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ORIGINAL PAPER

Floral diversity and environment during the middle Siwalik sedimentation (Pliocene) in the Arunachal sub-Himalaya

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Abstract

A comprehensive morphotaxonomical evaluation of diverse angiospermic dicotyledonous leaf impressions recovered from the middle part of the Siwalik succession (Subansiri Formation: Pliocene) of Arunachal Pradesh, eastern Himalaya, India, shows that the leaf remains are comparable to modern *Glochidion* J. R. Forst. and G. Forst. (Phyllanthaceae), *Bauhinia* L., *Callerya* Endl. (Fabaceae), *Mitragyna* Korth. (Rubiaceae), *Beilschmiedia* Nees (Lauraceae), *Uvaria* L. (Annonaceae), *Neolamarckia* Bosser (Rubiaceae), *Sorindeia* Thouars (Anacardiaceae), *Lagerstroemia* L. (Lythraceae), and *Premna* L. (Lamiaceae). Among these taxa, seven species are new to the Neogene floras of the Indian subcontinent. Analyses of the floral assemblage, with respect to the present-day distribution pattern of modern equivalent taxa and the physiognomic characters of the recovered fossil leaves, suggest that a tropical evergreen forest was growing in a warm humid climate in the region at the time of deposition. This qualitative climatic data is also corroborated by our previously published quantitative data obtained from a CLAMP (climate leaf analysis multivariate program) analysis on the middle Siwalik floral assemblage. The presence of some Southeast Asian elements in the fossil assemblage provides clear evidence of free exchange of taxa across southern Asia in the Pliocene.

Keywords Leaf impressions · Middle Siwalik · Pliocene · Palaeoenvironment · Phytogeography · Arunachal Pradesh

Introduction

"Siwalik" sediments are made up of a thick (~ 7000 m) succession of Neogene 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 (Parkash et al. 1980; Bora and Shukla 2005). 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 (Karunakaran and Ranga Rao 1979; Ranga Rao et al. 1979). In the Arunachal Pradesh sector, 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 (Karunakaran and Ranga Rao 1979; Kumar and Singh 1982; Ranga Rao 1983; Kunte et al. 1983; Agarwal et al. 1991; Kumar 1997; Anand-Prakash and Singh 2000; Joshi et al. 2003; Singh 2007). Its northern limit is defined by the Main Boundary Fault (MBF) separating it from the pre-Tertiary succession; while in the south, the Brahmaputra alluvium of the Brahmaputra Plain defines its boundary. The Main Frontal Thrust (MFT) separates Siwalik sediments from the Quaternary Assam alluvium (Kumar 1997; Joshi et al. 2003) (Table 1). The Siwalik sediments lying along the foothills of Arunachal Pradesh are subdivided into the lower Siwalik (Dafla Formation, Middle to Late Miocene), the middle Siwalik (Subansiri Formation; Pliocene), and the upper Siwalik (Kimin Formation, Late Pliocene to Early Pleistocene) exposed in reverse stratigraphic order (Joshi et al. 2003). In places, the contacts between the lower, middle, and upper Siwalik are also tectonised and faulted.

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Table 1 Generalized lithotectonic sequence in Arunachal Pradesh (after Joshi et al. 2003)

Geological unit		Brief description
North		
Gondwana Group		Carbonaceous shale, sandstone, and coal
	……….Main Boundary Faults………..	
Lower Siwalik (Dafla Formation)		Well indurated sandstone, shale, and siltstone with plant fossils
	……………..Thrust……………………	
Middle Siwalik (Subansiri Formation)		Weakly indurated sandstone, shale, and siltstone with plant fossils
	………………..Thrust………………….	
Upper Siwalik (Kimin Formation)		Sand, rock, and claystone/shale with plant fossils and fossil wood
	…………Main Frontal Fault…………	
Assam Alluvium/Quaternary deposits		
South		

In comparison to lower and upper Siwalik strata, the Arunachal middle Siwalik succession (Pliocene) has received little attention for palaeobotanical study in relation to phytostratigraphy and palaeoenvironment due to the inaccessibility of most of the fossil-bearing terrains in this area. Recently, we have investigated plant megafossils collected from this succession, reported a variety of taxa, and discussed in a preliminary way their palaeoecological significance (Khan and Bera 2014; Khan et al. 2015, 2016, 2017). We have documented leaf impressions comparable to extant *Persea*, *Lindera*, *Shorea*, *Calophyllum*, and *Glochidion*. Here, we study diverse angiosperm leaf impressions collected from the middle Siwalik horizons (Subansiri Formation: Pliocene) of the West Kameng District of Arunachal Pradesh, eastern Himalaya (Table 2). In combination with our earlier reported palaeobotanical data, the present study allows us to discuss the palaeoclimate and phytogeography of the area in more detail.

Materials and methods

During our field campaign, fossil leaf impressions were collected from roadside exposures along the Kameng River in the Bhalukpong area, West Kameng District of Arunachal Pradesh (situated between 26.46444° N and 29.498333° N and 91.497222° E and 97.415556° E), eastern Himalaya, India (Fig. 1). Siwalik sediments in and around the fossil localities belong to the Subansiri Formation (Pliocene; middle Siwalik), which is characterised by poorly indurated, medium- to very coarse-grained, salt and pepper-textured multistoried sandstones, with grey shale intercalations, siltstones, and conglomerates with plant fossils. The Siwalik sediments of Arunachal Pradesh were deposited between 13 and 2.5 Ma based on both detrital fission-track data and palaeomagnetism (Chirouze et al. 2012). The transition between the lower and middle Siwalik is dated at about 10.5 Ma and the middle to upper Siwalik transition is at 2.6 Ma (Chirouze et al. 2012).

Identifications were made by comparison with modern angiosperm leaves collected from forests adjacent to the fossil exposures, as well as with herbarium sheets of modern taxa kept in the Central National Herbarium (CAL), Sibpur, Howrah, West Bengal. Macroscopic images of fossil and relevant extant specimens were photographed using a digital camera (Canon Power Shot A720IS) (Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, and 13). Photographs showing macromorphological details of fossil leaves and their nearest living relatives were taken using an incident light compound microscope (Stemi SV 11, Zeiss). For descriptions of leaf impressions, the terminologies of Ellis et al. (2009) were used. The order of angiospermous fossil leaves in the systematic palaeobotany section is after the prevalent classification of flowering plants according to Angiosperm Phylogeny Group (APG IV 2016). All the fossil specimens including holotypes (CUH/PPL/B/64; CUH/PPL/B/50; CUH/PPL/B/66; CUH/PPL/B/1A; CUH/PPL/B/70; CUH/PPL/B/36; CUH/PPL/B/1A$_1$; CUH/PPL/B/9; CUH/PPL/B/52; CUH/PPL/B/73) studied are preserved in the Herbarium and Museum, Department of Botany, University of Calcutta (CUH).

Table 2 Comparable modern forms, corresponding forest types and present day distribution of recovered fossils from the middle part of the Siwalik sediments (Pliocene) of Arunachal sub-Himalaya (Pearson and Brown 1932; Brandis 1971; Santapau and Henry 1973; Hazra et al. 1996)

Fossil taxa	Modern equivalent taxa		Forest types	Present-day distribution
	Species	Family		
Pteridophytes				
Thelypteridaceophyllum tertiarum Joshi and Mehrotra, 2003; Khan et al. 2007	cf. *Ampelopteris* sp.	Thelypteridaceae	Evergreen	Bengal, Nilgiris, usually grows in moist shady places or along streams
Angiosperms				
Uvaria neograndiflora Khan, Bera M et Bera S, sp. nov.	*Uvaria grandiflora* Roxb.	Annonaceae	Evergreen	Southern China (400–1000 m), India, Sri Lanka, Thailand, Malaysia, Vietnam, Laos, Sumatra, Borneo, Java, Indonesia, Philippines
Persea mioparviflora Khan and Bera 2014	*Persea parviflora* Spreng.	Lauraceae	Evergreen	India (Khasi Hills, Assam, at 1219–1524 m) and the Malayan region
Persea preglaucescens Khan and Bera 2014	*Persea glaucescens* (Nees) D. G. Long	Lauraceae	Evergreen	China (Yunnan), Bangladesh, Bhutan, India (Western Ghats and adjoining hill ranges, sub-Himalayan tract), Myanmar and Nepal
Lindera neobifaria Khan and Bera 2014	*Lindera bifaria* Benth.	Lauraceae	Evergreen	China, Myanmar, Bhutan, India, Nepal, and Vietnam In India, this species occurs in the Himalaya from Kumaon eastwards (1524 m), Manipur, Upper Assam, Mishmi Hills, and Khasi Hills (914–1219 m)
Beilschmiedia plioroxburghiana Khan, Bera M et Bera S, sp. nov.	*Beilschmiedia roxburghiana* Nees	Lauraceae	Evergreen	Eastern Himalaya, Nepal, Sikkim, Assam, Malaysia, Thailand, Indo-China (250–2000 m)
Bauhinia siwalika Lakhanpal and Awasthi, 1984	*Bauhinia* sp.	Fabaceae	Evergreen	India, Sri Lanka, Vietnam, and southeastern China
Callerya precinerea Khan, Bera M et Bera S, sp. nov.	*Callerya cinerea* (Benth.) Schot	Fabaceae	Evergreen	Sikkim, ascending to 4000 ft., Assam Chittagong, and Myanmar
Calophyllum suraikholaensis (Awasthi and Prasad 1990); Khan et al., 2009, 2011, 2015, 2017	*Calophyllum polyanthum* Wall.	Calophyllaceae	Evergreen	India, Bangladesh, and Myanmar
Calophyllum siwalikum Khan, R.A.Spicer and Bera, 2017	*Calophyllum inophyllum* L.	Calophyllaceae	Evergreen	West coast from Mumbai, on the east coast from Orissa southwards, Andaman, and Myanmar (Tenasserim); in coastal settings within the tropics, from Madagascar to Australia and the Pacific
Glochidion palaeogamblei Khan and Bera 2012	*Glochidion gamblei* Hook. F.	Phyllanthaceae	Evergreen	Sikkim, Terai, and Myanmar
Glochidion siwalikum Khan, Bera M et Bera S, sp. nov.	*Glochidion zeylanicum* (Gaertn.) A. Juss.	Phyllanthaceae	Evergreen to semi-evergreen	China, Bangladesh, India, Indonesia, Japan, Malaysia, Sri Lanka, Thailand, Vietnam; Australia, Pacific islands (Solomon Islands) (100–600 m)
Lagerstroemia jamraniensis Prasad, et al., 2004	*Lagerstroemia speciosa* (L.) Pers.	Lythraceae	Moist deciduous	China, India, Sri Lanka, Myanmar, Thailand, Malaysia, Indonesia,

Table 2 (continued)

Fossil taxa	Modern equivalent taxa		Forest types	Present-day distribution
	Species	Family		
				Laos, Cambodia, Vietnam, Philippines
Sorindeia subansiriensis Khan, Bera M et Bera S, sp. nov.	*Sorindeia madagascariensis* Thouars ex DC.	Anacardiaceae	Evergreen	East tropical Africa (Somalia, Kenya, Tanzania, Zambia, Mozambique, Madagascar)
Shorea siwalika (Antal and Awasthi 1993) Khan et al. 2015	*Shorea assamica* Dyer.	Dipterocarpaceae	Evergreen	Upper Assam at the foot of Naga hills, in Sibsagar and Lakhimpur Districts
Shorea pliotumbuggaia Khan, Spicer RA et Bera, 2016	*Shorea tumbuggaia* Roxb.	Dipterocarpaceae	Dry mixed deciduous	India (Andhra Pradesh and Tamil Nadu)
Shorea bhalukpongensis Khan, Spicer RA et Bera, 2016	*Shorea tumbuggaia* Roxb.	Dipterocarpaceae	Dry mixed deciduous	India (Andhra Pradesh and Tamil Nadu)
Neolamarckia paleocadamba Khan, Bera M et Bera S, sp. nov.	*Neolamarckia cadamba* (Roxb.) Bosser	Rubiaceae	Evergreen	South Asia (India, Bangladesh, Bhutan, Nepal, Sri Lanka) and Southeast Asia (Myanmar, Thailand, Indonesia)
Mitragyna tertiara Konomatsu and Awasthi 1999	*Mitragyna parvifolia* (Roxb.) Korth.	Rubiaceae	Mixed deciduous	Sub-Himalayan region, central India, and Myanmar
Premna pliobengalensis Khan, Bera M et Bera S, sp. nov.	*Premna bengalensis* Clarke	Lamiaceae	Evergreen	Sub-Himalayan tract from Nepal eastwards (300–900 m)

