Fossil woods and their significance

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Fossil woods are the most striking and frequently occurring megaplant remains in sedimentary rocks. They store a wealth of information about palaeoclimate, palaeoecology, phytogeography and evolution. Without them our knowledge about the arborescent plants of the past would have remained largely incomplete. They are of great economic importance as a source of energy since they form the major component of our coal and lignite.

XYLEM or wood is a complex tissue made up of more than one type of cells working together as a unit. It results from the activity of a special meristem, the vascular cambium, and constitutes the bulk of woody gymnospermous or angiospermous tree trunks. The xylem as a whole is meant to conduct water and mineral salts upwards from the root to the leaves and to give mechanical strength to the plant body. Xylem consists of (i) tracheids, (ii) vessels or tracheae, (iii) wood fibres, and (iv) wood parenchyma. The first two are called 'tracheary elements' and are concerned with conduction. They are non-living at maturity. Wood fibres mainly provide mechanical strength to the plant body and are usually dead cells. However, fibres with living protoplast and nuclei have been found to occur in many woody plants[1]. All the three xylem components are lignified and thick walled. Wood parenchyma is associated with storage of starch, oils and many other ergastic substances and consists of living cells. Sometimes parenchyma cells develop secondary walls and become lignified[1,2]. Wood is a fairly compact and hard material which resists decay and for this reason it often gets fossilized and is found most frequently in fossil records. The study of the anatomy of xylem or wood is called xylotomy.

Fossilization of wood

Wood may become fossilized in various ways though the main process is always by burial. The burial may be violent as happens in the case of volcanic eruption by lava flows or by extensive floods but usually it is gradual and gentle as may be observed in the peat bogs, lakes, rivers and along the sea shores. The burial material such as sand or mud slowly consolidates into rock. The wood under preservation often gets flattened forming coaly fossils called compressions. Due to flattening, the original structure of the wood in compression is usually crushed and is obscured. However, such flattening is generally prevented by the process of fossilization known as petrifaction and permineralization[3] in which the wood becomes partly or even completely replaced by minerals, usually by silica, in the form of opal, chalcedony or agate but sometimes by iron pyrites or calcium carbonate[3–6]. The wood is thus changed into stony fossils and unlike in compressions, the original shape and internal microscopic structures of such woods are well preserved. Petrified woods allow sectioning and examination of the tissue under microscope. Many petrified woods such as those of Deccan intertrappeans are preserved in this way. Internal structure may also be preserved perfectly when wood is fossilized as a charcoal-like material called 'fusain' which was probably formed by charring of trees due to forest fires. Petrifactions are the most frequently occurring type of fossil woods (Figure 1 *b*, *d*). Their occurrence in the arid and treeless landscape of Kutch and Rajasthan is of particular significance as a striking reminder of dense forests which must have flourished there millions of years ago. Sometimes we get moulds or casts of fossil woods. They are in a way the negatives of the plant material. The mould faithfully reproduces the surface features of the stem or wood, such as the design of bark, knots, wound and leaf bases. However, if other sediments get into the cavity of the mould and solidify, a cast or a possible replica of the original material is formed. Moulds and casts depict only the external form of fossil wood (Figure 1 *c*). Bark is very rarely found intact in fossil woods. It is the first casualty in transportation and early degradation of wood. Presence of bark in fossil woods provides an evidence of quick burial. It also indicates that the fossil has not drifted too far from its place of origin and hence is of considerable significance in determining the provenance of fossil woods. The tree trunks and branches have been recovered from the high tide water marks of sea in the Piram island, off the coast of Bhavnagar in Gujarat. It seems that as these woods drifted into the ancient sea, they were attacked by wood eating animals such as marine wood borer, *Teredo*, a bivalve mollusc, before fossilization. The borings made by penetration of these worms are often seen preserved in the fossilized woods (Figure 1 *b*). These woods were often fossilized as petrifactions with iron pyrites. A large number of

