Fossil wood flora from the Siwalik Group of Arunachal Pradesh, India and its climatic and phytogeographic significance

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The plant fossil records from the Siwalik Group of Arunachal Pradesh, India are far from satisfactory due to remoteness and dense vegetation of the area. We report seven fossil woods of which three belong to the Middle Siwalik (Subansiri Formation), while the rest are from the Upper Siwalik (Kimin Formation). The modern analogues of the fossils from the Middle Siwalik are *Lophopetalum littorale* (Celastraceae), *Afzelia-Intsia* and *Sindora siamensis* (Fabaceae) and from the Upper Siwalik are *Miliusa velutina* (Annonaceae), *Calophyllum tomentosum* and *Kayea* (Calophyllaceae) and *Diospyros melanoxylon* (Ebenaceae). The dominance of diffuse porosity in the fossil woods indicates a tropical climate with low seasonality (little variation) in temperature, while a high proportion of large vessels and simple perforation plates in the assemblage infer high precipitation during the deposition of the sediments. The aforesaid inference is in strong agreement with the previous quantitative reconstruction based on fossil leaves. Several modern analogues of the fossil taxa are now growing in low latitudes possibly due to an increase in seasonality (increased variation) in temperature caused by the rising Himalaya.

Keywords. Megaflora; systematics; Neogene; northeast India; palaeoclimate.

1. Introduction

The Siwalik denotes low elevation (varying from a few hundred metres to ~1200 m) mountain ranges formed in between the lesser Himalaya (in the north) and the Gangetic Plains (in the south), due to the rising Himalaya since the middle Miocene (Karunakaran 1974). It extends all along the Himalayan foot-hills covering a distance of ~2400 km from Sindh of Pakistan in the west to Assam in the east attaining a width of 20–25 km. The Siwalik sediments were deposited in a fluvial environment, in coarsening-upward succession and

are divided into three subgroups, namely Lower, Middle and Upper Siwalik (Pilgrim 1910; Johnson *et al.* 1985; Ranga Rao *et al.* 1988; Valdiya 2002).

The flora archived in the Siwalik Group is very important for the study of vegetation in relation to climate change that occurred due to the rising Himalaya since the middle Miocene (Prasad 2008; Khan *et al.* 2014a). The fossil flora discovered from the Himalayan foreland basin is predominantly based on leaves and fruits, while the wood flora is still very meagre (Prasad 2008; Srivastava *et al.* 2014). Most of the fossils recovered from the Siwalik Group are from the foot-hills of

northwest Himalayan region (Prasad 2006; Shashi *et al.* 2006, 2008); however, from northeastern Himalayan region the fossil data is still far from satisfactory because of the remoteness of the area (Srivastava *et al.* 2014). In view of the aforesaid reasons, it is important to discover more fossils from the Siwalik of northeastern part of India to study the vegetation *vis-à-vis* climate change caused due to the rising Himalaya. A comparative study of northeastern and western parts of the Siwalik flora would be very useful for the study of evolution of continental climate caused by the upheaval of Himalaya. In northeastern region (NER), the Siwalik sediments (Lower, Middle and Upper) are exposed in Arunachal Pradesh (ARP), where floristic assemblage is predominantly based on leaves and fruits (Singh and Prakash 1980; Joshi and Mehrotra 2003, 2007; Joshi *et al.* 2003a,b; Bera *et al.* 2004, 2014; Khan and Bera 2007, 2010, 2014, 2016, 2017; Khan *et al.* 2008, 2009, 2011, 2014b, 2015, 2016, 2017; Bera and Khan 2009; Srivastava and Mehrotra 2009) with a meagre wood flora (Mehrotra *et al.* 1999; Joshi *et al.* 2003b). The dominant families are Calophyllaceae, Combretaceae, Dipterocarpaceae, Fabaceae and Lauraceae.

In the present communication, we report seven fossil woods from the Middle and Upper Siwalik sediments of Arunachal Pradesh (figures 1a, 3).

2. Regional geology

In NER, Arunachal Pradesh (ARP) has the largest land area and is bounded by countries like China in the north, Bhutan in the west and Myanmar in the east. About 80% of the geographical area of ARP is covered by lush green vegetation. In ARP, the Siwalik is exposed as a linear belt along the foot-hills whose northern part is limited by Main Boundary Fault (MBF) from the overlying Gondwana rocks, while the southern part is trammled by Main Frontal Fault (MFF) from the underlying alluvium deposits. In ARP, the Siwalik is classified into three formations such as Dafla (middle-late Miocene), Subansiri (Pliocene) and Kimin (late Pliocene–early Pleistocene) which are equivalent to Lower, Middle and Upper Siwalik sub-divisions of northwestern Himalaya (Karunakaran and Ranga Rao 1979). These three sub-divisions are separated from each other by reverse faults and are arranged in reverse stratigraphic order (table 1) (Kumar 1997; Joshi and Chakraborty 2001). The magnetostratigraphic study of the Siwalik

sediments from West Kameng district suggests that these sediments were deposited between 13 and 2.5 Ma and the changeover from Lower to Middle Siwalik occurred at ~ 10.5 Ma, while that from Middle to Upper Siwalik took place at ~ 2.6 Ma (Chirouze *et al.* 2012). Lithologically, the Lower Siwalik consists of an alternation of fine- to medium-grained sandstones and variegated mudstones which were deposited by a meandering river, while the Middle Siwalik is of medium- to coarse-grained, grey, mica-rich salt-and-pepper coloured sandstones which were deposited by a braided river (Tandon 1991). The Upper Siwalik comprises pebble and cobble conglomerates formed as alluvial fan deposits near the mountain front.

