REVISION OF SOME DIPTEROCARPACEOUS WOODS
PREVIOUSLY DESCRIBED FROM THE TERTIARY
OF SOUTH INDIA

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ABSTRACT

The present paper consists of the revision of five species of fossil dipterocarpaceous woods, viz. Dipterocarpxylon indicum, Shoreoxylon holdeni, S. mortandranse, S. megaporosum and Anisopteroxylon cuddalorense, described by Ramanujam (1956, 1960) from the Tertiary of South India, near Pondicherry, South Arcot district, Tamil Nadu (Madras). On re-investigation these were found very similar to the wood structure of the genus Dryobalanops Gaertn. f. and hence transferred to the genus Dryobalanoxylon Den Berger. The first species, i.e. Dipterocarpxylon indicum, is renamed as Dryobalanoxylon indicum (Ramanujam) comb. nov., and the remaining four species, found identical with each other, are placed under Dryobalanoxylon holdeni (Ramanujam) comb. nov.

GENERAL DESCRIPTION

Genus — Dryobalanoxylon Den Berger, 1923

1. Dryobalanoxylon indicum (Ramanujam) comb. nov.

Pls. 1-2, Figs. 1, 3, 5-8; Text-figs. 1-4

Dipterocarpxylon indicum Ramanujam, Palaeobotanist, vol. 4, pp. 51-54, Pl. 2, Figs. 12-14; Text-figs. 11-14, 1956.

In connection with the comparison of a new fossil wood resembling that of Dipterocarpus (Awasthi, 1965), I happened to consult the type material and slides of Dipterocarpxylon indicum Ramanujam (1956). On re-examination of the type slides the anatomical features of D. indicum were found to be different from those reported by Ramanujam (1956). The most important anatomical difference among the woods of Dipterocarpaceae is the nature and distribution of gum canals. The gum canals in the type material of D. indicum are in concentric tangential rings whereas they have been described by Ramanujam (1.e.) as diffuse or in pairs. Having concentric rings of gum canals this fossil wood cannot belong to Dipterocarpus, since this genus is characterized by the presence of gum canals as diffuse or in pairs.

Besides, the illustrations of this fossil wood were also found to be doubtful. The photomicrograph illustrating a cross-section of Dipterocarpxylon indicum (Ramanujam, 1956, Pl. 2, Fig. 12) does not look to be a fossil wood at all. The same figure, included in his Ph.D. thesis (Ramanujam, 1955, Pl. 11, Fig. 52), is illustrated as cross-section of the modern wood of Dipterocarpus pilosus. In case of
fossil wood it seems that Ramanujam happened to take a cross-section from a region in between two concentric rings of gum canals thus missing them altogether. On the other hand the smaller vessels, which are almost equal to the size of the gum ducts, were misunderstood as solitary gum ducts and shown as such in the figures (RAMANUJAM, 1955, PL. 11, FIGS. 49-50).

In order to investigate thoroughly, more sections (cross, tangential and radial longitudinal) were prepared from the type specimen (B.S.I. P. Museum No. 4964) and examined critically. On re-examination of the fossil wood a number of anatomical features have been found which were previously not described properly. It is, therefore, necessary to give here a revised description before comparing it with modern species.

