Further contribution to the low latitude leaf assemblage from the late Oligocene sediments of Assam and its phytogeographical significance

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An assemblage of fossil leaves is described from the late Oligocene (Chattian 28.1–23 Ma) sediments of Assam, which was located in a low palaeolatitude ($\sim 10^{\circ}$ – 15° N) during the period of sedimentation. It includes four new fossil leaves resembling *Firmiana* and *Pterygota* of the Malvaceae *s.l.* and *Paranephelium* and *Sapindus* of the Sapindaceae. The present study suggests that the floral migration between India and southeast Asia had occurred after the late Oligocene. Our study is in congruence with the earlier published data suggesting a floral migration had occurred after the complete suturing of two landmasses by the Neogene.

1. Introduction

Globally, the late Oligocene (Chattian 28.1–23 Ma) was the time of last significant global warmth period on our blue planet Earth (Zachos *et al.* 2001). In India, the only well known exposure of the late Oligocene sedimentary basin is in northeastern part, where substantial tectonic activity has been going on since the onset of the Indian and Eurasian plate collision at ~ 56 Ma (Qinghai *et al.* 2012).

The Makum Coalfield is a well known basin having exposure of the late Oligocene sediments. The coalfield is important because (i) it is one of the largest coal producing basins in northeast India and (ii) it contains a well diversified low latitude palaeoflora (Awasthi *et al.* 1992; Awasthi and Mehrotra 1995; Mehrotra *et al.* 2009; Srivastava and Mehrotra 2010a, 2012, 2013a, b; Srivastava *et al.* 2012a). Infact, there is no other Oligocene sedimentary basin in the Indian subcontinent which

contains such a rich and diversified assemblage of plants. The basin was situated at a low palaeolatitude, i.e., $\sim 10^{\circ}$ – 15° N (Molnar and Stock 2010) and the sediments were deposited in a deltaic, mangrove or lagoonal environment (Awasthi and Mehrotra 1995; Mehrotra *et al.* 2003; Srivastava *et al.* 2012b). The coalfield consists of Baragolai, Ledo, Namdang, Tikak, Tipong and Tirap collieries, lies in between the latitudes $27^{\circ}15'$ – $27^{\circ}25'$ N and longitudes $95^{\circ}40'$ – $95^{\circ}55'$ E (figures 1 and 2) and is located along the outermost flank of the Patkai range. On the southern and southeastern sides are the hills, which rise abruptly to heights of 300–500 m from the alluvial plains of the Buri Dihing and Tirap rivers respectively.

The fossils collected for the present study belong to the Tikak Parbat Formation being considered to be late Oligocene (Chattian 28.1–23 Ma) in age on the basis of regional lithostratigraphy (Pascoe 1964), remote sensing (Ganju *et al.* 1986) and

Keywords. Makum coalfield; Malvaceae; Palaeogene; Sapindaceae; Tikak Parbat Formation; Barail.

Figure 1. Map of Assam showing the fossil locality in the Tinsukia District.

Figure 2. Simplified geological map of Makum Coalfield, Assam (after Ahmed 1996).

biostratigraphic controls (Kumar *et al.* 2012). The formation has five coal seams confined within the basal 200 m section (Misra 1992).

The Tikak Parbat Formation constitutes alternations of sandstone, siltstone, mudstone, shale, carbonaceous shale, clay and coal seams (Misra 1992). However, the plant remains are mainly confined to the grey carbonaceous and sandy shales.

The formation is underlain by 300 m of predominantly massive, micaceous or ferruginous sandstones that incorporate the Baragolai Formation, which is successively underlain by 1100–1700 m of thin-bedded fine-grained quartzitic sandstones with thin shale and sandy shale partings that constitute the Naogaon Formation (Mishra and Ghosh 1996). The three formations together represent the

Barail Group (figure 2). In Barail Group, there is an upward trend of marine to non-marine palaeo-environments, which symbolizes the infilling of a linear basin on the eastern edge of the Indian plate. The detailed sedimentary information of the Tirap mine section has been given by Kumar *et al.* (2012).

2. Material and methods

Material for the present study was collected from the Tirap colliery of the Makum Coalfield, Tinsukia District, Assam (figures 1, 2). The specimens were first cleared with the help of a fine chisel and hammer and then photographed in natural low angled light using 10 megapixel digital camera (Canon SX 110). The terminology used in describing the fossil leaf is based on Hickey (1973), Dilcher (1974) and Ellis *et al.* (2009). The type specimens are housed in the museum of the Birbal Sahni Institute of Palaeobotany, Lucknow.

3. Systematic description

Order: Malvales Juss.

