

Fossil wood *Shoreoxylonornatum* from upper Miocene sediments of Sarkaghat, Himachal Pradesh: Palaeoclimatic and biogeographic implications

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ABSTRACT

A fossilized wood, discovered for the first time in the Middle Siwalik (Upper Miocene) sediments of NaladKhad in the Sarkaghat area, Mandi District, Himachal Pradesh, has been identified as *Pentacmesuavis* A. DC. (Synonym *Shoreasiamensis* (Kurz) Miq.), belonging to the family Dipterocarpaceae. The wood exhibits distinctive anatomical features, including concentric vertical gum canals, vasicentric tracheids, and predominantly solitary vessels of varying sizes, diffuse and diffuse-in-aggregate apotracheal parenchyma, heterocellular xylem rays, and thick-walled fibers. The comparable extant species currently found in south-east Asia's tropical evergreen to moist deciduous forests, suggests that a tropical humid climate with high precipitation prevailed in the region during the Upper Miocene. The co-occurrence of *ShoreaRoxb.* with other dipterocarpaceous and fabaceous taxa indicates a lush tropical vegetation sustained by consistent warmth and humidity. Fossil evidence further confirms *ShoreaRoxb.* widespread presence across the Indian subcontinent from the early Eocene to the Plio-Pleistocene.

Key-Words: Anatomy, Fossil wood, Himachal Pradesh, PalaeoclimatePhytogeography, Sarkaghat area, *ShoreaRoxb.* (Dipterocarpaceae), Siwalik (Upper Miocene)

INTRODUCTION

The Siwalik sediments exposed between the Himalayan Frontal Thrust (HFT) in the south and Main Boundary thrust (MBT) in the north contains post collisional fluvial molasse sediments by erosion of the rising Himalaya ranging in age from 18.3 Ma (Johnson et al, 1985) to 0.22 Ma (Ranga Rao, 1972). The fossil locality (N 31° 44' 26" E 76° 43'33") lies along the National Highway 70 very near to Sarkaghat area of Mandi District, Himachal Pradesh (Fig. 1). More than 150 specimens of leaf impressions were collected from middle Siwalik beds exposed in a road cutting section (N31° 44.265': E76 °.43.339') about 7Km from Sarkaghat town on the left side of main road which leads to Dharampur and easily approachable through vehicle. About 8 km from the leaf fossil site is the NaladKhad section (N. 31°46'N, E.76°43'E) from where few fossil woods were collected for the present study. This section has been magnetostratigraphically studied and dated by earlier workers, Brozovic and Burbank (2000). The NaladKhad section is located at, on the western limb of the Sarkaghat anticline, and in the Jawalamukhi thrust sheet. It is characterized by mainly thick units of fine to coarse, dark grey indurate, multistoried sandstones with red,

yellow and brown pedogenic mudstones. From western Siwalik belt, the palaeobotanical work has been carried out from the Siwalik of the Nalagarh (Prakash, 1975, 1979; Yadav, 1989) Jawalamukhi and Ranital (Ghosh and Ghosh, 1958; Lakhanpal, 1967, 1968, 1969; Lakhanpal and Dayal, 1966, Lakhanpal and Awasthi, 1992) and Bilaspur (Prasad, 2006). In view of the previous meagre work on the western Siwalik belt of Himachal Pradesh, authors surveyed different Siwalik fossil localities and collected large number of plant fossils from the Middle Siwalik sediments of Sarkaghat in Mandi District, Himachal Pradesh (Fig. 1). Investigation on the fossil woods and of Sarkaghat area revealed the occurrence of phytogeographically important genus, *ShoreaRoxb.* of the family Dipterocarpaceae which has been described and discuss in detail herewith.