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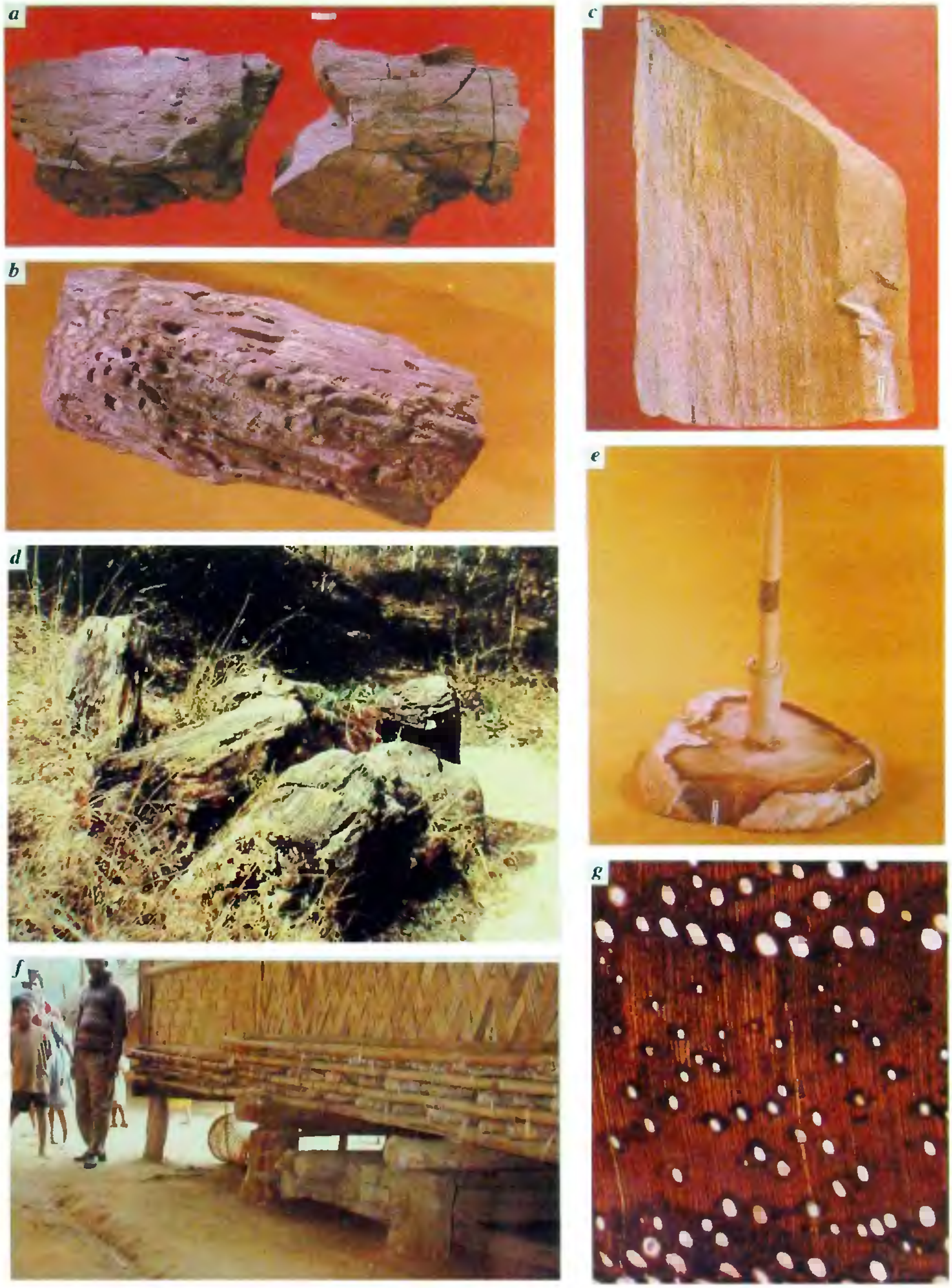