The sediments of Dafla Formation (Lower Siwalik) consist of indurated, medium- to fine-grained, well sorted, bluish-grey sandstone and bluish-grey, greenish-grey, and nodular silty shale. Stringers and small lenses of lignitic coal aligned parallel to the bedding plane are frequent. In the Lower Siwalik, bed forms are laminated to massive, large trough, festoon, planar curved, and tabular cross beds together with ripple cross laminations (Joshi and Chakraborty 2001). The Subansiri Formation (Middle Siwalik) named after the Subansiri River (Karunakaran and Ranga Rao 1979) is gradationally underlain by the Dafla Formation and overlain by the Kimin Formation. Lithologically, it is characterized by the presence of salt-and-pepper coloured, coarse- to medium-grained grey micaceous, soft, thick bedded massive sandstones (figures 2, 3d) and represents the valley filled deposits frequented by ephemeral streams. Total cumulative thickness of the Subansiri Formation is ~ 4200 m (Raju and Misra 2009) of which upper ~ 650 m is exposed in the study area. Moreover, the Kimin Formation (Upper Siwalik) whose composite thickness is ~ 2300 m, is gradationally underlain by the Subansiri Formation and unconformably overlain by the alluvium deposits. The lithology is mainly represented by loosely packed, very coarse to fine-grained, friable, grey sandstone which is highly limonitised at places (figure 2; table 1).

3. Materials and methods

Several fossil wood samples were collected from the areas having the exposures of Middle and Upper Siwalik (figures 1, 3). The wood pieces were sampled from the large trunks embedded in the section with the help of a chisel and hammer. All

Figure 1. (a) Map showing the study area. (b) Generalized geological map of the study area (1. Pappu Nala, 2. Near 7 km post on the Itanagar–Banderdeva road, 3. One km before Nirjuli on the Nirjuli–Banderdeva road).

the unearthed fossil wood samples were sectioned transversally and longitudinally (i.e., radially and tangentially). The standard method of grinding and polishing with different grades of carborundum powder was used during slide preparation and finally mounted in Canada balsam (Lacey 1963).

All type of slides are housed in the museum of the Birbal Sahni Institute of Palaeosciences, Lucknow (India). The slides were examined under transmitted light microscope. Total seven fossil woods are described from the Middle and Upper Siwalik sediments of Arunachal Pradesh. Of them,

Table 1. Generalised litho-tectonic succession in Arunachal Pradesh (after Joshi and Chakraborty 2001).

Gondwana	Carbonaceous shale, sandstone and coal with plant fossils
-----MBF-----	
Lower Siwalik	Well indurated sandstone, shale and siltstone with abundant plant fossils
-----Fault-----	
Middle Siwalik	Weakly indurated sandstone with concretions, shale, siltstone and conglomerates with abundant plant fossils
-----Fault-----	
Upper Siwalik	Sandrock, claystone/shale and boulder beds/gravel beds with abundant plant fossils especially petrified and carbonized wood
-----Main Frontal Fault-----	
Assam alluvia/Quaternary deposits	

three fossil woods belong to the Middle, while four are from the Upper Siwalik sediments. The fossil woods were identified after comparing them with modern woods both from thin sections available at the Birbal Sahni Institute of Palaeosciences, Lucknow (BSIP) and published literature (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; Ilic 1991; <http://insidewood.lib.ncsu.edu/>). We followed the anatomical terms given by Wheeler *et al.* (1986) and the International Association of Wood Anatomists (1989) while describing the fossil woods (<http://insidewood.lib.ncsu.edu/>, Gregory *et al.* 2009).

4. Systematic description

Family: Annonaceae

Genus: *Polyalthioxyton* Bande (1973)

Polyalthioxyton arunachalensis Srivastava, Mehrotra and Srikarni, sp. nov.
(figure 4a–e)

Specific diagnosis: Wood diffuse porous. Vessels round to oval, mostly small to medium, solitary and in radial pairs, evenly distributed; perforations simple. Axial parenchyma uniseriate, closely spaced scalariform bands. Rays 1–6 seriate, uniseriates rare; ray tissue weakly heterogeneous. Fibres thick walled, non-septate.

Holotype: Specimen no. BSIP41159; figure 4.

Type horizon: Upper Siwalik (= Kimin Formation).

Type locality: Near 7 km post on the Itanagar–Banderdeva road.

Age: Late Pliocene–Early Pleistocene.

Etymology: The specific name is after Arunachal Pradesh.

Description: Wood diffuse porous (figure 4a). Growth rings not observed. Vessels round to oval, mostly small, occasionally medium, tangential diameter range 59–118 μm and average about 75 μm , solitary and in radial pairs, 35–40 per mm^2 , evenly distributed, filled with dark coloured gummy deposits (figure 4a, b); vessel elements 79–148 μm in length with horizontal to oblique ends; perforations simple. Axial parenchyma apotracheal, uniseriate, closely spaced scalariform bands (figure 4b); cells 31–44 μm in length and 28–31 μm in width. Rays 1–6 seriate, 15–18 per mm (figure 4c, d); uniseriates rare, mostly made up of procumbent cells with 1 or 2 rows of upright or square cells, 5–96 μm in width and 132–1557 μm in height; ray to ray fusion present; ray tissue weakly heterogeneous, procumbent cells 27–31 μm in radial length and 10–19 μm in tangential height; upright cells 28–32 μm in tangential height and about 20 μm in radial length (figure 4e). Fibres polygonal in cross section, thick walled, non-septate.

Affinities: The important structural features of the fossil are: diffuse porous wood, vessels filled with gummy deposits, thin, closely spaced scalariform bands of axial parenchyma, moderately broad and mostly homocellular rays and non-septate fibres which indicate its affinities with Annonaceae (Pearson and Brown 1932; Kribs 1959; Ilic 1991). The other closely allied families are Ebenaceae, Lecythidaceae and Sapotaceae. Ebenaceae can be differentiated from our fossil in having narrower rays, while the other two families are generally characterized by heterocellular rays (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; Ilic 1991). According to Chowdhury and Tandan (1958), most of the genera of the Annonaceae are xylotomically homogeneous and difficult to be distinguished. However, the present fossil shows maximum resemblance with *Miliusa* Lesch., especially *M. velutina* (Dunal) Hk. f. & Th. (slide no. BSIP2275).