**REVISED DESCRIPTION**

**Topography** — Wood diffuse-porous (Pl. 1, Fig. 1). Growth rings not seen. Vessels visible to the naked eye as crowded dots in cross-section, medium to large, a few small, almost exclusively solitary, multiples not observed, evenly distributed (Pl. 1, Fig. 1), 8-16 vessels per sq. mm; tyloses not seen due to heavy crystalliferous infiltration. Vasicentric tracheids indistinguishable in cross-section from paratracheal parenchyma, recognized in tangential section by the presence of bordered pits. Parenchyma paratracheal, apotracheal; paratracheal parenchyma vasicentric, forming thin sheath of 1-3 cells around the vessels, occasionally tending to become aliform and aliform-confluent (Pl. 1, Fig. 5; TEXT-Fig. 1); apotracheal parenchyma associated with the concentric rings of gum canals (Pl. 1, Fig. 5), each 6-8 cells wide; diffuse parenchyma not seen. Xylem rays moderately broad, 20-60 μ in width, 7-8 rays per mm, each separated by 2-10 tangential rows of fibres, 1-5 (mostly 3-4) seriate (Pl. 1, Fig. 3; TEXT-Figs. 2-3); ray tissue heterogeneous; rays consisting of 1-15 marginal rows of upright cells at one or both the ends; sheath cells also present (Pl. 1, Fig. 3; TEXT-Fig. 3); uniseriate rays homocellular as well as heterocellular (Pl. 1, Fig. 6); rays upto 90 cells and 1900 μ in height. Fibres (Fibre-tracheids) aligned in radial rows between the two consecutive xylem rays.

**Gum canals** vertical, arranged in tangential rings (Pl. 1, Figs. 1, 5; TEXT-Fig. 1), embedded within parenchyma band.

**Elements** — Vessels circular to oval, mostly oval due to compression (Pl. 1, Fig. 5), upto 250 μ, r.d. upto 300 μ, thin-walled; vessel-members short to medium, 225-975 μ in length, with truncated ends; perforations simple; pits leading to contiguous tracheids large, 8-10 μ in diameter, circular, vestured, with small circular or slit-like orifices (Pl. 2, Fig. 7); pits leading to contiguous parenchyma and ray cells almost similar to vessel-tracheid pits. Vasicentric tracheids almost similar to parenchyma cells in cross-section. Parenchyma cells those occurring in the immediate vicinity of the vessels somewhat peripherally flattened, circular to oval or orbicular, t.d. 20-28 μ, r.d. 24-36 μ, 50-115 μ in length; chambered crystalliferous parenchyma strands present; infiltration dark. Upright Ray cells 50-80 μ in tangential height, 32-48 μ in radial length, procumbent ray cells 20-28 μ in tangential height, 48-160 μ in radial length. Fibres (Fibre-tracheids) angular, mostly hexagonal in cross-section, sometimes tangentially flattened, 16-32 μ in diameter, non-septate, very thick-walled, with narrow lumen (Pl. 1, Fig. 5), common walls 6-12 μ in thickness; pits bordered, vestured (Pl. 2, Fig. 8; TEXT-Fig. 4), 8-10 μ in diameter. Gum canals circular, 80-100 μ in diameter.

**AFFINITIES AND DISCUSSION**

Comparison with the modern woods — In having such important anatomical features as vertical gum canals, solitary vessels, vasicentric tracheids, multiseriate and heterogeneous xylem rays the present fossil wood shows undoubted affinities with the family Dipterocarpaceae. Except the two genera, Monotes and Marquesia, the family is characterized by the presence of vertical gum canals (METCALFE & CHALK, 1950). Excluding these two genera the woods of this family can be divided into two groups on the basis of the arrangement of gum canals.

I. Gum canals always in concentric rows, e.g. Shorea, Doona, Hopea, Isoptera, Parashorea, Pentacme, Balanocarpus, Dryobalanops and Doticarpus.
II. Gum canals diffuse, solitary and also in short tangential rows, e.g. Anisoptera, Dipterocarpus, Vateria (Stemonoporus), Vatica (Pachynocarpus), Upuna, Cotylelobium and Monoporandra.

In possession of concentric rings of gum canals the present fossil wood can be referred to the genera included in the first group. From a general survey of the thin sections and published data on the anatomy of these woods it has been found that Ramanujam's *Dipterocarpoxylon indicum* resembles that of the genus *Dryobalanops*. The important anatomical features of this genus by which it can be distinguished from other genera, are—vessels exclusively solitary or nearly so and fibres thick-walled with distinct bordered pits (Metcalfe & Chalk, 1950, pp. 215-218).

