features of the fossil leaf. On critical examination the most favorable comparison is with the leaves of *S. leprosula* Miq., *S. pauciflora* and *S sericea* especially in shape, size, texture and venation pattern (Plates IV, 2; V, 2, 5), although the secondary veins of the last two species are comparatively narrowly spaced and less acute. Moreover, in *S. pauciflora* and *S. sericea* secondary veins are alternate to opposite in contrast to the alternate secondary veins of our Plio-Pleistocene leaf. So, these features undoubtedly suggest its affinity with those of extant *Shorea leprosula* of the family Dipterocarpaceae (Fig. Plate IV, 1-4).

So far, only one fossil taxon exhibiting close resemblance with the modern *S. leprosula* has been recorded from the upper Miocene sediments of the West central Nepal under the name *S. nepalensis* (Konomatsu and Awasthi, 1999). Because the present fossil leaf exhibits more or less the same architectural features as the previously described fossil specimen of

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Konomatsu and Awasthi (1999), and also shows resemblance to extant taxon *S. leprosula*, the same specific name is assigned to our Plio-Pleistocene leaf specimen.

4.6. Systematics of the Plio-Pleistocene fruiting calyx

Species: *Shorea chandernagarensis* Khan, Spicer RA et Bera, sp. nov. (Fig. 3, e; Plate IV, 1, 5)

Holotype: CUH/PPL/C/f/7 (Fig. 3, e; Plate IV, 1)

Type locality: Road cuttings along the Chander Nagar-Gohpur road in Papumpare district.

Type horizon: Upper part of the Siwalik sediments (Kimin Formation, upper Pliocene to lower Pleistocene).

Collectors: Mahasin Ali Khan and Subir Bera.

Etymology: The epithet "*chandernagarensis*" recognizes Chander Nagar area, the locality where sepal lobe was collected.

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

Diagnosis: Calyx lobe with entire margin and parallelodromous venation; lobe base narrow; 9 longitudinal primary veins independent of each other, arising from the base; secondary veins (tertiaries) fine, percurrent.

Description: The holotype specimen (CUH/PPL/C/f/7) is a fruiting calyx lobe impression (Fig. 3, e; Plate IV, 1, 5); the lobe is elliptic to lanceolate, tapering gradually toward the base, 4.3 cm long and 1.9 cm wide, length to width (L/W) ratio 4.4/1; the lobe base is 0.2 cm wide; the lobe apex is missing; the margin is entire; seemingly 9 longitudinal parallel primary veins preserved, independent of each other, originate from the lobe base and radiate towards apex, all the primary veins are fine in thickness on the basal half, gradually thinning even more

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upward, the four middle primaries are somewhat thicker than the outermost lateral ones; arching secondaries that might branch from the primary not preserved; secondary veins are not clearly preserved, seemingly fine, percurrent; detailed venation pattern not clearly preserved.

Comparison: The identification of the fossil fruiting calyx lobe is based upon similarities in external architectural features (lobe size, shape, no of primary veins, and nature of secondary and tertiary veins). Comparisons were made with the modern fruiting calyx lobes of *Shorea leprosula*, *S. stellata*, *S. obtusa* and *S. talura* (Plate II, 4-7) showing apparent similarity with the fossil calyx lobe (Fig. 3, e; Plate IV, 1, 5). The fossil specimen shows the closest resemblance in external morphological characters (i.e. in shape, size and no of primary veins) with the persistent calyx lobes of the extant species *S. leprosula* Miq. (Fig. 3, e; Plate IV, 1, 5, 6). The fossil represents the first record resembling *S. leprosula* reproductive remains. Its occurrence is not at all surprising given that *Shorea* leaf impressions occur in the same sediments. Because the Plio-Pleistocene reproductive structure was not found in organic connection with the leaf like extant *S. leprosula* (Plate IV, 1), and is different from the earlier reported reproductive specimens (Table 3), a new specific name is here assigned to it. As a calyx lobe recovered from the Chander Nagar area of Papumpare district of Arunachal Pradesh, we propose a new species, *Shorea chandernagarensis* Khan et al. sp. nov.

5. Discussion

5.1. Paleoclimatic implications

Plant fossils are often the best tool to reconstruct the palaeoclimate and palaeoenvironment of the studied region, and in this instance we employ the concept of Nearest Living Relative (NLR) (Mosbrugger and Utescher, 1997) to infer past conditions. This approach presupposes that fossil plants and their modern relatives share similar physiological requirements for

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climate. The occurrence of winged fruit, fruit wings and impression and compression of leaves provides unambiguous evidence that *Shorea* trees lived in the Arunachal sub Himalaya during the middle Miocene to lower Pleistocene. *Shorea* is widely considered to be the classic component of Asian moist equatorial rain forests and has been used as the unequivocal indicator for the existence of tropical rain forests and moist climate in geologic epochs (Shi and Li, 2010 ; Shukla et al., 2012). It is noteworthy that some other tropical trees, such as *Mangifera indica*, *Dracontomelum mangiferum* (Anacardiaceae); *Chonemorpha macrophylla* (Apocynaceae); *Pongamia pinnata*, *Millettia pachycarpa*, *Dalbergia rimosa*, *Pongamia pinnata*, *Millettia extensa* (Fabaceae); *Macaranga denticulata*, *Croton caudatus* (Euphorbiaceae); *Combretum chinense*, *C. decandrum* (Combretaceae), *Dysoxylum procerum*, *D. costulatum* (Meliaceae); *Shorea assamica*, *Dipterocarpus* sp., *D. turbintus* (Dipterocarpaceae); *Actinodaphne angustifolia*, *A. obovata*, *Lindera pulcherrima*, *L. bifaria Litsea salicifolia*, *Cinnmomum bejolghota, Persea glaucescens*, *P. parviflora* (Lauraceae); *Calophyllum polyanthum* (Calophyllaceae); *Knema glaucescens* (Myristaceae); *Canarium bengalense* (Burseraceae); *Quercus lamellosa*, *Q. semicarpifolia* (Fagaceae); *Elaeocarpus lanceaefolius* (Elaeocarpaceae), *Berchemia floribunda* (Rhamnaceae), *Gynocardia odorata* (Achariaceae) are also recorded from the Mio-Pleistocene sediments of Arunachal Pradesh (Bera et al., 2004; Khan and Bera, 2007; Bera and Khan, 2009; Khan et al., 2011; Khan and Bera, 2014 a, b; Khan et al., 2014a, b; Khan et al., 2015). So, the NLRs of the present fossil specimens, along with NLRs of our earlier described fossil assemblage from the same region support the inference that the ancient forests were tropical evergreen and this strongly indicates that warm and humid climatic conditions prevailed in the region in Miocene to Pleistocene times. This is consistent with our earlier quantitative study (Khan et al., 2014a) using CLAMP (Climate Leaf Analysis Multivariate Program) on 80 different morphotypes of fossil leaves from the Arunachal Siwalik (Mio-Pleistocene) indicating a MAT (mean annual

temperature) 23.6º–25.3ºC ± 2.8ºC; a CMMT (cold month mean temperature) 16.9ºC–21.2ºC ± 4ºC and a WMMT (warm month mean temperature) of 27.8–28.3ºC ± 3.3ºC. The analysis also indicated a weaker than present monsoonal climate with growing season precipitation (GSP) of 174–242cm ± 92 cm during the Miocene-Pleistocene (Khan et al., 2014a). So, multivariate physiognomic analysis of Neogene Siwalik leaves shows mean annual temperature varied by only 1.7°C from lower to upper Siwalik times, which is far smaller than the uncertainty in the method (± 2.8°C). Overall the Arunachal Siwalik climate appears to have been remarkably uniform over the past 13 million years.

5.2. Phytogeographic implications

Members of *Shorea* are the representative component of tropical rain forests in Southeast Asia and hold important economic and ecological significance, but their origin and migration are controversial. Information on *Shorea* fossils, particularly the more convincing reproductive structures, not only can provide important information for reconstructing palaeoclimate, but also improve our knowledge of the phylogenetic history of the genus.

