Innovation and stasis : gymnosperms from the early Permian Jambi flora

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Wood anatomical variability in Early Permian ‘araucarioids’[6]

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Abstract

Although araucarioid wood is poor in diagnostic characters, well in excess of 200 Late Paleozoic species have been described. This study presents a large-scale anatomical analysis of this wood type based on the fossil wood collections from the Early Permian Mengkarang Formation of Sumatra, Indonesia. Principal Component Analysis visualisation, in conjunction with uni- and multivariate statistical analyses clearly show the wood from the Mengkarang Formation to be a contiguous micromorphological unit in which no individual species can be distinguished. Pycnoxylic wood species described previously from this collection or other collections from the Mengkarang Formation fall within the larger variability described here. Based on comparison with wood from modern-day Araucariaceae, the Early Permian specimens can be differentiated from extant (but unrelated) “araucarioids” by a few (continuous) characters.

Introduction

Pycnoxylic wood (wood with mainly tracheary elements and little parenchyma) from the Late Palaeozoic is generally considered to be poor in diagnostic characters (Gothan 1905; Jeffrey 1913; Frentzen 1931). Consequently, the difficulty concerned with distinguishing and classifying both modern, as well as fossil, araucarioid wood have been recognised by authors for a long time (e.g. Kraus 1882; Philippe 2011). This lack of anatomical variability is compounded by insufficient knowledge regarding the extent of intraspecific variation in wood characters in (fossil) wood (Kraus 1882; Jeffrey 1913; Frentzen 1931) as influenced by both ecology and cambial age.

Despite the low number of diagnostic characters in this wood type, a high number of species have been established within fossil araucarioid woods, particularly within the overlapping fossil genera *Araucarioxylon* and *Dadoxylon*. An overview published by Schultze-Motel (1962) recorded 45 species of *Araucarioxylon* (with a further 17 attributions to the genus as *Araucarioxylon* sp.) and 144 species of *Dadoxylon* (with an additional 20 as *Dadoxylon* sp.). Later, an update by Giraud (1991) listed a further 57 new species of *Dadoxylon* (in addition to 12 non-specific attributions to the genus). Philippe (2011) estimated that about 400 species of *Araucarioxylon* have now been described in total. It needs to be stated at the outset that any possibility of a phylogenetic connection between fossils assigned to *Araucarioxylon*, in addition to the term 'araucaroid', with modern *Araucariaceae* wood is unclear. In the absence of attached fructifications or other characters, this wood type is only classifiable as a 'primitive gymnosperm'. These terms simply indicate a similarity to Araucariaceae wood anatomy, in particular with regard to the hexagonal bordered tracheid pits.

One explanation for such a proliferation of described species of *Araucarioxylon* and *Dadoxylon* is that descriptions of new species of fossil wood are often based on only a very small number of specimens from a geographically limited area. One aspect of palaeobotany that has been much neglected over the years is an understanding of the degree of background variation in anatomical characters that occurs naturally within and between taxa as a result of intrinsic and extrinsic factors (Kraus 1882; Carlquist 1975, 1977). This is highly relevant to Late Palaeozoic fossil wood taxa where the observed variation can occur within a single tree, between trees of the same population, and between trees of differing ecology. However, given the high degree of anatomical variation in modern-day gymnosperms (Bailey & Faull 1934; IAWA Committee 2004; Falcon-Lang 2005), which are anatomically comparable to their Late Palaeozoic precursors, the level of variability within their Late Palaeozoic counterparts is also expected to be considerable. The dangers of strong over-classification (i.e. 'splitting') due to an underestimation of anatomical variability in individual species are obvious. With this in mind, a large-scale, quantitative approach, involving a comprehensive analysis of a large number of fossil pycnoxylic wood specimens, both those assigned to published fossil taxa and as yet unassigned collections could lead to a better delimitation of usable anatomical boundaries that would aid identification and classification of early gymnosperm wood.

During expeditions to the south-western part of the Jambi Province, Sumatra (Indonesia) over the period 2003–2008 fossil wood specimens were collected from the Early Permian Mengkarang Formation (sensu Suwarna et al. 2000; Suwarna 2006), which includes spectacular examples of (in situ) tree trunks (Fig. 5.2).

An earlier larger collection of fossil wood from the same region and predominantly from the same formation was collected by Posthumus during the 1920s and 1930s (Posthumus 1927). This was studied by Kramer as part of his work on the Tertiary woods of Southeast Asia (Kramer 1974a, b). He erected the (Tertiary) araucarioid species, *Dammaroxylon kaurioides* from this material and designated another 122 specimens of araucarioid fossil wood from Jambi as Coniferae incertae sedis (i.e. pycnoxylic wood of unknown affiliation).

A small number of specimens were collected in the 1980s from the same area. These were studied by Vozenin-Serra (1985, 1989) and attributed to two species of pycnoxylic wood: *Dadoxylon (Cordaioxylon) roviengense* Vozenin-Serra and *Dadoxylon saxonicum* (Goeppert) Frentzen. (These specimens were not available to us for inclusion in this study.)

The woods from these previous collections together with the material collected between 2003–2008 amount to some 160 specimens of fossil wood from a single, relatively small, geographic region.

Although part of this material has previously been described as Tertiary, it does appear to have been collected from the Early Permian Mengkarang Formation, as it was collected from the same localities as the more recent collections. We expect, therefore, that this material will not differ anatomically from the material that was collected more recently from these same localities and which is Early Permian in age.

Studies on variability in modern gymnosperm wood (Kraus 1882; Bailey & Faull 1934; IAWA Committee 2004; Falcon-Lang 2005) indicate that both intra- and intertree variability can be considerable. Therefore, we expected the fossil wood material in this combined Jambi collection to show a large amount of variability with regard to those characters used in the identification of such material, such as ray height and width (seriation) and ray density. In order to evaluate the degree of variation, a largescale quantitative analysis of both discrete and continuous characters exhibited by these fossils was performed. For a broader perspective on the amount of variability present in the Jambi collection, we also compared the material from this Early Permian collection with a small set of the anatomically similar, but phylogenetically at best very remote, modern-day Araucariaceae.

Given the different species established in the past, based on fossil gymnosperm wood from Jambi, we expected to find some clearly distinguishable fossil wood species, defined by a distinct set of characters. However, in light of the limited amount of diagnostic characters offered by araucarioid wood, we expect the number of distinct fossil species to be small. In order to ascertain this, we subjected the dataset to multivariate analysis.

Materials and methods

Geological context

All the fossil wood material analysed here is collected from the Mengkarang Formation, which is found to the southwest of the town of Bangko, in Jambi Province, Sumatra, Indonesia (Fig. 5.1).

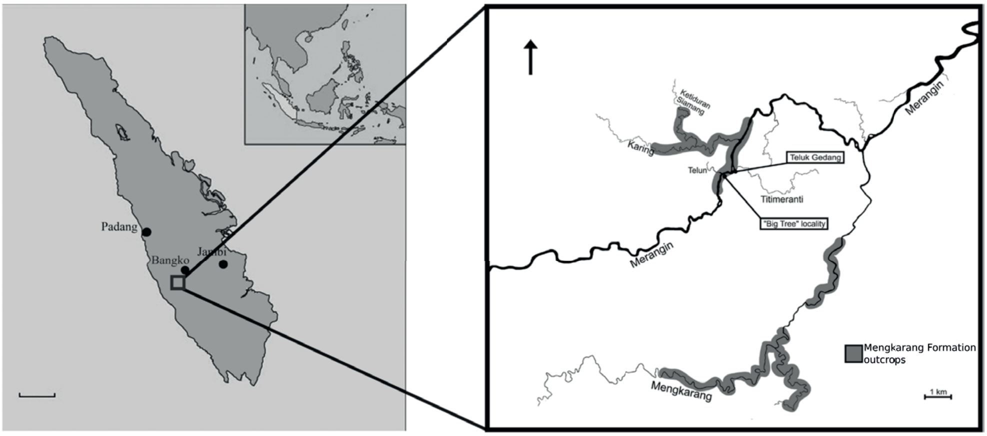


Figure 5.1: A map of Sumatra, Indonesia with insert showing the area southwest of Bangko: the Merangin River, its tributaries and the area where all the fossil wood material discussed was collected. The sections along the rivers where the Mengkarang Formation crops out are indicated.