Family: Malvaceae Juss. *s.l.*

Genus: *Firmiana* Marsili

Species: *F. oligocenica* Srivastava and Mehrotra, sp. nov. (figures 3a, 4a, c)

Description: Leaf simple, palmately lobed, three lobes seen; preserved lamina length of single lobe 6.5 cm, maximum width of single lobe 3.6 cm (near the middle); apex attenuate; base cordate; margin entire; texture chartaceous; attachment with petiole normal, preserved length and width 1.7 × 0.24 cm; venation pinnate, actinodromous; primary veins stout in thickness, 5 in number, nearly straight; secondary veins 8 pairs visible, 0.4–0.7 cm apart, predominantly alternate, angle of divergence moderate–wide acute (57°–74°), more or less uniform, moderately thick, smoothly curved; intersecondary veins not seen; tertiary veins percurrent and recurved, angle of origin RR; other features not visible.

Affinities: The characteristic features of the fossil leaf, viz., palmately lobed lamina, attenuate apex, cordate base, entire margin, actinodromous venation and percurrent tertiary veins suggest its close affinity with that of *Firmiana*–*Sterculia* of the family Malvaceae *s.l.* (formerly Sterculiaceae). A large number of herbarium sheets of *Firmiana colorata* Roxb. (= *Sterculia colorata* Roxb.), *Pterygota alata* Thwaites (syn. *Sterculia alata* Roxb.),

Sterculia acerifolia Hemsl., *S. bidwilli* Hk. ex Benth., *S. coccinea* Roxb., *S. diversifolia* G. Don, *S. foetida* Linn., *S. guttata* Roxb., *S. pallens* Wall. ex Hochr., *S. platanifolia* L. f., *S. rupestris* Benth., *S. trichosiphon* Benth., *S. versicolor* Wall. and *S. urens* Roxb. of the same family were examined in the Central National Herbarium, Howrah and the Forest Research Institute, Dehradun. After making comparison with them it was concluded that the fossil is close to *Firmiana colorata* (= *S. colorata*) (Herbarium sheet no. FRI 123878) and *S. urens* (Herbarium sheet no. FRI 1856) (figures 3b, 4b, d). The fossil also shows some resemblance with *Acer pictum* Thunb. of the family Sapindaceae but more acute angle of divergence of secondary veins and presence of both random reticulate and percurrent

Figure 3. (a) Fossil leaf of *Firmiana oligocenica* sp. nov. showing shape, size and venation pattern; and (b) modern leaf of *Sterculia urens* showing similar shape, size and venation pattern as in the fossil leaf (scale bar = 1 cm).

Figure 4. (a) Apical portion of a lobe of the fossil leaf (*F. oligocenica* sp. nov.) showing attenuate apex (red arrow); (b) apical portion of a lobe of the modern leaf (*S. urens*) showing similar apex (red arrow); (c) basal portion of the fossil leaf showing actinodromous venation and cordate base (white arrow) and petiole (red arrow); and (d) basal portion of the modern leaf showing similar actinodromous venation and cordate base (white arrow) and petiole (red arrow) (scale bar = 1 cm, unless otherwise given).

tertiaries in the latter differentiate it from the fossil leaf. In *Sterculia acerifolia*, *S. bidwilli* and *S. diversifolia* lamina is deeply lobed, while in *S. pallens* and *S. trichosiphon* lamina lobing is small as compared to that of the fossil. *Pterygota alata* Thwaites (syn. *Sterculia alata* Roxb.), *Sterculia coccinea*, *S. foetida*, *S. guttata*, *S. rupestris* and *S. versicolor* are different from the fossil in having unlobed lamina. In *S. platanifolia*, the angle of divergence of secondary veins is more acute in comparison to that of the fossil.

As far as the authors are aware, there is no fossil record of *Firmiana* but fossil leaf and fruit of *Sterculia* are known from various Cenozoic horizons. A fossil fruit of *Sterculia*, viz., *S. palaeovillosa* was described by Mehrotra (2000a) from the same horizon from where the present fossil was collected. Bande and Srivastava (1990) have described a fragmentary leaf of *Sterculia villosa* from the late Cenozoic sediments of Mahuadanr, Palamu District, Bihar. *Sterculia kathgodamense* described by Prasad (1994) from the Lower Siwalik sediments of Kathgodam, *S. tertiara* described

by Shashi *et al.* (2006) from the Lower Siwalik sediments of Champawat District, Uttaranchal, *S. mioensifolia* as well as *S. premontana* described by Prasad and Pandey (2008) from the late Miocene sediments of Surai Khola, Nepal and *Sterculia versicolor* described by Singh and Prasad (2010) from late Tertiary sediments of Latehar District, Jharkhand have unlobed lamina in contrast to the lobed lamina of the present fossil. A fossil leaf described by Carvalho *et al.* (2011) as *Malvaciphyllum macondicus* from the Palaeocene sediments of South America shows some similarity with the present fossil but its dentate margin makes the difference. As the present fossil shows close resemblance with *Firmiana* and *Sterculia*, the authors have preferred the name *Firmiana* as per alphabetical order. As it is different from all the known records, it is being described as *Firmiana oligocenica* Srivastava and Mehrotra, sp. nov., the specific epithet is after its age. The present fossil becomes the first record of *Firmiana*.