The fossil record of *Shorea* is rich (Fig. 4) and such fossils are found in sediments ranging from Eocene to Holocene (Fig. 5, a, b; Tables 4). The earliest reliable fossil record of *Shorea* (foliage and fruit fossils) is from the late Eocene of South China (Feng et al., 2013); numerous post-Eocene *Shorea* fossils were reported from India (Bande and Srivastava, 1990; Prakash et al., 1994; Prasad, 1994; Antal and Prasad, 1996, 1997; Awasthi and Mehrotra, 1997; Srivastava and Saxena, 1998; Bera and Banerjee, 2001; Prasad et al., 2004; Gurusamy and Kumarasamy, 2007; Joshi and Mehrotra, 2007; Khan and Bera, 2010; Tiwari et al., 2012; Shukla et al., 2012, 2013; Khan et al., 2015; Fig. 5, b, c; Table 4) and from the main land masses of Southeast Asia (Merrill, 1923; Den Berger, 1923; Schweitzer, 1958; Prakash, 1965b; Prakash, 1973; Sukiman, 1977; Prakash and Bande, 1980). However, we do not have

any convincing record of the genus *Shorea* from the Indian Palaeogene (Bande, 1992; Mehrotra, 2003). By the early Miocene the India and Eurasian plates were firmly sutured and plant migrational exchange between India and the main land masses of Southeast Asia from China was taking place judged by the available macrofossil records (Jacques et al., 2015). The oldest record of the genus in India is from the Miocene sediments (Table 4). Following that the genus became widespread in peninsular India (Eyde, 1963; Prakash, 1965a; Prakash and Awasthi, 1970; Awasthi, 1974; Roy and Ghosh, 1981; Awasthi and Srivastava, 1992; Prakash et al., 1994; Bera and Banerjee, 2001; Tiwari et al., 2012) as well as in the Himalayan foothills (Prakash and Awasthi, 1971; Prasad and Prakash, 1988; Antal and Awasthi, 1993; Prasad, 1994; Antal and Prasad, 1996, 1997; Awasthi and Mehrotra, 1997; Mehrotra et al., 1999; Prasad et al., 2004; Joshi and Mehrotra, 2007; Khan and Bera, 2010; Khan et al., 2015). However, Prasad et al. (2009) attempted to track the affinities of some fossil palynomorphs recovered from late Palaeocene-early Eocene (~55-50 Ma) sedimentary deposits of western and northeastern Indian region and compared them with the pollen of *Shorea* type; but identification is dubious. Macrofossils are believed to be much more reliable in identification than pollen in the family Dipterocarpaceae.

In the middle Miocene, the seasonal, monsoonal climate of the early Miocene became warmer and moister because of the Himalayan uplift (Morley, 2000). *Shorea* underwent a drastic increase in geographic distribution, species diversity, and abundance, becoming the dominant group in the Miocene forests of the Indian subcontinent (Prakash, 1965a; Ramanujam and Rao, 1967; Prakash and Awasthi, 1970, 1971; Awasthi, 1974; Roy and Ghosh, 1981; Prasad and Prakash, 1988; Awasthi and Srivastava, 1992; Antal and Awasthi, 1993; Awasthi and Mehrotra, 1997; Antal and Prasad, 1996, 1997; Prakash et al., 1994; Prasad, 1994; Srivastava and Saxena, 1998; Prasad et al., 2004; Gurusamy and Kumarasamy, 2007; Joshi and Mehrotra, 2007; Khan and Bera, 2010; Shukla et al., 2012, 2013).

Nevertheless, increasing aridity and seasonality in the late Miocene and Pliocene (Morley, 2000) led to their gradual disappearance along with rain forests across most parts of India. This is in conformity with the fewer fossil evidences of *Shorea* during the post-Miocene period (Bande and Srivastava, 1990; Bera and Banerjee, 2001; Tiwari et al. 2012; Khan et al., 2015) (Table 4; Fig. 5, a).

A large number of fossil records of *Shorea* also come from the Siwalik sedimentary strata of India i.e. Darjeeling, Uttaranchal, Arunachal Pradesh Siwalik sector (Antal and Awasthi, 1993; Prasad, 1994; Antal and Prasad, 1997, 1996; Mehrotra et al., 1999; Prasad et al., 2004; Joshi and Mehrotra, 2007; Khan and Bera, 2010; Khan et al., 2015) and Nepal (Konomatsu and Awasthi, 1999; Prasad et al., 1999, Prasad and Pandey, 2008). Here we report the occurrence of three distinct leaf remains along with one winged fruit and two fruiting calyx lobes, resembling those of modern *Shorea*, from the Siwalik sediments (middle Miocene to lower Pleistocene) of Arunachal sub-Himalaya. So, the present record of *Shorea* foliage and reproductive remains in appreciable number, together with earlier records, suggest that this taxon was a common forest element growing in parts of northern, central and eastern Himalayan sectors during Siwalik sedimentation (middle Miocene-lower Pleistocene).

Modern *Shorea* taxa similar to those of our Mio-Pleistocene specimens are now confined to the evergreen-deciduous forests of India and neighboring Southeast Asia where the conditions are more suitable for their luxuriant growth. *Shorea obtusa*, the nearest modern counterpart of our Miocene fossil specimen, is a deciduous tropical tree (10-30 m tall) growing in Myanmar, Thailand, Cambodia, Laos and Vietnam (Brandis, 1971). *Shorea tumbuggaia* Roxb., a comparable modern taxon of our Pliocene fossil specimens, is an endemic Indian medicinal tree species under threat due to loss of habitat, human interference and unregulated harvesting of oleoresin for trade (Savithramma, 2011). It is an endemic tree to Andhra Pradesh and Tamil Nadu in India (Brandis, 1971, Ankanna and Savithramma,

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2011). *Shorea leprosula* Miq., a nearest modern counterpart of Plio-Pleistocene specimens, is a large tree (reaching up to 60 m in height) found to grow in Peninsular Thailand, Peninsular Malaysia, Sumatra and Borneo (Gamble, 1972). In Peninsular Malaysia, it is one of the most common and widespread emergent species on well-drained sites on deep clay soil in lowland dipterocarp forests (below 700 m altitude), lower hill slopes, and valleys in hill dipterocarp forests (Ashton, 1982; Manokaran et al., 1992).

It is interesting to note that among the nearest relatives of the three studied species, *Shorea tumbuggaia* is endemic to India at present but the other two i.e. *Shorea leprosula* and *Shorea obtusa* are totally absent from Indian tropical forests suggesting differential adaptability of these taxa to changing ecoclimatic conditions (Fig. 6). Gradual changes in climatic conditions and physiography mainly as a result of collision of the Indian and Eurasian plates, strong uplift of Himalayas, and strengthening and fluctuation in the monsoonal conditions during Neogene time, brought considerable alteration and diversification in floral patterns (Molnar et al., 1993). Some taxa could adapt to the changed climatic conditions and continued to flourish there, while others either suffered extinction from the region or migrated to suitable area with tropical littoral and swampy conditions. So, it is assumed that *S. leprosula* and *S. obtusa* might have disappeared from the present day vegetation in the area of the fossil localities and moved to tropical forests of South-east Asia with more congenial ecoclimatic conditions for their survival.

So far, the present fossil taxa *S. obtusa*, *Shorea tumbuggaia* and *S. leprosula* are not reported from both the Palaeogene and Neogene of Southeast Asia (Bande and Prakash, 1986; Mehrotra et al., 2005) and their present occurrence from the Neogene of Arunachal sub-Himalaya suggests a probable migration of two dipterocarpaceous taxa *S. obtusa* and *S. leprosula* from Indian landmass to Southeast Asian regions after the land connections between these two land masses were established (Fig. 6, a, c). On the other hand, *Shorea*

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tumbuggaia migrated to other parts of the Indian land mass where conditions are more suitable for its luxuriant growth occurred due to climate change most probably associated with continued uplift of Himalaya (Fig. 6, b).

Shorea exhibits significant diversity with different species (i.e., *S. obtusa*, *S. tumbuggaia*, *S. leprosula*, *S. assamica*; *S. bracteolata*; *S. ridleyana*) bearing entire-margin leaves, winged fruits and fruiting wings; a diversity of form seen in the Arunachal sub-Himalaya since Mio-Pleistocene time. This may imply that the tropical zone of Arunachal sub-Himalaya has been one of the centers for diversification within the genus. However, Miocene-Pliocene species of *Shorea* (*S. assamica*; *S. buchananii*; *S. roxburghii*; *S. macroptera*; *S. ovalis*; *S. superba*; *S. robusta*; *S. minor*) have also existed in different regions of India, so detailed scenarios for the historical biogeography of *Shorea* still require further evidence from palaeobotany and molecular phylogeny.

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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. Earlier records of leaf remains of *Shorea* from Cenozoic sediments of India and abroad showing their main morphological characters.