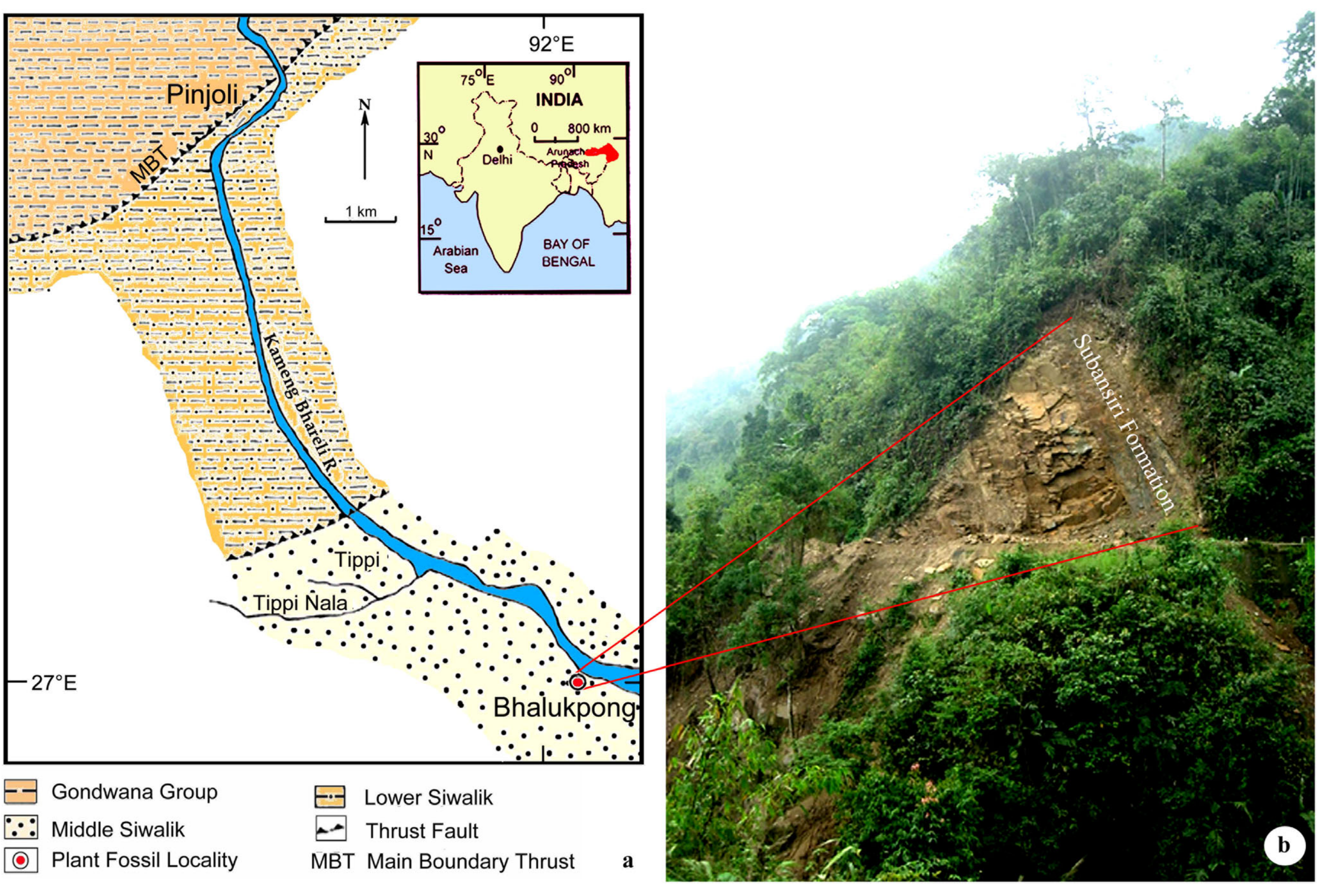

Fig. 1 **a** Location of the study area in West Kameng District, Arunachal Pradesh, India, and a geological setting of the area around Bhalukpong; the red square indicates the fossil locality. **b** Exposed section from the Bhalukpong-Tawang road cutting section

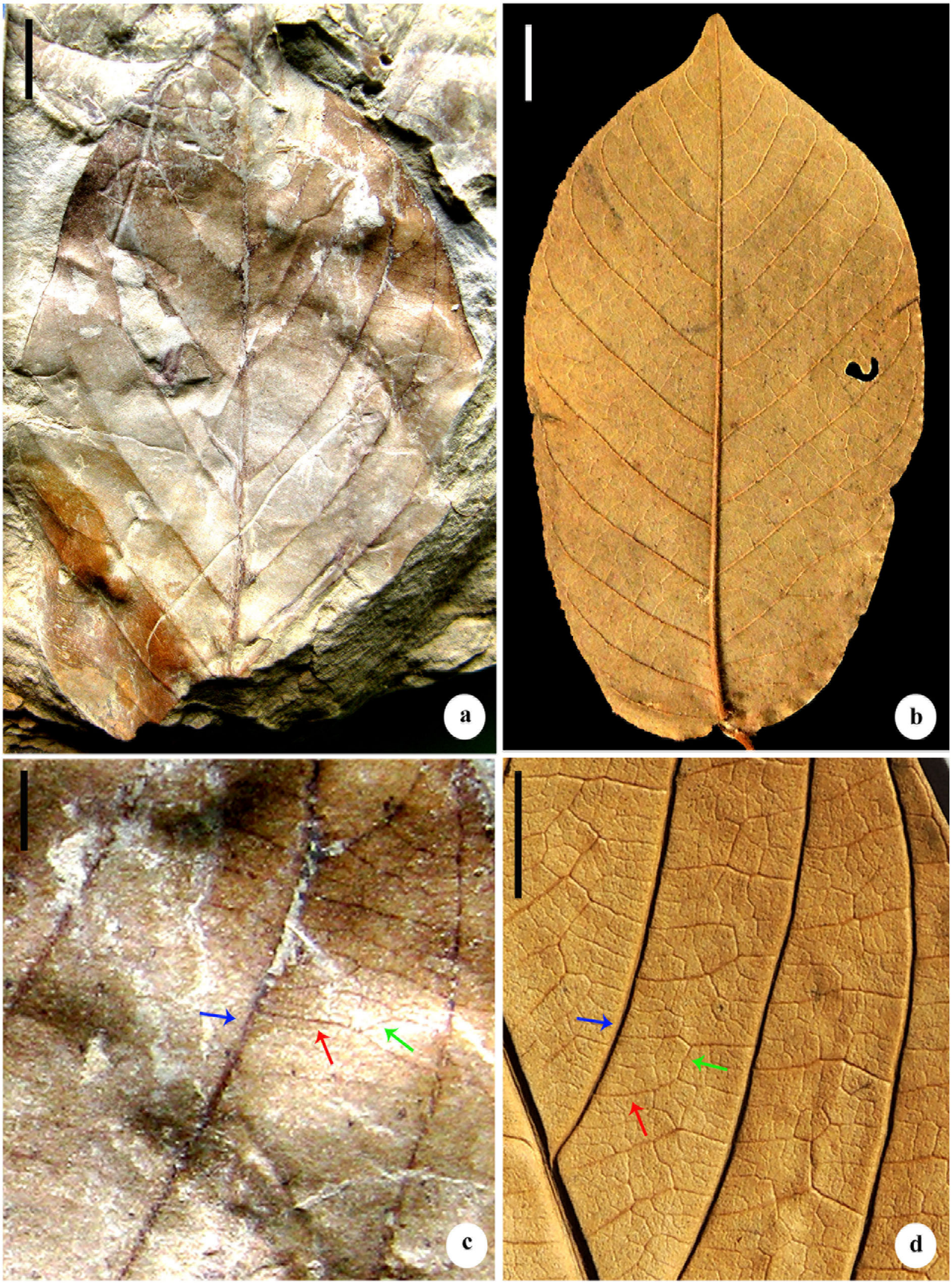

Fig. 2 **a** *Uvaria neograndiflora* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype CUH/PPL/B/52). **b** *Uvaria grandiflora* Roxb.—modern leaf with similar shape, apex, and venation pattern. **c** *Uvaria neograndiflora*—a part of the fossil leaf magnified to show details of secondary (marked by blue arrow), tertiary (marked by blue arrow), and quaternary (marked by blue arrow) venation. **d** *Uvaria grandiflora*—a part of the modern leaf magnified to show similar secondary (marked by blue arrow), tertiary (marked by blue arrow), and quaternary (marked by blue arrow) venation (scale = 1 cm)

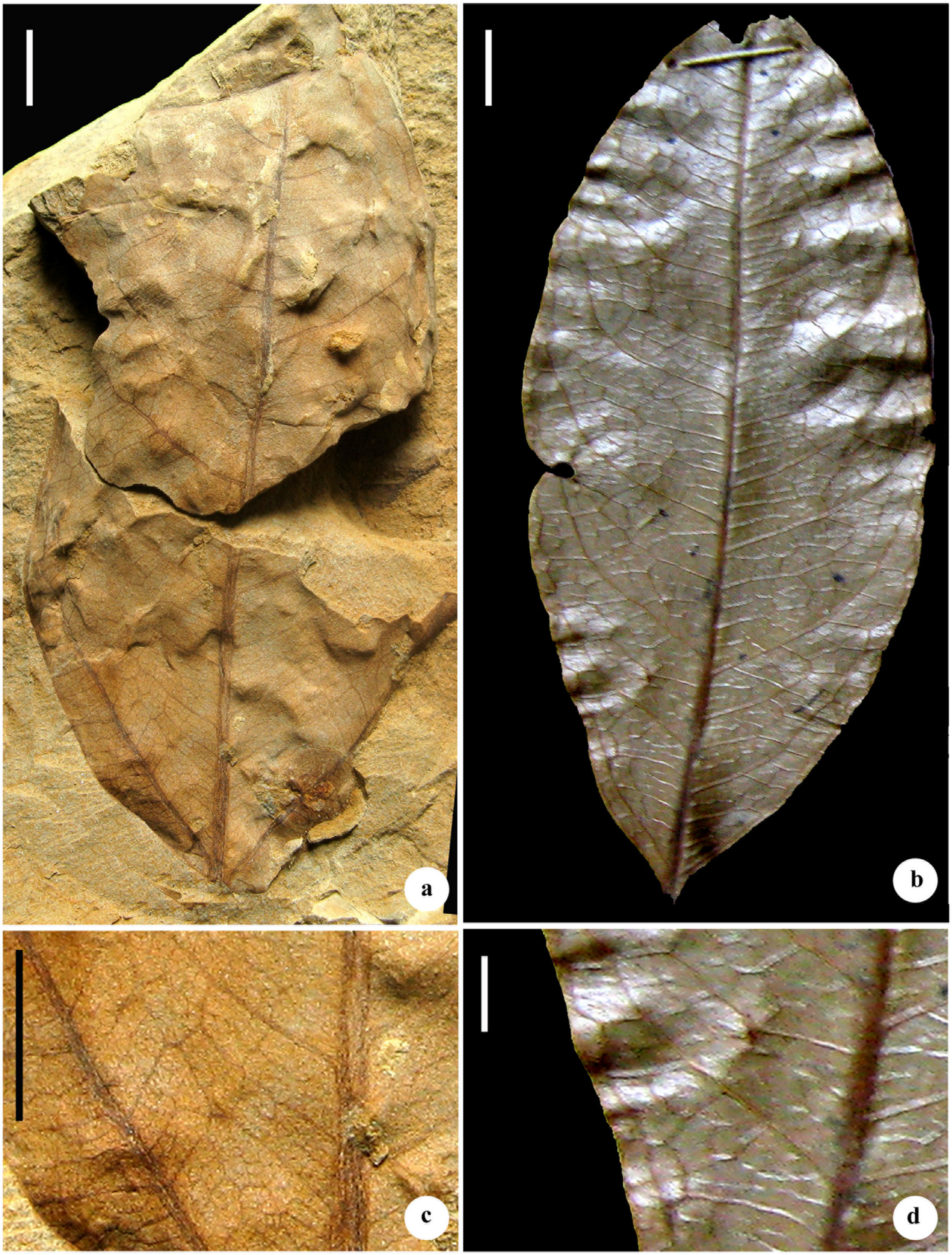

Fig. 3 **a** *Beilschmiedia plioroxburghiana* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype CUH/PPL/B/66). **b** *Beilschmiedia roxburghiana* Nees—modern leaf with similar apex, base, and venation pattern. **c** *Beilschmiedia plioroxburghiana*—a part of the fossil leaf magnified to show details of tertiary venation. **d** *Beilschmiedia roxburghiana*—a part of the modern leaf magnified to show similar tertiary venation pattern (scale = 1 cm)

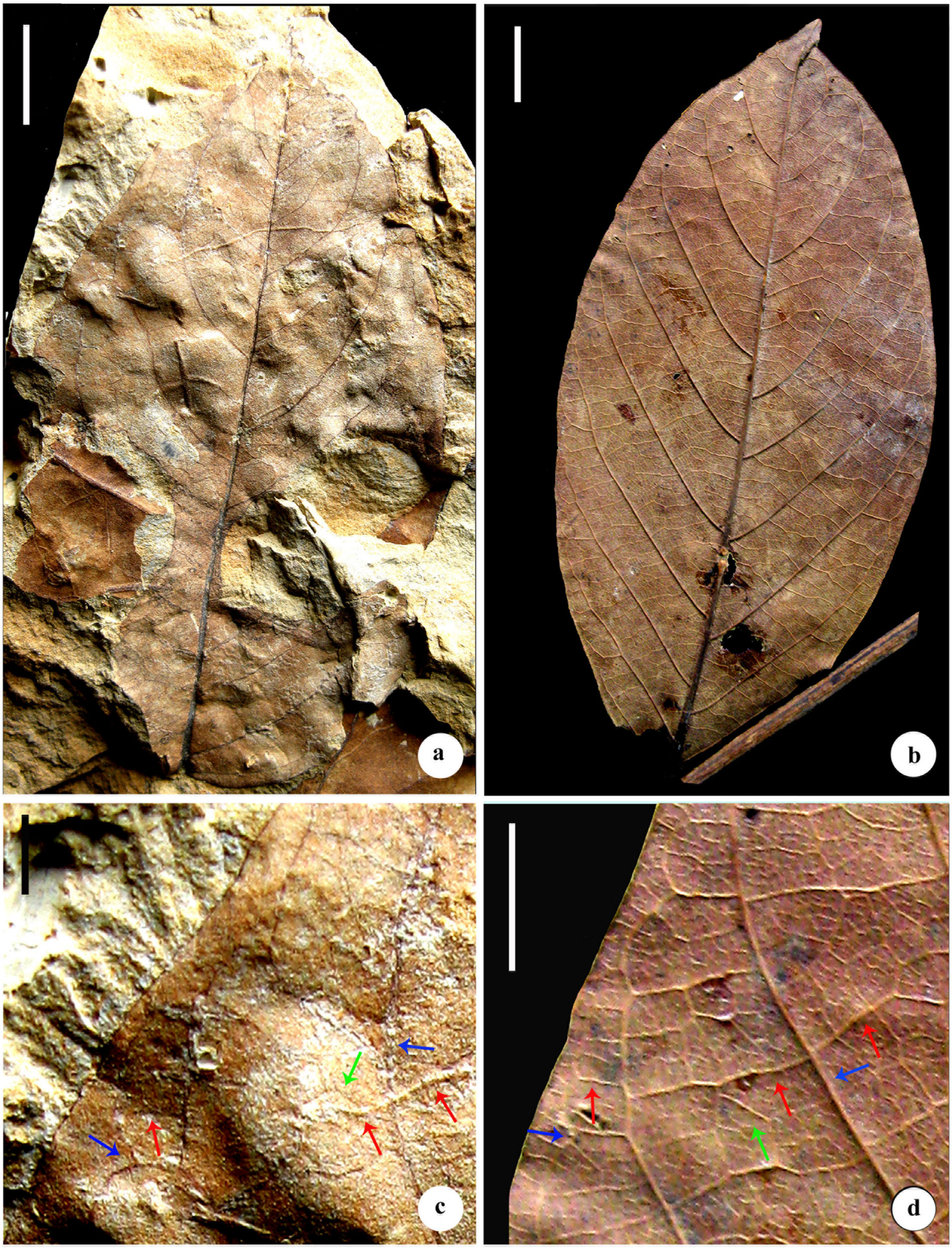

Fig. 4 **a** *Callerya precinerea* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype CUH/PPL/B/50). **b** *Callerya cinerea* (Benth.) Schot—modern leaf with similar apex, base and venation pattern. **c** *Callerya precinerea*—a part of the fossil leaf magnified to show details of secondary (marked by blue arrows), tertiary (marked by red arrows), and quaternary (marked by green arrow) venation. **d** *Callerya cinerea*—a part of the modern leaf magnified to show similar secondary (marked by blue arrows), tertiary (marked by red arrows), and quaternary (marked by green arrow) venation pattern (scale = 1 cm)