Figure 1 ***a–g***. ***a***, A carbonized wood sample from the Rajpardi lignite mine, District Bharuch, Gujarat; ***b***, A petrified wood eaten by marine wood borers (*Teredo*) from the Piram Island, off the coast of Bhavnagar, Gujarat; ***c***, A wood cast from the Paleogene sediments near Barmer, Rajasthan; ***d***, Petrified tree trunks lying scattered in a fossil wood locality at Tiruvakarrai in Tamil Nadu; ***e***, A decoration piece made of a fossil wood from Ginkgo petrified forest, State of Washington, USA (courtesy Dr Uttam Prakash); ***f***, Petrified wood logs used as support pillars/bases by villagers in their houses near Garobadha, Garo Hills, Meghalaya; ***g***, Transverse section of a fossil wood of *Lagerstroemia* (*Lagerstroemioxylon*) from Bikaner, Rajasthan, showing ring porous nature of the wood. (×15).

woods have also been preserved and described in the form of compressions from the lignite mines of India such as Rajpardi in Gujarat[7], Neyveli in Tamil Nadu and from the Tertiary sediments of Kerala and Maharashtra[8] (Figure 1 *a*) besides Andaman–Nicobar Islands[9]. Such type of woods have also been reported from the Plio-Pleistocene sediments of the Karewa lakes of Kashmir[10]. Sometimes calcified woods have also been found at different places. Pleistocene woods are also found sometimes in the inland lakes. Thus all kinds of fossil woods have been reported from India.

Identification of fossil woods

The identification of fossil woods requires detailed observation of their internal microscopic structures. Sometimes anatomical details are well preserved, particularly in cherty material. To study fossil woods, thin sections are cut in various planes such as transverse, tangential and radial, which help to build up the three-dimensional picture of the fossils as is the case for the study of extant woods. These sections are then ground, polished and examined under microscope. This method was first applied to petrified woods as early as in 1831 by Henry Witham and was followed by later palaeobotanists[11]. Anatomical features such as growth rings, tracheids, vessels, parenchyma, rays, fibres, resin canals and various kinds of minute pits, etc. are then examined (Figures 1 *g*, 2 *b–m*). Based on these characters, fossil woods can be identified and classified under various taxa and groups. Sometimes minute microscopic details are not preserved or remain obscure which makes it difficult to identify such woods to generic or specific levels.

Indian fossil woods

Oldest fossil woods from India come from the Palaeozoic sediments. A large number of fossil woods are known from the Lower Gondwana (Permian) formations of India. The vast forests of the Permian which covered much of Indian landmass during 245 m.y. –280 m.y. are represented in our coal seams by wood compressions and also by well-preserved petrifactions. All the known Indian Palaeozoic woods belong to Gymnosperms. The compression form is represented by *Vertebraria* Royle, referable to *Glossopteris*[12,13] irrespective of the fact of its being a stem or a root. The petrified woods have been described under various artificial genera, a comprehensive list of which has been given by Prasad[14]. These woods occur primarily in the Lower Barakar and Upper Raniganj and equivalent Kamthi formations of the Lower Gondwana. Surprisingly no wood has been reported from the Talchir, Karharbari and Kulti (Barren Measures) formations.

*Raniganj Formation/ *Kamthi Formation
Kulti Formation (Barren Measures)
*Barakar Formation
Karharbari Formation
Talchir Formation

(General sequence of Lower Gondwana formations of India, those containing fossil woods are marked by an asterisk).

