Innovation and stasis

Gymnosperms from the early Permian Jambi flora

Menno Booi

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Naturalis Biodiversity Center, Leiden University
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This too shall pass

Presumed to be from an ancient Sufi legend

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1

Introduction

The Late Carboniferous and Early Permian was a period of climatic transition mirroring that of the present day. The earth was moving from a long period dominated by glacial cycles into an era of general warming, culminating in the Early Triassic (Gastaldo, et al., 1996, DiMichele et al., 2001, Sun et al., 2012, Montañez & Poulsen, 2013). This change in climate is reflected in the Late Paleozoic vegetational fossil record, where the classic ever-wet forest mire associations slowly make way for genera with a greater resistance to seasonal drought (DiMichele et al., 2006). However, although this pattern is seen occurring in Euramerica in the latest Carboniferous to Early Permian, it is not seen in the Cathaysian region (notably in North China) until the Middle Permian (Hilton & Cleal, 2007).

It is not known whether this pattern of delayed climatic and floristic changes only applied to the North- and South China region, or whether this was seen throughout the eastern shore of the Paleo-Tethys Ocean. There is also uncertainty concerning the reconstruction of Late Paleozoic tectonic plate configuration of this region, as demonstrated by the numerous differing propositions, and whether these might explain the apparent difference in climatic conditions (Hilton & Cleal, 2007). An Early Permian flora from the eastern region of the Paleo-Tethys might throw an interesting light on the developments in an, at that time, tectonically very fragmented part of the world (Metcalfe, 2009, 2011).

What is the Jambi Flora?

The Jambi Flora is a fossil flora found as part of the Early Permian Mengkarang Formation that outcrops along several rivers in the vicinity of the town of Bangko (Merangin Regency, Jambi) in Middle Sumatra. Since its discovery in the early 20th century it has been the subject of several studies. However, major questions have still been left unanswered. A recent reinvestigation of the Jambi Flora, coupled with several expeditions (2003, 2004, 2006, 2008) to the area where the flora was found, has provided the opportunity to get a clearer understanding of this flora in a taxonomical, ecological and paleogeographical light.

History

The Jambi flora was first discovered by the Swiss geologist Tobler (1917, 1924), whose collections of plant fossils from the region were sent to the Dutch paleobotanist Jongmans for investigation. Jongmans' and Gothan's (1925) subsequent descriptions of the material formed the first publication on the 'Jambi Flora'. The next, dedicated expedition to the area in 1925 led to a comprehensive publication on the geology and paleontology of what would later be named the Mengkarang Formation (Jongmans & Gothan, 1935, Zwierzycki, 1935). The taxonomic work was based on material collected by Zwierzycki (geological samples) and Posthumus (palaeobotanical samples) from various localities along two rivers in the area (the Mengkarang and the Merangin) and several tributaries of the Merangin

(Zwierzycki, 1935). In addition, Jongmans and Gothan (1935) briefly discussed the floral composition of each 'locality' and remarked on the differences between them. They described some localities as characterised by associations that were virtually 'European' in composition, while others were dominated by elements with a more 'Asian' affinity. They also noted that the flora was overall more 'European' in character than those known from North China.

Further substantial publications on the flora or its geology did not appear until Suwarna et al. (19942), who introduced the name Mengkarang Formation, for what were previously named the 'Karing Beds' by Zwierzycki (1935).

The existing collection was taxonomically revised by Van Waveren et al. (2007) and comparison to the various Chinese palaeoflora provinces indicated the strongest affiliation with the North Cathaysia palaeoflora. This revision gave an insight into the potential of this flora, but also led to many questions that could not be answered with the available data. This in turn led to a reinvestigation of the area during several expeditions (2003, 2004, 2006 & 2008), organised and led by Van Waveren . The new material of fossil plants collected during those expeditions proved to be so interesting that it formed the basis for a number of papers (chapters 2-6).

Geology of the Mengkarang Formation

The Mengkarang Formation (at the section along the Merangin) through the Mengkarang Formation is of Late Asselian age (296.77 to 296.14Ma), as shown by isotopic age evaluation. Reconstruction of the original environment shows it to have been a volcanic slope. As such, it represents a system with high and constant influence from volcanism, such that all deposits are (reworked) volcanoclastic in nature; lava- , pyroclastic- and gravity flows occur frequently. From this we can deduce a dynamic ecosystem with frequent disruptions having a destabilizing influence, commonly providing opportunities for recolonization of areas laid bare by such events (Van Waveren, et al., in preparation).

The Mengkarang Formation is exposed along the Merangin River as a large, continuous outcrop of some 500 meters in thickness. This allows the study of the fossil flora and its different associations within the context of the geological development.

Plant associations of the Jambi flora

One of the problems with the earlier collection of the Jambi flora is that, in its present condition, it contains no detailed information about the localities where the specimens were obtained. Only the river or stream along which the locality (or localities) was situated are indicated. There is little information about the number of localities along each river, except for the remark that there were multiple localities along the Mengkarang River and that the material from these localities has been combined on grounds of similarity (Jongmans & Gothan, 1935). Posthumus (1927) likewise mentioned that, when collecting, the species composition did not vary much between localities.

However, initial observations in the field during the recent expeditions suggested dissimilarities in floristic composition between localities along the same river. This is confirmed when we look at a visual representation of relative abundances of genera per locality, showing the more abundant localities discovered infrom the collections of the recent expeditions (Fig. 1.1), ordered according to a Detrended Correspondence Analysis (Hill & Gauch, 1980). Here we see a clear distinction in species composition and relative abundances between the various localities. These localities can be broadly divided into two groups, namely those that are dominated by (marattialean) ferns and cordaites (Merangin 1 to Ketiduran Siamang 1, in Fig. 1.1), and those in which these groups play a more modest role (Merangin 3 to Ketiduran Siamang 2 in Fig. 1.1). The latter group can be further subdivided into floras that are dominated by lycopsids and calamites (Mengkarang 4, Merangin 3 in Fig. 1.1), and floras that are dominated by Early Permian pteridosperm genera (Merangin 4 and Ketiduran Siamang 2 in Fig. 1.1, see chapters 2, 3 and 4). However, 'transitional' associations between these also occur, such as localities in which cordaites, marattialean ferns and lycopsids together are the main constituents.

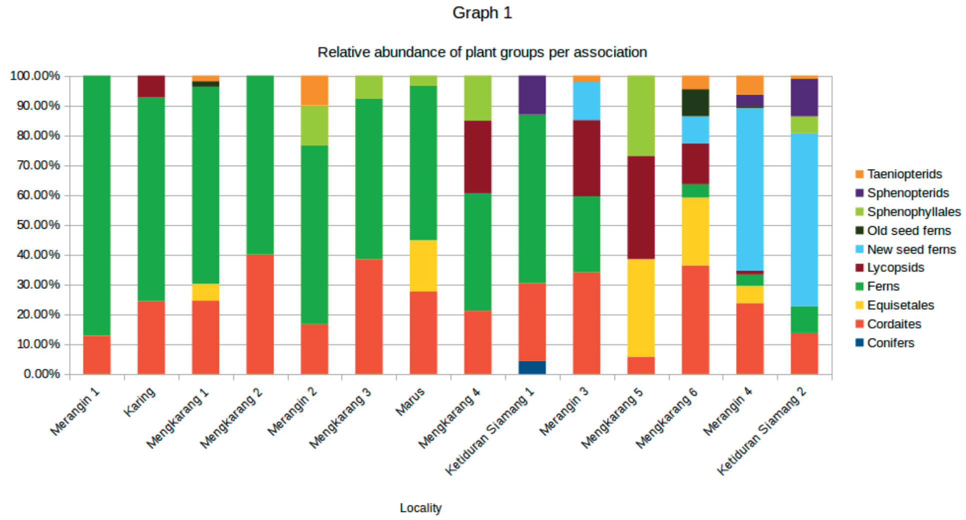

Figure 1.1: Relative abundances of phylogenetic groups for the more abundant localities from the Mengkarang Formation (as collected during the recent expeditions). Order of localities is determined by a DCA (Detrended Correspondence Analysis).

Cordaites can thrive in a broad array of ecological circumstances (Falcon-Lang & Bashforth, 2005, Raymond et al., 2010), and are a common factor throughout all plant associations in the Mengkarang Formation. Not only are leaves of cordaites never absent from any of the plant associations of the Mengkarang Formation, but among the fossilized remains are also numerous pieces of fossilized (araucarioid) secondary wood (of a type that might have been produced by cordaites), giving the impression of an area that was at most times densely forested (chapter 4, chapter 5).

Late Paleozoic marattialean tree ferns similarly are found in various ecologies, but do appear to be less suited to conditions of permanent standing water (DiMichele & Phillips, 2002). Lycopsids, on the other hand, appear more limited in their tolerance for more well-drained habitats (Phillips & DiMichele, 1992), hence their occurrence would probably signify wetter conditions. The same goes for the larger types of Equisetales (e.g. *Calamites*), which are sometimes found co-occurring with lycopsids in the assemblages. Particularly those associations that have high numbers of both lycopsids and Equisetales can be interpreted as classic forest mire associations, such as were common in the Euramerican paleotropics, especially in the Middle Carboniferous (Phillips et al., 1985, Galtier, 1996). Such associations signify ever-wet and relatively stable conditions. In contrast, there are two localities dominated by conspicuous Late Paleozoic seed ferns. It is striking that these localities, as well as two others where Equisetales feature prominently, are the only ones in which marattialean ferns are largely absent. It is with the gymnosperm species from these localities in the first place, that the first three chapters are concerned.

Synopsis

The Early Permian forest mire associations of the Jambi flora are, on the whole, remarkably similar to the Late Carboniferous assemblages from identical ecologies in Europe and North America. However, the associations that seem to reflect drier habitats and in which (presumed) gymnosperms play a more dominant role are host to a number of remarkably early occurrences of certain Permian genera, notably from the gigantopterids and the peltasperms, which are often also both morphologically distinctive and endemic to this flora. Such early occurrences are usually associated with circumstances in which the likelihood of preservation of plants growing outside of habitats with a solid geological preservation potential has become increased (Looy et al., 2014).

An example of such a morphologically unique species is the seed fern *Macralethopteris hallei*, the subject of chapter 2. Although already described by Jongmans & Gothan in 1935, the recent expeditions rendered much more and more complete material from this enigmatic seed fern. This has allowed a more detailed description of its morphology, comparing it to several contemporaneous similarly large-leaved alethopterid-like (seed)ferns, as well as an evaluation on its possible habitus and habitat.

One of the most characteristic pteridosperm groups found in contemporaneous assemblages throughout the palaeo-equatorial region is the order of the Peltaspermales (DiMichele, et al., 2005). This morphologically highly diverse group finds its origin at the end of the Late Carboniferous in Euramerica and is represented in the Jambi flora by three different genera. These are the subject chapter 3, where a particular emphasis is placed on what their occurrence in the Jambi flora can say about the paleogeography of the region in the Early Permian.

Probably the most morphologically distinct pteridosperm group of the Early Permian, the gigantopterids, is the subject of chapter 4. This group is characterised by various forms of anastomosing- or net venation in their leaves, a relatively uncommon feature in seed ferns at this time. However, the rather diverse morphology of the venation found in this group has led several authors to suggest that the gigantopterids are not a monophyletic group. Yet, the leaves and fronds of species within particular gigantopterid genera that come from such (paleo-)geographically distant areas as North America and North China can show an almost perfectly homologous morphology. The gigantopterids are represented in the Jambi flora by two endemic genera, *Gothanopteris* and *Palaeogoniopteris*. These are explored in the context of their (morphologically) related counterparts from China and North America to see whether common patterns can be discerned that could shed more light on the evolution and phylogeny, as well as the driving factors behind its development.

Another feature of the Mengkarang Formation is the abundance of fossilized wood, usually found as driftwood, but also as some spectacular examples of *in situ* specimens. This has provided the opportunity to do an unprecedented large-scale morphological analysis on araucarioid wood from a single region. The results are found in chapter 5, as well as their ramifications for the taxonomy of this type of fossil wood, of which hundreds of species have been described, despite the paucity of its diagnostic characters.

Chapter 6 represents a further exploration of this material in an ecological and taphonomical context. It mainly consists of a detailed analysis of a particularly large *in situ* tree trunk that is found along the Merangin River, using cathodoluminescence SEM. Both its ecology and its taphonomy are explored, in particular the circumstances surrounding its burial. This is supplemented by information from two other examples of *in situ* tree trunks from the Mengkarang Formation along the Merangin River.

2

New material of *Macralethopteris* from the Early Permian Jambi flora (Middle Sumatra, Indonesia) and its palaeoecological implications[1]

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Abstract

New material of the Early Permian alethopterid genus *Macralethopteris* is examined in detail. The material stems from different locations and statistical comparison of the morphological differences between collections suggests that the material is derived from several populations of a single species. Comparison is made with related Cathaysian and Euramerican species, showing the isolated occurrence of *Macralethopteris* in the Cathaysian region. Characteristics of the species and possible ecological implications suggest that *Macralethopteris* hallei grew in more mesic circumstances than usually associated with alethopterids. It is argued that *M. hallei* might have been a relatively small alethopterid with possible cormous growth.

Introduction

The Permian flora of Jambi (Sumatra, Indonesia) was first extensively described by Jongmans and Gothan in 1935, and recently revised by Van Waveren et al. (2007). This flora was reinterpreted as a flora of predominantly Cathaysian affinity (*sensu* Halle, 1927).

One of the endemic Cathaysian seed ferns from Jambi is *Macralethopteris hallei* Jongmans et Gothan, a robust Early Permian alethopterid species. It was first described and depicted from a few fragmentary specimens from the Shansi region of North China as *Alethopteris* sp. by Halle (1927). A few years later, more and better preserved material was found and collected in a different area allowing a more accurate and complete description of the species. This time the material came from an area in the southwestern part of the province of Jambi, Sumatra, Indonesia. The material, collected in 1925 by Posthumus, was described by Jongmans and Gothan (1935), and, on the basis of its large pinnule size and very dense venation, assigned to a new genus: *Macralethopteris*. Although this Indonesian material was larger, more detailed and more numerous than the specimens available to Halle, it was still rather fragmentary, consisting of small parts of pinnae with only incomplete pinnules preserved. Reinvestigation of the area in 2004 and 2006 supplied a new amount of material from this Cathaysian species that far exceeds that of the previous collections, both in quality of preservation, as in size and number of the specimens.

The Permian sediments from Jambi (Mengkarang Formation) consist of clays and siltstones grading into fine sandstones, alternating with pyroclastic deposits (tuffs) and coal seams of varying thickness, deposited in a delta plain environment (Van Waveren et al., 2005, 2006, 2007). Volcaniclastics and fluvially reworked volcaniclastics dominate (Tobler, 1919; Zwierzycki, 1935). Fusulinids found in the limestones at the base of the Permian Jambi sediments (Mengkarang Formation) were considered by Vachard (1989) to be indicative of a late Asselian (earliest Permian) age. Recently, Ueno (2006, pers. comm.) presented a second analysis, based on material he collected in 2004, and considered the fusulinids of these limestones to be roughly indicative of an Asselian-Sakmarian Age.

There are striking similarities in the composition of a number of Early Permian floras throughout the world. In particular, the occurrence of gymnosperm taxa from the morphogenus Taeniopteris and the appearance of large-leaved pteridosperms such as *Protoblechnum* and *Supaia* are common factors between a number of Euramerican and Cathaysian floras (DiMichele et al., 2000, 2001a, 2006b). The emergence of such large-leaved species has been treated by Asama (1962) in his reconstruction of trends towards the simple leaf as seen in the flora of the Shansi region (North China province). The Early Permian flora from Jambi also contains these particular floral elements (Van Waveren et al., 2005, 2007). Where seed ferns are present in the Jambi floral associations, they are usually a dominant element (Van Waveren et al., 2005). These seed fern-dominated associations alternate with more common ever wet forest mire associations mainly consisting of sphenopsids, pecopterids and lycopsids. The taphonomy of the seed fern remains indicates that they have not been significantly altered by transportation and that they were flushed into the system by a likely short-distance, highenergy event. These plants were probably representatives of a flora growing in the better drained areas, outside the ever wet coal-forming areas (Van Waveren et al., 2005; DiMichele et al., 2006b). This is further substantiated by the fact that plants typical for ever wet habitats are virtually or completely absent in these floras, although they can be well represented in other parts of the section, i.e., the typical forest mire associations. This suggests that the seed fern-dominated association existed outside the coal-forming, ever wet habitats, and that, from time to time, this material was washed into the wetland areas.

In the Late Carboniferous, a general drying trend started in the tropical regions, which persisted far into the Permian, leading to the eventual disappearance of the ever wet forest mire floras in the Euramerican region. Many different causal factors have been proposed as mechanisms driving this climate change. One of the main factors appears to have been a general warming of the Earth's climate, with the onset in the late Westphalian of a first large interglacial (González, 1990, and references therein) and continuing into the Early and Middle Permian. Although the general trend was one of warming and drying of the tropical climate, it was subject to large fluctuations (González, 1990; Montanez et al., 2007). Not only did this climate change lead to a warming of the global climate, but, as a consequence of the shrinking of the polar circulation cells causing the Intertropical Convergence Zone (ITCZ) to migrate (laterally) over an increasingly larger area, also to the distribution of precipitation over a larger region and increased seasonality in the Late Palaeozoic palaeotropics (Gastaldo et al., 1996; Ziegler et al., 2003).

In the last decades much research has been carried out on the effect of this drying trend on the Euramerican coal swamp flora, in particular the palaeomoisture reconstructions for Pennsylvanian coal swamps of North America, such as those based on coal ball data (DiMichele and Phillips, 1996), and the consequences this had for both habitat heterogeneity and vegetation composition (DiMichele et al., 2001b). Up until now, little has been written about the impact it had on the flora of the Cathaysian region. In the past, the assumption seems to have been that the Cathaysian region was only mildly affected by this drying trend, or that the drying trend occurred in Cathaysia much later than in Euramerica. Seasonality in Euramerica does appear to have arrived earlier and more forcefully than in Cathaysia (Ziegler et al., 2003). Coupled with a position in the palaeoequatorial belt favouring high precipitation (Patzkowsky et al., 1991), as well as tectonic processes resulting in basinal areas (Kerp, 1996; Cleal and Thomas, 2005; Hilton and Cleal, 2007), this could explain the persistence of coal swamp floras in Cathaysia into the Early Permian. Although much has been written about the changes in vegetation caused by the climate change and consequent changes in the ecology of the tropical mires, little is known about the possible effects this had on plant morphology.

For a better understanding of the species *Macralethopteris hallei* and its ecology, an emended diagnosis is needed, based on the old and the new material originating from several locations in the region, leading to a better-defined taxon. First, a comparison will be made of the material from the different localities to establish if we are dealing with a single species. Subsequently, the material will be compared with similar morphogenera and species from Cathaysia and Euramerica to get a clear view of its morphological relations. Finally, some hypotheses will be offered towards explaining the appearance of plant groups with relatively large pinnae in the Early Permian mesoxeric floras with possible implications for the growth form of *Macralethopteris*.

Material and methods

Material

Locations

All the fossil-bearing localities are situated in the vicinity of the town of Bangko, Jambi province, Sumatra, Indonesia (Fig. 2.1). All the material was collected from the Mengkarang Formation (Van Waveren et al., 2005).

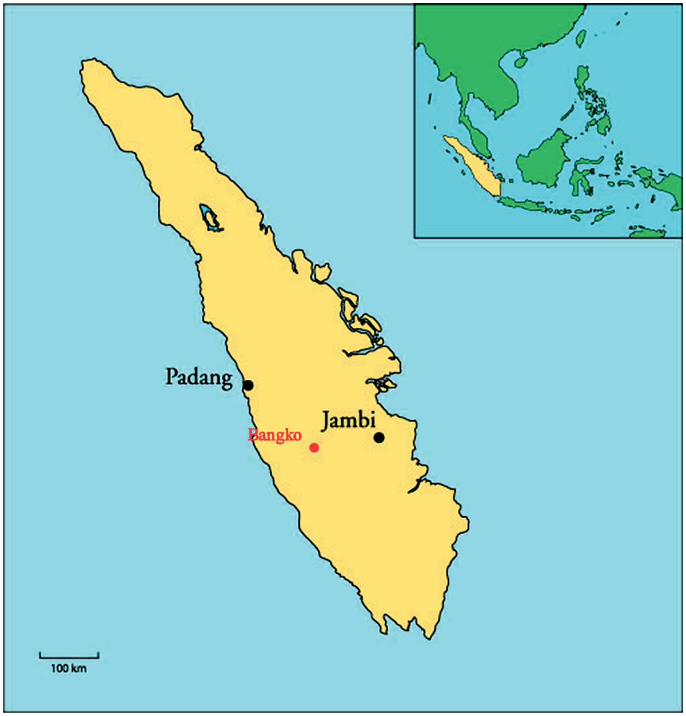

Figure 2.1: Map of the island of Sumatra, with the location of the town of Bangko indicated.

The material collected in 1925 by Posthumus, is from a riverbank along the small river Ketiduran Siamang. The sediment is finely laminated and rich in fine organic debris. Further details as to the location or sedimentology are not known. The specimens are fragmentary, consisting of rather small pieces of pinnae in which not a single pinnule is preserved in its entirety. Details like the delicate, dense venation are hardly discernible.

The majority of the material collected in 2004 and 2006 derives from a single locality along the Merangin River. It was found in layers consisting of fine to medium coarse silt with a clay fraction. The specimens are often (almost) entire pinnae, with a varying amount of visible detail.

Another, much smaller, collection was made in 2006 at a locality along the Ketiduran Siamang River. These fragmented specimens occur in coarser, sandy sediment. Although this material was collected from the banks of the same Ketiduran Siamang River as the 1925 material, the fossil-bearing sediment is rather different. The specimens collected in 1925 are embedded in organic-rich fine-grained sediment, i.e., fine sand to silt, whereas the sediment matrix of the specimens collected in 2006 from the Ketiduran Siamang River is slightly coarser grained, without the organic component. Another marked difference is the fact that the 1925 material consists of small pinnae segments, whereas the 2006 material consists almost exclusively of isolated pinnules, which suggests that the latter have been transported over some distance, were fragmented by a high-energy transport, or had become fragmented before transport.

Some morphological characteristics visible in the material from the Merangin locality are indistinct or absent in the specimens from the Ketiduran Siamang collections. This is due to the fragmentary nature of the specimens and the low quality of preservation.

Sedimentology of the Mengkarang Formation along the Merangin River (partially after Van Waveren et al., 2005)

The Mengkarang Formation has a thickness of 360 m along the Merangin River (Fig. 2.2) and is underlain by an intrusive granite body. Almost all of the sediments in the formation are pyroclastic and fluvially reworked deposits (Tobler, 1919; Zwierzycki, 1935). The facies associations presented below are based on lithofacies and fossil content (Van Waveren et al., 2005).

Description of the section (Fig. 2.2)

At the base of the section (0–1 m, facies association I) a mudstone holds scarce brachiopods and ammonites.

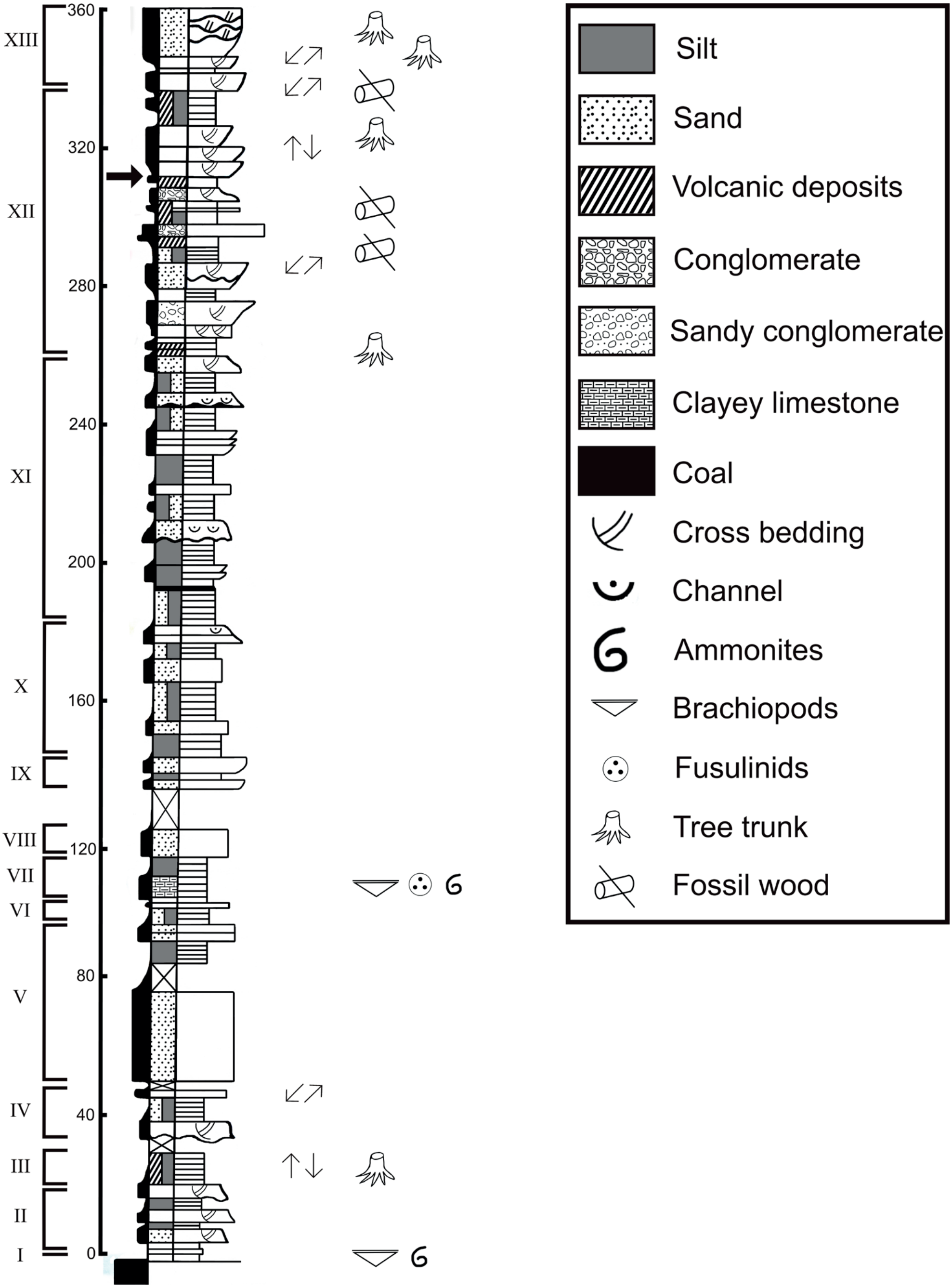

Figure 2.2: Simplified sedimentological log of the Mengkarang Formation along the Merangin river. The arrow on the left hand side indicates the *Macralethopteris* locality.

Light-grey sandstone bodies with plant remains (ferns, calamites, cordaites) and roots alternate with dark blocky shales (1–21 m, facies association II). The shales contain paleosol features and both macroand microfossil remains are absent. The sand bodies are massive (~6 m thick) and bedded (~2–3 m thick), fining upwards and have a channel geometry.

Between 21 and 30 m (facies association III) alternating thin layers of fine silicified sand and tuff encase a large silicified in situ tree trunk, 2.5 m high and 2 m in diameter. Sediments have been deposited asymmetrically against the tree. Bidirectional current patterns are present. Between 30 and 35 m no outcrop is present, probably because of the presence of soft, fine-grained sediment.

From 35 to 47 m (facies association IV) sandstones locally contain hummocky cross stratification. Thinly bedded clays and sands alternate and a single thin coal layer was observed. Large-scale cross bedding shows bidirectional currents.

From 47 to 98 m (facies association V) several very massive coarse sandstones alternate with thinly bedded clays. The sandstones containhigh-angle foresets accentuated by small pebbles.

Between 98 and 106 m (facies association VI), two 1 m thick coal layers alternate with middle-grained sand bodies, silts and silty sands with roots and plant remains (ferns, calamites, cordaites). From 106 to 118 m (facies association VII) dark mudstones with marine fossils (crinoids) are succeeded by a clayey limestone with fusulinids, which is overlain by a succession of dark marls with brachiopods.

From 118 to 125 m (facies association VIII) thick and massive, badly sorted, coarse sandstones occur.

Between 125 and 140 m, the succession is not exposed and likely consists of soft, easily weathered fine-grained sediment.

Between 140 and 145 m (facies association IX), two coarsening-upward beds alternate with shales. No floral or faunal elements were found.

From 145 to 188 m (facies association X), grain size decreases. Bed thickness varies considerably, between 0.5 m and 5 m. Dark blocky shales commonly occur underneath the finer sandstones. Thin coal layers are common. The sediments hold root systems and plant remains (ferns, calamites and cordaites, sometimes Lepidodendrales).

From 188 to 260 m (facies association XI) several middle- to coarse-grained sand bodies of 1.5 m to 3 m alternate with fine sand beds of 0.5 m or less and shales. Here again thin coal beds and dark blocky shales are observed beneath the sand bodies. The sand bodies show both fining and coarsening trends.

From 260 to 340 m (facies association XII) coarsening-up middle- to coarse-grained sandstone bars, lavas and pyroclastic sediments occur. In the lowest pyroclastic bank an in situ tree trunk has rooted (33 cm wide, 10 cm high).1 to 3 m thick, coarse agglomerate bodies reflect an increase in supply of coarse sediment. In between these coarse beds, finer grained clayey siltstone intervals occur. One particular interval is positioned just above a lava bed (~15 cm thick) and below an agglomerate. This interval contains different flora elements (*Macralethopteris*, *Taeniopteris*, gigantopterids and sphenopterids) than those found in the delta plain associations (ferns, calamites and cordaites). It consists of a set of beds with a total thickness of 70 cm and is comprised of four beds separated by 3–5 cm thick clays. The lowest bed (10 cm) is a clayey siltstone. It holds the most diverse flora, consisting of *Macralethopteris* (40%), *Gothanopteris bosschana* (10%), *Taeniopteris densissima*, *T*. cf. *multinervia* (10%) and *Cordaites* leaves. The next bed (20 cm) consists of clayey and sandy siltstone. Here a decreased diversity is observed, the association consisting of *Macralethopteris* (40%), *Cordaites* (40%) and *Calamites* (20%). The following few cm of clays are dark and rich in *Cordaites* leaves. The 13 cm thick bed deposited on top of the clays consists of a very fine sandy siltstone. Here the flora is even less diverse and consists of *Calamites* (50%) and *Cordaites* leaves (50%). The upper bed of fine silty sandstone overlies a few cm thick clay with a high amount of *Cordaites* leaves. It is 20 cm thick and the relative abundance of *Cordaites* leaf fossils reaches 75%, with 25% *Calamites*.

In the upper part of the section (340–360 m, facies association XIII), middle- to coarse-grained sand bodies alternate with dark blocky shales containing paleosol features and a shale holding large taeniopterid leaves. In many places the sandstone bodies enclose in situ calamite stems and indicate bidirectional currents. Bar-shaped sandstone bodies are coarsening-upward and grain size is dominantly middle. Circa 10 casts of in situ tree bases, with diameters of 47 to 170 cm, were found in the upper sandstone body. The plant remains in these sandstone deposits clearly show an orientation parallel to the main current direction.

Interpretation

Sea level fluctuations will have affected the accommodation space along the Merangin River section. Autocyclicity and tectonic activity including volcanism may also have been important factors in the alternation of the different depositional environments. The shoreline has not significantly shifted along the section, as can be deduced from the silty limestones and the regular occurrence of structures reflecting bidirectional currents. Marine deposits characterize the base of the section (0–120 m). The central part of the section represents a delta plain (120–260 m). Braided river and/or fan-delta deposits in the upper part of the section (260–360 m) reflect increased relief and/or irregularities in sediment supply, likely related to volcanism or climate.

Marine fossils in facies association I indicate a shallow-marine environment. The subsequent fining-upwards shallow channel fills (facies associations II and III) are interpreted as elements of a tidally influenced delta plain, because of the presence of bidirectional current patterns, their plant fossil content and the in situ tree. The dark blocky shales can be interpreted as immature gleys indicating waterlogged conditions. The asymmetrical deposition of the sediment around the tree suggests burial by repeated crevasse splays (Rygel et al., 2004). Facies association IV, with hummocky cross-stratification indicative of deposition below normalweather wave base (Duke et al., 1991), represents a shallow-marine environment. It grades over a small vertical distance (~1–2 m) into coastal swamp deposits with coals. A badly sorted sandstone with small pebbles accentuating high-angle foresets is interpreted to have been deposited close to the delta front (facies association V). Facies association VI with thin coal seams was deposited in the delta plain. It grades over less than 4 m into a clayey fusuline limestone (facies association VII) reflecting a rise of the relative sea level. This interval represents the deepest (~10–20 m) marine conditions during deposition of the succession. The thick-bedded coarse sandstones (facies associations VIII and IX) are again interpreted as delta front deposits. Facies association X represents a delta plain where the thin sand bodies were formed as crevasse splays fed by a meandering system. Facies association XI represents deposits of a meandering system with several crevasse splays. The thin coal deposits within this facies represent mires. The coarsening-upward beds, agglomerates, lava bed and the silty mudstone are interpreted as alternating fluviovolcanic and alluvial plain deposits (cf. Verstappen, 2000). The coarsening-upward sandstones (facies association XIII) with structures indicative of bidirectional currents are interpreted as bars in the mouth of a tidally influenced fan delta. The dark blocky shales are interpreted as immature gleys indicating waterlogged conditions. The finer sediments reflect more quiet depositional conditions, either in periods with limited supply of coarsegrained sediment or at sites temporarily lateral to the main transport paths.

Interpretation of the Macralethopteris locality of facies association XII

Extrusive rocks and volcaniclastic sediments are dominantly present and alternate with silty clays in which the Macralethopteris material is found. There is a lack of structures in these silty clay beds. Orientation of the plant fossils in the bed varies from parallel to the bed to, less commonly, oblique to the bed. The position between two volcanic deposits (a lava and an agglomerate) indicates that the general setting of this fine-grained interval of facies association XII can be interpreted as a transition area between volcanic landforms (for example, fluviovolcanic fans) and alluvial landforms (for example, an alluvial — or deltaic plain). A similar transition is observed in the present day Toba volcanic area of Sumatra

(Verstappen, 2000). The silty mudstones of the facies represent the sediments brought into the basin by the volcanic mudflows (lahars) that are common in such type of setting.

Methods

Statistical comparisons of the material from the different localities were made using a non-parametric Mann–Whitney U-test for two independent samples (SPSS 15.0.1). Results are given as p, where p stands for the probability that the two means derive from a sample of the same population. The material from Ketiduran Siamang collected in 2006 was excluded from statistical comparison, since the number and size of those specimens does not allow for reliable results (see Table 2.1). Likewise, in characters where the size of one of the samples was less than 7, no reliable statistical comparison could be performed. Cuticles were obtained following methods described by Kerp (1990), Krings and Kerp (1997) and Kerp and Krings (1999).

Results

Systematic part[2]

Macralethopteris hallei Jongmans et Gothan emend. Booi (Fig. 2.3, Plates 2.1 and 2.2).

Selected synonyms:

1927	*Alethopteris* sp. Halle-Halle, p. 111, pl. 24: figs. 13–15.
1935	*Macralethopteris Hallei* Jongmans et Gothan-Jongmans and Gothan, p. 130–132, pl. 40: figs. 2–5, pl. 41: fig.1.
1939	*Alethopteris Hallei* (Jongmans et Gothan)-Stockmans and Mathieu, p. 69, pl. X, fig. 1, 1a.
1974	*Alethopteris hallei* (Jongmans et Gothan) Stockmans et Mathieu–'Gu and Zhi', p.112, pl. 78, figs. 1–3.

Emended diagnosis

Pinnae broad to slender, ovate to linear. Rachis strong, broad, grooved longitudinally. Pinnules arranged suboppositely, opposite and alternating configurations also occurring; pinnules densely spaced, at semi-acute angle with rachis; shape slender lanceolate to slightly ovate-oblong, often contracted near base, apex rounded-acute, margin entire, narrowly confluent at base (connate), slightly decurrent on basiscopic side. Midvein distinct, straight and prominent. Secondary venation very dense, lateral veins bifurcating once near base, almost perpendicular to midvein; some seemingly arising directly from pinna rachis. Terminal pinnules elongated.

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[2] All measurements in mm unless indicated otherwise. Numbers in parentheses indicate average value of the character and the upper and lower value of the 95th percentile.

Table 2.1: N indicates the number of specimens from which measurements were taken, p indicates the statistical probability that both measurements come from the same population (T-test), NS is 'not significant'.

	Ketiduran Siamang (1925 locality)	N
(Minimal) Length pinna	-	-
Width pinna	-	-
Width ultimate rachis	2.69 (±1.59)	11
Shape pinnule	-	-
Length pinnule	-	-
Width pinnule (broadest point)	13.61 (±1.75)	24
Width pinnule (contracted point)	-	-
Width pinnule (at base)	15.36 (±1.36)	7
Angle pinnule/rachis	70.81° (±6.51)	37
Distance between pinnules	1.80 (±1.05)	16
Shape margin	entire	-
Shape pinnule apex	-	-
Midvein appearance	strong, in level with lamina	-
Width midvein	1.32 (±0.2744)	46
Length midvein	53.05	1
Distance midvein/top	-	-
Lateral vein shape	straight, slightly curved at base	
Angle lateral vein at midvein	76.67° (±7.50)	6
Angle lateral vein at margin	78.00° (±7.58)	9
Angle lateral vein	85.00° (±3.54)	5
Lateral vein bifurcation	common, once, near base	-
Lateral vein density (N/cm margin)	43.50 (±0.71)	2

Measurements in millimeters, unless indicated otherwise

Merangin (2004 & 2006 locality)	N	p	Ketiduran Siamang (2006 locality)	N
99.53 (±31.06)	34	-	-	-
62.91 (±20.87)	18	-	-	-
1.62 (±0,5984)	43	p<0.01	-	-
lanceolate	-	-	lanceolate	
35.91 (±10.43)	91	-	40.37	1
9.00 (±1.57)	158	p<0.001	9.61 (±1.82)	2
8.02 (±1.52)	127	-	-	-
11.25 (±2.01)	136	p<0.001	7.69	1
67.34° (±9.08)	182	0.05	-	-
2.21 (±1.20)	173	NS	0.4375 (±0.32)	4
entire	-	-	entire	-
acute, rounded	-	-	acute, rounded	-
strong, in level to slightly sunken	-	-	clear, in plane to sunken	-
0.85 (±0.1744)	186	p<0.001	1.01 (±0.3415)	7
34.86 (±5.62)	14	-	-	-
2.38 (±0.95)	16	-	-	-
straight to slightly curved, curving more strongly at base and margin	-	-	straight	-
79.35° (±7.76)	63	-	-	-
78.45° (±7.62)	62	NS	-	-
81.07° (±5.90)	42	-	80°	-
common, once, near base	-	-	-	-
62.68 (±6.05)	68	-	-	-

Cuticle: epidermal cells elongate, cell walls straight.

Description

Complete fronds are unknown. Pinnae are broad to slender, ovate to linear, on average 63 mm wide (30–(63)–92) and up to at least 180 mm long (58–(100)–182). The rachis is robust, 0.7–(1.8)–7.1 mm broad and longitudinally striated.

Pinnules mostly arranged suboppositely, though opposite and alternating configurations also occur. The pinnules are rather densely spaced, the distance between them at the broadest point averages 2.1 mm (0.0–(2.1)–4.0); they are never overlapping and arise from the rachis at an angle of about 68° (51–(68)–86). The pinnules are slenderly lanceolate in shape, sometimes even slightly ovate to oblong. They reach up to 61 mm in length (15–(36)–61), and a width at their broadest point of 9.6 mm on average (5.7–(9.6)–17.0). Near the base, they often show a slight contraction of the lamina. Pinnules are tapering from about two thirds towards the top and end in an acutely rounded apex. The pinnule margin is entire, usually narrowly confluent at the base (connate), and they are only very slightly decurrent at the base on the lower (basiscopic) side.