Table 3. Earlier records of fossil winged fruits of the *Shorea* from Cenozoic sediments of India and abroad showing their main morphological characters.

Table 4. Fossil record of *Shorea* from Cenozoic sediments of India and abroad.

Fig. 1. Map showing the location of the area. MBT - Main Boundary Thrust, MCT - Main Central Thrust, STD - South Tibetan Detachment, IYTS - Indus-Yarlung-Tsangpo suture. Faults are shown in grey. (Modified from Khan et al., 2014a)

Fig. 2. (a). Lithological column for part of exposed road-section along the Itanagar-Bandardewa road in Papumpare district (upper part of the Siwalik strata); (b). Lithological column for part of exposed road-section along Bhalukpong road, West Kameng district (middle part of the Siwalik strata); (c). Lithological column for part of exposed road-section along Pinjoli road near culvert no. 48/1 in West Kameng district (lower part of the Siwalik strata).

Fig. 3. (a). Line drawing of fossil leaf of *Shorea pliotumbuggaia* Khan, Spicer RA et Bera sp. nov. showing shape, size, primary vein (red arrow), secondary veins (blue arrows), marginal feeding trace (scooping out the edge of leaf margin; indicated by yellow arrow) and leaf mining (black arrow); (b). Line drawing of modern leaf of *Shorea tumbuggaia* Roxb. showing similar shape, size, primary vein (red arrow), secondary veins (blue arrows) and marginal feeding trace (yellow arrow); (c). Line drawing of a wing-like persistent calyx lobe of *Shorea bhalukpongensis* Khan, Spicer RA et Bera sp. nov. showing showing characteristic parallel primary veins (green arrows); (d). Line drawing of a wing-like persistent calyx lobe of modern *Shorea tumbuggaia* showing similar primary venation pattern (green arrows); (e). Line drawing of persistent calyx lobe of *Shorea chandernagarensis* Khan, Spicer RA et Bera sp. nov. showing parallel primary veins (blue arrow) and secondary transverse veins (red arrow); (f). Line drawing of a fruit of *Shorea pinjoliensis* Khan, Spicer RA et Bera sp. nov. showing characteristic parallel primary veins (red arrows) (Scale Bar = 1 cm).

Fig. 4. Map showing the distribution of modern *Shorea* and the localities of fossil *Shorea*.

Fig. 5. (a) Bar diagram showing the diversity of fossil *Shorea* in different geological epoch (PH= Pleistocene-Holocene; PP=Plio-Pleistocene; P=Pliocene; MP=Mio-Pliocene; M=Miocene and E=Eocene) (b) Bar diagram showing the diversity of fossil *Shorea* in different geological period; (c) Bar diagram showing the percentage of fossil *Shorea* in different geographical areas.

Fig. 6. Map showing modern distribution and fossil locality of studied taxa of *Shorea*. (a) showing modern distribution and fossil locality of studied taxon of *Shorea obtusa*; (b) showing modern distribution and fossil locality of studied taxon of *Shorea tumbuggaia*; (c) showing modern distribution and fossil locality of studied taxon of *Shorea leprosula*.

Plate I. *Shorea obtusa* leaves. (1, 2). Fossil leaf of *Shorea mioobtusa* Khan, Spicer RA et Bera sp. nov. showing obtuse apex and base, shape, size and venation pattern; (3). Modern leaf of *S. obtusa* Wall. showing same nature of apex and base, similar shape, size and venation pattern; (4). Enlarged portion of the fossil leaf showing primary vein (red arrow), secondary vein (yellow arrow) and tertiary vein (blue arrow); (5). Enlarged portion of the modern leaf of *S. obtusa* showing similar primary vein (red arrow), secondary vein (yellow arrow) and tertiary vein (blue arrow) (Scale Bar = 1 cm); (6). *Shorea mioobtusa* Khan, Spicer RA et Bera sp. nov.- Adaxial cuticle, anticlinal wall (white arrow) (Scale Bar = 10 µm); (7). *Shorea obtusa* Wall. - Adaxial cuticle with same type of anticlinal wall (white arrow) (Scale Bar = 10 µm); (8). *Shorea mioobtusa* - Abaxial cuticle, paracytic type stomata (white arrow) (Scale Bar = 10 µm); (9). *Shorea obtusa* - Abaxial cuticle, paracytic type stomata (white arrow) (Scale Bar = 10 µm).

Plate II. Winged fruits of fossil and modern species of *Shorea*. (1). A well-preserved fruit of *Shorea pinjoliensis* Khan, Spicer RA et Bera sp. nov. showing spherical spherical fruit body (white arrow) and wing-like persistent calyx lobe (red arrow); (2). Enlargement of Fig. 1 showing characteristic parallel primary veins (white arrows); (3). Winged fruit of modern *Shorea roxburghii*. (4). Winged fruit of modern *S. stellata*. (5). Winged fruit of modern *S. obtusa*. (6). Winged fruit of modern *S. leprosula*. (7). Winged fruit of modern *Shorea talura* (Scale Bar = 1 cm).

Plate III. Winged fruits and leaves of *Shorea tumbuggaia* leaves. (1). Fossil leaf of *Shorea pliotumbuggaia* Khan, Spicer RA et Bera sp. nov. (black arrow) along with persistent calyx lobe of *Shorea bhalukpongensis* Khan, Spicer RA et Bera sp. nov. (red arrow); (2). Fossil leaf of *Shorea pliotumbuggaia* Khan, Spicer RA et Bera sp. nov. showing shape, size, primary vein (red arrow), secondary veins (blue arrows), marginal feeding trace (scooping out the edge of leaf margin; indicated by yellow arrow) and leaf mining (black arrow); (3). A well-

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preserved wing-like persistent calyx lobe of *Shorea bhalukpongensis* Khan, Spicer RA et Bera sp. nov. showing showing characteristic parallel primary veins (green arrows); (4). A wing-like persistent calyx lobe of modern *Shorea tumbuggaia* showing similar primary venation pattern (green arrows); (5). Modern leaf of *Shorea tumbuggaia* Roxb. showing similar shape, size, primary vein (red arrow), secondary veins (blue arrows) and marginal feeding trace (yellow arrow) (Scale Bar = 1 cm).

Plate IV. Winged fruits and leaves of *Shorea leprosula* leaves. (1). Fossil leaf of *Shorea nepalensis* Konomatsu and Awasthi along with persistent calyx lobe of *Shorea chandernagarensis* Khan, Spicer RA et Bera sp. nov. (white arrow); (2). Modern leaf of *Shorea leprosula* Miq. along with persistent calyx lobes; (3). Enlarged portion of the fossil leaf showing primary vein (red arrow) and secondary veins (blue arrows); (4). Enlarged portion of the modern leaf of *S. leprosula* showing similar primary vein (red arrow) and secondary veins (blue arrow); (5). Enlarged portion of persistent calyx lobe of *Shorea chandernagarensis* showing parallel primary veins (black arrows) and secondary transverse veins (red arrows); (6). Enlarged portion of the persistent calyx lobe of *Shorea leprosula* showing similar parallel primary veins (black arrows) and secondary transverse veins (red arrows) (Scale Bar = 1 cm).

