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A Fossil Wood of Dipterocarpaceae from Pliocene Deposit in the West Region of Java Island, Indonesia

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ABSTRACT

Fossil woods in Java Island have been excavated and sold for outdoor ornaments or indoor decoration purposes since 30 years ago. These fossils are in danger of being drained out without known identities, composition and history. This study was aimed to find out the botanical identity and geographical aspect of a newly recovered silicified fossil wood from Banten area in the west region of Java Island. The fossil trunk 28 m in length and 105 cm in diameter was buried in a tuffaceous sandstone layer. The age of the stratum was thought to be Lower Pliocene. A small sample was cut from the outer part of the log and then ground to obtain thin section for anatomical observation. The main anatomical features of the fossil wood are as follows: wood diffuse porous; vessel almost exclusively solitary, vascicentric tracheid present; axial intercellular canal present, distributed in long tangential rows; fibers with distinctly bordered pit. These features show affinities of the fossil wood to the extant wood *Dryobalanops* of the family Dipterocarpaceae, regardless of the fact that this genus is no longer exists living in the natural forest of the present day Java Island.

Keywords: fossil wood, Dipterocarpaceae, *Dryobalanoxylon*, Pliocene, Java Island.

INTRODUCTION

Fossil woods in Java have become a commodity, excavated and sold since 30 years ago for ornamental purposes or just for collections by hobbyist. Unfortunately their origin and identity are mostly unknown so they tell nothing except their strange old appearance. It would be more meaningful if their origin, age and identity were known. Very little is known about paleo-vegetation in Java even though it has been subject of study since 19th century.

Study on the tertiary flora in Java Island was started by Goppert in 1854, Ettingshouses in 1883 and then by Crie in 1888 (Krausel, 1925). Their study mainly was based on fossil leaves with only a few fossil woods. Goppert described 37 species in 21 genera and several families such as Palmae, Fagaceae, Moraceae, Lauraceae, Ebenaceae, Sapotaceae, Rhamnaceae, and Celasteraceae. Among Goppert's materials there were 3 specimens which-according to Krausel (1925)-belongs to Dipterocarpaceae. The samples were similar to his earlier discovery, *Dipterocarpoxylon javanense* (Krausel, 1922b). In the same year Krausel (1922a) had also discovered several species of *Dipterocarpoxylon* in South Sumatra.

Crie (1888) described 9 species of plant fossils from Pliocene deposit in Gunung Kendang-Java. Two of the plant fossils belong to Dipterocarpaceae. One fossil wood sample described by Crie as *Naucleoxylon spectabile* (Rubiaceae), was redescribed as *Dipterocarpoxylon spectabile* (Dipterocarpaceae), by Krausel (1926). Krausel's findings were then criticized by Den Berger (1923, 1927). Several of *Dipterocarpoxylon* fossil wood described by Krausel turned out to be *Dryobalanoxylon*, because they have resin canals distributed in long tangential rows. *Dipterocarpoxylon* on the other hand, has resin canals diffusely distributed or in short tangential rows.

After Krausel's studies, Schweitzer (1958) described 1 species of *Vaticoxylon*, 5 species of *Dipterocarpoxylon*, 4 species of *Dryobalanoxylon*, and 2 species of *Shoreoxylon* from Pliocene beds in Java Island, along with other species of the same genera and family from Tertiary and Quartenary beds in Sumatra and Borneo. Many years later, unaware of the previous studies, we conducted a survey on fossil woods at fossil yards of three fossil wood collectors in

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West Java (Mandang and Martono, 1996). We found that 80% of 199 samples examined were belongs to Dipterocarpaceae. Unfortunately the origin of the sample was uncertain, and anatomical descriptions of each genus were not made. The study was based on the features that could be observed with hand lens only. So, this finding should be confirmed by further study on anatomical features of samples collected from well determined horizons.