Detailed comparison of the present fossil wood was made with the thin-sections of the two available species of *Dryobalanops*, viz. *D. aromatica* Gaertn. f. and *D. oblongifolia* Dyer. Of these, *D. oblongifolia* shows good general resemblance with it.

In view of the close resemblance with the woods of *Dryobalanops* the present fossil wood, *Dipterocarpoxylon indicum* Ramanujam is transferred to the genus *Dryobalanoxylon* Den Berger, 1923.

*Comparison with the fossil species*—So far 11 species of *Dryobalanoxylon* Den Berger have been described from the Tertiary of South east Asia as listed below in Table 1.

All these fossil woods differ quite markedly from the present fossil wood in some significant characters. In *Dryobalanoxylon tobleri* and *D. spectabile* the paratracheal parenchyma is comparatively less than in the present fossil wood. In *D. sumatrense* and *D. neglectum* the fibres are thin-walled, while in the present fossil wood they are very thick-walled and the lumen is visible only under high magni-
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TABLE 1 — LIST OF THE FOSSIL WOODS REFERRED TO DRYOBALANOXYLON DEN BERGER

<table>
<thead>
<tr>
<th>Name</th>
<th>Locality</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Dryobalanoxylon toberli</em> (Kräusel) Den Berger 1923</td>
<td>South Sumatra</td>
<td>Tertiary</td>
</tr>
<tr>
<td>D. toberli (Kräusel) Den Berger (?) Schweitzer 1958</td>
<td>West Java</td>
<td>Pliocene</td>
</tr>
<tr>
<td>2. <em>D. spectabile</em> (Cré) Den Berger 1927</td>
<td>Java</td>
<td>Tertiary</td>
</tr>
<tr>
<td>D. spectabile (Cré) Den Berger (?) Schweitzer 1958</td>
<td>West Java</td>
<td>Tertiary</td>
</tr>
<tr>
<td>3. <em>D. javanicum</em> (Kräusel) Den Berger 1927</td>
<td>Java</td>
<td>Tertiary</td>
</tr>
<tr>
<td>4. <em>D. sumatrense</em> Schweitzer 1958</td>
<td>West Java</td>
<td>Early Pliocene</td>
</tr>
<tr>
<td>5. <em>D. borneense</em> Schweitzer 1958</td>
<td>Middle Sumatra</td>
<td>Miocene</td>
</tr>
<tr>
<td>6. <em>D. mirabile</em> Schweitzer 1958</td>
<td>Middle Sumatra</td>
<td>Quaternary</td>
</tr>
<tr>
<td>7. <em>D. bangkoense</em> Schweitzer 1958</td>
<td>South coast of Seram and Middle Sumatra</td>
<td>Quaternary</td>
</tr>
<tr>
<td>8. <em>D. neglectum</em> Schweitzer 1958</td>
<td>Middle Sumatra</td>
<td>Quaternary</td>
</tr>
<tr>
<td>9. <em>D. musperi</em> Schweitzer 1958</td>
<td>West Java</td>
<td>Tertiary or Quaternary</td>
</tr>
<tr>
<td>10. <em>D. rotundatum</em> Schweitzer 1958</td>
<td>Middle Sumatra</td>
<td>Quaternary</td>
</tr>
<tr>
<td>11. <em>D. khmerinum</em> (Boureau) Schweitzer 1958</td>
<td>Cambodia</td>
<td>Quaternary</td>
</tr>
</tbody>
</table>

Diagnosis: *Dryobalanoxylon indicum* (Ramanujam) comb. nov.