GEOLOGY OF THE AREA

The Sarkaghat Anticline is exposed in the northeast part of the Kangra reentrant of the Himachal Sub-Himalaya along the northerly dipping Main Boundary Fault (MBF). Between the NNW-SSE trending AwahDevi-Lamba Graon syncline in south and Main Boundary Fault (MBF) in north .It is a regional structure in the

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Paleogene-Siwalik belt around west Sarkaghat. Based on litho-association, grain size, compactness and internal geometry of beds, five mappable lithostratigraphic units of the Siwalik Group have been classified viz. Nahan Formation of the Lower Siwalik Subgroup, Dewal and Mohargarh formations of the Middle Siwalik Subgroup and Pinjor and Kalar formations of the Upper Siwalik Subgroup within the MBF related Sarkaghat Anticline structure. The Nahan Formation (i.e. Chinji Formation) consists of fine grained, compact, grey white, occasionally flaggy sandstone with minor brick red mudstone/claystone along the core portion of the anticline. It shows gradational contact with the underlying Kasauli Formation of the Sirmur Group. The Dewal Formation (i.e. Nagri Formation) of the Middle Siwalik Subgroup comprises medium grained, grey to buff-brown and less compact sandstone and brick red to purple siltstone and friable red-brown to variegated color, nodular claystone/ mudstone with or without intra-formational conglomerate (IFC) lenses. Overlying the Dewal Formation with gradational contact, the Mohargarh Formation (i.e. Dhok Pathan Formation) comprises rather friable, massive, multistoried, medium to coarse grained, greenish-grey micaceous sandstone having polygonal cracks/fractures, pebbly conglomerate horizons and occasionally grey/ khaki mudstone bands. Having pebblier conglomerate bands, this litho-assemblage of the Mohargarh Formation differ from litho-pack of the Mohargarh Formation exposed in other parts of the Siwalik belt, probably due to proximal part of the Siwalik belt

The Mohargarh Formation show local erosional unconformity with the overlying coarserudaceous sediments of the Pinjor Formation around Baddu, Laungni and Duhgni areas. The Pinjor Formation comprises alternate sequence of coarse to gritty sandstone and polymictic, pebbly conglomerate almost in equal proportion along with minor grey to reddish brown siltstone/mudstone. This lithostratigraphic unit is well exposed around Kharot, Riyur, and Khera area. The successive lithostratigraphic unit the Kalar Formation (i.e. Boulder Conglomerate Formation) of the Upper Siwalik Subgroup conformably overlies the Pinjor Formation and well exposed around Marhi, Tihra, Kamlagarh and Dolan areas up to MBF in the northeast. This unit is well exposed along the footwall vicinity of the SE segment of

the MBF around Sarkaghat area. It comprises polymodal and polymictic boulderyconglomerate sequence along with sandy to muddy matrix and coarse sandstone/mudstone lenses. The clast size increases in younging direction towards MBF (up to >2 m diameter boulders). The clasts are composed of different colored quartzite, sandstone, granite/gneiss, mud stone, and limestone, slate and basic rocks in descending order of abundance in Sarkaghat Anticline area. Almost all the formations contain burnt wood/ charcoal pocket and thin carbonized layers. The pole plot of bedding data also indicates that the Sarkaghat anticline structure is a gentle, asymmetrical, inclined fold having northwesterly plunge (average 28° towards 333°) with steeper northern limb. The geometry and kinematics of the MBF, upright Sarkaghat anticline, joints and cum minor secondary faults of the area suggest the NE-SW trending, sub-horizontal maximum tectonic compression axis of the terminal phase of Himalayan tectonics to form the MBF related Sarkaghat Anticline in the area. Cande and Kent (1992) also correlated the local magnatic polarity stratigraphy (MPS) to the global magnetic polarity stratigraphic time scale (MPTS).