Recently, Srivastava and Kagemori (2001) reported one other dipterocarps fossil wood, *Dryobalanoxylon bogorensis,* from Pliocene deposit in Leuwiliang, West Java. So up to now there are already 5 species of *Dryobalanoxylon* fossil wood have been found in Java. Discovery of many Dipterocarpaceae fossil woods in Java is interesting, because Dipterocarpaceae is not a dominant family in the natural forest of the present day Java Island. In this paper, we presented a detailed description of a newly discovered dipterocarps fossil wood. The occurrence and possible causes of its extinction from Java Island are discussed.

MATERIAL AND METHODS

A silicified fossil wood log sizing 28 meter in length and 105 cm in diameter were excavated from a rubber wood plantation near Leuwidulang village, Maja District, Lebak Prefecture, Banten Province, Java Island. The coordinate of the site is approximately SL $06^0$26', EL $106^0$23' (Fig. 1). According to the geology map composed by Rusmana *et al.* (1991), the site is situated in Genteng Formation. The age of the formation was thought to be lower Pliocene (van Bemmelen, 1949). The fossil wood was buried in a rather soft; fine grained, grayish color tuffaceous sandstone. It was broken into 15 pieces about 2 m each after the silification process occurred, and apparently no further silification occurred thereafter. There is no deposition of new silica layer in the transverse faces of the broken logs, as have been seen in some other fossil wood.

A piece of sample was taken from the outer part of the log and then cut and ground to obtain thin sections of transverse, radial, and tangential face. Observation and description follow the format of the IAWA List of Microscopic Features suitable for hardwood identification (Wheeler *et al.* 1989). Vessel length was measured from tip to tip. Ray height was also measured from tip to tip, the total height of multiseriate and uniseriate portions. Number of observation for each quantitative character also follows the list as long as permissible by the available slide. For each quantitative character, mean value and standard error of the mean are given.

The results of observation were compared with the description of extant wood described by Desch (1941), Chu (1974), and Ilic (1995). Samples of extant wood in the xylarium of the Forest Products Research Institute in Bogor, Indonesia, were also used for comparison. Comparisons were also made with other fossil wood of the same genus from Sumatra, Borneo, and Java (Krausel, 1922a; Krausel, 1922b; Krausel, 1926; Den Berger 1923, 1927; Schweitzer, 1958, Srivastava and Kagemori, 2001).

RESULT AND DISCUSSION

Systematic

Sub Class : Dicotyledons
Family : Dipterocarpaceae
Genus : *Dryobalanoxylon* Den Berger, 1923
Species : *Dryobalanoxylon lunaris* Y. Mandang and N. Kagemori sp. nov. (Fig. 3-8).

Diagnostic features:

Wood diffuse porous, vessel almost exclusively solitary, vascicentric tracheid present; axial resin canals present, distributed in concentric rows; fibers with distinctly bordered pit; ray exceeds 2000 μm tall, prismatic crystal present in enlarged parenchyma cells.

Description:

Wood: diffuse porous.

Growth ring: regularly spaced parenchyma bands containing concentric rows of axial resin canal resemble growth ring boundaries.

Vessel: evenly distributed, almost exclusively solitary (92%), a few in radial or oblique pairs; tangential diameter 195-257 μm, average 22±10 μm; radial diameter 217-339 μm, average 274±12 μm; frequency 5-8 per mm^2, average 6±0.6 per mm^2; length 440-970 μm, average 751±46 μm; end wall horizontal to slightly oblique; intervessel pit not observed; vessel ray pit not observed; perforation plate simple; tyloses common; deposit not observed.

Vascicentric tracheid: present, with 2-3 rows of bordered pit.

Parenchyma: both paratracheal and apotracheal: paratracheal vascicentric, tendency to aliform with narrow and short to long wing; apotracheal mainly in regularly spaced concentric bands encircling axial resin canals, a few diffuse in aggregates forming short tangential lines between the rays.

Rays: heterocellular with 1-4 rows of upright cells; 1-4 seriate, mostly 3-4 seriate; up to 2980 μm tall, average 1405±567 μm (range 5-90 cells high, commonly 30-60 cells high); frequency 5-7, average 5.8±0.6 per tangential mm; tend to be storied in some places; occasionally 2 or 3 rays are longitudinally connected.