Plate V. *Shorea* leaves. (1). Modern leaf of *Shorea stellata*; (2). Modern leaf of *S. pauciflora*; (3). Modern leaf of *S. thorelii*; (4). Modern leaf of *S. talura*; (5). Modern leaf of *S. sericea*; (6). Modern leaf of *S. roxburghii* (Scale Bar = 1 cm).
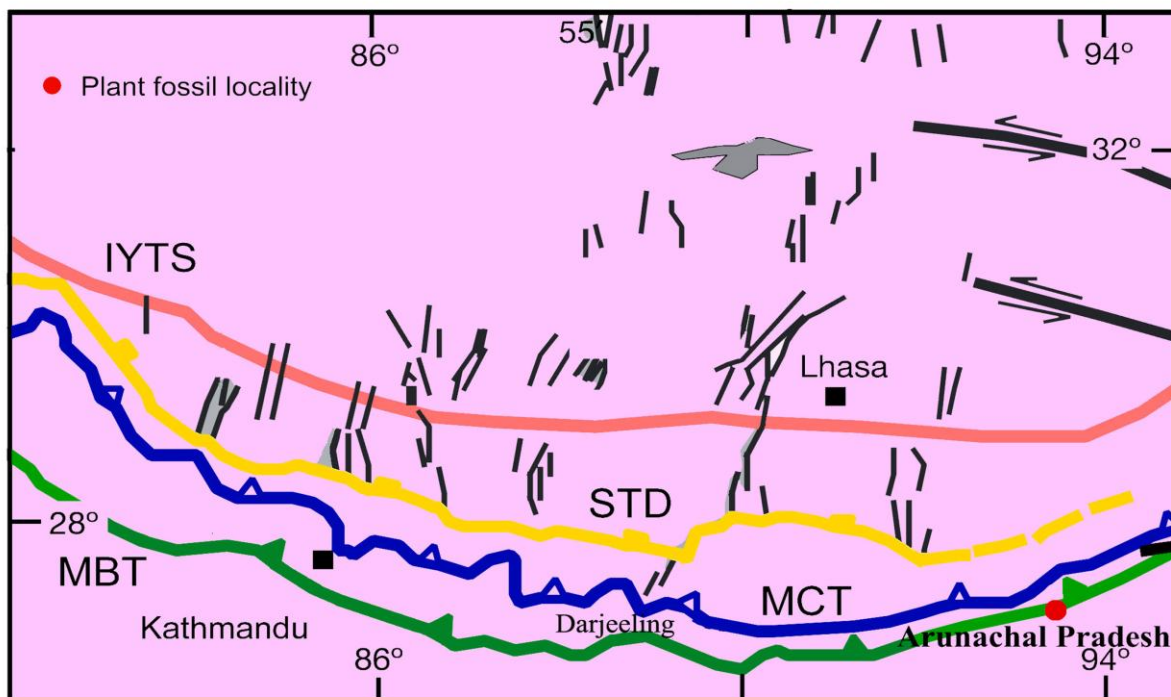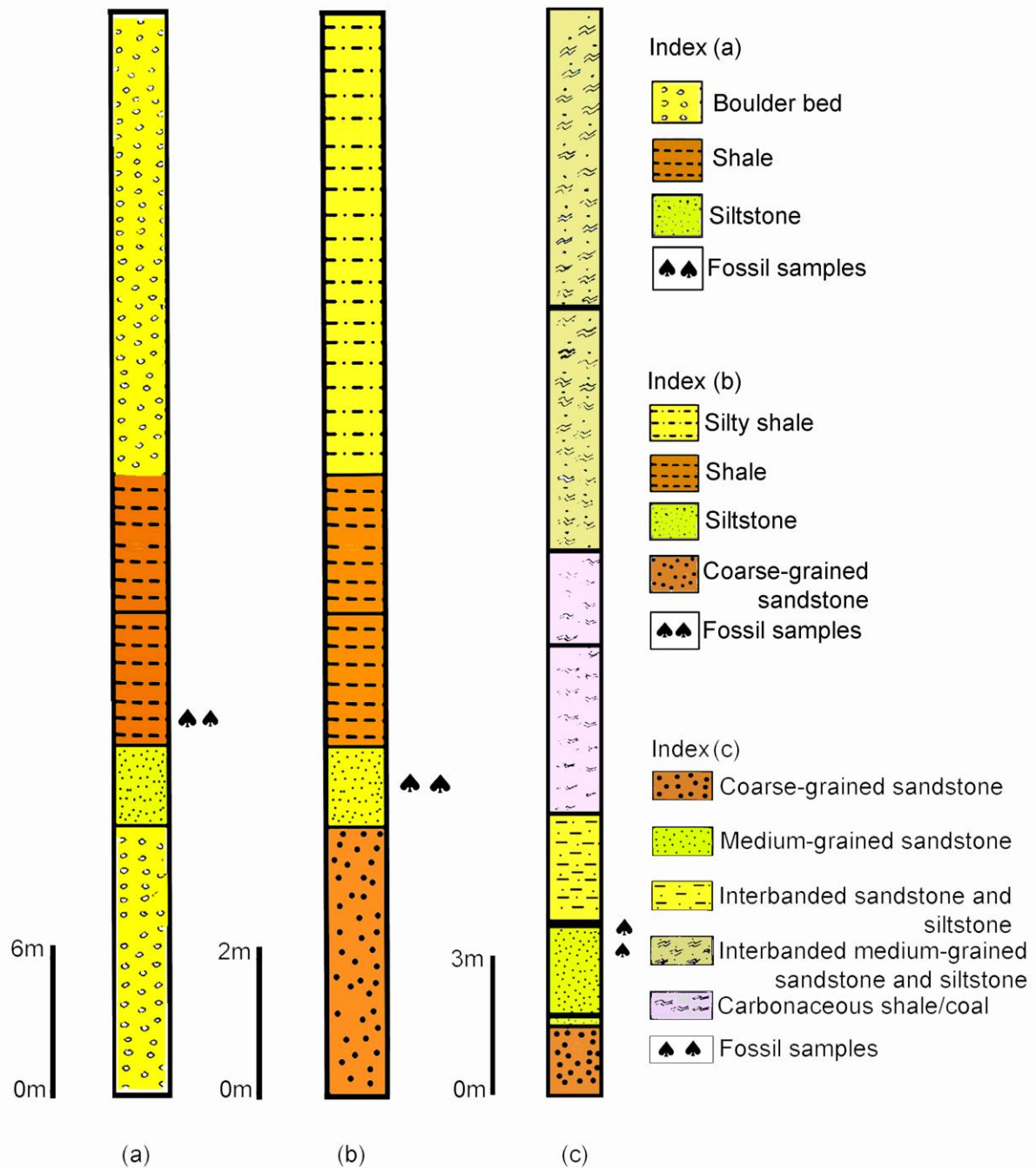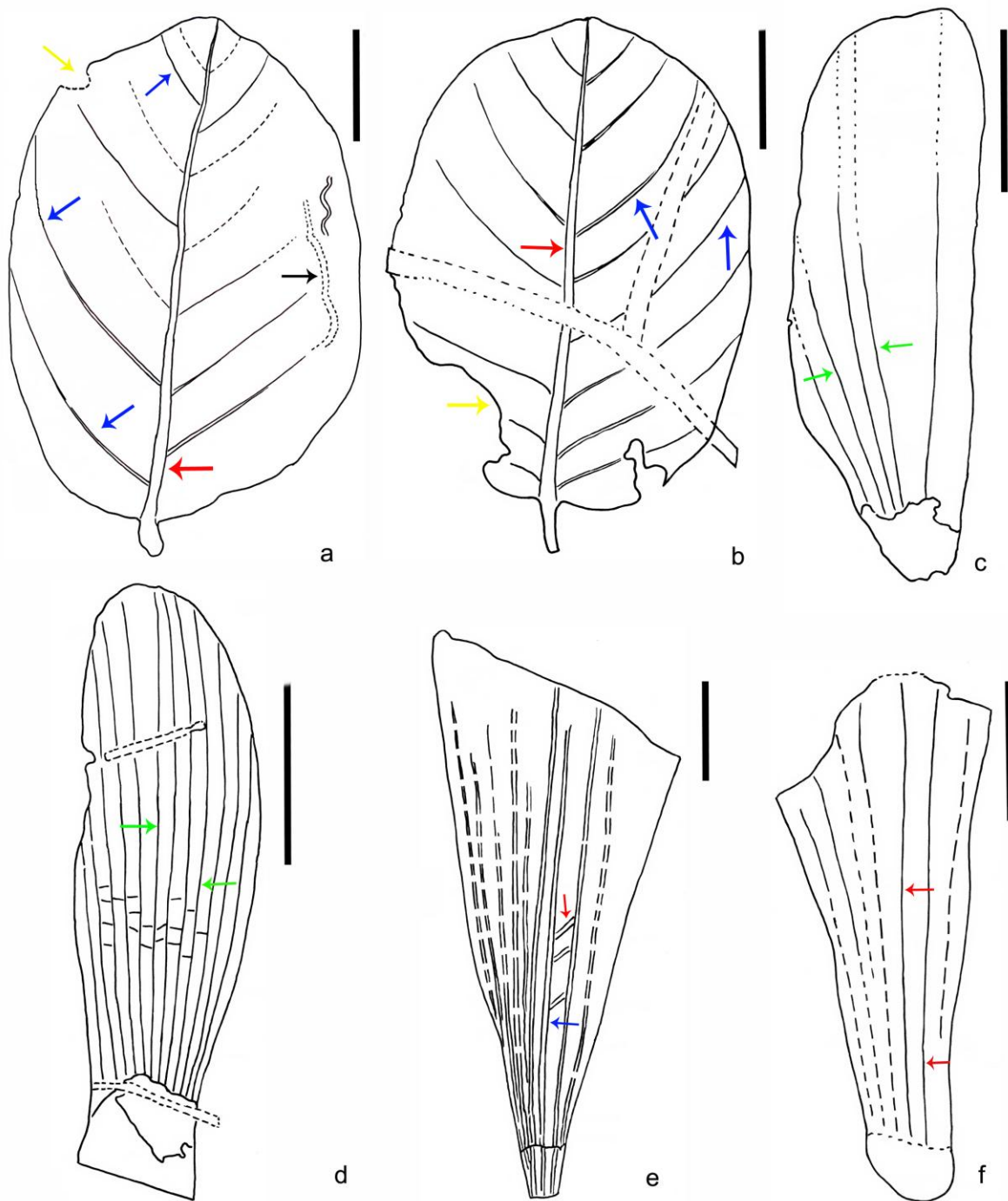
Fig. 1