Kramer (1974) instituted the genus *Polyalthioxyton* for the fossil woods of *Polyalthia* Bl., *Platymitra*

Figure 2. Generalized lithology of the study area.

Boerl., *Stelechocarpus* Hooker f. & Thomson and other xylotomically similar taxa. Bande (1973) also established the genus *Polyalthioxylon* for the fossil woods of *Polyalthia* only. Prakash (1978) preferred Kramer's genus as most of the genera of the Annonaceae are homogeneous in their

wood anatomy. According to the botanical code of nomenclature (Rule 12A), a taxon can bear only one correct epithet, that is, the earliest. Therefore, we have preferred *Polyalthioxylon* Bande. To date five species of *Polyalthioxylon*, namely *P. indicum* Prakash (1978) from the Siwalik of

Figure 3. (a) Showing an Upper Siwalik locality situated 1 km before Nirjuli. (b) A Middle Siwalik locality of Pappu Nala showing a fossil wood embedded in sandstone. (c) An Upper Siwalik locality situated at 7 km post on the Itanagar–Banderdewa road. (d) A section of the Middle Siwalik locality of Pappu Nala showing salt-and-pepper coloured sandstone.

Uttar Pradesh, *P. oldhavenense* [Crawley \(2001\)](#) from the Palaeogene of the United Kingdom, *P. parapaniense* [Bande \(1973\)](#) from the Deccan Intertrappean beds of India, *P. platymitroides* [Kramer \(1974\)](#) and *P. stelechocarpoides* [Kramer \(1974\)](#) from the Neogene of southeast Asia are known. The present fossil is distinct from all of them in having narrower rays and therefore, is described as *Polyalthioxylon arunachalensis* sp. nov., the specific name indicating its occurrence in Arunachal Pradesh.

Miliusa comprises small trees and shrubs found in India, southeast Asia and Australia. *M. velutina* is a tree distributed in the deciduous forest of northern and central India. It is also found in sub-Himalayan tract from Ganges eastwards, in Assam, Odisha, Andhra Pradesh, Madhya Pradesh and Myanmar ([Chowdhury and Tandan 1958](#)).

Family: Calophyllaceae

Genus: *Calophylloxyton* [Lakhanpal and Awasthi \(1965\)](#)

Calophylloxyton cuddalorensis [Lakhanpal and Awasthi \(1965\)](#)
(figure 5a–f)

Description: Wood diffuse porous (figure 5a). Growth rings absent. Vessels circular to oval, tangential diameter range 52–266 μm and average 104 μm , mostly solitary, arranged in oblique radial lines, 7–11 vessels per mm^2 , tylosed (figure 5a, b); vessel elements 111–117 μm in length with horizontal to oblique ends; perforations simple. Vasicentric tracheids present (figure 5e), pits 3–4 μm in diameter, arranged in 1 or 2 rows. Axial parenchyma apotracheal banded, bands mostly continuous, 2–8 cells wide, band width 46–136 μm ,

Figure 4. *Polyalthioxylon arunachalensis* Srivastava *et al.*, sp. nov. (a) Transverse section (Ts) showing shape, size and distribution of vessels. (b) Ts showing closely spaced uniseriate scalariform bands of axial parenchyma. (c) Tangential longitudinal section (Tls) showing distribution of rays. (d) Tls showing structure of rays and non-septate fibres. (e) Radial longitudinal section (Rls) showing weakly heterogeneous ray tissue.

distance between two bands 250–409 μm (figure 5a, b). Rays uniseriate, 2–35 cells or 48–567 μm high, width 11–19 μm (figure 5c, d); ray tissue weakly heterogeneous, mostly made of procumbent cells with 1 or 2 rows of upright or square cells (figure 5f); procumbent cells 12–18 μm in tangential height and 46–58 μm in radial length; upright or square cells 44–48 μm in tangential height and 40–47 μm in radial length (figure 5f). Fibres polygonal in cross section, moderately thick walled, non-septate.

Figured specimen: Specimen no. BSIP41160.

Horizon: Upper Siwalik (= Kimin Formation).

Locality: 1 km before Nirjuli on the Nirjuli–Banderdeva road.

Age: Late Pliocene–Early Pleistocene.

Affinities: The diagnostic features of the fossil wood, viz., diffuse porous wood, simple perforations, mostly solitary vessels arranged in oblique radial lines, vasicentric tracheids, continuous thick apotracheal bands of axial parenchyma, exclusively uniseriate rays and non-septate fibres indicate its close affinities with Clusiaceae and *Parinari* Aubl. of the Chrysobalanaceae (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; Miles 1978;

Figure 5. *Calophylloxyton cuddalorensis* Lakhanpal and Awasthi showing (a) distribution of vessels and apotracheal bands of axial parenchyma, (b) vessels arranged in an oblique pattern, (c) uniseriate rays, (d) distribution of rays and non-septate fibres, (e) vasicentric tracheids, and (f) weakly heterogeneous ray tissue.

Ilic 1991). However, *Parinari* can be differentiated in having thinner bands of axial parenchyma (Kribs 1959). Tandon and Purkayastha (1958) provided a key to separate various genera of the family Clusiaceae and a perusal of this key indicates that our fossil is very close to *Calophyllum* L. and *Mesua* L. Both these genera are now placed in Calophyllaceae. Our fossil can be differentiated from *Mesua* in having comparatively less thick walled fibres and less closely spaced axial parenchyma bands (Lakhanpal and Awasthi 1965; Prakash 1966a) and hence, can be assigned to *Calophyllum*. Published

descriptions and photographs (Pearson and Brown 1932; Tandon and Purkayastha 1958; Kribs 1959; Miles 1978; Ilic 1991; <http://insidewood.lib.ncsu.edu/>) of its various species were consulted for detailed comparison. In addition, wood slides of several species of *Calophyllum*, namely *C. apetalum* Willd. syn. *C. wightianum* Wall. ex Planch. & Triana, *C. blancoi* Planch. & Triana, *C. brasiliense* Cambess. (syn. *C. lucidum* Benth.), *C. calaba* L. (syn. *C. retusum* Wall. ex Planch. & Triana), *C. Costatum* F.M. Bailey, *C. ferrugineum* Ridl., *C. inophyllum* L., *C. obliquinervium* Merr.,

C. papuanum Lauterb., *C. polyanthum* Wall. ex Planch. & Triana, *C. tacamahaca* Willd. (syn. *C. spectabile* Willd.), *C. tetrapterum* Miq. (syn. *C. floribundum* Hook. f. and *C. venustum* King) and *C. tomentosum* Wight were also available for comparison at the Birbal Sahni Institute of Palaeosciences, Lucknow. The present fossil wood is identical to *C. tomentosum* Wight (slide no. BSIP232).