Wood diffuse-porous. Growth rings absent. Vessels mostly medium to large, t.d. up to 250 μ, r.d. up to 300 μ, exclusively solitary; vessel-members 225-795 μ in length; perforations simple; pits leading to contiguous tracheids large, 8-10 μ in diameter, vested; tyloses present. Vasicentric tracheids forming thin sheath of 1-2 cells wide around the vessels. Parenchyma paratracheal, apotracheal; paratracheal parenchyma vasicentric to occasionally extending sideways forming aliform to occasionally aliform confluent; apotracheal parenchyma present, associated with the concentric rings of gum canals, each band 6-8 cells in width. Xylem rays 1-5 (mostly 3-4) seriate; rays markedly heterogeneous; rays homocellular to mostly heterocellular, consisting of procumbent cells through the median portion and about 1-15 marginal rows of upright cells at one or both the ends; sheath cells occasionally present; rays up to 90 cells and 1900 μ in height. Fibres (Fibre-tracheoids), nonseptate, pits bordered, 8-10 μ in diameter. Gum canals vertical, in concentric tangential rings, circular, 80-100 μ in diameter.

Holotype — B.S.I.P. Museum No. 6964.
Locality — Murattandichavadi (Morton-dra), about 8 km W.N.W. of Pondicherry, South Arcot district, Tamil Nadu (Madras).

II. *Dryobalanoxylon holdeni* (Ramanujam) comb. nov.

Pl. 2, Figs. 9-13; Text-figs. 5-9

2. *Shoreoxylon mortandranse* Ramanujam, *Ibid.*, vol. 4, pp. 48-51, Pl. 1, Fig. 8; Pl. 2, Figs. 9-11; Text-figs. 8-10, 1956.


In 1956 Ramanujam described two species of *Shoreoxylon*, viz. *S. holdeni* and *S. mortandranse* showing affinities with the woods of *Shorea*. Again in 1960 he described two more fossil dipterocarpaceous woods, viz. *Shoreoxylon megaporosum* and *Anisopteroxylon cuddalorensense*, showing resemblance with those of *Shorea* and *Anisoptera* respectively. While going critically through their published descriptions and figures and examining their type slides they were found very similar to the wood structure of *Dryobalanops*. Hence they should also be placed under the genus *Dryobalanoxylon* Den Berger.

Ramanujam (1956) described the fibres in *S. holdeni* as typically libriform, nonseptate, having numerous, small or narrowly bordered, circular pits. Since among those genera having gum canals in concentric rings fibre-tracheids are found only in *Dryobalanops* this fossil should be placed under the genus *Dryobalanoxylon* Den Berger (1923). Besides the presence of fibre-tracheids (fibres with bordered pits), the fossil wood under revision also possesses exclusively solitary vessels which is another important feature of *Dryobalanops*. Thus Ramanujam’s *Shoreoxylon holdeni* cannot be a fossil of *Shorea* and is transferred to the genus *Dryobalanoxylon* and named as *D. holdeni* (Ramanujam) comb. nov.

Similarly, in *Shoreoxylon mortandranse* (sic.) Ramanujam described the fibres as libriform to semilibriform, very thick-walled, nonseptate, pits numerous, simple or narrowly bordered and round to flat-
tended. On re-examination of the type slides the nature of the fibres was found essentially the same as in his *S. holdeni*. He distinguished it from *S. holdeni* on the basis of the following differences: (1) presence of abundant aliform parenchyma, (2) apotracheal parenchyma confined mainly in the vicinity of resin canals, (3) rare occurrence of vasicentric tracheids and (4) rays broader and higher with different arrangement of vertical cells. In fact there is no basic difference between the two, there being a difference only in their preservation; *Shoreoxylon holdeni* is comparatively better preserved than *S. mortandranse*. The type and distribution of paratracheal parenchyma is the same in both the species. The vasicentric tracheids and fibre-tracheids are also present in both. However, the former being better preserved vasicentric tracheids and fibre-tracheids are seen in it more clearly; whereas in the latter they are not so distinct due to poor preservation, but they are definitely present as can be seen in the type slides. Thus *Shoreoxylon mortandranse* is identical with *S. holdeni*.