Index (a)

- Boulder bed
- Shale
- Siltstone
- Fossil samples

Index (b)

- Silty shale
- Shale
- Siltstone
- Coarse-grained sandstone
- Fossil samples

Index (c)

- Coarse-grained sandstone
- Medium-grained sandstone
- Interbanded sandstone and siltstone
- Interbanded medium-grained sandstone and siltstone
- Carbonaceous shale/coal
- Fossil samples

(a)   (b)   (c)

Fig. 2

Fig. 3
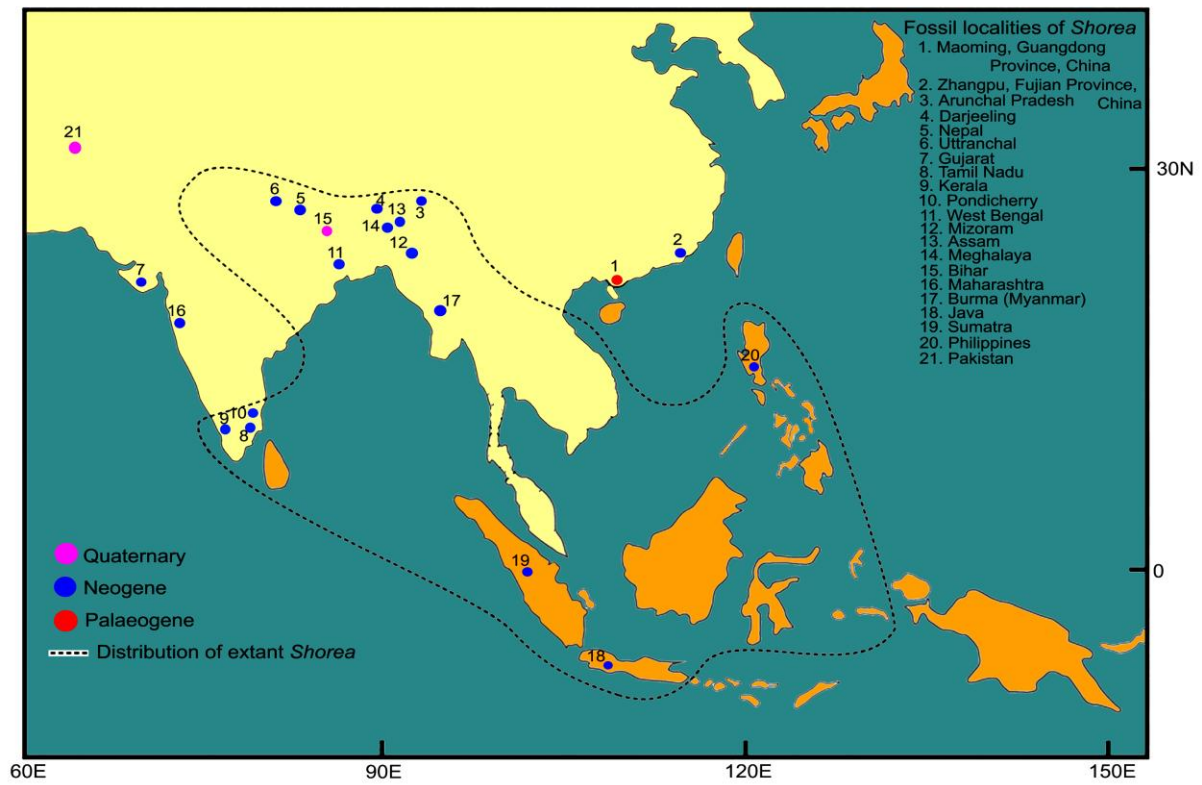
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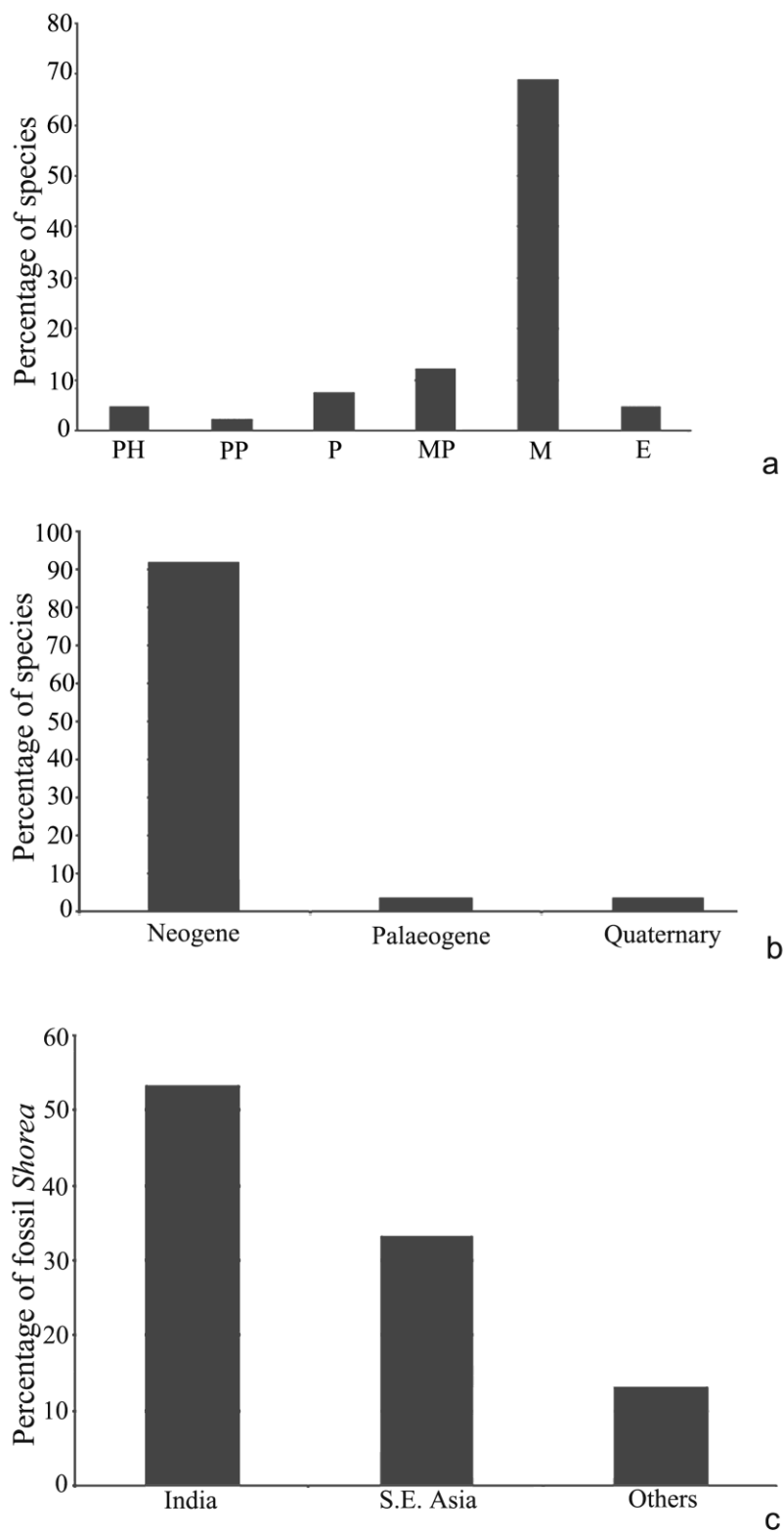