The Mengkarang Formation has been dated, based on fusulinid analysis, as Late Asselian to Sakmarian in age (Vachard 1989; Ueno et al. 2007). A more recent analysis of brachiopods indicates a Sakmarian age (Hasibuan et al. 2000), whilst an unpublished analysis of zircons found in the pyroclastic deposits encasing the large tree trunk mentioned above, returned a Middle to Late Asselian age (Schmitt et al., pers. comm.). In addition, all compression flora (i.e. not fossil wood), collected from the Mengkarang Formation, can be attributed to early Permian taxa.

Outcrops of this Formation are found along the Merangin River as well as its tributaries in this area. Even though the Merangin River cuts through the Mengkarang Formation, its tributaries (with exception of the Mengkarang River) largely follow a single set of strata (Fig. 5.1). Therefore, the rivers can be grouped into stratigraphical horizons. The oldest is the Telun horizon and comprises material found along the Telun River or near the Telun mouth along the Merangin (including the locality of the large in situ tree). The younger Ketiduran Siamang horizon consists of material found along the Ketiduran Siamang River. The youngest Karing horizon is the material found along the Karing River. Finally, the Mengkarang River is less chronologically constrained since the Mengkarang River cuts through all the strata of the Mengkarang Formation.

The Mengkarang Formation is characterised as volcanic in origin, with evidence of periodic partial flooding (Donovan et al. 2013). It consists of both marine and fluvial deposits, including lime stones, (reworked) pyroclastics and thin coal seams. Its abundant compression floras represent both classic Late Palaeozoic forest mire associations, as well as more xeric vegetation types (Van Waveren et al. 2007; Booi et al. 2008, 2009a, b).

Collections

During an expedition to Jambi Province in 1925 Posthumus (1927) collected a large amount of fossil wood from along the Merangin River and several of its tributaries; 178 specimens in total, of which 137 are of gymnosperm wood, the remainder being angiosperm woods (Dipterocarpaceae). These are reported by Posthumus as having been collected from the Karing Schichten formation (Zwierzycki 1935), which is now considered to be equivalent to the Mengkarang Formation sensu Zwierzycki (1935). The Mengkarang Formation is unconformably overlain by Tertiary strata and the possibility exists that some specimens might actually originate from those much younger layers. This is the case for the Dipterocarpaceae, which, as described by Schweitzer (1958), all derive from a single locality along the Merangin River.

Recent expeditions (2004, 2006 and 2008) to the area have collected an additional 22 specimens of gymnosperm fossil wood (no angiosperm fossil wood was found). Some of these specimens were found as loose boulders (float) along the Merangin River and its tributaries. These are large fossil wood fragments that had become dislodged from the sediment by river action and subsequently washed into the river and have been collected from the river bed. However, some of the logs have been found still encased in the Early Permian outcrops.

Additionally, almost half of the newly collected fossil wood specimens were found as (near) in situ, upright tree trunks along the Merangin River, encased in the pyroclastic deposits of the lowest part of the Mengkarang Formation.

One of these, a large tree trunk (2.4 m high, 3.3 m from the root base, 1.9 m in diameter at the distal end and 2.37 m in diameter at the proximal (base) end) was found encased in alternating layers of tuff on the western bank of the Merangin River (Fig. 5.2). On both sides of the trunk supporting structural roots are visible, the longest extending 3.44 m from the root base (Fig. 5.2C).

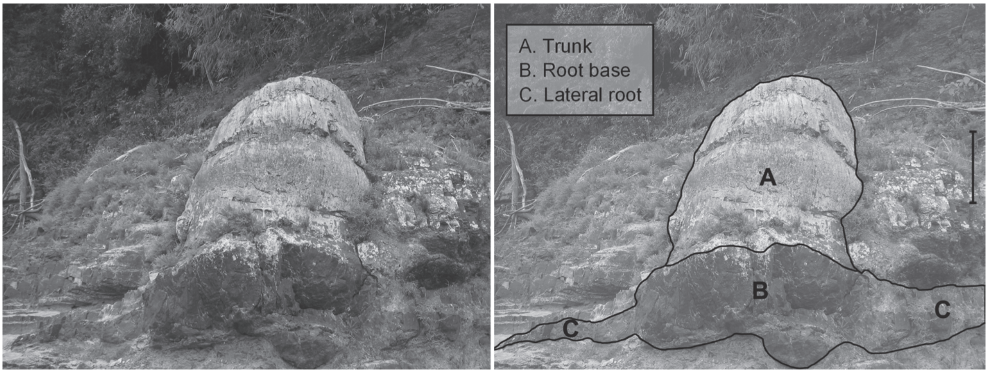


Figure 5.2: The large in situ tree trunk found on the bank of the Merangin River. The schematic overlay in one of the pictures illustrates the different parts of the trunk. – A: Trunk. – B: Root base. – C: Lateral support root on either side. Scale bar is 1 metre.

Eight large logs were found on the eastern bank of the Merangin River, directly opposite the large tree trunk described above and possibly from the same layer (although this could not be verified, as the outcrop is not exposed on this side). These logs range in height from 55 cm to 160 cm, and in diameter from 95 cm to 180 cm, with an average diameter of 128 cm.

Thin sections

Two sets of thin sections exist for the specimens of the original collection of Jambi fossil wood. The first set was made for Kramer's work (1974a, b) on fossil wood from Indonesia from the Jambi fossil wood specimens collected by Posthumus. A second set was made of all these specimens from the original Jambi collection by J. van der Burgh at a later date. Both sets are housed at the Laboratory of Palaeobotany and Palynology of Utrecht University, The Netherlands. The latter set was used for the analysis in this paper, as it is the most complete.

Thin sections were also made of all the fossil wood collected in 2004–2008 expeditions. These are housed in the Naturalis Biodiversity Center.

All thin sections used measure at least 1.5 by 1.5 cm, and are usually larger.

Extant material

Thin sections (three planes of section) of six species of extant Araucariaceae (*Agathis macrophylla* (Lindl.) Mast., *Ag. dammara* (Lamb.) Rich., *Ag. robusta* (C. Moore ex F. Muell.) Bailey, *Araucaria angustifolia* (Bertol.) Kuntze, *Ar. cunninghamii* Aiton ex D. Don, *Ar. bidwillii* Hook.) were used for comparative purposes. These slides are housed in the collection of the Herbarium of the Naturalis Biodiversity Center (NHN-Leiden).

All analyses detailed below were applied to both the fossil and the modern wood specimens.

Throughout this paper, specimen numbers starting with U are part of the older original collection (housed in the Laboratory of Palaeobotany and Palynology of Utrecht University) and specimen numbers starting with NAT are part of the newly collected material (housed in the Naturalis Biodiversity Center, Leiden).

Multivariate analysis

Choice of characters

Of the sets of thin sections made from the 137 gymnosperm wood specimens in the original collection, only 85 sets were of wood of sufficient quality of preservation to include in this study.

Where possible, characters used are based on the IAWA list of microscopic features for softwood identification (IAWA Committee 2004). However, it deviates from the characters usually used for description and differentiation of species of araucarioid wood, because we tried to use as few compound characters as possible. For example, a character such as ray density (in tangential view) can be seen as a ‘compound character’ that is determined by five separately distinguishable characters, namely ‘size of tracheids’, ‘size of ray cells’, ‘ray seriation’, ‘ray height’ and ‘number of tracheid cells between rays’. In such a case the latter five characters were used instead of the first, in order to have a character set that described the anatomy in as much detail as possible. Table 5.1 shows the characters chosen for the measurements and briefly explains them. For every character at least 25 measurements were taken per specimen. Averages of these measurements were subsequently used in the analyses. Given that no growth rings were observed in any of the fossil wood sections and relative deformation is less in the radial plane than in the tangential plane, the radial diameter of each cell was measured.

Preservation determined the choice of measured characters and therefore important characters such as crossfield pits had to be excluded from the analysis since they could only be observed in 14% of fossil specimens. However, the description and measurements of the cross-field pits is included in the general description of the material.

Table 5.1: The characters used in the multivariate analyses and statistics and their descriptions.

Character
Radial tracheid diameter (TS)
Number of tracheids between rays (TS)
Ray height (number of cells, TLS)
Ray width (number of cells, TLS)
Radial ray cell length (RLS)
Ray cell height (RLS)
No of tracheid pit rows (1-5 seriate, RLS)
Bordered pit diameter (RLS)

Methods used

Principal Components Analysis (PCA) was chosen as it provides a visual representation of the multivariate pattern in the dataset. PCA was performed on the correlation matrix. The components in a PCA are hypothetical variables (the components) that represent the maximum of variance in the data. All actual variables contribute to each component (eigenvector) and the relative amount of a single variable's contribution to the component is referred to as the "loading". The relative ability of a component to account for the variability in the dataset is represented by its eigenvalue (Hammer & Harper 2006).