The midvein is prominent, straight and sometimes slightly sunken, ending about 2 mm from apex, about 1 mm in width (0.6–(0.94)–1.85).

The lateral venation is very dense, lateral veins bifurcate only once, usually very near the base (at the midvein). Lateral veins leave the midvein at about 70° (50–(70)–90), curve near the base and run towards the margin at an angle of 81° (76–(81)–90). They curve again slightly near the margin, which they reach at an angle of 79° (63–(79)–90). Several lateral veins appear to arise directly from the main rachis, but details may be obscured due to less than optimal preservation (see Bocheński, 1960, on architecture of alethopterid venation). Density at the pinnule margin is 62 veins/cm (44–(62)–71).

Only single pinnae were found and complete terminal pinnules are unknown, although some almost complete specimens are present (Plate 2.1, Fig. 2.1).

Only very fragmentary pieces of cuticle could be obtained, in which the epidermal cells are elongate, with straight cell walls.

Comparison of Macralethopteris material from the different Jambi localities

For reasons outlined under Material, comparison of the material will only include two of the three collections described in Table 2.1. There are notable differences in the size of certain leaf characters between the collections (see Table 2.1). While the distance between the pinnules and the angles of the lateral veins appear not to be significantly different between the two populations, the pinnae from the 1925 collection are generally much larger, particularly with regard to the width of the pinnules (p b 0.001), width of the midveins (p b 0.001), width of the rachis (p b 0.01) and angle of the pinnules with the rachis (p b 0.05).

Plate 2.1: Figure 1: *Macralethopteris hallei* Jongmans and Gothan (no. MerXI–2) (bar = 1 cm). Figure 2: *Macralethopteris hallei* Jongmans and Gothan (no. MerXI–2), detail (bar = 1 cm).Figure 3: *Macralethopteris hallei* Jongmans and Gothan (no. MerXI–59), detail pinna apex (bar = 1 cm).

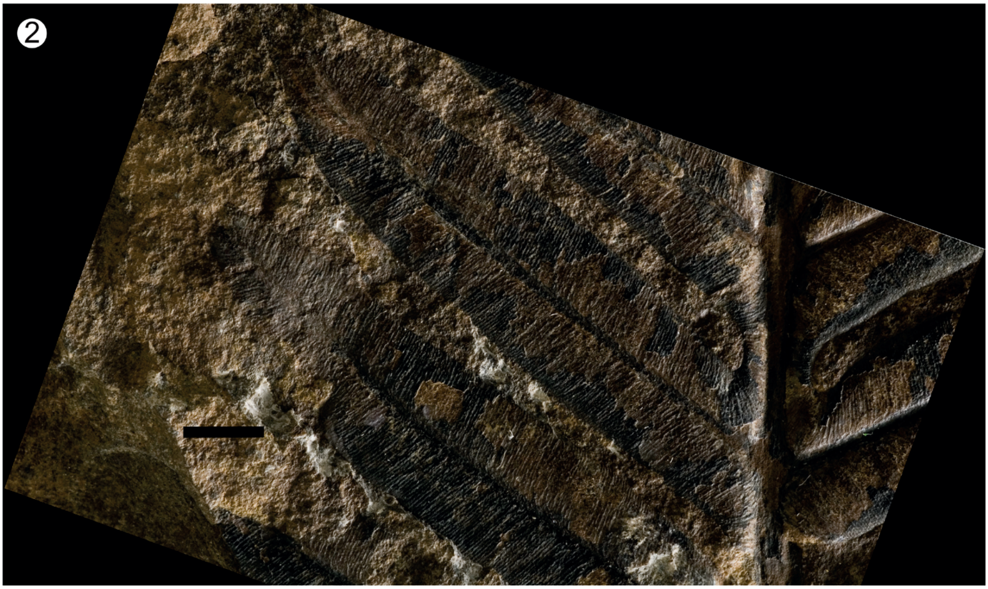

Plate 2.2: Figure 1: *Macralethopteris hallei* Jongmans and Gothan (no. MerXI–36) (bar = 1 cm). Figure 2: *Macralethopteris hallei* Jongmans and Gothan (no. MerXI–36), detail (bar = 0.5 cm).
Comparison of the morphology of the *Macralethopteris* material from the different localities (the 2006 Ketiduran Siamang material is excluded from statistical comparison, see Material and methods)

These differences between the populations may be explained by three different factors.

The first factor that should be taken into account is that the two populations are not exactly of the same age. Although the two localities are approximately situated in the same plant horizon (Jongmans and Gothan, 1935), a precise correlation of the localities is not possible. This means that the differences between the two populations might be attributable to a difference in evolutionary development and that they represent closely related phylogenetic stages.

The second aspect considering the difference in pinnule size between these two populations is a difference in ecology. Amount of available moisture, intensity of solar irradiation and soil composition are just a few of many factors that could influence the habitus of a species and thus pinnule size to a significant degree (Parkhurst and Loucks, 1972). Little is known about the locality from which the 1925 material was collected, neither the exact position nor the sedimentology. The lithology of the specimens of finely laminated, finegrained substrate suggests that deposition took place under lowenergy conditions and its fine lamination and high organic content is indicative of slow deposition as may occur on river banks, a floodplain or semi-lacustrine environment. The recently collected material is found in coarser sediment, probably deposited as part of a gravity flow.

A third explanation might be a difference in growth stage, in which case the new material would represent a young, barely established population of *Macralethopteris*, while the older material may represent more mature individuals.

Of course, the morphological differences between the two populations may be due not to a single cause, but to a combination of two or three of the factors mentioned above.

Although there is a clear difference between the two populations, this difference pertains mostly to the dimensions of some of the characters in the pinnae. These are insufficient grounds to distinguish two different species (see Table 2.1); therefore, all specimens are assigned to *Macralethopteris hallei*.

Comparison with other alethopterid species

In Table 2, several species are listed with properties akin to those of *Macralethopteris hallei*.

Stockmans and Mathieu (1939), in re-evaluating the work by Jongmans and Gothan (1935), questioned the validity of the genus *Macralethopteris*. They regarded it as a subgenus of *Alethopteris* at most, because the sole characteristic that would set it apart from other *Alethopteris*-species is its pinnule size. In the same publication, they described new species of *Alethopteris* with pinnules that are sometimes even larger than those of *Macralethopteris*.

However, the almost absent decurrency at the lower (basiscopic) side of the pinnule base and, most of all, the remarkably dense venation set *Macralethopteris* clearly apart from true *Alethopteris* species. Vein density is seen as one of the most significant discriminating characteristics for *Alethopteris* species; Šimůnek (1996) and Zodrow and Cleal (1998) have shown that it appears to be a very stable character. Although previous authors did not discuss the almost symmetrical nature of the pinnules, this is also a strong argument in favour of accommodating *Macralethopteris hallei* in a separate genus from *Alethopteris* Sternberg. *Alethopteris* Sternberg is characterized amongst others by a marked decurrency of the lamina on the basiscopic side, giving the pinnules a strongly asymmetrical appearance. This is very poorly developed in *Macralethopteris*, which has rather densely spaced pinnules that are almost symmetrical in outline, sometimes even *Callipteridium*-like. Therefore, we retain *Macralethopteris* as a separate morphogenus.

Stockmans and Mathieu (1939) described two new *Alethopteris* species from the Kaiping flora of China that show some superficial similarities with *M. hallei*. The first, *Alethopteris straelenii*, has falcate pinnules, unlike *Macralethopteris*, and the vein density is lower. The larger width of the rachis and the fact that the lateral veins reach the margin perpendicularly, also distinguishes it from *Macralethopteris* (see Table 2.2). The second is *A. gothanii*, which shows a strong resemblance to *M. hallei*, but differs from it in the clear decurrency of its pinnule base, the lower density of the lateral veins, its broader rachis and its broader pinnules (see Table 2.2). For these reasons we retain *Alethopteris gothanii* as a separate species and we do not include it in the synonymy of *M. hallei*, as has been proposed by 'Gu and Zhi' (1974, p.116). This also means that the large specimen illustrated by 'Gu and Zhi' (1974, plate 78, fig. 2) as *Alethopteris hallei* should be included in *Alethopteris gothanii*. The broadly spaced pinnules, clear basal decurrency of the basiscopic margin as well as the very acute pinnule apices of this specimen set it clearly apart from *Macralethopteris hallei*.

Comparing *Macralethopteris hallei* with the common Euramerican Early Permian alethopterids, e.g. *Alethopteris schneideri* (Sterzel) Sterzel, 1918 and *A. zeilleri* (Ragot) Wagner, 1968, the Euramerican species differ in having much smaller and semi-ovate pinnules with obtusely rounded apices and in the venation density, which is higher in *M. hallei*.

The reconstruction of a pinna segment of *Macralethopteris* by Wagner (1968) shows several pinnules that are not connected at the base or that are even slightly cordate. Gothan and Weyland (1954) already emphasized this particular character. Examination of the material available to Gothan and Weyland (1954), Wagner (1968) and the newly collected specimens indicates that *Macralethopteris* may have non- or barely confluent pinnule bases, but this is very rare as only 2% of the newly collected specimens show this feature. Fig. 2.3 shows a new reconstruction of a part of a pinna, based on the new material, together with the one by Wagner (1968).

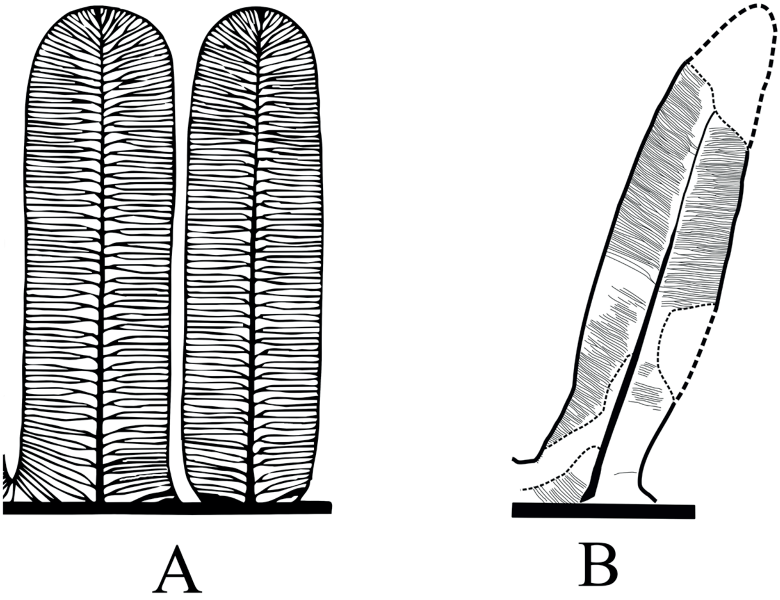

Figure 2.3: Comparison of pinnule reconstruction of *Macralethopteris* by Wagner (1968) (A) and Booi (B).

The most remarkable characteristic of *Macralethopteris* is its high vein density (60–65/cm). The only alethopterid having a more-or-less comparably high vein density is *Alethopteris lancifolia* Wagner, although this species has only about 50 veins/cm according to Wagner (1961). This latter species is known from the early Langsettian (Westphalian A) and pinnules have a different shape, as they start to taper at about half the pinnule length and taper far more rapidly.

General morphology in comparison with several alethopteroid species

Macralethopteris and the material that has been reclassified by Hill et al. (1985) as *Qasimia tobaensis* (basionym *Taeniopteris tobaensis*) are very similar, but according to Hill et al. (1985) the venation is different, and, especially the pinnule attachment (with contracted base) distinguishes it from Macralethopteris. Furthermore, Li et al. (1982) describe *Q. tobaensis* in the original publication as sporangia-bearing. Because the new material of *Macralethopteris* has rendered cuticles and no fertile pinnules were found, and because of the close morphological similarity to *Alethopteris*, we suggest that *Macralethopteris* is a seed fern, like all other true alethopterids.

Table 2.2: Measurements of the new material of *Macralethopteris hallei* and those of several comparable species from the Late Carboniferous and Early Permian

	A. straeleni Stockmans & Mathieu, 1939	**A. gothani Stockmans & Mathieu, 1939**	**A.? shengi Sze, 1954**
Shape pinna	-	parallelsided	linear
(Minimal) Length pinna	120	110	-
Width pinna	-	-	80-90
Ornamentation ultimate rachis	striate	striate	keeled
Width ultimate rachis	4-5	2-3	4
Shape pinnule	slightly curved, contracted at base on anterior side	ovate-elongated, contracted at base on anterior side	ovate to oblong, more or less linear, gradually tapering
Length pinnule	50-70	35-40	48
Width pinnule (broadest point)	15-18	12	22
Width pinnule (contracted point)	-	-	-
Width pinnule (at base)	-	-	-
Angle pinnule/rachis	55°	50-60°	50-60°
Distance between pinnules	(1-)2	-	-
Shape margin	-	-	entire
Shape pinnule apex	-	-	obtuse
Shape pinnule base	-	-	slightly decurrent, with slight auriculate distal expansion
Midvein appearance	very strong, slightly curved near top	clear, reasonably strong, reaching top	strongly decurrent, bending slightly forward, persisting almost to apex
Width midvein	-	-	-
Length midvein	-	-	-
Distance midvein/top	-	-	-

A. lancifolia Wagner, 1961	A. zeilleri (Ragot, 1955) Wagner, 1968	A. schneideri (Sterzel, 1881) Sterzel, 1918	M. hallei Jongmans & Gothan, 1935 (new material)
-	-	linear, tapering slightly at base and clearly near apex, apex somewhat decurrent	ovate-linear
-	-	-	99.53 (±31.06)
-	-	-	62.91 (±20.87)
faintly striate	-	-	striate
0.5	0.5-1	up to 10	1.62 (±0,5984)
lanceolate, borders tapering from halfway pinnulelength	distinctly confluent	catadromically concave, anadromicly convex, ovate to broadly linear	lanceolate-ovate
10-40	15-25	up to 14	35.91 (±10.43)
4-8	6-8	up to 8	9.00 (±1.57)
-	-	-	8.02 (±1.52)
-	-	-	11.25 (±2.01)
oblique	70°	65°	67.34° (±9.08)
-	close	often slightly overlapping	2.21 (±1.20)
-	parallel to subparallel	curved downward	entire
bluntly acuminate	broadly rounded	rounded	acute, rounded
connected, decurrent on basiscopic side	basiscopically somewhat decurrent, acroscopically straight	auriculately extended margin on catadromic side, basal pinnules with slightly cordate base	connected, slightly decurent on basiscopic side
distinct, straight, persisting into apex	moderately thick, straight, persisting into apex	strong	strong, in plane to slightly sunken
-	-	-	0.85 (±0.1744)
-	-	¾ of pinnule length	34.86 (±5.62)
-	-	-	2.38 (±0.95)

Table II Measurements of the new material of *Macralethopteris hallei* and those of several comparable species from the Late Carboniferous and Early Permian (*continued)*

	A. straeleni Stockmans & Mathieu, 1939	**A. gothani Stockmans & Mathieu, 1939**	**A.? shengi Sze, 1954**
Lateral vein shape	straight, slightly curved at base	very delicate and dense	very dense and thick, arching
Angle lateral vein at midvein	-	-	-
Angle lateral vein at margin	perpendicular	perpendicular (to oblique near top)	-
Angle lateral vein	-	-	-
Lateral vein bifurcation	common, once to twice, near base	common, once, at or near base	common, once to thrice, first bifurcation near base
Vein density (N/cm margin)	40	38-40	-
Geological age	Permian	Permian	Carboniferous-Permian

Unless indicated otherwise, all measurements in millimeters

A. lancifolia Wagner, 1961	**A. zeilleri (Ragot, 1955) Wagner, 1968**	**A. schneideri (Sterzel, 1881) Sterzel, 1918**	**M. hallei Jongmans & Gothan, 1935 (new material)**
thin, close, numerous, curving slightly at the midvein	straight, sometimes curving slightly near midvein	straight, curving slightly upward at margin and curving strongly downwards at midvein	straight to slightly curved, curving more strongly at base and margin
-	-	acute	79.35° (±7.76)
right angle	right or nearly right angle	-	78.45° (±7.62)
-	-	perpendicular to midvein	81.07° (±5.90)
once, common, at irregular intervals	once or twice at irregular intervals	regularly twice bifurcated	common, once, near base
50	30-35	40	62.68 (±6.05)
Upper Westphalian A-Westphalian B	Stephanian A-Middle Permian	Lower to Middle Permian	Asselian(-Artinskian)

Macralethopteris hallei also shows similarities to *Alethopteris*? *shengi* described by Sze (1954), especially in size and the venation. However, the strongly curved lateral veins of the latter differ from those of *Macralethopteris* and are more comparable to those of *Protoblechnum*, as was already indicated by Sze.

Jongmans and Gothan (1935) assigned three more species to the genus *Macralethopteris*. The first is *Macralethopteris missouriensis* (White) Jongmans et Gothan (basionym *Taeniopteris missouriensis* White). *Taeniopteris missouriensis* as described and illustrated by White (1893) is a species showing a remarkably variable morphology. Smaller, apical pinnules on the fronds show alethopterid morphology, with lanceolate pinnules and broadly decurrent basiscopic pinnule bases. Although pinna arrangement is similar, the pinnule attachment appears less rigid than is usual in alethopterids. However, non-apical parts show a strongly cordate pinnule attachment, while alethopterid pinnules are almost invariably connate. Wagner (1968, p. 21) regarded the relationship between *Macralethopteris hallei* and“*Taeniopteris*” *missouriensis* as doubtful and stated: “if this species [*Taeniopteris missouriensis*] is considered characteristic of *Macralethopteris*, then it must be accepted that a Neuropteroid pinnule insertion may occur in certain parts of the frond”. The many new *Macralethopteris hallei* specimens, however, do not show any tendency towards a ‘neuropteroid’ (cordate) attachment of the pinnules, but unequivocally show an alethopterid, connate morphology. Therefore, the inclusion of *T*. *missouriensis* White in *Macralethopteris* cannot be justified.

A second of the species assigned to *Macralethopteris* by Jongmans and Gothan (1935) is *M*. *serrata* (Halle) Jongmans et Gothan (basionym *Taeniopteris*? *serrata* Halle), originally described and illustrated in Halle’s Shansi flora (1927). Its pinnules are not decurrent at the base, even clearly contracted. The general morphology of the pinnules shows a flat, thin lamina rather than the thick lamina found in almost all alethopterids. For these reasons, it is hard to see any morphological similarities between this species and alethopterids in general and therefore we do not think this species should be included in the genus *Macralethopteris*.

Jongmans and Gothan (1935) transferred *Taeniopteris jejunata* Grand’Eury, 1877, a form with pinnate leaves, to *Macralethopteris*. Later, Remy (1953) established the genus *Ilfeldia* for taeniopterid fern fronds with lateral sporangia, with as a single species *Ilfeldia jejunata*. According to Cridland and Morris (1960) *Taeniopteris jejunata* is a pinnate leaf. Such pinnate fronds are also known from Ilfeld (Germany), where the fertile material described by Remy (1953) as *Ilfeldia jejunata* was collected. It should be noted that the name *Taeniopteris jejunata* is still commonly used. Leaves of *Taeniopteris jejunata* are usually neuropterid or heart-shaped at base and pedunculate (Remy, 1953). Moreover, pinnules of *T*. *jejunata* are larger than those of *M*. *hallei* are and not vaulted.

Jongmans and Gothan (1935) furthermore compared with a specimen of *Desmopteris chonsonensis*, described and illustrated by Kawasaki (1934). The specimen on the poor-quality photograph in Kawasaki indeed looks similar, but the drawing of the venation (Kawasaki, 1934, pl. LVII, fig. 152a) clearly shows repeatedly bifurcating lateral veins comparable to those found in *Comia*, rather than a typical, simply bifurcating alethopterid venation pattern.

Remy (1953) suggested to include *Taeniopteris* (?) *auriculata* (Carpentier, 1920) in *Macralethopteris*, on the grounds of using *Macralethopteris* as a genus for sterile pinnate taeniopterid leaves; pending the availability of material with fructifications that would allow a more precise classification. However, *Macralethopteris* is a genus for alethopterid foliage and none of the species mentioned above fit the generic diagnosis of this genus.

It is remarkable that, even when *Macralethopteris* is so abundant, like in the locality where the 2004 *Macralethopteris* material was collected, only single pinnae have been found. Although this might be inherent to the fragmentary nature of the material, it raises the question whether *Macralethopteris hallei* might have had simply pinnate fronds.

Macralethopteris hallei differs from all other alethopterids in the high venation density and the *Callipteridium*-like pinnule configuration. Furthermore, pinnules are larger than in most other alethopterids. Nevertheless, it should be emphasised that all other characters are clearly alethopterid. With regard to the general shape of pinnules and pinnae it has the strongest morphological resemblances to the group of (Late Carboniferous) alethopterids with semi-acute pinnule apices, such as *A. lonchitica* Sternberg, *A. urophylla* (Brongniart) Goeppert and *A. bohemica* Franke.

Discussion

Macralethopterid ecology and implications

Ecology

The morphology of the pinnules of *Macralethopteris* points to rather mesic growing conditions. Its remarkably thick, coriaceous lamina is a character that is strongly correlated with habitats characterized by high solar irradiation (Givnish, 1988). Furthermore, a very dense venation is usually found correlated with high potential transpiration (Uhl et al., 2002), although this correlation seems to be less unequivocal when it pertains to Palaeozoic pteridosperms (Uhl and Mosbrugger, 2002). The slight change in lateral vein angle near the margin of the leaf can be interpreted as the result of flattening of a pinnule margin that was originally curved downwards, a further aspect that would point to a habitat with a high amount of solar irradiation (Arens,1997 and references therein). However, the xeromorphic features are perhaps also partially attributable to a relatively primitive vascular system in these seed ferns (Stidd, 1981).

DiMichele et al. (2006a) describe the Westphalian habitat of medullosan pteridosperms such as alethopterids as “clastic floodplain environments, from better drained levees and streamsides to soggy soil areas”. However, *Macralethopteris* is found in the Mengkarang Formation as part of a mesoxeric assemblage that also includes the early gigantopterid *Gothanopteris bosschana*, and the gymnosperms *Taeniopteris densissima* and *T*. cf. *multinervia*. This means that, as an assemblage, it can be equated with other Early Permian “seasonally dry” floras, such as described from the Permian of Texas (DiMichele et al., 2006b). These floras are interpreted as vegetation types adapted to seasonal drought and a lower ground water table. These mesophytic assemblages are usually found alternating with assemblages of ever wet floras. In the case of this Early Permian flora from Sumatra, they are seen as colonizing the well-drained, drier areas of the tropical ever wet regions. These had grown increasingly patchy in ecology towards the end of the Carboniferous as a result of a general drying of the tropical climate (DiMichele and Phillips, 1996; Gastaldo et al., 1996; DiMichele et al., 2001b, 2006b).

Trends in Early Permian gymnosperm communities

The Asselian age of the Jambi flora places it as slightly older than the oldest layers from Shansi (see Hilton and Cleal, 2007, fig. 4). Viewing the present *Macralethopteris* material in the light of the younger Cathaysian species (*Alethopteris gothanii*, *A. straelenii*), it becomes clear that, while *Macralethopteris* has a unique morphology, there is a general trend in the Cathaysian region for some alethopterid species to develop larger pinnules. Although the *Macralethopteris* material from Jambi already shows rather large pinnules, we can see they are still significantly smaller than those found in the younger strata in China, specifically those mentioned above from the Kaiping area (see Table 2.2). We assume that the Cathaysian alethopterids mentioned above are phylogenetically related to the Carboniferous Euramerican alethopterids. Trigonocarp seeds, generally attributed to medullosalean seed ferns (e.g. *Alethopteris*) are known from the Jambi flora (Jongmans and Gothan, 1935, p.165, plate 55, fig. 7), although they have not been found in direct association with *Macralethopteris* leaf remains. All these Early Permian Cathaysian alethopterids are found associated with a flora of mesoxeric character, implying drier ecological growing conditions than those in which the Carboniferous Euramerican alethopterids are found.

In addition, the tendency towards larger pinnules in these Cathaysian alethopterids is not unique. A large number of the species that are found in Early Permian mesoxeric floras have rather large ‘leaves’ or ultimate leaflets (or pinnules). Examples of these are gigantopterids, seed fern species belonging to the *Protoblechnum–Supaia–Comia* complex (or supaioid complex) and taeniopterids. Asama (1960, 1962) already described the tendency in these xeromorphic floras towards larger-leaved plants in his studies on changes in leaf morphology through time, and specifically those that occurred in the Cathaysian Shansi flora. He noted that in various taxa from this flora, such as sphenopsids, peltasperms, pteridosperms and gigantopterids, there was a common trend towards increasingly larger pinnules or leaves. Laveine et al. (1977) put forward a more extensively argued hypothesis as to the morphological changes taking place in pteridosperm fronds during the Late Carboniferous and Early Permian on similar lines as those proposed by Asama. They concluded that fusion and neotenic processes (Asama's retardation) led not only to larger pinnules but also to smaller fronds. Kerp (1996) described a comparable trend towards smaller fronds in peltasperms from the Permian of Europe.

It is difficult to understand why larger pinnules in these Cathaysian alethopterids (and in the mesophytes in general) should coincide with drier (local) climate. A larger leaf, respectively leaflet behaving like an individual leaf unit, will cause a thicker boundary layer at the leaf surface, which then in turn will reduce the water loss through evaporation from the stomata. However, this effect would be detrimental since larger leaves heat up far more quickly than smaller ones and in so doing the temperature of the leaf would rapidly reach a point where the processes within the leaf would suffer (Parkhurst and Loucks, 1972; Givnish, 1979, 1988). In extant vegetation worldwide, an increase in leaf size is, on the whole, associated with an increase in (mean) temperature and precipitation (Givnish, 1979; Traiser et al., 2005).

Growth strategy

We can question whether an alethopterid leaflet can be regarded as an individually functioning leaf unit, or whether an alethopterid frond in its entirety should actually be viewed as a single, deeply divided, large frond. The answer for this might be found in the ontogeny of (semi-) compound leaves, but up till now it still remains unclear whether such leaves should be viewed as a collection of smaller leaves or whether they function as a very deeply divided, lobed leaf (Champagne and Sinha, 2004). This is further complicated by the sparse knowledge of the actual physiology of an extinct plantgroup like the pteridosperms. It is possible to regard the frond as the actual functioning leaf unit instead of the individual pinnules. Given the possibility of a bi- or even monopinnate habitus for *Macralethopteris hallei*, this would mean a significant reduction in functional leaf size when compared with the large alethopterid fronds of the Euramerican Carboniferous.

The xeromorphic features described above would also fit a different growth strategy, namely that of a liana-like habitus. The limitations in water transport and the increased solar irradiation caused by growth in the higher parts of the canopy often result in xeromorphic characters in plants with climbing habits. This habitus was reasonably common throughout various pteridosperm groups during the Late Carboniferous and Early Permian (Krings et al., 2003b). However, the sturdy build of the pinnules of *Macralethopteris hallei* and its (presumed) small frond size would provide enough support for the plant to have a 'solitary' habitus and not to have to rely on other plants for support, as climbing plants do. Nor are any other characteristics like climber hooks, flexuous stipes or similar features that are found in other climbing pteridosperms (Kerp and Krings, 1998; Krings et al., 2003a,b), present in *Macralethopteris hallei*.

Macralethopteris could also have been a self-supporting part of the upper canopy. In which case the xeromorphic features would be due to high irradiation and high wind movement. However, there is a large presence of *Cordaites* leaves in the association in which *Macralethopteris* is found. These are probably related to the large tree trunks throughout the section, at least part of which are cordaitean in origin (Vozenin-Serra, 1985). This makes it less likely that *Macralethopteris* would have formed the upper canopy.

The fact that only single pinnae are found in the material, without indications of a bipinnate morphology, points to a growth habitus for *Macralethopteris* that was significantly smaller than that of the majority of Permocarboniferous medullosan pteridosperms. DiMichele et al. (2006a) and others have hinted at the possibility of a cormous habitus for alethopterids with large fronds (or pinnae). Such a growth strategy does appear to fit the sturdy fronds of *Macralethopteris*. In the light of climate changes bringing about an increase in monsoonal seasonality in the Permocarboniferous tropics (Patzkowsky et al., 1991; Ziegler et al., 2003), this could have further implications. DiMichele et al. (2006b) have shown that mesoxeric floras of the Early Permian tropics were growing in environments that can be interpreted as 'seasonally dry'. While conditions were certainly less extreme in the Early Permian tropics of Jambi, it could be that in such a situation of growing seasonality, pteridosperms (and other members of the gymnosperm assemblages), that were growing in better drained habitats, would have had increasing difficulty surviving the drier periods. A cormous rhizome, such as found in the extant marattialean fern genus *Angiopteris*, could have enabled them to survive the more severe dry periods by shedding their fronds and using the corm as a survival mechanism, similar to most present-day cormous plants in seasonal climates. To a certain extent, this would also explain the development of the larger pinnules, since these would not have evolved as a consequence of a general drying climate, but partially as an adaptation to a temporarily (seasonally) wetter environment.

Conclusions

The recently found material of *Macralethopteris* sheds new light on the morphology of this Permian alethopterid. Although the material from the different localities shows variability in some characteristics, this is in all likelihood due to the fact that the material stems from different populations, growing under different ecological conditions. The genus *Macralethopteris* is undoubtedly morphologically close to *Alethopteris*, but there are still enough characteristic differences to retain them as separate genera. The fronds of *M. hallei* show a morphology adapted to mesoxeric growing conditions and are found as part of an assemblage interpreted as a mesophytic flora. There is a strong possibility that *M. hallei* had a simply pinnate frond and a cormous rhizome.

3

Comia and *Rhachiphyllum* from the early Permian of Sumatra, Indonesia[3]

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Abstract

Recent expeditions to the Early Permian formations of Jambi, Sumatra, have produced material of a new species of peltasperm affinity, *Comia variformis* nov. sp., with a remarkably broad morphological range that touches on several other Permian taxonomic groups. It is found in association with material attributable to the callipterid genus *Rhachiphyllum*, in addition to *Supaia*-like material and an *Autunia* fructification, corroborating a peltasperm affinity. Palaeogeographic relationships of the morphologies found in *C. variformis* and the other material show strong relationships with North China and even the Angaran region, suggesting a migration zone running from the North China Block to the West Sumatra–West Myamar terrane.

Introduction

Early Permian climate and tropical plant ecology

Changes in climate during the Late Carboniferous to Early Permian caused a major transformation in the vegetation of the tropical lowlands. Water-dependant plant groups mostly disappeared and more drought-resistant seed fern and other gymnosperm lineages appeared and claimed an increasingly dominant role (Gastaldo et al., 1996; DiMichele and Phillips, 1996; DiMichele et al., 2001; Cleal and Thomas, 2005). Subsequently, the Early Permian saw a high diversification of these plant groups (Wang, 1996; DiMichele et al., 2005, 2006).

From the Latest Carboniferous and Early Permian onwards, associations dominated by peltasperms and other seed plants become increasingly common (Kerp, 1996, 2000; DiMichele et al., 2005, 2008). These associations are generally found in deposits belonging to, or stemming from habitats with drier conditions and better-drained soils, than found in the coal swamp environment. Evidence of seasonal drought is commonly found (DiMichele et al., 2006; Montañez et al., 2007). These changing ecological circumstances would have led to more adaptations in water-use efficiency for the vegetation, as is demonstrated by features in their morphology (for example, Krings et al., 2005), than was common in the wetter swamp or swamp margin habitats.

Much of the earliest, large-scale occurrences of these more mesoxeric seed fern/gymnosperm assemblages took place in the western part of Euramerica (Mamay and Breed, 1970; DiMichele et al., 2000, 2001, 2005). Genera belonging to the gigantopterids, the callipterids, *Comia* and species belonging to the *Protoblechnum/Compsopteris/Supaia*-complex, are found as a part of Early Permian assemblages in the USA (Texas and Utah), Mexico and Venezuela, that appear to be indicative of seasonally dry conditions (Weber, 1997; DiMichele et al., 2006; Chaney and DiMichele, 2007; Ricardo-Branco, 2008).

Compared to the Euramerican region, Cathaysia seems less affected by the changing climate. During the Late Carboniferous and Early Permian, lycopsids remain a dominant factor in the Cathaysian wetland vegetation (Ziegler, 1990; Shen, 1995), while disappearing from the Euramerican tropics. Although similar seed fern and gymnosperm assemblages are found in the Early Permian of Cathaysia and Euramerica, the Texas and Utah floras show a closer resemblance (on a generic level) to the Middle Permian Cathaysian floras than to the European palaeofloras of the Early Permian (Shen, 1995; DiMichele et al., 2005; Hilton and Cleal, 2007). This similarity is difficult to align with the heterogeneity of the Early Permian tropical climate, where ever-wet conditions persisted in part of the Cathaysian region, while the western Euramerican part of the tropical zone became increasingly arid (Ziegler, 1990; Patzkowsky et al., 1991; Ziegler et al., 2003; Hilton and Cleal, 2007).

The Jambi flora

The so-called Jambi flora is a compression/impression flora of the Early Permian Mengkarang Formation from the province of Jambi in Sumatra, Indonesia. It was first elaborately described in 1935 by Jongmans and Gothan and interpreted as a Late Carboniferous Euramerican flora with Cathaysian elements. In a reinvestigation of the existing collection by Van Waveren et al. (2007), the material was reinterpreted as an Early Permian Cathaysia-type flora, an interpretation that had already been suggested by Posthumus (1927), albeit on different grounds. It contains Euramerican elements, and is particularly similar to North and Northwest Chinese floras in species composition. Gondwanan species are entirely absent (Van Waveren et al., 2007).

The composition of the floral assemblages of the Mengkarang Formation (Van Waveren et al., 2005; Booi et al., 2008) suggests a division into (at least) two separate associations that are distinct in both species composition and ecology. The first is a typical Late Carboniferous-type swamp flora, containing Lepidodendrales, pecopterids, sphenopsids and *Cordaites*. The second is a flora that is dominated by a variety of seed ferns and other gymnosperms, such as *Macralethopteris*, callipterids, *Sphenopteris*, taeniopterids and gigantopterids, next to rarer, more hydrophilous elements such as sphenopsids and pecopterid ferns. This latter assemblage is interpreted as a more mesic flora occurring in slightly betterdrained soils, and as representing plants that are occasionally washed in from higher lying ground (Van Waveren et al., 2005; Booi et al., 2008). Although very different in species composition, the associations are broadly comparable in both diversity and preservation of the fossils suggesting a taphonomically comparable amount of transport. The two assemblages alternate in the formation and thus are interpreted as two distinct floras that inhabited neighbouring environments.

In the older collections from the Mengkarang Formation no material of callipterids sensu stricto was found. In the expeditions to the area in 2004 and 2006, a large amount of new fossil material of a peltasperm (comioid and callipterid) affinity was found in association with a floral assemblage of the latter, mesic type. This material exhibits a very diverse morphology. The early Early Permian (Asselian–Sakmarian) age for the Mengkarang formation (see Materials) that contains the callipterid material places it close in age to the first Euramerican peltasperms (*Autunia*, *Rhachiphyllum*) of the latest Carboniferous (Kerp, 1988, 1996). The (probable) location of the Jambi strata is as the southeastern part of the Indochina block (Barber et al., 2005) and the palaeoclimate in the Cathaysian region was different from the increasingly drier circumstances prevailing in the Euramerican tropics (Patzkowsky et al., 1991).

Next to the genera *Autunia*, *Rhachiphyllum* and *Peltaspermum*, the current notion of many authors (Kerp, 1996; Wang, 1997; Naugolnykh, 1999; DiMichele et al., 2005; Krings et al.,

2005) is that several other large-leaved Late Palaeozoic morphogenera, like *Protoblechnum*, *Compsopteris*, *Comia*, *Glenopteris* and *Supaia*, can also be tentatively included in the peltasperms. This is based both on the repeated association of these leaf genera with peltasperm fructifications such as *Autunia* and *Sandrewia* and on the similarity of the venation patterns of these genera to callipterid venation.

We will give a detailed description of the new material, followed by a comparison with morphologically related groups and species. The aim is to get a clearer view of the general morphology of the material, its relationship with other genera and the factors that shaped its morphology. Subsequently, the possible implications for the palaeoecology of the Jambi flora will be discussed. Finally, we will look into the relationships of our fossil material with other species and their bearing on the palaeogeography of the region.

Materials

The material described here is from the Early Permian Mengkarang Formation of Middle Sumatra. All localities are situated in the vicinity of the town of Bangko, Jambi province (Fig. 3.1). The Mengkarang formation was deposited in a back-arc basin subject to volcanic activity and occasional marine incursions (Booi et al., 2008). Deposition took place in a

Figure 3.1: Map of the island Sumatra, Indonesia. The small town of Bangko indicated, in the neighbourhood of which all the localities are situated.

delta plain setting, with volcanic deposits interfingering with their alluvially reworked products (Tobler, 1922, 1923, Zwierzycki, 1935; Van Waveren et al., 2005). The formation consists of several continuous outcrops, containing marine, terrestrial and volcanic deposits. Marine- and delta plain deposits characterize the lower part of the formation, while braided river and fan delta deposits make up the upper part (Booi et al., 2008).

A single limestone layer is found in the Mengkarang Formation. The fusulinids found in this limestone were considered by Thompson (1936) as Early Permian and by Vachard (1989) to be indicative of the Late Asselian (earliest Permian). A recent analysis, based on material collected in 2004, determined that the fusulinids of the limestones are indicative of a Sakmarian age (Ueno et al., 2007).

The material treated here was collected at two different locations in the Mengkarang Formation, situated about 2 km apart (Fig. 3.2). One is situated along the small Ketiduran Siamang stream, the other lies on the bank of the Merangin River. The majority of the material comes from the first locality. Both locations are inundated for most of the year and only accessible at the height of the dry season. At both exposures, the fossils are found exclusively in one particular layer, about 15 cm thick, consisting of silty claystone. The sediment matrix at the Ketiduran Siamang locality has a lower fine organic fraction than that

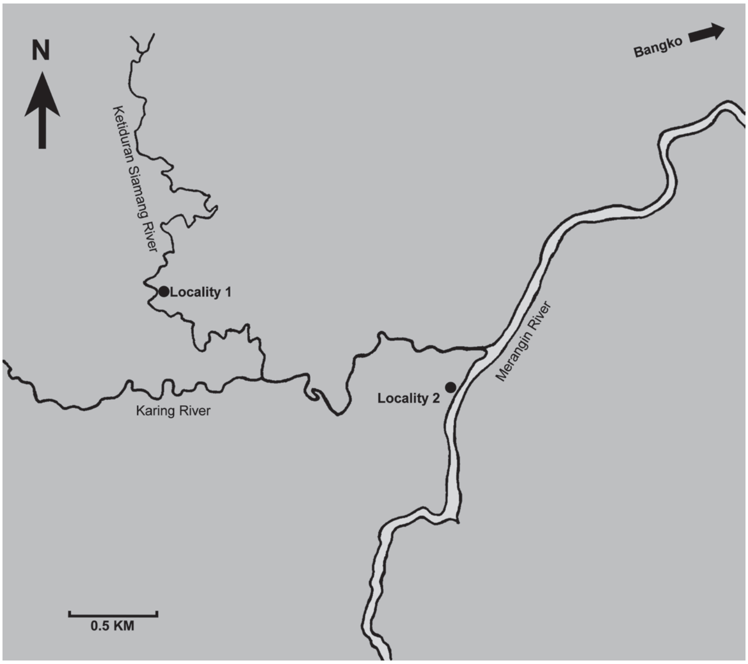

Figure 3.2: Map of the two localities where the material was found. Locality 1 along the Ketiduran Siamang River, locality 2 along the Merangin River.

of the Merangin locality and occasionally contains semi-rounded pebbles. No sedimentary structures are present and the amount of fossil plant material is high. The plant fossils occur both as impressions and as compressions and show very little signs of transport. Deposition possibly took place during a short-distance mass flow event (Van Waveren et al., 2005), initiated by a rainstorm that would also explain the high concentration of fossil leaf material.

Even though reasonably well-preserved compression leaf fossils are present, no cuticle material could be recovered.

Systematic part[4]

About 60 specimens of broadly peltaspermean affinity were found in the two localities. The fossil material shows a remarkably high variation in gross morphology. The material will first be described in general terms before being divided into three groups that will be discussed separately.