The genus *Firmiana* consists of about 12 species of trees found in Old World tropics (Mabberley

1997). *Firmiana colorata* (= *Sterculia colorata*) is found in Pegu, Bangladesh, western peninsula and Sri Lanka. *Sterculia* consists of 150 species distributed in tropical areas of the world (Mabberley 1997). *S. urens* Roxb. is found in northwest India, Assam, Bihar, eastern and western peninsula and Sri Lanka (Hooker 1872–1897).

Specific diagnosis: Leaf palmately lobed, three lobes seen; apex attenuate; base cordate; margin entire; texture chartaceous; attachment with petiole normal; venation pinnate, actinodromous; secondary veins eight pairs visible, 0.4–0.7 cm apart, predominantly alternate, angle of divergence moderate-wide acute, smoothly curved; intersecondary veins not seen; tertiary veins percurrent and recurved, angle of origin RR.

Holotype: Specimen no. BSIP 40061.

Horizon: Tikak Parbat Formation.

Locality: Tirap Colliery, Tinsukia District, Assam (27°17'20"N, 95°46'15"E).

Age: Late Oligocene (Chattian 28.1–23 Ma).

Number of specimens studied: One.

Genus: *Pterygota* Endl.

Species: *P. palaeoalata* Srivastava and Mehrotra, sp. nov. (figures 5a–c, 6b, c)

Description: Leaf more or less complete, symmetrical, mesophyll, narrow elliptic; preserved lamina length 25.3 cm and maximum width 10.1 cm (near the middle part); apex attenuate; base slightly broken, symmetrical, cordate; margin entire; texture chartaceous; venation pinnate, actinodromous, basal, perfect; mid-vein curved in upper half of lamina, moderate in thickness, three pairs of lateral primaries arising from the base of mid-vein, the outer lateral vein on each side thin and arising at right angle (92°), two inner lateral primaries on each side stout, arising at an angle of 38°–80°, curving upward and running up to nearly half of the length of lamina; secondary veins arising from primaries fine, angle of divergence moderate-wide acute (62°–76°), 2.1–3.1 cm apart, predominantly alternate, moderate in thickness, smoothly curved and joining superadjacent secondary veins through the tertiary veins; intersecondary veins absent; tertiary veins percurrent, simple, recurved, oblique in relation to mid-vein, angle of origin AR-AA, alternate-opposite; marginal ultimate venation looped; quaternary veins orthogonal; areoles predominantly quadrangular, imperfect, random; veinlets branched; leaf mines frequently present all over the surface of lamina.

Affinities: The characteristic features of the fossil leaf, viz., narrow elliptic shape, attenuate apex, cordate base, actinodromous venation, percurrent tertiary veins and absence of intersecondary veins suggest its close affinity with that of *Pterygota* (syn. *Sterculia*) of the family Malvaceae s.l. (formerly Sterculiaceae). A number of herbarium sheets were examined in the Central National Herbarium, Howrah and the Forest Research Institute, Dehradun. After making comparison with a large number of taxa of the family Malvaceae such as *Brachychiton acerifolium* Macarthur and Moore, *Firmiana colorata* Roxb. (= *Sterculia colorata*), *Firmiana simplex* (L.) W. Wight, *Kleinhovia hospita* L., *Pterygota alata* Thwaites (= *S. alata* Roxb.), *Sterculia acerifolia* Hemsl., *S. bidwilli* Hk. ex Benth., *S. coccinea* Roxb., *S. diversifolia* G. Don, *S. guttata* Roxb., *S. pallens* Wall. ex Hochr., *S. platanifolia* L. f., *S. rubiginosa* Zoll. ex Miq., *S. rupestris* Benth., *S. trichosiphon* Benth., *S. urens* Roxb., *S. versicolor* Wall. and *S. villosa* Roxb., it may be inferred that the fossil shows similarity with that of *Pterygota alata* (Herbarium sheet no. FRI 3330) (figures 5d, 6a, d, e). In *Firmiana simplex*, *Sterculia acerifolia*, *S. bidwilli*, *S. platanifolia*, *S. trichosiphon*, *S. urens* and *S. villosa*, the leaves are lobed in contrast to the unlobed lamina of the present fossil. *Brachychiton acerifolium*, *Sterculia coccinea*, *S. diversifolia*, *S. rubiginosa* and *S. versicolor* have eucamptodromous venation which differentiates them from the fossil. Though *Sterculia guttata* and *S. rupestris* have actinodromous venation, occurrence of only one pair of lateral primaries makes them different from the present fossil. Similarly, *Firmiana colorata* (= *Sterculia colorata*) has only two pairs of lateral primaries unlike the present fossil. *Sterculia pallens* has both lobed and unlobed lamina and actinodromous venation but the apex is acute-obtuse in contrast to the present fossil where it is attenuate. In *Kleinhovia hospita*, the venation is actinodromous but the distance between two secondary veins is comparatively less which makes it different from the fossil.