The outlines for the different groups within the PCA scatter plots have been illustrated by also plotting their convex hulls. These connect the most extremely positioned data points for each group, and illustrate the extent of the variance for a certain group of fossil wood specimens.

All data processing was done using PSPP, R and Paleontological Statistics (Hammer et al. 2001). Where results and their standard deviations are stated, the standard deviations are given in parentheses preceded by the '±' sign.

Results

Anatomy of the fossil wood (Plate 5.1)

Description:

Composition: Homoxylous (pycnoxylic) wood (Plate 5.1A). Without resin canals. No growth rings observed.

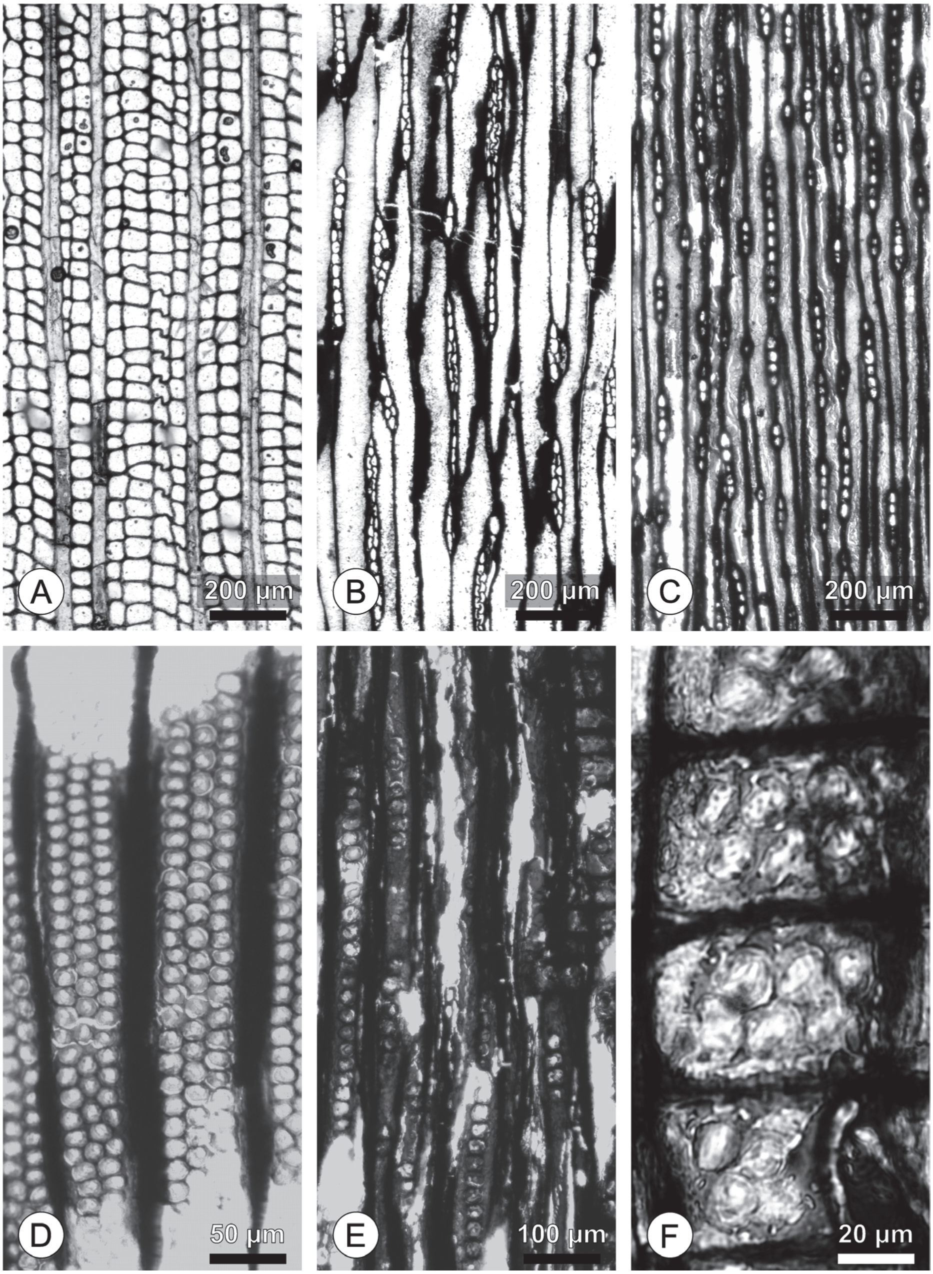


Plate 5.1: Wood anatomy of the pycnoxylic fossil wood from the Mengkarang Formation. – A: U–2188, transverse section, uni– and biseriate rays. – B: U–1744, tangential section, uni– and biseriate rays. – C: U–1584, tangential section, uniseriate rays. – D: U–1768, radial longitudinal section, three rows of bordered pits on a tracheid wall. – E: NAT–40, radial longitudinal section, one row of bordered pits on a tracheid wall. – F: 2030, radial longitudinal section, polygonal cross–field pits.

Rays: Rays uniseriate (83.4%), biseriate (16.5%) or very rarely triseriate (0.1%), 1.17 cells wide on average (± 0.400). Rays usually 1–30 cells high (95.2%), on average 11.1 (±10.2) cells high. Ray cells all procumbent; usually 18–38 μm (97.7%) high, on average 26 μm (± 4.7); ray cell length (in radial direction) very variable, 75–238 μm (96.6%), on average 150 μm (± 38.3). Rays laterally separated by 1–10 tracheids (99.8%), mostly 1–6 (94%), at an average of 3.47 tracheids (± 1.86).

Tracheids: Usually rectangular to square in transverse section, 32–82 μm (96.3%) in radial diameter, 55.7 μm (± 11.8) on average.

Bordered pits: Alternate, in rows of 1–5 pits across on the radial tracheid wall.Mostly 1–3 pits across (98.1%), rarely four pits (1.5%) or five pits (0.4%), on average 1.8 (± 0.75) pits. The pits vary in outline from round (43.3%) to rounded hexagonal (46.4%) to hexagonal (10.3%). and measure 10–20 μm in diameter (99.1%) with an average size of 15 μm (± 2.3). The shape of the pit aperture varies strongly, from lenticular (15.1% of specimens) to lenticular-oval (34.9%) to oval (30.2%) to oval-round (14%) to round (5.8%).

Cross-field pits: Araucarioid type. Number of pits per cross-field varies from one to eight, but commonly between one and five (97.3%), with an average of 2.26 (±1.26) pits per cross-field. Polygonal to round or slightly oval. Varying in arrangement from isolated to completely crowding the cross-field, with up to three alternating horizontal rows.

Statistical analysis of the data

Test for normality

In an attempt to ascertain the distribution of the data for the different characters of the fossil wood, a Shapiro-Wilk test for normal distribution was performed on all data for the characters listed in Table 5.2. This test is generally considered to be the more powerful (Stephens 1974) compared with other tests for normality, with a smaller chance of false positives compared to, for example, the Kolmogorov-Smirnov test. It shows that only the characters tracheid cell diameter and ray cell length agree with the test's null-hypothesis of normal distribution at an alpha-level of 0.05.

Principal Components Analysis

If we apply the most basic approach in using any component with an eigenvalue larger than 1 (see Table 5.3), the first 3 components all appear valid candidates for the PCA, with the first two components being the most meaningful. However, both the low eigenvalues of the first 5 components and the small differences between them also illustrate the relatively weak explanatory power of all those components. Given these results, we have decided to present graphically only the results for the first two components here.

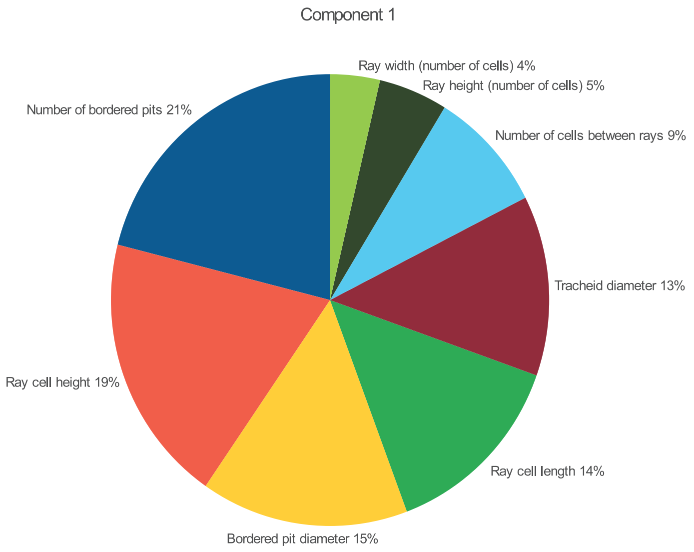
Table 5.2: The results of the Shapiro-Wilk test for normality. W indicates the test result. The last column (N) indicates the number of specimens in which the character was measured. * indicates the p-values significant at an alpha of 0.05.