General morphological observations

The frond was at least once pinnate, possibly bipinnate. The pinnae are more than 100 mm long (only fragments of complete pinnae are preserved). The main rachis is approximately 3.4 mm in width (2.4– (3.4)–4.5), although specimens with a rachis of almost 10 mm width occur. The angle of the pinnules with the rachis is, on average, 59° (55–(59)–63), but quite variable, ranging from 30–40° to 90° in some specimens. Distance between pinnules at their broadest point (acroscopic margin to basiscopic margin) is 4.3 mm (3.5–(4.3)–5.2) and at their base (midvein to midvein) is 18 mm (17–(18)–19).

Pinnule length averages around 47 mm (44–(47)–50). However, very few pinnules were preserved complete and only some of the smaller pinnules could be measured in their entire length. The actual average pinnule length is probably much higher. The longest (almost complete) pinnule found measured 79 mm. Pinnule width is less variable, about 13 mm (12–(13)–14).

The midvein of the pinnules is 0.81 mm (0.77–(0.81)–0.86) in width, ending about 5.5 mm from the apex of the pinnule. The lateral veins depart from the midvein at about 22° (19–(22)–26) and the angle of the lateral vein at the margin is 67° (61–(67)–73), at a density of 19 veins per cm leaf margin (18–(19)–21).

Several veins in lobed pinnae arise from the base of a slightly more prominent lateral vein running through the middle of the lobe, making an angle with this ‘lobe vein’ of about 44° (36–(44)–52). The ‘lobe vein’ can be quite prominent, in some cases causing the pinna

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[4] Measurements are mm, unless otherwise indicated; figures in parentheses in indicate the average value and the values of the range of the character (as 95 % confidence interval).

lamina to develop a plicate character (Plate 3.3: 1). However, the venation pattern is much simpler in a few specimens with entiremargined pinnules and does not contain these 'lobe veins'. These specimens will be treated separately as Group 2.

Crenation or (deeply incised) lobing of the pinna margin is common throughout the material, but in most specimens the incisions in the margins are never deeper than about 1/3 of the width of the lamina (measured from the midvein to the margin). However, in a handful of specimens the lobes have far deeper incisions, up to 1/2–3/4 of the lamina, resulting in a pinnulate margin. A single specimen belonging to this group (Plate 3.5: 1) also shows an apical bifurcation of the rachis as well as intercalary pinnules. Based on these characteristics, this deeply incised material will be treated separately from the rest of the specimens as Group 3.

Group 1

This group comprises the large majority of the material and consists of pinna fragments with elongate pinnules that have entire to undulate and (subdentately) crenate margins. Crenate margins are found in about 50% of all specimens and 80% have an undulating to crenate pinnule margin. Some of the specimens are apical fragments (Plate 3.1: 3, Plate 3.4: 1; Fig. 3.3A,B,D), but the majority of the material consists of more basal material, as indicated by a thicker rachis (Plate 3.1: 1, Plate 3.2: 1–2, Plate 3.3: 1,2,4). The lowermost pinnules of the apical fragments have a length/width ratio of about 4.5:1; in the more basal specimens, it is about 4.8:1. Pinnules are usually up to 70 mm in length.

Pinnae with entire to moderately undulating margins usually have sessile attachment to the rachis with broadly attached to connate pinnules at the base (Plate 3.1: 3, Plate 3.4: 1; Fig. 3.3A,B,C,D,E). At the base, these pinnules are slightly contracted acroscopically and sometimes have an auriculate lobe on the decurrently sloping basiscopic margin (Fig. 3.3C,D — indicated with arrow).

In these specimens the midvein is often found to be placed asymmetrically, nearer the acroscopic side at about 1/3 of the width of the pinnule (Plate 3.1: 3,Plate 3.4: 1; Fig. 3.3A,B,D).

More strongly undulating to crenate margins are associated with pinnae that are elongate–lanceolate in shape and broadly to narrowly attached to the rachis (Plate 3.1: 1, Plate 3.2: 1,1a; Fig. 3.3F,G), but generally not connected at the base.

Pinnae with a subdentate leaf margin are broadly lanceolate to subovate in shape and invariably strongly attenuate near the base, although the lamina always reaches the rachis. The apex of the pinnule is sometimes acuminately elongated, with reduced dentations of the margin (Plate 3.2: 2, Plate 3.3: 1,2,4; Fig. 3.3H). These pinnae are associated with a broad rachis, reaching a width of up to almost 10 mm (Plate 3.3: 4).

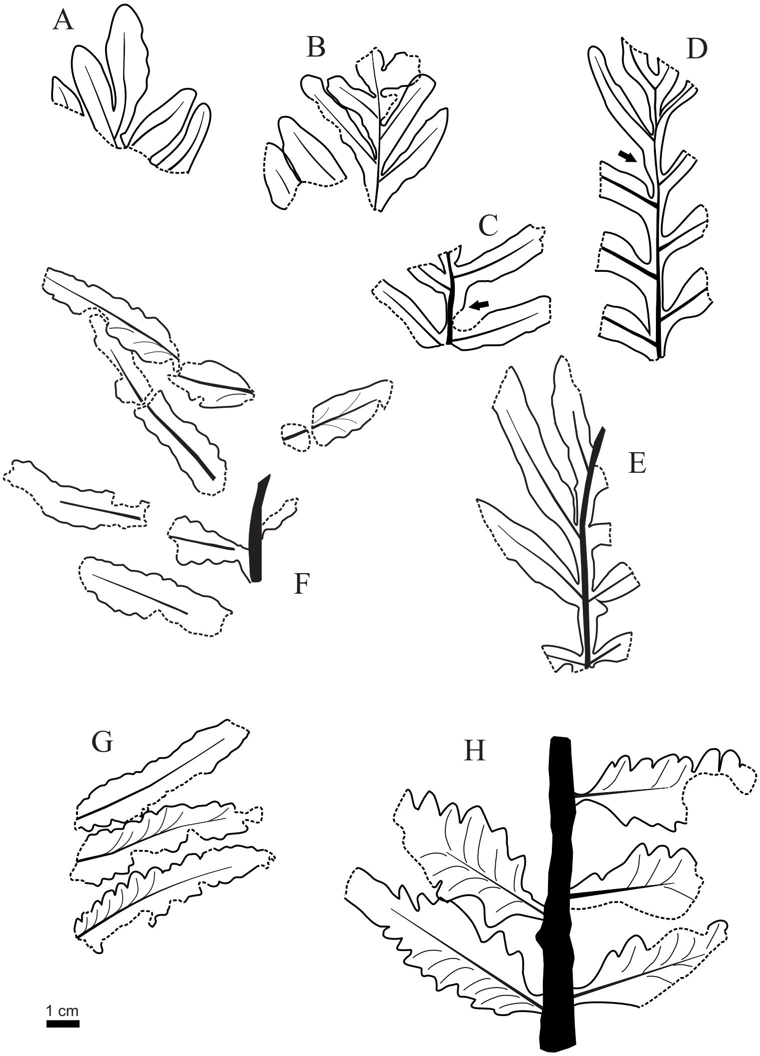

Figure 3.3: Outline drawings for several specimens from Group 1 (*Comia variformis*).

Lateral venation is usually evenly spaced, and consists of fasciculate groups of veins, with one central vein that is more prominent than the surrounding veins of that fascicle. Fascicles are placed at regular intervals and all veins branching from a single fascicle run broadly parallel to each other. Fasciculation of lateral veins becomes more pronounced and regular with an increasing amount of marginal lobing, resulting in one prominent, clear and often sunken 'midvein' corresponding to every lobe (Fig. 3.4). Fasciculated bundles of veins or fascicles, consisting of about 12 (11–(12)–14) veins alternate with small groups of interfascicular (non-fasciculated veins), usually about 1–2.

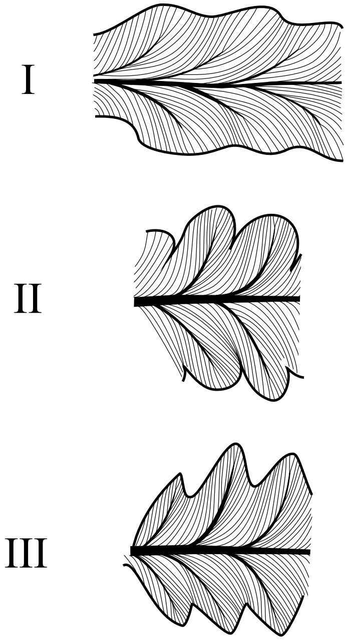

Figure 3.4: Semischematic drawings of venation patterns found in the material of Group 1 (*Comia variformis*).

Morphological diversity of the material of Group 1

The large variation in several characters in this group of specimens could lead to the conclusion that they represent more than one species. However, all the specimens are found in a single layer in both localities, and the same extent of morphological variation is present in both assemblages. Moreover, for all the pluriform characters intermediary forms are present. The patterns of undulation to (subdentate) lobing of the margin show a gradual transition, ranging from entiremargined pinnules to undulating, to fully crenate and subdentate pinnules (for example, Plate 3.2: 1,1a,2; Fig. 3.3G). Morphology of the pinnule base also shows a gradual range of variation from broadly attached and connate to increasingly attenuate. Additionally, the material with entire-margined pinnules and those with subdentate margins are found in both localities within the same sedimentary bed. Throughout this material, the venation consists of fascicular bundles alternating with interfasciculate veins.

It is therefore unlikely that the material represents several species. Due to its fragmentary nature, it is difficult to determine whether the morphological variation existed within a single frond [as has previously been seen in other seed ferns (see Rees and Cleal, 1993)], or was produced by several fronds (for example, in different stages of growth). We conclude that there is enough morphological coherence to interpret the material of Group 1 as stemming from a single species, and it will be interpreted and reconstructed as such.

Reconstruction of the frond for Group 1

The imparipinnately arranged, entire-margined apices (Plate 3.1: 3, Plate 3.4: 1) are interpreted as the apex of the frond. These are succeeded by the pinnules with slightly more undulate margins (Plate 3.2: 1,1a), followed by those with crenate margins (Plate I, 1). The large, lanceolate-ovate pinnules (Plate 3.2: 2, Plate 3.3: 1,2,4) with subdentate margin have been found attached to the broadest rachis and are therefore interpreted as the most basal part of the frond.

Generic attribution

The general characters of the material include pinnate fronds, consisting of large and broad pinnae with entire to crenate and subdentate margins, and fasciculate lateral venation with interfasciculary veins. This combination of characters allows attribution of this material to the Permian genus *Comia* (Zalessky, 1934; Raskassova, 1963). [For comparison with the morphologically similar (fern)genera *Fascipteris* and *Validopteris*, see Huang, 1977, table 3 and Mamay et al., 2009, table 2, (translation with revised terminology)]. Below we offer several comparisons with other *Comia* species that have the closest morphological resemblance to the present material.

Comparisons for Group 1 (Table 3.1)

There is a strong similarity between this material and *Comia kuqaensis* Wu (1985) from the Late Permian of Kuqa, southern Xinjiang (Northwest China), specifically with the specimens with distinctly crenate margined pinnules, although in *C. kuqaensis* the pinnules appear more deeply lobed. The general venation architecture is also comparable. However, the tendency for the basal lobes in *C. kuqaensis* to overlap with the main rachis is a feature not seen in the material from Group 1, where crenate pinnules have a strongly attenuate pinnule base.

There is a similarity between the present material and *Comia tarimensis* Wu (1985) from the Late Permian of Kuqa, southern Xinjiang (Northwest China), especially with the specimens with subdentate pinnule margins. The venation architecture is also comparable. However, the dentations of the pinnule margins in *C. tarimensis* are slanted towards the pinnule apex making them more serrate than dentate, that is not seen in the present material. Additionally, the pinnule base in *C. tarimensis* appears more broadly attached than is seen in the subdentate pinnules of the material from Group 1.

There is some similarity in general pinnule shape between the present material and *Callipteris*? *laceratifolia* Halle (as illustrated in 'Gu and Zhi', 1974, plate 93, figs. 1, 2). However, the strongly elongated lobes, the small lobing at the pinnule apex and, in particular, the absence of both a central fasciculate 'midvein' (in the lobes) and interfasciculate veins in *C.*? *laceratifolia*, are clear differences with the material of Group 1. Moreover, overall

Table 3.1: Comparison of morphological characters between the material of *Comia variformis* and several selected morphologically related species.

	Comia kuqaensis Wu Shao-Zu, 1985	*Comia tarimensis* Wu Shao-Zu, 1985	*Comia dentifolia* Rasskasova, 1963
Frond appearance	bipinnate	bipinnate	large, simply pinnate
Frond length			
Frond width	180	140	
Apex appearance			
Apex bifurcation present			
Primary rachis appearance			thick
Rachis width		3-4	
Ultimate pinna width			
Ultimate pinna appearance			
Ultimate rachis width			
Pinnule appearance		lanceolate	large, linear to linear-lanceolate, nearly flat
Pinnule attachment	contracted	decurrent	connivent
Pinnule arrangement			close to each other
Distance between pinnules at middle			
Distance between pinnules at base			
Pinnule angle	about 65°-70°	40°-50°	60°-90°
Pinnule length		-	
Pinnule width at broadest point		-	
Terminal pinnule appearance			
Margin	incised-lobed	lobed	cut into more or less large oval-triangular lobes/teeth with acuminate, obliquely forward directed apices

Comia dentata Radczenko forma ***multinervia*** Fefilova, 1973	*Callipteris lobulata* Fefilova, 1973	*Comia variformis* nov. sp.
probably broadly lanceolate, at least once pinnate	-	large, at least simple pinnate
>148	>102	>91
> 160	>67	-
-	-	-
no	no	no
broad, coarsely striate	coarsely striate	very broad basally, longitudinally striate, tapering towards apex
12 (±0.76)	1.6 (±0.53)	3.40 (±2.48)
-	-	-
-	-	-
-	-	-
lanceolate	lanceolate	broadly lanceolate to lanceolate-ovate, apex sometimes slightly elongated, ligulate
connected, strongly constricted at apical side, broadly decurrent on distal side, forming ‘lobe’	connected, strongly constricted at apical side, broadly decurrent on distal side, forming small lobe	broadly attached apically to strongly attenuate basally
subopposite	alternating	moderately distant, subopposite
-	-	4.4 (±2.8)
-	-	18 (±4.1)
60-70°	about 80°	58º (±15)
132	27 (±6.3)	> 45
26 (±2.3)	11 (±1.3)	13 (±4.8)
-	-	-
crenate	lobed to slightly dentate	entire to crenate to subdentate

Table 3.1: Comparison of morphological characters between the material of *Comia variformis* and several selected morphologically related species. (*continued*)

	Comia kuqaensis Wu Shao-Zu, 1985	*Comia tarimensis* Wu Shao-Zu, 1985	*Comia dentifolia* Rasskasova, 1963
Midvein appearance			thick, weakly percurrent, straight, persists almost to pinnule apex
Midvein width			
Distance midvein-top			
Lateral vein appearance			Alternating at pinnule base, forming gently arching bundles of simple, nearly parallel veins, corresponding to lobes/teeth of margin; interfascicular veins once bifurcate, ending in notches between lobes/teeth, parallel to fascicles
Number of veins per fascicle	8-12	10-14	4-7
Number of interfascicular veins	2-3	1-2	2-3
Lateral vein arrangement/density (N/cm leaf margin)	-	-	
Lateral vein angle at midvein			50
Lateral vein angle at margin			
Lateral vein angle at 'lobevein'			
Lateral vein bifurcation			
Occurrence			Ambarskaya Formation, latest Permian

Comia dentata Radczenko forma ***multinervia*** Fefilova, 1973	*Callipteris lobulata* Fefilova, 1973	*Comia variformis* nov. sp.
strong, slightly sunken	clear, straight	moderately clear, slender, straight to curving with pinnule
1.7 (±0.11)	0.41 (±0.17)	0.80 (±0.20)
-		-
clear, curving, forming fasciculated bundles within crenated lobes	very clear, curving	widely spaced, curving strongly towards margin, forming bundles fasciculated at base
		12 (±2.4)
		1-2
14 (±1.8)	-	19 (±3.5)
acute	acute	22º (±10)
obtuse	obtuse	69º (±16)
very acute	-	44° (±10)
-	frequent, occuring in middle third of pinnule lobe	infrequent
Cis-Urals, Russia, early Late Permian	Cis-Urals, Russia, early Late Permian	Mengkarang Formation, Indonesia, Earliest Permian

morphology of the material of ‘Gu & Zhi’, both of the pinnule and the pinna, is far more reminiscent of *Psygmophyllum* (Schimper, 1870), than it is of callipterid morphology.

Comia dentifolia Raskassova (1963) from the latest Permian (Ambarskaya Formation) of Angara has some striking similarities with the present material, particularly in the dentately lobed leaf margin. However, the leaf margin appears to be serrate, with apically slanted teeth in one of the figured specimens (Raskassova, 1963, plate 1, fig. 1), a characteristic that is not seen in this group.

The material described by Fefilova (1973) from the Permian of the Fore-Urals (or Cis-Urals) as *Comia dentata* Radczenko f. *multinervia* Fefilova also shows similarities to the material of Group 1. However, the general shape of the pinnules is linear-lanceolate, while in this group they are far more ovate and always attenuate. In contrast, they are broadly connected at base in the material of Fefilova. When comparing the present material with the Permian *Callipteris lobulata* Fefilova, 1973, there are strong similarities in the subacute lobing of the margin and the attenuate leaf bases of the pinnules. However, the central ‘lobe vein’ in the specimens from Group 1 is far more prominent than in *C. lobulata* and the lateral venation leaves the midvein under a more acute angle.

There is a similarity between the present material and the Late Carboniferous and Permian Angaran species *Odontopteris rossica* Zalessky (1927), both in the general shape of the pinnae and in the shape of the lobed margin. However, pinnae of *O. rossica* are both more deeply incised and more irregular than seen in the material of Group 1. In addition, although ultimate venation appears fasciculated in *O. rossica*, no clear interfascicular veins can be seen in the specimens as depicted by Zalessky (1927, plate XLIII, fig. 1,1a) and the central vein in a lobe is also less pronounced.

Although similar morphologies to the material of Group 1 can be found among several species of *Comia* and morphologically similar genera, no species could be found that matches the characteristics of our material or its morphological variation. We therefore will describe it as a new species within the genus *Comia*.

Specific diagnosis

Comia variformis Booi nov. sp., Plate 3.1: 1–3, Plate 3.2: 1,1a,2, Plate 3.3: 1,2,4, Plate 3.4: 1. Fronds large, at least once pinnate; ultimate pinnae more than 100 mm in length; ultimate rachis broad, with distinct longitudinal striations, gradually tapering towards apex, simple; pinnule arrangement opposite to alternate, at an oblique angle with the rachis, moderately broadly spaced, not overlapping.

Pinnules relatively large, lanceolate to broadly lanceolate, spatulate in apical part of frond, apex rounded to obtuse; apical lanceolate pinnules broadly attached to rachis, usually connected; more basal broadly lanceolate pinnules attenuate at base; margin entire in apical parts to undulating to distinctly crenate to subdentate in basal parts; pinnules getting smaller towards the apex, apex consisting of several imparipinnately arranged linear-spatulate pinnules with a single apical enlarged pinnule; midvein clear, slender, slightly sunken beneath the plane of the lamina, almost reaching the apex.

Lateral veins broadly spaced, arising from midvein at an acute angle and gradually curving outwards towards margin, which they reach at an obtuse angle; forming fascicles with about 11 veins and single central more prominent fasciculate vein. Fascicles alternate with 1–2 nterfasciculary veins.

Etymology: named variformis for its large morphological variability (Latin root).
Type locality: small outcrop along the Ketiduran Siamang stream. (Longitude: S: 02°-09′-10.9″/latitude: E: 102°-08′-26.3″, locality 1 in Fig. 3.2).
Type stratum: Mengkarang Formation.
Type material: holotype: Nationaal Natuurhistorisch Museum, Leiden (NNM), Kes2–9 (Plate 3.3: 4).
Additional material: paratypes: NNM Kes2–11; Kes2–18; MerXIII-12.
Stratigraphical range: early Early Permian (Asselian–Sakmarian).

Divergent material

Uncommonly, very slender, linear-shaped leaves are also found in the material, usually as single pinnules, but sometimes arranged as if attached to a single rachis (Plate 3.1: 2). The shape combined with the rather 'laterally compressed' look of the venation leads us to interpret them as pinnules that were not fully developed. We will include this material in the species described above as cf. *Comia variformis*.

Description of material from Group 2 (Plate 3.4: 2–3; Fig. 3.5)

Fasciculation of the lateral venation appears to be virtually or completely absent in a small number of specimens that have some similarity to the material of pinnules with entire margins from Group 1. These reach a length of at least 46 mm, but at a length/width ratio of at least 7:1. Some of these rather long, entire-margined pinnules are found attached to a broad rachis in one of the specimens (Plate 3.4: 3), indicating that these pinnules could occur at some distance from the apex.

This latter specimen in particular, in combining slender lanceolate pinnules with a clear midvein and outward curving venation, invites comparison with species belonging to the *Protoblechnum/Compsopteris/Supaia*-complex. The high length–width ratio in particular is

Table 3.2: Comparison of morphological characters between the material of *Rhachiphyllum* sp. and several selected morphologically related species.

	Autunia conferta (Sternberg) Kerp, 1988	*Rhachiphyllum schenkii* (Heyer) Kerp, 1988	*Callipteris changi* Sze, 1954
Frond appearance	bipinnate, oval, widest at middle, immature fronds pinnate	bipinnate to tripinnate, slender, lanceolate (small fronds), ovate to oval (larger fronds)	very large, bipinnate-tripinnate
Frond length	up to 800		-
Frond width			-
Apex appearance		monopodial	-
Apex bifurcation present	overtopping or dichotomous, dichotomy of 30°-45°		-
Primary rachis appearance	robust, longitudinally striate, basal part naked and thickened	robust, longitudinally striated, basal part naked	striated, somewhat scabrous
Rachis width	5-18 (basally)		very thick, up to 4 mm
Ultimate pinna width	-	-	-
Ultimate pinna appearance	subopposite to alternate, angle of 30°-60° with rachis, angle decreases near apex	suboppositely to alternately attached	distant, alternate, linear, somewhat asymmetrical, slightly longer on outer sides, 40°-60° with rachis
Ultimate rachis width			-
Pinnule appearance	usually vaulted, lamina thick, ovate, obtuse, rarely acute	variable, arcuate, oblong or prolonged, degree of lobing and prolongation decreases apically, not vaulted	oval to linear oblong, curving outward, distinctly blunt/ obtusely rounded at apex, lamina thick
Pinnule attachment	oblique to strongly decurrent, connate to non-connate, prolonged and strongly lobed to pinnatifid	oblique, deccurent	united, especially in upper parts by decurrent lamina, greatly reduced at distal side
Pinnule arrangement			alternate to subopposite
Distance between pinnules at middle			-
Distance between pinnules at base			very close to rather distant

Callipteris obese Huang, 1977	*Callipteris hongshanensis* Huang 1977	*Rhachiphyllum* sp.
at least bipinnate	large, at least bipinnate	large, at least bipinnate
-	-	-
-	-	-
-	-	overtopping asymmetrical bifurcation
-	-	yes
-	robust, thick	slender
-	-	-
-	-	-
-	inserted at acute angle	-
-	-	-
arched, obovate, apex round	lanceolate	alethopteroid
barely connected, strongly constricted on apical side, broadly decurrent on distal side	broadly attached, barely connected, slightly decurrent on distal side	broadly attached and connected
opposite to subopposite	opposite to alternate	closely spaced
reasonably broadly spaced	reasonably close, sometimes overlapping (with intercalated pinnules)	0.72 (±1.0)
-	-	-

Table 3.2: Comparison of morphological characters between the material of *Rhachiphyllum* sp. and several selected morphologically related species. (continued)

	Autunia conferta (Sternberg) Kerp, 1988	*Rhachiphyllum schenkii* (Heyer) Kerp, 1988	*Callipteris changi* Sze, 1954
Pinnule angle			perpendicular to rachis, more oblique near apex
Pinnule length	3.5-20 (at about 1/3 below apex)		-
Pinnule width at broadest point			-
Pinnule lobe length			
Pinnule lobe width			
Terminal pinnule appearance			-
Margin	straight, arcuate to crenulate (in apical regions of frond)	entire, slightly lobed (smaller fronds), distinctly lobed to pinnatifid	-
Intercalated pinnules	in two lateral furrows, covering part of rachis, apically increasing in length, increasing in width	resembling other pinnules, increasing in length apically	more rounded with somewhat contracted base, midrib little less distinct
Midvein appearance	strong, sunken, decurrent at base, arching, dividing pinnule unequally	not sunken, relatively thin, more pronounced in larger and lobed pinnules, flexuous to gently arching	sunken, distinct, decurrent and strong at base, tapering upwards
Midvein width			-
Distance midvein-top			-
Lateral vein appearance	thick, closely spaced, nearly straight to arcuate, parallel, subsidiary veins in basiscopical part	thin, widely spaced, arcuate, subsidiary veins thin, arcuate	relatively strong, especially at base, arching towards margin, some directly from rachis
Lateral vein arrangement/density (N/cm leaf margin)			-
Lateral vein angle at midvein			narrow angle, about 20°-30°
Lateral vein angle at margin			oblique

Callipteris obese Huang, 1977	*Callipteris hongshanensis* Huang 1977	*Rhachiphyllum* sp.
-	-	40º (±4.1)
35	30-35	> 70
19	12-15	21 (±2.6)
		1.14 (±0.16)
		0.58 (±0.06)
-	-	-
entire	entire	entire
-	identical to other pinnules	-
unclear	clear, slightly curved with pinnule	moderately clear, slender
-	-	-
-	-	-
unclear	clear, straight, sparse	widely spaced, curving strongly towards margin
18-22	16-18	-
-	obtuse	-
37-40°	obtuse	-

Table 3.2: Comparison of morphological characters between the material of *Rhachiphyllum* sp. and several selected morphologically related species. (continued)

	Autunia conferta (Sternberg) Kerp, 1988	*Rhachiphyllum schenkii* (Heyer) Kerp, 1988	*Callipteris changi* Sze, 1954
Lateral vein angle at 'lobevein'			-
Lateral vein bifurcation	single or once bifurcated, usually near midvein	up to 5 times (average 2-3), subsidiary up to 3 times	usual, but sometimes absent
Occurrence	Middle Europe, Moscovian (Late Carboniferous)-Sakmarian (Early Permian)	Middle Europe, Moscovian (Late Carboniferous)-Rotliegendes (Early Permian)	N China, Middle Permian-Late Permian

Callipteris obese Huang, 1977	*Callipteris hongshanensis* Huang 1977	*Rhachiphyllum* sp.
-	-	-
-	often once halfway midvein and margin	infrequent
Heilongjiang, N China, Late Permian	Heilongjiang, N China, Late Permian	Mengkarang Formation, Indonesia, Earliest Permian

reminiscent of the morphology of some species attributed to *Supaia* (for example, White, 1929; DiMichele et al., 2007, fig. 12–14). Specifically the specimen shown in Plate 3.4: 2 and Fig. 3.5A has some remarkable similarity with some of the material depicted by DiMichele et al. (2007, fig. 12) as cf. *Supaia anomala*. A similar likeness, in general frond shape, next to shape and venation of the pinnules, exists with *Iniopteris sibirica* Zalessky (1934), particularly as depicted by Huang (1977, textfig. 7).

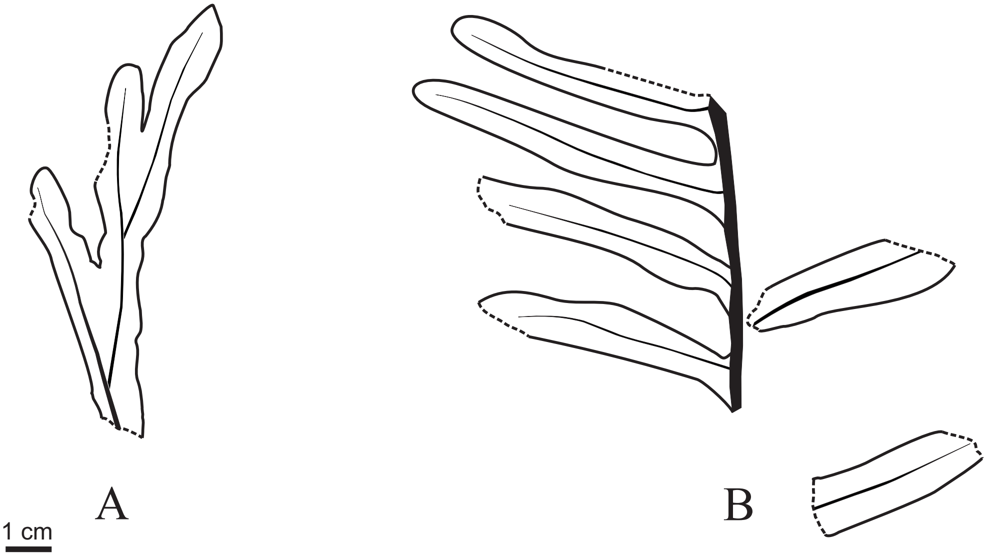

Figure 3.5: Outline drawings for several specimens from Group 2 (cf. *Supaia* sp.).

The sparseness of this particular material does not allow any further treatment at this time. We will provisionally attribute it to the genus *Supaia* as cf. *Supaia* sp., in preference to other morphologically similar genera like *Protoblechnum* or *Compsopteris*, because of its slender ribbon-like pinnules. However, we acknowledge the problematic nature of attributing a small group of specimens to one of these insufficiently defined genera.

Description of material of Group 3

This group of 4 specimens consists of leaf fragments with strongly lobed pinnules, in one specimen attached to a rachis that shows a dichotomously bifurcated apex (Plate 3.5: 1) with overtopping pinnules. The rachis is robust, striate and about 3–4 mm wide. The pinnules are 17 mm (12–(17)–22) wide on average, and are at least 50 mm (43–(50)– 56) long (no complete pinnules were found). These have a midvein of about 0.97 mm (0.73–(0.97)–1.2) wide.

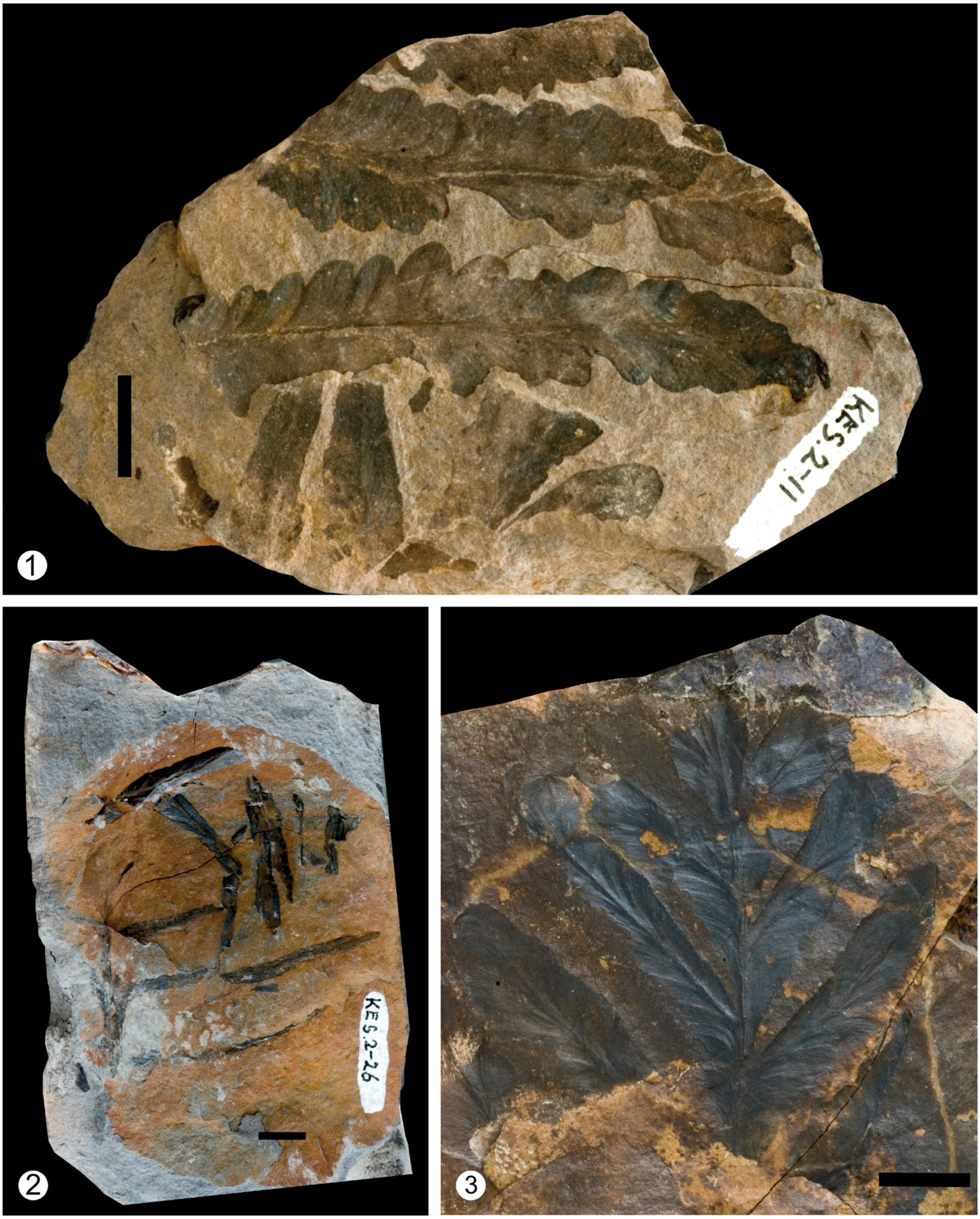

Plate 3.1: 1.*Comia variformis* (Kes2–11) paratype, Scale bar = 1 cm.2.cf. *Comia variformis* (Kes2–26). Scale bar = 1 cm.3.*Comia variformis* (MerXIII–12) paratype. Scale bar = 1 cm.

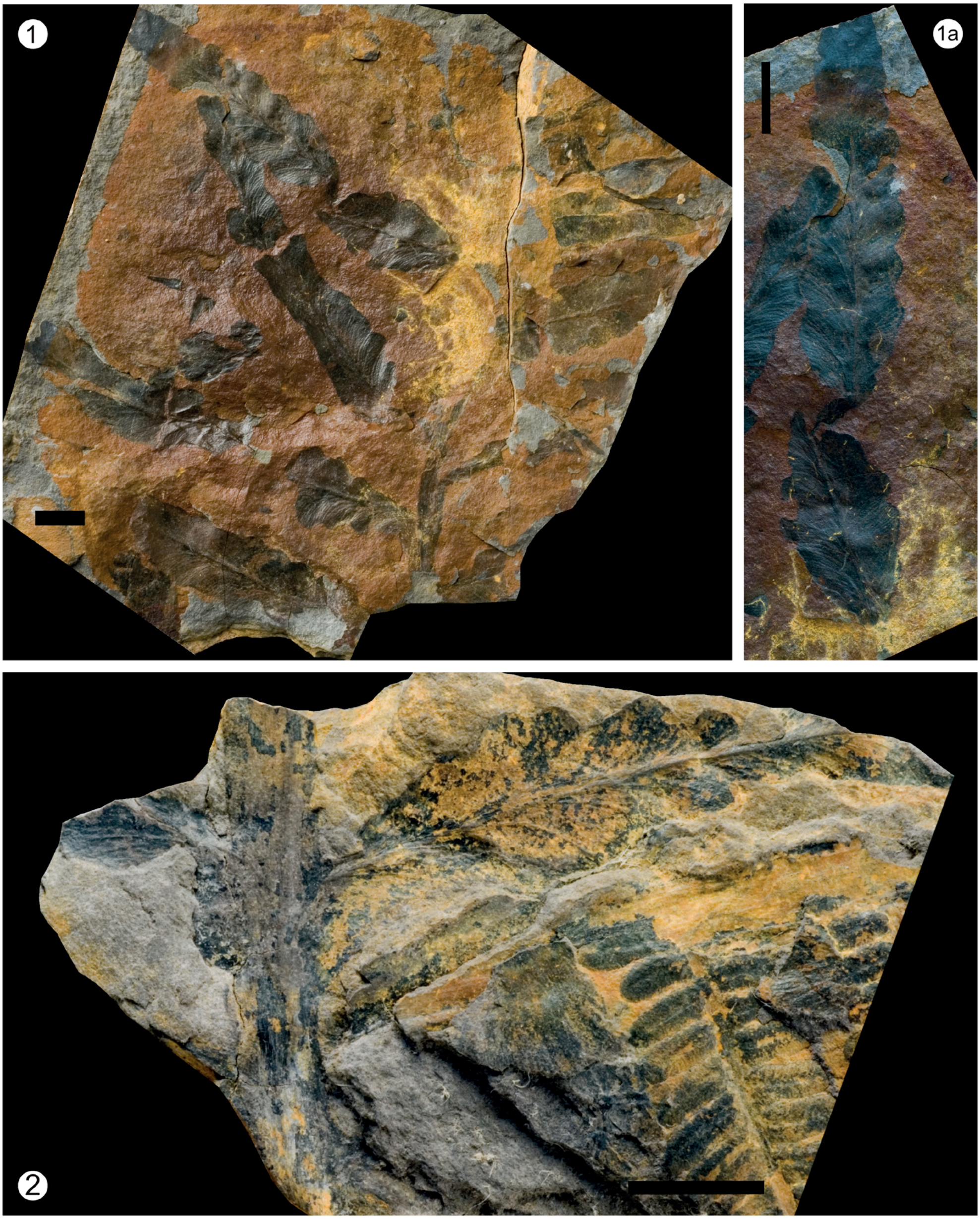

Plate 3.2: Figure 1:Comia variformis **(Kes2–18) paratype, Scale bar = 1 cm. Figure 1a:*Comia variformis* (Kes2–18) paratype, detail Scale bar = 1 cm. Figure 2:*Comia variformis* (KS06–IV–5), Scale bar = 1 cm.**

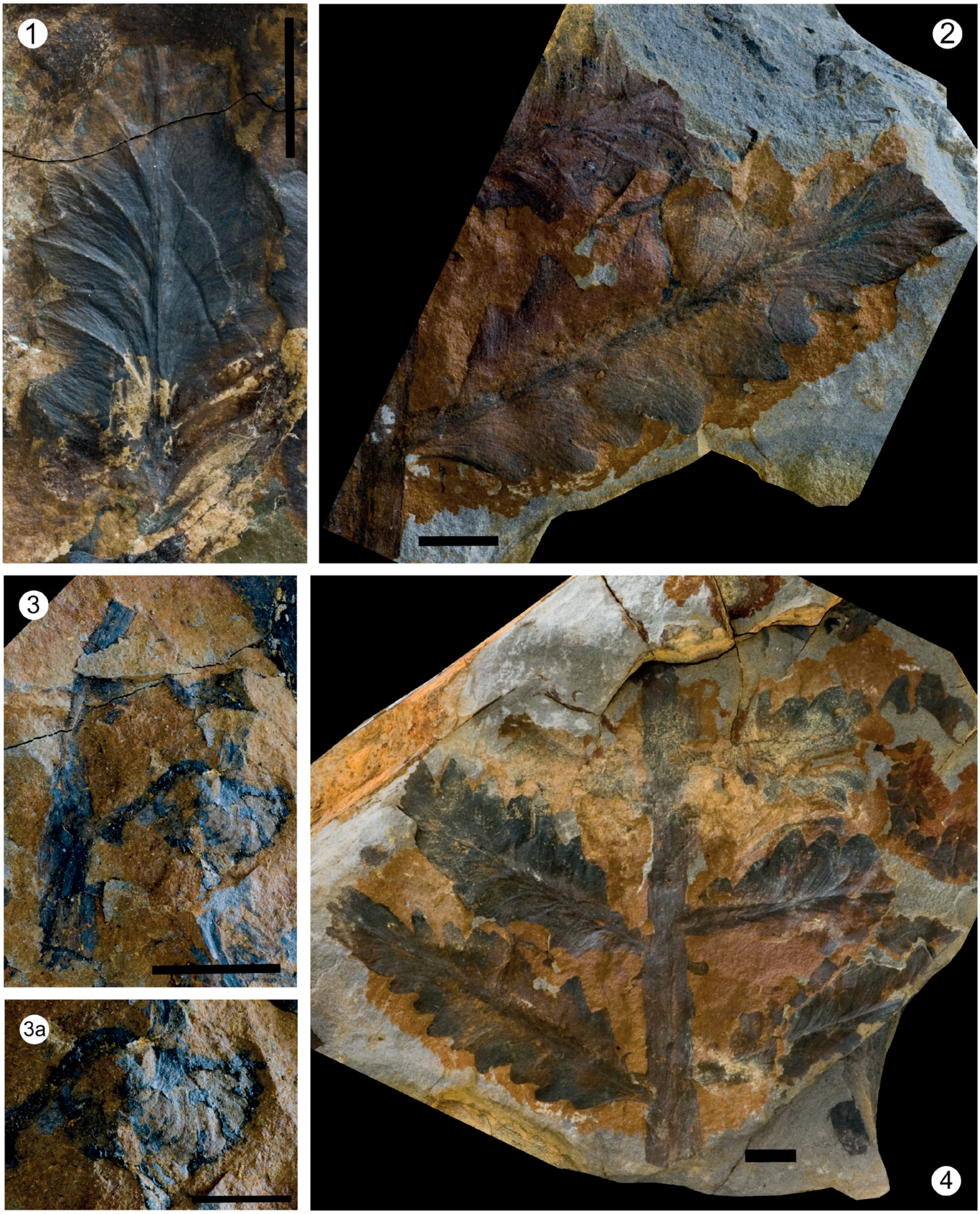

Plate 3.3: Figure 1.*Comia variformis* (MerXIII–12). Scale bar = 1 cm. Figure 2.*Comia variformis* (Kes2–9), counterpiece of Figure 4, detail Scale bar = 1 cm. Figure 3.*Autunia* sp. fructification (Kes2–5D). Scale bar = 1 cm. Figure 3a. *Autunia* sp. fructification, detail (Kes2–5D). Scale bar = 0.5 cm. Figure 4.*Comia variformis* (Kes2–9) holotype. Scale bar = 1 cm.