Most of these woods have been reported from West Bengal (Raniganj Coalfield), Bihar (Jharia Coalfield) and Maharashtra (Kamthi Formation). A few records are also known from Andhra Pradesh, Madhya Pradesh and Uttar Pradesh (Singrauli Coalfield, Mirzapur District). Most of the fossils consist only of secondary wood but some of them possess homo- to heterocellular pith with sclerotic or secretory cells and endarch primary xylem. In these Lower Gondwana woods the secondary xylem is pycnoxylic, more or less uniform and mostly possesses araucarioid pittings but sometimes a mixture of araucarioid and abietoid pits along with taxinean spirals. The presence of well-defined growth rings in these woods indicates some climatic fluctuations. The xylem rays are homogeneous, generally 1–2 seriate, the cross field pits may be one to many, circular, bordered, araucarioid and taxodioid. These woods have often been found in coal-bearing beds in association with impressions of representatives of the *Glossopteris* flora. Although these woods are undoubtedly gymnospermous, their further affinities cannot be ascertained in the absence of any other supporting evidence. They could represent any of the orders like Glossopteridales, Cordaitales. Taxales and Ginkgoales. Gymnosperms were the most dominant group of plants in the Permian of India as has also been revealed by a large number of foliar taxa[15]. They continued their dominance throughout Mesozoic and Early Cretaceous. Birbal Sahni enhanced the significance of fossil woods by naming a new and enigmatic group of gymnosperms as Pentoxyleae after the characteristic wood genus *Pentoxylon* Srivastava (Figure 2 *a*, *b*) reported from the Rajmahal Hills of India[16], then considered to be Jurassic in age. The group Pentoxyleae has been accorded the status of an order Pentoxylales by later palaeobotanists. The age of the Rajmahal sediments has since been revised as Lower Cretaceous. The woods of Pentoxylales are remarkable in having poly 'steles' or many vascular 'bundles'[17]. *Pentoxylon sahnii* frequently had five steles. The name of the genus and the group was derived from this feature. Five was the commonest number of steles though the number varied. The secondary wood was compact and markedly eccentric with a much greater development towards the centre of stem with distinct growth rings (Figure 2 *b*). Although polystelic features of the stems show resemblance with Palaeozoic medullosan