MATERIAL AND METHODS

The plant fossils comprising fossil woods, leaf, fruit and seed impressions have been collected from several fossil localities exposed in and around Sarkaghat area in the Himalayan foot hills of Himachal Pradesh. The petrified fossil wood described and discussed in this text was collected from NaladKhad section, near manufacturing bridge ($N31^\circ 45.519'$: $E76^\circ 42.576'$) about 17 km from Sarkaghat on Dharampur Road, Mandi District, H.P. The fossil wood has been cut into thin slices through transverse, Tangential longitudinal and Radial longitudinal with the help of diamond edged blade and then ground into thin sections on grinding disc by using different grades of carborandum powder. The prepared sections (TS, TLS and RLS) will be examined under high power microscope and their identification has been done with the modern taxa on the basis of published literature on anatomy and through examination of wood slides of modern plants housed in the Xylaria of Birbal Sahni Institute of

Palaeobotany, Lucknow. For the description of the fossil wood, we follow Wheeler *et al.* (1986) and International Association of Wood Anatomists (1989). The photographs of the wood slide showing a variety of anatomical features have been taken with the help of camera attached to the microscope. The fossil specimen and Photographs/ Negatives have been deposited in the Museum of Birbal Sahni Institute of Palaeosciences, Lucknow.

Systematics of fossil wood

Family: Dipterocarpaceae

Genus: *Shoreoxylon* Den Berger, 1923

Shoreoxylonornatum (Trivedi and Ahuja) Bande and Prakash, 1980
(Figures A-G)

1979 *Shoreoxylonornatum* Trivedi and Ahuja, p. 646, figs. 1-5

1980 *Shoreoxylonornatum* (Trivedi and Ahuja) Bande and Prakash, p.

Material: This species is based on a single piece of secondary wood measuring about 6cm in length and 4cm in diameter.

Description: Wood diffuse- porous. **Growth rings** absent. **Vessels** mostly small to large, t.d. 70-305µm, r.d. 65-310 usually solitary, usually compressed due to pressure during fossilization, sometimes in radial multiples of 2-3, 7-10 per sq mm; tyloses present (Figs. A, B); perforation simple; intervessel pits vestured, 4-8 µm in diameter (Fig. G). **vasicentric tracheids** occurring in the immediate vicinity of vessels, intermingled with parenchyma. **Parenchyma** paratracheal and apotracheal; paratracheal parenchyma scanty to paratracheal rarely vasicentric forming 1-3 seriate, interrupted sheath around the vessels; apotracheal parenchyma diffuse to diffuse-in-aggregate, apotracheal parenchyma also present, surrounding the gum canals (Figs. A, B). **Xylem rays** fine to broad, 1-5 (usually 4-5) cells or 15-105 µm wide and 3-55 cells or 160-1350 µm in height, rays homo to heterocellular with 1-5 marginal rows of upright cells at the ends, sheath cells almost continuously arranged in one or both the flanks (Figs. C, D, E). **Ray tissues** heterogeneous; procumbent cells 14-25µm in tangential height and 20-150µm in radial length; upright cells 35-55µm in tangential height and 20-30µm in radial length (Fig. E). **Fibres** semi-libriform, moderately thick-walled, nonseptate,

10-30 µm in diameter and 320-650 µm in length; interfibre pits could not be seen (Fig. F). **Gum canals** normal, well preserved vertically arranged in concentric rows, enclosed by thick apotracheal bands of parenchyma and 80-160 µm in tangential diameter (Fig. B).

Specimen: BSIP Museum specimen no. 41236.

Horizon and Age: Middle Siwalik Formation, Upper Miocene.

Locality: NaladKhad section, near manufacturing bridge (31° 45.519':76° 42.576'), about 17 km from Sarkaghat on Sarkaghat – Dharampur Road, Mandi District, H.P.

Affinity with extant taxa

The diagnostic features of the present fossil wood are the presence of normal, vertical gum canals in concentric rings, vasicentric tracheids, mostly solitary and small to large sized vessels, diffuse and diffuse-in aggregate apotracheal parenchyma, heterocellular xylem rays and thick-walled fibres. These features collectively indicate its affinity with the modern woods of the family Dipterocarpaceae. On the basis of the distribution of gum canals the woods of this family has been divided into following three groups.