Ramanujam (1960) also described another species of *Shoreoxylon*, *S. megaporosum*, on the basis of some minor differences from the earlier species. According to him (Ramanujam, 1960, p. 110) this species differs from his *S. holdeni* in possession of bigger vessels, very sparse vasicentric tracheids and in the distribution of xylem parenchyma. In this case also no essential difference was found when compared with the photomicrographs of *S. holdeni* and *S. mortandranse*. He described the vessels as very large, with 250-525 μ in diameter. On the basis of this feature he distinguished it from all species of *Shoreoxylon*. From the photomicrograph the vessels do not appear to be very large. On measuring the diameter of the vessels with the scale in mm and dividing it with the magnification it came to about 300 μ, which is nearly equal to the vessel diameter of the previously described species. Besides its similarity in the shape, size and distribution of vessels this shows similar types and distribution of paratracheal parenchyma, vasicentric tracheids, xylem rays and fibre-tracheids as in the above revised species. Hence *Shoreoxylon megaporosum* should also be merged with them.

The last species being revised here is *Anisopteroxylon cuddalorense*. Ramanujam (1960) has shown its resemblance with the modern woods of *Anisoptera*. From the description and photomicrographs its affinities with *Anisoptera* appear to be doubtful. Although the type slides of this species could not be obtained for re-examination the description and photomicrographs were found sufficient to revise its affinities. Ramanujam has mentioned the presence of solitary and diffuse gum ducts similar to those of *Anisoptera*. In fact no such gum ducts are present in this fossil wood; the smaller vessels are often filled with dark contents which he considered as solitary gum ducts. In possession of other important anatomical features, such as the type and distribution of the vessels, paratracheal and apotracheal parenchyma, vasicentric tracheids, 1-4 seriate xylem rays and fibre-tracheids it also showed closest resemblance with the wood of *Dryobalanops*. As regards the type and distribution of gum canals they are definitely of concentric type though they are not present in the photomicrograph (Ramanujam, 1960, Pl. 17, Fig. 12). It may be due to the fact that such gum canals are sometimes widely or irregularly spaced and may or may not be present in the smaller cross-sections photographed.

Thus it is evident that all these four species of fossil dipterocarpaceous woods are identical with each other and possess all the anatomical details of the genus *Dryobalanops*. Hence they should be transferred to the genus *Dryobalanoxylon* Den Berger and named as *Dryobalanoxylon holdeni* (Ramanujam) comb. nov., which has priority over other specific epithets.

In having a combination of all the anatomical features described below, it differs from all the hitherto known species of *Dryobalanoxylon*.

It differs from *Dryobalanoxylon summary* and *D. neglectum* in having thin walled fibres. In *D. tobleri* and *D. spectabile* the paratracheal parenchyma is comparatively less than in *D. holdeni*. The vessels in *D. borneense* are smaller (small to medium) whereas in *D. holdeni* they are medium to large. In addition to paratracheal parenchyma, *D. mirabile* and *D. javanense* possess diffuse parenchyma, while in *D. holdeni* the diffuse parenchyma
is absent. In *D. bangkoense* and *D. rotundatum* the paratracheal parenchyma is more abundant. The xylem rays in *D. khmerinum* are up to 8-seriate. Lastly, it differs from *D. indicum* (Ramanujam) comb. nov. mainly in the ray character. The xylem rays in *D. holdeni* are less in height, i.e. up to 30 cells in height. Moreover, the paratracheal parenchyma in *D. holdeni* is comparatively more and mostly aliform to aliform-confuent.

**DIAGNOSIS**

*Dryobalanoxylon holdeni* (Ramanujam) comb. nov.