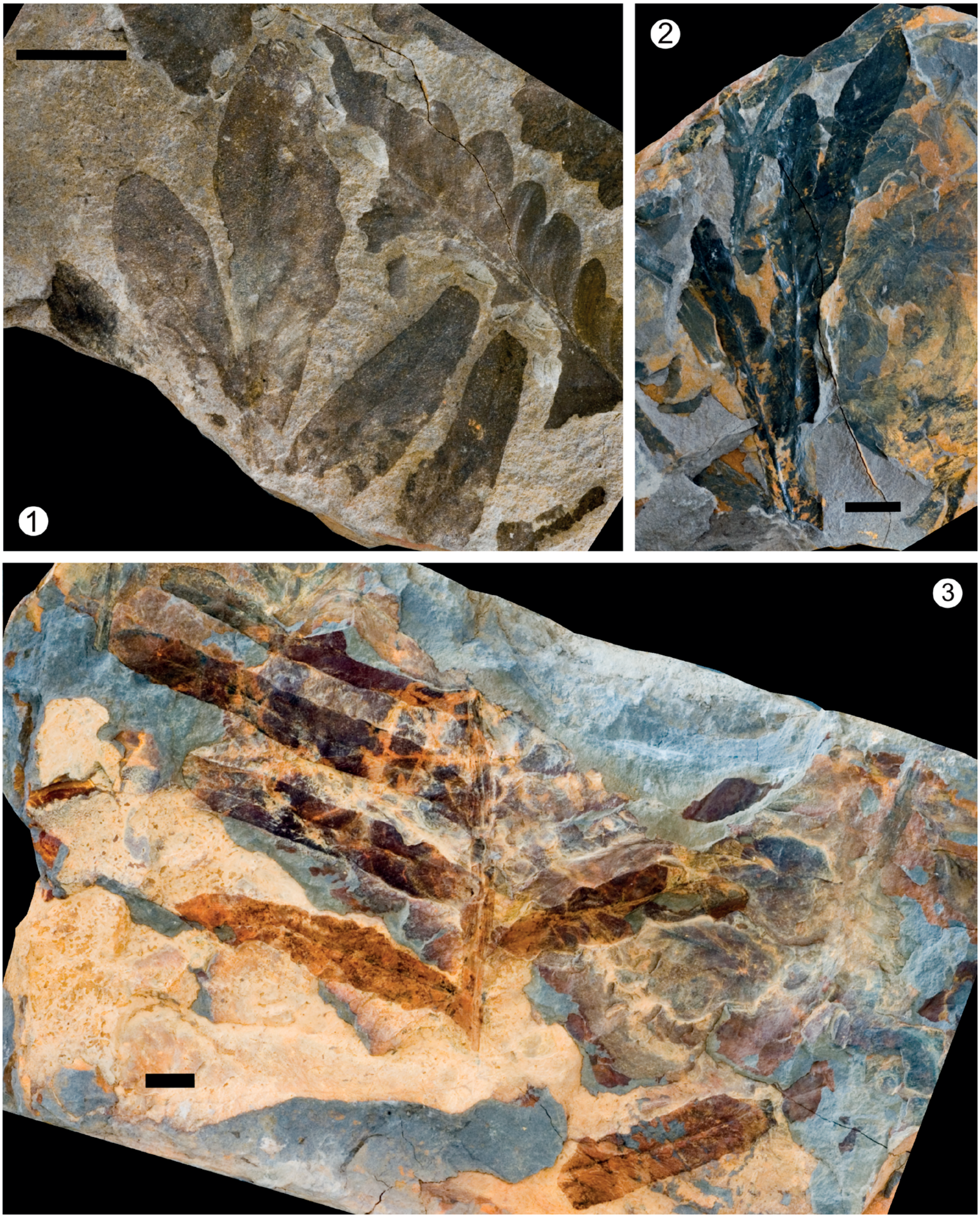

Plate 3.4: Figure 1.*Comia variformis* (Kes2–11) Scale bar = 1 cm. Figure 2.cf. *Supaia* sp. (Kes2–19) Scale bar = 1 cm (retouched). Figure 3.cf. *Supaia* sp. (Kes2–8), Scale bar = 1 cm (retouched).

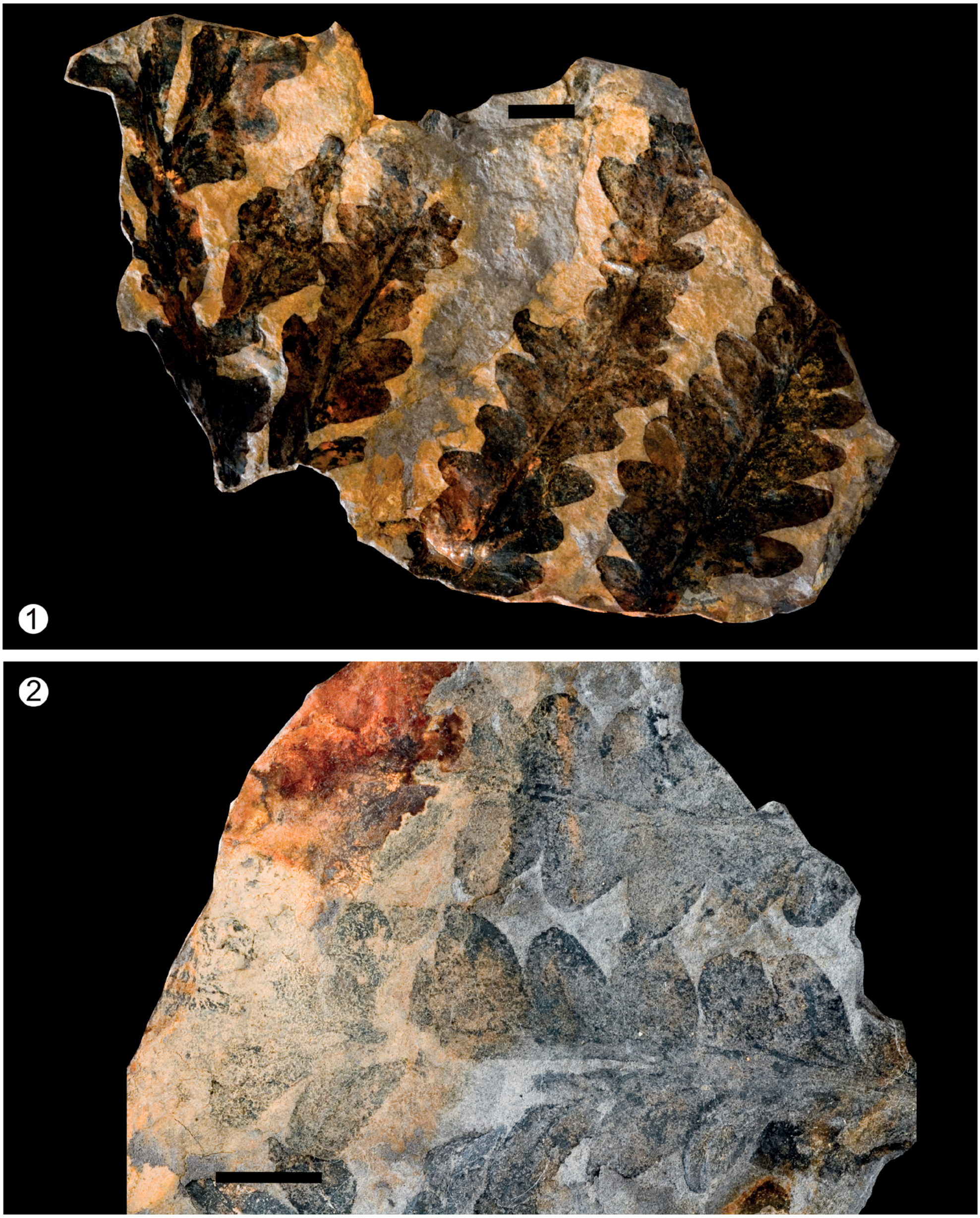

Plate 3.5: Figure 1. Rhachiphyllum sp. (Kes2–5A) Scale bar = 1 cm (retouched).Figure 2. Rhachiphyllum sp. (KS06–IV–3). Scale bar = 1 cm.

Intercalated pinnules (attached directly to the rachis) are present in one of the specimens belonging to this group (Plate 3.5: 1). These are similar in general shape and venation to the lobes of the associated pinnules (Plate 3.5: 1–2; Fig. 3.6).

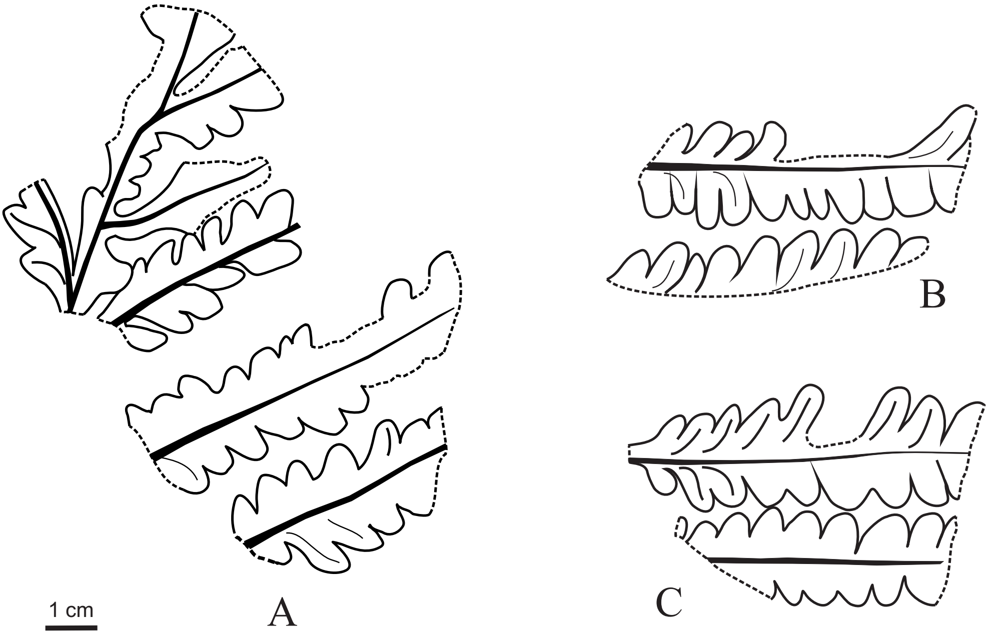

Figure 3.6: Outline drawings for several specimens from Group 3 (*Rhachiphyllum* sp.).

Venation is fairly broadly spaced, but details are only uncommonly visible. Every lobe has a prominent central vein, that arises from the midvein of the pinnae at a very acute angle (almost parallel to the midvein) and curves with the shape of the pinnule, reaching the margin at a perpendicular angle. At regular intervals smaller veins branch from this central vein at an acute angle and curve running almost parallel to the central vein.

Comparisons for Group 3 (Table 3.2)

Compared with *Autunia conferta* (Sternberg) Kerp, the material from Group 3 shows general similarities in the overall shape of the pinnules as well as with the nature of lobing present in them. However, the angle under which the lateral venation arises from the midvein in the present material is more acute (almost parallel to the midvein) than in *A. conferta*. Additionally, the pinnules of the present material appear to lack the vaulted appearance and sunken midvein that is characteristic of *A. conferta*.

Rhachiphyllum schenkii (Heyer) Kerp has similarly shaped pinnules, However, *R. schenkii* exhibits only monopodial apices, while the preserved pinna apex in this material is dichotomously bifurcate. Additionally, the intercalated pinnules of *R. schenkii* appear far more elongated than they are in the present material.

There is a distinct resemblance with both the overall shape of fronds of *Callipteris changi* Sze (1954) and the arrangement and shape of the pinnules. However, the lateral venation in the pinnules of *C. changi* appears to have both more bifurcated and denser veins than are seen in the material from Group 3.

There is similarity in general morphology between the present material (see Plate 3.5: 2) and *Callipteris obese* Huang, 1977, but the very thick rachis exhibited by that species has not been found in this morphogroup.

There is a similarity between the material of Group 3 and *Callipteris hongshanensis* Huang, 1977, in particular with the specimen depicted in Plate 3.5: 1, but the pinnules of *C. hongshanensis* appear to be more acuminate and the lateral venation shows far more bifurcations than are seen any of the present specimens.

Systematic conclusion for Group 3

Among existing callipterids no described species could be found that fits the material described as Group 3. However, the characters present in the material including the deeply lobed to pinnulate terminal branches, alethopteroid pinnae, outward curving pinnate venation and intercalated pinnules do allow the material to be ascribed to callipterids sensu stricto (Kerp 1988, Kerp and Haubold, 1988). The small number of the specimens and the relatively poor preservation of the material withhold us from describing it as a new species and we therefore will only bring it under the genus for callipterid leaf material with unknown reproductive structures as *Rhachiphyllum* sp.

Additional peltasperm material

The following specimen of a megasporophyll was found in close association with the specimens at the Ketiduran Siamang locality: *Autunia* sp., Plate 3.3: 3,3a.

Description

A single disc shaped megasporophyll, apparently peltately attached to small stalk. It consists of at least nine clearly visible ‘ribs’, arranged in a fan shaped form, about 10 mm wide and 7 mm long.

Extensive comparison with other *Autunia* species is not possible, as the fructification involved consists of just a single detached megasporophyll. The clear and pronounced ribbing is more in accordance with European species such as *A. milleryensis* (Renault) Krasser

(Krasser, 1919; Kerp, 1988), and less with those of *A. shanxienis* Wang (1997) that were found in association with *Supaia* fronds.

General discussion

Affinity and ecology of Comia variformis nov. sp.

The lateral venation of *C. variformis* is typically comioid in character, although, particularly in the character of its crenate to subdentate pinnule margins, it seems more affiliated with the species found in the Northern Cathaysian region, than with the species known from the localities the southern United States.

The most remarkable aspect of the material is the broad morphological diversity, ranging from broadly attached and connate pinnules at the top to subdentate pinnules with strongly attenuated attachment at the base.

Several authors (Asama, 1960, 1962; Laveine et al., 1977; Kerp, 1996; Naugolnykh, 1999) have mentioned an apparent trend in Late Carboniferous and Permian pteridosperms towards an increase in the size of the pinnules through fusion, leading to a general reduction in overall size of the fronds. The high variability, the large amount of semilobate to entire-margined pinnules and the large size of the pinnules found in *C. variformis* suggest that this species might be the result of a similar reduction in frond size from an unknown ancestor. In this it differs from most, if not all, other species of *Comia*. It is not uncommon for *Comia* fronds to have a non-uniform morphology in which pinnule attachment becomes more constricted basally and pinnule margins become less entire towards the base. However, *C. variformis* seems to exhibit these characteristics to a higher degree than is commonly seen in this genus.

It is difficult to indicate a particular causing factor behind this morphological variability. A mix of sun and shade leaves in the assemblage could have caused the large variation in pinnule characters, that is, the leaves were formed under different conditions of light intensity. A similar case of leaf shape dimorphism was proposed for *Scytophyllum bergeri* (Kustatscher et al., 2007) as well as for *Komlopteris nordenskioeldii* and *Ctenozamites cycadea* (Barbacka and Van Konijnenburg-Van Cittert, 1998), but substantiating data from, for example, cuticles could not be obtained for *C. variformis*. Zwieniecki et al. (2004) suggested a method of ascertaining whether morphologically different leaves could represent sun- and shade leaves of the same plant by using the gradient in leaf venation density. Unfortunately, there was insufficient detailed material available of *C. variformis* to perform such an analysis.

Strongest correlation between leaf margin morphology and climatic factors appears to be with mean annual temperature (MAT), where presence of entire-margined leaves in the vegetation increases with increasing MAT (Wolfe, 1979; Royer et al., 2005). However, this method mainly applies to the relationship between entire leaf margins vs. toothed leaf margins and does not in the first place allow application to lobed leaves. Moreover, previous data are based on leaves from dicotyledonous, woody species; the application of these results to an unrelated group such as the Palaeozoic peltasperms could be questionable.

A general plant physiological approach might be less ambiguous. Sisó et al. (2001) have shown that lobed leaves have a lower hydraulic resistance than an entire-margined leaf and that the hydraulic resistance decreases even more with more pronounced lobing of the leaf margin. They proposed that this might be a mechanism for adjusting water balance in different atmospheric conditions.

The presence of both entire-margined and lobed pinnules in *C. variformis* could be a reflection of a very heterogeneous habitat. Certainly, when compared with most other species of *Comia* found in the Amerosinian region or Angara their generally more uniform morphology within the fronds compared to the pluriform variation found in the material of *C. variformis* is striking.

Mamay et al. (2009) report the comioids from the Artinskian of north-central Texas as the earliest occurrence for the group yet. The Asselian to Sakmarian age of *Comia variformis* would make this an even earlier occurrence of this particular morphogenus.

Palaeogeographical implications

The callipterids sensu stricto (*Autunia*, *Rhachiphyllum* and *Peltaspermum*) first emerge in the fossil record in localities from Central and Western Europe in the latest Carboniferous (Kerp, 1988, 1996). They are also found in assemblages from the Early Permian of the southwestern United States (DiMichele et al., 2005) and the Middle- to Late Permian of the North China Block (Shen, 1995) and Angara (Meyen, 1982) (Fig. 3.7).

Taxa with less strongly established peltasperm affinity are less common in Europe, although both *Protoblechnum* (Broutin, 1977) and *Supaia* are found in Early Permian localities from northern Spain (Doubinger and Heyler, 1975; Gand et al., 1997; Galtier and Broutin, 2008) and the Czech Republic (Stamberg, 1997). They are well represented in the Early Permian of the United States [*Supaia*, *Glenopteris*, *Comia*, *Auritifolia* (DiMichele et al., 2005; Chaney et al., 2009; Mamay et al., 2009)], the Middle- to Late Permian of China [*Protoblechnum*, *Compsopteris*, *Supaia* (Shen, 1995)] and *Angara* [*Compsopteris* (Meyen, 1982)], Fig. 3.7. In addition, a single specimen of Comia has been found in the Middle Permian Gharif flora of Oman (Berthelin et al., 2003).

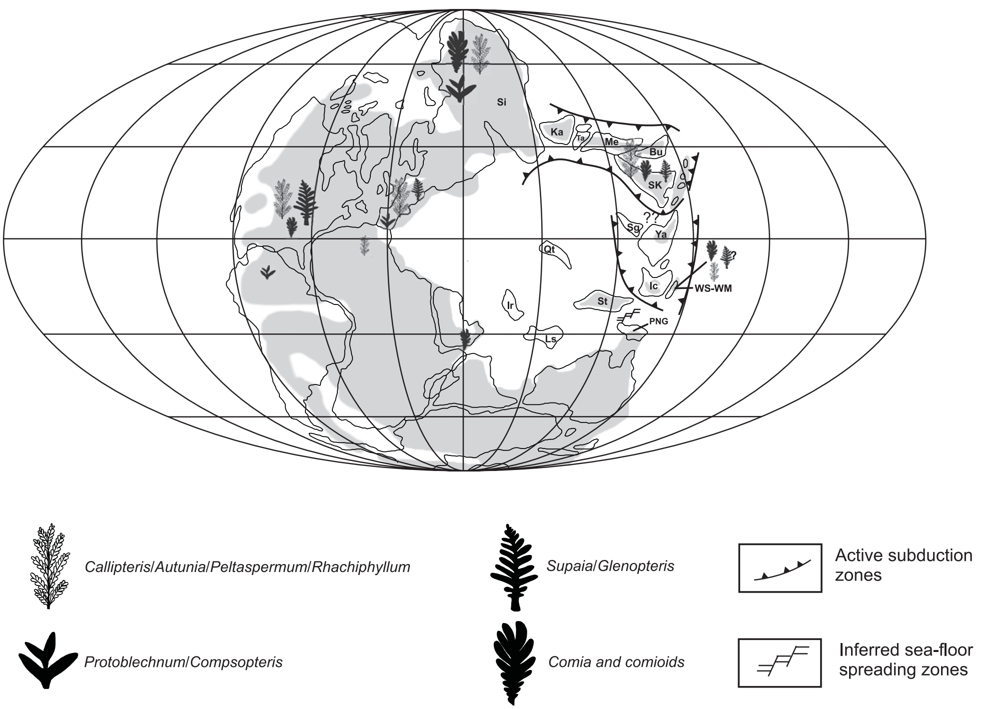

Figure 3.7: Palaeogeography of the Early Permian (modified from Ziegler et al., 1997; Barber et al., 2005; Shi, 2006). Si. Siberia; Ka. Kazakhstan; Me. Central Mongolia–Ergun; Ta. Tarim; Bu.Bureya–Jiamusi; SK. Sino–Korea (North China); Ya. Yangtze (South China); Ic. Indochina; WS–WM. West Sumatra–West Myamar; Sg. Sanpang–Garze; St. Shan–Thai (Sibumasu); PNG.Papua New Guinea; Ls. Lhasa; Qt. Qiangtang; Ir. Iran. With distributions of the callipterid plant groups (Smaller symbols indicate less than 10 occurrences, larger symbols indicate 10or more reports. Mainly based on data with coordinates submitted to GBIF (http://www.gbif.org).

Palaeogeographical reconstructions of the Late Palaeozoic eastern Palaeo-Tethys region are numerous. In the past decades, data from various disciplines have led to divergent results (McLoughlin, 2001; Li and Powell, 2001). Of late, reconstructions mainly based on biotic palaeogeographical province configurations (Shi, 2006; Hilton and Cleal, 2007), both marine and continental, are approaching a consensus view.

Current palaeogeographic and plate tectonic reconstructions of the region have the South China (Yangtze) Block grouped with Indochina Block as a single landmass (Barber et al., 2005; Metcalfe, 2006; Shi, 2006; Metcalfe and Sone, 2008), situated between the Palaeo-Tethys and the Palaeo-Pacific. The North China (Sino-Korea) Block connects to the Siberian Block in the north via a ‘bridge’ of smaller terranes (Shi, 2006). The North- and South China and Indochina blocks share a common flora usually referred to as the Cathaysia flora (Halle, 1927, Shen, 1995) or eastern Amerosinian flora (Hilton and Cleal, 2007). Wetland floras can only migrate from one (micro-)continent to the next through close connection between the wetlands (Hilton and Cleal, 2007). This implies that the Northwest China-, North China-, South China- and Indochina Blocks were situated in close proximity to each other and also located in a generally comparable climate zone, because of the similarities in the floras found on these blocks.

Papua New Guinea has an Early Permian mixed flora consisting of elements from both the Cathaysian and the Gondwana floral provinces (Jongmans, 1940, 1941; Hopping and Wagner, 1962; Rigby, 2001; Playford and Rigby, 2008), that includes some of the earliest occurrences of Gigantonoclea (Rigby, 1996, 2001). This implies a link with the Sibumasu (Shan-Thai) Block, where this genus is found in the younger late Early Permian (Kungurian-Wordian, Kon'no, 1963; Asama, 1966; Li and Shen, 1996). Following Shi (2006), we have situated Papua New Guinea with the Sibumasu Block to the south of the China- and Indochina Blocks in our reconstruction (Fig. 7).

The West Sumatra terrane, on which the Mengkarang Formation is found, is commonly placed as a landmass situated at the southern end of the Indochina block (Barber et al., 2005), possibly extending along the eastern edge of this block (Crow, 2008, pers. comm.) during the Early Permian. Comparison of shared taxa between the Early Permian Jambi flora and the Chinese floras of the same period indicate a similarity with North China, and an even stronger similarity with the floras of Northwest China (Van Waveren et al., 2007). The affiliation of the Jambi flora with floras found in North- and Northwest China suggests the presence of a northerly migration zone connecting the West Sumatra–West Myamar terrane with these continents. Migration of floral elements by a southerly route seems far less likely, because the Gondwanan elements that are present in the Early Permian flora of Papua New Guinea have not been found on West Sumatra–West Myamar.

From the comparisons above it can be concluded that *Comia variformis* is, in its morphology, unmistakably most related to Cathaysian species of *Comia*. In the Cathaysian region, species of *Comia* have been found only on the North China Block (Shen, 1995). This strengthens the already established 'North- and Northwest China-character' of the Jambi flora (Van Waveren et al., 2007). Another aspect of *C. variformis* is that, where the lower pinnules are concerned (subdentate, lanceolate-ovate pinnules), some of the most relevant, morphologically comparable species are found in the Angaran flora province. Angaran influences in the Cathaysia floras are not unique, since several mixed Cathaysian-Angaran floras are found, particularly on the North China block (Naugolnykh, 2000; Sun, 2006).

The presence of material belonging to *Autunia*, *Rhachiphyllum* and cf. *Supaia* further enhances the connection with the Permian floras of the North China block, since specimens from sensu stricto peltasperms in the Cathaysian region are known exclusively from North China.

There is the possibility of convergence in *Comia variformis* with the morphologies found in the Angaran species. Since all these taxa presumably originally developed from the same pan-palaeotropical ever-wet flora, convergent trends are likely. However, the high northern latitude at which the Angara floras are found (Fig. 3.7) indicates that ecological circumstances would have differed and suggests a subtropical to temperate climate. On the other hand, the waning or absence of a boreal northern icecap (Beauchamp, 1994) during the Middle Permian might have had a significant influence on the distribution of the climate zones in the northern hemisphere.

Although convergent trends cannot be excluded completely, the most parsimonious solution is the presence of a (temporary) Early Permian migration zone connecting the West Sumatra terrane to parts of the North China Block. It is not known if this zone crossed the South China Block, because of the absence of a plant fossil record for the earliest Permian for South China (Shen,1995). During the Early Permian, migration between the North- and South China Block would have been hampered by the presence of a sea barrier, although there is the possibility of the presence of a shelf sea between the North- and South China Blocks (Shi, 2006). Shi (2006) mentions the presence of Cathaysian marine micropalaeontological elements in his Sino-Mongolian Japanese province for the Middle Permian. The palaeogeographical vicinity of these two provinces and the observation of common elements in the marine faunas (Barber & Crow, in prep.) suggest that the North China block, the West Sumatra–West Myamar terrane and the Indochina Block might have been placed closer to each other in the Early Permian than is usually proposed (Fig. 3.7).

Conclusions

C. variformis is an exceptional species within the genus *Comia*, whose morphological variation seems to go beyond that usually seen in comioid species. Yet, all the leaf types found are undeniably of a comioid morphology, due to the presence of fasciculation combined with interfascicular veins. Comparisons show *C. variformis* to be morphologically closely related to species from North China and Angara. The presence of *Rhachiphyllum* and *Autunia* material strengthens this similarity. This suggests the presence of a migration zone between North China and West Sumatra–West Myamar and the possibility that Indochina and North China were in closer proximity to each other in the Early Permian than is generally assumed.

4

The Jambi gigantopterids and their place in gigantopterid classification[5]

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Abstract

The gigantopterids are a pan-palaeotropical Late Palaeozoic (to Early Mesozoic) plant group with unknown affiliations. Two gigantopterid species, both sole representatives of their respective genera, are known from the Early Permian Mengkarang Formation of Jambi (Sumatra, Indonesia). Through an emendation of the Jambi gigantopterids, based on the old and newly collected material, and a subsequent analysis of the leaf morphology of several gigantopterid genera, we conclude that the Jambi species are similar to the other gigantopterids, but do not appear to be related to them directly. We propose a possible scenario for the evolution of gigantopterid leaf morphology, based on marginal leaf growth, with implications for the validity of the gigantopterids as a natural group.

Introduction

The gigantopterids are a morphologically recognizable, but loosely defined, plant group containing leaf fossils with pinnate venation in which higher orders of the venation form anastomosing or reticulate patterns. A conclusive diagnosis of the group has never been given. All unequivocal finds are from the Permian and come from palaeotropical China and other parts of South-East Asia, in addition to the Middle East, Turkey, North America, Mexico and Venezuela (Table 4.1). Only rarely have gigantopterid leaves been found with attached reproductive structures (Li & Yao, 1983b). This means that the foundation for coherence of the different genera commonly included in this group is almost completely morphological and the phylogenetic validity of this taxon or group is under debate (Mamay et al., 1988; Wang, 1999; Glasspool et al., 2004a).

Table 1 Occurrence of the genera ascribed to the gigantopterids.

	North America, Mexico & Venezuela	Southeast Asia	Turkey & Middle East
Gothanopteris		•	
Palaeogoniopteris		•	
Gigantopteridium	•	•	
"Gigantopteridium" marginervum	•	•	
Zeilleropteris	•	•	
Cathaysiopteris	•	•	•
Evolsonia	•		
Gigantonoclea	•	•	•
Gigantopteris		•	•
Trinerviopteris		•	
Delnortea	•		
Neogigantopteridium		•	
Lonesomia	•		

Classification

History of gigantopterid leaf morphology

The first gigantopterid leaf fossils were described by Schenk (1883) from specimens collected in China by Von Richthofen under the name of *Megalopteris nicotianaefolia* Schenk. Since *Megalopteris* was already in use as a genus [*Megalopteris* (J.W.Dawson) E.B.Andrews] for a distinct group of leaf fossils from the Middle Palaeozoic (Dawson, 1871), the species was later assigned the name *Gigantopteris nicotianaefolia* Schenk ex Potonié (Potonié, 1902).

In 1935, Jongmans & Gothan described two new gigantopterid species from the Mengkarang Formation of Jambi Province (Middle Sumatra), Indonesia, and considered them to indicate that the Early Permian Jambi flora belonged to the ‘Cathaysia flora’ (then also known as the ‘Gigantopteris flora’) (Jongmans & Gothan 1935). They named these species *Gigantopteris bosschana* Jongm. & Gothan and *Gigantopteris mengkarangensis* Jongm. & Gothan.

Koidzumi (1934, 1936) published a reclassification of the gigantopterid leaf forms, which had been lumped into the single genus *Gigantopteris* Schenk ex Potonié until that time. The classification, with the absence of associated fossilized stems or fructifications, was based purely on morphological leaf characters and thus dealt with morphotaxa only (for an explanation of the term morphotaxon, see Materials and Methods). Koidzumi united the known gigantopterid species in the family Gigantopteridaceae and divided them into five tribes and eight genera: Palaeogoniopteridieae Koidz.(Palaeogoniopteris Koidz., Gigantopteridium Koidz., Zeilleropteris Koidz.), Gothanopteridieae Koidz. (Gothanopteris Koidz.), Cardioglossieae Koidz. (Cardioglossum Koidz.), Cathaysiopteridieae Koidz. (Cathaysiopteris Koidz.) and Gigantopteridieae Koidz. (Gigantopteris, Gigantonoclea Koidz.). *Gigantopteris bosschana* was reclassified as *Gothanopteris bosschana* and *G. mengkarangensis* as *Palaeogoniopteris mengkarangensis* (Koidzumi, 1936). This new classification has been almost universally adopted.

In 1959, Asama undertook a new classification of the gigantopterids based mainly on the different levels of venation in gigantopterid leaves (Asama, 1959). He supported this classification with his ‘growth retardation theory’, which, in the case of the gigantopterids, sought to explain leaf evolution through the fusion of segments, leading to an increase in leaf size and complexity of venation. To illustrate this hypothesis, he compiled several ‘series’ of (possible) evolutionary lineages for the gigantopterids. Later studies (Yao, 1978; Li & Yao, 1980, 1982) concluded that, in the light of a better understanding of the stratigraphy and correlation of Cathaysian strata, most of Asama’s proposed evolutionary sequences proved unsupportable. Asama’s work on gigantopterid phylogeny has not been accepted in general, except by Boureau & Doubinger (1975). Asama’s ‘*Emplectopteris*-series’ however, leading from *Emplectopteris triangularis* Halle to *Gigantonoclea taiyuanensis* (Asama) Gu & Zhi in unicoherent to tricoherent stages, has found support and seems to be consistent with the current knowledge of the Cathaysian fossil record (Liu & Yao, 1992; Li et al., 1995; Wang, 1999), although there is still disagreement about whether the frond architecture of *Emplectopteris* Halle can be reconciled with the more reduced architecture found in *Gigantonoclea* (Liu, Wang & Yao, 1996).

Since the classification of Koidzumi, both species from Jambi have remained the only representatives of their respective genera, affirming their unique morphology among gigantopterids. The Early Permian (Asselian-Sakmarian) age of the Mengkarang Formation (Ueno et al., 2007; Booi et al., 2008) implies that they belong to the earliest occurrences of gigantopterids in the fossil record, with all other genera occurring only from the late Early Permian onwards (Li et al., 1995; DiMichele et al., 2005).

Analysing the gigantopterid leaf morphology

It has been suggested by many authors (Asama, 1959, 1960; Meyen, 1984, 1987; DiMichele et al., 2005) that the general leaf morphology of the gigantopterids in the majority of the lineages developed through fusion of pinnules with relatively simple venation patterns, resulting in more complex fused patterns in which the original venation patterns appear to be conserved. To gain more insight into this question, we provide a purely morphological analysis of the different venation patterns present in several gigantopterid genera. The approach used involves the analysis and deconstruction of the known patterns, and is meant to provide a visual aid for the discussion of gigantopterid leaf venation patterns. As a guideline, we take the rule that any venation structures present in the known gigantopterid species must have been present in some form in the venation of the ancestral forms as well.

In addition, through an emendation of the descriptions for the Jambi species, based on the older and newly collected material, we aim to develop a more detailed description of the habit and morphology of the Early Permian gigantopterid species from Jambi. Subsequently, the Jambi gigantopterids will be evaluated within the framework of an analysis of the morphologies of gigantopterid leaf venation patterns to ascertain their position relative to other gigantopterid morphologies. We discuss the concept of polyphyletic composition of the gigantopterids within the context of their possible evolutionary morphological development. These aspects will then be evaluated within the framework of the current understanding of gigantopterid evolution.

Materials and methods

The material under review stems, in part, from the 1925 expedition to the Jambi region (described by Jongmans & Gothan 1935) and is supplemented by material collected during the 2003, 2004 and 2006 expeditions to the area (Van Waveren et al., 2005).

Material of *G. bosschana*, collected in 1925, comes almost exclusively from one (or more) localities along the small Ketiduran Siamang River. It comprises about 17 small pinna fragments. A single specimen that, according to Jongmans & Gothan (1935), belongs to *G. bosschana* is from a locality along the Mengkarang River. The material of *G. bosschana* collected in 2004 and 2006 stems from a single locality along the Merangin River. It comprises three pinna fragments with well-preserved venation, found in siltstone and associated with *Macralethopteris* Jongm. & Gothan, *Taeniopteris* Brongn., *Sphenopteris* Brongn., *Calamites*

Brongn. and *Cordaites* Unger. (For details on the sedimentology of this location, see Booi et al., 2008.)

Material of *Palaeogoniopteris mengkarangensis*, collected during the expedition of 1925, was found exclusively in one (or more) localities along the Mengkarang River. It comprises only four pinna fragments. The *P. mengkarangensis* material collected in 2004 also stems from a locality along the Mengkarang River. It comprises three specimens found in coarse siltstone layers, reasonably rich in fine organic debris. It was found in association with material of *Calamites*, *Callipteridium* C.E.Weiss, *Cordaites* and *Lepidodendron* Sternb.

Fusulinids found in a limestone layer at the base of the Mengkarang Formation were considered by Vachard (1989) to be indicative of the Late Asselian (earliest Permian). A second analysis, based on material collected in 2004, determined that the fusulinids of the limestones are indicative of a Sakmarian age (Ueno et al., 2007).

The nature of a morphotaxon

The nomenclatural concept of the morphotaxon for fossil plants was first introduced in the 2000 edition of the International Code for Botanical Nomenclature (ICBN, St Louis code; Greuter et al., 2000). It served to replace the earlier concepts of 'organ genus' and 'form genus'. In the 2006 Vienna code (ICBN, 2006), the morphotaxon is defined as 'a fossil taxon which, for nomenclatural purposes, comprises only the parts, life-history stages, or preservational states represented by the corresponding nomenclatural type'. In every other aspect, these taxa follow the same rules for status, typification and priority as nonfossil plant taxa. Most of the genera ascribed to the gigantopterids are only known in the form of leaf morphogenera. This means that, in the following comparisons and analyses, we attempt to classify a group of leaf morphogenera. This should not be confused with a classification of actual plant genera.

Descriptive terminology

Since Schenk (1883) and Koidzumi (1934, 1936),various terminologies have been applied to describe the morphology of the gigantopterid species. Here, we adopt the term 'sutural vein' for those veins or veinlike structures that are not part of the regular venation and appear to have come about as a result of the fusion process. These occur either as the result of fusion between ultimate venation arising from adjacent penultimate veins or from fusion of the ultimate venation of two adjacent antepenultimate veins. Structures similar to sutural veins, but without clear connection to the ultimate or penultimate venation, might be better described as 'sutural lines'. The terminology for the general venation takes the central vein of the (fused) leaf as a starting point, considering this to be the 'first-order vein (primary venation)'. Subsequent venation branching from this central vein is named the 'venation of the second order (secondary venation)', 'third order (tertiary venation)', etc. (Fig. 4.1).

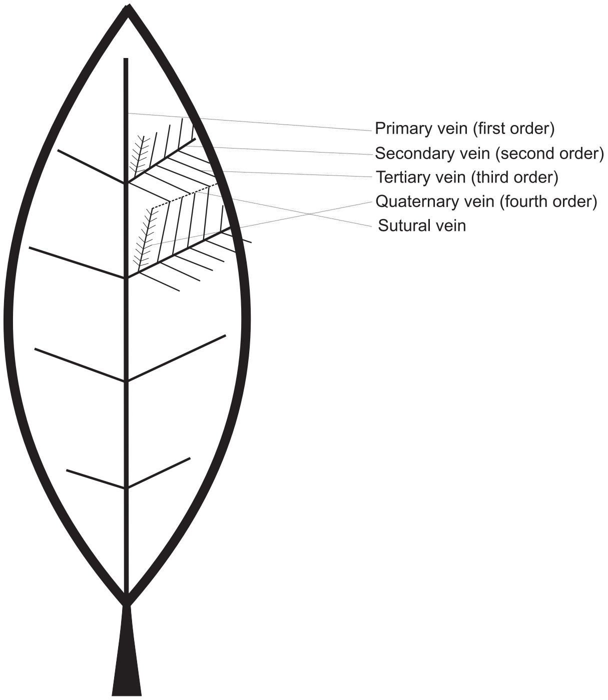

Figure 4.1: Schematic representation of a leaf with pinnate venation with orders of venation and sutural vein indicated.