	Shapiro-Wilk		N
	W	*p (asymp. 2-tailed)*	
Tracheid diameter	0.980	0.157*	95
Number of tracheids between rays	0.970	0.027	96
Ray height	0.956	0.004	88
Ray width	0.923	0.000	92
Radial ray cell length	0.992	0.915*	83
Ray cell height	0.886	0.000	94
Number of rows of bordered pits	0.926	0.000	96
Bordered pit diameter	0.970	0.027	95

Table 5.3: The eigenvalues for all the components available for the PCA. The values in the middle column indicate the percentage of the total amount of variance in the dataset that the components account for. In the last column the characters that contribute most to the respective component are mentioned.

Component	Eigenvalue	% variance	Description
1	2.279	28.48	Dominated by 'number of rows of bordered pits', 'ray cell height' and 'bordered pit diameter'
2	1.299	16.24	Dominated by 'tracheid diameter' and 'ray cell width'
3	1.139	14.24	Dominated by 'ray height' and 'ray width'
4	0.9737	12.17	Dominated by 'number of cells between rays'
5	0.9480	11.85	Dominated by 'ray height'
6	0.5314	6.643	Dominated by 'ray cell width'
7	0.4356	5.445	Dominated by 'ray cell height'
8	0.3946	4.932	Dominated by 'number of bordered pits' and 'tracheid diameter'

The loadings of component 1 indicate that the characters of ‘ray cell height’ (19%), ‘number of rows of bordered pits’ (21%) and ‘bordered pit diameter’ (15%) together account for more than half (55%) of its variance (see Fig. 5.3).



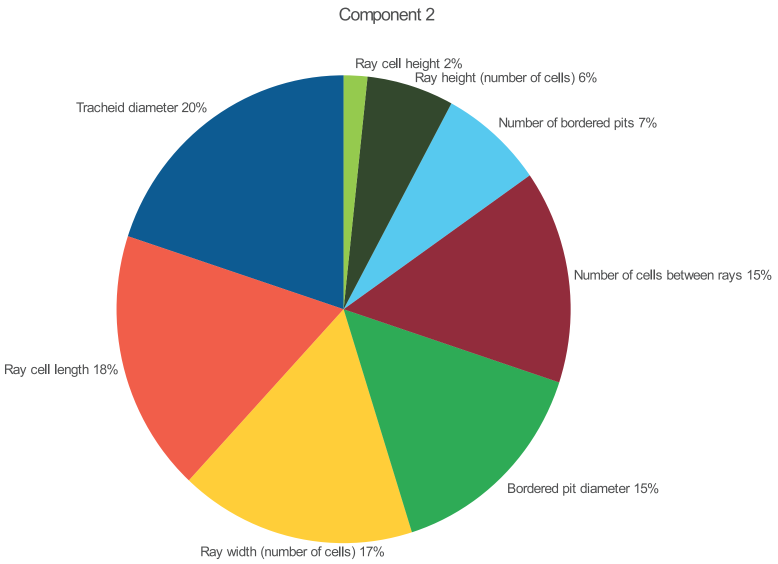


Figure 5.3: Two pie charts describing the relative contributions (loadings) of the characters used in the PCA to components 1 and 2.

The loadings of component 2 show that ‘tracheid diameter’ (20%), ‘ray cell length’ (18%) and ‘ray width (number of cells)’ (17%) together account for more than half (55%) the variance described by this component (see Fig. 5.3).

In the PCA scatter plot for components 1 & 2 in Figure 5.4, different symbols are used for the relative stratigraphic position within the Mengkarang Formation of the samples by indicating the groups of rivers and streams along which the specimens were found (as detailed above).

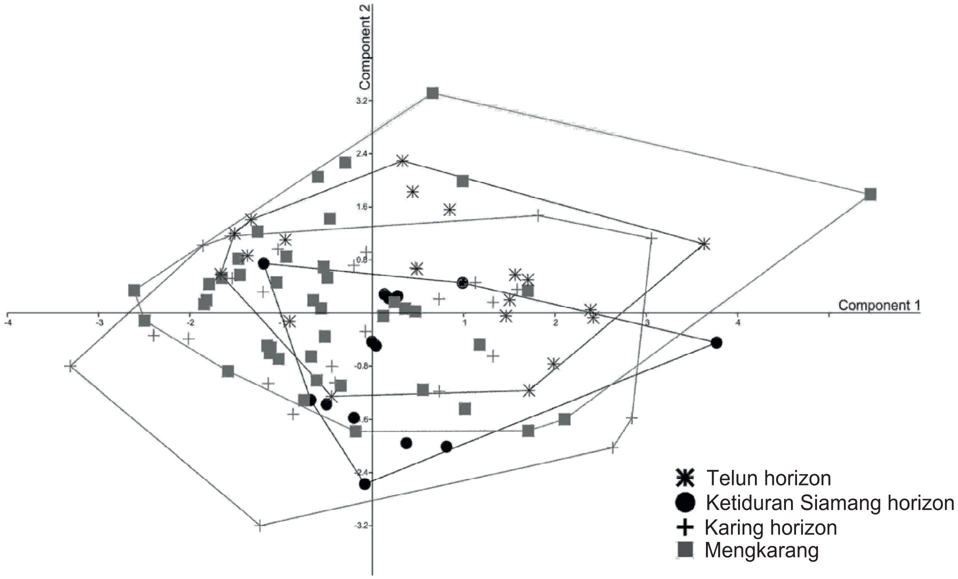


Figure 5.4: The PCA scatter plot for components 1 and 2. The symbols indicate the groups of rivers and streams where the respective specimens were found. This shows the distribution of anatomical and morphological variability by river along which they were found.

Largest variability is observed for specimens found along the Mengkarang River, although the extent of the variability in the upper right corner of the plot (Fig. 5.4) is mainly accounted for by two ‘outliers’. The other localities exhibit lower amounts of variability and strongly overlap.

In the second PCA scatter plot for components 1 & 2 (Fig. 5.5), the different symbols indicate either the specimens from the original collection or the recently collected material. The variability found in the original, bigger collection is larger than that of the recently collected material, but the two collections overlap completely (see also Table 5.4). To further determine how the two collections relate in measurable characters, a test for equality of means was performed.

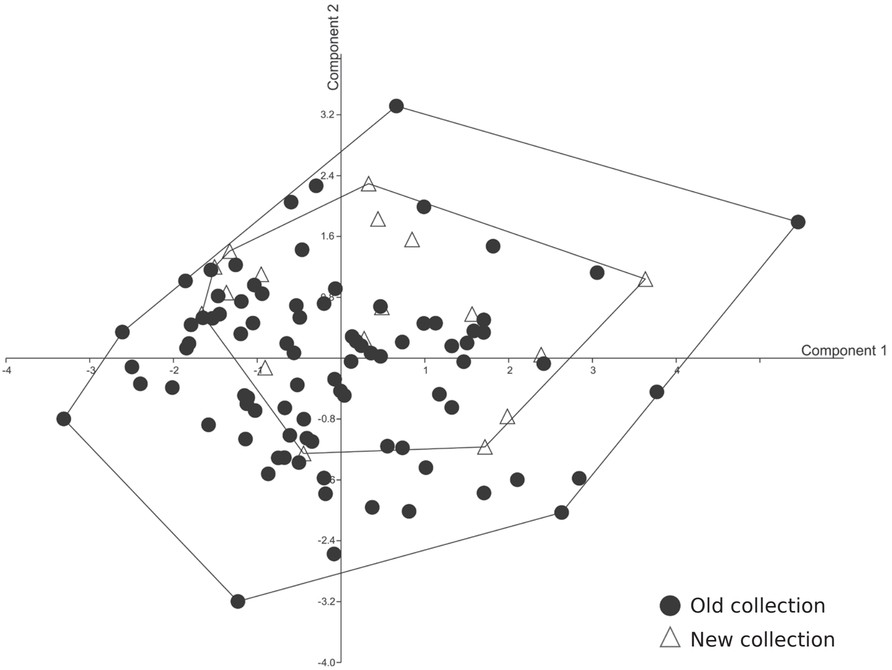


Figure 5.5: The PCA scatter plot for components 1 and 2. The symbols indicate whether the specimens come from the original or the recently collected material. This shows the differences in distribution of anatomical and morphological variability between these two collections.