Wood diffuse-porous. Growth rings absent. Vessels small to large (mostly large), t.d. 60-280 μ, r.d. 60-300 μ, exclusively solitary, about 9-15 vessels per sq. mm; perforations simple; pits leading to contiguous tracheids large, 8-10 μ in diameter, bordered, vested with small circular or slit-like orifices; tyloses. Vasicentric tracheids forming thin sheath of 1-2 cells around the vessels. Parenchyma paratracheal, apotracheal; paratracheal parenchyma vasicentric to aliform, enclosing a few neighbouring vessels; apotracheal parenchyma associated with concentric ring of gum canals, forming bands, each band 2-7 cells in width. Xylem rays fine to moderately broad, 20-80 μ in width, 1-4 seriate; ray tissue markedly heterogeneous, consisting of procumbent cells in the median thickened portion and 1-5 uniseriate marginal rows of upright cells at one or both the ends, sheath cells occasionally present; rays up to 30 cells and 900 μ in height. Fibres (Fibre-tracheids) nonseptate thickwalled, walls 4-8 μ in diameter; pits bordered, circular, about 8 μ in diameter, with small circular or slit-like orifices. Gum canals vertical, arranged in concentric rings, 40-60 μ in diameter.

**Holotype** — B.S.I.P. Muscum No. 4969. **Locality** — Mortanda (also called Murattandichavadi), about 8-10 km W.N.W of Pondicherry, South Arcot district, Tamil Nadu (Madras).

**Distribution of Dryobalanops Gaertn. f.**

This genus consists of 9 species (WILLIS, 1966, p. 367; FOXWORTHY, 1946), distributed in Sumatra, Borneo and Malay peninsula. The home of this genus is Borneo where all the species are found. It is totally absent in India and adjacent countries. So far 13 species of *Dryobalanoxylon* (including the 2 spp. described in the present paper) are known from South India, Java, Sumatra, Borneo and Cambodia. This suggests that the genus *Dryobalanops* was distributed more widely during the Tertiary period than today.

**ACKNOWLEDGEMENTS**

The author is deeply indebted to Dr. R. N. Lakhanpal for his guidance and keen interest in this work. The author is also grateful to the authorities of the Forest Research Institute, Dehra Dun, for all the facilities given and permission to consult their xylarium.

**REFERENCES**


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EXPLANATION OF PLATES

Plate 1

Dryobalanoxylon indicum (Ramanujam) comb. nov.

Dryobalanops oblongifolia
2. Cross-section to show the nature and distribution of vessels, parenchyma and gum canals similar to fossil wood. \( \times 14 \).

Dryobalanoxylon indicum (Ramanujam) comb. nov.
3. Tangential longitudinal section showing nature and distribution of the xylem rays. \( \times 40 \). (B.S.I.P. Museum, Slide No. 3890).

Dryobalanops oblongifolia
4. Tangential longitudinal section showing similar type and distribution of xylem rays. \( \times 60 \).

Dryobalanoxylon indicum (Ramanujam) comb. nov.
5. Magnified cross-section showing vessel-tracheid parenchyma, fibres (thick-walled) and gum canals (G.C.). \( \times 63 \). (B.S.I.P. Museum, Slide No. 3889).
6. Radial longitudinal section showing heterocellular xylem ray. \( \times 110 \). (B.S.I.P. Museum, Slide No. 3891).

Plate 2

Dryobalanoxylon indicum (Ramanujam) comb. nov.
8. Tangential longitudinal section showing fibre-tracheids (fibres with bordered pits). \( \times 240 \). (B.S.I.P. Museum slide No. 3890).

Dryobalanoxylon holdeni (Ramanujam) comb. nov.
9. Fibre-tracheids in radial longitudinal section showing abundant bordered pits. \( \times 210 \). (B.S.I.P. Museum, Slide No. 3892).

Dryobalanoxylon holdeni (Ramanujam) comb. nov.
11. Magnified cross-section showing vessels, aliform to aliform-confluent parenchyma. \( \times 63 \). (B.S.I.P. Museum, Slide No. 3894).
12. Tangential longitudinal section showing xylem rays. \( \times 60 \). (B.S.I.P. Museum Slide No. 3895).
13. Radial longitudinal section showing heterocellular xylem rays. \( \times 60 \). (B.S.I.P. Museum, Slide No. 3892).