‘Subsidiary veins’ are veins of the ultimate order arising directly from veins of the antepenultimate order (for example, third-order veins arising directly from first-order veins). ‘Accessory veins’ are veins of, usually, ultimate order originating at the base of veins of the penultimate order and running more or less parallel to venation of the antepenultimate order. ‘Accessory meshes’ are meshes that are derived, at least partially, from anastomosing accessory veins.

Systematic palaeobotany

Gothanopteris bosschana (Jongm. & Gothan) Koidz. emend. nov. Booi (Figs. 4.2 & 4.3).

1927 *Gigantopteris americana* White: Posthumus, p. 4 (Wrongful attribution)

1935 *Gigantopteris bosschana* Jongm. &Gothan, p. 139–142, Taf. 46, Taf. 47, Fig. 1

1936 *Gothanopteris bosschana* (Jongm. & Gothan) Koidz., p. 136

1959 *Gothanopteris bosschana* (Jongm. & Gothan) Koidz.: Asama, p. 67

2007 *Gothanopteris bosschana* (Jongm. & Gothan) Koidz.: Waveren et al., p. 14–16

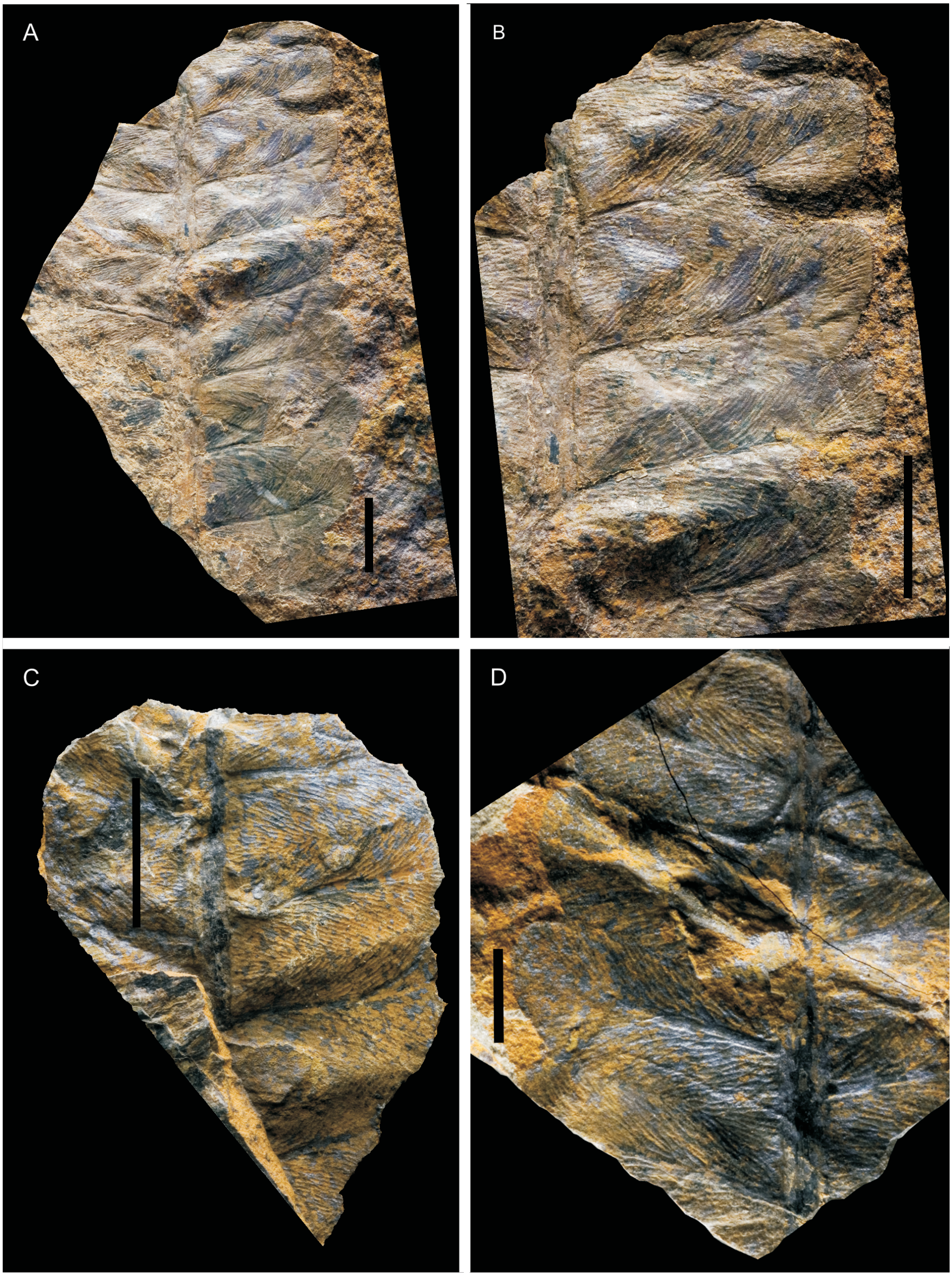

Figure 4.2: A, ***Gothanopteris bosschana*** (MerXI–9). Scale bar, 1 cm. B, ***Gothanopteris bosschana*** (MerXI–9), detail. Scale bar, 1 cm. C, ***Gothanopteris bosschana*** (MerXI–27A). Scale bar, 1 cm. D, ***Gothanopteris bosschana*** (MerXI–27C). Scale bar, 0.5 cm.

Emended diagnosis (see Table 4.2): Leaves broadly ribbon-like, tapering in width towards one side, margin crenate. Primary venation broad, longitudinally irregularly striate; secondary venation at almost perpendicular angle to first-order venation, subopposite to alternate, regularly spaced, distinct, straight to slightly curved from halfway towards leaf margin, tapering, dissolving into several veinlets identical to tertiary venation; third-order venation at slightly acute angle to second-order venation, regularly spaced, bifurcating and fusing, forming elongated meshes with acute tips; third-order venation fusing halfway between two secondary order veins to form an indistinct sutural vein, running parallel to second-order venation; veins similar to third-order veins from first-order vein (subsidiary veins), bifurcating and fusing, forming elongated meshes, fusing with third-order venation running from base of secondary veins forming basal triangular areas between bases of second-order veins.

Description: The material consists of fragments of broadly linear-lanceolate leaves with a crenate margin. The largest fragments are more than 86 mm in length (complete fronds were in all probability much larger) and, on average, 30 mm [23–(30)–36 mm] in width. Veins of the first order are broad, about 2.2 mm wide [1.8–(2.2)–2.6 mm], sunken beneath the plane of the lamina, with irregular longitudinal striations. Veins of the second order leave the first-order veins at an angle of 76 ° [74–(76)–77 °] and are broad at the base, about 0.74 mm [0.71–(0.74)–0.78 mm]. They run straight or slightly curved upwards (curving only in the upper half of the vein) towards the margin of the lamina. They taper gradually and disappear at about three-quarters to four-fifths of the way towards the margin, dissolving into several third-order veins. The second-order venation is evenly spaced, veins are about 7.2 mm [6.9–(7.2)–7.6 mm] apart and positioned alternately to suboppositely (although opposite configurations occur) on both sides of the first-order vein. There is a tendency for the secondary venation to become more closely spaced with the tapering of the margin.

The third-order venation arises from the second-order veins at an angle of 44 ° [42–(44)–45 °]. It is regularly spaced and it usually bifurcates once or twice at regular intervals throughout the lamina. Neighbouring third-order veins anastomose regularly and form elongated, ellipsoid-hexagonal meshes with acute tips. Third-order venation arising from two neighbouring secondary veins also fuses halfway between these secondary veins to form an indistinct sutural vein that runs parallel to the veins of the second order, from the edge of the subsidiary venation to the margin.

Subsidiary veins originate directly from the firstorder vein in the spaces between two veins of the second order. They bifurcate regularly and anastomose with neighbouring veins, forming meshes similar to those found in the regular third-order venation, and curving slightly towards the sutural vein. This venation forms triangular areas delineated by the first-order vein (at the base) and the regular third-order venation originating from the base

Table 2 Generic and specific diagnosis of *Gothanopteris bosschana* by Jongmans and Gothan (1935), with subsequent emendations by Koidzumi(1936) and Asama (1959) and Booi.

	Jongmans and Gothan (1935)	Koidzumi (1936)
Frond	Probably bipinnate; Pinnules fused (like in *Pecopteris unita*) to pinnae with crenate margins and rounded margins. Every crenation corresponding to a pinnule	Probably simple, broadly ribbon-like, probably very long; pinna margin grandi-crenate
Rachis (primary venation)		Robust, very stout
Secondary venation	Perpendicular to rachis, distinct for 3/4 of its length, tapering strongly, longitudinally striate	Originating at nearly right angle to rachis, straight, parallel, forking into several veinlets and dissolving before reaching the margin
Tertiary venation	Between two midveins (secondary veins), arising diagonally from them, consisting of lengthened meshes	Freely branching and anastomosing, forming a network of obliquely elongate meshes (principal tertiary vein absent)
Sutural vein	Indistinct, formed from the venation of two neighbouring secondary veins (not a true vein)	Between the secondary veins, generally very indistinct
Venation from rachis		Proximal ramifications of the basal tertiary join with tertiary venation directly from adjacent rachis

Asama (1959)	Booi
Frond shape unknown; Leaf broadly ribbon-like, unicoherent; leaf margin grandi-crenate	Leaves broadly ribbon-like, margin crenate
Robust, very stout	Broad, longitudinally irregularly striate
Originating at nearly right angle to rachis, straight, parallel, forking into several veinlets and dissolving before reaching the margin	At almost perpendicular angle to first order venation, subopposite to alternate, regularly spaced, distinct, straight to slightly curved, dissolving into tertiary venation before reaching the margin
Freely branching and anastomosing to form a network of obliquely elongate meshes (principal tertiary vein absent)	At slightly acute angle to secondary venation, regularly spaced, bifurcating and fusing, forming elongated meshed with acute tips,
Between the secondary veins, generally very indistinct	Tertiary venation fusing halfway between two secondary veins, forming indistinct sutural vein, running parallel to second order veins
Proximal ramifications of the basal tertiary join with tertiary venation directly from adjacent pinna-rachis	Subsidiary veins from first order veins, bifurcating and fusing, forming elongated meshes, fusing with regular third order venation forming triangular areas between bases of second order veins

of the neighbouring second-order veins (at the sides). These ‘triangles’ of subsidiary venation are often found to lie slightly above the plane of the lamina, with the most distal tip of the ‘triangle’ being most elevated above the plane of the lamina.

The size of the meshes in the regular ultimate venation is variable; they are 2 mm in length [1.9–(2.0)–2.2 mm] and 0.3 mm in width [0.28–(0.29)– 0.30 mm]. A comparable amount of variability exists in the meshes of the subsidiary venation, the meshes measuring 2 mm in length [1.9–(2.0)–2.2 mm] and 0.3 mm in width [0.28–(0.29)–0.30 mm].

Comparisons (for comparison with Palaeogoniopteris mengkarangensis, see below): Comparison with other gigantopterids shows that *G. bosschana* shows similarity with *Gigantopteridium americanum* (White) Koidz. (as already noted by Jongmans & Gothan 1935). Primarily at the level of ultimate and penultimate venation, there are some convergences between this species and *G. bosschana*. Elongated meshes, both in the ultimate venation and in the venation arising directly from the first-order vein, are present in both species. However, the meshes occur frequently and regularly throughout the pinnae in *G. bosschana*, whereas they occur uncommonly in *Gm. americanum*. In both species, the subsidiary venation arising from the first-order vein forms triangular areas between two second-order veins. However, the tendency for large bundles of ultimate venation to arise from a single vein attached to the ultimate venation is not present in *G. bosschana*. A similar pattern in the ‘triangular areas’ of *Gigantopteridium huapingense* (Feng) Shen, in which the entire venation arises from a single vein attached to the first-order vein (see Liu & Yao 2002, text fig. 3), is also absent in *G. bosschana*.

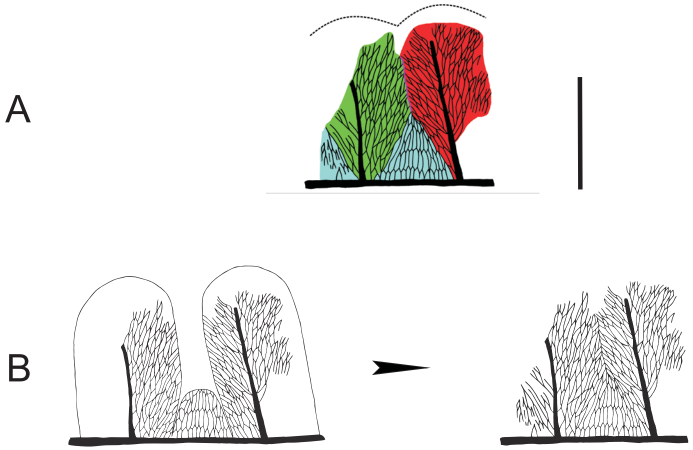

Figure 4.3: A, Semi-schematic drawing of venation pattern in *Gothanopteris bosschana*, based on specimens MerXI-9 and MerXI-27A (see Fig. 2), with venation from different origins and sutural veins indicated with different colours. Scale bar, 1 cm. B, Deconstruction of *G. bosschana*.

Comparing *G. bosschana* with the genus *Cathaysiopteris*, the arrangement of ultimate and penultimate orders of venation is similar, but the regular elongated anastomosing of the last order venation seen in *G. bosschana* is absent in *Cathaysiopteris*, and the 'accessory meshes' found in the Chinese species *Cathaysiopteris whitei* (Halle) Koidz. (see Yao & Liu 2002, plate I, fig. 4) are not found in *G. bosschana*.

There is also a similarity at the level of ultimate and penultimate venation with the 'younger' leaves of *Gigantonoclea lagrelii* (Halle) Koidz. (for example, see Wang, 1999, text, fig. 2C). The elongated meshes in the ultimate venation, the crenate leaf margin and the indistinct (absent?) sutural vein are all similarities with *G. bosschana*. The interaccessory meshes at the base of the penultimate venation in *Gc. lagrelii* are not present in *G. bosschana*, although the preservation of the specimens is not of sufficient quality to completely exclude the possible presence of such a character.

Superficially, there is a similarity between *G. bosschana* and the genus *Gigantopteris* in the presence of regularly reticulate venation throughout the lamina. However, the venation pattern in *Gigantopteris*, in which the ultimate venation forms polygonal meshes within the polygonal meshes of the penultimate venation (Glasspool et al., 2004a), is not seen in *G. bosschana*, in which meshing only occurs on one level of venation and is not polygonal.

In Asama's (1959) 'evolutionary series' for the gigantopterids, *Gothanopteris* was included as the sole member of the '*Lonchopteris* series', indicating a possible phylogenetic connection with that genus based on a similarity in venation. Although the two genera share the character of anastomosing meshes in the ultimate venation, the meshes in *Gothanopteris* are of a different, far more elongated, nature than those in *Lonchopteris* Brongn. (a medullosalean frond morphogenus). Additionally, a connection between these genera would not explain the origin of the subsidiary venation arising straight from the third-order vein that forms the triangular areas of venation perpendicular to the first-order vein, which occurs in between the second-order veins of *Gothanopteris*, as a similar architecture cannot be found in *Lonchopteris*.

Palaeogoniopteris mengkarangensis (Jongm. & Gothan) Koidz. emend. Booi (figs 4.4 & 4.5).

1935 *Gigantopteris mengkarangensis* Jongm. & Gothan, p. 143–144, taf. 47, figs 2–4.
1936 *Palaeogoniopteris mengkarangensis* (Jongm. & Gothan) Koidz., p. 133–134
1959 *Palaeogoniopteris mengkarangensis* (Jongm. & Gothan) Koidz.: Asama, p. 67
2007 *Palaeogoniopteris mengkarangensis* (Jongm. & Gothan) Koidz.: Waveren, et al., p. 14–16

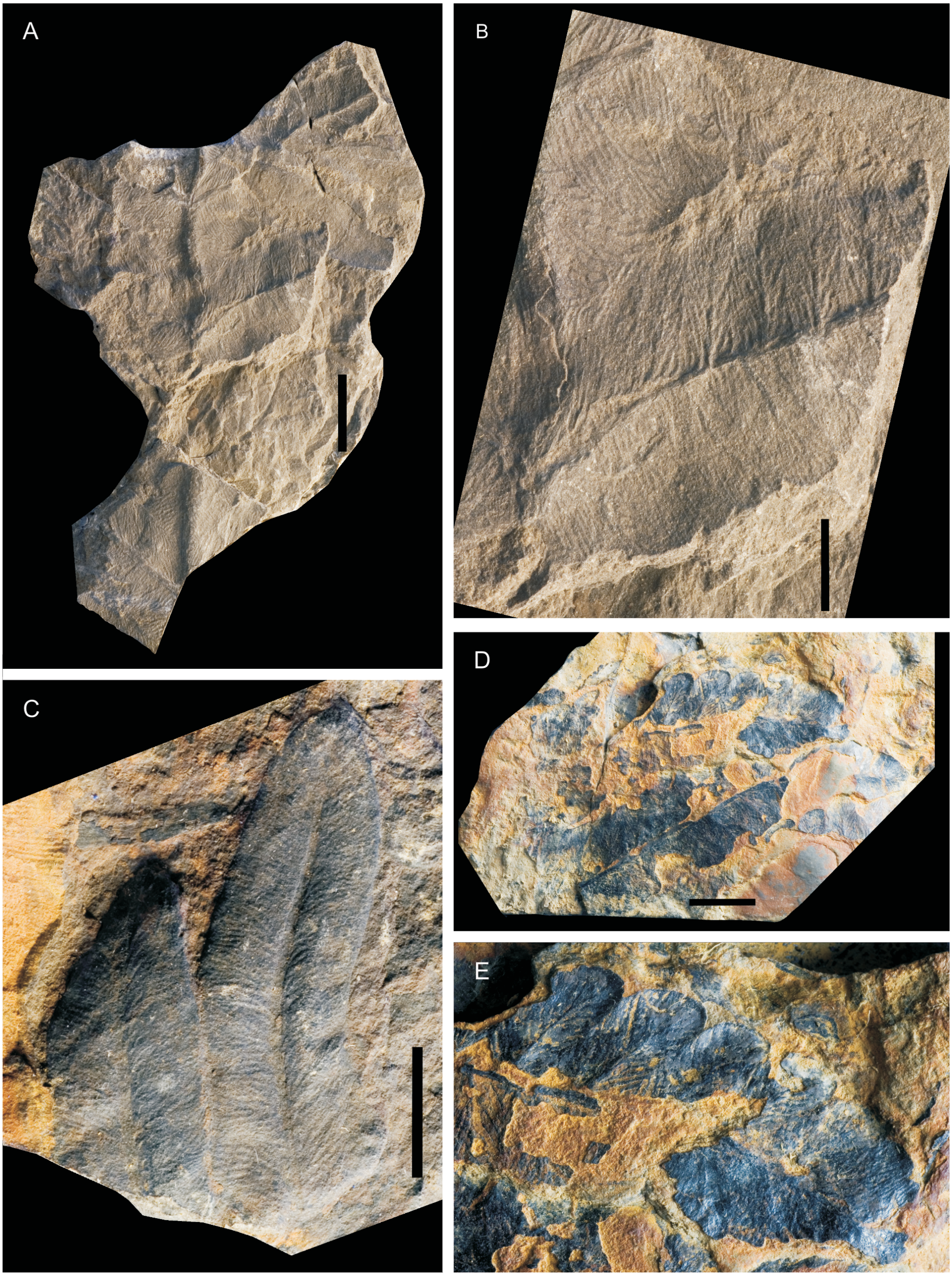

Figure 4.4: A, *Palaeogoniopteris mengkarangensis* (45 352). Scale bar, 1 cm. B, *Palaeogoniopteris mengkarangensis* (45 352), detail. Scale bar, 0.5 cm. C, *Palaeogoniopteris mengkarangensis* (45 355). Scale bar, 1 cm. D, *Palaeogoniopteris mengkarangensis* (MenU2-A4). Scale bar, 1 cm. E, *Palaeogoniopteris mengkarangensis* (MenU2-A4), detail.

Emended diagnosis (see Table 4.3): Fronds at least once pinnate; first-order vein distinct, sunken; pinnae at obtuse angle to first-order vein, broadly linearlanceolate, narrowly confluent at base; second-order vein straight, broad, sunken, curving outward at base, persisting almost to pinna apex; margin entire to crenate; third-order venation simple to infrequently bifurcate and at obtuse angle to second-order vein in apical pinnules; third-order venation in more basal pinnae frequently bifurcated at base and forming pinnate clusters, clusters sometimes with more distinct central vein (midvein) giving rise to pinnate fourth-order veins, third- to fourth-order veins forming distinct sutural veins halfway between the pinnate clusters, running parallel to pinnate third- (to fourth-) order venation. Largest pinnae with decurrently sloping basiscopic lamina. Here third- (to fourth-) order venation fusing with venation straight from rachis, anastomosing and forming irregularly polygonal meshes.

Description: Leaves are at least bipinnate. Pinnae can be longer than 75 mm. The first-order vein is distinct and sunken beneath the level of the lamina. It is about 1.8 mm wide [1.3–(1.8)–2.3 mm] and is longitudinally irregularly striate. Pinnae are positioned at an angle of about 68 ° [61–(68)–74 °] to the rachis and close to each other, often touching. They are broadly linear-lanceolate in shape, broadly attached and narrowly confluent at base. The second-order vein is clear and straight, about 0.87 mm [0.64–(0.87)–1.1 mm] broad. It runs straight, hardly tapering and persists almost up to the apex of the pinnule. Pinna size varies from smaller pinnae with partly simple thirdorder venation to larger pinnae with pinnately branching third- to fourth-order venation.

Third-order venation varies with pinnule shape and size, leaving the midvein under an obtuse, although variable, angle of about 65 ° [46–(65)–84 °]. In the smaller entire-margined pinnae (Fig. 4.4C), which are about 9 mm wide, third-order venation varies from straight and unforked (near the pinna apex) to frequently pinnately branching up to halfway towards the pinna margin in the more basal parts of the pinnule. Here third-order veins form elongate clustered groups. In the larger pinnae with a crenate margin (Fig. 4.4A, D), the clustering of lateral veins is more pronounced, leading to the formation of a distinct central ‘midvein’ in every cluster with distinctly less prominent venation arising from it in a ‘herringbone’ pinnate pattern, effectively forming a fourth order of venation. Halfway between clusters, lateral veins fuse to form a sutural vein that runs from close to the midvein to the pinnule margin, parallel to the vein clusters. Every cluster corresponds to a crenation, with the widest point (‘apex’) of the crenation coinciding with the central part of the cluster. In the basiscopic, decurrently sloping base of the larger pinnae, subsidiary venation from the first-order vein bifurcates and anastomoses frequently, forming a reticulate pattern consisting of polygonal meshes.

Table 3 Generic and specific diagnosis of *Palaeogoniopteris mengkarangensis* by Jongmans and Gothan (1935) with

	Jongmans & Gothan (1935)	**Koidzumi (1936)**
Frond	Pinnae separate, usually crenate at the margin, every crenation corresponding to a fused pinnule	Lanceolate in outline, pinnate. Pinnae ovate-oblong, proximal base alato-decurrent to the next node, distal base suddenly contracted, grandi-crenate, opposite, touching with decurrent wing, distant above
Rachis (primary venation)		
Secondary venation		Stout, originating at acute wide angle to rachis
Tertiary venation	One for every fused pinnule, midvein	Distinct, originating at very wide angle to secondary veins
Quaternary venation	Arising both from the tertiary and the secondary veins, at an acute angle, delicate, bifurcating, non-anastomosing	Copiously forked or pinnate from secondary veins, on both sides of the secondary vein in each lobe
Sutural vein	Distinct, between the fused pinnules	From each opposite pair of quaternary veins, between the tertiary veins, quaternary venation from secondary veins also fusing with sutural vein
Venation from rachis (subsidiary venation)		Anastomosing on the proximal side of the distal basal lobe
Remarks	Every fused pinnule with 'veinbundle' with midvein, next to additional veinbundles from the secondary venation. For the most part without mesh venation. Meshes only occur in area (corner) between primary and secondary venation	

n subsequent emendations by Koidzumi(1936) and Asama (1959) and Booi.

Asama (1959)	Booi
At least unipinnate, with unicoherrent pinna; Pinnae ovate-oblong, abaxial base alato-decurrent to the next node, adaxial base suddenly contracted, grandi-crenate, opposite, touching with decurrent wing, distant above	Fronds at least once pinnate, pinnae at obtuse angle to primary vein, broadly linear-lanceolate, narrowly confluent at base, pinnae margin entire to crenate
	Distinct, sunken
Stout, originating at acute angle to rachis	Straight, broad, sunken, curving downwards at base, persisting almost to pinna apex
Non-bifurcating, arising from the secondary veins at an acute angle and directly from the primary vein	At obtuse angle to second order vein, simple to infrequently bifurcate in apical pinnae, in more basal pinnae frequently bifurcate at base and forming pinnate clusters
	Distinct, formed by fused venation halfway between pinnate clusters of tertiary (quaternary?) venation, running parallel to tertiary venation
	Present in larger pinnae, in decurrently sloping basiscopic part of pinna, fusing with tertiary venation anastomosing and forming irregularly polygonal meshes

Comparisons: There appears to be little similarity with the other Jambi species, *G. bosschana*. Branching patterns in the tertiary venation are of a pinnate nature in *P. mengkarangensis*, whereas, in *G. bosschana*, they bifurcate and anastomose. Anastomosing of veins occurs commonly between neighbouring ultimate (tertiary) veins in *G. bosschana*, whereas, in *P. mengkarangensis*, they only occur where the ultimate venation of two neighbouring tertiary veins meet (forming a sutural vein). The morphological variation found in the material of *P. mengkarangensis*, ranging from pinnae with simple venation to pinnae with compound venation structures, is not found in *G. bosschana*.

As already remarked by Jongmans & Gothan (1935), *P. mengkarangensis* is similar in several morphological characters to *Gigantopteridium*. In frond morphology, there is a similarity between the two in the pinnate construction of the frond, but, whereas first-order pinnae in *P. mengkarangensis* are still separate, they have become 'fused' in *Gigantopteridium*. There is a correspondence in the relative sparseness of fusing in the venation of the ultimate order. In addition, ultimate order venation in both taxa is monopodial in nature, but, in *Gigantopteridium*, a central 'midvein' structure, although occasionally distinct (Liu & Yao, 2002), is far less pronounced than it is in *P. mengkarangensis*.

There is a similarity between *P. mengkarangensis* and the genus *Cathaysiopteris*, most clearly in the ultimate and penultimate venation. In both taxa, venation arises from a centralized 'midvein' under an obtuse to acute angle and fuses midway between these central veins in a sutural vein running parallel to the central veins. However, in all known species of *Cathaysiopteris*, there are three orders of venation, whereas *P. mengkarangensis* has at least four orders. In addition, a clear difference with the Cathaysian species *Cathaysiopteris* whitei is the origin of the sutural vein. In that species, it originates close to the base of the central vein, forming meshes parallel to the main rachis (so-called 'accessory meshes'; see Yao & Liu 2002, plate I, fig. 4), whereas, in *P. mengkarangensis*, the sutural vein arises from the main rachis. In a comparison with the Euramerican species *Cathaysiopteris yochelsonii* Mamay (Read & Mamay, 1964; Mamay, 1986), differences are more marked, as *P. mengkarangensis* lacks its secondary venation that remains unforked up to the margin.

There is a clear similarity between *P. mengkarangensis* and *Zeilleropteris* [the Cathaysian species *Z. yunnanensis* (Zeiller) Koidz. and *Z. yujiaensis* (Huang) Li & Yao and the North American *Z. wattii* Mamay]. There are similar branching patterns in the ultimate venation, but, whereas they are curved in *Zeilleropteris*, they appear far more rigid and straight in *P. mengkarangensis*. In addition, in *Zeilleropteris*, the ultimate venation arising from neighbouring secondary veins is fused between those veins, whereas this is not so in *P. mengkarangensis*.

Palaeogoniopteris was classified by Asama (1959) as the only member of the '*Callipteridium* series', presumably because of a broad morphological similarity to this genus. Why the genus *Callipteridium* (Medullosales) was singled out for similarity by Asama, in preference to other genera with pinnate venation, was not made clear. There is a similarity in last order venation between the two genera, but both the callipterid genus *Autunia* Krasser (Peltaspermales) and species from the morphogenus *Pecopteris* (Brongn.) Sternb. (as already indicated by Jongmans & Gothan 1935), and especially the zygopterid genus *Nemejcopteris* Barthel, come closer in resembling the general simple and rigid pinnate venation pattern.

Outside the gigantopterids, at the level of ultimate venation and organization of the pinnae, there is a similarity with some species of the morphogenus *Pecopteris*. Jongmans & Gothan (1935) drew specific comparison with *Diplazites unita* (Brongn.) Göpp. (= *Pecopteris unita* Brongn.), and there is a strong similarity in the organization of ultimate order venation with a central, well-developed 'midvein' from which the lateral veins arise at a slightly obtuse angle and run straight to the 'margin'. A convergence along the same lines also exists with certain callipterid species, such as *Autunia conferta* (Sternb.) Kerp, and with *Nemejcopteris* (Barthel, 1968), all of which have the same pinnate organization of lateral venation in the pinnae that exists in *P. mengkarangensis*.

Discussion and conclusions

Frond morphology of the Jambi gigantopterids

Gothanopteris bosschana

The material of *G. bosschana*, all incomplete leaf fragments, shows a remarkably consistent morphology. All specimens show parts of a strap-like leaf with lobed but parallel margins, slightly tapering to one side. This, and the consistency of morphology, suggests that this morphology presents a good indication of the architecture of the entire leaf.

No evidence of an attachment to venation of a lower order was found, giving no indication that these leaves were part of a larger (pinnate) frond. However, the fragmented nature of the fossils suggests that a certain amount of transport has taken place and as such does not allow reliable speculation as to the existence of compound leaves. Given the relative sparseness of the material, no further information regarding the general habit of this species can be gained from the specimens.

Palaeogoniopteris mengkarangensis

The material of *P. mengkarangensis*, shows a rather varied morphology of a transitional nature. The material ranges from single pinnules with a simple to occasionally branched venation (Fig. 4.4C) to once pinnate fragments in which venation of the pinnules consist of units of lateral venation separated by sutural veins (Fig. 4.4A). The material shows a gradual transition between these morphologies.

The material is interpreted as a bipinnate frond. The pinnae with simple venation are also the smallest and most slender pinnae among the material. They are therefore tentatively interpreted as the most apical pinnae. The pinnae with branching venation and sutural veins would then represent the more basal portions of the frond. Only in some of the material from this last group a basiscopic decurrent basal part of the pinna is fully developed (Fig. 4.4A, B). These are also the fragments in which the pinnules are most widely spaced and are interpreted as the most basal pinnae in the frond. There is no indication in the material of more than a bipinnate layout of the frond.

The classification history of the Jambi gigantopterids

In 1936, in his reclassification of the gigantopterids, Koidzumi moved Jongmans & Gothan's *Gigantopteris bosschana* to the new genus *Gothanopteris* (family Gigantopteridaceae, tribe Gothanopteridieae), the tribe characterized by ribbon-like, simple fronds and absent or indistinct sutural veins. *Gigantopteris mengkarangensis* Jongm. & Gothan was placed in the genus *Palaeogoniopteris* (family Gigantopteridaceae, tribe Palaeogoniopteridieae), the tribe characterized by the (clear) presence of sutural veins and pinnately or monopodially forked tertiary veins. The two other genera included in this tribe by Koidzumi are *Gigantopteridium* and *Zeilleropteris*. The unique morphology of the Jambi species was later confirmed by the isolated placement of *Gothanopteris* and *Palaeogoniopteris* in the classification of Asama (1959), who viewed them as phylogenetically unrelated to the North Cathaysian gigantopterids and as descended from different ancestry (Asama, 1959, 1975).

Li & Yao (1983a) offered a comprehensive analysis of possible phylogenetic relations between different genera and groups within the gigantopterids. In their phylogenetic diagram (Li & Yao, 1983a, table 1), both *Gothanopteris* and *Palaeogoniopteris* are positioned as possibly having evolved from Late Palaeozoic *Alethopteris* Sternb. In addition, *Palaeogoniopteris* is proposed as a possible ancestor to *Zeilleropteris yujiaensis* (Huang, 1980), and *Gothanopteris* as a possible ancestor to the Triassic species *'Gigantopteris' ferganensis* Brick (Krishtofovich, 1957, p. 289, fig. 271). Little morphological relationship appears to exist between *Palaeogoniopteris* and *Z. yujiaensis*. The polygonal meshes and the distinct sutural veins found in the ultimate order venation in *Palaeogoniopteris* are not seen in *Z. yujiaensis*. In addition, the ultimate and penultimate venation and the sutural veins of *Z. yujiaensis* leave the second-order venation at an angle of about 30 ° and curve slightly towards the leaf margin. All of these structures are situated at an almost right angle to the second-order venation in *Palaeogoniopteris*, are more distinct there and run almost straight. There appears to be little morphological similarity between *G. bosschana* and the material of *'Gigantopteris' ferganensis*. There is similarity in the general crenate-dentate shape of the pinna and the subsidiary venation that occurs between the second-order veins. However, *G. bosschana* has neither the prominent, widely spaced tertiary veins seen in *'G.' ferganensis*, nor its anastomosing fourth-order venation.

Glasspool et al. (2004a) proposed a provisional division of the gigantopterids, in which the genera *Gothanopteris*, *Cathaysiopteris*, *Cathaysiopteridium* Li, *Neogigantopteridium* Yang, *Palaeogoniopteris* and *Zeilleropteris* would be grouped together based on their shared characteristics of (clear) sutural veins and the absence of polygonal meshes in the ultimate order venation. This group should then be considered as separate from the 'true' gigantopterid genera *Gigantopteris* and *Gigantonoclea* (including *Cardioglossum*, with which it shares regular polygonal venation throughout the lamina).
A similar form of morphological grouping was put forward by DiMichele et al. (2005) for the American gigantopterids, dividing them into two groups, one with (uniform) reticulate venation (*Gigantonoclea*) and the other with ultimate venation with a herringbone pattern (*Gigantopteridium*, *Cathaysiopteris*, *Delnortea* Mamay, *Evolsonia* Mamay and *Lonesomia* Weber). This latter group could be further subdivided into a group with three orders of venation (*Cathaysiopteris* and *Gigantopteridium*) and a group with four orders of venation (*Delnortea*, *Evolsonia* and *Lonesomia*).

Although these divisions of the gigantopterids can accommodate *Gothanopteris*, in *Palaeogoniopteris* there seems to be a tendency towards polygonal meshes in the basiscopic decurrent lobes of the more basal pinnules (although different in character from those found in *Gigantopteris* or *Gigantonoclea*). In this, it appears to be unique among gigantopterids, as in all other genera the (pen-)ultimate venation appears to consist either almost entirely of polygonal meshes (*Gigantopteris*, *Gigantonoclea*) or of anastomoses of a more simple, nonpolygonal nature (*Cathaysiopteris*, *Gigantopteridium*, *Neogigantopteridium*, *Delnortea*, *Zeilleropteris*, *Gothanopteris*). This means that, where *Palaeogoniopteris* is concerned, the division proposed by Glasspool et al. (2004a) is not applicable in the strictest sense, as it contains characters of both of the proposed groups. However, the division offers a good general rule for the grouping of gigantopterids on morphological grounds and might reflect a true phylogenetic division.

The preceding comparisons and classifications show that the Jambi gigantopterids display broadly the same venation characteristics as those found in Cathaysian and Euramerican gigantopterids. However, there are differences that appear to preclude the possibility to propose any reliable phylogenetic connections on morphological grounds. The details of the morphological and possible phylogenetic position of the Jambi gigantopterids relative to other gigantopterid genera will be explored in the following sections.

Gigantopterid affinities in the literature

Since the early work on gigantopterids, new finds of gigantopterid material have considerably increased the information about gigantopterid anatomy and possible affinities. This has provided a clearer perspective on gigantopterid diversity throughout the world; however, the origin of the gigantopterids is still unclear. Doubt is cast on whether the gigantopterids should be considered a valid order or suprafamilial taxon. Some authors (Mamay et al., 1988; Wang, 1999; Glasspool et al., 2004a) have expressed the opinion that the gigantopterids should not be viewed as a taxonomically coherent clade, but as an artificial group, held together only by similarities in the venation.

Fructifications or reproductive structures attributable to gigantopterids, which could shed light on possible affinities, have only rarely been found (Li & Yao, 1983b). These were interpreted as seeds and pollen-bearing organs related to cycadophytes by the original authors. However, they also remarked on the similarity of these possible reproductive structures to marratialean synangia. Hill & Camus (1986) considered that the question of whether these structures described by Li & Yao (1983b) were related to seed ferns or (marattialean) ferns was undecided.

Through the years, authors have attributed gigantopterid species to various plant groups, because of the lack of information from reproductive organs. Schenk (1883) described the original material of *Gigantopteris* (*Megalopteris*) as a 'höchst ausgezeichneter Farn' ('very clear fern'), and compared it to extant species of *Polypodium* L. and *Acrostichum* L. with undivided fronds on the basis of a general morphological similarity. Zeiller, in 1907, designated it as an 'alleged fern' and found similarities in the venation with the extant fern genus *Goniopteris* C.Presl and species from *Polybotrya* Humb. & Bonpl. ex Willd. and *Diplazium* Sw., in particular in his specimens that were later reclassified as *Zeilleropteris* (Zeiller, 1907). Koidzumi (1936) referred to the gigantopterids as 'fern-like plants'. Zhu & Zhang (1995), in a revision of *Gigantonoclea cardiophylla* Zhu & Geng, reclassified it as *Trinerviopteris cardiophylla* (Zhu & Geng) Zhu, and concluded that it was a true fern on the basis of the presence of (sterile) sori. They considered this newly established genus to be intermediate between *Gigantonoclea* and *Gigantopteris*.

Others found affinity with particular seed fern clades or with the gymnosperms in general. Gigantopterids from the Shansi flora were described by Halle (1927) as probably belonging to the pteridosperms. Meyen (1984), based on Asama's assertion that the Cathaysian gigantopterids have a phylogenetic link with *Emplectopteris*, allied them to Callistophytales. Later, following the find by Li & Yao (1983b) of attached reproductive structures with *Gigantonoclea* leaves, both *Gigantonoclea* and *Gigantopteris* were placed in Gigantonomiales by Meyen (1987), and later as a member of Emplectopteridaceae within that order by Cleal (1993). The North American gigantopterids, on the other hand, were attributed by Meyen

(1987) to the peltasperms, based on the presence of fructifications similar to *Harrisiothecium* B.Lundbl. microsporangiate capsules, that White (1912) described as occurring in association with *Gigantopteridium americanum*. Li & Taylor (1998, 1999) discussed two new stem species based on permineralized stem fragments from the Upper Permian of Guizhou, China. The first of these, *Aculeovinea yunguiensis* H.Li & Yao (1983a), based on the information from leaf morphology and reproductive structures available at that time, suggested *Alethopteris* and *Callipteridium* (by way of *Emplectopteris* and *Emplectopteridium* S.Kawas.) as the ancestors to all the species found in the gigantopterids. DiMichele et al. (2005) considered the American and Chinese gigantopterids to represent separate clades, although they proposed that both could have evolved from the peltasperms, on the basis of the similarity in venation patterns and, particularly in the case of the American forms, supported by the repeated association with peltasperm reproductive organs. Anderson, Anderson & Cleal (2007) classified *Gigantonoclea* in the callistophytalean Emplectopteridaceae (based on the presumed relationship with the genus *Emplectopteris*), and *Gigantopteris* in the family Gigantopteridaceae (Gigantopteridales, Cycadopsida) following Li & Yao(1983b) and Wang (1999).