Given the difference in sample size between the old and the new collections, and the deviations from normal distribution, we have to use a test such as a two-group permutation test, which does not rely on assumptions of normality or equality of variances. Performing this test using a permutation with 10,000 replicates and the Mahalanobis squared distance measure, results in a p-value of 0.16 for the hypothesis of both means being equal, which is significant for the alpha level of 0.05.

In his work on Tertiary fossil wood from Southeast Asia, Kramer (1974a, b) treated a large number of araucarioid specimens from Indonesia, mostly collected from several rivers that cut through the Mengkarang Formation (specifically, the Karing, Mengkarang, Ketiduran Siamang and Tantan Rivers). He ascribed 7 specimens of araucarioid fossil wood (all of them collected from the rivers mentioned above) to the genus *Dammaroxylon* as *D. kauri-oides* nov. spec. and designated their age as Early Quaternary or Late Tertiary, although on what basis was not made clear. The genus *Dammaroxylon* had been established earlier by Schultze-Motel (1966) for *Dadoxylon*-type secondary wood from the Late Cretaceous with the distinguishing character of "Randzellen" ("border or marginal cells", visible as wavy line above and below a ray in radial view).

Table 5.4: The most important characters for the two collections of fossil wood specimens (original and recent) separate and combined. Standard deviations are indicated with the ± symbol.

		Newly collected material	Older collection	Older collection and newly collected material
Tracheids	*Shape*	rounded square	rounded square	rounded square
	Diameter	60µm (±7.9)	55µm (±7.3)	56µm (±7.4)
	Pitting	1 to 4-seriate, 2.04 (±1.35)	1 to 5-seriate, 1.79 (±0.54)	1-3(-5) seriate, 1.82 (±0.539)
	Bordered pit diameter	16µm (±1.1)	15µm (±1.5)	15µm (±1.4)
Rays	*Number of tracheid cells between rays*	3.10 (±1.61)	3.62 (±1.85)	3.47 (±1.82)
	Height (number of cells)	10.7 (±10.4)	11.4 (±9.76)	11.1 (±9.86)
	Width (number of cells)	1.15 (±0.356)	1.17 (±0.411)	1.17 (±0.400)
	Radial cell length	151µm (±34.9)	153µm (±34.8)	150µm (±34.8)
	Cell height	27µm (±2.8)	27µm (±3.3)	26µm (±3.2)
Number of CF pits		1 to 5, 3.13 (±1.42)	1 to 8, 2.20 (±0.976)	1 to 8, 2.27 (±1.01)

Kramer (1974a) further described 122 specimens, the majority of them specimens collected from the Mengkarang and Karing Rivers, as Coniferae incertae sedis. He subsequently divided a subset of 14 of them, which were particularly well-preserved, into three groups based on differences in a number of anatomical characters. These were intended to be treated at a later date in a separate paper, which never materialised. He distinguished these three different pycnoxylic architectures:

- Similar to *Dammaroxylon kaurioides* Kramer, but without "border cells" (i.e. "Randzellen").
- Similar to group 1 (above), but with smaller radial bordered pits (vertically 9–11 µm, horizontally 10–12 µm in diameter). Usually in 3–5 vertical rows (sometimes 6–7), the pit apertures appear slightly oblique to horizontal and almost reach the edge of the bordered pit.
- Similar to group 1 (above), but with rays usually 1 to rarely 2 cells in width and often much higher (up to 120 cells; on average 30–40 cells).

In the third PCA scatter plot (Fig. 5.6), the *D. kaurioides* holotype (as well as the other specimens assigned by Kramer (1974a) to *D. kaurioides*) and the Coniferae incertae sedis groups that Kramer differentiated in the Jambi material are marked. Both the *D. kaurioides* specimens, as well as the Coniferae incertae sedis groups, fall within the larger variability of the remainder of the fossil specimens. (With the notable exception of one of the specimens of the Coniferae incertae sedis 2, which is an outlier in the upper right quadrant.) Additionally, there is a partial overlap between the D. kaurioides specimens with Coniferae incertae sedis 1. Each of the groups does appear to inhabit a constrained part of the overall morphological variability present in the collection.

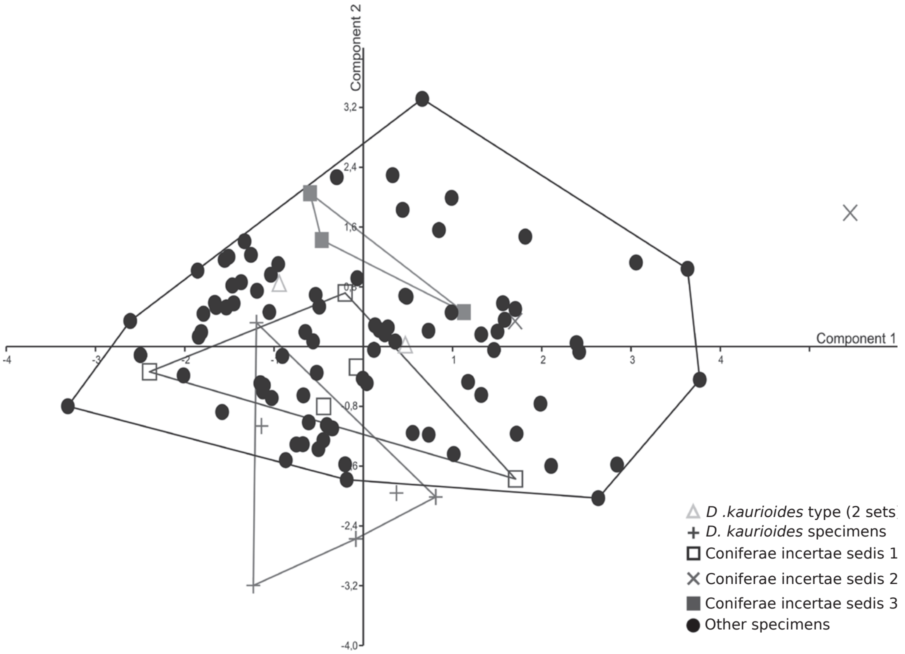


Figure 5.6: The PCA scatter plot for components 1 and 2. The symbols indicate the D. kaurioidesholotype and the different Coniferae incertae sedis groups proposed by Kramer. This shows thedistribution of anatomical and morphological variability in these groups.

In a fourth PCA scatter plot (Fig. 5.7) for components 1 & 2, the measurements from the extant Araucariaceae species have been included for comparison. The plot shows that the two groups do inhabit adjacent, but separate morphological spaces. This is mostly due to the variability that is explained by component 2. The character loadings for component 2 show that the characters of ‘border pit diameter’ (21%), ‘ray height’ (20%) and ‘number of cells between rays’ (17 %) together account for more than half (58%) of the variability (Fig. 5.8). In order to analyse to what extent characters other than the ‘bordered pit diameter’, ‘number of cells between rays’ and the ‘ray height’ contributed to the position of the extant Araucariaceae specimens relative to the fossil material, these were excluded from the data set for the last PCA scatter plot (Fig. 5.9). Here the two groups show considerably more overlap.