Lakhanpal and Awasthi (1965) instituted the genus *Calophylloxyton* to include the fossil woods showing resemblance with *Calophyllum*. So far, the following four species of the fossil genus were described from the Neogene of India: *Calophylloxyton indicum* Lakhanpal and Awasthi (1965) and *C. cuddalorensis* Lakhanpal and Awasthi (1965) from the Cuddalore Sandstone of South Arcot District, Tamil Nadu, *C. eoinophyllum* Prakash (1966a) from the Tipam Group of Deomali, Arunachal Pradesh (Khan *et al.* 2017) and *Calophylloxyton* sp. from the Warkalli beds of south India (Awasthi and Anhuja 1982). In addition, two more species, namely *C. intermedium* Müller-Stoll and Mädél-Angeliewa (1986) from the Tertiary of West Java and *C. tiebaghiense* Salard-Cheboldaef *et al.* (2012) from the Cenozoic of New Caledonia are also known. Our fossil wood is identical to *C. cuddalorensis*, while other species can be differentiated in having thicker rays, thinner axial parenchyma bands or lesser vessel frequency. Hence, the present fossil has been kept under *Calophylloxyton cuddalorensis*.

Calophyllum is a genus of about 80 species of trees distributed in tropics of both the hemispheres, but majority is found in the Indian subcontinent and southeast Asia. *C. tomentosum*, the modern comparable species of the fossil, occurs in the evergreen forests of Western Ghats, ascending up to 1500 m elevation (Tandon and Purkayastha 1958).

Genus: *Kayeoxyton* Chowdhury and Tandan (1949)

Kayeoxyton assamicum Chowdhury and Tandan (1949)
(figure 6a–f)

Description: Wood diffuse porous (figure 6a). Growth rings absent. Vessels circular to oval, tangential diameter range 38–104 µm and average 61 µm, almost solitary, tylosed, rarely forming oblique arrangement, 13–28 vessels per mm² (figure 6a, b); vessel elements 27–111 µm in length with horizontal to oblique ends; perforations simple. Vasicentric tracheids rarely present. Axial

parenchyma apotracheal banded, bands mostly continuous, sometimes broken, 3–13 cells wide, bandwidth 95–160 µm, regularly spaced. Rays 22–24 per mm, 1–2, rarely 3 seriate; uniseriate 2–4 cells or 62–121 µm high, 9–12 µm in width, multiseriate 16–23 cells or 144–515 µm in height, 19–23 µm in width (figure 6c, d); ray tissue heterogeneous; rays mostly made up of procumbent cells with extensions of 1–5 rows of upright cells, uniseriate rays made of upright cells; procumbent cells 10–15 µm in tangential height and 21–51 µm in radial length; square cells 25–40 µm in tangential height, 28–41 µm in radial length (figure 6f). Fibres libriform, polygonal in section, non-septate, 36–58 µm in width; occasionally with bordered pits (figure 6e).

Figured specimen: Specimen no. BSIP41161.

Horizon: Upper Siwalik (= Kimin Formation).

Locality: 1 km before Nirjuli on the Nirjuli–Banderdeva road.

Age: Late Pliocene–Early Pleistocene.

Affinities: The characteristic features of the fossil wood are: diffuse porous wood, thick apotracheal banded axial parenchyma, solitary and tylosed vessels, simple perforation plates, vasicentric tracheids, 1–3 seriate rays and non-septate libriform fibres with bordered pits. They indicate its affinities with the family Clusiaceae (Pearson and Brown 1932; Kribs 1959; Miles 1978; Ilic 1991). Chowdhury and Tandan (1949) prepared a list of taxa having diffuse porous woods with alternate bands of parenchyma and fibres and concluded that only *Kayea* Wall. of the Clusiaceae (now placed under Calophyllaceae) has the tendency to form oblique radial pattern. The other closely allied genera of the family are *Calophyllum* L. and *Mesua* L. which have larger but fewer vessels with more pronounced oblique pattern (Tandon and Purkayastha 1958). In view of the above-mentioned facts, the present fossil shows maximum similarities with *Kayea*. Tandon and Purkayastha (1958) studied woods of two species of *Kayea*, namely *K. kunsteleri* King and *K. nervosa* T. And. and found both of them anatomically indistinguishable.

Chowdhury and Tandan (1949) established the genus *Kayeoxyton* to include fossil woods showing affinities with *Kayea*. The only species of the fossil genus known so far is *K. assamicum* Chowdhury and Tandan described from the Tipam Group (late Miocene) of Assam. Later on, Prakash and Tripathi (1975) and Bande and Srivastava (1988) also recorded it from the Neogene of Assam and

Figure 6. *Kayeoxylon assamicum* Chowdhury and Tandan showing (a) distribution of vessels and thick apotracheal bands of axial parenchyma, (b) shape, size and distribution of vessels, (c) structure of rays, (d) mostly 1–2 seriate rays and non-septate fibres, (e) pits in fibres, and (f) heterogenous ray tissue.

West Bengal, respectively. As our fossil is also very similar to *Kayeoxylon assamicum*, it has been assigned to it.

Kayea is a tropical genus of small to medium trees and occurs in south and southeast Asia. Five species of it are found in India and Myanmar. In India, they are found in Assam, Sikkim and Andamans, especially in sub-montane forests (Tandon and Purkayastha 1958).