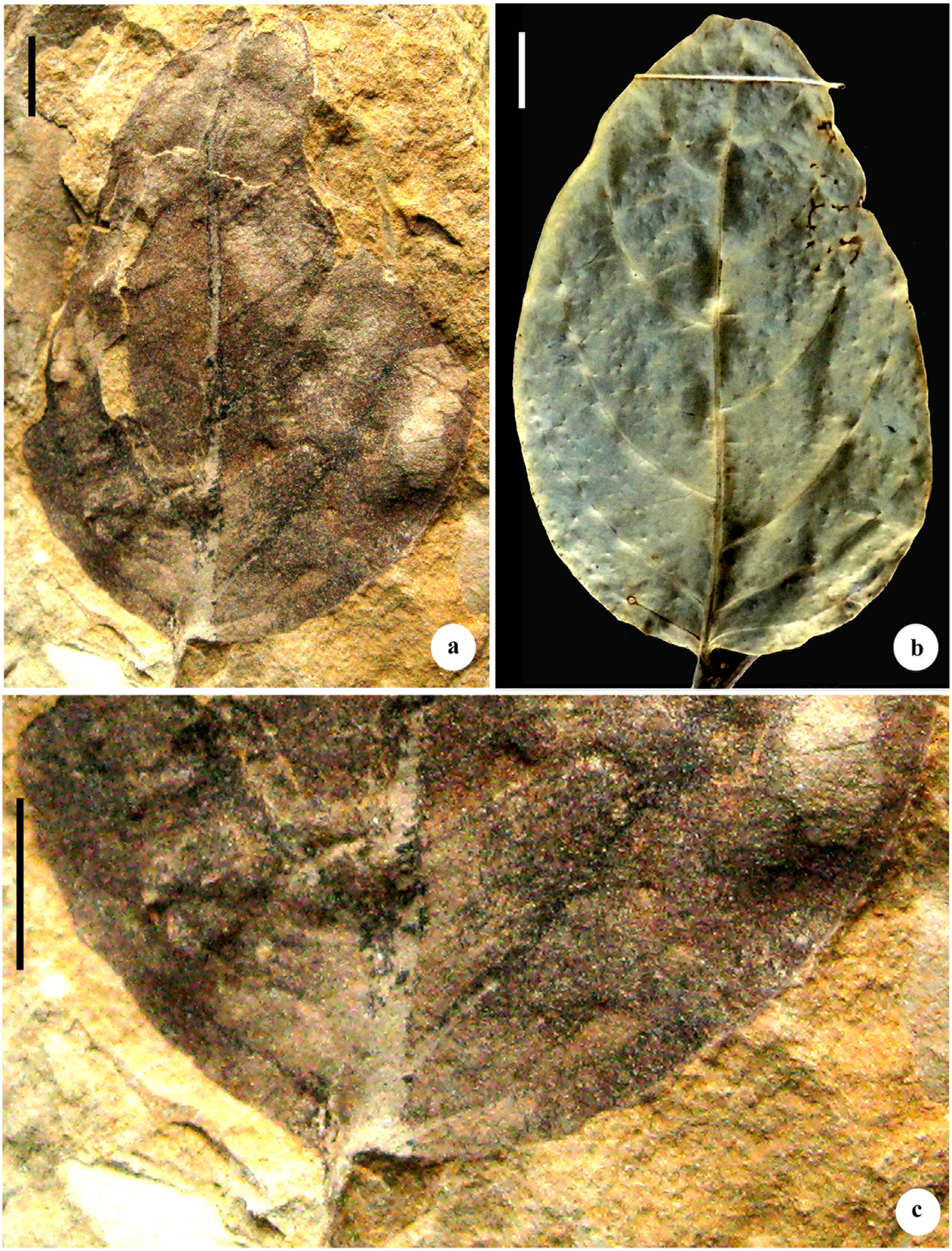

Fig. 5 **a** *Glochidion siwalikum* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype CUH/PPL/B/64A). **b** *Glochidion zeylanicum* (Gaertn.) A. Juss.—modern leaf with similar size, shape, and venation pattern. **c** *Glochidion siwalikum*—basal part of the fossil leaf magnified to show details of venation (scale = 1 cm)

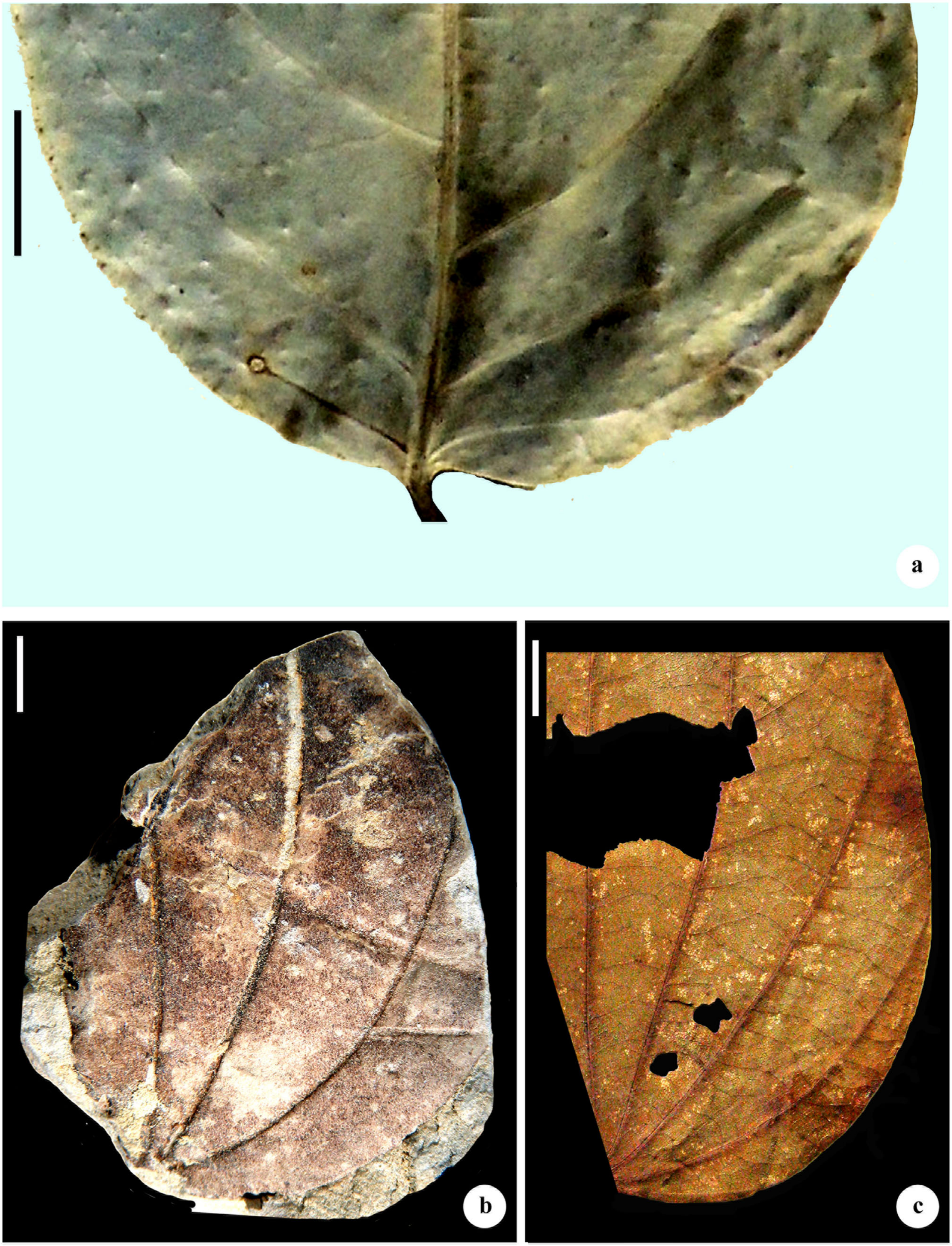

Fig. 6 **a** *Glochidion zeylanicum*—basal part of the modern leaf magnified to show similar venation pattern. **b** *Bauhinia siwalika* Lakhanpal and Awasthi—fossil leaflet (specimen no. CUH/PPL/B/9). **c** *Bauhinia* sp.—modern leaflet with similar acrodromous venation pattern (scale = 1 cm)

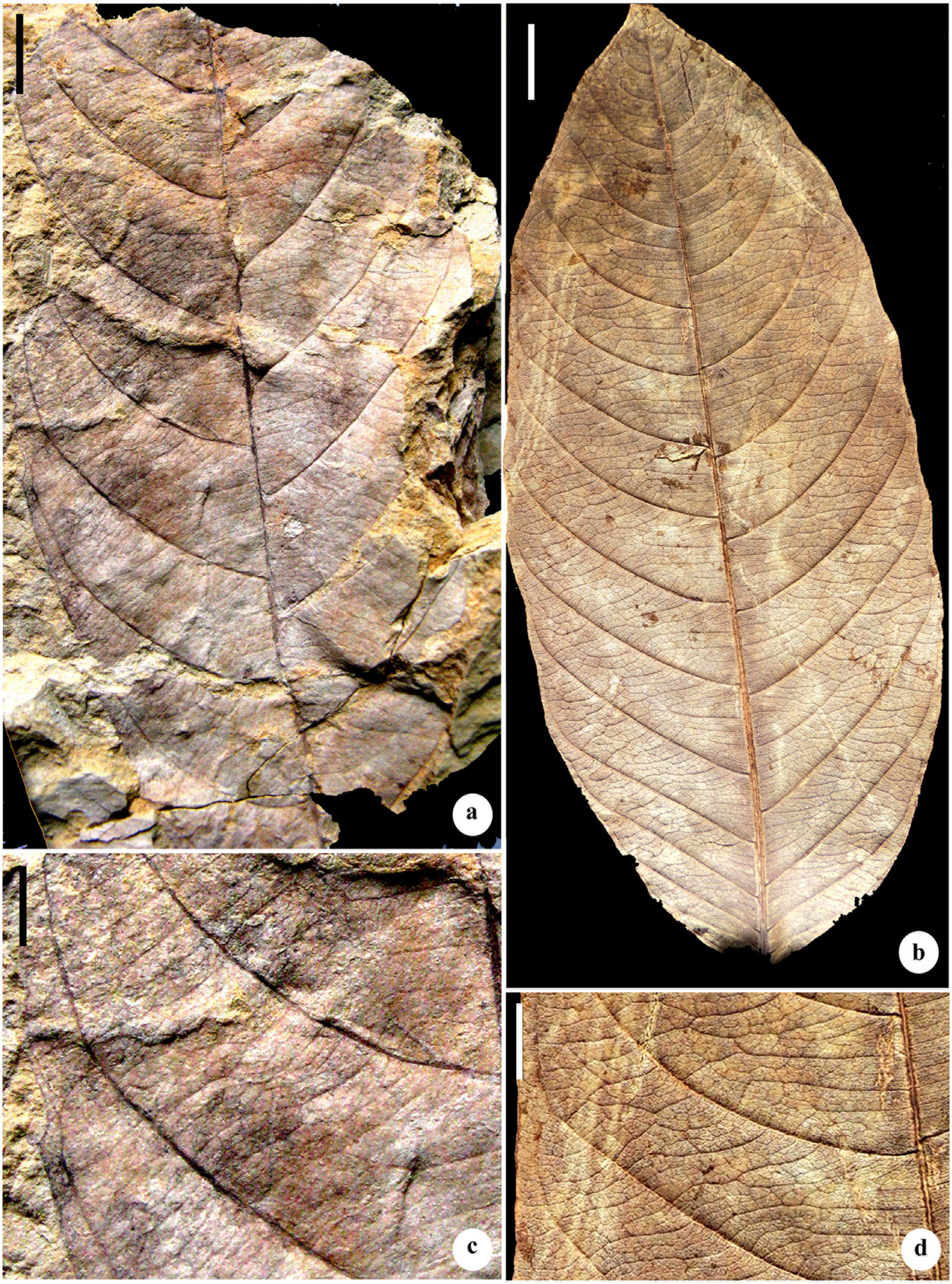

Fig. 7 **a** *Lagerstroemia jamraniensis* Prasad, et al.—fossil leaf (specimen no. CUH/PPL/B/73). **b** *Lagerstroemia speciosa* (L.) Pers.—modern leaf with similar venation pattern. **c** *Lagerstroemia jamraniensis*—a part of the fossil leaf magnified to show details of secondary and tertiary venation. **d** *Lagerstroemia speciosa*—a part of the modern leaf magnified to show similar secondary and tertiary venation patterns (scale = 1 cm)