Fiber: very thick walled, with distinctly bordered pits.

Intercellular canal: axial resin canal present, distributed in concentric rows, some definitely not full circle; almost regularly spaced and the distance between rows are 0.5 mm to 2 mm; tangential diameter 91-242 μm, average 129 ± 17 μm: other

canals are diffuse as single canals among the axial elements.

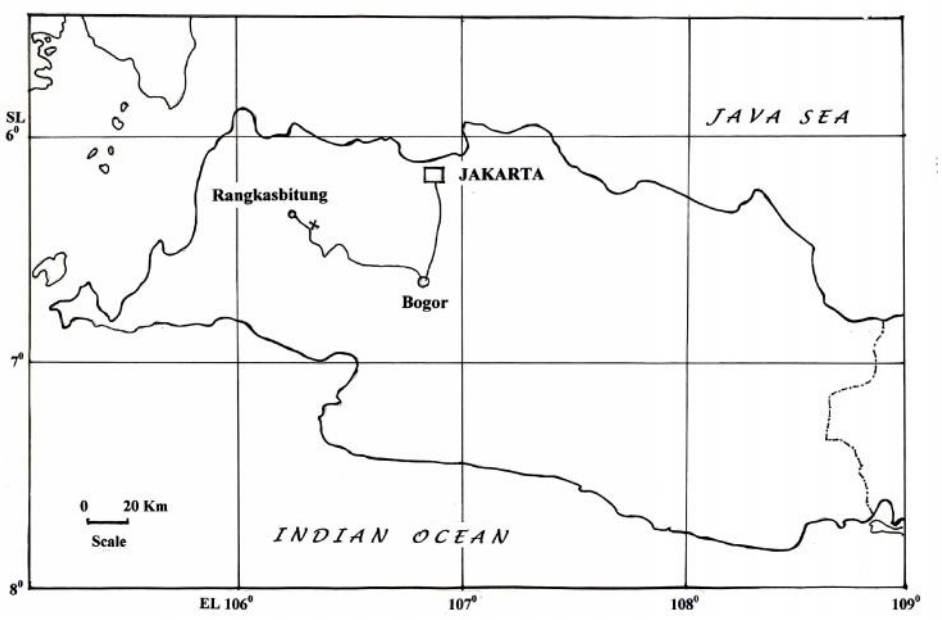

Figure 1. Map of West Java showing the site of fossil wood under study (x).

Figure 2. The fossil wood *Dryobalanoxylon* after being excavated near Rangkasbitung.

Mineral inclusion: prismatic crystals present in the enlarged parenchyma cells.

Holotype: BF 93, Forest Products Research Institute, Bogor, Indonesia.

Size: length, 28 m; diameter at breast height, 105 cm.

Origin: Leuwidulang, Banten, West Java.

Horizon: Genteng Formation

Age: Lower Pliocene

Repository: Forestry Museum Jakarta, Indonesia

Similarities to extant woods

The combinations of diffuse porous and the occurrence of vascicentric tracheids and axial resin canal are characteristics of Dipterocarpaceae family. Vessels almost exclusively solitary, resin canal distributed in long concentric lines and fibers with distinctly bordered pit indicated that the Leuwidulang fossil wood, *Dryobalanoxylon lunaris*, is closely related to modern *Dryobalanops* Gaertner f. (Table 1.). *Dryobalanoxylon lunaris* differs from modern *Dryobalanops* wood mainly in ray height and in size of resin canals. It has much taller rays and has much bigger resin canal.

Dryobalanoxylon lunaris has resin canals distributed in closely spaced tangential rows resembling growth ring boundaries. Among modern *Dryobalanops,* only *Dryobalanops fusca* has the same distribution of resin canal as in *Dryobalanoxylon lunaris.* However *Dryobalanops fusca* has much shorter and narrower rays. Furthermore, the diameter of resin canal in modern *Dryobalanops* woods is less than 100 μm (Ilic, 1994).