Group I- Gum canals absent, e.g.

Monotes and *Marquesia*.

Group II- Gum canals present, always inconcentric rings, e.g.

Shorea, *Doona*, *Hopea*. *Isoptera*, *Parashorea*, *Pentacme*, *Balanocarpus*, *Dryopbalanops* and *Doona*

Group III- Gum canals diffuse solitary and in short tangential rows, e.g.

Anisoptera, *Dipterocarpus*, *Vateria*, *Vatica*, *Upuna*, *Cotylelobium* and *Monoporandra*

Due to the presence of concentric rings of gum canals the present fossil wood can be assigned to the genera included in Group II. Although the fossil wood shows somewhat near resemblance with the woods of *Parashorea* but differs from the present fossil wood in having somewhat narrow, 1-6 (usually 3-5) seriate xylem rays with occasional sheath cells on one or both the flanks. However, in the fossil wood the rays are 1-5 seriate with almost complete row of sheath cells on both the flanks. *Balanocarpus* and *Dioticarpus* are also different in possessing mostly small to medium-sized vessels. *Balanocarpus* can further be differentiated due to

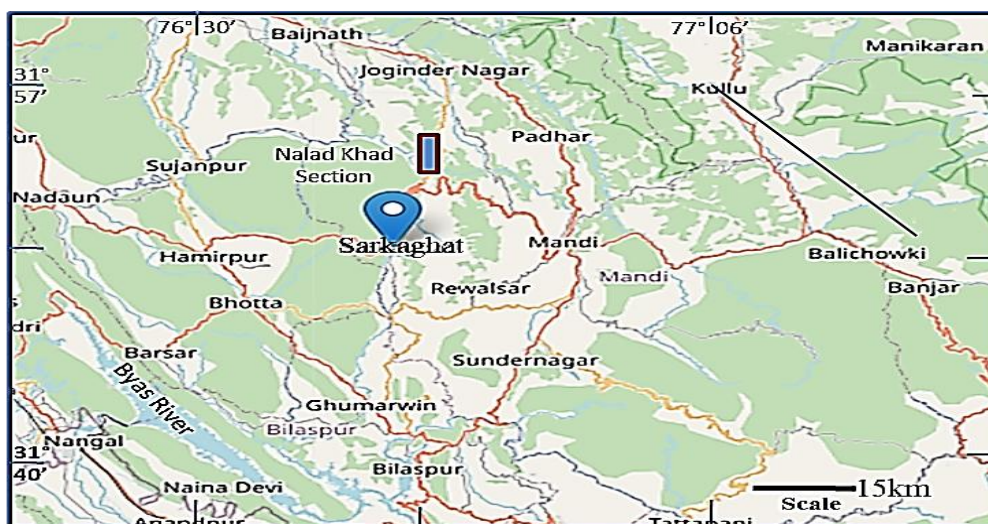


Figure 1: Google map showing location of the study area in Sarkaghat, Mandi district, Himachal Pradesh, India indicating the occurrence of fossil wood

the presence of ripple marks (*B. heinii*). *Dryobalanops* possesses almost exclusively solitary vessels and thick-walled fibers with distinct bordered pits. The wood of *Hopea* can also be easily differentiated from the present fossil wood in possessing mostly small-sized vessels and upright cells interspersed among the procumbent cells of the rays. However, in the present fossil wood there are mostly medium to large vessels and upright cells are only arranged at the ends of the rays. The woods of *Isoptera* differ from the present fossil in possessing small, spindle shaped rays without sheath cells. Similarly, *Doona* can be differentiated in having abundant paratracheal parenchyma varying from aliform to confluent and uniseriate xylem rays in contrast to scanty or vasicentric, paratracheal parenchyma and 1-5 seriate xylem rays in the present fossil wood.