Family: Celastraceae

Genus: *Lophopetalumoxylon* Mehrotra et al. (1984)

Lophopetalumoxylon indicum Mehrotra et al. (1984) (figure 7a–e)

Description: Wood diffuse porous (figure 7a). Growth rings distinct, delimited by fibrous tissue. Vessels deformed due to compression, mostly small, tangential diameter range 72–97 µm and average 74 µm, solitary and in radial pairs, about 24 per mm², without tyloses and evenly distributed; vessel elements 42–141 µm in length with horizontal to oblique ends; perforations simple (figure 7a, b); intervessel pits bordered, alternate, 5–7 µm in diameter (figure 7d). Axial parenchyma

Figure 7. *Lophopetalumoxylon indicum* Mehrotra *et al.* showing (a) thin apotracheal bands of axial parenchyma, (b) thick walled fibres and structure of vessels, (c) uniseriate rays, (d) intervessel pits, and (e) homogeneous ray tissue.

apotracheal in the form of thin (2–4 celled), wavy bands (figure 7a, b); cells 6.5–8.5 µm in length and 5–6 µm in width. Rays uniseriate, 20–21 per mm, 2–8 cells or 28–154 µm high, 4–6 µm in width, made up of procumbent cells (figure 7c); ray tissue homogeneous, ray cells 17–43 µm in radial length and 11–21 µm in tangential height (figure 7e). Fibres angular in cross section, thick walled, non-septate, 3–4 µm in diameter. Intercellular canals absent.

Figured specimen: Specimen no. BSIP41162.

Horizon: Middle Siwalik (= Subansiri Formation).

Locality: Along Pappu Nala near the Naharlagun–Banderdeva road.

Age: Early Pliocene.

Affinities: The characteristic features of the fossil wood are: diffuse porous wood, vessels small solitary and in radial pairs, simple perforations, bordered alternate intervessel pits, thin apotracheal bands of axial parenchyma, uniseriate, homocellular rays, non-septate thick walled fibres and absence of intercellular canals. These characters cumulatively indicate their resemblance with

Celastraceae (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; Miles 1978; Ilic 1991). The fossil also shows some resemblance with *Bauhinia* L. of the Fabaceae and *Terminalia* L. of the Combretaceae. The former can be differentiated from the present fossil in having either storied rays or heterogeneous ray tissue, while the latter is distinct in possessing generally paratracheal parenchyma and septate fibres. Nigam (1963) proposed a key to differentiate various Indian genera of the Celastraceae and a perusal of this key indicates that our fossil is close to *Lophopetalum* Wight and *Kokoona littoralis* Lawson (syn. *Lophopetalum littorale* Ridl.), especially with the latter (slide no. BSIP3419).

Mehrotra *et al.* (1984) instituted the genus *Lophopetalumoxylon* for the fossil woods resembling *Lophopetalum*, including *L. littorale*. Its only species, *Lophopetalumoxylon indicum* was described from the Deccan Intertrappean beds of Dindori District, Madhya Pradesh (Mehrotra *et al.* 1984). The present fossil is identical to it and therefore, is kept under the same species.

Lophopetalum littorale, the modern comparable form of the fossil, is a large tree growing in Myanmar on low lands inundated during the rains (Nigam 1963).

Family: Ebenaceae

Genus: *Ebenoxylon* Felix (1882)

Ebenoxylon siwalicus Prakash (1981)
(figure 8a–d)

Description: Wood diffuse porous (figure 8a). Growth rings present marked by denser fibres (figure 8a). Vessels mostly small to medium, crushed due to compression, tangential diameter range 28–77 μm and average 66 μm , radial diameter 43–210 μm , solitary and in radial multiples of 2–6, 16–21 per mm^2 , evenly distributed, tylosed (figure 8a); vessel elements 180–206 μm in length with horizontal to oblique ends; perforations simple; intervessel pits alternate, round, about 6–7 μm in diameter. Axial parenchyma paratracheal scanty and apotracheal thin (mostly one celled thick) reticulate (figure 8a). Rays 1–3 (mostly 1–2) seriate, 25–30 per mm; uniseriates made up of upright cells, 3–23 cells or 76–861 μm high, 6–16 μm in width; multiseriates made up of procumbent cells with 1–4 rows of upright cells, 18–60 μm in width and 18–40 cells or 288–931 μm high (figure 8b, c); ray-to-ray fusion observed; ray cells mostly filled with dark contents; ray tissue heterogeneous,

procumbent cells 43–55 μm in radial length and 17–27 μm in tangential height, upright cells 32–46 μm in radial length and 54–60 μm in tangential height (figure 8d). Fibres angular in cross section, thick walled and non-septate.

Figured specimen: Specimen no. BSIP41163.

Horizon: Upper Siwalik (= Kimin Formation).

Locality: Near 7 km post on the Itanagar–Banderdeva road.

Age: Late Pliocene–Early Pleistocene.

Affinities: The characteristic features of the fossil wood such as diffuse porous wood, small to medium vessels arranged in radial multiples of 2–6, simple perforations, mostly thin reticulate axial parenchyma, predominantly 1–2 seriate rays, heterogeneous ray tissue and non-septate fibres indicate its affinity with modern woods of the families Apocynaceae, Ebenaceae, Myrtaceae, Rubiaceae and Sapotaceae (Pearson and Brown 1932; Metcalfe and Chalk 1950). However, the occurrence of vasicentric tracheids in woods of Apocynaceae, Myrtaceae, Rubiaceae and Sapotaceae differentiates them from the present fossil. Moreover, some genera of Myrtaceae have exclusively solitary vessels. Among various genera of the Ebenaceae, woods of *Diospyros* Linn. show near resemblance with the present fossil (Pearson and Brown 1932; Kribs 1959; Miles 1978; Kazmi 1982; Ilic 1991; <http://insidewood.lib.ncsu.edu/>). Besides published description and photographs, wood slides of the following species of *Diospyros*, namely *D. evena* Bakh., *D. guianensis* (Aubl.) Gürke, *D. kurzii* Hiern, *D. macrophylla* Bl., *D. malabarica* (Desr.) Kostel., *D. melanoxydon* Roxb., *D. pentamera* (F. Muell.) Woods and F. Muell., *D. pyrrhocarpa* Miq. and *D. virginiana* L. were consulted. The present fossil shows maximum resemblance with *D. melanoxydon*.