As far as the fossil leaf record of *Pterygota* is concerned, it is known from various Cenozoic horizons. Bande and Srivastava (1990) have described a fossil leaf of *Pterygota alata* from the late Cenozoic beds of Mahuadanr, Palamu District, Bihar. It shows similarity with the present fossil in a combination of characters. *Pterygota cordata* (cf. *P. alata*) described by Awasthi and Mehrotra (1995) has two pairs of lateral primaries with secondary veins only. Under such conditions, it is difficult to compare it with the present fossil. A very fragmentary specimen cf. *Pterygota alata* is also described by Mathur *et al.* (1996) but due to its fragmentary nature its identification becomes doubtful.

Figure 5. (a) A fossil leaf of *Pterygota palaeoalata* sp. nov. showing shape, size and venation pattern; (b) text diagram of the fossil leaf showing insect mines (brown arrows), primary vein (red arrow), recurved and percurrent tertiary veins (blue and green arrow); (c) basal portion of the fossil leaf showing actinodromous venation, i.e., middle primary (black arrow) and several lateral primary veins (white arrows) emerging from the single locus (red arrow) and percurrent tertiary veins (yellow arrows); and (d) basal portion of the modern leaf showing actinodromous venation, i.e., middle primary (black arrow) and several lateral primary veins (white arrows) emerging from the single locus (red arrow) and percurrent tertiary vein (yellow arrow) (scale bar = 1 cm).

Fossil leaf described as *Malvaciphyllum macondicus* (Carvalho *et al.* 2011) from the Palaeocene sediments of South America shows some similarity with the present fossil but its dentate margin makes the difference. Therefore, a new species, *Pterygota palaeoalata* Srivastava and Mehrotra, sp. nov., has been created, the specific epithet is after the modern species – *Pterygota alata*.

The genus *Pterygota* consists of about 20 species distributed throughout the tropics of Old World (Willis 1973). *P. alata* is a tall evergreen tree found in the evergreen forest of north-east India (particularly Assam) and Western Ghats but reaches its best development in Chittagong, Myanmar and Andamans (Ramesh Rao 1958).

Figure 6. (a) A modern leaf of *Pterygota alata* showing similar shape, size and venation pattern as in the fossil (figure 5a, b); (b) apical portion of the fossil leaf (*P. palaeoalata* sp. nov.) where two secondary veins (white arrows) join each other (yellow arrows); (c) middle portion of the fossil leaf showing primary vein (black arrow), secondary veins (red arrows), recurved and percurrent tertiary veins (yellow and white arrows); (d) middle portion of the modern leaf showing similar primary vein (black arrow), secondary veins (red arrows), recurved and percurrent tertiary veins (yellow and white arrows) and (e) marginal portion of the apical part of the modern leaf where two secondary veins (yellow arrows) join each other (black arrow) (scale bar = 1 cm).

Specific diagnosis: Leaf symmetrical, narrow elliptic; apex attenuate; base symmetrical, cordate; margin entire; texture chartaceous; venation pinnate, actinodromous, basal, perfect; three pairs of lateral primaries arising from the base of mid-vein, the outer lateral vein on each side thin and arising at right angle, two inner lateral primaries on each side stout, arising at acute angle, curving upward and running up to nearly half

of the length of lamina; secondary veins arising from primaries fine, angle of divergence moderate-wide acute, predominantly alternate, smoothly curved and joining superadjacent secondary veins through the tertiary veins; intersecondary veins absent; tertiary veins percurrent, simple, recurved, oblique in relation to mid-vein, angle of origin AR-AA, alternate-opposite; marginal ultimate venation looped; quaternary veins orthogonal;

Figure 7. (a) Fossil leaf of *Paranephelium makumensis* sp. nov. showing shape, size, venation pattern and attenuate apex (red arrow); (b) enlarged portion of the fossil leaf showing pentagonal areole (yellow arrow); and (c) a modern leaf of *Paranephelium xestophyllum* showing similar shape, size, venation pattern and attenuate apex (red arrow) (scale bar = 1 cm, unless otherwise mentioned).

areoles predominantly quadrangular, imperfect, random; veinlets branched.

Holotype: Specimen no. BSIP 40062A.

Horizon: Tikak Parbat Formation.

Locality: Tirap Colliery, Tinsukia District, Assam (27°17'20"N, 95°46'15"E).

Age: Late Oligocene (Chattian 28.1–23 Ma).

Number of specimens studied: One.

Order: Sapindales Juss. ex Bercht. and Presl

Family: Sapindaceae Juss.

Genus: *Paranephelium* Miq.