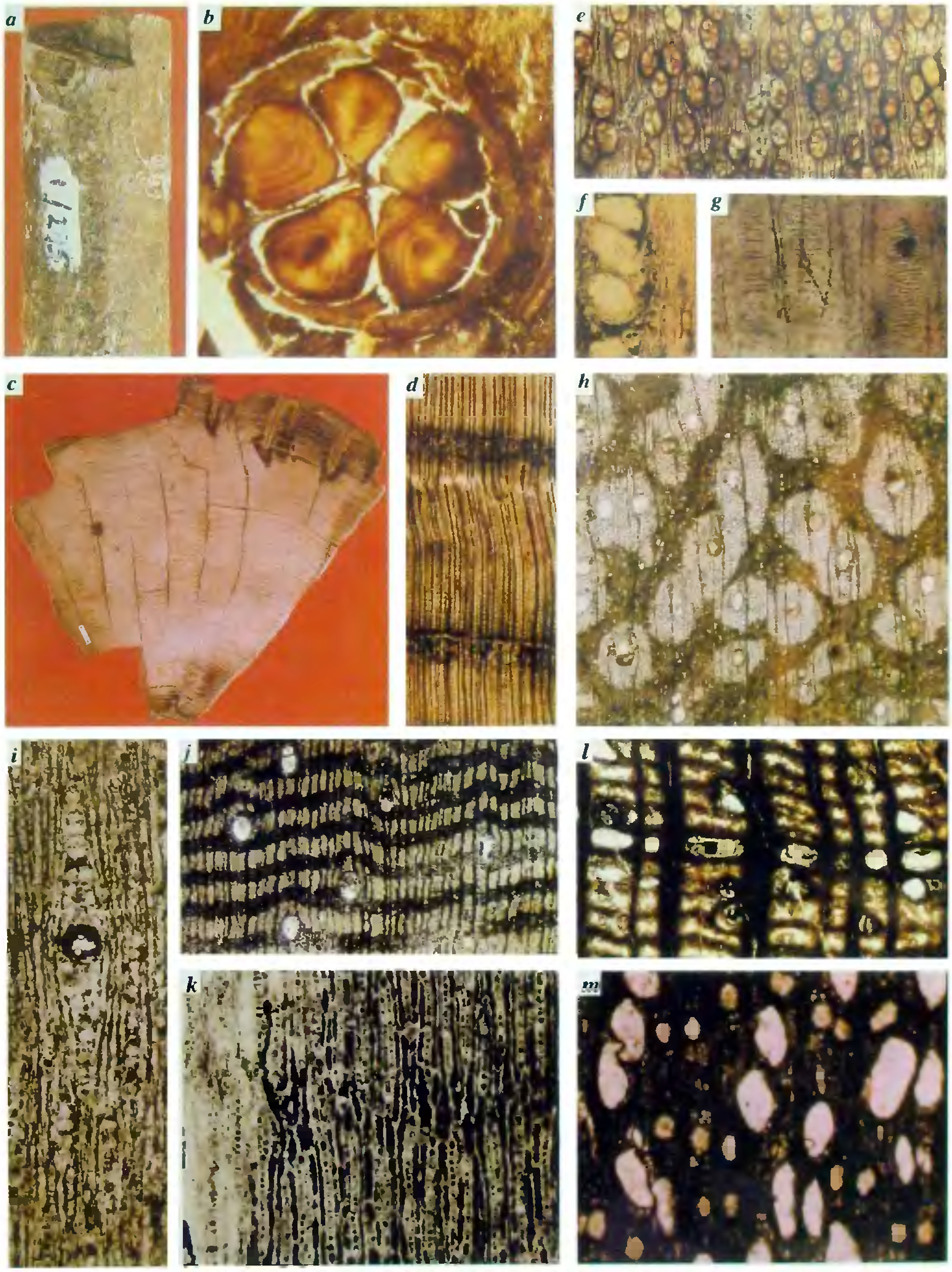

Figure 2 *a–m*. ***a***, A specimen of *Pentoxylon sahnii* (× 2); ***b***, Transverse section of *Pentoxylon sahnii* showing polysteles, eccentric pycnoxylic wood and growth rings (× 10); ***c***, Transverse section of *Sahnioxylon rajmahalense* showing distinct growth rings (× < 1/2); ***d***, Transverse section of *Sahnioxylon rajmahalense* showing size difference in growth rings of early and late wood (× 15); ***e***, Transverse section of a fossil wood showing highly tylosed solitary vessels (× 20); ***f***, Tyloses in a vessel as seen in longitudinal section of a fossil wood (× 70); ***g***, Radial longitudinal section of *Hydnocarpoxylon indicum* Bande and Khatri showing scalariform perforations in the vessels (×100); ***h***, Transverse section of a fossil wood of *Isoberlinia* (an African genus) from Kachchh showing abundant paratracheal parenchyma (× 20); ***i***, Longitudinal section of a fossil wood of *Mangifera* (*Mangiferoxylon scleroticum* Awasthi) showing radial gum canal in the rays (× 70); ***j***, Transverse section of a fossil wood of *Millettioxylon indicum* Awasthi showing banded type of parenchyma (× 20); ***k***, Longitudinal section of *Millettioxylon indicum* Awasthi showing storied arrangement of xylem rays (× 70); ***l***, Transverse section of *Sterculinium kalagarhense* Guleria showing banded parenchyma and traumatic gum canals forming a row (× 20); ***m***, Transverse section of *Dipterocarpoxylon pondicherriense* Awasthi from Kachchh showing large solitary vessels and small axial gum canals (× 15).

ferns, they differ in having pycnoxylic wood as seen in gymnosperms.