Felix (1882) established the genus *Ebenoxylon* for the fossil woods of *Diospyros*. Total 15 species of the genus are known from various parts of the world and are mentioned below: *Ebenoxylon aegypticum* Kräusel (1939) and *E. ebenoides* Kräusel (1939) from the Tertiary of Libya, *E. indicum* Ghosh and Kazmi (1958) from the late Miocene–Pliocene of Arunachal Pradesh, *E. arcotense* Awasthi (1970, 1984) from the late Miocene–Pliocene of Pondicherry, *E. kartikcherraense* Prakash and Tripathi (1970) from the Tipam Sandstone (late Miocene) of Assam, *E. mohgaoense* Chitale and Patil (1972) and *E. deccanensis* Trivedi and Srivastava (1982) from the Deccan Intertrappean beds of central

Figure 8. *Ebenoxylon siwalicus* Prakash showing (a) thin reticulate lines of axial parenchyma, (b) distribution of rays, (c) structure of 1–2 seriate rays and non-septate fibres, and (d) heterogeneous ray tissue.

India, *E. bavaricum* Selmeier (1976) from the Miocene of Bavaria, *E. miocenicum* Prakash (1978), *E. siwalicus* Prakash (1981), *E. kalagarhensis* Prasad (1989) and *E. palaeocalendula* Prasad (1993) from the Siwalik sediments of Uttarakhand, *E. obliquiporosum* Awasthi and Anhuja (1982) from the late Miocene–Pliocene of Kerala, *E. burmense* Du (1988) from the Pliocene of Myanmar and *E. neyveliensis* Mukherjee and Prasad (2013) from the late Miocene–Pliocene Neyveli lignite deposits of Tamil Nadu. Many of them are based on minor

characters, possibly due to intraspecific variations and, therefore, are difficult to be distinguished. The present fossil was compared with all of them and found close to *Ebenoxylon siwalicus* Prakash. The other species have either thinner rays or more paratracheal parenchyma.

Diospyros is a genus of about 450–500 species widely distributed in tropical and mild temperate regions of the world. *D. melanoxylon*, the modern counterpart of the fossil, is a common tree of mixed deciduous forests of peninsular India (Kazmi 1982).

Figure 9. *Hopeoxylon eosiamensis* Prakash showing (a) distribution of small to medium vessels, (b) concentric rows of vertical canals enclosed in axial parenchyma bands, (c) structure of rays, (d) 1–4 seriate rays and non-septate fibres, and (e) heterogeneous ray tissue.

Family: Fabaceae

Genus: *Hopeoxylon* (Navale) Awasthi (1977)

Hopeoxylon eosiamensis Prakash (1981)
(figure 9a–e)

Description: Wood diffuse porous (figure 9a). Growth rings delimited by thin bands of terminal parenchyma enclosing gum canals, bands 340–760 μm apart (figure 9a, b). Vessels round to oval, mostly small to medium sized, tangential diameter range 42–78 μm and average 63 μm , radial diameter 44–138 μm , solitary and in radial multiples

of 2 to 3, 22–30 per mm^2 , evenly distributed, dark brown gummy deposits present inside the vessels (figure 9a); vessel elements 147–180 μm in length with horizontal to oblique ends; perforations simple. Axial parenchyma paratracheal and apotracheal; paratracheal vasicentric forming 1–3 celled sheath around the vessels to aliform to confluent; apotracheal terminal enclosing the gum canals and thin short broken bands also observed (figure 9a, b). Rays 1–4 (mostly 2–3) seriate, 18–22 per mm ; uniseriats rare, 6–9 cells or 150–160 μm high, 11–27 μm in width; multiseriats 2–5 seriate, mostly

made up of procumbent cells with 1 or 2 rows of upright or square cells, 18–46 μm in width and 12–27 cells or 155–588 μm in height (figure 9c, d); ray tissue heterogeneous, procumbent cells 36–56 μm in radial length and 11–14 μm in tangential height; upright or square cells 19–36 μm in tangential height and 24–38 μm in radial length (figure 9e). Fibres polygonal in cross section, thick walled, non-septate, 5–7 μm in diameter. Gum canals normal, vertical in concentric rings and embedded in parenchyma bands, 80–150 μm in diameter (figure 9b).

Figured specimen: Specimen no. BSIP41164.

Horizon: Middle Siwalik (=Subansiri Formation).

Locality: Along Pappu Nala near the Naharlagun–Banderdeva road.

Age: Early Pliocene.

Affinities: The characteristic features of the fossil wood, viz., concentric rings of gum canals embedded in terminal parenchyma bands, vasicentric to aliform-confluent axial parenchyma, simple perforations, 1–4 seriate rays with heterogeneous ray tissue and non-septate fibres indicate its affinity with the xylogenically similar taxa *Copaifera* Linnaeus, *Detarium* Jussieu and *Sindora* Miquel of the Fabaceae (Metcalf and Chalk 1950; Normand 1950; Kribs 1959; Ilic 1991). The fossil does show superficial resemblance with *Daniella* Benn. and *Sindoropsis* J. Léonard of the Fabaceae and *Shorea* Roxb. ex C.F. Gaertn. of the Dipterocarpaceae. However, *Daniella* is distinct in having storied elements; *Sindoropsis* has slightly narrower rays and intercellular canals in short tangential rows, while *Shorea* can be differentiated in having vasicentric tracheids (<http://insidewood.lib.ncsu.edu/>). Besides published literature, wood slides of two species of *Detarium*, namely *D. macrocarpum* Harms and *D. senegalense* J.F. Gmel. and seven species of *Sindora*, viz., *S. beccariana* de Wit, *S. echinocalyx* Prain, *S. irpicina* de Wit, *S. siamensis* Miq. (syn. *S. cochinchinensis* Baill.), *S. supa* Merr., *S. tonkinensis* A. Chev. and *S. velutina* Baker were available for study. Of them, our fossil shows maximum resemblance with *S. siamensis* Miq. The genus *Copaifera* occurs in tropical America and Africa, while *Detarium* is confined to tropical Africa only. *Sindora* is usually found in southeast Asia, Hainan, western Malaysia, Celebes and Molucca (Ridley 1967; Willis 1973).