Species: *P. makumensis* Srivastava and Mehrotra, sp. nov. (figures 7a, 8a, c)

Description: Leaf symmetrical, mesophyll, narrow elliptic; preserved lamina length 15.6 cm,

maximum width 5.5 cm (near the middle); apex seemingly attenuate; base broken; margin entire, wavy; texture chartaceous; venation pinnate, eucamptodromous; primary vein stout in thickness, slightly curved; secondary veins 14 pairs visible, 0.7–1.9 cm apart, predominantly alternate, angle of divergence moderate-wide acute to right (55°–93°), abruptly curved just near the margin, moderate in thickness; intersecondary veins present, simple, 1–2; tertiary veins percurrent, simple, forked, angle of origin OA-AR; areoles well developed and quadrangular to pentagonal in shape.

Affinities: The characteristic features of the fossil leaf, viz., symmetrical lamina, narrow elliptic shape, attenuate apex, entire margin, eucamptodromous venation, moderate-wide acute to right angle of divergence of secondary veins, simple intersecondaries and percurrent tertiary veins suggest its close similarity with the modern leaf of

Figure 8. (a) A middle portion of the fossil leaf (*P. makumensis* sp. nov.) showing secondary veins with eucamptodromous venation (white arrows), primary and tertiary veins (yellow and red arrows); (b) a middle portion of the modern leaf (*P. xestophyllum*) showing similar secondary veins with eucamptodromous venation (white arrows), primary and tertiary veins (yellow and red arrows); (c) enlarged portion of the fossil leaf showing intersecondary (white arrows), secondary (yellow arrows) and primary veins (red arrow); and (d) enlarged portion of the modern leaf showing similar intersecondary (white arrows), secondary (yellow arrows) and primary veins (red arrow) (scale bar = 0.5 cm).

Paranephelium Miq., particularly *P. xestophyllum* Miq. (= *P. hystrix* Smith) (Herbarium sheet no. FRI 42582) (figures 7c, 8b, d) of the family Sapindaceae. A large number of herbarium sheets were examined in the Central National Herbarium, Howrah and the Forest Research Institute, Dehradun. The fossil also shows similarities with *Xerospermum noronhianum* Bl., *Sapindus detergens* Roxb., *S. mukorossi* Gaertn., *S. thwaitesii* Hiern, *Lepisanthes burmanica* Kurz of the Sapindaceae and *Mangifera indica* L. and *Bouea oppositifolia* Meisn. of the Anacardiaceae. Both *Xerospermum noronhianum* and *Sapindus detergens* are very much similar to the fossil leaf but the angle of divergence of secondary veins is more acute in them than in the fossil. In *Sapindus mukorossi*, secondary veins are smoothly curved near the margin in contrast to the present fossil where they are abruptly curved. In *S. thwaitesii*, the angle of divergence of secondary veins is wide acute to right and tertiary veins are random reticulate which make the major difference from the fossil. *Lepisanthes burmanica* is also very much similar but the distance between the two secondary veins is lesser in it than in the fossil. *Mangifera indica* shows similar features as found in the fossil but the distance between the two secondary veins is comparatively less and tertiary veins are percurrent, recurved-retroflexed and orthogonal reticulate unlike the present fossil. *Bouea oppositifolia* also shows some similarities with the fossil leaf but the angle of divergence of secondary veins is wide acute to right and margin is not wavy in it; this marks the difference.

As far as the fossil record of *Paranephelium* is concerned, its only fossil, *Paranephelium seriaensis* (Prasad and Dwivedi 2008), is known from the middle Miocene sediments of western Nepal. It has acute apex, distance between two secondary veins is 0.7–1.2 cm, angle of divergence of secondary veins is moderate acute and shows absence of intersecondary veins; all these features are in contrast to the present fossil leaf where apex is attenuate, secondaries are comparatively far apart with moderately acute to right angle of divergence and intersecondary veins are present. Therefore, a new species, *Paranephelium makumensis* Srivastava and Mehrotra, sp. nov., has been created, the specific epithet is after the Makum Coalfield.

Paranephelium is a small genus consisting of four species distributed in southeast Asia and western Malaysia. It is small-to-medium sized tree of the lower canopy or higher understorey of the primary rain forest, mixed deciduous forest or dry evergreen forest, especially in the moist part near streams, sometimes in secondary forest, rarely in scrub; typical of lowlands and the lower hillside (Davids 1984). *Paranephelium xestophyllum*, a closely comparable species of the fossil, is a small evergreen

tree found mainly in the primary rain forest, also in mixed deciduous, dry evergreen, partly secondary or disturbed forest, rarely in (seasonal) swamp. It is distributed in China, Myanmar, Thailand, Indo-chinese peninsula, Malayan peninsula, Sumatra, Kalimantan and Philippines (Davids 1984).

Specific diagnosis: Leaf symmetrical, narrow elliptic; apex attenuate; margin entire; texture chartaceous; venation pinnate, eucamptodromous; primary vein stout in thickness; secondary veins 0.7–1.9 cm apart, predominantly alternate, angle of divergence moderate–wide acute to right, abruptly curved near the margin; intersecondary veins present, simple, 1–2; tertiary veins percurrent, simple, forked; areoles quadrangular to pentagonal in shape.