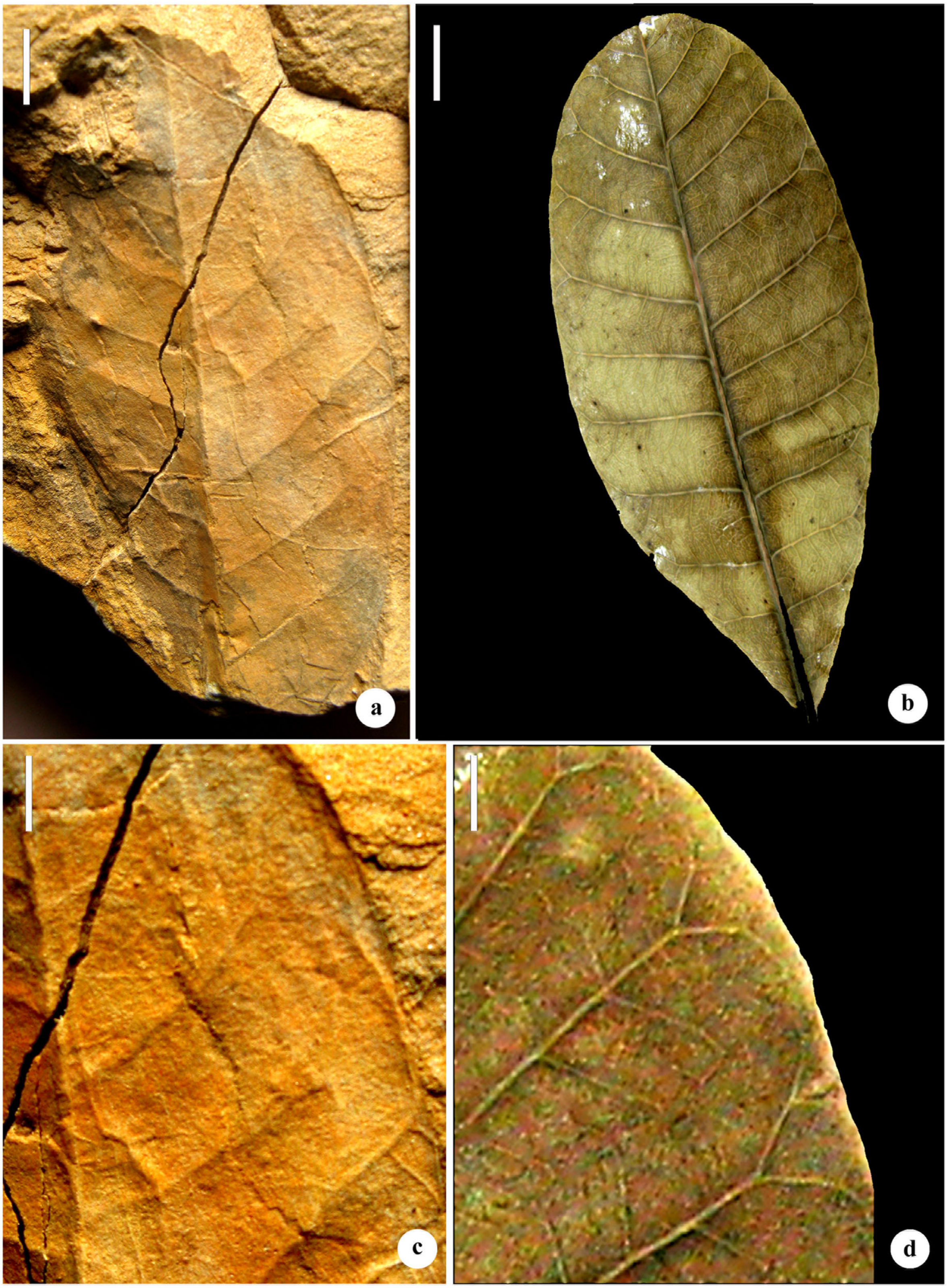

Fig. 8 **a** *Sorindeia subansiriensis* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype: CUH/PPL/B/70). **b** *Sorindeia madagascariensis* Thouars ex DC.—modern leaf with similar shape, size, and venation pattern. **c** *Sorindeia subansiriensis*—a part of the fossil leaf showing primary (marked by white arrow), secondary (marked by red arrows), intersecondary veins (marked by green arrows), and tertiary veins (marked by blue arrow). **d** *Sorindeia madagascariensis*—a part of the modern leaf showing similar venation pattern (marked by arrows) (scale = 1 cm)

Fig. 9 **a** *Neolamarckia paleocadamba* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype CUH/PPL/B/1A) (scale = 1 cm)

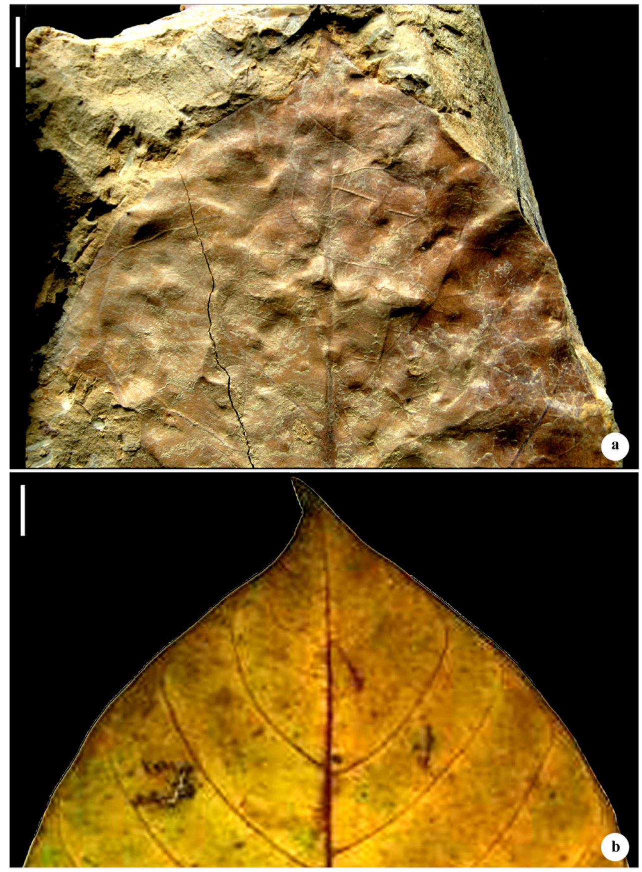

Fig. 10 **a** *Neolamarckia paleocadamba* Khan, Bera M et Bera S, sp. nov.—apical part of the fossil leaf showing acuminate apex. **b** *Neolamarckia cadamba* (Roxb.) Bosser—apical part of the modern leaf showing similar nature of apex (scale = 1 cm)

Results

The fossil leaf impressions recovered from the middle part of the Siwalik sediments (Pliocene: Subansisri Formation) of Arunachal sub-Himalaya are identified as *Uvaria neograndiflora* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *U. grandiflora* Roxb.) (Fig. 2a, b, c, d), *Beilschmiedia palaeoroxburghiana* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *B. roxburghiana* Nees) (Fig. 3a, b, c, d), *Callerya precinerea* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *C. cinerea* (Benth.) Schot) (Fig. 4a, b, c, d), *Glochidion siwalikum* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *G. zeylanicum* (Gaertn.) A. Juss.) (Figs. 5a–c and 6a), *Bauhinia siwalika* Lakhanpal and Awasthi (similar to the modern leaf *Bauhinia* sp.) (Fig. 6b, c), *Lagerstroemia jamraniensis* Prasad, et al. (similar to the modern leaf *L. speciosa* (L.) Pers.) (Fig. 7a, b, c, d), *Sorindeia subansiriensis* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *S. madagascariensis* Thouars ex DC.) (Fig. 8a, b, c, d), *Neolamarckia precadamba* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *N. cadamba* (Roxb.) Bosser) (Figs. 9a; 10a, b; 11a, b), *Mitragyna tertiara* Konomatsu and Awasthi (similar to the modern leaf *M. parvifolia* (Roxb.) Korth.) (Fig. 12a, b, c, d), and *Premna pliobengalensis* Khan, Bera M et Bera S, sp. nov. (similar to the modern leaf *P. bengalensis* Clarke) (Fig. 13a, b, c, d). Systematic descriptions of only the newly described fossil leaf impressions are provided below.

Systematic Palaeobotany

Family Annonaceae Juss.
Genus *Uvaria* L.

Species *Uvaria neograndiflora* Khan, Bera M et Bera S, sp. nov. (Fig. 2a, c)

Holotype: CUH/PPL/B/52
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng district (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession (Subansiri Formation: Pliocene).
Etymology: Adding the prefix "neo" to the modern comparable specific epithet *grandiflora* derives the specific name.

Diagnosis: Simple, symmetrical; wide elliptical, maximum lamina length 7.3 cm and maximum width 5 cm; apex attenuate; base broken; margin entire; texture chartaceous.

Venation pinnate, camptodromous-eucamptodromous; primary vein (1°) single, prominent, straight, moderate in thickness; secondary veins (2°) about 7 pairs visible, alternate, distance between two secondaries 0.5 to 0.9 cm, angle of divergence acute, narrow less than 45°; uniform, some of them joining superadjacent secondaries near the margin; inter-secondary veins absent; tertiary veins (3°) fine, percurrent, simple, oblique in relation to midvein, predominantly alternate, closely placed; quaternary veins (4°) fine, orthogonal reticulate, irregular.

Remarks: The main characteristic features of the present fossil leaf are the narrow obovate shape, attenuate apex, entire margin, chartaceous texture, camptodromous-eucamptodromous venation, secondary veins arising at an acute angle, percurrent, simple, oblique, and closely placed tertiary veins. These features are common in the modern leaves of the family Annonaceae. Size, shape, texture, and venation pattern strongly indicate that the present fossil shows its closest affinity with extant leaves of *Uvaria*. Comparisons were also made with the modern leaves of other two genera viz., *Artabotrys* R.Br. and *Polyalthia* Blume of the Annonaceae, showing apparent similarity with the fossil specimen. *Polyalthia* differs in having more acute angles of origin of the secondaries as compared to the fossil, while *Artabotrys* differs in having an acuminate apex as compared with the attenuate apex in the fossil.

To find out the nearest modern counterpart of the fossil specimen, herbarium sheets of all available species of *Uvaria* were examined and we found that only two species of *Uvaria* viz., *U. zeylanica* Deless. ex DC. and *U. grandiflora* Roxb., show resemblance with the present fossil specimen. *U. zeylanica* differs in having alternate to opposite secondary veins and prominent intersecondary veins. Leaves of *U. zeylanica* are also narrower than the fossil leaf. So, the fossil specimen shows closest resemblance with the modern leaves of *Uvaria grandiflora* Roxb. (C. N. Herbarium Sheet No. 10764) in size, shape, and vein architecture (Fig. 2b, d).

To date, five fossil leaves resembling modern *Uvaria* have been described from Eocene to Miocene sediments of India (Prasad 1994; Antal and Prasad 1998; Shukla and Mehrotra 2014) and China (Tao 2000; EGCFC 1978). Two of them, namely *Uvaria siwalicus* Prasad and *Uvaria ghishia* Antal and Prasad, were described from the Siwalik sediments (middle Miocene) of India. *Uvaria siwalicus* differs in having an acute apex, while *U. ghishia* is different in having a wide acute angle of origin of secondaries. Another Indian species *Uvaria palaeozeylanica* Shukla and Mehrotra from the Early Eocene differs in having alternate to opposite secondary veins and intersecondary veins. However, our new species is characterised by alternate secondary veins and the absence of intersecondary veins. Two Chinese species, i.e. *Uvaria lincangensis* Tao and Chen (Tao 2000) of the Late Miocene and *U. yunnanensis* Li (EGCFC 1978) of the Oligocene, differ from our fossil specimen mainly in having an oblong-lanceolate and a narrow elliptic shape, respectively. Because the present fossil is different from any previously described fossil leaves of *Uvaria*, it is assigned a new specific epithet, i.e. *Uvaria neograndiflora* Khan, Bera M et Bera S, sp. nov.

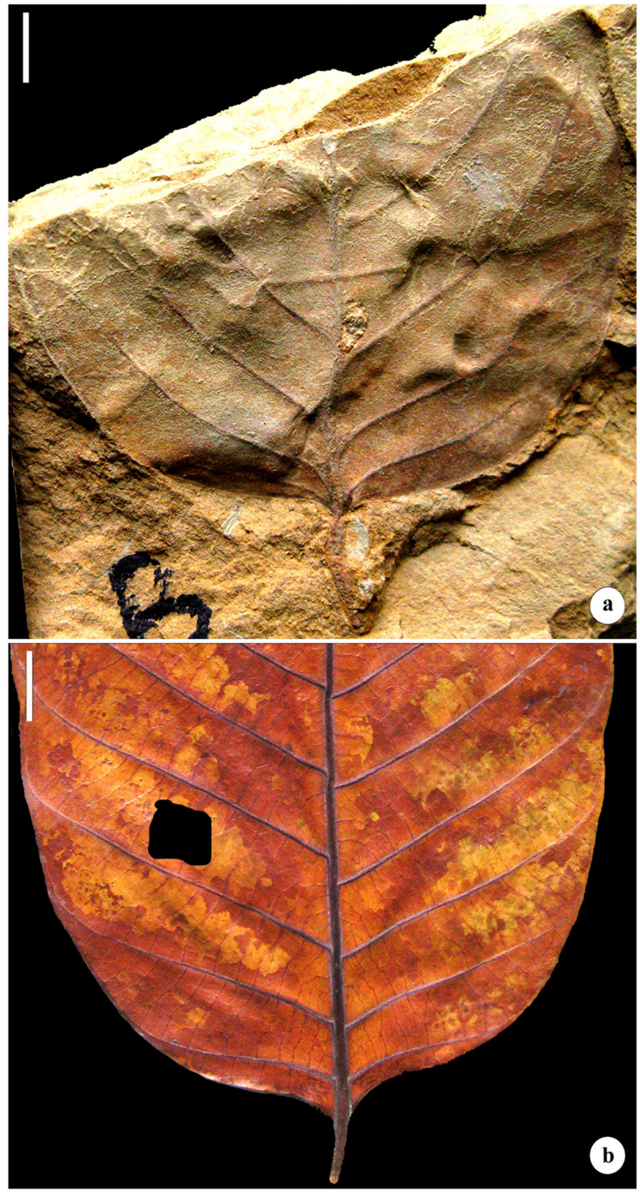

Fig. 11 **a** *Neolamarckia paleocadamba* Khan, Bera M et Bera S, sp. nov.—fossil leaf (CUH/PPL/B/1A$_1$). **b** *Neolamarckia cadamba*—modern leaf with similar shape, base, and venation pattern (scale = 1 cm)