The earliest records of flowering trees in India, in the form of a large number of petrified woods, have been reported from the Deccan Intertrappean sediments of Late Cretaceous–Early Tertiary of Central India of about 65 m.y. age. They represent varied dicot genera, even woody lianas, *e.g.*, *Aristolochioxylon*, and a number of palms[18] which are the characteristic components of any moist tropical forest. Similarly a large number of modern genera are represented by their fossil woods in the Neogene sediments[8,19]. Widespread occurrence of fossil woods of Dipterocarpaceae, the dominance of leguminous woods along with wood remains of Sapotaceae, Ebenaceae and Rosaceae help to demarcate the Neogene flora of India from the Palaeogene. Gymnosperms were rare during the Tertiary. With the advent of angiosperms they obviously declined fast and became a moribund group. They are represented by the rare occurrence of woods of *Araucarioxylon* and *Podocarpoxylon*, the two typical southern gymnosperm genera until the invasion of northern conifers in India such as *Abies*, *Cupressus* and *Pinus*, whose wood remains have been found in the Pliocene–Pleistocene deposits of Kashmir[10]. Thus the fossil woods are an important source of information in tracing the antiquity of extant arborescent plants.

Discussion

As stated earlier, wood provides mechanical strength to the plant body and conducts water and mineral salts from roots to leaves. These functions are vital to terrestrial life. Thus the development of woody or vascular plants was a critical factor in the initial conquest of land by plants around 410 m.y. ago (Ludlovian) during the Upper Silurian period. The evidence for this was provided by Obrhel[20] by his discovery of *Cooksonia* (*C. hemispherica*), an extremely simple plant consisting of small, naked or leafless, dichotomizing axes with slender cetrarch protosteles bearing terminal sporangia, from the Middle Ludlovian deposits of Bohemia, belonging to sub-division Rhyniophytina[21,22]. *Cooksonia* is thus considered to represent geologically the oldest vascular plant known to date. The vascular system consists of slender strand of annular tracheids[23]. The middle Devonian (Givetian, about 370 m.y. ago) period heralded the initiation of the cambial activity leading to the secondary growth (*Schizopodium*). Thus the anatomical studies of fossil woods has enabled us to understand how the pioneering land plants evolved from the earliest seaweed-like forms to some of the first large trees such as *Archaeopteris* and *Callixylon*, the pro-Gymnosperms which first appeared in the Middle Devonian about 380 m.y. ago[24]. Likewise polysteleic nature of *Pentoxylon* and related stems along with pycnoxylic wood have provided some kind of connecting link between the ferns (Medullosan type) and the gymnosperms.

The study of fossil woods has provided substantial data about palaeoclimate, palaeoecology, palaeogeography, phytogeography and evolutionary characters[8,18,19,25–34].

Analysis of growth rings in fossil woods provides information about palaeoclimate[35,36]. Depending on changes in radial cell diameter within the growth ring and the variation in the ring width, it is possible to extrapolate climate information. This study of tree rings to reconstruct past and present climate is called 'dendroclimatology' which is a subfield of 'dendrochronology'[37]. This kind of study has lately been seriously undertaken in our country[38,40]. Dendrochronological research could contribute to a better understanding of the dynamics of monsoon[41]. Growth rings are normally distinct and well defined in trees of temperate regions with pronounced seasonal changes. Accordingly, Permian to Early Cretaceous Indian woods show well developed and distinct growth rings (Figure 2 *b–d*) on account of palaeolatitudinal position of Indian Plate in cooler region at that time[42,43]. Growth rings are usually not well marked and indistinct in the woods of tropical trees (Figure 2 *e*, *j*, *l*) with a few exceptions like *Tectona grandis*, etc.[44–46].