Holotype: Specimen no. BSIP 40063.

Horizon: Tikak Parbat Formation.

Locality: Tirap Colliery, Tinsukia District, Assam (27°17'20"N, 95°46'15"E).

Age: Late Oligocene (Chattian 28.1–23 Ma).

Number of specimens studied: One.

Genus: *Sapindus* Plum.

Species: *S. palaeoemarginatus* Srivastava and Mehrotra, sp. nov. (figures 9a, c, e)

Description: Leaf complete, symmetrical, mesophyll, suborbiculate elliptic; preserved lamina length 6 cm; maximum width 5 cm near the middle; apex emarginate; base symmetrical, obtuse to round; margin entire; texture coriaceous; venation pinnate eucamptodromous; primary vein stout in thickness, nearly straight; secondary veins 5 pairs visible, 0.5–0.6 cm apart, predominantly alternate, angle of divergence wide acute (68°–78°), uniform, moderately thick, uniformly curved; intersecondary veins present, simple; tertiary veins random reticulate, other features not visible.

Affinities: The characteristic features of the fossil leaf, viz., suborbiculate elliptic shape, emarginate apex, obtuse to round base, eucamptodromous venation, simple intersecondaries and random reticulate tertiary veins suggest its close affinity with that of *Sapindus* of the family Sapindaceae. A large number of herbarium sheets of *Sapindus* species, namely *S. attenuatus* Wall., *S. detergens* Roxb., *S. emarginatus* Vahl, *S. lawriifolius* Vahl, *S. mukorossi* Gaertn. and *S. thwaitesii* Hiern were examined in the Central National Herbarium, Howrah and the Forest Research Institute, Dehradun. After making comparison with

them, it is suggested that the present fossil is close to *S. emarginatus* (figure 9b, d, f). The other species such as *S. attenuatus*, *S. detergens* and *S. mukorossi* have attenuate apex and acute base and are thus different from the present fossil. In *S. laurifolius* and *S. thwaitesii* shape of leaf is elliptic and base is acute unlike the present fossil. *Ceriops roxburghiana* Arn. of the family Rhizophoraceae is also very similar to the present fossil leaf but it has brochidodromous venation which differentiates it from the present fossil.

As far as fossil record of *Sapindus* leaf is concerned, it is known from both India and abroad. From India, only two types of leaves are known, viz., leaf type D and leaf type E comparable to *S. bilinicus* and *S. falcifolius* respectively (Deshmukh and Sharma 1978). In both these leaves, the apex is acute and acuminate respectively and the base

is acute; these features differentiate them from the present fossil. *Sapindus graecus* and *S. falcifolius* are known from the late Oligocene sediments of Bulgaria (Bozukov *et al.* 2008). In the former the leaf is narrow elliptic with attenuate apex and acute base which make the difference from the present fossil, while in the latter the leaf is elliptic in shape. *S. falcifolius* is also known from the middle Miocene of Morilor Valley of Romania (Paraschiv 2004). Its leaf is asymmetrical, oblong-lanceolate in shape with cuneate base and acuminate apex; all these features differentiate it from the present fossil. As the present fossil is distinct from all known species, it is being described under a new species, *Sapindus palaeoemarginatus* Srivastava and Mehrotra, sp. nov., the specific name is after the modern species – *Sapindus emarginatus*.

Figure 9. (a) Fossil leaf of *Sapindus palaeoemarginatus* sp. nov. showing shape, size and venation pattern; (b) modern leaf of *Sapindus emarginatus* showing similar shape, size and venation pattern as in the fossil; (c) apical portion of the fossil leaf showing emarginate apex (red arrow); (d) apical portion of the modern leaf showing similar emarginate apex as in the fossil (red arrow); (e) a portion of fossil leaf showing secondary and intersecondary veins (red and yellow arrows); and (f) a portion of the modern leaf showing similar secondary and intersecondary veins as in the fossil (red and yellow arrows) (scale bar = 1 cm).

The genus *Sapindus* is a tree or shrub consisting of 15 species found in tropical and warm climate; about 7 species are found in India. *S. emarginatus* Vahl is a common tree, found mostly in West Bengal and peninsular India in deciduous and evergreen forests (Santapau and Henry 1973).

Specific diagnosis: Leaf symmetrical, shape suborbiculate elliptic; apex emarginate; base symmetrical, obtuse to round; margin entire; texture coriaceous; venation eucamptodromous; angle of divergence of secondary veins wide acute; inter-secondary veins present, simple; tertiary veins random reticulate.

Holotype: Specimen no. BSIP 40064A.

Horizon: Tikak Parbat Formation.

Locality: Tirap Colliery, Tinsukia District, Assam (27°17'20"N, 95°46'15"E).

Age: Oligocene (Chattian 28.1–23 Ma).

Number of specimens studied: One.