There should be silica bodies inside the ray cells of *Dryobalanoxylon* as in modern *Dryobalanops* but it might have been dissolved during silification. The occurrence of silica bodies in ray cells is useful in differentiating modern *Dryobalanops* from *Shorea (sections Rubroshorea and Richetia)*, *Parashorea*, and *Hopea.* It seems impossible however to use this feature for differentiation of sillicified fossil woods, so we have to rely on other features.

Comparison with other fossil wood

Seventeen species of *Dryobalanoxylon* fossil woods have been found, of which 3 were found in India, 1 in Cambodia, 1 in Vietnam, and 11 species in Indonesia (Table 2: Schweitzer 1958; Srivastava et al,

2001). Anatomical features of *Dryobalanoxylon* from Indonesia are summarized in Table 3, 4 and 5, compared to the recently recovered fossil wood from Leuwidulang, *Dryobalanoxylon lunaris.*

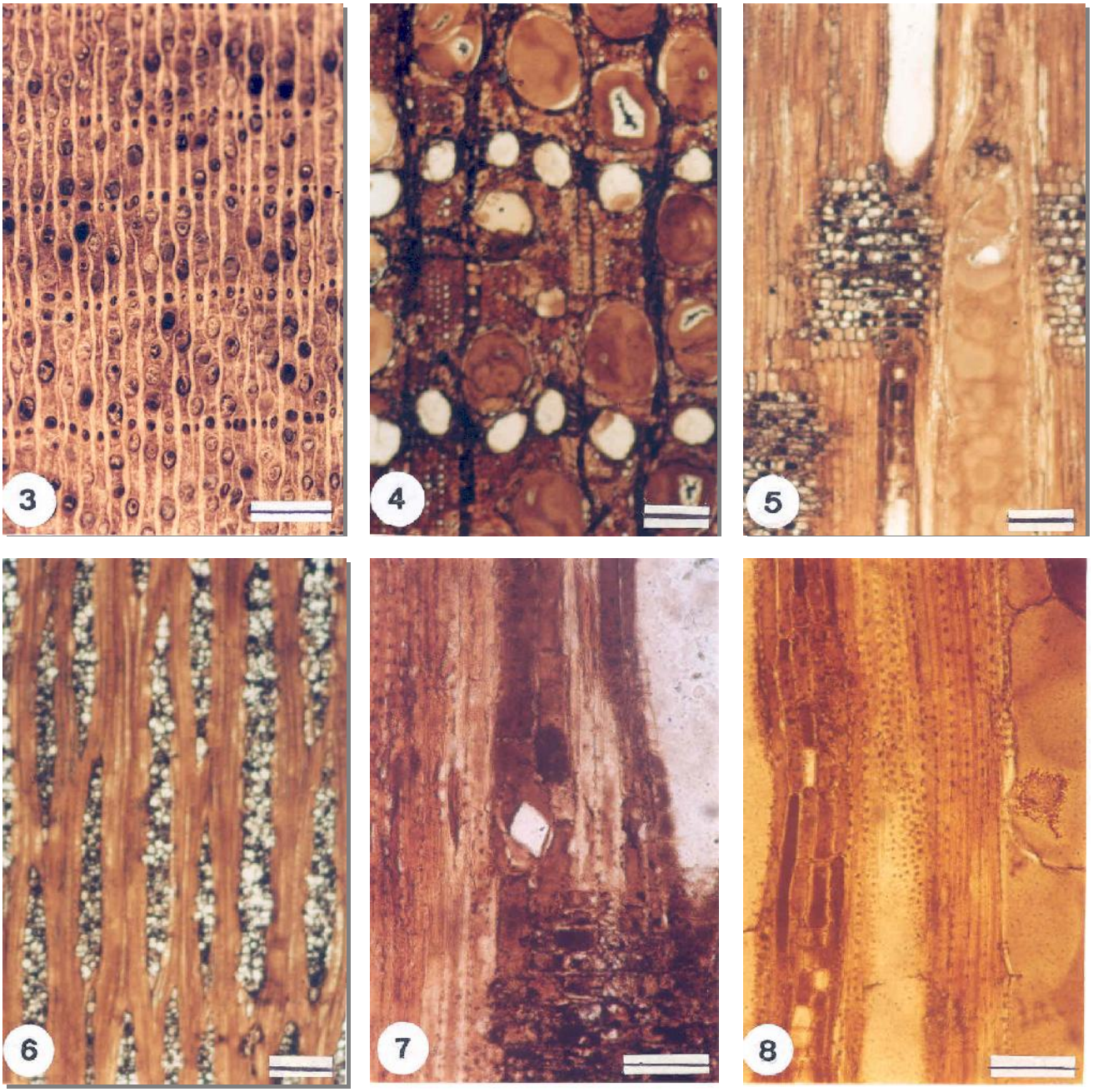

Figure 3-8. *Dryobalanoxylon lunaris*: (3) transverse surface (scale bar = 1 mm); (4) transverse surface (scale bar = 200 μm); (5) radial surface (scale bar = 200 μm); (6) tangential surface (scale bar = 200 μm); (7) radial surface, showing crystal in enlarged parenchyma cell (scale bar = 100 μm); 8) radial surface, showing vascicentric tracheids (scale bar = 100 μm).

Dryobalanoxylon lunaris differs from the other *Dryobalanoxylon* fossil wood mainly in vessel length and in mineral inclusions. *D. lunaris* has much longer vessel elements and has crystal inclusions in the enlarged parenchyma cells. *D. lunaris* also differs from most of the other *Dryobalanoxylon* fossil woods in ray height. *D. lunaris* has rays up to 90 cells high, the same with *Dryobalanoxylon sumatrensis*. However *D. sumatrensis* has much shorter vessel elements, and has no crystals in its parenchyma.

Phytogeography