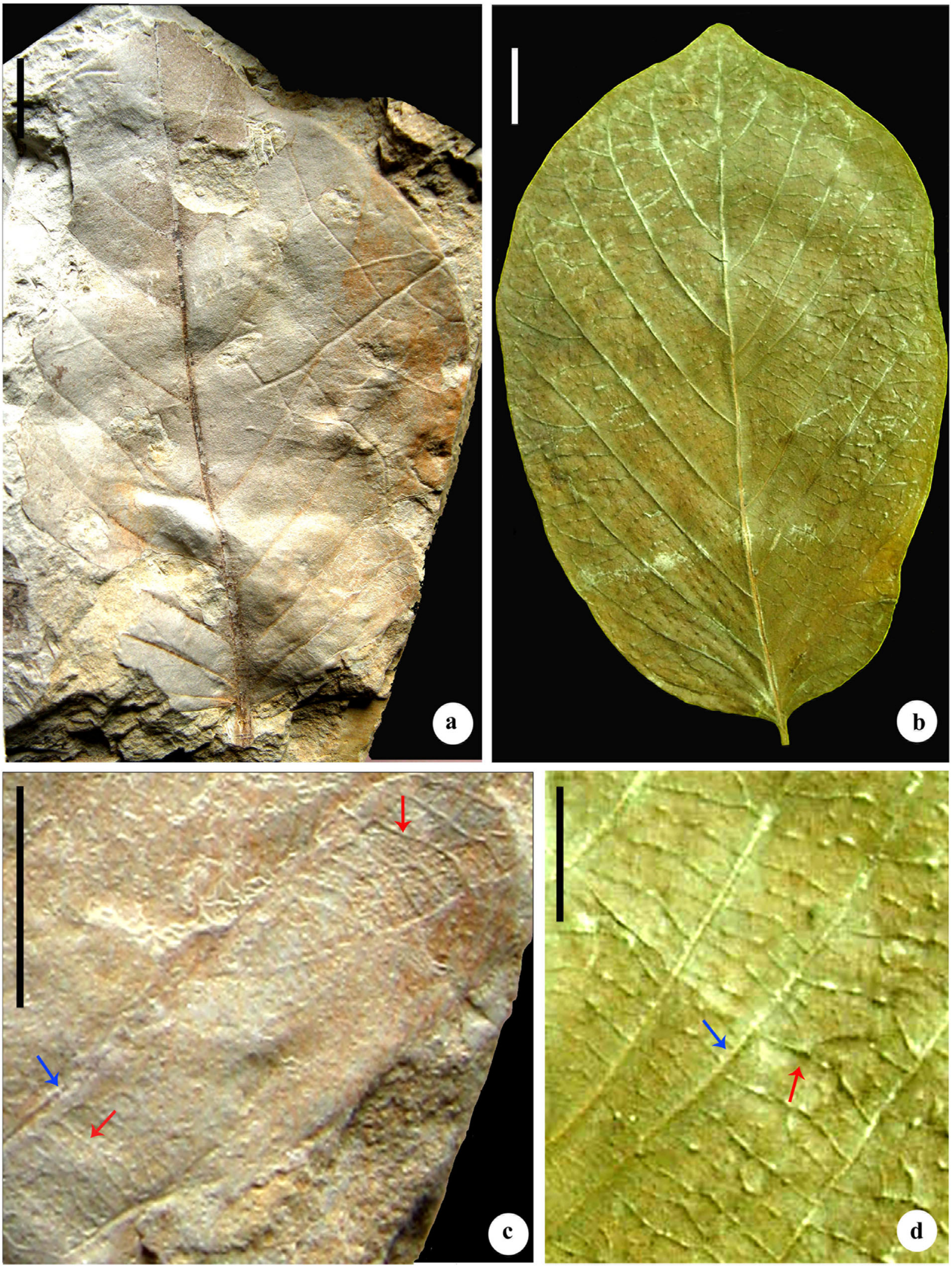

Fig. 12 **a** *Mitragyna tertiara* Konomatsu and Awasthi—fossil leaf (specimen no. CUH/PPL/B/52). **b** *Mitragyna parvifolia* (Roxb.) Korth.—modern leaf with similar apex, base, and venation pattern. **c** *Mitragyna tertiara*—a part of the fossil leaf magnified to show details of secondary (marked by blue arrow) and tertiary venation (marked by red arrows). **d** *Mitragyna parvifolia*—a part of the modern leaf magnified to show similar secondary (marked by blue arrow) and tertiary (marked by red arrow) venation pattern (scale = 1 cm)

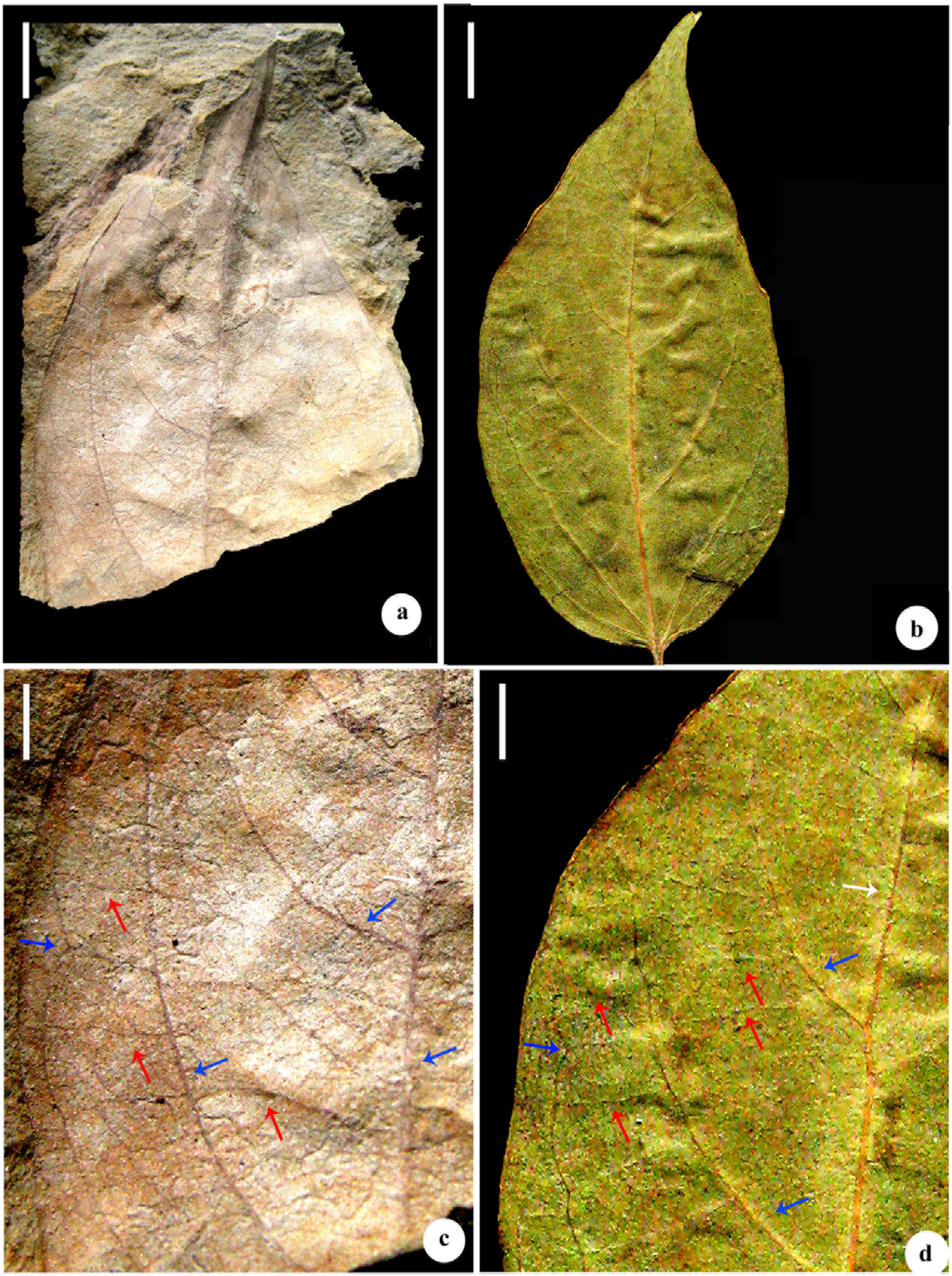

Fig. 13 **a** *Premna pliobengalensis* Khan, Bera M et Bera S, sp. nov.—fossil leaf (holotype CUH/PPL/B/36A). **b** *Premna bengalensis* Clarke—modern leaf with similar shape, apex, and venation pattern. **c** *Premna pliobengalensis*—a part of the fossil leaf magnified to show details of primary (marked by white arrow), secondary (marked by blue arrows), and tertiary venation (marked by red arrows). **d** *Premna bengalensis*—a part of the modern leaf magnified to show similar primary (marked by white arrow), secondary (marked by blue arrows), and tertiary (marked by red arrows) venation pattern (scale = 1 cm)

Family Lauraceae Juss.
Genus *Beilschmiedia* Nees

Species *Beilschmiedia plioroxburghiana* Khan, Bera M et Bera S, sp. nov. (Fig. 3a, c)

Holotype: CUH/PPL/B/66
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng district (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession (Subansiri Formation: Pliocene).

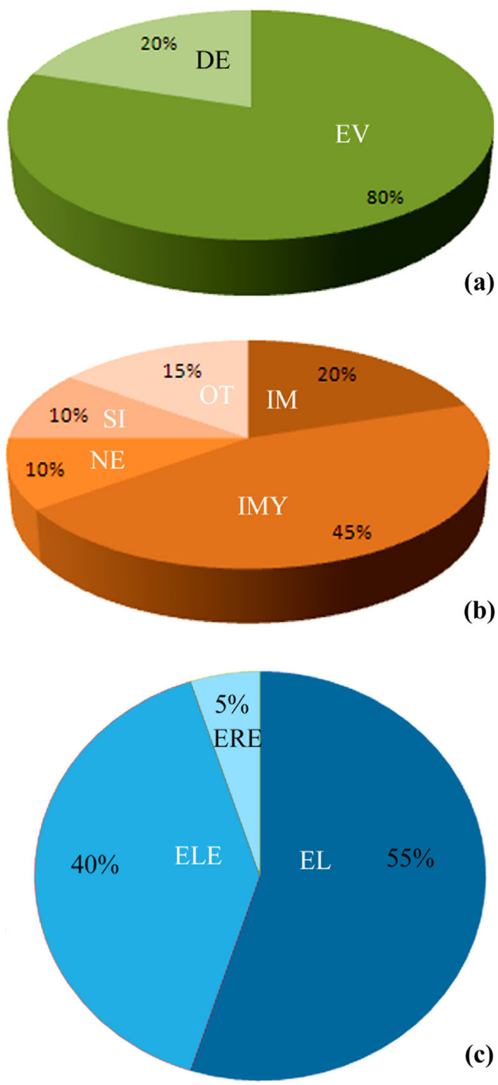

Fig. 14 **a** Diagrammatic representation of different types of forest elements of middle Siwalik (Pliocene) flora of Arunachal Pradesh (DE, deciduous; EV, evergreen). **b** Diagrammatic representation of Middle Siwalik (Pliocene) flora of Arunachal foothill represented in the present-day flora of different geographical regions (NE, Northeast India; SI, South India; IMY, India and Myanmar; IM, India and Malaya Peninsula; OT, Others). **c** Diagrammatic representation of Pliocene flora of Arunachal sub-Himalaya in three different categories (EL, extant local taxa; ELE, extant but locally extinct taxa; ERE, extant but regionally extinct taxa)

Etymology: Adding the prefix “plio” to the modern comparable specific epithet *roxburghiana* derives the specific name.
Diagnosis: Leaf symmetrical, elliptic; preserved lamina length 12 cm and width 5.2 cm; apex acute; base acute; margin entire; texture coriaceous.

Venation pinnate, eucamptodromous to brochidodromous; primary vein single, prominent, more or less straight, stout; secondary veins (2°) six visible, anastomosing near margin, 0.8–1.2 cm apart, usually alternate, angle of divergence acute (about 50°–60°), moderate, thick, uniformly curved up, and joined to superadjacent secondary at a nearly obtuse angle, usually unbranched; intersecondary veins present, simple, abundant; tertiary veins (3°) fine, predominantly orthogonal reticulate, occasional percurrent, almost straight, sometimes branched, oblique in relation to midvein, predominantly alternate and close; quaternary veins (4°) fine, orthogonal reticulate.

Remarks: The diagnostic features of this fossil leaf, such as the elliptic shape, acute apex and base, entire margin, eucamptodromous to nearly brochidodromous venation pattern, presence of intersecondary veins, and the acute angle of divergence of 2° veins curved towards the margin, suggest its affinity with modern leaves of family Lauraceae. In order to compare and find out the nearest generic affinity of the present fossil leaf, several modern genera of Lauraceae were examined. The fossil specimen shows resemblance with the extant leaves of five genera of Lauraceae such as *Phoebe* Nees, *Actinodaphne* Nees, *Beilschmiedia* Nees, *Litsea* Lam., and *Persea* Mill. Leaves of some species of *Phoebe* show fairly good resemblance with the fossil leaf but the secondaries in *Phoebe* run more or less straight towards the margin and in the fossil specimen they are more curved. *Actinodaphne* and *Persea* differ in having relatively more sparsely arranged secondary veins. However, *Litsea* differs in having relatively more sparsely arranged tertiary veins. On critical examination, it was found that the fossil shows better resemblance with the leaves of *Beilschmiedia*.

In order to find out specific affinity, herbarium sheets of all the available species of this genus were critically examined and it was found that four species of *Beilschmiedia* come close to the fossil, viz., *B. cylindrica* S. K. Lee and Y. T. Wei; *B. delicata* S. K. Lee and Y. T. Wei; *B. robusta* C. K. Allen, J. Arnold and *B. roxburghiana* Nees. The base in *B. delicata* and *B. robusta* is cuneate; whereas in the fossil specimen, it is acute. *B. cylindrica* differs in having obovate leaf blade. On the basis of leaf morphology (size, shape, nature of apex and base, texture, and venation pattern), *B. roxburghiana* Nees (C. N. Herbarium Sheet No. 371857) shows the closest resemblance to the fossil specimen (Fig. 3b, d). It is worth noting that *Beilschmiedia* has not been recorded previously from the Cenozoic sediments of India.