Asama's (1959) evolutionary 'series' for the gigantopterids found its origin in a number of fern and gymnosperm genera, such as *Emplectopteris*, *Emplectopteridium*, *Konnoa* Asama, *Lonchopteris*, *Callipteridium*, *Supaia* C.D.White and *Pecopteris*.

The analysis of gigantopterid cuticles from some species confirms the gymnosperm affiliation of several stomatal characters. Yao & Crane (1986) analysed some cuticles obtained from leaves with gigantopterid morphology and concluded that they were pteridosperms on the basis of the presence of amphistomatic leaves and stomata with six subsidiary cells producing two to six overarching papillae. Li & Tian (1990) and Li et al. (1994), in their analysis of cuticles from *Gigantonoclea guizhouensis* Gu & Zhi, could only confirm an uncertain relationship with gymnosperms, with a possible phylogenetic position between the pteridosperms and the angiosperms, as none of the stomatal characters could provide a definite affiliation to known cuticular morphologies. Yao & Liu (2004) observed a close relationship of characters found in the lower cuticle of *Gigantopteridium marginervum* Yao & Liu with *Aipteris confluens* Brick, although they concluded that no real affiliation could exist because of the large differences in gross leaf morphology between these species. Guo, Tian & Chang (1993) stated, on the basis of an analysis of cuticles from *Gigantonoclea hallei* Gu & Zhi and *Gigantopteris dictyophylloides* Gu & Zhi, that the presence in both of these species of the two characters of paracytic stomata and sinuous epidermal cell walls was exceptional among Late Palaeozoic plants, and that these features, in combination with the simple leaves and anastomosing venation, might suggest an evolutionary connection between the gigantopterids and ancestral angiosperms. Bifurcated fronds are a common feature in gigantopterids.

Bifurcated fronds occur in the American species *Cathaysiopteris yochelsonii*, *Zeilleropteris wattii* and *Gigantopteridium americanum*, as well as in the Chinese species of *Gigantonoclea* (Yao & Liu, 2002). Although bifurcations occur in both Chinese and American species of gigantopterids, they appear to be most common in American species of *Cathaysiopteris*, *Zeilleropteris* and *Gigantopteridium*. As bifurcated leaves are much more commonly found in seed ferns (for example, Medullosales) than in ferns, it suggests an affiliation with the first group for at least part of the gigantopterids.

From the preceding overview, it can be concluded that, although the affiliation of the gigantopterids as a group seems to be broad, most appear to lie with the gymnosperms. Affiliations within the gigantopterids are even less clear. Although several attempts have been made in the past to reconstruct the phylogenetic tree of the gigantopterids (Asama, 1959; Li & Yao, 1983a; Yang, 1987), a completely satisfactory solution remains to be found. The common thread in this preceding research appears to be the effort of compiling a coherent phylogenetic framework for the gigantopterids on the basis of the known species. However, the assumption must be that most stages in gigantopterid evolution are absent from the known fossil record. Therefore, an analysis of the venation patterns present in these taxa might shed more light on the evolution and possible ontogeny of the gigantopterids.

Analysis and deconstruction of the venation patterns in several gigantopterids (figs 4.3, 4.5–4.8)

Most gigantopterids give the impression that the previously existing venation patterns are preserved in fused forms (Asama, 1959, 1960; Meyen, 1984, 1987; DiMichele et al., 2005). In some cases, part of the venation pattern could have either disappeared or become slightly deformed and altered in the fusion process. In the following analyses, sutural veins are interpreted as lines that separate groups of (often pinnate) venation and could represent the lines along which fusion could have taken place, either between the ultimate venation of neighbouring penultimate veins, or between the ultimate venation of neighbouring antepenultimate veins. The reconstructions are based on the assumption that, where fusion would occur in pinnate leaves, the first evolutionary stage of fusion would be that occurring between the ultimate venation arising from neighbouring penultimate veins (individual pinnules), possibly followed by the fusion between the venation arising from neighbouring antepenultimate veins (neighbouring pinnae).

Both *Gigantopteris* and *Gigantonoclea* (including *Cardioglossum*, see Glasspool et al., 2004a) and the intermediate genus *Trinerviopteris* (Zhu & Zhang, 1995) will be excluded from this deconstruction. Wang (1999) extensively treated *Gigantonoclea*, and a reliable and generally accepted evolutionary history, which has its origin in *Emplectopteris*, exists for this genus (Asama, 1959; Wang, 1999). *Gigantopteris* (including *Trinerviopteris*) (Glasspool et al., 2004b) as a genus is too diverse to be treated within the framework of this paper. The Mexican species *Lonesomia mexicana* Weber 1997) will also be excluded, because no specimens have yet been found that show the venation of this species in sufficient detail.

The choice of the gigantopterid species analysed below was determined mainly by the availability of reliable depictions or drawings. Greater morphological variation that could be present in some species will probably be underrepresented.

Morphological analysis and deconstructions

Gothanopteridieae

Gothanopteris (Fig. 4.3): The analysis and deconstruction of the morphology of *Gothanopteris* shows two areas in which venation from different origins meets and appears to fuse. One is the vague sutural vein (or sutural line), where the ultimate venation meets between the penultimate veins. The other is the triangular delineation, where the subsidiary venation reaches the regular ultimate venation. If we separate the different areas of the pinna along these lines, the subsidiary venation that stands at a different angle to the regular ultimate venation must be interpreted as originally having been a part of the pinna that was distinct from the regular pinnules. We interpret it here as an intercalated pinnule which was present in the initial stage. Another possible interpretation would be that the subsidiary venation consists of the remains of a strongly reduced pinnule, but the absence of any remnant of a midvein in this part makes this a less likely solution. The anastomosations of the ultimate venation are too regular to have been the result of deformation during the fusion process and are therefore interpreted as having been present in the original unfused form.

Palaeogoniopteridieae

Palaeogoniopteris (Fig. 4.5): The morphology of *Palaeogoniopteris* shows one area in which venation from different origins meets and appears to fuse at the distinct sutural veins (often, but not always, extending all the way to the second-order vein) that separate the pinnate ultimate venation of the pinnae. The venation pattern that occurs in the decurrently sloping margin of the larger pinnae (Figs 4.4B, 4.5A) is far more complex, and a possible solution for resolving this pattern, taking the origins of the subsidiary venation as a starting point, is given in Figure 4.5A. Judging by the direction of the individual veins and their origin in both the first-order venation (subsidiary veins) and second-order veins, they are interpreted as originally having been individual pinnules sloping down from the pinnae into the basal basiscopic part of the rachis. The fusion process conflated these pinnules and the anastomosing venation patterns are the result of intersecting veins that mostly retained their original orientations. An alternative explanation is that these patterns originated through fusion of the pinnae with an intercalated pinnule. However, the angle of the subsidiary venation corresponds with that of the venation of the basiscopic side of the neighbouring pinna. In the case of an intercalated pinnule, a venation direction perpendicular to the first-order vein would be expected.

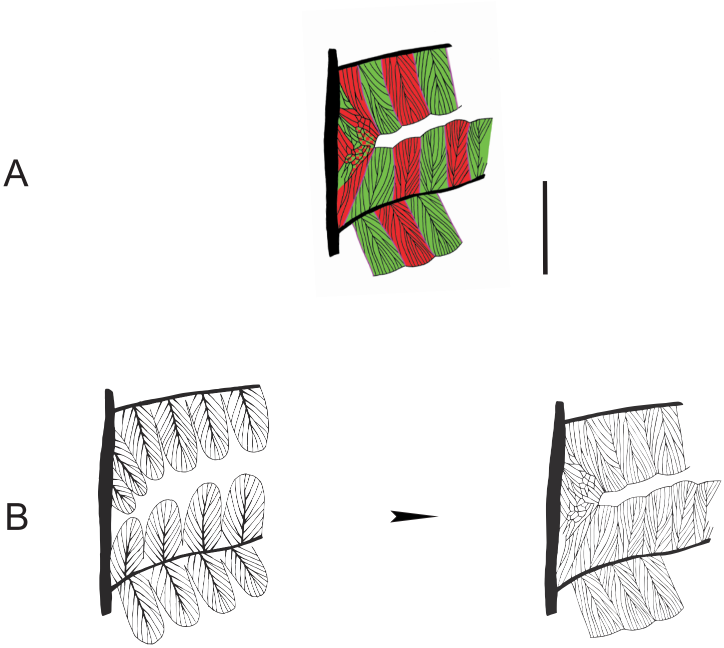

Figure 4.5: A, Semi-schematic drawing of venation patterns throughout several pinnules of *Palaeogoniopteris mengkarangensis,* based on specimens 45 352 and 45 355 (see Fig. 4), with venation from different origins and sutural veins indicated with different colours. Checkered area indicates venation of unclear origin. Scale bar, 1 cm. B, Deconstruction of *P. mengkarangensis.*

Gigantopteridium (Fig. 4.6): *Gigantopteridium americanum* (White, 1912) occurs in the late Early Permian of North America and *Gm. huapingense* in the Middle Permian of south China (Shen, 1995). Despite the geographical and chronological distance, the differences between the species are relatively slight and occur mainly in general frond morphology and in the angle between the first- and third-order venation. Therefore, they fall under the same (morpho)genus (Liu & Yao, 2002).

Analysis of the morphology of *Gigantopteridium* reveals two areas in which venation from different origins meets. The first is where the ultimate venation of two penultimate veins fuses to form a sutural vein parallel to the penultimate veins. A second presents itself if we interpret each point at which the ultimate venation branches off from the penultimate venation as originally constituting a separate pinnule. A slight deformation of the original venation patterns (mainly in *Gm. huapingense*) might have occurred, resulting in occasionally anastomosing veins. In addition, some of the original ultimate venation seems to have been lost. When we separate the different venation structures along these proposed lines, it reveals a section of subsidiary venation between the penultimate veins. In *Gm. huapingense*, the subsidiary venation runs mainly perpendicular to the first-order vein and at a noncongruent angle to the ultimate venation. This distinguishes it from the regular pinnae and it is therefore interpreted as originally having been an intercalated pinnule. In *Gm. americanum*, on the other hand, the subsidiary venation runs in the same direction as the neighbouring basiscopic ultimate venation. In addition, it displays the same type of 'bundled', pinnate venation as occurs in the regular ultimate venation. They are therefore interpreted as pinnules sloping down from the penultimate order vein (sensu Laveine, Coquel & Loboziak, 1977).

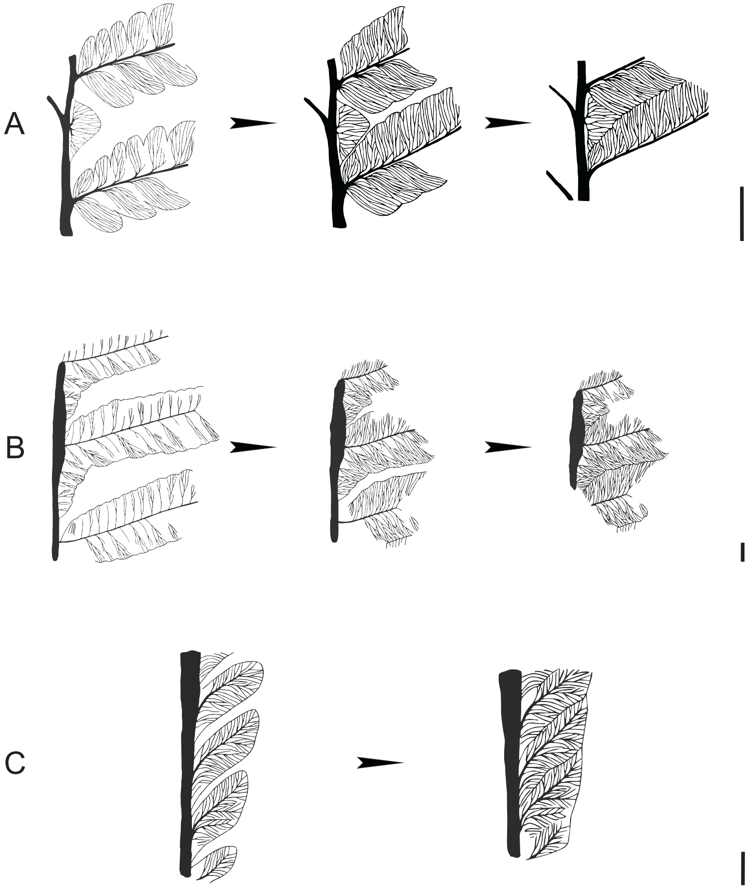

Figure 4.6: Deconstruction of three species included in the genus *Gigantopteridium*. A, Original *Gm. huapingense* redrawn from Liu & Yao (2002, text fig. 3). B, Original *Gm. americanum* based on White (1912, plate 46, fig. 2). C, Original '*G.*' *marginervum* based on Yao & Liu (2004, plate I, fig. 1). Scale bars, 1 cm.

Gigantopteridium marginervum from the Middle Permian of south China is a morphologically related species. Yao & Liu (2004) originally classified this species as *Gigantopteridium*, but DiMichele et al. (2005) called this attribution into question, because of the presence of marginal circumferential veins in the secondary venation, not seen in other species of *Gigantopteridium*. Despite this, it can be deconstructed along similar lines as the other *Gigantopteridium* spp., although the individual pinnules are here more clearly delineated by the sutural veins than is usual in this genus.

Zeilleropteris (Fig. 4.7A, B): The known species of *Zeilleropteris* include *Z. wattii* (Mamay, 1986), Z. *yujiaensis* and *Z. yunnanensis* (Zeiller, 1907), which has a roughly similar venation pattern to *Z. yujiaensis*; the first is found in the late Early Permian of North America and the last two come from the Late Permian of north(east) China. An analysis of the known venation morphology shows two areas in which venation from different origins meets. One occurs at the point at which the ultimate venation from two adjacent antepenultimate veins meets and fuses. The other occurs where the ultimate veins between two neighbouring penultimate veins fuse, forming meshes. The subsidiary veins adjacent to the penultimate order veins appear to slant acroscopically; therefore, these are interpreted here as having originally been subsidiary veins of a basiscopically decurrent part of the lamina.

Cathaysiopteridieae

Cathaysiopteris (Fig. 4.7C, D): *Cathaysiopteris whitei* from north China and *Cathaysiopteris yochelsonii* (Read & Mamay, 1964; Mamay, 1986) from North America are strikingly similar in almost all aspects of their morphology. The main differences between the two species is the presence of accessory veins in *C. whitei* (Yang, 1987; Liu & Yao, 1992), which give rise to the sutural vein and are absent in *C. yochelsonii*, and the smaller angle under which the tertiary venation leaves the secondary venation in *C. whitei*.

An analysis of the morphology of *Cathaysiopteris* shows one area in which venation from different origins clearly meets and fuses along the sutural vein that runs parallel to the penultimate veins (as described above). If we divide the venation pattern along this line, it results in the individual pinnules forming a pinnate leaf with a regular venation of three distinct stages. In *C. whitei*, the accessory veins are interpreted in an analogous manner to similar veins seen in *Emplectopteris* (for example, Liu et al., 1996, text, fig. 5) and *Gigantonoclea* (for example, Wang, 1999, text, fig. 2C), so that, in the deconstructed form, they end in the deeply sinuated part between the pinnules. In the case of *C. yochelsonii*, which lacks these accessory veins and has subsidiary veins arising from the first-order venation, it is also likely to suppose that the pinnules were originally connate at the base.

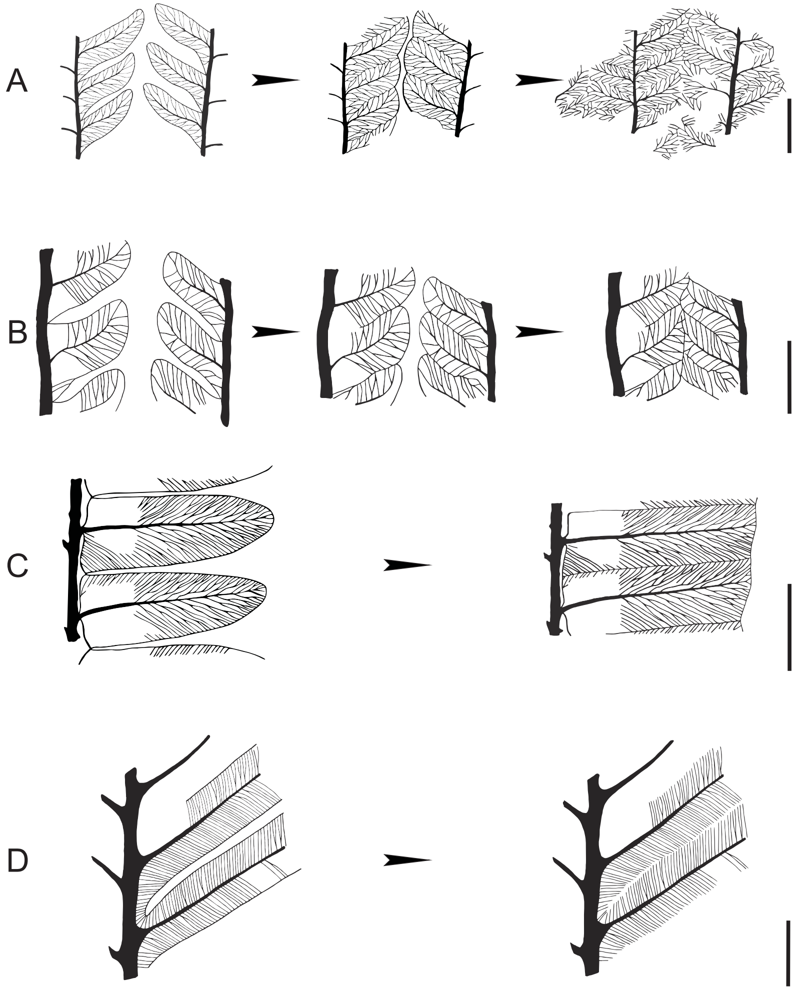

Figure 4.7: Deconstruction of two members of Palaeogoniopteridieae, both from the genus *Zeilleropteris*. A, Original *Zeilleropteris wattii* based on Read & Mamay (1964, plate 19, fig. 1). B, Original *Z. yujiaensis* redrawn from Huang (1980, fig. 37). Deconstruction of two members of Cathaysiopteridieae. C, Original *Cathaysiopteris whitei* based on Gu & Zhi (1974, text fig. 103, no.1) and Liu & Yao (1992, text fig. 5). D, Original *C. yochelsonii* after DiMichele et al. (2005, fig. 13C). Scale bars, 1 cm.

Unclassified

Evolsonia (Fig. 4.8A): Deconstructing the single known species of *Evolsonia*, *E*. *texana* Mamay, poses problems as a result of some irregularity in the venation patterns. This may partly be caused by the less than detailed preservation of the original specimens of Mamay (1989). An analysis of the morphology shows two areas in which venation from different origins comes together. One is where the ultimate venation from two neighbouring antepenultimate veins meets (resulting in an interlocking pattern), and the other is between the ultimate venation from two neighbouring penultimate veins. In both cases, vague sutural lines, indicated as broken lines in the original drawing by Mamay (1989), mark these areas. Separating the venation along these lines reveals individual pinnules with pinnate venation of varying complexity. The individual pinnules appear to have become fused without much deformation in the venation.

Neogigantopteridium (Fig. 4.8C): The single species of *Neogigantopteridium*, *N. spiniferum* Yang (1987) from the Permian of Yuxian, China, can be deconstructed along rather similar lines to *Zeilleropteris*, as it shares most of its characteristics with that genus. The fusion processes seem to have led to little or no deformation of the original venation. An analysis of the known venation morphology suggests two areas in which venation from different origins meets and fuses. The first is at the point at which the ultimate venation from two adjacent antepenultimate veins meets and anastomoses. The second occurs where the ultimate veins between neighbouring penultimate veins anastomose, forming meshes. The subsidiary veins neighbouring the penultimate order veins appear to slant acroscopically; therefore, these are interpreted here as having originally been subsidiary veins of a small basiscopically decurrent part of the lamina.

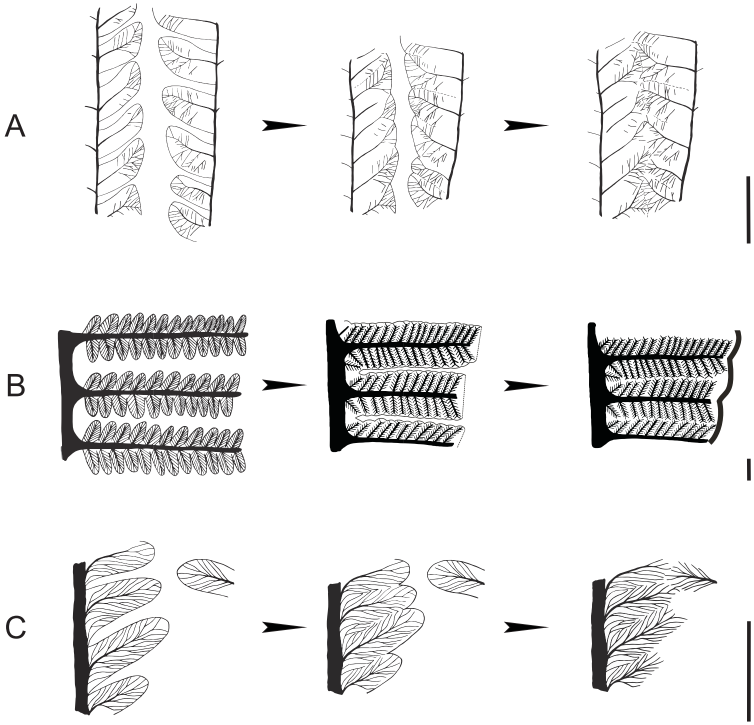

Figure 4.8: Deconstruction of three members of the gigantopterids without assigned supergeneric classification. A, Original *Evolsonia texana* redrawn from Mamay (1989, fig. 14). B, Original *Delnortea abbottiae* based on Mamay et al. (1988, figs 18, 19). C, Original *Neogigantopteridium spiniferum* redrawn from Yang (1987, text fig. 9). Scale bars, 1 cm.

Delnortea (Fig. 4.8B): The single known species of *Delnortea*, *D. abbottiae* Mamay (Mamay et al., 1984, 1988), has a very regular morphology in which no indications are present of any deformation of the pre-existing venation patterns. Areas in which the venation of different origins meets are both between the fourth-order veins and between the third-order veins. The only possible areas in which the original parts of the pinna would have become fused are between the ultimate venation from two adjacent antepenultimate veins and between the ultimate venation of two adjacent penultimate veins. Separating the venation along these lines reveals pinnules with uniformly and rigidly pinnate ('herringbone') venation.

Interpretation of gigantopterid morphology

Features of the deconstructed forms

From the deconstruction of the different species found in the gigantopterids, several general features resulting from the fusion process can be found.

Deconstructing the known venation patterns in these gigantopterid forms results in pinnae with recognizable separate pinnules that often have a simple form of pinnate venation. In some instances (*G. bosschana*, *Gm. huapingense*), structures with venation at a right angle to the rachis are found, without a clear central vein. These could be interpreted as former intercalated pinnules or, alternatively, as broad connate areas between pinnules. From this, we conclude that there is a tendency for most of the original features of the leaf morphology to be retained in the fused forms.

Sutural veins are most commonly seen between ultimate venation from adjacent pinnules or from adjacent pinnae. However, their occurrence is not a completely regular feature in gigantopterids. It is, for example, unclear why they occur between ultimate venation from adjacent penultimate veins in *Palaeogoniopteris*, but are absent between ultimate venation from adjacent penultimate veins in *Zeilleropteris*. A possible reason underlying this irregularity might be that a sutural vein would originate as a border vein of the original pinnule and that the emergence of a sutural vein is formed through merging of these border veins. However, although *'Gigantopteridium' marginervum*, in particular, still appears to have preserved the border veins in the known leaf morphology, in most gigantopterid genera no real substantiating evidence for this idea can be found. An alternative explanation for the origin of a sutural vein might be a strongly reduced pinnule. This would be most likely where sutural veins are prominent, as in Palaeogoniopteris. In such cases, the sutural vein could be the remnant of a penultimate vein where the ultimate venation was either strongly reduced or became completely fasciculated. Finally, some uncertainty also exists about whether sutural veins should in all cases be considered true veins, containing conducting vascular tissue, or are sometimes only sclerenchymal thickenings of the lamina. Unfortunately, evidence from, for example, permineralized gigantopterid leaves, which could shed light on these questions, has not yet been found.

History of leaves and venation patterns

The most basic division among tracheophyte leaf types is that between microphyllous and megaphyllous leaves. Microphyllous leaves are characterized by their small size and usually only have a single vascular trace, whereas megaphyllous leaves usually have branching venation and a large variety of leaf shapes (Foster & Gifford, 1959; Tomescu 2008). Megaphyllous leaves have developed independently at least twice in the history of vascular plants, in ferns and in seed plants (gymnosperms and angiosperms), although the actual number might be much higher (Boyce & Knoll, 2002). Different scenarios based on morphological data have been proposed, and can differ strongly in the number and affiliation of independent emergences of megaphyllous leaf growth (Friedman, Moore & Purugganan, 2004, and references therein). However, there is so much variety in the different genetic pathways of leaf formation, even within the angiosperms, that the number of independent emergences of megaphyllous leaf growth is likely to be high (Tomescu, 2008). More data from molecular studies outside the angiosperms is needed to resolve this question.

The main distinction within megaphyllous plant groups is between taxa with discrete marginal leaf growth and those with diffuse intercalary growth. Ferns and most gymnosperms belong to the first group (Zurakowski & Gifford, 1988; Boyce, 2007; H. Kerp, Palaeobotany Research Group, University of Münster, 2008, pers. comm.), whereas leaves indicative of the second group are found in Gnetales and the angiosperms (Esau, 1965; Hagemann & Gleissberg, 1996).

Venation pathways and patterning are primarily determined by active proximal transport of distally produced auxin (Gälweiler et al., 1998; Scarpella et al., 2006) and a subsequent complex process of auxin focusing and auxin drainage towards preexisting veins (Poli, Jacobs & Cooke, 2003; Scarpella et al., 2006; Boyce, 2008, fig. 1.1). Marginal growth usually results in parallel running venation with occasional dichotomous bifurcations. Net venation is uncommon in taxa with marginal leaf growth, but occurs in several extant fern taxa, for example *Ophioglossum* L., *Christensenia* Maxon and, and a number of filicalean lineages (for example, Dipteridaceae). Among extinct gymnosperm megaphylls, we find net venation in Liginopteridales, Glossopteridales and the gigantopterids (Taylor & Taylor, 1993; Trivett & Pigg, 1996; Boyce, 2008).

However, a distinction can be drawn between two different types of net venation. The first seemingly comes about through lateral fusion of parallel venation, resulting in more or less elongated meshes oriented parallel to the general venation, and is further characterized by a lack of hierarchy in vein width. In the other, the venation is regularly seen to curve in on itself, and usually has clearly distinguishable hierarchical orders of vein size, next to blind vein endings. Amongst extant plants, the last type is exclusively observed in angiosperms (Trivett & Pigg, 1996).

Remarks on gigantopterid ecology and habit

Several authors have described gigantopterid species as climbing plants. In the material from Shansi, Halle (1927, 1929) found several hook-bearing pinnae associated with and attributable to *Gigantopteris nicotianaefolia* and *Gc*. *lagrelii*. He interpreted these as climbing structures and the species as lianas. Li & Taylor (1998, 1999) interpreted permineralized stem remains, belonging to *Gigantonoclea* and *Gigantopteris*, as lianas or vines growing in a tropical rainforest environment on the basis of general ecology, morphology, stellar architecture and the presence of hooks and spines. They interpreted *Gigantopteris* (*Vasovinea*) as growing in the open sunlight part of the canopy and *Gigantonoclea* (*Aculeovinea*) as growing in the shady understorey.

The gigantopterid habitat has sometimes been characterized as wet to very wet. Li et al. (1994) described *Gigantonoclea* guizhouensis as probably living in a tropical climate with high precipitation. Beck & Labandeira (1998) described a Permian flora from north Texas, dominated by the gigantopterids *Cathaysiopteris*, *Gigantopteridium* and *Zeilleropteris*, as riparian. Wang (1999) interpreted *Gc*. *lagrelii* as an aquatic plant with partially submerged leaves.

Other authors have found gigantopterid ecology to be more mesic in nature. Mamay (1989) compared the large leaves of *Evolsonia* to those found in present-day tropical understorey vegetation, but also remarked on their coriaceous texture and occurrence in depositional settings interpreted as subject to periodic drought. Wang (1999) described *Gigantonoclea pubescens* Wang as growing in open sunlight and under arid conditions.

It has been suggested (most notably by Asama 1959, 1960) that the emergence and development of the gigantopterids was climatologically driven. A similarity in ecological circumstances would provide analogous selective pressures that could result in convergent evolutionary patterns. However, the preceding evidence shows that gigantopterids have been interpreted as growing in a variety of different habitats, varying from forest mires to areas subject to periodic drought. It is therefore unlikely that climatological circumstances and ecology would have been the only factors that shaped gigantopterid evolution.

Gigantopterid leaf growth

One of the main problems in gigantopterid classification is the rarity of directly associated (attached) reproductive structures. Li & Yao (1983b) described them from leaves attributable to *Gigantonoclea* (ovulate- and pollen-bearing organs) and Zhu & Zhang

(1995) described them from *Trinerviopteris* (sori). Another find of 'rounded bodies' in *Gigantonoclea*-like leaves was described as *Linophyllum xuanweiense* by Zhao et al. (1980). In all of these cases, no pollen or spores could be obtained from the specimens. In addition, the specimens show only little detail because of bad preservation, and belong to Chinese genera with polygonal venation. As sori and other reproductive structures are so rarely found on the leaves, although fairly large amounts of leaf material from most gigantopterid taxa have been collected, this strongly suggests that most gigantopterid taxa had reproductive structures that were separate from the leaves.

Boyce (2005) argued that the medullosalean seed fern morphology, in which the reproductive structures are integrated in the fronds (for example, Zodrow 2004), places limitations on the morphological variability of these fronds. In geologically younger seed fern clades, such as the Peltaspermales, in which reproductive organs have become separate from the vegetative parts of the plant, leaf shape would no longer be limited by the dual vegetative/reproductive role. [Another option is leaf heteromorphy, such as seen in *Gigantonomia* Li & Yao (1983b), where the presumed ovules are found in leaves that are much narrower than sterile ones.] This would help to explain why the relatively large and entire leaves, which characterize the gigantopterids, are not seen in ferns or seed ferns before the Late Palaeozoic. It strengthens the case for a possible gigantopterid affiliation with a Late Palaeozoic seed fern group, such as the peltasperms, as already proposed by Meyen (1987) and DiMichele et al. (2005).

Next to the location of the reproductive structures, another limiting factor in leaf size might be the marginal leaf growth that characterizes both ferns and gymnosperms. Marginal leaf growth allows for only a limited range of possible venation patterns, in which ultimate veins are always oriented towards the margin where growth occurs and always end in that margin (Boyce, 2007, 2008). Although anastomoses can occur, they are usually of a far simpler nature than those found in modern-day angiosperms (Roth-Nebelsick et al., 2001).

Larger leaves, because of a resulting thicker boundary layer surrounding the lamina and hindering the diffusion path of transpiration, heat up more quickly (Givnish, 1979). (This is analogous to the wellestablished positive correlation between potential transpiration and leaf venation density; Uhl & Mosbrugger 2002; Uhl, Walther & Mosbrugger, 2002.) In order to mitigate these consequences, an increase in water transport efficiency through higher venation density is a necessity. However, the options towards this, within a framework of marginal leaf growth, are limited. Although extreme cases of densely packed parallel venation are known from the fossil record, such as in leaves of *Cordaites* or *Macralethopteris* (Booi et al., 2008), this would have a significantly negative effect on the amount of space in the lamina available to photosynthetic parenchyma. Alternatively, a reticulate pattern can lead to higher venation densities with far less consequences for blocking solar radiation.

Venation densities in gigantopterids can reach 5 mm of vein length per square millimetre of leaf surface, compared with an average vein density of 2 mm of vein length per square millimetre of leaf surface in regular Palaeozoic laminate leaves (Boyce, 2008). In addition, although several plant groups, such as *Comia* Zalessky and *Protoblechnum* Lesq./*Compsopteris* Zalessky, developed larger leaves in the Early to Middle Permian (Laveine et al., 1977; Kerp,1996; Naugolnykh, 1999), no other Palaeozoic plant group developed the leaf sizes for entire leaves that we see in the gigantopterids.

Therefore, a case could be made that two factors were elemental in the evolution of the gigantopterids, the first being the segregation of reproductive and vegetative structures in the plant, and the second the need for high vein densities for better water transport in larger leaves.

One of the main questions to be answered is what the physiological process might have been that would have led to these large leaves and reticulate venation. Unfortunately, little research has been performed on the developmental mechanisms of gymnosperm leaf growth, and even less is known about extinct groups of gymnosperms, such as seed fern clades. However, assuming a similar process of marginal growth such as seen in present-day ferns and gymnosperms, the active leaf meristem would always have been situated at the margins of the individual leaflets or pinnules. It is possible to imagine that, where marginal meristems would have touched as, for example, between two neighbouring pinnules, the meristem might have fused, a process perhaps analogous to that described as leading to sympetaly or syncarpy in present-day angiosperms (De Laet et al., 1995; Endress, 2001). However, the exact mechanism behind this is still unclear. In addition, whether this process took place ontogenetically or phylogenetically, or through a combination of these, is yet to be determined. The end result of such a first evolutionary stage of fusion may have looked something like the morphology seen in the Jambi gigantopterids *G. bosschana* and *P. mengkarangensis* (Figs 4.3, 4.5), but also in some species of *Gigantonoclea* [for example, *Gc. lagrelii* (Wang, 1999, text fig. 2A, B, text fig. 3)]. A further fusion of the apical marginal meristem of pinnules of neighbouring pinnae would have then led to the coherent leaves with three or four orders of venation that we see in most gigantopterids. Following this line of reasoning, the fusion of individual pinnules forming a coherent leaf can be seen as a strategy towards reticulate venation in plant groups whose possibilities for leaf venation patterns were limited by their marginal leaf growth.

The fusion process, outlined above, appears to have been conservative in nature; much of the original form of the fused pinnules is still present in the fused leaves. In this context, the one exception among gigantopterid taxa appears to be *Gigantopteris*, in which none of the pinnulate structures that can be seen in all other gigantopterid genera can be found. Instead, the venation of *Gigantopteris* is characterized by two orders (first and second) of clearly pinnate venation, but culminates in the penultimate and ultimate venation (fourth and fifth order) characterized by polygonal venation, one surrounding the other. In several *Gigantopteris* spp., these ultimate orders of venation also feature blind vein endings (Glasspool et al., 2004a). In these characteristics, the venation of *Gigantopteris* is radically different from that found in all other gigantopterid genera, and is suggestive of a different and derived mechanism of laminar vascular growth from that commonly seen in fern and gymnosperm leaves.

Possible phylogenetic implications of the deconstructed morphologies (Table 4.4)

Similarities in the morphologies of the deconstructed forms allow the gigantopterid species analysed above to be divided across four distinct groups based on the characters of their venation (Table 4.4). The first division divides the forms across two groups, one with anastomosing ultimate venation and one with pinnate ultimate venation. The latter group can be further subdivided according to the presence of additional characters. This results in three more groups, the first with only simple pinnate venation, the second with pinnate venation and subsidiary veins (in a decurrent basiscopic lamina) and the third with pinnate venation and intercalated pinnules. Some of these morphological boundaries can be crossed (for example, reductions can result in the loss of intercalated pinnules or a decurrently sloping lamina). However, it can be postulated that these four groups represent the minimum of distinct morphologies that were present in the earlier morphologies of these gigantopterid genera.

The most remarkable aspect of the morphology of *Gothanopteris* among the gigantopterids analysed here is the regularity and homogeneous occurrence of the anastomosing ultimate venation. In this respect, it appears to be much more closely related to genera such as *Gigantopteris* and *Gigantonoclea* than to most gigantopterids, in which the venation patterns are of a far more pinnate nature. However, the meshes in *Gothanopteris* are elongated, not distinctly polygonal and appear in only one hierarchical order of venation, which sets it clearly apart from the morphologies seen in most of *Gigantonoclea* and, particularly, in *Gigantopteris*.

The general morphology of the venation of *Palaeogoniopteris* is commonly found throughout several gigantopterid genera (see Table 4.4). However, although most gigantopterid fronds are interpretable as originally having been pinnate, usually this original morphology has become completely fused throughout the original frond. Palaeogoniopteris mengkarangensis is an exception to this rule as, in this species, the venation from adjacent secondary veins is still separate. In addition, the combination of pinnate venation with polygonal meshes found in *Palaeogoniopteris* is not seen in other forms of gigantopterids.

This number of nonoverlapping morphologies found in the gigantopterids supports the assertion of other authors (Mamay et al., 1984; Glasspool et al., 2004a) that the gigantopterids are a phylogenetically diverse and polyphyletic group, mainly held together by a homoplasious or convergent trend towards the fusion of pinnules, resulting in larger leaves and an increase in reticulation of the venation patterns caused by the fusing of venation. Moreover, the variation in basic morphologies, as shown in the deconstructions, suggests multiple emergence from several different Late Palaeozoic plant families. This recurring evolutionary pattern is seen throughout the palaeotropical zone, in the North American part of Euramerica and on the Asian subcontinents. The absence of any gigantopterid finds from the known European fossil record could even suggest independent emergence on both sides of the Amerosinian region, further increasing the polyphyletic diversity of this group. In general, the Jambi species appear to be morphologically similar to other gigantopterid genera, but also contain unique features that set them apart, thus making any direct phylogenetic connections unlikely.

Table 4 Characteristics of the venation patterns of the deconstructed gigantopterid species. Grouping according to similarities.

General pattern	Additional characteristics	Group	Species
Anastomosing venation	Anastomosing venation and intercalated pinnules	I	*Gothanopteris bosschana*
Pinnate venation	Simple pinnate venation	II	*Palaeogoniopteris mengkarangensis* *Cathaysiopteris whitei* *Evolsonia texana* *Delnortea abbotiae*
	Pinnate venation, subsidiary veins and decurrent basiscopic lamina	III	*Zeilleropteris wattii* *Zeilleropteris yujiaensis* *Zeilleropteris yunnanensis* *Cathaysiopteris yochelsonii*
	Pinnate venation and intercalated pinnules	IV	*Gigantopteridium huapingense*

Table 5 Proposed affiliations of the gigantopterids or groups within the gigantopterids. Specification of the basis for the interpretation is given in the table, the particular affiliations are indicated by colours.

	Schenk (1883)	Zeiller (1907)	Halle (1927)	Koidzumi (1936)	Asama (1959)
Gigantopterids (general)					
Gigantopteris	Leaf morphology	Leaf morphology	Leaf morphology		
Gigantonoclea			Leaf morphology		Leaf morphology
Trinerviopteris					
Gothanopteris					Leaf morphology (*Lonchopteris*)
Palaeogoniopteris					Leaf morphology (*Callipteridium*)
Gigantopteridium					(*G. americanum*)
Zeilleropteris		Leaf morphology			Leaf morphology (*Z. yunnanensis*)
Cathaysiopteris			Leaf morphology		Leaf morphology (*C. whitei*)
Evolsonia					
Neogigantopteridium					
Delnortea					
“*Gigantopteridium marginervum*"					
Cathaysian gigantopterids					
American gigantopterids					

Meyen (1984)	Li & Yao (1983a)	Li & Yao (1983b)	Li & Taylor (1998)	Li & Taylor (1999)	DiMichele et al (2005)
				Stem morphology	
	Reproductive structures	Reproductive structures (attached)	Stem morphology		
	Leaf morphology				
	Leaf morphology				
	Leaf morphology				
	Leaf morphology				
Leaf morphology					
Reproductive structures (association)					Reproductive structures (association)

5

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).