Dipterocarpaceae in natural forest of the present day Java Island represented only by 5 genera i.e. *Anisoptera*, *Dipterocarpus*, *Hopea*, *Shorea* (*Antho-shorea*) and *Vatica* (Prawira, 1976). Their occurrences are so rare and therefore they are not

considered as economically important trees in the area. There are no records of *Dryobalanops* occurrence in Java Island except those recently planted in arboretum and experimental forest using seed brought from other islands.

Table 1. Comparison between *Dryobalanoxylon lunaris* fosil wood and *Dryobalanops* wood.

Anatomical features	***Dryobalanops* Gaertner f.**			***Dryobalanoxylon lunaris***
	Desch, 1941	**Chu, 1974**	**Ilic, 1994**	
Wood				
Diffuse porous	+	+	+	+
Growth ring boundaries	+ resembling	.	-	+ resembling
Vessel				
Mostly solitary	+	+ 89-95%	+ 90-95%	+ (92%)
Tangential diameter (μm)	182 (*D.a.*); 181 (*D.o.*)	180-232	130-240 (160-220)	190-257 ā = 228
Frequency/mm^2	8.9 (*D.a.*) 7.7 (*D.o.*)	.	5(8-12)17 5 (*D.f.*) 17 (*D.r.*)	6-8 ā = 6.5
Length (μm)	.	.	.	440-970 ā = 751
Tyloses	+	+	+	+
Vascicentric tracheid				
Presence	+	+	+	+
Parenchyma				
Diffuse in aggregates	+	+	+	+
Vascicentric, incomplete	+	+	+	+
Aliform	tendency	+	tendency	tendency
Confluent	.	(+)	.	.
Banded	+	+	+	+
Ray				
Heterocellular	+	+	+	+
Marginal cells	.	1-3	1-3	1-4
Sheath cells	.	(+)	(+)	(+)
Width, seriate	.	1-6	1-3-6	1-4 (3-4)
Height, cells	.	.	.	5-90 (30-60)
Height (μm)	.	< 2000	up to 1000	744-2900 ā= 1405
Frequency per mm	.	.	4-6(8)	5-7
Storied structure	usually in *D.a.*	tendency except in *D.r.*	.	tendency
Fiber				
Distinctly bordered pit	.	+	(+)	+
Wall thickness	.	.	moderately thick to thick	thick
Resin canal, axial				
Diffuse	.	.	.	+
Long tangential rows	+	+	+	+
Diameter (μm)	< vessel	< vessel	40-70	91-242 ā = 129
Mineral inclusion				
Silica in ray cells	+	+	+	?
Silica in parenchyma	.	.	sparse in *D.b.* & *D.o.*	.
Crystals in parenchyma	+ *(D.o.)*	(+) *D.f.* & *D.r.*	(+) *D.k., D.l. D.o., D.r.*	+