4. Discussion and conclusion

The family Malvaceae consists of ~250 genera with ~4500 species distributed in tropical to temperate regions of the world (Carvalho *et al.* 2011). Recent studies have merged Sterculiaceae, Tiliaceae and Bombacaceae into the expanded Malvaceae (Bayer *et al.* 1999; Bayer and Kubitzki 2003) and nine subfamilies have been recognized based on various morphological and anatomical synapomorphies as well as molecular data (Judd and Manchester 1997; Alverson *et al.* 1998, 1999; Bayer *et al.* 1999) in contrast to 10 families concept (Baum *et al.* 1998; Cheek 2006; Heywood *et al.* 2007). In the present paper we have followed Malvaceae *s.l.* for describing the fossil malvalean leaves as it is used by a majority of modern taxonomists. The fossil record of the family dates back to late Campanian–early Maastrichtian of Mexico (Estrada-Ruiz *et al.* 2010); late Cretaceous sediments of Texas (Wheeler and Lehman 2000); middle-late Palaeocene sediments of Columbia (Carvalho *et al.* 2011); early Miocene of Czech Republic (Kvaček 2004). In India, the oldest fossil record of the family is known from the Deccan Intertrappean sediments of central India (Chitale and Sheikh 1973); also recorded from the late Paleocene, late Oligocene and Neogene sediments of northeast India (Srivastava and Mehrotra 2010b), Neogene sediments of western, southern and northern India (Guleria 1992; Prasad 2008).

The family Sapindaceae (Sapindales) contains 142 genera and 1900 species (Buerki *et al.* 2009)

which are predominantly pantropical in distribution. Some taxa such as *Acer* L., *Aesculus* L., *Atalaya* Bl., *Diplopeltis* Endl. and *Dodonaea* Jacq. are distributed in temperate regions with main centre of diversity in south Asian region. The family is also economically important for fruits like *Dimocarpus longan* Lour., *Litchi chinensis* Sonn., *Paullinia cupana* Kunth; wood like *Aesculus* L. (Buerki *et al.* 2009). It consists of four sub-families such as Xanthoceroideae, Hippocastanoideae, Dodonaeoideae and Sapindoideae (Stevens 2001) which diverged between 116 and 98 Ma, and spread mainly from Laurasia while southeast Asia persisting as a significant area in the evolution of the family (Buerki *et al.* 2011). The fossil record of the family is known from the Oligocene and Miocene sediments of Africa; late Oligocene–early Miocene of southeast Bulgaria (Bozukov *et al.* 2008); Miocene sediments of Romania (Paraschiv 2004); late Miocene sediments of Poland (Walther and Zastawniak 2005); and Eocene of Oregon (Manchester 1994; Wheeler *et al.* 2006). From India, the oldest fossil record of the family is from the Deccan Intertrappean sediments of Maharashtra (Kar *et al.* 2004) and central India (Dayal 1965; Chitale and Shallom 1969; Mehrotra 1987). It is also known from the late Palaeocene, late Oligocene and Neogene sediments of northeast India (Srivastava and Mehrotra 2010b); Siwalik sediments of northern India (Prasad 2008) and Neogene sediments of Gujarat and Pondicherry (Guleria 1992).

Phytogeographically, the family Malvaceae *s.l.* is important for India and southeast Asia indicating the migration of taxa in deep time (Bande and Prakash 1986). The family is represented in India by the genus *Sterculia* from the Maastrichtian–Palaeogene sediments while it made its first appearance in the Neogene sediments of Myanmar as *Sterculinium foetidense* (Prakash 1973; Guleria 1983). Likewise, another genus *Pterospermum* was present in the Palaeogene sediments of Borneo as *Phyllites* (*Pterospermum*) *gracilis* (Geyler 1875), while it made its first appearance in the Neogene sediments of India (Awasthi *et al.* 1980; Antal and Awasthi 1994; Antal and Prasad 1996; Roy and Mukhopadhyay 2005; Srivastava *et al.* 2012c). Similar is the case for the genus *Grewia* which was recorded from the Deccan Intertrappeans (Maastrichtian–Danian) (Prakash and Dayal 1965; Paradkar and Dixit 1984; Bande and Srivastava 1995; Khare *et al.* 2000; Srivastava and Guleria 2000) and late Palaeocene sediments (Mehrotra 2000b) of India. This genus was later recorded from the Neogene sediments of South Vietnam and Myanmar (Serra 1981; Gottwald 1994). The above records suggest that a free floral migration occurred from India to southeast Asia and *vice-versa* after the complete suturing of the Indian and Asian plates during the

Table 1. Distribution of the modern comparable species in different forest types.