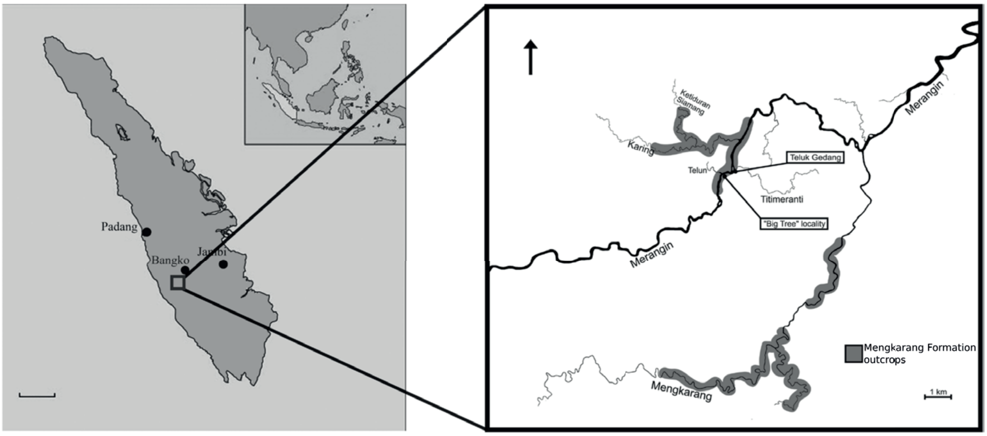


Figure 5.1: A map of Sumatra, Indonesia with insert showing the area southwest of Bangko: the Merangin River, its tributaries and the area where all the fossil wood material discussed was collected. The sections along the rivers where the Mengkarang Formation crops out are indicated.

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).

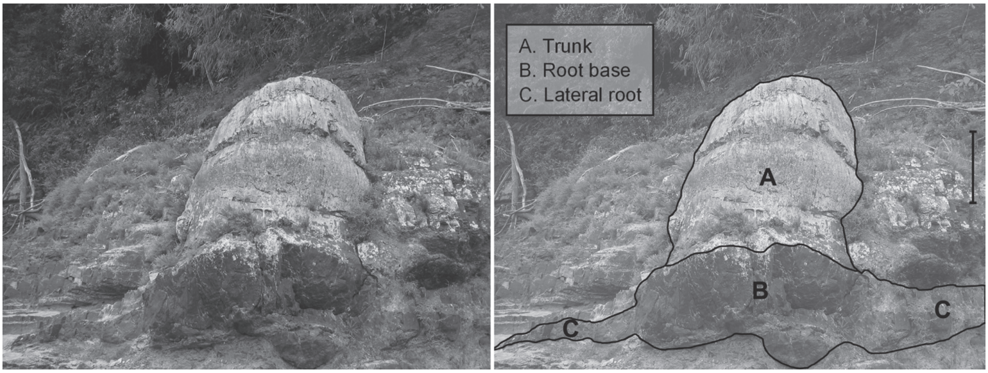


Figure 5.2: The large in situ tree trunk found on the bank of the Merangin River. The schematic overlay in one of the pictures illustrates the different parts of the trunk. – A: Trunk. – B: Root base. – C: Lateral support root on either side. Scale bar is 1 metre.

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.

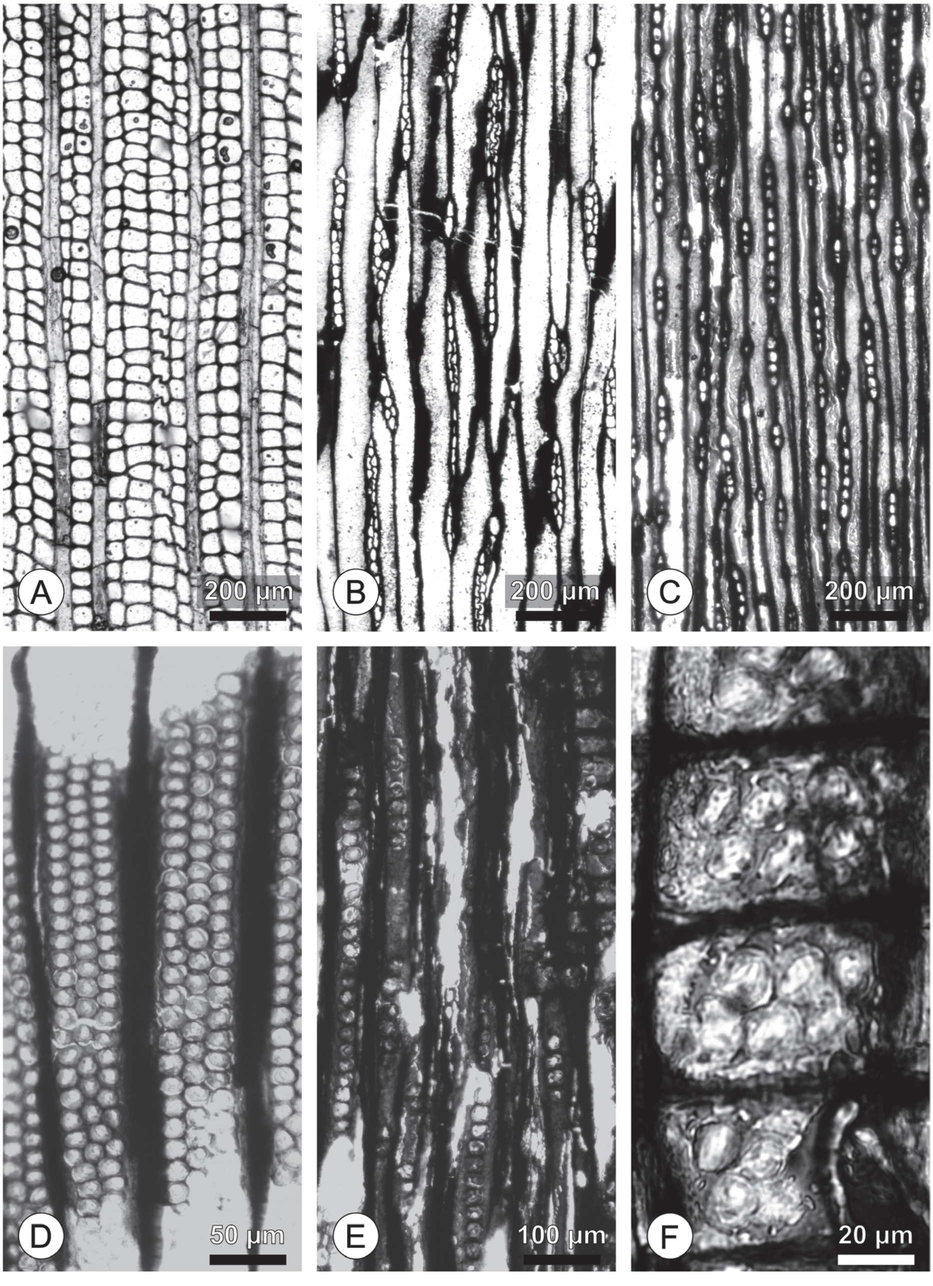


Plate 5.1: Wood anatomy of the pycnoxylic fossil wood from the Mengkarang Formation. – A: U-2188, transverse section, uni- and biseriate rays. – B: U-1744, tangential section, uni- and biseriate rays. – C: U-1584, tangential section, uniseriate rays. – D: U-1768, radial longitudinal section, three rows 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.

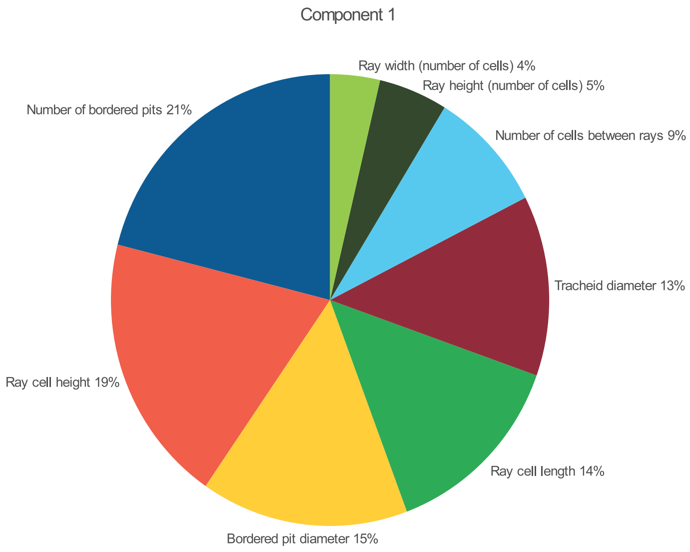
Table 5.2: The results of the Shapiro-Wilk test for normality. W indicates the test result. The last column (N) indicates the number of specimens in which the character was measured. * indicates the p-values significant at an alpha of 0.05.

	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).



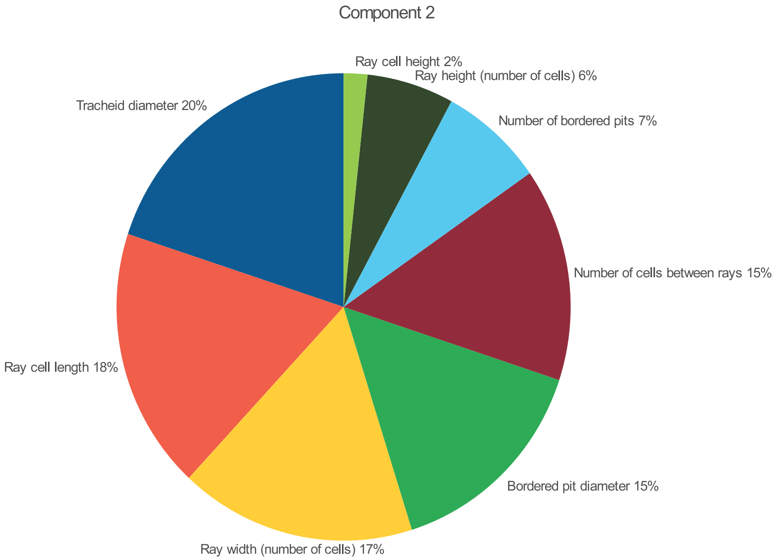


Figure 5.3: Two pie charts describing the relative contributions (loadings) of the characters used in the PCA to components 1 and 2.

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).

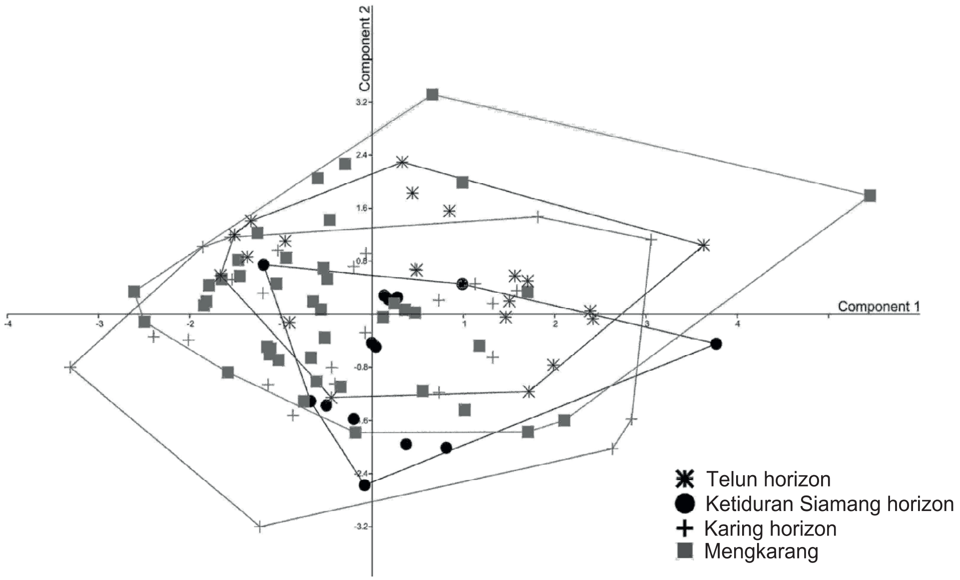


Figure 5.4: The PCA scatter plot for components 1 and 2. The symbols indicate the groups of rivers and streams where the respective specimens were found. This shows the distribution of anatomical and morphological variability by river along which they were found.

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.

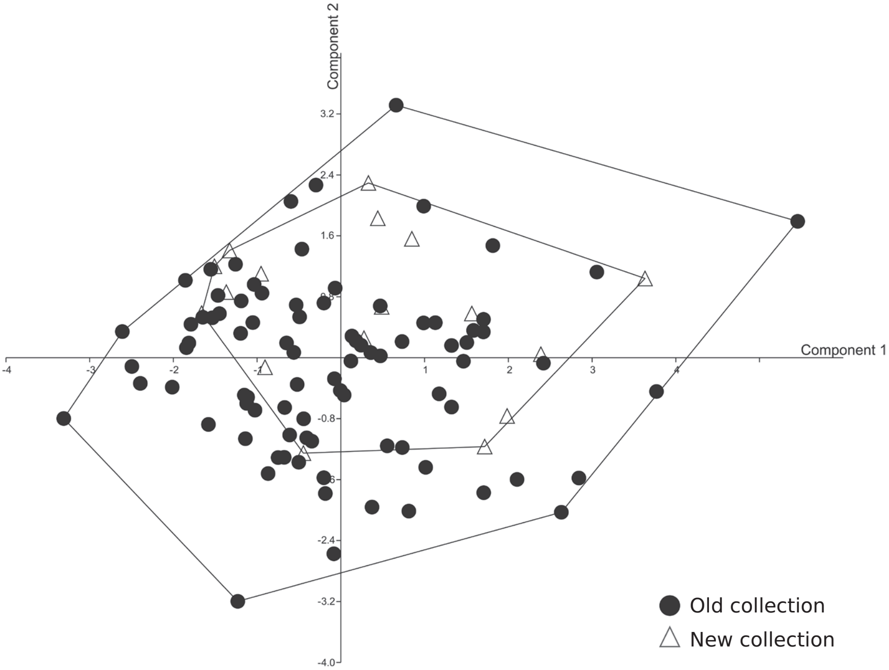


Figure 5.5: The PCA scatter plot for components 1 and 2. The symbols indicate whether the specimens come from the original or the recently collected material. This shows the differences in distribution of anatomical and morphological variability between these two collections.

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. kaurioides* 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.

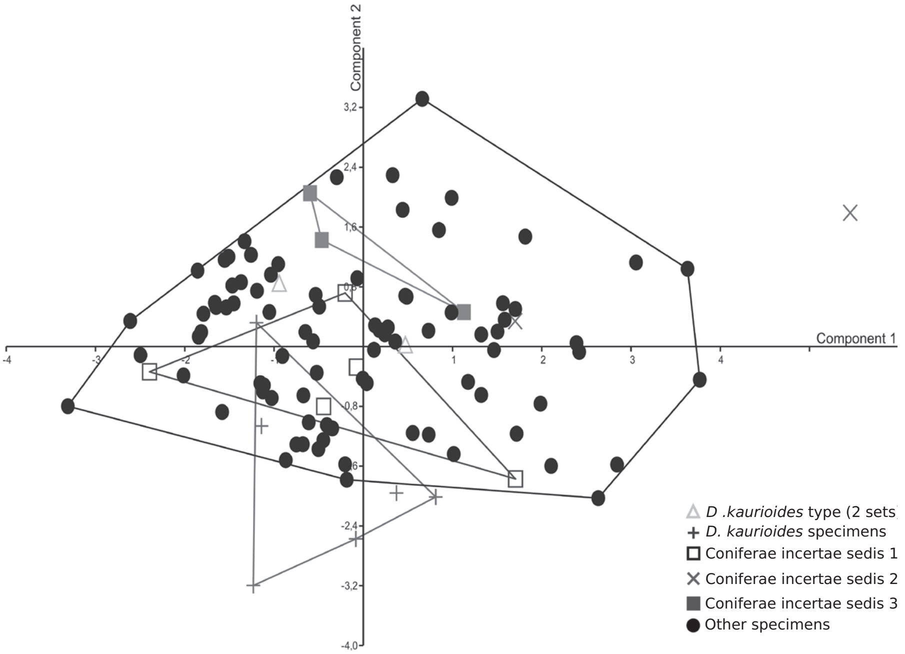


Figure 5.6: The PCA scatter plot for components 1 and 2. The symbols indicate the D. kaurioidesholotype and the different Coniferae incertae sedis groups proposed by Kramer. This shows thedistribution of anatomical and morphological variability in these groups.

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.

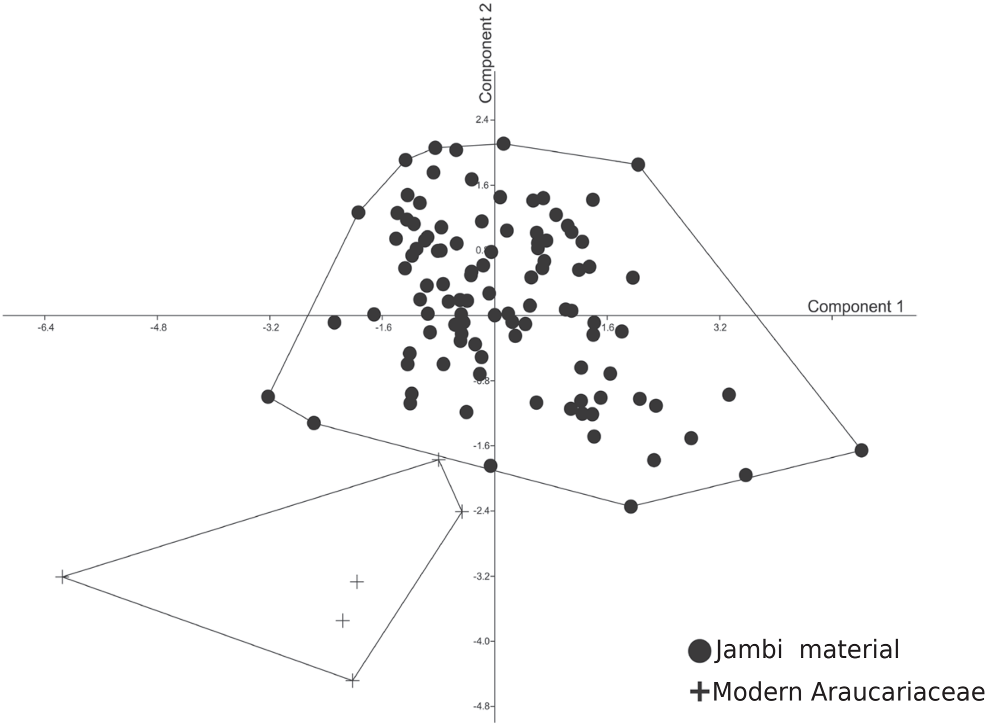


Figure 5.7: The PCA scatter plot for components 1 and 2 for the dataset including both the fossil wood from the Mengkarang Formation and the measurements taken from six modern Araucariaceae. The symbols indicate the older Mengkarang Formation derived material and the measurements taken from modern Araucariaceae. 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.

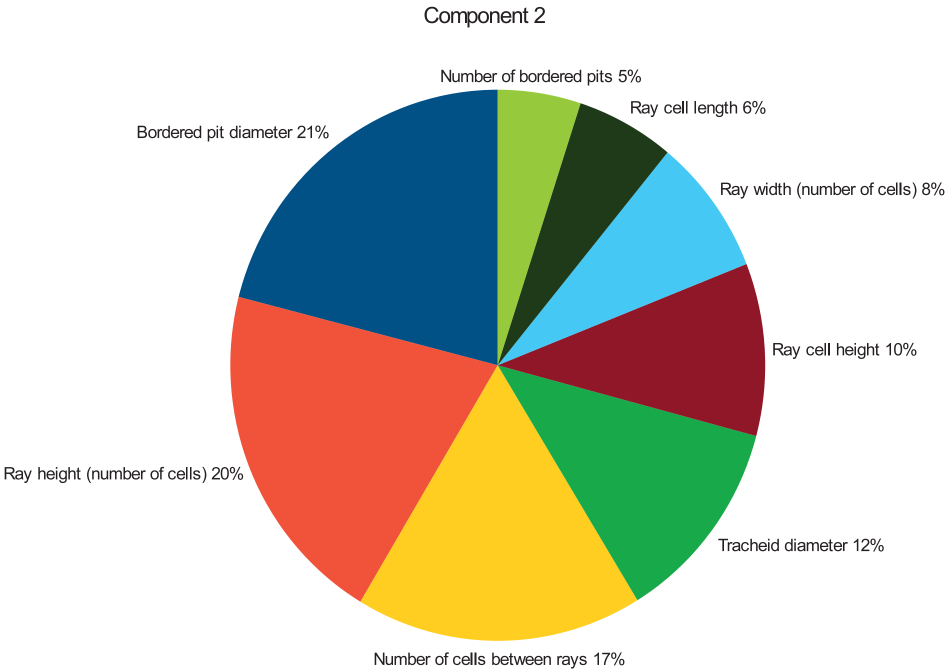


Figure 5.8: A pie chart describing the relative contributions (loadings) of the characters used in the PCA to components 1 and 2 of the dataset including both the fossil wood from the Mengkarang Formation and the measurements taken from six modern Araucariaceae.

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.

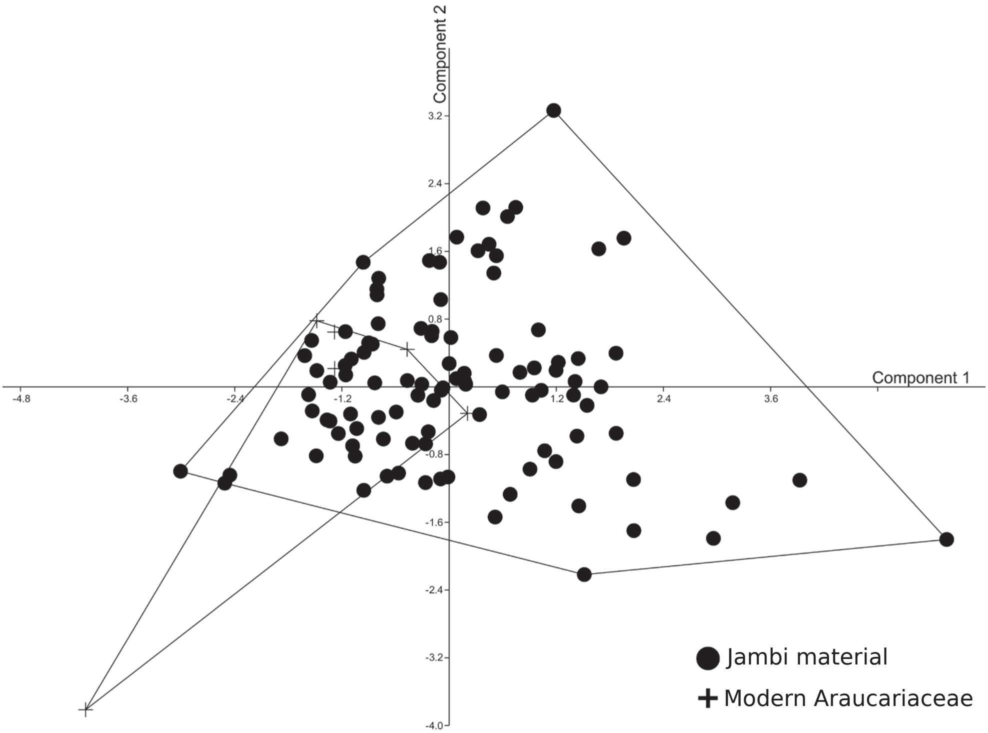


Figure 5.9: The PCA scatter plot for components 1 and 2 for the same dataset as used in Figure 7, but excluding the characters of 'number of tracheid cells between rays', 'ray height (number of cells)' and 'bordered pit diameter', showing the differences and overlap of remaining wood anatomical characters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

6

Burial and preservation of a fossil forest on an Early Permian (Asselian) volcano (Merangin River, Sumatra, Indonesia)[7]

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[7] Submitted to Geological Journal.

Abstract

In situ fossil forests, commonly silicified, may yield abundant palaeoecological and taphonomic data. The Early Permian (Asselian) Mengkarang Formation of the western Jambi Province, Sumatra, is well exposed in the valley of the Merangin River. No consensus regarding the depositional environment of this section had been reached hitherto. This section preserves abundant evidence of a Permian forest which grew at the foot of an active volcano, where pyroclastic flows often made way and destroyed the vegetation, and where epiclastic reworked pyroclastics rapidly entombed the vegetation. The present assessment is based on a detailed study of three localities using multiple lines of evidence, including petrography, palynofacies analysis and silica typing, including cathode luminescene methods. In situ Agathoxylon was near enough to the volcanic slope to be buried rapidly, shallow enough to avoid extreme crystallisation in the lumina and far enough from the metamorphic centre not to get recrystallized. All these combined contingencies make this a most unique find that provides significant insights into a rarely studied palaeoecological setting from the Early Permian.

Introduction

Silicified *in situ* fossil forests hold a wealth of palaeoecological information. Their preservational histories have intrigued scientists for centuries. Among the most famous is the Triassic fossil forest discovered by Darwin in 1835 in Argentina. It consists of 52 fossil *Araucarites* (Darwin, 1846) buried by a wet pyroclastic base surge flow (Brea *et al*., 2009). The classic Carboniferous Joggins section, first described by Lyell and Dawson (1853), is typified by more than 60 horizons of lycopsids (club mosses and related taxa) where preservation follows from an inter-distributary deltaic system prone to disturbance, and where crevasse splays and bay fills entombed the standing trees (Calder *et al*., 2006). A different preservational setting is found in the alluvial Petrified Forest Member in the Triassic Chinle Formation of Arizona, where trees are large and countless, but not *in situ* (Gastaldo and Demko*,* 2011). Preservation in the Chinle Formation is explained in a broad geological context by a transition from a low stand to a climbing system track; burial is alluvial. A particularly interesting case is the very detailed silicification of the Middle Pennsylvanian peat-forming vegetation from the Radnice basin in Czech Republic. Various consecutive ash falls entombed lepidodendrales (scale trees) in growth position (Opluštil *et al*., 2009). The spectacular Chemnitz occurrence, in the Early Permian of Germany, consists of a petrified forest ecosystem holding 53 araucarioid trunks in growth position, which were buried by both pyroclastic flows and ashes (Rößler *et al*., 2012).

The Mengkarang Formation outcrops along the Merangin River in the western Jambi province on Sumatra (Zwierzycki, 1935). The 1925 map of the Jambi expeditions marked the position of a '*Dadoxylon*' locality in this river valley. More than 125 fossil wood samples from this expedition were counted in the collections of the University of Utrecht. The 2004-2006-2008 expeditions to this province of Sumatra confirmed the presence of numerous horizons holding *in situ* and transported wood. A full taxonomic inventory has been determined for the total of 157 gymnospermous samples collected from the Mengkarang Formation both during the 1925 and the 2004-2006-2008 expeditions (Booi *et al*., 2014).

As seen from the above few examples, the circumstances of silicification of *in situ* forest systems are generally depicted as either pyro- or epiclastic, that is, volcanic or alluvial. The Early Permian Mengkarang Formation on western Sumatra represents a true dilemma as no consensus on its depositional setting has been achieved hitherto. Reviewing the relevant literature, there is an unresolved controversy with respect to the details of the circumstances of silicification of the trees because the depositional setting of the Mengkarang Formation is depicted on stratigraphic maps as having an inter-fingering alluvial and volcanic character (Suwarna *et al*., 1994). Indeed, originally the deposits outcropping along Merangin section were considered chiefly volcanic (Zwierzycki, 1935) and it is only lately that the alluvial character of the Mengkarang Formation has been emphasized (Suwarna, 2006).

Discrimination between pyroclastic and epiclastic sedimentary rocks is complex, not only because the nomenclature is generic, but also because volcanic landforms result from near-simultaneous constructive and destructive forces (Thouret, 1999). To elucidate the preservational history of the Jambi silicified forest, we present:

1. the detailed analysis of three exposures where contemporary erosion has prepared what could be considered a palaeorelief;
2. the petrography of the entombing rocks;
3. the organic micropaleontology of the shales; and
4. the X-ray diffraction and the cathode luminescence results of the silicified wood.

Geological setting

Rapids in the Merangin and Mengkarang rivers expose the strongly silicified Palaeozoic volcanic and alluvial sedimentary rocks in the foothills of the Barisan Mountains in the west of the Merangin Regency of the province of Jambi on Sumatra (Fig. 6.1A). The Mengkarang Formation was named by Suwarna *et al*. (1994); previously, Zwierzycki (1935) had defined these rocks as the ‘Karing Beds’ in a continuous stratigraphic sequence overlain by the ‘Salamuku Beds’ and in turn by the ‘Air Kuning Beds’. The regional mapping programme by the Geological Research and Development Centre, now the Pusat Survei Geologi, revised the local stratigraphy into two interleaving formations, namely the Mengkarang (mainly sedimentary) and Palepat (mainly volcanic) formations (Suwarna *et al*., 1994). Suwarna *et al*. (1998) introduced the Telukwang Formation which interleaved with the Mengkarang Formation (below) and the Palepat Formation (above).

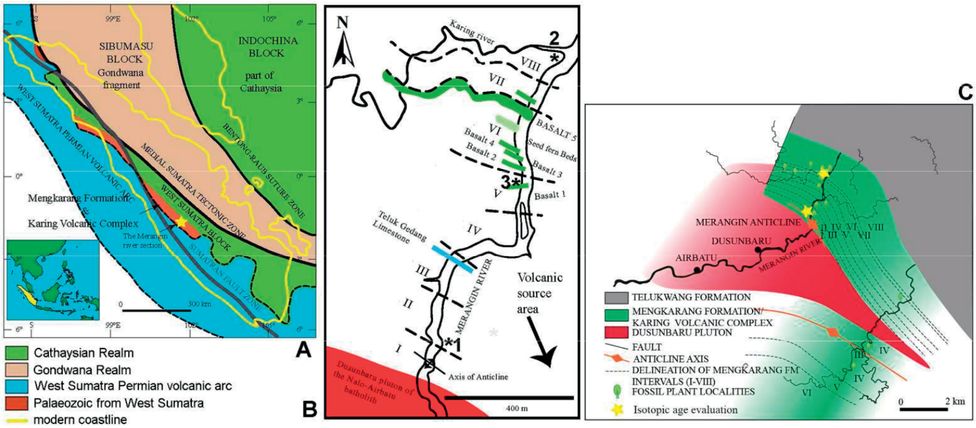


Figure 6.1: Tectonic and locality maps. (A) Position of the Merangin River section in a geological context. Sumatra and nearby landmasses outlined in yellow. Inset map shows the position of Sumatra (yellow) in south-east Asia. (B) Map of the geology of the Merangin River section. Intervals I–VIII, identified informally herein, will be described in detail in a forthcoming paper (Van Waveren et al,., research in progress). Key: 1, 2, 3 = localities discussed in text; blue = limestone; pale green = seed fern beds; dark green = basalt.

The sedimentation of the Mengkarang Formation has been described as predominantly of epiclastic/floodplain origin (Suwarna, 2006), ranging from mire to swamp deposits and including marine intercalations. The Telukwang Formation overlies the Mengkarang Formation and is mainly composed of debris derived from the erosion of the volcanic centre that formed during the life of a volcanic complex.

The stratigraphic correlation of the Mengkarang Formation has been the subject of a long running debate and as a result the Jambi palaeoflora has been commonly referred to as being of 'Permo-Carboniferous' in age in the literature (Hutchison, 2007). Lately, Ueno (*in* Crippa *et al*., 2014) studied fusulines from Teluk Gedang and determined an Asselian age (Early Permian), thus confirming the work of Fontaine and Gafoer (1989).

The North China and Euramerica affinities of the Jambi palaeoflora were first recognized by Jongmans and Gothan (1935), and its tropical ecology and geographic affinities have been confirmed by Van Waveren *et al*. (2007). Barber and Crow (2003) suggested that the West Sumatra Block was detached from the Cathaysian palaeobiographic area and inserted behind the East Sumatra Block, that is, behind Sibumasu. The former location of the West Sumatra Block relative to Cathaysia remains an active area of research. Barber and Crow (2003) placed the West Sumatra Block outboard of the southern Cathaysia margin, as have Ferrari *et al*. (2008). Consideration of Palaeotethyan marine faunal provinces, and Cathaysian and Euramerican plant provinces, have indicated that western Sumatra should be placed at a similar equatorial latitude as the Indochina Block (Booi *et al*., 2009; Crippa *et al*., 2014).

In this account the volcanic sequences within the Mengkarang Formation are referred to as dacitic products of 'Karing Volcanic Complex' (Crow and van Waveren, 2010). The Karing Volcanic Complex was a volcanic centre at the foot of which the sediments in the Mengkarang Formation were deposited.

Material and Methods

Table 6.1 lists the sample numbers used for this study, giving a brief description of each sample and indicating the type of analysis applied. These samples were collected from a trio of three-dimensional exposures along the Merangin River, informally named Localities 1-3 herein (Figs 6.1B, 6.2).

1. An exposure on the basal eastern side of the Merangin section (latitude 02^0 10' 9.39", longitude 102^0 08' 59.88") was examined, making a panoramic picture of the section and taking a stratigraphic logs at a scale of 1/100. This site is notable for the large *in situ* roots and trunk of an *Agathoxylon*.

2. The exposure on the western bank on the top of the section at the mouth of the Karing River, indicated on the 1935 map as yielding *Dadoxylon* (latitude 02^0 09’ 08.65”, longitude 102^0 09’ 13.04”), was also mapped in detail both in plan view and as a section scale 1/100.
3. A further locality halfway through the section (latitude 02^0 09’ 17.05”, longitude 102^0 09’ 09.54”) was examined as it contained large root systems in the Gurami beds, equally illustrated with a stratigraphic log at a scale of 1/100.

Table 6.1: Applied methods for each sample type

sample number	description	method
30	pyroclastic accretion wedge/ alluvial deposits	petrography
31	pyroclastic accretion wedge/ alluvial deposits	petrography
35	pyroclastic accretion wedge/ alluvial deposits	petrography
37	pyroclastic accretion wedge/ alluvial deposits	petrography
38	pyroclastic accretion wedge/ alluvial deposits	petrography
39	pyroclastic accretion wedge/ alluvial deposits	petrography
40	pyroclastic accretion wedge/ alluvial deposits	petrography
41	pyroclastic accretion wedge/ alluvial deposits	petrography
42	pyroclastic accretion wedge/ alluvial deposits	petrography
44	pyroclastic accretion wedge/ alluvial deposits	petrography
45	pyroclastic accretion wedge/ alluvial deposits	petrography
46	pyroclastic accretion wedge/ alluvial deposits	petrography
48	pyroclastic accretion wedge/ alluvial deposits	petrography
49	pyroclastic accretion wedge/ alluvial deposits	petrography
128	pyroclastic accretion wedge/ alluvial deposits	petrography
129	pyroclastic accretion wedge/ alluvial deposits	petrography
133	pyroclastic accretion wedge/ alluvial deposits	petrography
134	pyroclastic accretion wedge/ alluvial deposits	petrography
153	pyroclastic accretion wedge/ alluvial deposits	petrography
J16	pyroclastic accretion wedge/ alluvial deposits	petrography
J17	pyroclastic accretion wedge/ alluvial deposits	petrography
J18	pyroclastic accretion wedge/ alluvial deposits	petrography
J27	pyroclastic accretion wedge/ alluvial deposits	petrography
132	pyroclastic accretion wedge/ alluvial deposits	petrography/palynofacies
49	shales	palynofacies
46	shales	palynofacies
44	shales	palynofacies
45	shales	palynofacies

Table 6.1: Applied methods for each sample type (continued)

sample number	description	method
TGBT I	in situ Big Tree (B.T.) top	X-ray diffraction, Colour of cathode luminescence
TGBT H	in situ B.T. middle	X-ray diffraction, Colour of cathode luminescence
TGBT B	in situ B.T. base	X-ray diffraction, Colour of cathode luminescence
55	in situ B.T. veins	X-ray diffraction, Colour of cathode luminescence
39	in situ roots on accretion wedge of B.T.	X-ray diffraction, Colour of cathode luminescence
51	in situ Psaronius	X-ray diffraction, Colour of cathode luminescence
TG-II	tree base opposite river in situ tree at Teluk Gedang	X-ray diffraction, Colour of cathode luminescence
TG-III	tree base opposite river in situ tree at Teluk Gedang	X-ray diffraction, Colour of cathode luminescence
32	Merangin float with veins down stream of batholith	X-ray diffraction, Colour of cathode luminescence
33	Merangin float with veins down stream of batholith	X-ray diffraction, Colour of cathode luminescence
34	Merangin float with veins down stream of batholith	X-ray diffraction, Colour of cathode luminescence
36	Merangin float with veins down stream of batholith	X-ray diffraction, Colour of cathode luminescence
71	Merangin float with veins down stream of batholith	X-ray diffraction, Colour of cathode luminescence

Although Locality 1 is the most important exposure, comparison to Localities 2 and 3 provides additional relevant information on the forest beds (Figs 6.1B, 6.2).

Petrography of volcanic deposits

The rock samples assembled along the Merangin section were sent to Mikina Petrolab in Poland, where uncovered polished slides were prepared for polarization microscopy. For each slide, 300 points were counted. The grain classes recognised included the numbers of grains of quartz, feldspars, dark mafic minerals, calcareous skeletons and calcareous cement, organic matter, lithic rock fragments and the percentage of matrix, cement or vitric groundmass. Seven classes of grain size are chosen: (1) tuffaceous shale or ash (<62 µm); (2) fine-grained tuffaceous siltstone or ash (62-125 µm); (3) fine-grained tuffaceous sandstone

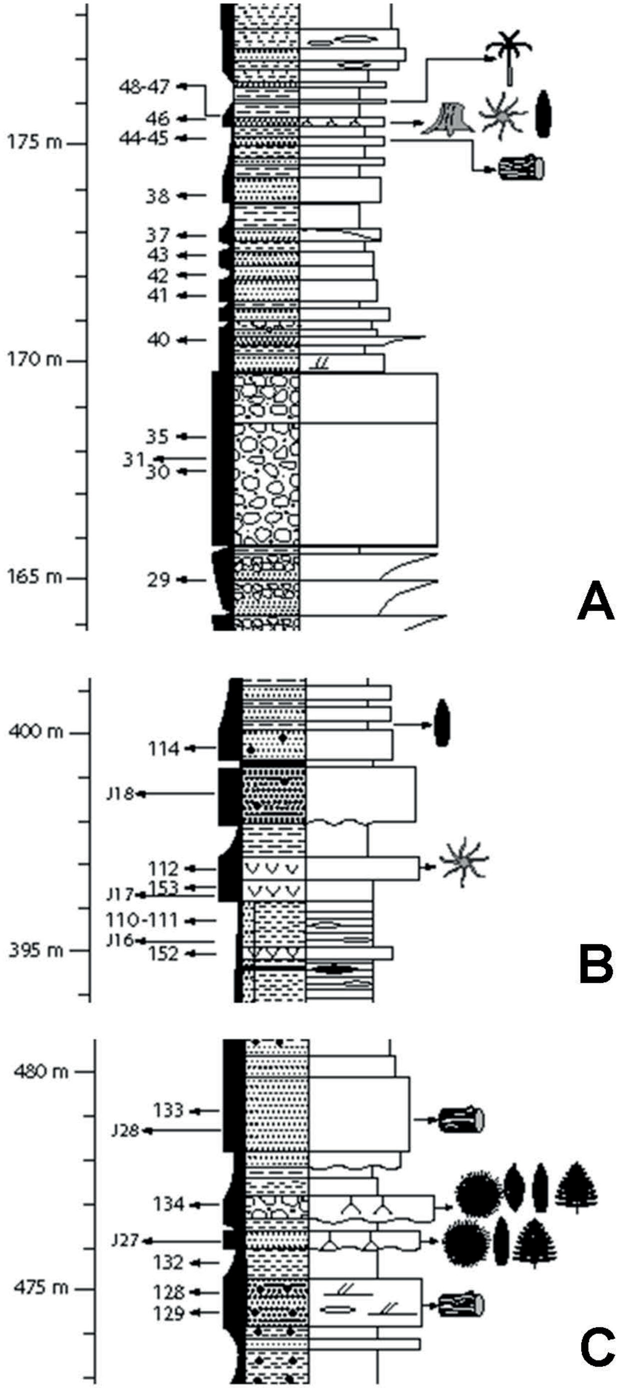


Figure 6.2: Measured sections of key sequences. (A) In situ *Agathoxylon* section through the four wedges (Locality 1). (B) Section through the two levels with roots as natural coke (Locality 3). (C) Section through the two forested levels at Mouth Karing (Locality 2).

or tuff (125-250 μm); (4) medium-grained tuffaceous sandstone or tuff (250-500 μm); (5) coarse- to medium-grained, tuffaceous sandstone or tuff (500-1000 μm); (6) coarse-grained tuffaceous sandstone or lapilli (1000-2000 μm); and (7) gravel or tuff (>2000 μm). Rounding is scored in four categories: (1) angular; (2) sub-angular; (3) sub-rounded; and (4) rounded. Tuffs were differentiated using the criteria of Schmid (1981) where pyroclastic deposits with particles of less than 125 μm in size are considered ashes and those composed of particles larger 125 μm are considered tuffs. The percentages of the counts were used to determine the degree of similarity between the rocks by subjecting them to an agglomerative hierarchical clustering, where a cluster was formed between two samples when the squared Euclidean distance was smallest. This is Ward's method and was offered in PAST software (Hammer *et al*., 2001).