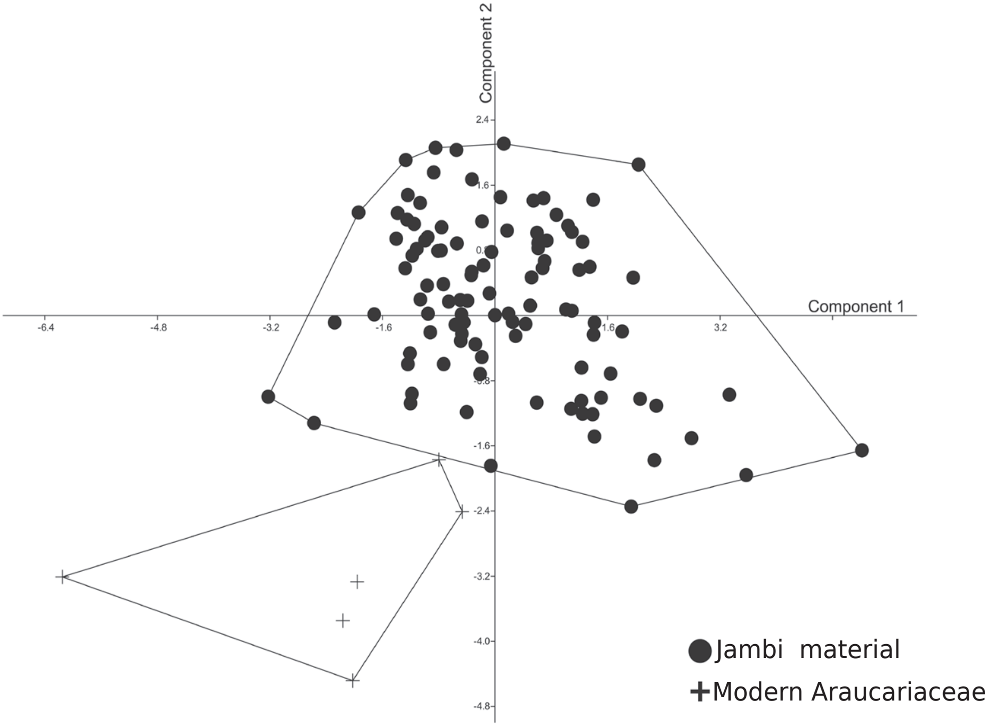


Figure 5.7: The PCA scatter plot for components 1 and 2 for the dataset including both the fossil wood from the Mengkarang Formation and the measurements taken from six modern Araucariaceae. The symbols indicate the older Mengkarang Formation derived material and the measurements taken from modern Araucariaceae. This shows the differences in distribution of wood anatomical variability between the Early Permian and modern species.

Discussion

Original and new collections

Table 5.4 offers an overview of the measurements of those specimens recently collected compared with those from the original collection and the collection as a whole. In all characters listed, the measurements taken from both groups are strikingly similar. These measurements alone give an indication that both sample sets (and, therefore, both collections) probably represent the same fossil wood morphotype.

Multivariate comparisons

The two-group permutation test indicates that it is not likely that the original and recently collected material derive from different populations. Therefore we will treat them as representative of the same statistical population. Our recently collected material is, either with certainty or with great likelihood, derived from a formation that has been dated as Early Permian in age. This implies that the material from the old collection, including that which was used by Kramer, is also likely to have derived from the same formation and should be viewed as Early Permian as well, in contrast to Kramer's own designation of his material as probably being Tertiary in age. Although, angiosperm Dipterocarpaceae have also been collected from this region, the fact that these have only been described from one single locality and have not subsequently been found during the recent expeditions, makes it likely that these derive from the overlying Tertiairy formations.

In Table 5.5 the properties of Kramer's *Dammaroxylon kaurioides* are listed and compared with those of all the araucarioid fossil wood specimens from the Mengkarang Formation. We can see great similarity between the specimens described by Kramer and those of the dataset of this study. The latter simply shows a larger range of variability in most characters, that probably is mostly due to the larger sample size.

Anatomy of Dammaroxylon kaurioides

For the holotype specimen of *Dammaroxylon kaurioides* Kramer (U-04732) there are two different sets of slides. The first is the original set made for and used by Kramer in his study (Kramer 1974a), the second is a set made later from the holotype specimen in Utrecht. (This was done in order to have a reference thin section, because the original thin sections were at that time considered to be lost.) The specimen from which these thin sections are taken (U-04732) is a semi-circular part (slice) of a trunk, measuring 19.2 × 10.0 × 4.50 cm; the original diameter of the trunk is estimated at about 20 cm. Table 5.6 shows the data from the description by Kramer, and compares it with measurements taken from (i) the original holotype slides for this study, (ii) the newly made slides of the holotype, (iii) all the specimens classified by Kramer as D. kaurioides and, finally, (iv) the entire collection from the region.

Measurements made during the course of this study from the original slides from the holotype along with those of Kramer generally agree well. However, when comparing these with the measurements taken from the newly prepared slides of the holotype, significant differences can be seen. The two seem to deviate particularly strongly in the characters of the diameter of the tracheids (measured in radial direction, both by Kramer and herein) and the size of the bordered pits. While the amount of possible intra-tree variability has already clearly been illustrated by Bailey and Faull (1934), Falcon-Lang (2005) and many others, it is still striking to see the amount of (non-overlapping) morphological variability present in a single fossil wood fragment. If nothing else, this clearly illustrates the problematic nature of describing a new species of fossil wood based on just a single set of slides.

Table 5.5: Wood anatomical ranges of all the fossil wood species described from fossil wood from the Mengkarang Formation. For comparison the description of all the material used in this paper is included. Standard deviations are indicated with the ± symbol.

		Agathoxylon spec. Booi et al., this paper	Dammaroxylon kaurioides Kramer, 1974a	Dadoxylon (Cordaioxylon) roviengensis Vozenin-Serra, 1985	Dadoxylon (cf.) saxonicum (Goeppert) Frentzen - Vozenin-Serra, 1985
Tracheids	*Shape*	rounded square	-	rectangular	square
	Diameter	33-83µm	55-70µm	30-88µm	48-80µm
	Bordered pits	1-3(-5) seriate; Ø 10-20µm, pit aperture lenticular to round	(1-)2(-3)-seriate, Ø 15-15.5µm (vertically), 15.5-17 µm (horizontally); pit apertures oblique 'cracks'	3-5-seriate, Ø 13-17µm, pit aperture crossed, oblique, lenticular	1-3-seriate, Ø 15-20µm (height/ width 0.75-1), pit apertures circular or elliptical
Rays	*Number of tracheid cells between rays*	1-10, usually 1-6	1-7, usually 3-4	-	-
	Height (number of cells)	1-30, 11.1 (±10.2)	1-50, usually 2-11	up to 52	up to 25
	Width (number of cells)	1 (83.4%)-2	1 (70%)-2	1-2	1(-2)
	Cell length	75-238 µm, 150µm (±38.3)	-	120-240µm	240-280µm
	Cell width	-	-	16-40µm	28-36µm
	Cell height	18-38 µm, 26µm (±4.7)	-	30-35µm	about 40µm
	Density	-	7-8/mm	7-9/mm	9-11/mm
	Number of CF pits	1-8, commonly 1-5	1-8, usually 2-4 (or 1)	2-9 (usually 3-5)	2-19 (mostly 4-6)

Vozenin-Serra (1985) studied two fossil wood specimens collected at Teluk Gedang (Fig. 5.1) along the Merangin River. She identified two “structural types” in the material (Table 5.5). One was assigned to *Dadoxylon (Cordaioxylon) roviengense* Vozenin-Serra, a species originally based on specimens from Cambodia of Triassic age. The other was assigned to *Dadoxylon saxonicum* (Goeppert) Frentzen, a species described from the Polish and French Stephanian as well as the Permian of former East Germany, Russia and China. The latter was later (Vozenin-Serra 1989) assigned to *Dadoxylon* cf. *saxonicum* (Goeppert) Frentzen. Both specimens were assumed to be Early Permian in age.

Table 5.6: The main characters of *Dammaroxylon kaurioides* from the original description of the holotype by Kramer (1974a), compared with our measurements of the two independently made slide sets of the holotype and the measurements of all the specimens assigned by Kramer to *D. kaurioides* combined. Standard deviations are indicated with the ± symbol.

		Dammaroxylon kaurioides Kramer, 1974a	Dammaroxylon kaurioides, holotype (original slides)	Dammaroxylon kaurioides, holotype (newly prepared slides)	Dammaroxylon kaurioides, all type specimens	Agathoxylon spec. Booi et al., this paper
Tracheids	*Diameter*	55-70μm	60μm (±10)	71μm (±6.8)	55μm (±7.4)	33-83μm, 56μm (±7.4)
	Pitting	1-3 seriate, usually 2	1-3 seriate, 1.6 (±0.49)	1-3 seriate, 1.4 (±0.50)	1-2(-3) seriate, 1.5 (±0.52)	1-3(-5) seriate, 1.82 (±0.539)
	Bordered pit diameter	15-15.5μm (vertically), 15.5-17μm (horizontally)	16μm (±0.96)	13μm (±1.5)	15μm (±1.4)	10-20 μm, 15μm (±1.4)
Rays	*Number of tracheid cells between rays*	1-7, usually 3-4	3.35 (±1.50)	3.5 (±1.80)	4.11 μm (±2.09)	1-10, 3.47 (±1.82)
	Height (number of cells)	1-50, usually 2-11	15.2 (±12.7)	12.5 (±10.5)	10.7 (±9.31)	11.1 (±9.86)
	Width (number of cells)	1 (70%)-2	1.22 (±0.420)	1.19 (±0.397)	1.25 (±0.444)	1 (83.4%)-2, 1.17 (±0.400)
Number of CF pits		1-8, usually 2-4 (or 1)	2.04 (± 1.09)	-	2.46 (±1.30)	1-8, 2.26 (±1.01)

The anatomy of *Dadoxylon (Cordaioxylon) roviengensis*, is almost identical to a large number of specimens in our dataset. Noteworthy differences are the high rays, that do occur throughout our dataset, but which do not seem to be predominantly associated with higher numbers of rows of bordered pits, as seems the be the case in *D. roviengensis*.