The Late Cretaceous–Early Tertiary Deccan Intertrappean flora is mainly represented by fossil woods whose study has provided the bulk of information about the composition of this flora. A large number of its woody dicot genera such as *Artocarpus*, *Barringtonia*, *Canarium*, *Dracontomelum*, *Drypetes*, *Garcinia*, *Homalium*, *Lophopetalum*, *Polyalthia*, *Sonneratia* and *Syzygium* indicate that at that time tropical humid conditions prevailed over the Indian peninsula[47]. Somewhat similar climatic conditions extended into the later half of the Tertiary as is revealed by a large number of woods of the dipterocarpaceous taxa (e.g., *Anisoptera*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Shorea*, etc.) along with those of *Calophyllum*, *Gluta*, *Cynometra* and *Afzelia-Intsia*. In addition to these, the occurrence of *Bauhinia*, *Cassia*, *Cordia*, *Mangifera*, *Ormosia*, *Sterculia*, *Terminalia*, etc., ranging from semi-evergreen to deciduous woody taxa in the Late Tertiary, indicates a gradual decrease in rainfall and evolution of drier conditions. Palaeogeographically the occurrence of fossil woods of *Sonneratia* in the Tertiary of central and western India and *Heritiera* in eastern India indicates the existence of coastal conditions far inland in the past than at present. Likewise fossil woods of *Lagerstroemia*, *Dracontomelum*, *Drypetes*, *Syzygium*, *Terminalia arjuna* and *Barringtonia* indicate the presence of water channels and damp or swampy conditions.

The occurrence of certain South American, African and Australian woods such as *Simarouba=Quassia*[48,49], *Hyphaene*[50] and *Eucalyptus*[51] in the Deccan Intertrappean (Late Cretaceous) sediments of Central India indicates the proximity of South America, Africa and Australia to India at that time. The occurrence of these taxa in India probably represents angiospermic remnants of the Gondwanaland flora. Similarly the presence of certain typical Malayan elements, largely represented by the woods of dipterocarpaceous genera[25] (Figure 2 *g*) and African taxa like *Isoberlinia* (Figure 2 *h*), *Entandrophragma*, etc.[52,53] in the Upper Tertiary sediments of India and their complete absence in the Deccan Intertrappean sediments indicate the invasion of such genera from the east and west respectively, after the establishment of land connections with India by early Miocene through Indonesia and Myanmar on one hand and via Ethiopia and Arabia on the other. Likewise the complete absence of woods or any other megafossils of northern conifers such as Pinaceae in the Miocene sediments of the Indian subcontinent indicates that these conifers entered into India after the uplift of the Himalayas at the end of Miocene when the conditions became cooler and conducive to their growth. The occurrence of a fossil wood of *Prunus* in the Miocene sediments of Ladakh[54] at a height of 4581 m indicates the uplift of the Himalayas by about 2445 m since then as *Prunus* does not grow above 2140 m at present. Based on detailed analysis of Indian fossil woods ranging from Deccan Intertrappeans to Neogene in age, Bande and Prakash[27] have been able to trace the evolutionary trends in the secondary xylem of dicot woods. Features like wide apotracheal parenchyma bands and storied structures of various elements such as rays, wood fibres and parenchyma are more advanced and hence they are found frequently in the younger Neogene woods in contrast to older Deccan Intertrappean woods (Figure 2 *j–l*). Similarly vessel members with scalariform perforations are more common in Deccan Intertrappean woods than in the younger Neogene woods since it is considered to be a primitive feature (Figure 2 *g*). Normal axial gum canals are present in the Neogene woods (Figure 2 *m*) whereas they are absent in the Pre-Neogene Indian woods.

Fossil woods are of great economic importance when they occur in large quantities as in the case of lignite and coal mines. Neyveli lignite is composed of large number of fossil woods and a number of carbonized woods have also been collected from the Rajpardi lignite mine of Gujarat[7,8] (Figure 1 *a*). Similarly Gondwana coals also consist of woody material[55] besides other vegetal remains. Such large deposits of lignites and coals are our major source of energy. In addition, petrified wood logs have been used by villagers as pillars and support bases for making their houses (Figure 1 *f*) in the north-east India and for marking the boundaries of fields in almost all other areas near fossil localities. They have occasionally been used as curios and for decorative purposes (Figure 1 *e*) after cutting and polishing.

The so-called fossil wood forests or parks with a large number of tree trunks as at Tiruvakarrai in Tamil Nadu (Figure 1 *d*), Mandla in Madhya Pradesh and Akal fossil park near Jaisalmer in Rajasthan, act as repositories of arborescent fossil plants and remind us of our luxuriant forests during the past.

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