Table 3 Physiognomic characteristics of the fossil flora recovered from the middle part of the Siwalik sediments (Pliocene) of Arunachal Pradesh [*U*, unlobed; *E*, entire; *P*, present; *A*, absent; *N*, normal; −, indistinct; *CH*, chartaceous; *CO*, coriaceous; *A*, acute; *O*, obtuse; *CU*, cuneate; *R*, round; *S*, simple; *C*, compound; *C*, close; *D*, distant; *C-D*, close-distant; *OV*, ovate; *OBV*, obovate; *E*, elliptic; *M II*, microphyll II; *M III*, microphyll III; *ME I*, mesophyll I; *ME II*, mesophyll II; *ME III*, mesophyll III; leaf sizes are from the CLAMP analysis (Wolfe 1993)]

Physiognomic characteristics										
Fossil taxa	Lamina	Size	Margin	Drip tip	Nature of petiole	Texture	Base	Organization	Venation pattern	Shape
Uvaria neograndiflora	U	ME I	E	P	–	CH	–	S	C	E
Persea mioparviflora	U	M III	E	A	–	CO	A	S	D	E
Persea preglaucescens	U	M III	E	–	–	CO	A	S	D	E
Lindera neobifaria	U	M III	E	P	–	CH	A	S	D	E
Beilschmiedia plioroxburghiana	U	ME III	E	A	–	CO	A	S	C	E
Bauhinia siwalika	U	ME I	E	–	–	CO	Cordate	C	D	OBV
Callerya precinerea	U	ME II	E	P	–	CH	O	C	C-D	E
Calophyllum suraikholaensis	U	M III	E	–	–	CH	A	S	C	E
Calophyllum siwalikum	U	M III	E	A	–	CH	CU	S	C	E
Glochidion palaeogamblei	U	M II	E	P	–	CH	A	S	D	E
Glochidion siwalika	U	M III	E	A	N	CO	R	S	D	OV
Lagerstroemia jamraniensis	U	ME III	E	–	–	CO	–	S	C	E
Sorindeia subansiriensis	U	ME I	E	–	–	CO	–	C	C-D	E
Shorea siwalika	U	ME I	E	–	–	CH	–	S	D	E
Shorea pliotumbuggaia	U	M III	E	A	N	CO	O	S	D	E
Neolamarckia paleocadamba	U	ME III	E	P	N	CH	A	S	D	E
Mitragyna tertiara	U	ME I	E	A	N	CH	O	S	C-D	OBV
Premna pliobengalensis	U	ME I	E	P	–	CH	–	S	C	E

Family Fabaceae Lindl.
Genus *Callerya* Endl.

Species *Callerya precinerea* Khan, Bera M et Bera S, sp. nov. (Fig. 4a, c)

Holotype: CUH/PPL/B/50
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng district (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession (Subansiri Formation: Pliocene).

Etymology: Adding the prefix "pre" to the modern comparable specific epithet *cinerea* derives the specific name.
Diagnosis: Leaf blade simple, symmetrical, elliptic; preserved lamina length 6.2 cm and width 4.1 cm; apex acuminate; base obtuse; margin entire; texture chartaceous.

Venation pinnate, simple, eucamptodromous to nearly brochidodromous; primary vein prominent, more or less straight, stout; secondary veins 12 pairs, alternate to sub-opposite, unbranched, 0.9–1.5 cm apart, uniformly curved up and joined to their superadjacent secondary, sometimes forming loop in the apical portion, angle of divergence acute, moderate (60°), alternate to sub-opposite, unbranched; tertiary veins (3°) fine, percurrent, the tertiaries arise from midrib looking like intersecondary veins but they join the secondary veins arising below them; sometimes branched, oblique to right angle in relation to midvein, predominately alternate and close to distant. Further higher venation details could not be seen.

Remarks: The diagnostic features of this fossil leaf blade, such as the elliptic shape, acuminate apex, obtuse base, entire margin, eucamptodromous to nearly brochidodromous venation pattern, and acute angle of divergence of 2° veins curved towards the margin, suggest its close resemblance to modern leaves of Fabaceae. In the details of leaf architecture, the Siwalik leaf blade shows close resemblance with the modern leaves of *Callerya*. In order to find out specific affinity, the herbarium sheets of all the available species (*C. atropurpurea* (Wall) Schot, *C. cineria* Benth., *C. speciosa* (Champ.) Schot) of this genus were critically examined and it was concluded that the modern leaves of *Callerya cineria* Benth. (C. N. Herbarium Sheet No. 112599) (Fig. 4b, d) show the closest similarity with the fossil leaf in shape, size, and venation pattern. *C. speciosa* differs in having acute apex and round base as compared with the acuminate apex and obtuse base in the fossil specimen, while *C. atropurpurea* differs in having an obtuse apex.

As far as the authors are aware, no fossil specimen showing affinities to the leaves of *Callerya* has so far been described from the Cenozoic sediments of India and this is the first record of *Callerya* from this region.

Family Phyllanthaceae Martynov
Genus *Glochidion* J. R. Forst. and G. Forst.

Species *Glochidion siwalikum* Khan, Bera M et Bera S, sp. nov. (Fig. 5a, c)

Holotype: CUH/PPL/B/64
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng District (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession of sediments (Subansiri Formation: Pliocene).
Etymology: The Latin epithet "*siwalikum*" is chosen in reference to the Siwalik deposits from where fossil leaves were recovered.
Diagnosis: Leaf simple, asymmetrical, ovate; preserved lamina length 6.9 cm and maximum width 4.8 cm; apex acute; base round; margin entire; texture coriaceous; 0.4 cm of petiole preserved, but incomplete.

Venation pinnate, simple, eucamptodromous; primary vein prominent, stout, almost straight; six pairs of secondary veins visible, alternate, 0.6–1 cm apart; gradually curved angle of divergence acute (about 50°), moderately thick, unbranched; tertiary veins percurrent, straight to sinuous, branched, oblique in relation to midvein, predominantly alternate and close; further high order venation not preserved.
Remarks: The characteristic features of the present fossil leaf such as its asymmetry, ovate shape, acute apex, round base, eucamptodromous venation, acute angle of divergence of secondary veins, and percurrent tertiary veins indicate that the present fossil belongs to the family Phylanthaceae. After the critical examination of a large number of herbarium sheets of different genera (*Phyllanthus* L.; *Cleistanthus* Hook. F. ex Planch.; *Aporosa* Blume; *Glochidion* Forst.; *Uapaca* Baill.; *Bridelia* Willd. etc.) of Phylanthaceae, it has been concluded that the extant leaves of *Glochidion* show closest similarity with the present fossil leaf. Herbarium sheets of all the available species (*G. zeylanicum* (Gaertn.) A. Juss., *G. benguetense* Elmer, *G. multiloculare* (Rottler ex Willd.) Voigt, *G. oblatum* Hook. f., *G. chlorophaes* Baill., *G. hirsutum* Muell. Arg., *G. daltonii* (M ll. Arg.) Kurz) of this genus have been studied in order to determine the nearest affinity of the fossil leaf and the present fossil shows closest similarity in shape, size, apex, and venation pattern with the extant leaf of *G. zeylanicum* (Gaertn.) A. Juss. (C. N. Herbarium Sheet No. 403357) (Figs. 5b and 6a). Both *G. chlorophaes* and *G. hirsutum* differ in having an obtuse base. However, *G. oblatum*, *G. multiloculare*, *G. benguetense*, and *G. daltonii* are different in having an acuminate to attenuate apex. *G. oblatum* also differs from the fossil specimen in having an elliptic laminar shape.

Three fossil leaves resembling the genus *Glochidion* have been reported so far from the Siwalik sediments of India, i.e. *Glochidion miocenica* Prasad 1994 (similarity with modern leaf *Glochidion chlorophaes* Baill.) known earlier from the Middle Miocene sediments of the Kathgodam area in the Himalayan foothills of Uttar Pradesh; *Glochidion palaeohirsutum* Antal and Prasad 1996 (similar to the modern leaf *Glochidion hirsutum* Muell. Arg.) known from Siwalik sediments of the Oodlabari assemblage, Darjeeling and *Glochidion palaeogamblei* Khan and Bera 2012 (similar to the modern leaf *Glochidion gamblei* Hook. f.) known from Siwalik sediments of the Arunachal sub-Himalaya. Both *Glochidion miocenica* and *Glochidion palaeohirsutum* differ from our specimen in having an obtuse base, while *Glochidion palaeogamblei* is different in having an attenuate apex. So, a new name *Glochidion siwalikum* is proposed here for the presently described fossil leaf.

Family Anacardiaceae (R.Br.) Lindl.
Genus *Sorindeia* Thouars

Species *Sorindeia subansiriensis* Khan, Bera M et Bera S, sp. nov. (Fig. 8a, c)

Holotype: CUH/PPL/B/70
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng District (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession (Subansiri Formation: Pliocene).
Etymology: The Latin epithet "*subansiriensis*" is chosen in reference to the Subansiri Formation from where fossil leaves were recovered.
Diagnosis: Leaf simple, asymmetrical; elliptic, maximum lamina length 7.5 cm and maximum width 4.8 cm; apex acuminate; base not observed; margin entire; texture coriaceous.

Venation pinnate, eucamptodromous-brochidodromous; primary vein single, prominent, straight, stout; secondary veins 0.8 to 1.2 cm apart, about 8 pairs preserved, mostly alternate, angle of divergence acute, less than 45°; intersecondary veins present; tertiary veins percurrent, simple, oblique; further venation orders not clearly seen.
Remarks: The characteristic features of the present fossil leaf are asymmetry with an elliptical shape, entire margin, eucamptodromous-brochidodromous venation, secondary veins arising at acute angle, the presence of intersecondary veins and percurrent tertiary veins. These features collectively indicate its affinity with modern leaves of the family Anacardiaceae. In order to compare and find the nearest generic affinity of the present fossil leaf, eight available modern genera (*Sorindeia* Thouars, *Mangifera* L., *Anacardium* L., *Rhus* L., *Bouea* Meisner, *Gluta* (L.) Ding Hou, *Drimycarpus* Hook. f., and *Semecarpus* L.) of Anacardiaceae were examined. *Mangifera*, *Drimycarpus*, and *Semecarpus* differ in having a comparatively larger size of lamina. *Anacardium* differs in having an obovate shape as compared to the elliptical shape in our fossil specimen. It also differs from our Siwalik fossil in having a round apex. *Gluta* differs in having an acute apex. On

the other hand, *Bouea* and *Rhus* differ from the fossil specimen by having relatively more closely arranged secondary veins. The fossil specimen shows the best resemblance in almost all the morphological characters with *Sorindeia*, especially *S. madagascariensis* Thouars ex DC. (C. N. Herbarium Sheet No. 98688) (Fig. 8b, c). This genus is endemic to Africa and is not found in the present-day vegetation of India or Asia. This is the first record of a *Sorindeia* fossil leaf from the Cenozoic sediments of India.

Family Rubiacae Juss.
Genus *Neolamarckia* Bosser

Species *Neolamarckia pliocadamba* Khan, Bera M et Bera S, sp. nov.
(Figs. 9a, 10a, and 11a)

Holotype: CUH/PPL/B/1A
Additional specimen examined: CUH/PPL/B/1A$_1$
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng District (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession (Subansiri Formation: Pliocene).
Etymology: Adding the prefix “plio” to the modern comparable specific epithet *cadamba* derives the specific name.
Diagnosis: Leaf simple, preserved specimen almost symmetrical, broad elliptic; preserved lamina length 7–14 cm and maximum width 7–10 cm; apex acuminate; petiole 1.3 cm in length; base in one specimen well preserved, acute; margin entire; texture chartaceous.

Venation pinnate, simple, craspedodromous type; primary vein prominent, straight, stout; secondary veins 8 pairs visible, angle of divergence acute to moderate (45°–65°), more acute one side of the leaf than on the other side of the leaf, alternate, 1–2.9 cm apart, curving uniformly; both inter-secondary and intramarginal veins absent; tertiary veins percurrent, mostly simple, relationship with midvein oblique, constant, predominantly alternate, and closely spaced. Further venation not well preserved.

Remarks: The aforesaid diagnostic features of the preserved fossil leaf impressions such as broad elliptic shape, acuminate apex, acute base, entire margin, uniformly curved secondaries, percurrent tertiary veins and absence of intersecondary and intramarginal veins collectively suggest their resemblance with the modern leaves of the family Rubiaceae. These features are found commonly in the three genera viz., *Mussaenda* L., *Randia* L. and *Neolamarckia* Bosser., of this family. Critical examination of the herbarium sheets of these genera and the present fossils revealed that the leaves of *Mussaenda* and *Randia* differ in having narrow elliptic laminae. The genus *Neolamarckia* comes closest to the present fossils. Further, in order to find out the nearest species, a number of herbarium sheets of two available species viz. *Neolamarckia cadamba* (Roxb.) Bosser and *Neolamarckia macrophylla* (Roxb.) Bosser were studied in detail and we concluded that the leaves of *N. cadamba* resemble the present fossil leaves in shape, size, and venation pattern (Figs. 10b and 11b). *N. macrophylla* differs from the fossil specimen by having opposite arrangement of secondary veins.

In earlier work, the generic name *Neolamarckia* was taxonomically treated as *Anthocephalus*. So far, only one fossil leaf of this genus, *Anthocephalus siwalika* Prasad and Awasthi 1996 (similar to *A. macrophyllus* Havil.) has been reported from the lower Siwalik sediments of Surai Khola, western Nepal. Because our fossil leaf shows dissimilarity to the fossil leaf of Nepal in size, shape, and venation pattern, we assign it to a new species *Neolamarckia pliocadamba* Khan, Bera M et Bera S, sp. nov.

Family Lamiaceae Martinov
Genus *Premna* L.