Fossil woods resembling *Sindora* and allied forms, such as *Copaifera* and *Detarium* were

described under the fossil genus *Hopeoxylon* (Navale) Awasthi (1977). So far nine species of the genus, namely *H. aethiopicum* (Lemoigne et al.) Lalitha and Prakash (1980) from the Miocene of Ethiopia, *H. arcotense* Awasthi (1977) from the Neogene of south India, *H. assamicum* Lalitha and Prakash (1980) from the Miocene of Assam and West Bengal (Bera et al. 2001), *H. eosiamensis* Prakash (1981) from the Lower Siwalik sediments of Uttarakhand, *H. indicum* (Navale) Awasthi (1977) from the Neogene of south India and Oligo-Miocene of Saudi Arabia (Prive-Gill et al. 1999), *H. libycum* (Boureau and Louvet) Lalitha and Prakash (1980) from the Palaeogene of Libya, Algeria and Tunisia, *H. migiurtinum* (Chiarugi) Lalitha and Prakash (1980) from the Miocene of Somalia, *H. sindoroides* (Kramer) Lalitha and Prakash (1980) from the Tertiary of West Kalimantan and *S. speciosum* (Navale) Awasthi (1977) from the Neogene of south, north (Prakash et al. 1988) and northeast India (Mehrotra et al. 2005) are known (Prakash et al. 1988, Prive-Gill et al. 1999). Of them, *H. arcotense* was considered by Prakash et al. (1988) as synonym to *H. speciosum*. The present fossil shows maximum resemblance with *H. eosiamensis* and hence has been assigned to it. The other species can be distinguished from our fossil in width, height and homogeneity of the rays.

Sindora siamensis, the modern comparable species of the fossil, is a large evergreen tree found in open semi-deciduous forests of Kampuchea, Laos, Malaysia, Thailand and Vietnam.

Genus: *Pahudioxylon* Chowdhury et al. (1960)

Pahudioxylon indicum Prakash (1979)
(figure 10a–f)

Description: Wood diffuse porous (figure 10a, b). Growth rings marked by terminal parenchyma (figure 10a). Vessels round to oval, mostly medium to large, tangential diameter range 76–199 μm and average 119 μm , mostly solitary, occasionally in radial pairs, 10–16 per mm^2 , evenly distributed, filled with black gummy deposits (figure 10a, b); vessel elements 59–173 μm in length with horizontal to oblique ends; perforations simple; intervessel pits alternate, vestured, 5–7 μm in size (figure 10e). Axial parenchyma both apotracheal and paratracheal; apotracheal terminal in the form of one-celled thick band, bands about 850 μm apart, paratracheal vasicentric to aliform to confluent (figure 10a, b). Rays 1–3 (mostly bi) seriate, 8–14

Figure 10. *Pahudioxylon indicum* Prakash showing (a) medium to large vessels and terminal parenchyma, (b) vasicentric to aliform axial parenchyma, (c) structure of rays, (d) 1–3 seriate rays and non-septate fibres, (e) vestured intervessel pits, and (f) homogeneous ray tissue.

per mm, irregularly storied, made up of procumbent cells, 11–21 μm in width and 3–22 cells or 60–286 μm in height (figure 10c, d); ray tissue homogeneous; ray cells filled with dark contents, 27–46 μm in radial length and 17–26 μm in tangential height (figure 10f). Fibres polygonal in cross section, thick walled, non-septate, 3.5–4.5 μm in diameter.

Figured specimen: Specimen no. BSIP41165.

Horizon: Middle Siwalik (= Subansiri Formation).

Locality: Along Pappu Nala near the Naharlagun–Banderdeva road.

Age: Early Pliocene.

Affinities: The important features of the fossil wood, viz., diffuse porous wood, growth rings

marked by terminal parenchyma, mostly solitary vessels filled with black gummy deposits, simple perforations, vestured intervessel pits, mostly aliform-confluent axial parenchyma, 1–3 seriate, homocellular, irregularly storied rays and non-septate fibres indicate its affinities with anatomically inseparable genera *Afzelia* Sm.-*Intsia* Thouars of the Fabaceae (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; Ramesh *et al.* 1972; Ilic 1991). However, our fossil resembles the best with *I. bijuga* (Colebr.) Kuntze (slide no. BSIP810). There are some more genera of the Fabaceae, namely *Aphanocalyx* Oliv., *Baiki-aea* Benth. & Hooker f., *Brachystegia* Benth., *Caesalpinia* L. and *Cassia* L. showing some resemblance with the fossil. *Aphanocalyx* in having

mostly exclusively uniseriate rays can be differentiated from our fossil, whereas *Baikiaea* possesses banded parenchyma also and is therefore, distinct from our fossil. In *Brachystegia* rays, vessel elements and fibres, etc., are all typically storied; *Caesalpinia* has all rays storied and often lack marginal parenchyma, whereas rays are generally non-storied in *Cassia*.