Further, from a detailed examination of thin sections and published literature on anatomy of all the available species of the genera belonging to this group, it has been found that the present fossil wood resembles the wood of the extant genus *Pentacme* A. DC. In order to find out the nearest modern equivalent of the present fossil wood, thin sections of modern woods of all the available species of *Pentacme* A. DC. were examined. A study of the anatomical characters of the species of *Pentacme* A. DC. indicates that the wood of *Pentacmesuavis* A. DC. (Syn. *Shoreasiamensis* (Kurz.) Miq. shows closest affinity with the present fossil wood.

FOSSIL RECORD AND COMPARISON

Schweitzer (1958) classified the fossil dipterocarpaceous woods which have gum canals in tangential bands into two form genera, viz., *Shoreoxylon* Den Berger (1923) and *Dryobalanoxylon* Den Berger (1923). The genus *Dryobalanoxylon* includes woods with both libriform fibers and fiber tracheids and exclusively solitary vessels while *Shoreoxylon* consists of woods possessing only libriform fiber. The first group includes only *Dryobalanops*, while the other one includes all the remaining genera of Shoreae group. More than 25 fossil woods resembling the genera of Shoreae group are described from India and abroad. Some of the available species are *Shoreoxylonpalembangense* (Krausel) Den Berger (1923), *S. dajmbiense* Den Berger (1923), *S. asiaticum* Schweitzer (1958), *S. maximum*, *Shoreoxylon cf. posthumi* Schweitzer (1958) from the Tertiary of Sumatra, *S. multiporosum*, *S. pulchrum* and *S. posthumi* Schweitzer (1958) from the Quaternary of Sumatra, *S. moroides* Den Berger (1927), *S. parvum* Schweitzer (1958) from the Pliocene of Java, *S. swendenbergi* (Schuster) Schweitzer (1958) from the Pliocene of East Indies, *S. burmense* Prakash (1965) and *S. irrawaddiensis* Prakash and Bande (1980) from the Tertiary of Burma, *S. evidens* Eyde (1963), *S. tipamense* Prakash and Awasthi (1970), *S. deomaliense* Prakash and Awasthi (1971) from the Tertiary of Assam, *S. speciosum* Navale (1963), *S. krauseli*

Ramanujam and Rao (1967, 1969) from Tertiary of South India. *Shoreoxylonburmense* Prakash reported from Tertiary of western India (Shukla *et al.*, 2013). The species recorded from the Indian subcontinent are quite different from our present fossil wood. *S. krauseli* and *S. irrawaddiensis* differ from the present fossil wood in having only 1 or 2 marginal rows of upright cells in the xylem rays as against 1-5 marginal row of upright cells in the rays of the fossil wood. *S. burmense* and *S. tipamense* also differ from the present fossil wood in the parenchyma distribution as the diffuse and diffuse-in - aggregate parenchyma is sparse. The xylem rays are with occasional sheath cells in *S. tipamense* as against 1-5 seriate xylem rays with complete row of sheath cells on one or both the flanks in the present fossil wood. *Shoreoxylon speciosum*, *S. evidens*, *S. deomalinese* and *S. arcotense* differ from the present fossil in the absence of apotracheal, diffuse and diffuse-in - aggregate parenchyma. The apotracheal parenchyma is found only enclosing the concentric gum canals, whereas in the fossil wood there is presence of apotracheal diffuse and diffuse-in-aggregate parenchyma. Besides, the xylem rays in *S. speciosum* are homogeneous as against heterogeneous rays in the present fossil wood. *S. indicum* can also be differentiated from the fossil wood in having abundant, confluent to banded paratracheal parenchyma and only 1-2 seriate marginal rows of upright cells in the xylem rays as against scanty to vasicentric paratracheal parenchyma and 1-5 rows of upright cells in the xylem rays of the fossil wood. *S. bengalensis* is also markedly different from this Siwalik fossil wood because diffuse and diffuse-in - aggregate parenchyma is absent. Thus from the above detailed comparison, it is quite evident that the present fossil wood is different most of the species of *Shoreoxylon* Den Berger (1923). It shows closest affinity with the fossil wood, *Shoreoxylonornatum* (Trivedi and Ahuja) Bande and Prakash, 1980 described from Lower Siwalik sediments of Kalagarh area, Uttarakhand. Therefore, the present fossil wood has been kept under the specific name *Shoreoxylonornatum* (Trivedi and Ahuja) Bande and Prakash.