Fig. 5
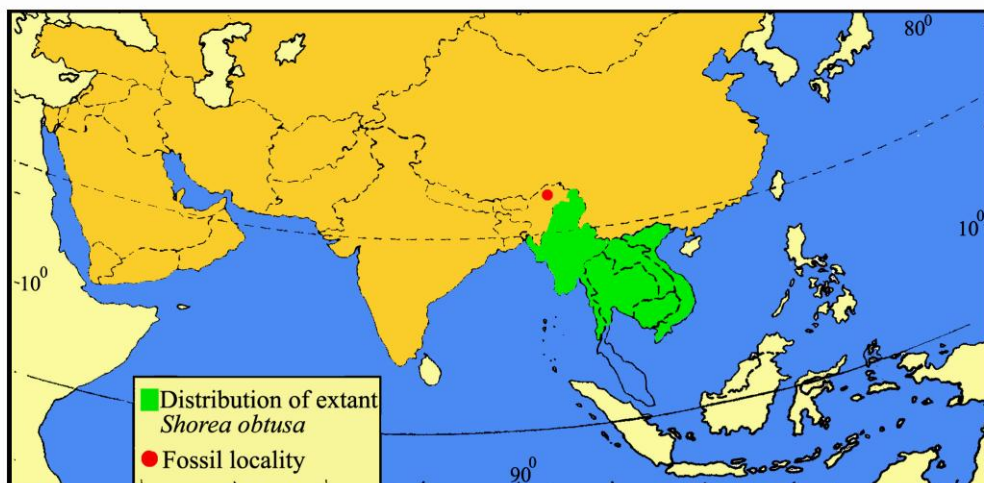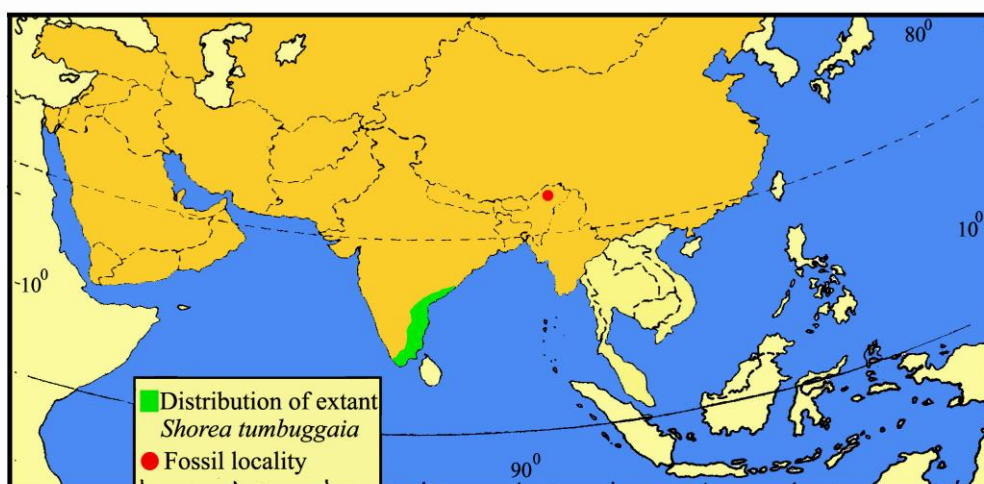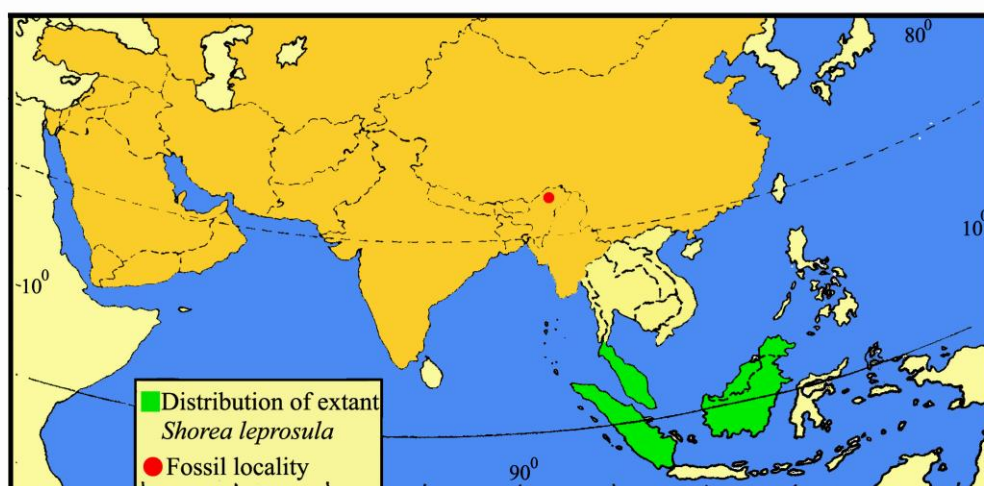
Fig. 6
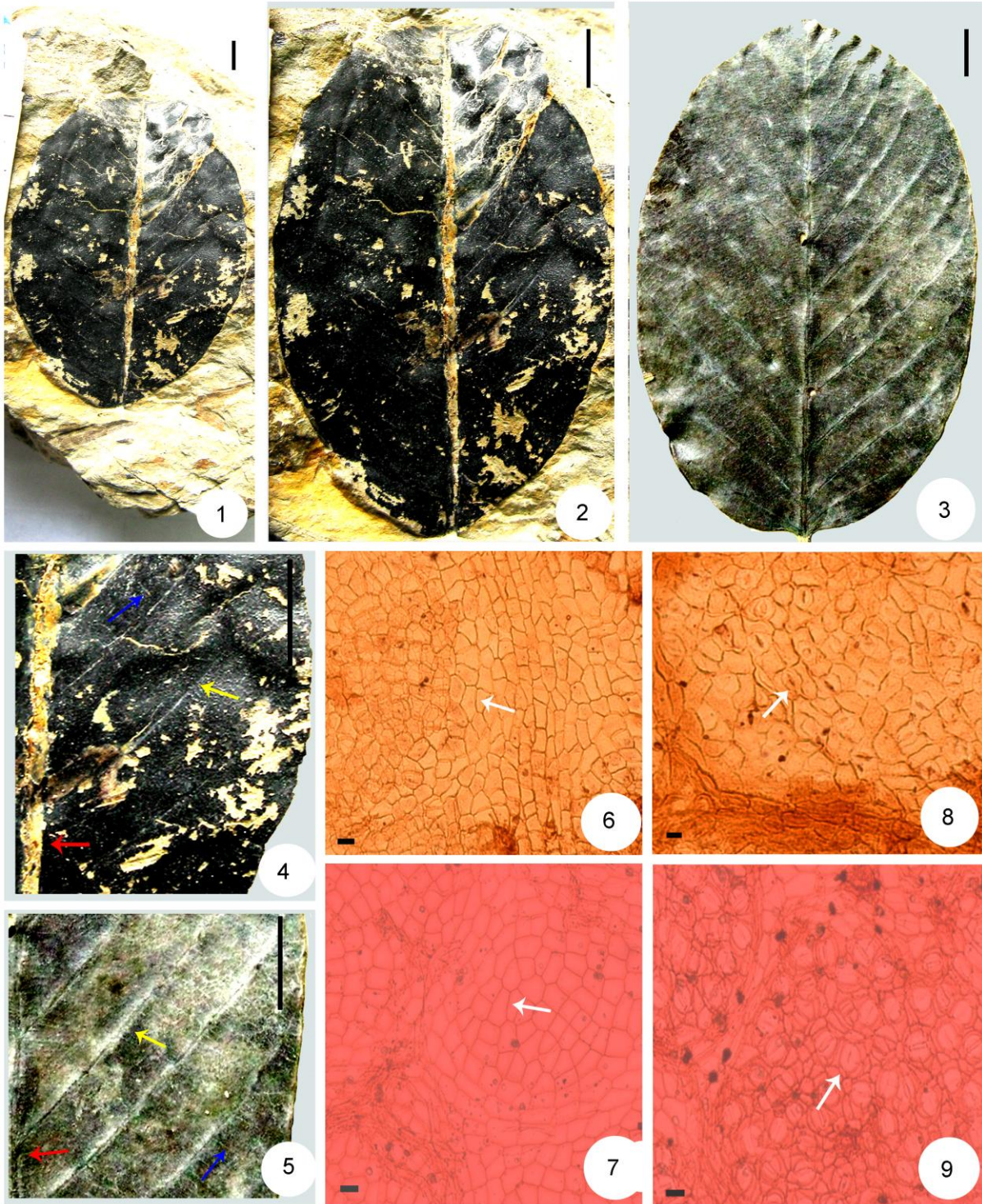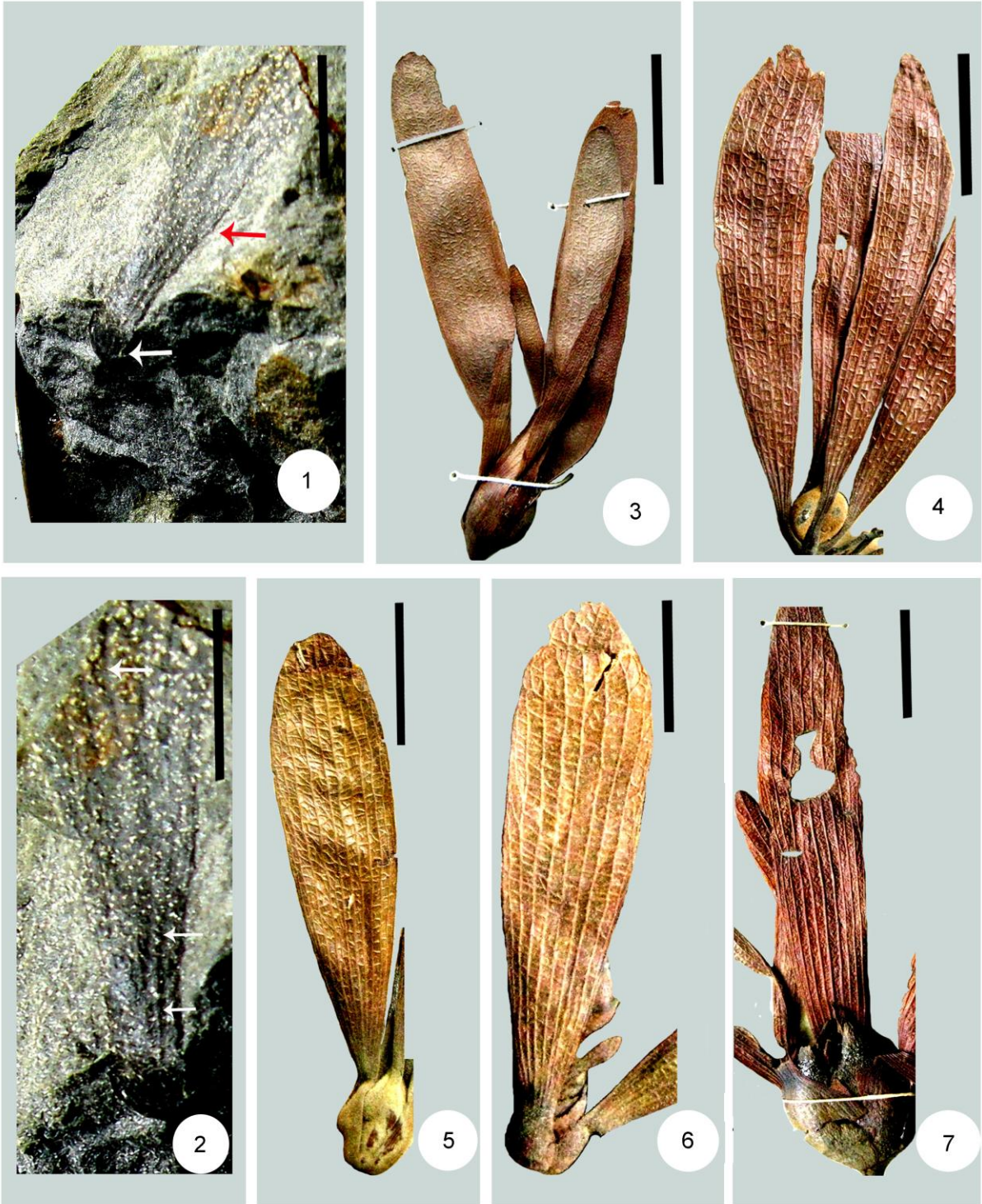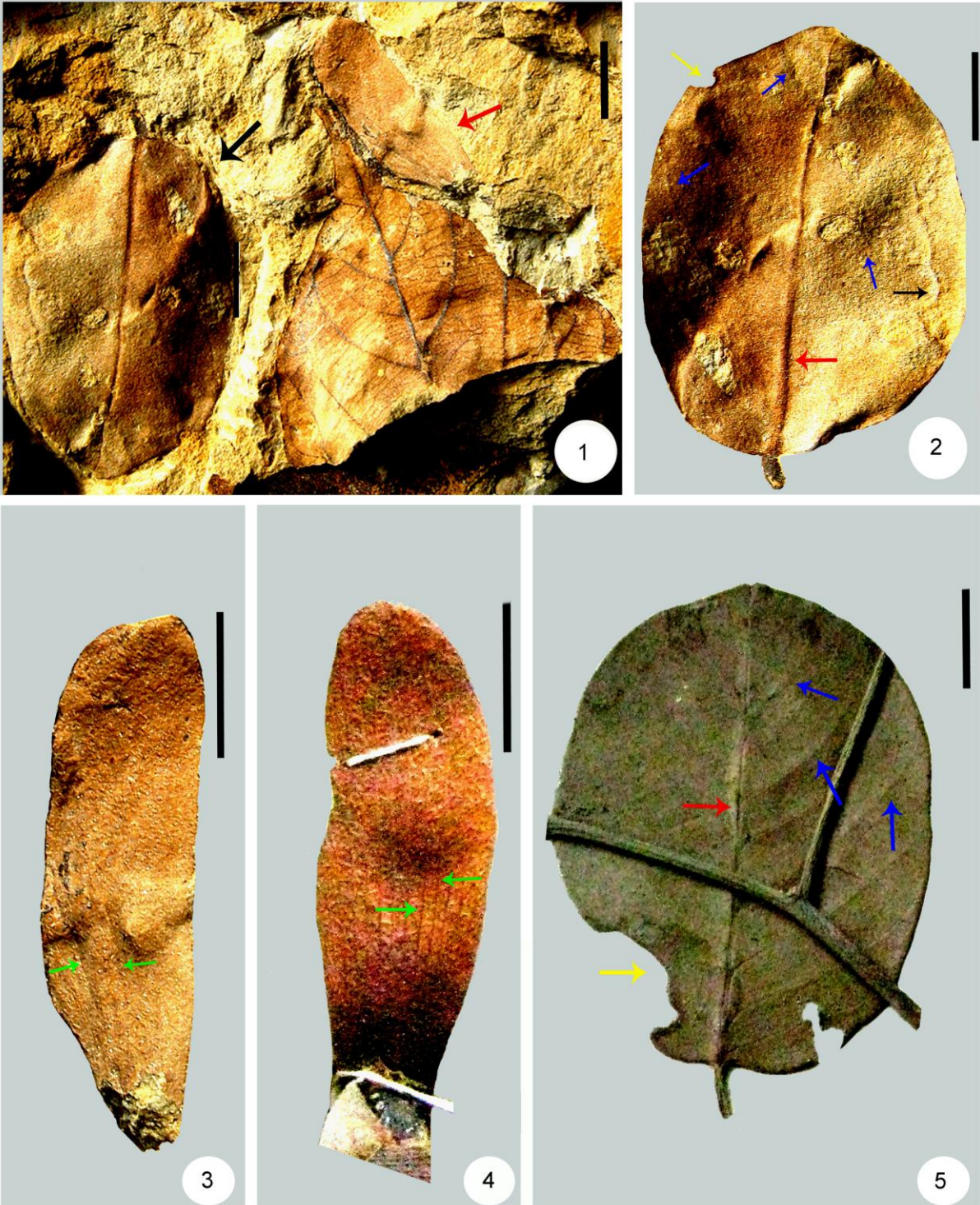
Plate I