Chowdhury *et al.* (1960) instituted the genus *Pahudioxylon* for the fossil woods showing similarities with those of *Pahudia* Miq. As *Pahudia* was already merged with *Afzelia*, Prakash (1966b) redefined the genus *Pahudioxylon* to include fossil woods of *Afzelia* and *Intsia* also. So far, 18 species of it are known from various Cenozoic exposures of the world: *P. bankurensis* Chowdhury *et al.* (1960), *P. bengalensis* Ghosh and Roy (1982) and *P. garbetaense* Bera and Banerjee (2001) from West Bengal, *P. sahnii* Ghosh and Kazmi (1961) from Tripura, *P. arcotense* Navale (1963) from Pondicherry, *P. deomaliense* Prakash (1966b) from Arunachal Pradesh, *P. assamicum* Prakash and Tripathi (1975) from Assam, *P. indicum* Prakash (1979) from Himachal Pradesh (all from India), *P. afzeloides* (Boureau) Prakash *et al.* and *P. kiliani* (Louvete) Prakash *et al.* from Indo-China and Algeria, respectively (Prakash *et al.* 1967), *P. menchikoffi* (Boureau) Müller-Stoll and Mädél-Angeliéwa (1967) from Algeria, *P. irregulare* (Felix) Müller-Stoll and Mädél-Angeliéwa and *P. pannonicum* (Felix) from Antigua and Hungary respectively (Müller-Stoll and Mädél-Angeliéwa 1967), *P. welkitii* Lemoigne and Beauchamp (1973) from Ethiopia, *P. gehannemense* Louvet (1975) from Libya, *P. paracochinchinense* Vozenine-Serra (1981) from South Vietnam and *P. furoni* (Koeniguer) Guleria (1984) and *P. aethiopicum* (Lemoigne *et al.*) Guleria (1984) from the Republic of Chad and Ethiopia, respectively (<http://insidewood.lib.ncsu.edu/>). Most of these species were established on the basis of minor variations and there is a possibility that some of them could be merged into one another. We have compared our fossil in detail, especially with the Indian species and found that our fossil shows maximum similarities with *P. indicum* Prakash (1979) known from the Siwalik of Himachal Pradesh. The only difference was in the frequency of vessels which is more in number in the present fossil. The other species are distinct in having either broader rays or thicker terminal bands of parenchyma. In order to avoid creation of a new species, we have kept our fossil under *Pahudioxylon indicum*.

Afzelia is a genus of 12 species distributed in tropical Africa and Asia (Willis 1973; Mabberley 1997), whereas *Intsia* consists of nine species found in offshore islands of tropical east Africa, Madagascar and tropical Asia. *Intsia bijuga*, the nearest comparable species of the fossil, occurs in tidal forests of Sunderbans, Andaman Islands and Myanmar.

5. Discussion

On land, the distribution of biota is mainly governed by its corresponding climatic conditions (Jansson 2003; Woodward *et al.* 2004) and this can be viewed even in the fossil records (Jansson 2003; Srivastava and Mehrotra 2013; Srivastava *et al.* 2015). So the fossil records are important to reconstruct the ancient climate and distribution of the organisms.

The Nearest Living Relative (NLR) approach is used for the reconstruction of palaeoecology and palaeoclimatology. This method considers that the climatic requirements of a fossil taxon are similar to the ones of its NLR and is confidently used by the palaeobotanists in the palaeoclimate reconstruction (Bande and Chandra 1990; Prakash *et al.* 1994; Estrada-Ruiz *et al.* 2007; Jeong *et al.* 2009; Srivastava *et al.* 2009; Feng *et al.* 2010; Bamford 2011; Mehrotra *et al.* 2011, 2013, 2016; Tiwari *et al.* 2012; Licht *et al.* 2014, 2015). The modern analogues of the fossil assemblage are: *Miliusa velutina* (Annonaceae), *Calophyllum tomentosum* and *Kayea* (Calophyllaceae), *Lophopetalum littorale* (Celastraceae), *Diospyros melanoxyton* (Ebenaceae), *Intia bijuga* and *Sindora siamensis* (Fabaceae). It is interesting to note that *Calophyllum tomentosum* is restricted to wet evergreen forests of Western Ghats and Sri Lanka, while *Kayea* is found in wet evergreen forests of south and southeast Asia. *Sindora siamensis* is deciduous to semi-evergreen tree now growing in southeast Asia. The modern analogues of the fossil assemblages are mainly growing in the tropical wet evergreen to moist deciduous forests indicating high rainfall; moreover, the presence of legumes and *Diospyros melanoxyton* indicates seasonality in the rainfall. The presence of *Lophopetalum littorale* and *Intsia bijuga* again supports the presence of high rainfall.

Plants have limited options to escape from adverse environmental conditions. Under such circumstances, they modify their external as well as

internal architectural features for adaption. The modification in architectural structures, regardless of their taxonomic affinities, can be viewed either externally (Bailey and Sinnott 1915, 1916; Wolfe and Upchurch 1987; Spicer *et al.* 2011) or internally (Carlquist 1975, 1977, 1988; Baas 1976, 1986). These modified architectural features are often used in the reconstruction of palaeoclimate (Bailey and Sinnott 1915, 1916; Wolfe 1979; Wheeler and Baas 1991, 1993; Wiemann *et al.* 1998; Poole 2000; Mehrotra *et al.* 2011; Spicer *et al.* 2011; Srivastava *et al.* 2012; Tiwari *et al.* 2012). In case of woods, several anatomical features have been identified which directly or indirectly represent their corresponding climatic conditions such as density and diameter of vessels, presence or absence of growth rings, diffuse porosity, vessel grouping, structure of perforation plate, intervessel pitting, extent of parenchyma and nature of ray (Wolfe and Upchurch 1987; Wheeler and Baas 1993; Woodcock and Ignas 1994). The characters such as diffuse porosity and indistinct growth rings in woods, large diameter of vessels with low density conjointly infer tropical climate with low seasonality (little variation) in temperature (Wheeler and Baas 1993; Woodcock and Ignas 1994). The dominance of diffuse porosity in woods of Lower and Upper Siwalik infers a tropical climate with little seasonality in the warm and cold month temperatures. The high proportion of large vessels and simple perforation plates in the present assemblages suggest high precipitation (Wolfe and Upchurch 1987). The presence of simple perforation plates often represents an adaptation to more efficient water transport (Wheeler and Baas 1993). All the aforesaid-inferences get more support from the previous quantitative palaeoclimate analysis, based on the leaf architecture, done by Khan *et al.* (2014a).

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