Legend: *D.a.= Dryobalanops aromatica; D.b. = Dryobalanops beccarii; D.f. = Driobalanops fusca; D.k. = D. keithii; D.l. = Dryobalanops lanceolata; D.o. = Dryobalanops oblongifolia; D.r. =Dryobalanops rappa*; ā = mean value; + (present); - absent; (+) some conform; . data not available; < less than.

In a recent survey in Leuweng Sancang Nature Reserve situated about 250 km south east of Jakarta, Sidiyasa (1985) found only 3 genera and 4 species of Dipterocarpaceae, these are *Dipterocarpus gracilis*, *Dipterocarpus hasseltii*, *Shorea javanica* and *Anisoptera costata*. In Yanlapa Nature Reserve, which is only about 10 km east of Leuwidulang village, the site of fossil wood being studied, Sutisna (1995) recorded only one species of Dipterocarpaceae that is *Dipterocarpus hasselti*. It was dominant only in 3 out of 12 plots surveyed. Jafarsidik and Anwar (1987) did not find any dipterocarps trees in Kali Bedahan mangrove forest, in seashore about 180 km east of Jakarta. Yamada (1975) also did not find dipterocarps trees in montane forest of Mt. Pangrango, about 100 km south of Jakarta.

The genus *Dryobalanops* now occurs only in Sumatra Island, Borneo Island and Peninsular Malaysia. There are two species of *Dryobalanops* in Sumatra and Peninsular Malaya: *Dryobalanops sumatrensis* Kosterm. (Syn. *D. aromatica* Gaertner f.) and *D. oblongifolia* Dyer. In Sumatra *Dryobalanops* occurs in most of the provinces except in Lampung and Bengkulu, the two provinces in the south part of the island. Genus *Dryobalanops* in Borneo Island consists of eight species that are *D. sumatrensis* Kosterm., *D. beccarii* Dyer, *D. fusca* V.Sl., *D. keithii* Sym., *D. lanceolata* Burck., *D. oblongifolia* Dyer and *D. rappa* Becc., and *D. oocarpa* V.Sl.

The discovery of *Dryobalanoxylon* fossil wood in this study conform to the previous observation conducted by Krausel (1922a, 1922b, 1926), den Berger (1923, 1927), Schweitzer (1958), Mandang and Martono (1996), and Srivastava and Kagemori (2001). The absence of extant wood in the present day natural forest of Java indicated that it must have extinct by some reasons. According to Endert (Steenis, 1963) the absence of several Sunda shelf elements in Java were due to serious effect of volcanic

activities in the Tertiary, and then destruction by agricultural practice. These reasons however did not satisfy Steenis. In part it may be right but he had a tentative idea that for a long time in the Tertiary, Java was consisted of islands arc which similar to that of the present Lesser Sunda Island.

Table 2. List of *Dryobalanoxylon* fossil woods in Indonesia.