Taxa	Tropical wet evergreen forest	Tropical semi- evergreen forest	Tropical moist deciduous forest	Littoral and swamp forest	Tropical dry deciduous forest	Tropical dry evergreen forest	References
Anacardiaceae							
<i>Lannea coromandelica</i>			+		+		Awasthi and Mehrotra (1995)
<i>Mangifera indica</i>	+	+	+		+		-do-
<i>Parishia insignis</i>			+				-do-
<i>Semecarpus anacardium</i>		+	+		+		Srivastava and Mehrotra (2012)
<i>S. kurzii</i>			+				-do-
Annonaceae							
<i>Alphonsea</i>	+						Srivastava and Mehrotra (2013a)
<i>Saccopetalum longiflorum</i>			+		+		Awasthi and Mehrotra (1995)
Apocynaceae							
<i>Alstonia</i>	+	+					-do-
Avicenniaceae							
<i>Avicennia officinalis</i>				+			-do-
Burseraceae							
<i>Santiria laevigata</i>	+	+		+			-do-
Calophyllaceae							
<i>Calophyllum polyanthum</i>	+					+	-do-
Clusiaceae							
<i>Garcinia</i>	+	+					-do-
<i>Kayea floribunda</i>	+						-do-
<i>Mesua</i>	+						-do-
<i>Poeciloneuron indicum</i>	+						Srivastava and Mehrotra (2013b)
Combretaceae							
<i>Terminalia catappa</i>				+			Awasthi and Mehrotra (1995)
<i>T. chebula</i>	+		+	+	+		-do-
<i>T. coriacea</i>					+		-do-
<i>T. crenulata</i>		+	+				-do-
Fabaceae							
<i>Butea frondosa</i>							Srivastava and Mehrotra (2010a)
<i>Entada phaseoloides</i>					+		Awasthi and Mehrotra (1995)
Lauraceae							
<i>Apollonias arnottii</i>	+	+	+				-do-
Lecythidaceae							
<i>Barringtonia racemosa</i>				+			Mehrotra (2000a)

Table 1. (Continued)

Taxa	Tropical wet evergreen forest	Tropical semi- evergreen forest	Tropical moist deciduous forest	Littoral & swamp forest	Tropical dry deciduous forest	Tropical dry evergreen forest	References
Malvaceae							
<i>Firmiana colorata</i>		+	+				Present communication
<i>Sterculia urens</i>	+		+		+		Present communication
<i>Pterygota alata</i>	+	+	+				Present communication
Meliaceae							
<i>Heynea trijuga</i>			+				Awasthi and Mehrotra (1995)
Memecylaceae							
<i>Memecylon amplexicaule</i>	+			+			-do-
Myristicaceae							
<i>Myristica sylvestris</i>	+						-do-
Phyllanthaceae							-do-
<i>Bridelia retusa</i>		+	+		+		-do-
Rhizophoraceae							
<i>Rhizophora mucronulata</i>				+			-do-
Sapindaceae							
<i>Nephelium</i>	+	+					-do-
<i>Paranephelium xestophyllum</i>	+			+		+	Present communication
<i>Sapindus emarginatus</i>				+	+		Present communication

Figure 10. Different forest types in the assemblage of Makum Coalfield.

beginning of Neogene (Srivastava and Mehrotra 2010b). There are several other families and genera which indicate the floral migration in between the two landmasses in the geologic past and this was discussed in great detail by Bande and Prakash (1986) and Tiwari *et al.* (2012).

For the reconstruction of palaeoclimate, qualitative and quantitative study was made on the flora of Makum Coalfield, Assam. Qualitative study is based on the floristic assemblages containing the families listed in table 1. Among them, the families such as Annonaceae, Burseraceae, Clusiaceae, Combretaceae, Lecythidaceae, Myristicaceae and Rhizophoraceae are typical pantropical (van Steenis 1962) and their presence in the Makum Coalfield palaeoflora provides evidence that the CMMT (cold month mean temperature) was not less than 18°C (Srivastava *et al.* 2012b). Similarly, the dominance of Fabaceae (Srivastava and Mehrotra 2010a) whose abundance and richness covary with temperature (Punyasena *et al.* 2008), also indicates a warm climate. The occurrence of Avicenniaceae and Rhizophoraceae is significant in terms of the depositional environment. These families are highly indicative of deltaic, mangrove or lacustrine deposition of sediments in the Makum Coalfield. The presence of palms like *Nypa* (Mehrotra *et al.* 2003) provides further evidence of a coastal plain environment where both temperature and humidity remained high throughout the year (Tomlinson 1990). The overall floristic assemblage indicates a dominance of moist conditions (figure 10). For quantitative study, CLAMP (Climate Leaf Analysis Multivariate Program) analysis was made on 80 different morphotypes of fossil leaves, including the presently described assemblage from the Tirap mine indicating MAT (mean annual temperature) $28.3^{\circ} \pm 3.7^{\circ}\text{C}$; CMMT $23^{\circ} \pm 5.5^{\circ}\text{C}$ and a WMMT (warm month mean temperature) of $33.6^{\circ} \pm 5.2^{\circ}\text{C}$ and a monsoonal climate during the late Oligocene (Srivastava *et al.* 2012b).

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