Comparing our dataset to Vozenin-Serra's description of the *Dadoxylon* (cf.) *saxonicum* specimen from Jambi, the one character in which they appear to differ is in the case of its rather large ray cells (240–280 μm in length, about 40 μm in height), which both in length and in height exceed the range commonly found in our dataset.

The comparisons with earlier descriptions of wood from the Jambi region show that on the whole our dataset is either almost indistinguishable from those described previously (as in the case of Kramer 1974a), or at least has strong overlap and similarities with them (as in the case of Vozenin-Serra 1985).

Overlap with Dadoxylon/Araucarioxylon

Endlicher (1847) erected the genus *Dadoxylon* as a genus exclusively intended for araucarioid wood, where previous fossil wood genera could apply to wood, leaves or fructifications. In a revision of fossil “conifer wood”, Kraus (1870) created the new genus for araucarioid wood *Araucarioxylon*. The diagnoses of the two genera strongly overlap (Gothan 1905; Philippe 2011) and both have been used to assign very similar kinds of pycnoxylic araucarioid fossil woods.

In a proposal to revise the nomenclature of cordaitalean (*Dadoxylon*-type) wood, Vogellehner (1964) determined both *Araucarioxylon* and the less commonly used *Cordaioxylon* to be junior synonyms of *Dadoxylon*. Additionally, Agathoxylon Hartig now turns out to be the single validly published genus for araucarioid secondary xylem without any special distinguishing characters (Philippe 1993, 2011; Rößler et al. 2014).

Dammaroxylon

The genus *Dammaroxylon* (Schultze-Motel 1966) was established for araucarioid secondary wood of a *Dadoxylon*-type (*Agathoxylon*) with the distinguishing character of “Randzellen”. These “Randzellen” are not actual cells, but are an artefact derived from the marginal intercellular spaces at the top and the bottom of a ray. While *Dammaroxylon* is a validly described genus (Philippe 1993), several authors (Schultze-Motel 1966; Kramer 1974a; Bamford & Philippe 2001) have stated that the marginal intercellular spaces, which create the impression of the so-called “Randzellen”, are a common feature in many types of extinct and extant wood. Therefore, the validity of this character as the sole basis for this genus can be questioned.

In the present material of *Dammaroxylon kaurioides*, this particular character could only rarely and with some uncertainty be observed. In fact, at first the feature could not be observed in any of the slides made from the specimens that were originally attributed by Kramer to *D. kaurioides*. It was only when turning to the thin sections originally made for Kramer’s own research, which are slightly thicker, that the feature could sometimes faintly be seen. And so, in addition to the reservations above, it should be said that to base an entire genus on the presence of a characteristic whose visibility is so dependent on small variations in preparation is at least problematic.

Statistical test results

Principal Component Analysis (PCA) results

The values of the individual character loadings (Fig. 5.3) for the two components used in the PCA are reasonably equally distributed. As no single character dominates in the loadings, it is unlikely that one character will offer a sufficient basis to subdivide the material. If any clear grouping will emerge from the PCA, it will come about through similarities in character combinations.

The scatter-clouds depicted in Figure 5.4–5.7 show no obvious individual grouping within the dataset as a whole (except in Fig. 5.7).

In the first PCA scatter plot (Fig. 5.4), where the specimens are marked by the rivers along which they were found, there is no clear differentiation in anatomy of specimens between the different localities. The specimens from the Mengkarang River locality show the largest variability, primarily caused by two ‘outliers’ in the top right quadrant of the plot. The rightmost of the two (specimen U-2185) is characterised by an average number of four rows of bordered pits across a tracheid, far more than the average (1.8 ± 0.75) of the whole dataset. The other’s position in the PCA are the result of a combination of character values. The other three groups of localities have strongly overlapping wood anatomical morphospaces.

The scatter plot in Figure 5.5 allows comparison of the original collection with the recently collected material. The plot shows that the recently collected material fits within the larger variability of the material of the original collection and no clustering of any sort can be discerned. This result, in combination with the direct comparisons of the measurements discussed previously, makes it safe to conclude that both collections are representative of the same anatomical variability.

The next PCA scatter (Fig. 5.6) has the specimens labelled that were identified by Kramer (1974a), both the *D. kaurioides* specimens and his three Coniferae incertae sedis groups. This scatter illustrates that, except perhaps in the case of the Coniferae incertae sedis 3, no sign of clustering can be seen. However, this is based on a group of three specimens, which makes it difficult to conclude that the clustering is meaningful. Note, however, the distance between the two scatter points that are derived from the two individual sets of slides made at different times from the same holotype specimen. The difference in measurements is reflected in their relative positions in the scatter plot. One would intuitively expect two samples from such a specimen of fossil wood to group much closer than they do here.

Adding measurements for the modern Araucariaceae specimens to the PCA data (Fig. 5.7), two discernible, although adjacent, groups can be determined. The difference between the two groups seems to take place mainly along the y-axis, as determined by component 2.

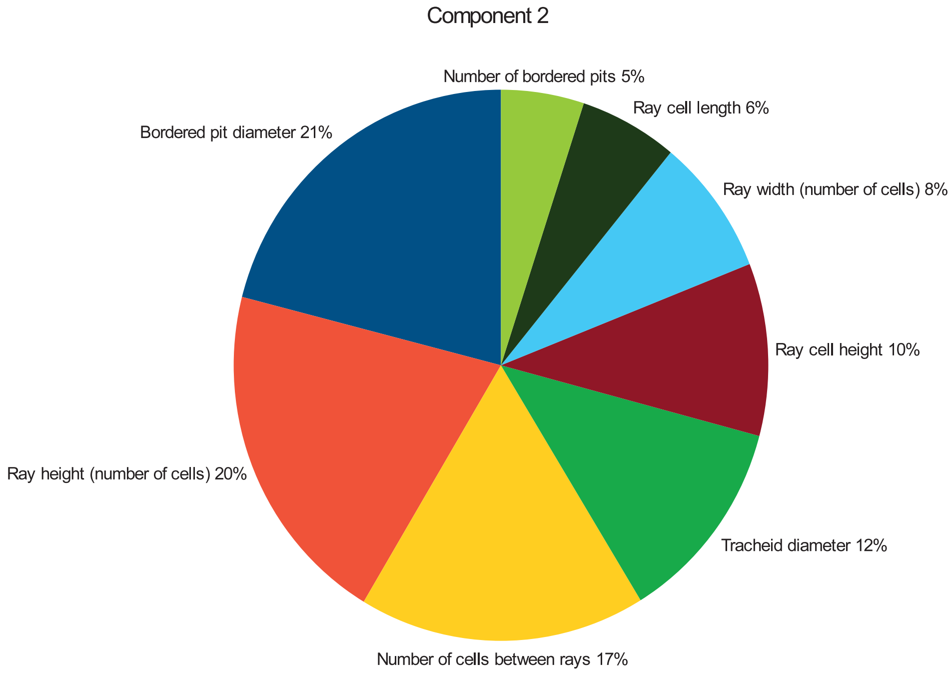


Figure 5.8: A pie chart describing the relative contributions (loadings) of the characters used in the PCA to components 1 and 2 of the dataset including both the fossil wood from the Mengkarang Formation and the measurements taken from six modern Araucariaceae.

From the relative contributions of the different characters for component 2 (Fig. 5.8), it can be seen that three characters are best explained by this component. These are 'bordered pit diameter', 'ray height (number of cells)' and 'number of tracheid cells between rays'. Removing these characters provides an indication to the extent they influence the end result. Figure 5.9 shows the same PCA as Figure 5.7, but with the characters mentioned previously eliminated from the analysis. Comparing these two plots it becomes clear that in Figure 5.9 the overlap between the two groups is now considerable. In this way, we have illustrated the three main characters in which the anatomy of our Permian material differs from the anatomy of modern Araucariaceae (see also Table 5.7): (i) number of tracheid cells separating the rays, which is considerably higher in the modern Araucariaceae than in the older material. This, indirectly, is a good measure for the density of the rays and indicates that ray density is much lower in the modern Araucariaceae compared with our Permian specimens; (ii) ray height (measured as number of cells) is much higher in the fossil material than in the modern specimens; (iii) bordered pit dimensions are smaller in the modern material. These characters appear to be to the main defining characters in which the Early Permian material differs significantly from modern Araucariaceae.