No.	Species	Origin	Age	Authors
1	*D. javanense*	Bolang, West Java	Tertiary	Krausel, 1922 Den Berger, 1923
		Tenjo, West Java	Pliocene	Schweitzer, 1958
2	*D. spectabile*	Bogor, West Java	Pliocene	Krausel, 1926 Den Berger, 1927
		Banten	Pliocene	Schweitzer, 1958
3	*D. tobleri*	Palembang, South Sumatra	Tertiary	Krausel, 1922 Den Berger, 1923
		Banten, West Java	Pliocene	Schweitzer, 1958
4	*D. rotundatum*	Jambi, Sumatra	Quaternary	Schweitzer, 1958
5	*D. musperi*	Bogor, West Java	Pliocene	Schweitzer, 1958
6	*D. mirabile*	Jambi, Sumatra	Quarternary	Schweitzer, 1958 Schweitzer, 1958
7	*D. neglectum*	Jambi, Sumatra	Quarternary	Schweitzer, 1958
		? Bogor, West Java	?	Schweitzer, 1958
8	*D. bangkoense*	Jambi, Sumatra	Quarternary	Schweitzer, 1958
		Banten, West Java	Pliocene Miocene	
9	*D. borneense*	East Kalimantan	Miocene	Schweitzer, 1958
10	*D. sumatrense*	Jambi, Sumatra	Pliocene	Schweitzer, 1958
11	*D. bogorensis*	Leuwiliang, West Java	Pliocene	Srivastava & Kagemori, 2001
12	*D. lunaris*	Leuwidulang, Banten, West Java	Pliocene	This report

Table 3. Comparison between *Dryobalanoxylon lunaris* and other *Dryobalanoxylon* fossil wood species: vessel features [Krausel, 1922b; Krausel, 1926; Schweitzer, 1958; Srivastava & Kagemori, 2001 (except for *D. lunaris*)].

Fossil species		Vessel features			
		Frequency per mm^2	Tangential diameter	Radial diameter	Vessel length
			«m		
D. javanense	a	8-16	70-210	65-275	.
	b	5-10	125-225	125-275 (250)	250-500
D. spectabile	a	10-16	95-170	130-270	400-700
	b	9-14	95-200	125-275 (200-250)	500
D. tobleri	a	8-16 (12-16)	80-230	100-330	250-550
	b	5-12	150-200	175-350	250
D. rotundatum		10-16 (14)	50-300		250-500
D. musperi		15-22	60-150 (100-125)		.
		10-15	60-200 (150-200)		
D. mirabile		9-22	75-175	100-275	150-500
D. neglectum		7-13	150-225	225-300	300-500
D. bangkoense		7-13	75-225	125-325 (250-275)	100-600
D. borneense		10-16	60-125	100-200	250-600
D. sumatrense		4-8	75-200	125-325	200-700
D. bogorensis		3-4	120-286	165-336	308-572
D. lunaris		5-8	195-257	217-339	440-970
		ā = 6.5	ā = 228	ā =274	ā =751

Legend: ( ) common value; ā : average; **.** data not available

The last explanation by Endert was not satisfactory because, eventhough agricultural practices might be significant in reducing the population of some elements in Java Island but it was unlikely the main cause of extinction of *Dryobalanops*. The fact is that *Dryobalanops* also does not occur in Lampung and Bengkulu, the two provinces in the southern part of Sumatra Island, where agricultural practices have not been as intensive as in Java. Furthermore, there are still considerable amounts of natural forest in these two provinces but still, *Dryobalanops* also does not occur there. So the cause of *Dryobalanops* extinction from Java and southern part of Sumatra was most likely by volcanic activities, which was occurred somewhere around the present day Sunda strait. *Dryobalanops* was obviously not able to withstand the continuous shower of volcanic ash. *Dryobalanops* is very sensitive as shown by formation of resin canals. Disturbance from outside of the plant stimulate the formation of resin canals in wood, which are mostly distributed in concentric lines. Continuous and heavy disturbance in wide areas must have caused mass extinction of *Dryobalanops* from West Java and southern part of Sumatra.