Plate II

Plate III
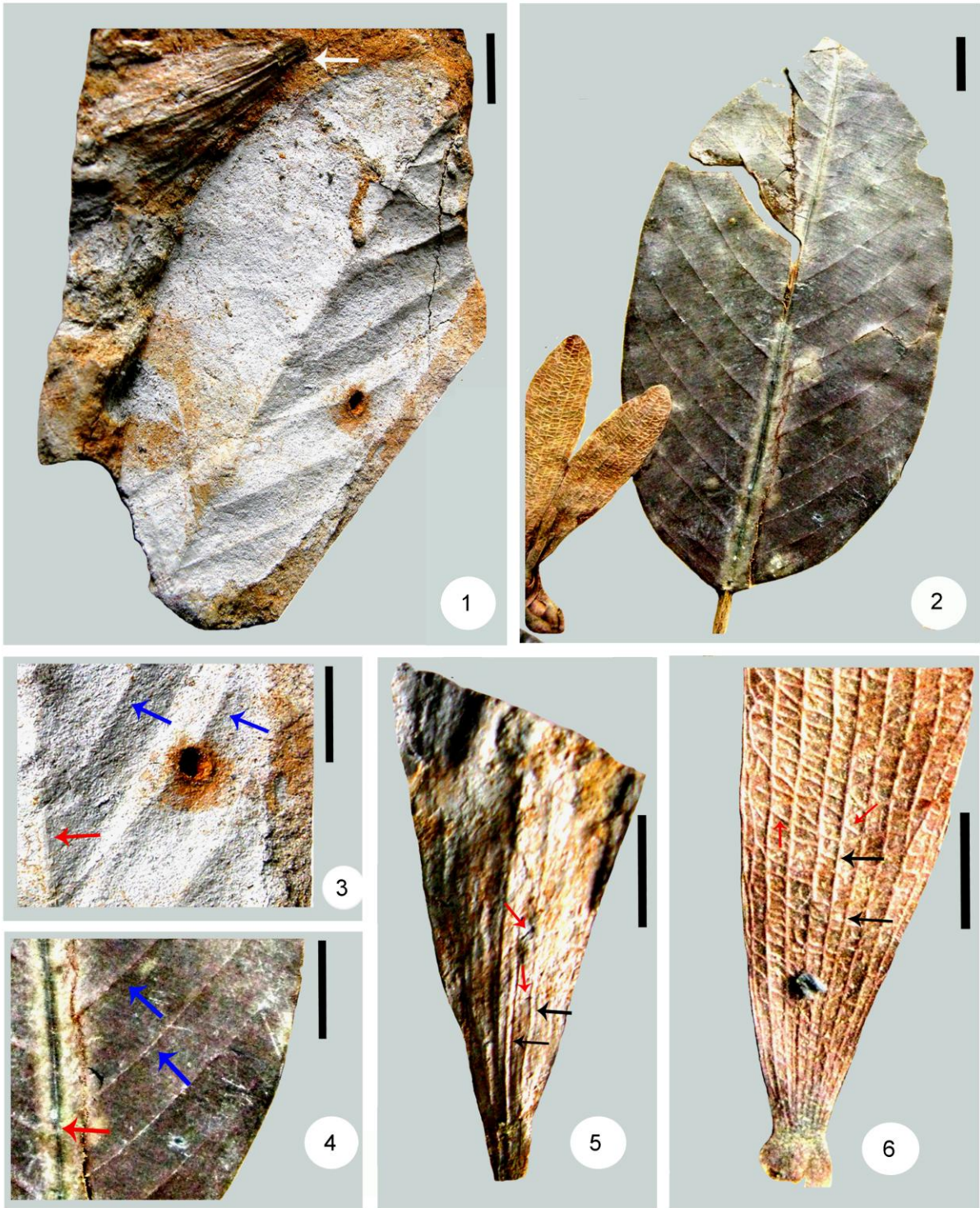
Plate IV

Plate V

Table 1.

North		
Gondwana Group		Carbonaceous shale, sandstone and coal
lower Siwalik (Dafla Formation)		well indurated sandstone, shale and siltstone with plant fossils
middle Siwalik (Subansiri Formation)	………Main Boundary Faults…….	weakly indurated sandstone, shale and siltstone with plant fossils
upper Siwalik (Kimin Formation)		sand rock and claystone/shale with plant fossils fossil wood
Assam Alluvium/ Quaternary deposits	…………….Thrust…………….	
South		
	…………….Thrust…………….	
	………Main Frontal Fault………	

Table 3.

Fossil species	NLR	Location and Age	1^0 veins	Shape	Apex	Length/ Width ratio (in cm)	Nature of secondary veins	Reference
Shorea mioassamica	*S. assamica* Dyer	Arunachal Pradesh; middle to upper Miocene	7	Linear lanceolate	Broken	3.2/1.2	At right angle	Khan and Bera, 2010
Shorea kachchhensis	*S. macroptera* Dyer	Kachchh of Gujrat; early Miocene	10-11	Linear lanceolate	Obtuse	5.8/1.4	70^0-80^0	Shukla et al., 2012
Shorea	*Shorea*	South	9-	Fruit	Roun	3.5/1to	Usually	Feng

maomingensis	*sericea* Dyer	China; late Eocene	18	body spherical to ellipsoidal; sepal lobe elliptic to obovate	ded to obtuse	7.5/1	alternate-percurrent, sinuous and straight; camptodromous marginally and apically.	et al., 2013
Shorea fujianensis	*Shorea hypochra* Hance	Southeast China, middle Miocene	11-13	Fruit body incomplete, ovoid; sepal lobe oblanceolate-lanceolate	Rounded	Ca. 4.5/1	Usually opposite percurrent, sinuous and straight, convex; perpendicular or at an obtuse or acute angle to the long	Shi et. al., 2014

							axis of the lobe.	
Shorea pinjoliensis sp. nov.	*Shorea* sp.	Arunachal Pradesh; middle to upper Miocene	7-8	Fruit body complete, spherical; sepal lobe seemingly elliptic to obovate	Broken	2.9/1	Seemingly fine, percurrent; further venation details not preserved.	Present study
Shorea bhalukpongensis sp. nov.	*S. tumbuggaia*	Arunachal Pradesh; Pliocene	Very faint; not clearly seen	Sepal lobe elliptic to lanceolate, 1.8 cm long and 0.6 cm wide; lobe	rounded	2.2/1	Not clearly preserved	Present study

				base 0.3 cm wide				
Shorea chandernag arensis sp. nov.	*Shorea leprosula* Miq.	Arunac hal Pradesh; upper Pliocen e to lower Pleisto cene	9	Calyx lobe 4.3 cm long and 1.9 cm wide; elliptic to lanceola te; lobe base narrow, 0.2 cm wide	Broke n	4.4/1	Seemingly secondary veins fine, percurrent .	Presen t study
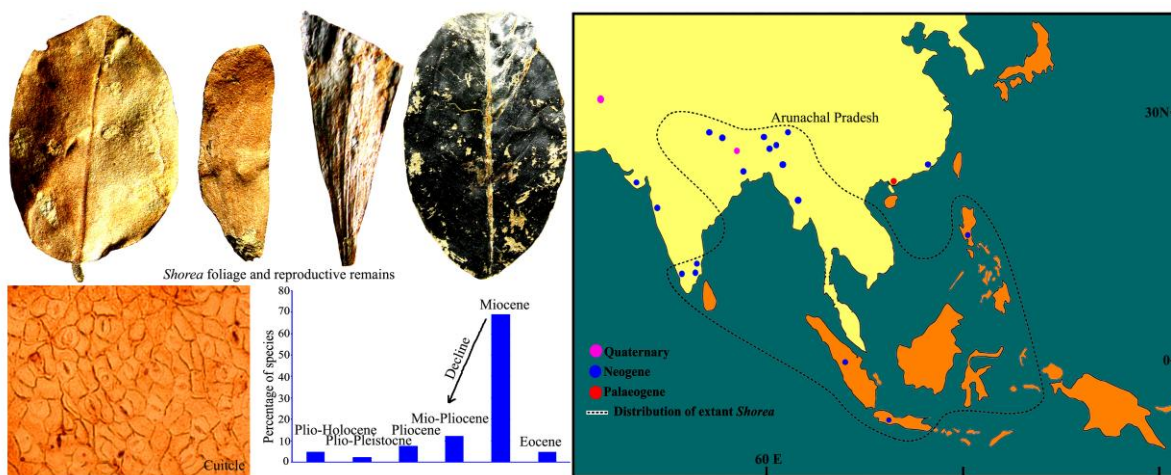
Graphical abstract

Highlights

- *Shorea* reproductive and leaf remains from the Mio-Pleistocene in Arunachal Pradesh.

- *Shorea* was a dominant forest element during Neogene (Miocene time).

- Tropical, warm and humid climatic conditions suggested during the deposition.

- Review the phytogeography and highlight the phytogeographic implication of *Shorea*.