RESULTS AND DISCUSSION

Dipterocarpaceae is one of the phytogeographically important family of the Asian rain forests (Ashton, 1982) of the order Malvales consisting of 470 species belonging to 17 genera. In India, the dipterocarpaceous species are mainly distributed in tropical peninsula from Karnataka coast to the tip of southern and northeast region. *Pentacme* A. DC. includes only 8 species which are widely distributed in the world from Sri Lanka and India on the west and throughout Burma and other countries of Southeast Asia up to Philippines in the east (Widiyatno *et al.*, 2013). *P. suavis* A. DC. (Syn. *Shorea siamensis* (Kurz) Miq. with which present fossil wood resembles is canopy tree of dry dipterocarps forests occurring in Malaya, South-east Asia, Myanmar, Thailand, Malaysia, Cambodia, Laos, and Vietnam (Pearson and Brown, 1932; Pooma *et al.*, 2017).

A number of fossil woods resembling the genus *Shorea* Roxb. are described from India and abroad under the organ genus *Shoreoxylon* (Den Berger, 1923). These are *Shoreoxylonpalembangense* (Krausel) Den Berger (1923), *S. djambiense* Den Berger (1923), *S. asiaticum* Schweitzer (1958), *S. maximum*, *Shoreoxylon cf. posthumi* Schweitzer (1958) from the Tertiary of Sumatra, *S. multiporosum*, *S. pulchrum* and *S. posthumi* Schweitzer (1958) from the Quaternary of Sumatra, *S. moroides* Den Berger (1927), *S. parvum* Schweitzer (1958) from the Pliocene of Java, *S. szvendmbergi* (Schuster) Schweitzer (1958) from the Pliocene of East Indies, *S. burmense* Prakash (1965) and *S. irrawaddiensis* Prakash and Bande (1980) from the Tertiary of Burma, and *S. burmense* Prakash from western India (Shukla *et al.*, 2013). *S. evidens* Eyde (1963), *S. tipamense* Prakash and Awasthi (1970), *S. deomaliense* Prakash and Awasthi (1971) from the Tertiary of Assam, *S. speciosum* Navale (1963), *S. krauseli* Ramanujam and Rao (1967, 1969), *S. indicum* and *S. arcotense* Awasthi (1974) from the Miocene-Pliocene of Cuddalore Series, South India, *S. bengalensis* Roy and Ghosh (1979) and *S. tipamense* Prakash and Awasthi (Bande and Prakash, 1980) from the Tertiary of West Bengal and *S. ornatum* (Trivedi and Ahuja) Bande and Prakash, (1980) and *S. siwalicus* (Prasad and Prakash, 1988) from Siwalik sediments of