The results of the present study, together with the early discovery on the abundance of Dipterocarpaceae fossil wood in the west region of Java, are indicative that this part of the island was connected by land to Sumatra and Borneo and Asia's main land once upon a time during the Tertiary period. Many plants from Asia must have been migrated through this land connection to Java even though some of them were then destroyed and extinct. The inability of *Dryobalanops* and other extinct genera to remigrate from upper part of Sumatra and Borneo in the later period might had been hampered among others by separation of these islands by sea water, as has been occurred at the end of Pleistocene epoch.

Table 4. Comparison between *Dryobalanoxylon lunaris* and other *Dryobalanoxylon* fossil wood: ray features [Krausel, 1922b; 1926; Schweitzer, 1958; Srivastava and Kagemori, 2001 (except for *D. lunaris*)].

Fossil species	Ray width (cells)	Ray height (cells)		Ray height («m)	Ray distance (cells)	Sheath cells	Storried structure
		Multi seriate	Unise-riate				
D. javanense	1-6 (3-5)	3-30	.	.			.
	1-6 (3-5)	3-45 (30)	.	.	2-19	+	.
D. spectabile	1-6 (3-6)	3-30	.	.			.
	1-4 (3)	3-35	up to 15	.	4-12	+	.
D. tobleri	1-6 (2-4)	10-50	.	.			.
	1-5 (2-4)	35-50	.	.	6-8	+	.
D. rotundatum	1-4 (2-3)	2-30 (18-22)	up to 15	.	2-20	-	+
D. musperi	1-4 (2-3)	20-35 (20-25)	up to 20	.	1-12	.	.
D. mirabile	1-5 (3-4)	20-30	.	.	2-12	-	.
D. neglectum	1-3	56	.	.	4-18	.	.
D. bangkoense	1-5 (3-4)	4-70 (25-40)	up to 15	.	2-23	.	.
D. borneense	1-3	55	.	.	3-9	+	.
D. sumatrense	1-5	4-90	up to 15	.	2-15	-	.
D. bogorensis	1-6	11-36	.	500-1200	.		.
D. lunaris	1-4 (3-4)	5-90 (30-60)	up to 20	744-2900 ā = 1405	.	-	tendency

Legend: ( ) common value; + present; - absent; . data not available

Table 5. Mineral inclusions and resin canal in *Dryobala-noxylon* fossil wood [Krausel, 1922b; 1926; Schweitzer, 1958; Srivastava and Kagemori, 2001 (except for *D. lunaris*)].

Fossil species	Crystal		Silica particles in ray	Resin canal diameter «m
	In ray	In paren-chyma		
D. javanense	.	.		30-80
	+?	.	+?	30-100
D. spectabile	.	.		30-120
			+	40-100
D. tobleri	+?	.		50-250
	.			50-100
D. rotundatum	.	.		50-100
D. musperi	+	.		40-75
D. mirabile	+	.	+?	60-200
D. neglectum	+	.		40-150
D. bangkoense	+?	.	+?	25-125
D. borneense	.	.	.	40-70
D. sumatrense	+	.	+?	75-110
D. bogorensis	-	-	-	33-100
D. lunaris	-	+	.	91-242

Legend: + present; - absent; +? questionable; . not mentioned.

CONCLUSION

The silicified fossil wood log excavated from Pliocene deposit near Leuwidulang village in Banten, Java Island, belongs to Dipterocarpaceae family. Anatomical features of the fossil wood showed that the fossil wood belongs to genus *Dryobalanoxylon* Den Berger. However, the fossil wood differs from the previously described *Dryobalanoxylon* fossil woods species in vessel length, ray height and crystals inclusion in the enlarged parenchyma cells, so it is unlikely that this specimen belong to any of them. It should therefore be assigned to another species, as we proposed *Dryobalanoxylon lunaris*.

The extant genus *Dryobalanops* Gaertner f. is now existing only in Sumatra, Borneo and Malay Peninsula. The occurrence of *Dryobalanoxylon* fossil wood in Java indicates that the ancestor of Dryobalanops was distributed in wider areas. Its extinction from Java was thought to be by volcanic activities. The inability of *Dryobalanops* to remigrate from Sumatra and Borneo in the later period might have been hampered by separation of these islands by seawater.

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