Species *Premna pliobengalensis* Khan, Bera M et Bera S, sp. nov.
(Fig. 13a, c)

Holotype: CUH/PPL/B/36
Type locality: Road cuttings along the Bhalukpong-Tawang road of West Kameng District (27.50706° N, 92.64259° E).
Type stratum: Middle part of the Siwalik succession (Subansiri Formation: Pliocene).
Etymology: Adding the prefix “plio” to the modern comparable specific epithet *bengalensis* derives the specific name.
Diagnosis: Leaf simple; nearly complete, except the basal portion, almost symmetrical; 5.1 cm long and 3.6 cm broad at the widest part; shape elliptic; margin entire; apex acuminate; petiole not preserved; texture smooth and chartaceous.

Venation pinnate, camptodromous–eucamptodromous type; primary vein moderate, markedly curved; 4–5 pairs secondary veins, alternate, angle of divergence of secondaries acute to moderate (45°–60°), in lower side more acute than upper, uniformly curved, unbranched, 0.6–1.1 cm apart; intersecondary veins simple; tertiary veins percurrent and forked, almost straight, oblique in relation to midvein, predominantly alternate and close; quaternary veins thin, poorly preserved, relatively randomly oriented.

Remarks: In possessing an elliptic shape, acuminate apex, entire margin, camptodromous to eucamptodromous venation, alternate, uniformly curved secondary veins, and percurrent tertiary veins the present leaf impressions resemble closely with the modern leaves of the family Lamiaceae. A critical examination of the herbarium sheets of available four genera viz., *Callicarpa* L., *Premna* L., *Gmelina* L., and *Tectona* L. f., of this family suggests that the leaves of *Premna* L. have nearest affinity with the fossil leaf. *Callicarpa* L. and *Tectona* L. f. differ in having a comparatively larger lamina size. However, *Gmelina* differs in having an ovate shape as compared to the elliptical shape in the fossil specimen. In order to find out specific affinity, the herbarium sheets all the available species (*Premna bengalensis* Clarke, *Premna punduana* Wall. ex Schauer, *Premna latifolia* Roxb.)

of this genus were critically examined and it was concluded that the leaves of *Premna bengalensis* Clarke (C. N. Herbarium Sheet No. 348042) show the closest similarity with the fossil leaf in shape, size, and venation pattern (Fig. 13b, d). In *P. punduana*, the secondary veins run more or less straight towards the margin, but in the fossil specimen they are more curved. *P. punduana* also differs in having a comparatively larger size of lamina. *P. latifolia* differs in having lanceolate-ovate and elliptic-ovate leaf blade.

As far as the authors are aware, there is only one fossil record of the genus *Premna* Linn., i.e. *Premna latifolia* (Singh and Prasad 2007) from the Late Tertiary sediments of the Mahuadnar Valley, Jharkhand. The present fossil leaf shows dissimilarity to the fossil leaf *Premna latifolia* Singh and Prasad 2007 in size and venation pattern. In our Siwalik specimen, the angle of divergence of secondaries is more acute in lower side than upper, whereas in *Premna latifolia* it is more acute in upper side than lower. It is therefore described as a new species *Premna pliobengalensis*.

Discussion

Here, we describe well-preserved leaf impressions from the middle part of the Siwalik sediments (Pliocene: Subansiri Formation) of Arunachal sub-Himalaya for the first time enhancing our knowledge of the flora during Siwalik (Pliocene) sedimentation. The fossil flora consists of a wide range of mostly woody plants represented by 20 species belonging to 11 families (Table 2). Lauraceae, represented by 4 species, is the most dominant family followed by Dipterocarpacae (three species in one genus), Fabaceae (two species in two genera), Anacardiaceae (two species in two genera), Rubiaceae (two species in two genera), Calophyllaceae (two species in one genus), and Phyllanthaceae (two species and one genus). Among the fossil species, seven species are new to the Neogene floras of Indian subcontinent. It is to be noted that almost all proposed new species are made here on the basis of single specimens (with part and counterparts) for their completeness and good preservation.

Palaeoclimate and palaeoecology

Here, we follow the principle of "Uniformity in the order of Nature," i.e. the physical and biological processes must have been the same in the past as in today's environment and vegetation (Cain 1944). One approach to the study of the palaeoclimate or palaeoecology of a particular area, particularly useful for Neogene material, is to compare the composition of fossil floras with that of modern vegetation for which the existing climatic conditions are known (Cain 1944; Mosbrugger and Utescher 1997). It is rather difficult to deduce the precise palaeoecology of an area prior to the Cenozoic period, because the modern vegetation is quite different from those of earlier periods. As the plant megafossils in our study belong to the Pliocene time and their NLRs (nearest living relatives) still exist in the forests of different geographical regions today, the general climate, topography, ecological peculiarities, distribution pattern, and type of forest complex during the Siwalik sedimentation of the Arunachal sub-Himalaya can be deduced with confidence. The other reliable approach for deducing palaeoclimate is the relationship that exists between leaf physiognomic characters of plant fossils and climate (Kovach and Spicer 1996; Herman and Spicer 1996; Wolfe and Spicer 1999; Jacobs 2002; Yang et al. 2015). Because the fossils in the present study are exclusively leaf impressions, this approach plays an important role in interpreting the palaeoclimate and palaeoecology because it is independent of systematic relationships of the species and errors in taxonomic assignment reducing considerably errors in palaeoecological and climate data interpretation (Wolfe and Spicer 1999).

The NLR method extrapolates known climatic requirement of modern taxa with the comparable and related taxa in the past (Axelrod and Bailey 1969; Hickey 1977). This method presupposes that fossil plants and their modern relatives share similar physiological requirements for climate (Mosbrugger and Utescher 1997). On the basis of NLRs, the floral assemblage of middle part of Siwalik succession consists of two major forest elements: (1) evergreen and (2) deciduous (Fig. 14a). In the Arunachal middle Siwalik assemblage, 80% of the taxa are evergreen including *Thelypteridaceophylum*, *Persea mioparviflora*, *Persea preglaucescens*, *Lindera neobifaria*, *Beilschmiedia plioroxburghiana*, *Shorea siwalika*, *Bauhinia siwalika*, *Callerya precinerea*, *Calophyllum suraikholaensis*, *Calophyllum siwalikum*, *Neolamarckia paleocadamba*, *Sorindeia subansiriensis*, *Glochidion palaeogamblei*, *Glochidion siwalika*, *Premna pliobengalensis*, and *Uvaria neograndiflora*. Deciduous elements of the ancient forests make up just 20% of the taxa including *Shorea pliotumbuggaia*, *Shorea bhalukpongensis*, *Mitragyna tertiara*, and *Lagerstroemia jamraniensis*. Thus, analysis of fossil floral assemblages with respect to the present-day distribution pattern of modern equivalent taxa (Table 2) suggests that wet evergreen type forests occurred in the area during the period of deposition, in contrast to the semi-evergreen vegetation occurring today in this area (Hazra et al. 1996). The dominance of evergreen elements in the assemblage indicates the prevalence of tropical, warm, and humid climate with abundant rainfall in contrast to relatively dry present-day climate in the area.

The physiognomic features of woody dicot leaves such as size, venation, density, texture, margin, shape, and nature of leaf tip, etc., have a close relationship with climate (Wolfe 1993; Wolfe and Spicer 1999; Yang et al. 2015); and when such features are recorded in fossil leaf impressions, this relationship provides reliable data on climatic conditions prevailing at the time of sedimentation. Drip tips, an extended leaf tip, are an important physiognomic feature of angiosperm leaves in wet tropical forests (Dorf 1969). Interestingly, 35% of the taxa in the Subansiri assemblage (such as *Lindera neobifaria*, *Callerya precinerea*, *Neolamarckia paleocadamba*, *Mitragyna tertiara*, *Glochidion palaeogamblei*, *Premna pliobengalensis*, and *Uvaria neograndiflora*) possess conspicuous drip tips, suggestive of a tropical humid climate during Siwalik sedimentation (Table 3). Considering all physiognomic data (e.g. all species having entire margined leaves; most taxa possessing large leaf sizes, i.e. mesophyll type leaves; Table 3) suggests that during Pliocene time the Himalayan foothills in Arunachal Pradesh enjoyed a tropical, warm, and humid climate with plenty of rainfall.

The aforesaid qualitative data are also consistent with our previously published quantitative climate data (Khan et al. 2014) using foliar physiognomic analysis. CLAMP (Climate Leaf Analysis Multivariate Program) analysis (Wolfe 1993; Teodoridis et al. 2011; Yang et al. 2011) on fossil leaf morphotypes (i.e. not assigned taxonomic affiliation) from the Arunachal middle Siwalik (Pliocene) indicated a MAT (mean annual temperature) of 23.6 °C ± 2.8 °C; a CMMT (cold month mean temperature), 16.9 °C ± 4 °C; a WMMT (warm month mean temperature), 28.1 °C ± 3.3 °C; a GSP (growing season precipitation), 198.1 ± 92 cm (Khan et al. 2014). The ratio of the precipitation in the three wettest months to the three driest months for the middle Siwalik samples is > 6:1 which defines them as monsoonal (Lau and Yang 1997; Zhang and Wang 2008). However, present-day ratio for that region is > 120:1 based on the same gridded dataset that was used to calibrate CLAMP. Although several methods have been used to measure the strength of the monsoon (Liu and Yin 2002; Liu et al. 2011; van Dam 2006), here we used the monsoon index (MSI) of Xing et al. (2012) because their MSI can be derived from the climate variables made by CLAMP analysis using the following expression: $\mathrm{MSI} = (3\mathrm{WET} - 3\mathrm{DRY}) \times 100/\mathrm{GSP}$. The higher MSI value, the more different the precipitation between the wet and dry seasons. When this equation is applied to the Arunachal middle Siwalik flora, the MSI value comes to 43.2 while that of the modern MSI is 54.7. So, during Pliocene time, the monsoon in the Arunachal area was slightly weaker than now.

Phytogeography

Phytogeography, an important aspect of palaeobotany, deals with the study of a fossil flora to know the past distribution and migration of taxa especially during the Cenozoic (Bande and Prakash 1986). During the predominantly Neogene orogenic uplift of the Himalaya, significant changes occurred in regional physiography, environment, and floral characteristics (Ding et al. 2017). As a result, organisms which could not adapt to the new environment gradually perished and new plants and animals replaced them and flourished.

The present-day distribution of the modern relatives of the 20 fossil taxa recovered from the middle part of the Siwalik sediments (Pliocene: Subansiri Formation) of Arunachal sub-Himalaya indicates that they grow in different geographical regions all over India and other adjoining countries (Table 2; Fig. 14b). In India, they are distributed mostly in northeastern and southern regions. In this middle Siwalik assemblage, the modern equivalents of four taxa (20%) including *Beilschmiedia roxburghiana*, *Persea parviflora*, *Uvaria grandiflora*, and *Glochidion zeylanicum* occur both in India and the Malaya Peninsula; and nine taxa (45%) including *Persea glaucescens*, *Lindera bifaria*, *Calophyllum polyanthum*, *Calophyllum inophyllum*, *Neolamarckia cadamba*, *Glochidion gamblei*, *Callerya cinerea*, *Lagerstroemia speciosa*, and *Mitragyna parvifolia* are found to grow both in India and Myanmar (Fig. 14b). This clearly indicates a free exchange of floral elements during Neogene time across southern Asia.

It is interesting to note that *Calophyllum polyanthum* is still distributed in Arunachal Pradesh, while *C. inophyllum* is conspicuously absent from the entire northeastern region of India, including Arunachal sub-Himalaya. This is possibly due to the different adaptability of these two species to changing ecoclimatic conditions. *Calophyllum inophyllum* is a littoral species growing on the Indian west coast around Mumbai and on the east coast from Orissa southwards, as well as the Andaman Islands and Myanmar (Tenasserim) (Pearson and Brown 1932; Brandis 1971). Distinct, but modest, elevation changes in the northeastern India area, possibly related to the Himalayan Orogeny since the Miocene, might have caused the disappearance of *C. inophyllum* from the entire eastern Himalaya and northeast Indian plains and a move to other littoral/coastal and swampy forests of India.

Based on the thorough survey of the recovered fossil taxa and the present-day distribution of their NLRs, we also categorized the Pliocene taxa of Arunachal sub-Himalaya into three types: extant local taxa (55%), extant but locally extinct taxa (40%), and extant but regionally extinct taxa (5%) (Fig. 14c). Extant local taxa are those taxa which have their NLRs presently growing in or near the fossil locality. Extant but locally extinct taxa are those taxa which have their NLRs growing in other parts of India but do not occur in the present-day flora of fossil locality. Comparable modern forms of these taxa are *Shorea assamica*, *Shorea tumbuggaia*, *Persea parviflora*, *Callerya cinerea*, *Glochidion gamblei*, *Calophyllum inophyllum*, *Lindera bifaria*, and *Premna bengalensis*. It is presumed that significant changes in the climate and/or modest elevation changes after middle Siwalik time (Pliocene) might be a possible reason for the disappearance of these taxa from the present-day vegetation. However, they are presently growing in the other regions of India including northeast region due to availability of suitable climatic conditions. Extant but regionally extinct taxa are those taxa whose NLRs have disappeared from India and now grow in other parts of the world. By gradual changes in climate and physiography mainly caused by a general global cooling, the strong uplift of the Himalaya brought considerable alteration and diversification in floral patterns (Mehrotra et al. 2005). Some of the taxa could adapt to the changed circumstances or already had wide environmental tolerances and continued to flourish in the eastern Siwalik region, while others either suffered local extinction or migrated to suitable areas with tropical littoral and swampy conditions.

The fossil record of Fabaceae and Dipterocarpaceae, dominant families of the Pliocene assemblage, shows that they were abundant in India during Neogene time (Bande and Prakash 1986; Prasad and Awasthi 1996); whereas during the Paleogene, they were only occasionally represented (Bande and Prakash 1986; Khan et al. 2016). This indicates that these two tropical families might have entered India during the Neogene after the establishment of land connections with those land areas where they were flourishing during the Paleogene.

Conclusions

Considering both qualitative and quantitative climate data of the recovered leaf fossils, the overall floristic composition indicates the existence of tropical evergreen vegetation under warm and humid climate during the deposition of the Siwalik sediments (Pliocene) in the Arunachal sub-Himalaya. The present study also provides clear evidence of free exchange of some Southeast Asian elements across southern Asia in the Pliocene.