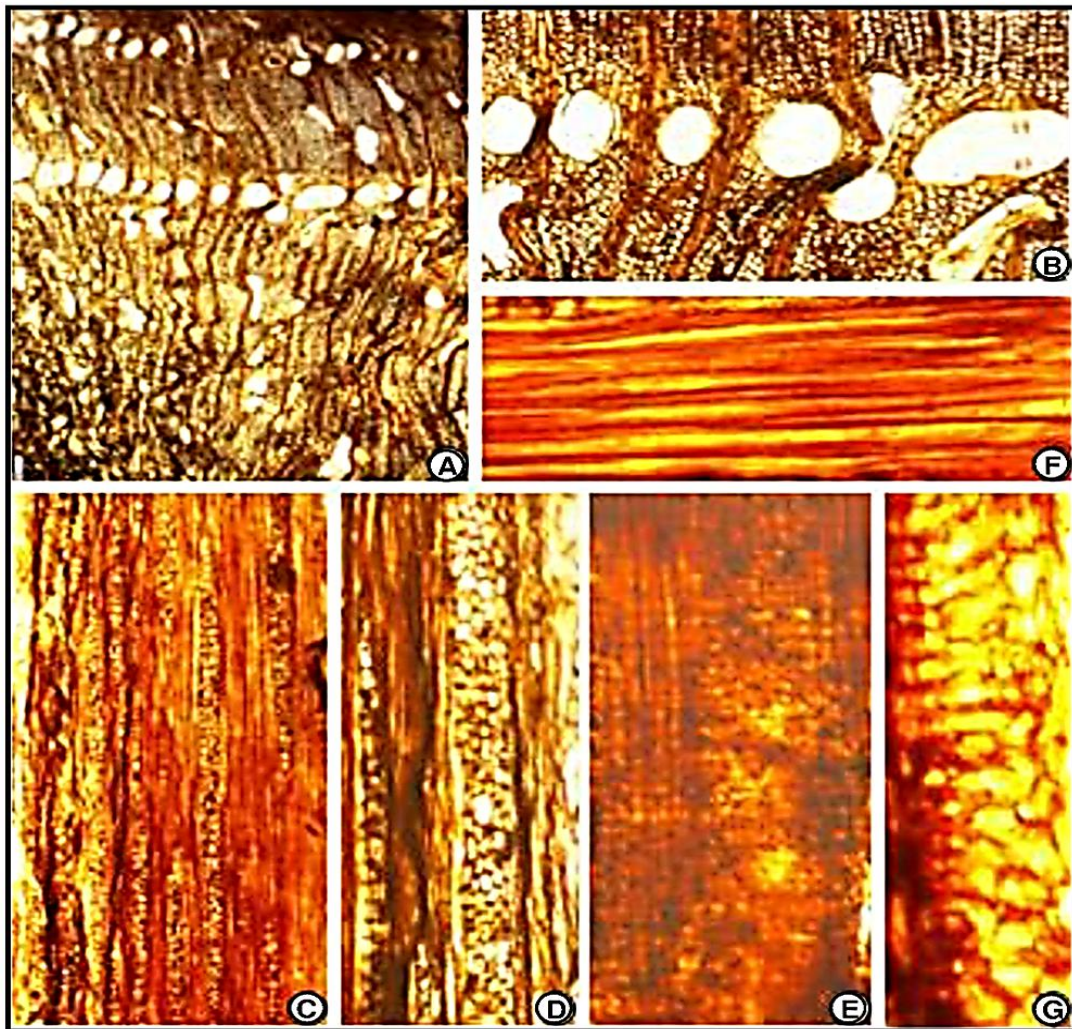


Figure3: *Shoreoxylon ornatum* (Trivedi & Ahuja) Bande and Prakash A. Cross section of fossil wood showing nature of vessels, xylem rays, fibre and gum canals. BSIP wood slide no - 41236-I.B. Cross section of fossil wood magnified to show detail of parenchyma, gum canal and compressed vessels. BSIP wood slide no - 41236-I. C. Tangential longitudinal section of fossil wood showing nature of xylem rays and parenchyma strand. BSIP wood slide no - 41236-II. D. Tangential longitudinal section of fossil wood showing detail of uniseriate and multiseriate xylem rays. BSIP wood slide no - 41236-II. E. Radial longitudinal section of fossil wood showing heterogeneous xylem rays. BSIP wood slide no - 41236-III. F. Tangential longitudinal section of fossil wood magnified to show detail of fibre strands. BSIP wood slide no - 41236-II. G. Tangential longitudinal section showing the nature of pits