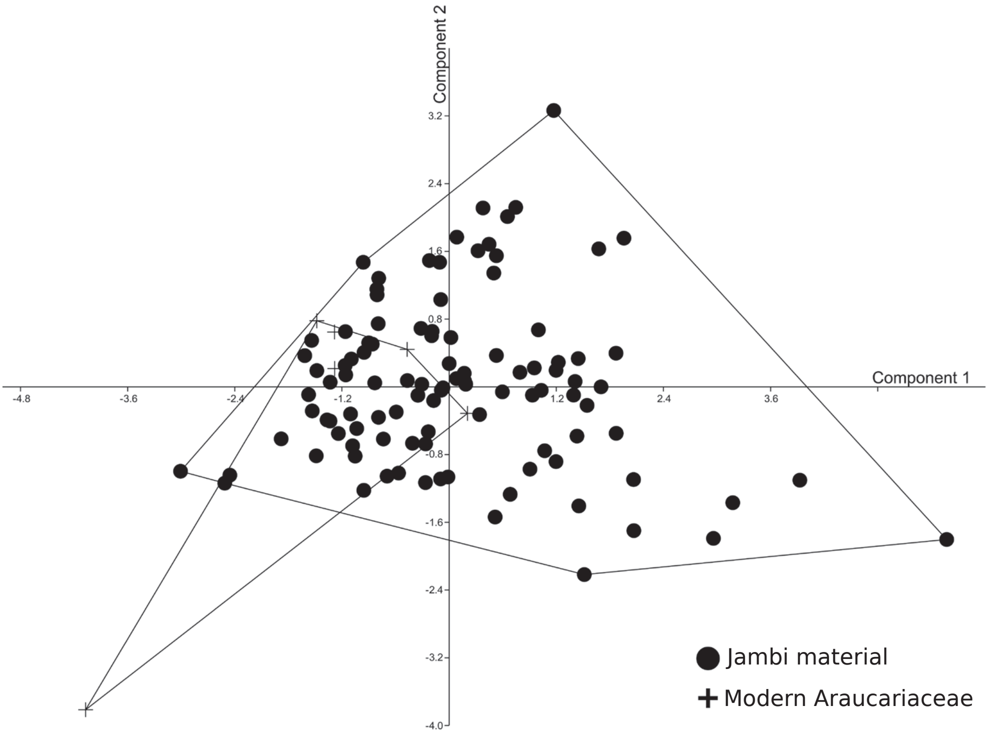


Figure 5.9: The PCA scatter plot for components 1 and 2 for the same dataset as used in Figure 7, but excluding the characters of 'number of tracheid cells between rays', 'ray height (number of cells)' and 'bordered pit diameter', showing the differences and overlap of remaining wood anatomical characters among the Early Permian and modern species.

Even though a large amount of anatomical variation is present in the araucarioid fossil wood from the Mengkarang Formation, it is impossible to divide the specimens into more than one coherent group. The possibility should be considered that the presence of a high number of species, overlapping but each distinct in anatomy, is giving the illusion of a single large homogeneously varied species, but this does not appear to be the most parsimonious solution. In such a case, a more heterogeneously distributed PCA plot would be expected. This is further confirmed by the fact that all specimens are fully comparable in regard to all qualitative characters (including the cross-field pits, where they could be observed).

Table 5.7: The main characters and their values from measurements for the Early Permian material and a small group of six modern Araucariaceae. Standard deviations are indicated with the ± symbol.

		Combined measurements for 6 modern Araucariaceae	**Agathoxylon spec. Booi et al., this paper**
Tracheids	*Shape*	rounded square	rounded square
	Diameter	25-64μm, 44μm (±8.0)	33-83μm, 56μm (±7.4)
	Pitting	1-6 seriate, 1.81 (±0.440), porus oval to lenticular	1-3(-5) seriate, 1.82 (±0.540), porus lenticular to round
	Bordered pit diameter	10-18μm , 13μm (±1.4),	10-20μm, 15μm (±1.4)
Rays	*Number of tracheid cells between rays*	(1-)7-9(-65), 8.32(±2.12)	1-10, 3.47 (±1.82)
	Height (number of cells)	1-20, 6.05 (±0.600)	1-30, 11.1 (±9.86)
	Width (number of cells)	1(-2), 1.01 (±0.020)	1-2, 1.17 (±0.400)
	Radial cell length	52 to 300μm, 187μm(±10.2)	75-238μm, 150μm(±34.8)
	Cell height	16 to 32μm high, 24μm(±0.94)	18-38μm, 26μm(±3.18)
Number of CF pits		1-9, 3.50 (±0.440)	1-8, 2.26 (±1.01)

Possible parent plants for this type of wood

Although there is insufficient direct evidence to directly link the Jambi fossil wood to Cordaitaleans, strong circumstantial evidence comes from the co-occurrence of both large amounts of *Araucarioxylon/Agathoxylon*-type wood and *Cordaites* leaves, where the latter are by far the most commonly occurring leaf form in the impression/compression floras of the Mengkarang Formation. Of the remaining species in those associations, which consist mainly of pecopterid ferns and (presumed) seed ferns (Jongmans & Gothan 1925, 1935; Van Waveren et al. 2005, 2007; Booi et al. 2008, 2009a,b), only the less commonly occurring *Dicranophyllum* leaves (Van Waveren et al. 2007) can be seen as an alternative leaf form that could possibly be associated with the araucarioid wood. The anatomical characters found in the fossil wood specimens treated here are not sufficient for an attribution to *Cordaites*. The presence of other characters, such as a septate pith of the *Artisia*-type (characteristic for *Cordaites*, although also occurring in other gymnosperms), or leaf traces in helical arrangement are needed.

Implications of the xylological variability for araucarioid wood taxonomy

From the preceding section it can be seen that this collection of fossil wood translates into a large cloud of anatomical variability, with no clear demarcating lines for distinguishing separate morphospecies. Moreover, when comparing species previously described from the same collection or from material from the same geological formation, these species seem to fit comfortably in the larger ‘morphospace’ described by the entirety of the material of both the original collection supplemented with the recently collected specimens. This, and the fact that dimensions in fossil wood are also heavily influenced by ecology and cambial age (cf. Bailey & Faull 1934; Anfodillo et al. 2013), throws into question the entire practice of distinguishing species of fossil wood solely on the basis of continuously varying characters, or even the presence or absence of certain characters. Very similar reservations have been put forward by Philippe (2011), and the analysis of this collection seems to strongly support his proposal to refrain from distinguishing individual species of araucarioid wood, but rather to view the entirety of variation found in araucarioid wood as a large continuous whole and as a single fossil species. A traditional Linnaean approach does not suffice where such a slowly evolving tissue as araucarioid secondary xylem is concerned, since even large timespans do not appear to result in truly significant discontinuities in character ranges. We suggest that this could lead to a non-Linnaean form of classification where ‘species’ are described as having certain morphological ranges over a certain set of anatomical characters. And where individual specimens are described based on their position within that range.

Early Permian material differs in only a few quantitative characters from the phylogenetically remote modern Araucariaceae, namely, the number of tracheid cells between rays, ray height (number of cells) and diameter of the inter-tracheid pits, although similarities in overall histology and the shared araucarioid inter-tracheid and cross-field pitting easily outweigh these differences.

Conclusions

All the araucarioid wood collected from the Mengkarang Formation can be viewed as deriving from the same statistical population and is, therefore, very probably of Early Permian age. In contrast to the earlier study designating the original collection as Tertiary in age.

The results of the comparisons and the PCAs show that Kramer’s *Dammaroxylon kaurioides* is a subset of the total amount of variation of all the araucarioid wood in the Jambi collections. This implies that the specimens assigned to *D. kaurioides* are not anatomically or morphologically distinct from the rest of the araucarioid wood from the Mengkarang Formation. The morphological space occupied by *D. kaurioides* is in reality part of a larger continuous whole. The single example of two independently made preparations from the holotype specimen of *D. kaurioides* makes clear how much variation is present even in a single specimen, which is only a fragment of the original tree. Even when compared with present-day Araucariaceae, the anatomical differences are slight and lie with only a few characters.

Because it is possible to describe the entire collection and the variation therein as a single, morphologically wide-ranging species, it becomes evident that clearly delineated Linnaean species are not the way forward for araucarioid fossil wood taxonomy.