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Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

References

Agarwal, R. P., Srivastava, A. K., & Maithani, A. (1991). Geology of the eastern Himalayan foothill belt of Bhutan and Arunachal Pradesh: an overview. *Himalayan Geology, 2*(2), 197–205.

Anand-Prakash, & Singh, T. (2000). Nature, composition, rank (maturation) and depositional environment of Siwalik coals from Arunachal Himalaya. *Himalayan Geology, 21*(1 &2), 17–29.

Antal, J. S., & Awasthi, N. (1993). Fossil flora from the Himalayan foothills of Darjeeling district, West Bengal and its palaeoecological and phytogeographical significance. *Palaeobotanist, 42*(1), 14–60.

Antal, J. S., & Prasad, M. (1996). Some more leaf-impressions from the Himalayan foothills of Darjeeling District, West Bengal, India. *Palaeobotanist, 43*, 1–9.

Antal, J. S., & Prasad, M. (1998). Morphotaxonomic study of some more fossil leaves from the lower Siwalik sediments of West Bengal, India. *Palaeobotanist, 47*, 86–98.

APG IV. (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society, 181*, 1–20.

Awasthi, N., & Prasad, M. (1990). Siwalik plant fossils from Surai Khola area, western Nepal. *Palaeobotanist, 38*, 298–318.

Axelrod, D., & Bailey, H. P. (1969). Palaeotemperature analysis of Tertiary floras. *Palaeogeography, Palaeoclimatology, Palaeoecology, 6*, 163–195.

Bande, M. B., & Prakash, U. (1986). The Tertiary flora of Southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-Malayan region. *Review of Palaeobotany and Palynology, 49*, 203–233.

Bora, D. S., & Shukla, U. K. (2005). Petrofacies implication for the Lower Siwalik Foreland Basin evolution, Kumaun Himalaya, India. *Special Publication of the Palaeontological Society of India, 2*, 163–179.

Brandis, D. (1971). Indian trees. Bishen Singh, Mahenra Pal Singh, Deradun.

Cain, S. A. (1944). *Foundation of plant geography*. New York: Harper & Brother Co.

Chirouze, F., Dupont-Nivet, G., Huyghe, P., van der Beek, P., Chakraborti, T., Bernet, M., & Erens, V. (2012). Magnetostratigraphy of the Neogene Siwalik Group in the far eastern Himalaya: Kameng section, Arunachal Pradesh, India. *Journal of Asian Earth Science, 44*, 117–135.

Ding, L., Spicer, R. A., Yang, J., Xu, Q., Cai, F., Li, S., Lai, Q., Wang, H., Spicer, T. E. V., Yue, Y., Shukla, A., Srivastava, G., Khan, M. A., Bera, S., & Mehrotra, R. (2017). Quantifying the rise of the Himalaya orogen and implications for the South Asian monsoon. *Geology, 45*, 215–218.

Dorf, E. (1969). Palaeobotanical evidences of Mesozoic and Cenozoic climatic changes. *Proceedings of the North American, paleontological Convention*, pp. 323–346.

Editing Group of Cenozoic Flora of China (EGCFC). (1978). *Fossils of plant in China*. Beijing: Science Press.

Ellis, B., Daly, D. C., Hickey, L. J., Johnson, K. R., Mitchell, J. D., Wilf, P., & Wing, S. L. (2009). *Manual of leaf architecture*. Ithaca, NY: Cornell University Press.

Hazra, P. K., Verma, D. M., & Giri, G. S. (1996). Materials for the flora of Arunachal Pradesh. *Botanical Survey of India, 1*, 1–693.

Herman, A. B., & Spicer, R. A. (1996). Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. *Nature, 380*, 330–333.

Hickey, L. J. (1977). Stratigraphy and palaeobotany of the Golden valley Formation (Early Tertiary) of western North Dakota. *GSA Memoirs, 150*, 181.

Jacobs, B. F. (2002). Estimation of low-latitude paleoclimates using fossil angiosperm leaves: examples from the Miocene Tugen Hills, Kenya. *Paleobiology, 28*, 399–421.

Joshi, A., & Mehrotra, R. C. (2003). A thelypteridaceous fossil fern from the Lower Siwalik of the East Kameng District, Arunachal Pradesh, India. *Journal Geological Society of India, 61*, 483–486.

Joshi, A., Tewari, R., Mehrotra, R. C., Chakraborty, P. P., & De, A. (2003). Plant remains from the Upper Siwalik sediments of West Kameng District, Arunachal Pradesh. *Journal Geological Society of India, 61*, 319–324.

Karunakaran, C., & Ranga Rao, A. (1979). Status of exploration for hydrocarbons in Himalayan region—contributions to stratigraphy and structure. *Geological Survey of India Miscellaneous Publication, 4*(5), 1–66.

Khan, M., De, B., & Bera, S. (2007). A fossil fern-leaflet of family Thelypteridaceae from the Middle Siwalik sediments of West Kameng District, Arunachal Pradesh. *Journal of the Botanical Society of Bengal, 61*(1), 65–69.

Khan, M., De, B., & Bera, S. (2009). Leaf-impressions of *Calophyllum* L. from the Middle Siwalik sediments of Arunachal sub-Himalaya, India. *Pleione, 3*(1), 101–106.

Khan, M., Ghosh, R., Bera, S., Spicer, R. A., & Spicer, T. E. V. (2011). Floral diversity during Plio-Pleistocene Siwalik sedimentation (Kimin Formation) in Arunachal Pradesh, India, and its palaeoclimatic significance. *Palaeodiversity and Palaeoenvironments, 91*, 237–255.

Khan, M., & Bera, S. (2012). *Glochidion palaeogamblei* sp. nov.—a new fossil leaf of Euphorbiaceae from the Pliocene sediments of Arunachal Pradesh, eastern India and its palaeoclimatic significance. In S. Panda & C. Ghosh (Eds.), *Diversity and conservation of plants and traditional knowledge* (pp. 149–154). Bishen Singh Mahendra Pal Singh: Dehra Dun.

Khan, M. A., & Bera, S. (2014). New lauraceous species from the Siwalik forest of Arunachal Pradesh, eastern Himalaya, and their palaeoclimatic and palaeogeographic implications. *Turkish Journal of Botany, 38*, 453–464.

Khan, M. A., Spicer, R. A., Bera, S., Ghosh, R., Yang, J., Spicer, T. E. V., Guo, S., Su, T., Jacques, F., & Grote, P. J. (2014). Miocene to Pleistocene floras and climate of the eastern Himalayan Siwaliks, and new palaeoelevation estimates for the Namling-Oiyug Basin, Tibet. *Global and Planetary Change, 113*, 1–10.

Khan, M. A., Bera, S., Ghosh, R., Spicer, R. A., & Spicer, T. E. V. (2015). Leaf cuticular morphology of some angiosperm taxa from the Siwalik sediments (middle Miocene to lower Pleistocene) of Arunachal Pradesh, eastern Himalaya: systematic and palaeoclimatic implications. *Review of Palaeobotany and Palynology, 214*, 9–26.

Khan, M. A., Spicer, R. A., Spicer, T. E. V., & Bera, S. (2016). 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. *Review of Palaeobotany and Palynology, 233*, 236–254.

Khan, M. A., Spicer, R. A., Spicer, T. E. V., & Bera, S. (2017). Evidence for diversification of *Calophyllum* L. (Calophyllaceae) in the Neogene Siwalik forests of eastern Himalaya. *Plant Systematics and Evolution, 303*, 371–386.

Konomatsu, M., & Awasthi, N. (1999). Plant fossils from Arumg Khola and Binai Khola Formation of Churia Group (Siwalik), west-central Nepal and their palaeoecological and phytogeographical significance. *Palaeobotanist, 48*, 163–181.

Kovach, W. L., & Spicer, R. A. (1996). Canonical correspondence analysis of leaf physiognomy: a contribution to the development of a new palaeoclimatological tool. *Palaeoclimates, 2*, 125–138.

Kumar, G. (1997). *Geology of Arunachal Pradesh* (pp. 1–217). Bangalore: Geological Society of India.

Kumar, S., & Singh, T. (1982). Sandstone dykes in Siwalik sandstone-sedimentology and basin analysis—Subansiri District (NEFA), eastern Himalaya. *Sedimentary Geology, 33*, 217–236.

Kunte, S. V., Ganju, J. L., & Dutta, N. K. (1983). Geology and structure of the Tertiary belt between Bargang and Pachin Rivers, Arunachal Pradesh. *Geological Survey of India, Miscellaneous Publication., 43*, 124–129.

Lakhanpal, R. N., & Awasthi, N. (1984). A late Tertiary florule from near Bikhnathore in West Champaran District, Bihar. In: *Symposium on Evolutionary Botany and Biostratigraphy* (pp. 587–596). Prof. A. K. Ghosh Commemoration Volume.

Lau, K. M., & Yang, S. (1997). Climatology and interannual variability of the Southeast Asian summer monsoon. *Advances in Atmospheric Science, 14*, 141–162.

Liu, X., & Yin, Z.-Y. (2002). Sensitivity of East Asian monsoon climate to the uplift of the Tibetan Plateau. *Palaeogeography, Palaeoclimatology, Palaeoecology, 183*, 223–245.

Liu, Y.-S., Utescher, T., Zhou, Z.-K., & Sun, B.-N. (2011). The evolution of Miocene climates in North China: preliminary results of quantitative reconstructions from plant fossil records. *Palaeogeography, Palaeoclimatology, Palaeoecology, 304*, 308–317.

Mehrotra, R. C., Liu, X. Q., Li, C. S., Wang, Y. F., & Chauhan, M. S. (2005). Comparison of the Tertiary flora of Southwest China and Northeast India and its significance in the antiquity of the modern Himalayan flora. *Review of Palaeobotany and Palynology, 135*, 145–163.

Mosbrugger, V., & Utescher, T. (1997). The coexistence approach—a method for quantitative reconstructions of Tertiary terrestrial palaeoclimatic data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology, 134*, 61–86.

Pearson, R. S., & Brown, H. P. (1932). *Commercial timbers of India. 1 & 2*. Government of India: Central Publication Branch, Calcutta.

Parkash, B., Sharma, R. P., & Roy, A. K. (1980). The Siwalik group (Molasse) sediments shed by collision of continental plates. *Sedimentary Geology, 25*, 127–159.

Prasad, M. (1994). Morphotaxonomical study on angiospermous plant remains from the foot hills of Kathgodam, North India. *Phytomorphology, 44*, 115–126.

Prasad, M., & Awasthi, N. (1996). Contribution to the Siwalik flora from Surai Khola sequence, western Nepal and its palaeoecological and phytogeographical implications. *Palaeobotanist, 43*, 1–42.

Prasad, M., Ghosh, R., & Tripathi, P. P. (2004). Floristics and climate during Siwalik (Middle Miocene) near Kathgodam in the Himalayan foot-hills of Uttranchal, India. *Journal of Paleaontological Society of India, 49*, 35–93.

Ranga Rao, A. (1983). Geology and hydrocarbon potential of a part of Assam-Arankan basin and its adjacent region. *Petroleum Asia Journal, 4*, 127–158.

Ranga Rao, A., Khan, K. N., Venkatachala, B. S., Sastri, V. V. (1979). Neogene/Quaternary boundary and the Siwalik. In Sastri, M. V. A. et al. (Ed.), *Proceedings of Field Conference on Neogene-Quaternary Boundary*, India (pp. 131–142).

Santapau, H., & Henry, A. N. (1973). *A dictionary of the flowering plants in India*. New Delhi: Publication and Information Directorate.

Singh, T. (2007). Geology of Itanagar capital complex, Arunachal Himalaya, with special reference to neotectonics. *Journal of the Geological Society of India, 70*, 339–352.

Singh, S. K., & Prasad, M. (2007). Late Tertiary leaf flora of Mahuadanr Valley, Jharkhand. *Journal of the Palaeontological Society of India, 52*(2), 175–194.

Shukla, A., & Mehrotra, R. C. (2014). Paleoequatorial rain forest of western India during the EECO: evidence from *Uvaria* L. fossil and its geological distribution pattern. *Historical Biology, 26*(6), 693–698.

Tao, J. R. (2000). *The evolution of the Late Cretaceous–Cenozoic floras in China*. Beijing: Science Press.

Teodoridis, V., Mazouch, P., Spicer, R. A., & Uhl, D. (2011). Refining CLAMP—investigations towards improving the Climate Leaf Analysis Multivariate Program. *Palaeogeography, Palaeoclimatology, Palaeoecology, 299*, 39–48.

van Dam, J. A. (2006). Geographic and temporal patterns in the late Neogene (12 –3 Ma) aridification of Europe: the use of small mammals as paleoprecipitation proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology, 238*, 190–218.

Wolfe, J. A. (1993). A method of obtaining climatic parameters from leaf assemblages. *United States Geological Survey Bulletin, 2040*, 1–73.

Wolfe, J. A., & Spicer, R. A. (1999). Fossil leaf character states: multivariate analysis. In T. P. Jones, & N. P. Rowe. (Eds.), *Fossil plants and spores: modern techniques* (pp. 233–239). London: Geological Society of London.

Xing, Y., Utescher, T., Jacques, F. M. B., Su, T., Liu, Y. (. C.)., Huang, Y., & Zhou, Z. (2012). Paleoclimatic estimation reveals a weak winter monsoon in southwestern China during the-Miocene: evidence from plant macrofossils. *Palaeogeography, Palaeoclimatology, Palaeoecology, 358–360*, 19–26.

Yang, J., Spicer, R. A., Spicer, T. E. V., & Li, C.-S. (2011). "CLAMP online": a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. *Palaeobiodiversity and Palaeoenvironments, 91*, 163–183.

Yang, J., Spicer, R. A., Spicer, T. E. V., Arens, N. C., Jacques, F. M. B., Su, T., Kennedy, E. M., Herman, A. B., Steart, D. C., Srivastava, G., Mehrotra, R. C., Valdes, P. J., Mehrotra, N. C., Zhou, Z. K., & Lai, J. S. (2015). Leaf form-climate relationships on the global stage: an ensemble of characters. *Global Ecology and Biogeography, 24*(10), 1113–1125.

Zhang, S. P., & Wang, B. (2008). Global monsoon summer rainy seasons. *International Journal of Climatology, 28*, 1563–1578.