Kalagarh, Uttarakhand. Besides, the fossil leaves showing their affinity with the genus *Shorea* Roxb. have also been described as *Shorea siwalica* from Siwalik of Darjeeling District of West Bengal and Arjun Khola, western Nepal (Antal and Awasthi, 1993; Prasad *et al.*, 2019); *Shorea miocenica* from Siwalik of Oodlabari, Darjeeling District, West Bengal (Antal & Prasad, 1996) and from Siwalik of Tinau Khola, Nepal (Konomatsu and Awasthi, 1999); *Shorea bengalensis* from Siwalik sediments (Middle Miocene) of Darjeeling District, West Bengal (Antal & Prasad, 1997); *Shorea*

neoassamica Prasad from Siwalik of Kathgodam, Uttarakhand (Prasad, 1994); *Shorea palaeoridleyana* Joshi and Mehrotra (2007) from east Kameng District of Arunachal Pradesh (Joshi & Mehrotra, 2007), *Shorea eutrapizifolia* from Koilabas area western Nepal (Prasad *et al.*, 1999); *Shorea palaeoeostellata* from Siwalik of Surai Khola, western Nepal (Prasad and Pandey, 2008); *Shorea palaeocurtisii* from Middle Miocene of Koilabas, western Nepal (Prasad and Dwivedi, 2008) and *Shorea nepalensis* from the Siwalik of Binai Khola, Nepal (Konomatsu & Awasthi, 1999).

Khan *et al.*, (2016) reported the occurrence of plant remains (Fossil leaf, winged fruit and fruiting calyx lobes) of the genus *Shorea* from Tertiary sediments of Arunachal Pradesh, India. On the basis of this discovery, they suggested that the genus *Shorea* had arrived in eastern Himalaya by the Mio-Pleistocene. Wilf *et al* (2022) documented some fossil leaves of *Shorea* from Late Tertiary of Borneo and also pointed out that these leaf fossil evidence is important for establishing the occurrence of dipterocarps in southeast Asian rain forests. Thus, the fossil record of the genus *Shorea* Roxb. indicates that it was widespread on the entire Indian subcontinent from the Early Eocene onwards up to the Pliocene-Pleistocene. This further indicates a more or less warm and humid climate supporting the luxuriant vegetation during the period as all the nearest living relatives of the present and earlier described fossils are distributed in the evergreen to deciduous forests of the Indo-Malayan region. On the basis of distribution pattern, the genus *Shorea* Roxb. is supposed to be of Malaysian origin, as the two-third of the total dipterocarp species occur there today and the region is also quite rich in its fossil records (Lakhanpal 1974; Sasaki 2006; Bansal *et al.*, 2019). According to them this, the family migrated from south-east Asia to India during the Neogene when the land connections were established between the two landmasses (Lakhanpal 1970; Awasthi 1994). The presence of above Dipterocarpaceous taxa in the Miocene sediments of north western India and its complete absence today in the region is a sign of drastic change in the climate which might be responsible for the complete extinction of the

family from the Himalayan foot hills of Himachal Pradesh, India.

CONCLUSION

Palaeobotanical analysis of plant fossils from the western Siwalik belt in Himachal Pradesh has identified petrified fossil wood resembling *Shorea* Roxb. of the Dipterocarpaceae family, with modern analogs like *Pentacme suavis* A. DC. (syn. *Shorea siamensis* (Kurz) Miq.), which no longer grow in the Himalayan foothills but thrive in Southeast Asia's tropical forests. The presence of these evergreen taxa during the Mio-Pliocene suggests that lush evergreen forests dominated the region, contrasting with today's mixed deciduous forests. Fossil records of *Shorea* and other dipterocarps in the Siwalik sediments indicate their migration from Southeast Asia during the Early Miocene, followed by extinction in the region, likely due to unfavorable conditions from Himalayan uplift. The distribution of *Shorea* species across eastern and southern India, extending to Sri Lanka via the Himalayan foothills during the Miocene-Pliocene, highlights their historical spread, with some populations persisting in these regions today.

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