Organic matter

The samples were cleaned and demineralized using standard preparation techniques for siliceous material (Pearson and Scott, 1999). Five palynomaceral categories are chosen, simplified after Van Waveren and Visscher (1994), and using as much as possible the terminology initiated by Whitaker (1984) and applied by the Rijks Geologische Dienst (Van der Laar and Van der Zwan,1996). Particulate organic matter (POM) is subdivided into Structureless Organic Matter aggregates (SOM), Equidimensional Particulate Organic Matter (EPOM) and Blade-like Organic Matter (BOM). These subdivisions pertain to the buoyancy of the particles; equidimensional particles are less buoyant than blade-like particles. Blade-like particles are composed either of tracheal organic matter (TOM) or exoskeletal fragments (EXOM) as described by Van Waveren (1993). For the rest, pollen, spores and algal remains are counted (P&S). For each preparation 100 points were point counted. Only two colour categories were counted, namely opaque and brown, as hyaline particles were considered to be (sub-)recent.

Silica type

Analysis and imaging were undertaken as described in Matysova *et al*. (2010). Imaging was achieved through optical microscopy in normal (PPL) and polarized (XPL) light [IRSM AS CR], and reflected light (RL) [IRSM AS CR]. Hot cathodoluminescence microscopy (CL) was applied at the Department of Geological Sciences, Faculty of Science, Masaryk University, Brno, Czech Republic, while hot cathodoluminescence microscopy and spectroscopy (CL) was done at the Institute of Mineralogy, TU Freiberg, Germany. Scanning electron microscopy (SEM; SE=secondary electrons/BE=back scattered electrons) was undertaken at the Laboratory of Electron Microprobe Analysis, Faculty of Science, Masaryk University. Analyses were done by energy or wavelength-dispersive X-ray spectroscopy (EDS/WDS) at the Laboratory of Electron Microprobe Analysis, Faculty of Science, Masaryk University, while X-ray diffraction (XRD) – measuring of planar fragments (cuttings after preparations of thin sections or polished blocks) – was done at the Analytical Laboratory, Institute of Inorganic Chemistry AS CR, Řež, Czech Republic.

Results

Locality 1 (Fig. 6.2A)

The *in situ Agathoxylon* locality consists of four stacked accretion wedges separated by ochre to red brown shales (Fig. 6.3). The wedges fan from base to top and from NW to NNW. The first wedge is particularly coarse-grained (Fig. 6.4A), and includes three fossil tree trunks of 0.30 m in width to 2.5 m in length, and 0.3-1.0 m in width and 0.2-1.0 m in length (Fig. 6.4B). The trunks are parallel to bedding. The deposits are typified by fining both in thickness and grain sizes in a NW direction, and a decrease in pebble densities is observed in the same direction. The change in lithofacies is associated with a change in colour from cream to a little darker.

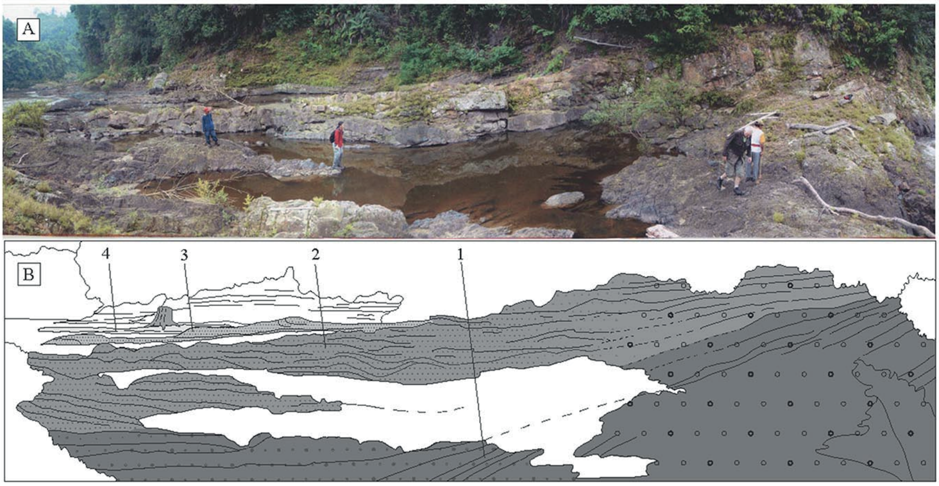


Figure 6.3: The *in situ Agathoxylon* locality (Locality 1) with the four accretionary wedges. (A) Panoramic picture of the four wedges. (B) Explanatory sketch of same view showing the individual flows, numbered 1 to 4.

The second wedge is barren of transported tree trunks and also fines in a NW direction, while changing in grain size and colour from light-coloured, pebbly and coarse-grained to dark grey and fine-grained. This flow has a positive relief, which it displays about halfway along the exposed wedge in the dark grey beds (Fig 6.4C). The positive relief is in association with apparent deep foresets dipping in the opposite direction to the thinning and current direction.

The third accretion wedge also carries tree trunks and in the same order of dimensions as described for the first flow. This wedge has no clear *in situ* trunks, but includes several scattered larger trunks that may have grown from the underlying shales; the exposure was too overgrown to determine this with confidence. This third wedge also displays a pronounced change in lithology from thick-bedded, coarse-grained, pebbly deposits to thinly-bedded, fine-grained, dark grey flows (Fig. 6.4D).

Figure 6.4: Aspects of the *in situ Agathoxylon* section (Locality 1). (A, C, D) Details of the pyroclastic accretion wedge. (A) Proximal thick and coarse-grained beds dipping to the left. (C) The convolute structure and positive relief halfway through the pyroclastic accretion wedge, seen on the opposite river bank. (D) The beds of the dark grey, fine-grained distal wedge. (B) Wood (arrowed) transported on the first pyroclastic accretion wedge. (E, F) *Agathoxylon* trunk. (E) In situ trunk showing the surrounding sedimentary beds. (F) Shallow channels next to the *in situ Agathoxylon*, which is just out of view to the left.

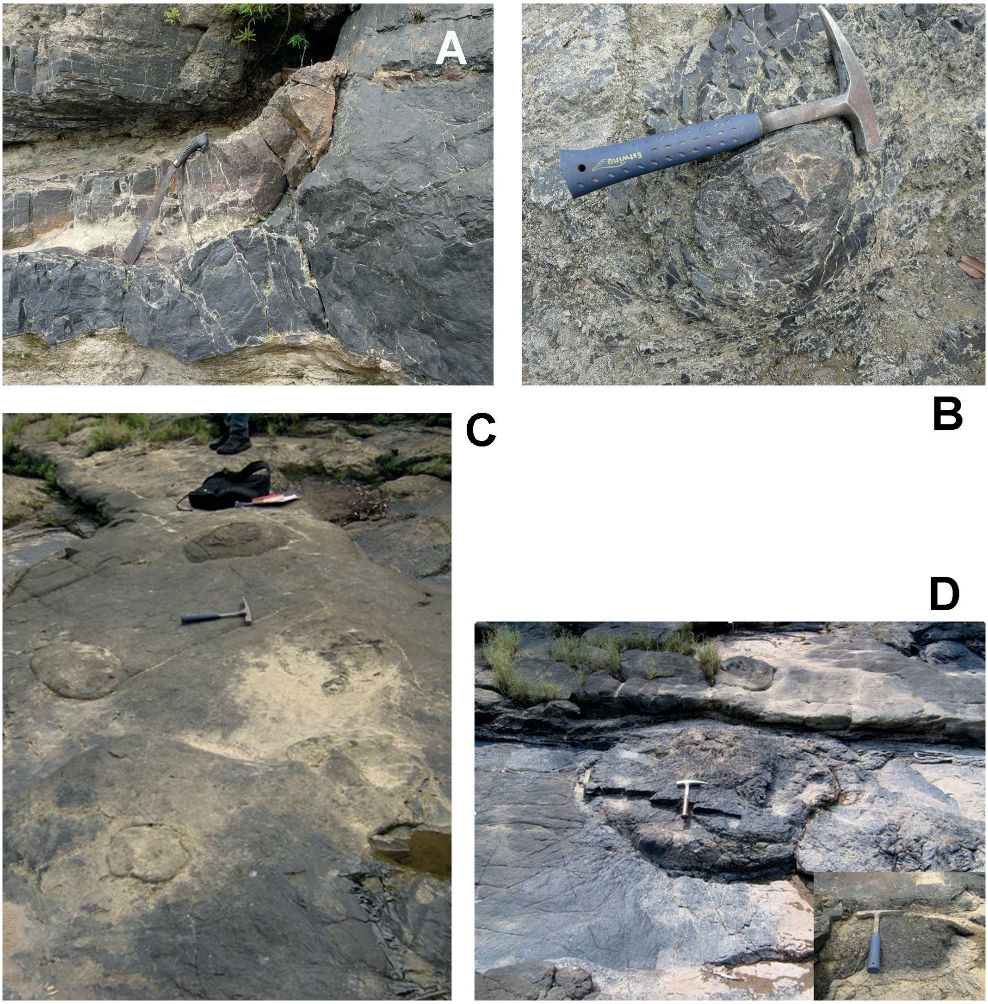


Figure 6.5: (A, B) Aspects of the in situ *Agathoxylon* section (Locality 1). (A) The root of the in situ *Agathoxylon* with a cohesive flow banked up against it. (B) An *in situ Psaronius* (Fig. 7B) with pyrite and carbonate mineralization that is also considered to relate to alluvial preservation. (C, D) '*Dadoxylon*' (Locality 2). (C) Cluster of '*Dadoxylon*' at the mouth of the Karing River. (D) Detail of '*Dadoxylon*' at the mouth of the Karing River; inset shows details of radial growth pattern.

The fourth set of beds thins in a NNW direction. On the relief it formed in a SSE direction, two *in situ* root systems had grown from light-coloured, coarse-grained, pebbly deposits. A thin soil in between the pebbly deposits may have been present, but, if so, is obviously concealed by present-day soils. These two root systems each have a diameter of approximately 1 m, but their trunks are not preserved. The *in situ Agathoxylon* is situated half way down the wedge, just above distal dark grey lenses (Fig. 6.4E). It is approximately 2.5 m in height, varying between 1.9 m (top) and 2.4 m (base, near the roots) in diameter, including the roots (measurements after Booi *et al*., 2014). All roots systems on the top and at the base of the palaeorelief have the same typical sinuous shape without bifurcations and without smaller visible side roots. These roots remain parallel to the sedimentary surface, yet the giant tree – that could be observed in cross section – has a dark 'lump' diving directly into the deposits while the two side roots thin rapidly sideward. Most typically, above and to the right of the tree when looking in a downstream direction, are slightly concave channel-like structures (Fig. 6.4F), in some examples with a coarser-grained lag. One bed on the other side of the shallow channels thickens against the tree, indicating that the sediment had some cohesion (Fig. 6.5A). Just above these forested beds (<1 m), an *in situ Psaronius* trunk base of 30 cm in both diameter and height was observed (Fig. 6.5B). Rare *Calamites* were found as transported plants in distal pyroclastic flows, but also *in situ* at different points along the section.

Locality 2 (Fig. 6.2B)

At the mouth of the Karing River, the exposures are three dimensional despite of the outcrop being large and the trunks strongly eroded. The slope of the foot of the volcano, as observed at Locality 1, is not so clear and is more gentle. Beds are strongly lithified, yet a few thin shale layers are very carbonaceous and form thin coal beds. An *in situ* forest is covered with shales and pebbly grey deposits where another forested level can be seen (Fig. 6.5C). A total of eleven trunks of various sizes could be counted, some of which interfere with each other (Fig. 6.6). A large *Taeniopteris* leaf impression was found in the claystones in between the two interfering forested horizons. The trees at the Karing locality, in spite of their size, have a star-shaped structure (Fig. 6.5D) which may represent a giant fern from which the shaft is preserved near the base of the tree.

Figure 6.6: Plan view of tree positions, informally labelled A–"G", at the mouth of the Karing River (Locality 2). Note the interference of two trunk marks "E" and F. Two specimens, "E" and "G", distinguished in the figure by quotation marks, are only considered trees with doubt.

Locality 3 (Fig. 6.2C)

The Gurami beds are typified by carbonaceous tree roots in a strongly lithified rock (Fig. 6.7A). These roots display the sinuous tapering shape without secondary roots which was also observed for the tree roots at the giant *in situ Agathoxylon* (Locality 1). The remains on and in the rock cannot be extrapolated into one single (or two) star-shaped root system(s) (Fig. 6.8). One of the roots clearly plunges into the rock (Fig. 6.7B). Petrographic analysis displays a deformed lignin with high vitrinite reflection (Fig. 6.7C).

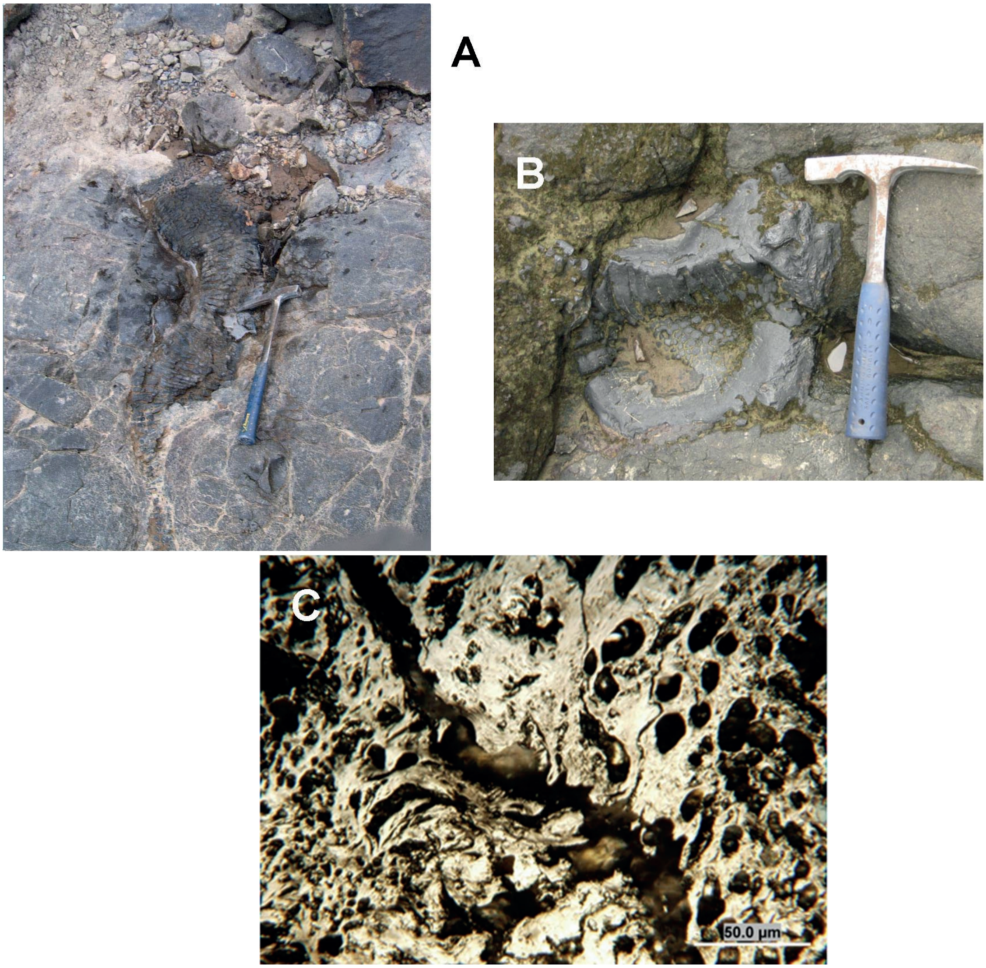


Figure 6.7: Aspects of the Gurami beds (Locality 3). (A, B) Early Permian naturally coalified roots penetrating into the basalt. (C) Petrography of the roots system. High vitrinite reflectance from fluorescence microscopy on poorly preserved, probably tracheal structures from the root system.

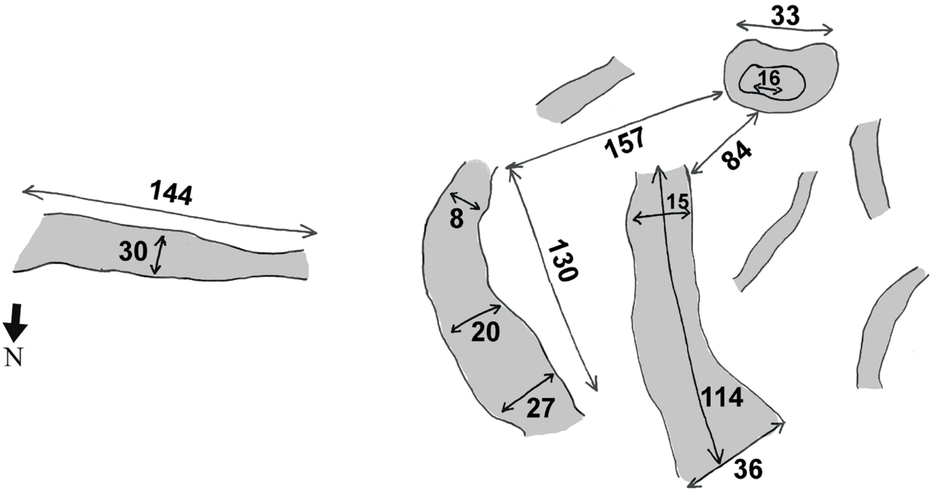


Figure 6.8: Field sketch of the roots at the Gurami basalt, measurements in cm (Locality 3). Measurements and field relations are accurate, but the overall scaling is approximate.

Petrography

The cluster analysis produced using Ward's method of the percentages of the different petrographic clast types within the four flows around the *in situ Agathoxylon* (Table 6.2; Fig. 6.9) indicates two main clusters, either having a vitric groundmass or having a matrix. The samples taken proximally in the accretion wedges are within the cluster characterized by the presence of a vitric groundmass (samples 30, 37, 40, 43). They have a higher percentage of crystals and a lower percentage of vitric groundmass than their distal equivalents from the same cluster (31, 37, 41). Early flows (30, 31) have a relatively high percentage of crystals, whereas later flows (40) have a higher percentage of vitric groundmass. These samples are pyroclastic tuffs and ashes. Samples characterized by matrix (42, 44, 45, 46, 48, 49) were taken, among others, from shallow channels and are epiclastic. They are differentiated by the percentage of tuffaceous grains. The composition of these grains hardly differs from those in the tuffs, yet they are epiclastic products of early reworking of the pyroclastic flows beneath. At the *in situ Agathoxylon* site (Locality 1), pyroclastic deposits are subjacent or lateral to the tree that grows into the reworked alluvial products of the pyroclastic deposits.

Samples from the mouth of the Karing River site (Locality 2) (samples 128, 132, J27; Table 6.2) fall within the epiclastic cluster, while the other samples (129, 133, 134) have a vitric groundmass and belong to the pyroclastic cluster. Here, inversely to Locality 1, epiclastic deposits are subjacent to the forested horizons. These were entombed into an epiclastic deposit, only later to be entombed in an overlying pyroclastic deposit.

Table 6.2: Percentages from petrographic point counts

Field number	Organic matter	SiO2	Feldspar	Lithic grains	CaCO3 rock fragments	Dark minerals	Clay minerals	Tuffaceous sand and silt	Animal CaCO3	CaCO3 cement	Vitric ground mass	Matrix	Lime matrix	Grain size	Texture
30	0	30.3	28	20.3	0	1	0	0	0	0	20	0	0	5	1
31	0	35	19.6	4.7	0	4	0	0	0	0	31.3	0	0	5	1
35	0	2.7	29.3	0.7	0	5.6	0	0	0	0	60.6	0	0	5	1
37	0.3	23	23.3	10.3	0	11.9	0	0	0	0	31	0	0	5	1
40	0	30	28.3	9.3	0	7.2	0	0	0	0	25	0	0	5	1
41	0.3	9.9	6.6	10.2	0	6.6	0	0	0	0	65.3	0	0	4	2
42	1.7	0	0	0	0	0	0	24.8	0	0	0	73.7	0	3	2
43	0	20.3	14.7	27.7	0	0.3	0	0	0	0	36.7	0	0	6	2
44	2	0	0	0	0	0	5.3	15.7	0	0	0	77	0	3	1
45	4.6	0	0	0	0	0	4.3	5.6	0	0	0	84.5	0	3	1
46	10	0	0	0	0	0	2.3	1.3	0	0	0	85.7	0	4	4
48	0	0	0	0	0	0	0	16	0	0	0	84	0	1	4
49	5.3	0	0	0	0	0	1.7	29.3	0	1.3	0	59.7	0	3	1
J16	0.7	0	0	0	0	0	12.3	37	0	0	0	48.3	0.3	2	4
J17	0	0	0	0	0	100	0	0	0	0	0	0	0	4	1
J18	3	0	0	0	0	0	11.2	35	0	0.3	0	50	0	2	4
110	29	0	0	0	0	0	0	0	0	0	0	71	0	2	1
111	0	0	0	0	0	100	0	0	0	0	0	0	0	3	1
114	0	0	0	0	0	0	3	70.7	0	3.3	0	22	0	4	4
152	0	0	0	0	0	72	0	0	0	14.2	0	0	13.6	3	1

Table 6.2: Percentages from petrographic point counts (continued)

Field number	Organic matter	SiO2	Feldspar	Lithic grains	CaCO3 rock fragments	Dark minerals	Clay minerals	Tuffaceous sand and silt	Animal CaCO3	CaCO3 cement	Vitric ground mass	Matrix	Lime matrix	Grain size	Texture
153	0	0	0	0	0	100	0	0	0	0	0	0	0	3	1
J27	6.3	0	0	0	0	0	10.6	33.3	0	4.3	0	44.6	0	3	2
128	17.2	0	0	0	0	0	6	0.7	0	1.3	0	74	0	2	1
129	0.7	9.3	6	47.3	0	1	0	0	0	10	25.3	0	0	5	4
132	17.7	0	0	0	0	0	18	8	0	0	0	56.3	0	1	1
133	0	10	5.3	51	0	6.3	0	0	0	12.7	7.3	0	7.3	1	0
134	0.7	10.7	7	36.7	0.7	4.7	0	0	0	5.7	27.7	0	6.7	3	3

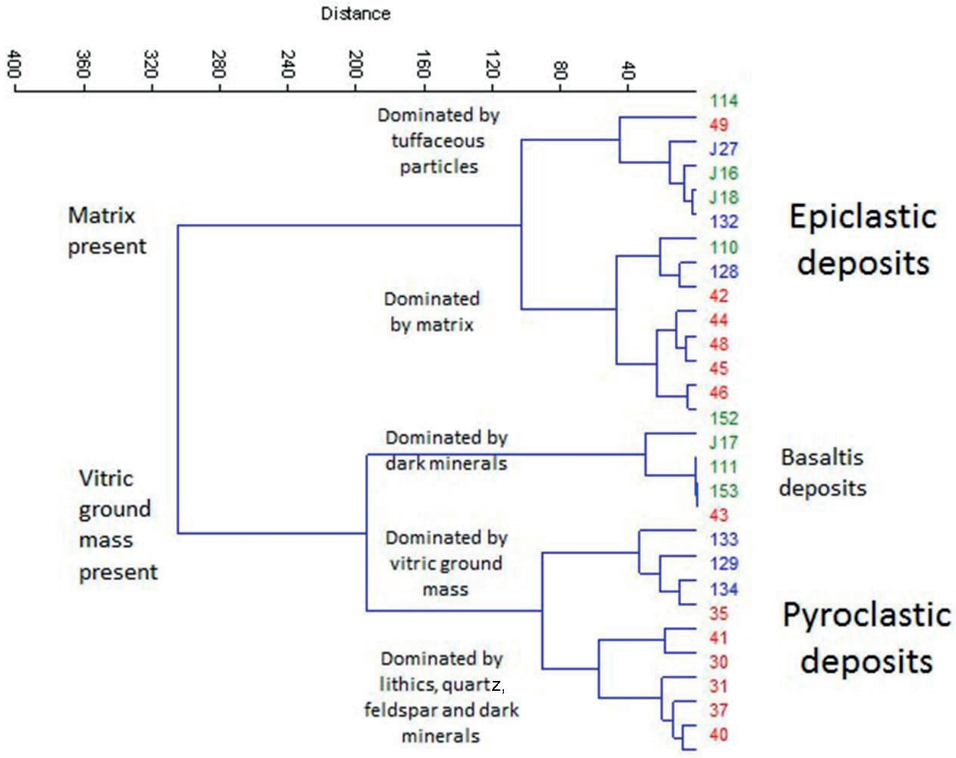


Figure 6.9: Cluster analysis of the petrographic point counts using Ward's method. Red numerals are the samples from around the *in situ Agathoxylon* (Locality 1); blue numbers are from the mouth of the Karing River (Locality 2); and green numbers are samples from the Gurami beds (Locality 3).

Samples from the Gurami beds (Locality 3) typically show the presence of four pyroclastic horizons with only poikiloblastic dark minerals, for example, basalts (111, 152, 153, J17). The rest of the samples are clustered with the epiclastic deposits (110, 114, J16, J18). The rock carrying the root fragments, and into which the tree root intrudes, is a basalt.

Silica type and preservation

Most petrographic slides (Table 6.3), from the *in situ Agathoxylon* site (Locality 1) and the floats along the Merangin River have outstanding secondary wood preservation (Fig. 6.10A); their detailed taxonomy was analyzed by Booi *et al*. (2014). In the present study, cathode luminescence was used to separate volcanic from diagenetic or metamorphic processes and products (Goètze *et al*., 2001).

Preservation at the Locality 1 varies. The root system of the tree is poorly preserved (Fig. 6.10B), whereas the rest of the wood is well preserved. The lumina are either homogeneously filled with opal, sometimes showing the primary and the secondary cell wall or even some cell material being pushed aside to the sides of the cell by the amorphous silica (Fig. 6.10A), or the silica display some fibrous to microcrystalline crystallisation from the cell walls. In other cases, larger crystals appear from the cell centre and destroy the lignin.

The lignin preservation is of poorer quality in samples found in the section below the level of the *in situ Agathoxylon* at Locality 1 (samples 32, 33, 36) and also next to it, while the crystallisation on the xylem is more often fibrous or microcrystalline. The roots at the same level as the tree top (on top of the fourth accretion wedge) (sample 39) are badly preserved and composed chiefly of fine-grained sedimentary mudrock. The *Psaronius* again is more silicified then these roots systems, but also badly preserved.

Petrographic composition of all silicified tree samples consisted chiefly of quartz. Minor components included kaoline (4, 2, 4 %), calcite (4, 0, 6 %), pyrite (6, 9, 5 %) and albite (5, 1, 5 %). The roots preserved at the Gurami beds (Locality 3) are fully made or organic carbon. The trees preserved at the Mouth Karing show only faint lignin remains (Fig. 6.10C)

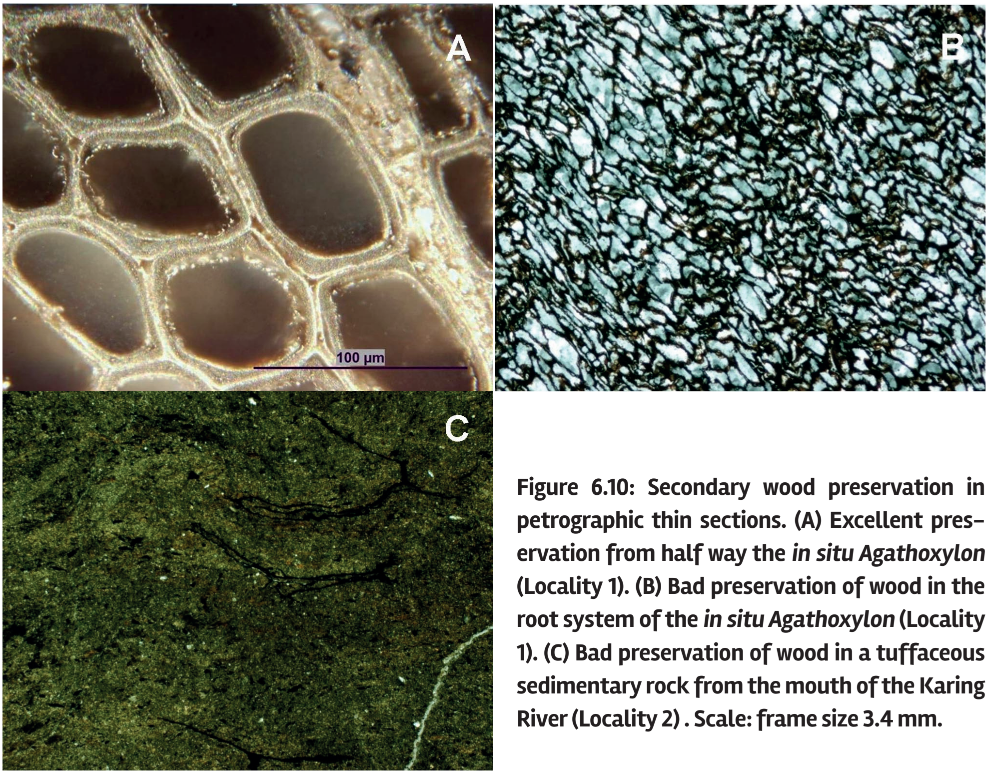


Figure 6.10: Secondary wood preservation in petrographic thin sections. (A) Excellent preservation from half way the *in situ Agathoxylon* (Locality 1). (B) Bad preservation of wood in the root system of the *in situ Agathoxylon* (Locality 1). (C) Bad preservation of wood in a tuffaceous sedimentary rock from the mouth of the Karing River (Locality 2) . Scale: frame size 3.4 mm.

Table 6.3: Characteristics of wood preservation

sample number	description	main component from X- ray diffraction	Other components from X-ray diffraction	mean coherence quartz length (nm)	colour of C.L. emission
TGBT-06 I	in situ Big Tree (B.T.) top	quartz (99%)	kaoline (0.8%)	99	red
TGBT-06 H	in situ B.T. middle	quartz (100%)	-	160	blue and red
TGBT-06 B	in situ B.T. base	quartz (100%)	-	94	blue and red
MR 39	in situ roots on accretion wedge of B.T.	quartz	pyrite	?	N.A.
MR 51	*in situ Psaronius*	quartz (81, 89, 80%)	calcite (4, 0, 6%), Pyrite (6, 9, 5%), albite (5, 1, 5 %), Kaoline (4, 2, 4 %)	124/147/137	N.A.
TG-III	tree base opposite river	quartz	-	285	blue and red
32	Float withveins	quartz	-	350	N.A.
33	Float with veins	quartz	-	136	N.A.
34	Float with veins	quartz	-	203	N.A.

Significance C.L. according to Goetze (1996)	Anatomical preservation xylem	Fill of lumina	Crystallisation from xylem	Cloudy centres visible
(ii) red indicates matrix quartz and quartz phenocrysts in volcanic rocks	good	homogeneous "empty cell"	fibrous	no
(i) blue to violet CL represents plutonic quartz as well as quartz phenocrysts in volcanic rocks, and high-grade metamorphic quartz while	very good	fibrous/ homogeneous	fibrous growing towards cell centre	no
(I) blue to violet CL represents plutonic quartz as well as quartz phenocrysts in volcanic rocks, and high-grade metamorphic quartz while	bad	not clear	homogenous	yes
(iv) non or weakly luminescent indicates authigenic quartz	undulating (deformed?)	microcrystaline	not clear	?
(iv) non or weakly luminescent indicates authigenic quartz	bad but recognizable	microcrystaline	not clear	no
(i) blue to violet CL represents plutonic quartz as well as quartz phenocrysts in volcanic rocks, and high-grade metamorphic quartz while	good	homogeneous "empty cell"	idem	yes
(iv) non or weakly luminescent indicates authigenic quartz	variable	microcrystaline/ fibrous	larger crystal growth in veins but also from xylem	sometimes
(iv) non or weakly luminescent indicates authigenic quartz	variable	microcrystaline/ fibrous	larger crystal growth in veins but also fromxylem	sometimes
(iv) non or weakly luminescent indicates authigenic quartz	variable	microcrystaline/ fibrous	larger crystalgrowth in veins but also from xylem	sometimes

Table 6.3: Characteristics of wood preservation (continued)

sample number	description	main component from X- ray diffraction	Other components from X-ray diffraction	mean coherence quartz length (nm)	colour of C.L. emission
36	Float with veins	quartz	-	226	N.A.
Gurami beds I	Transportedroots in basalt	albite (45%)	quartz (30%), clay minerals	N.A.	N.A.
Gurami beds II	Transported roots in basalt	albite (90%)	quartz (3%), clay minerals	N.A.	N.A.
Gurami bed/ powder	Transported roots in basalt	albite (96%)	quartz (3%)	N.A.	N.A.
Mouth Karing	Tree base	?	?	?	?

Significance C.L. according to Goetze (1996)	Anatomical preservation xylem	Fill of lumina	Crystallisation from xylem	Cloudy centres visible
(iv) non or weakly luminescent indicates authigenic quartz	variable	microcrystaline/ fibrous	larger crystal growth in veins but also from xylem	sometimes
N.A.	coal	N.A.	N.A.	N.A.
N.A.	coal	N.A.	N.A.	N.A.
N.A.	coal	N.A.	N.A.	N.A.
N.A.	sometimes visible	sediment	N.A.	N.A.

Cathode luminescence (CL)

The silica in the large *in situ Agathoxylon* (Locality 1) is typified by a double peak, one at 475 nm (blue) and one at 600 nm (red) (Fig. 6.11). Between the peaks in Figure 6.11B, the curve remains high, indicating the presence at 500 nm of green, and even remaining relatively high by the end of the spectrum at 750 nm and more (brown). While at the foot of the tree

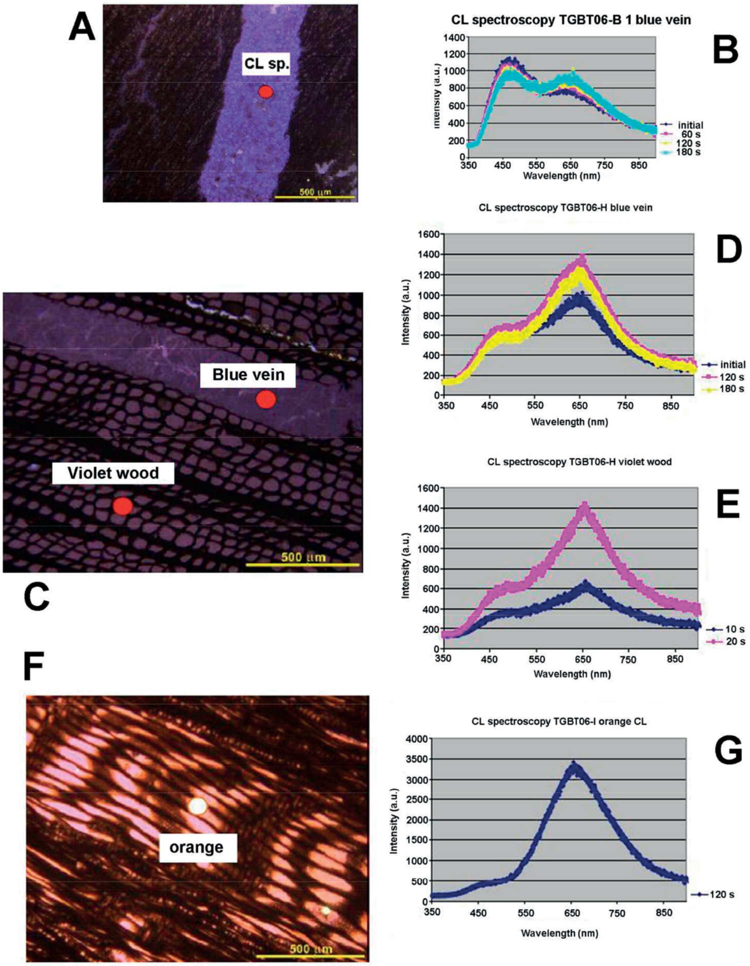


Figure 6.11: Hot Cathode Luminescence (CL) of the *in situ Agathoxylon*: (A, B) Sample from the tree base with the roots. (A) Petrographic thin section with cathode luminescence. (B) CL spectrum for different excitation periods. (C–E) Sample from the middle part of the tree. (C) Petrographic thin section with cathode luminescence within a vein (blue) and wood (violet). (D) CL spectrum for different excitation periods for the vein. (E) CL spectrum for different excitation periods for the wood. (F, G) Sample from the tree top. (F) Petrographic thin section with cathode luminescence. (G) CL spectrum for an excitation period of 120s.

the CL spectrum is high, both at blue and at red, halfway along the tree the first blue peak weakens and it becomes hardly visible at its top (Fig. 6.11).

Across the river from this locality, silica in the wood required extra excitation. It is consequently weak, yet still it has a faint double peak with a high at blue green and remains high in the brown spectrum (Fig. 6.12).

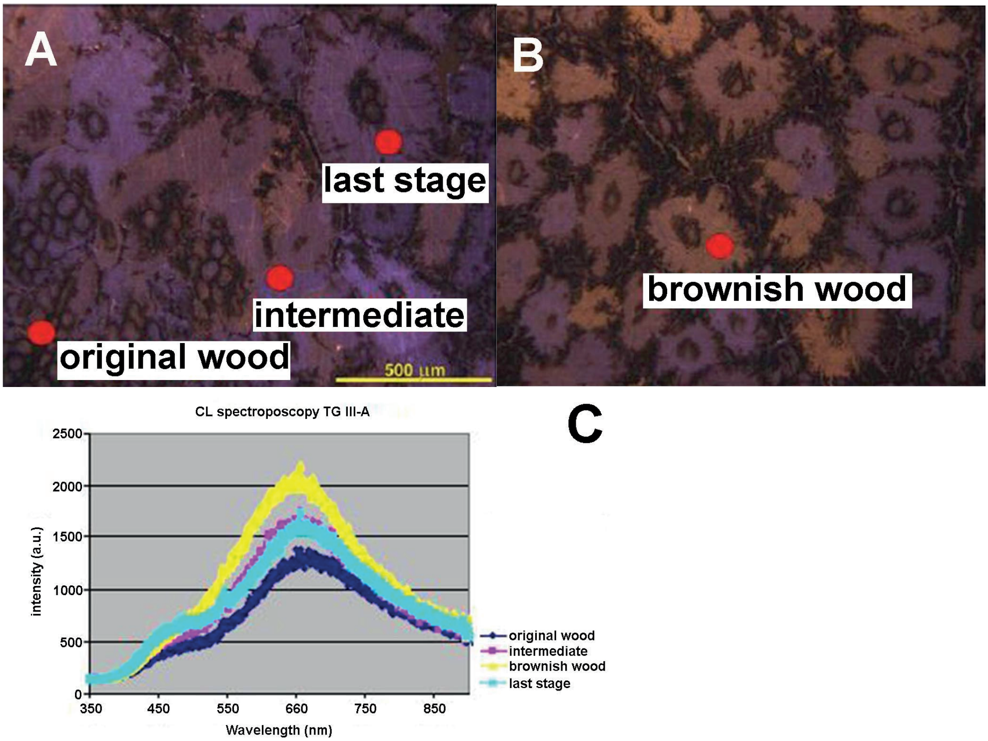


Figure 6.12: Hot cathode luminescence of a tree at Teluk Gedang across the river (Fig. 1B). (A) Petrographic thin section with three wood stages illuminated, namely original, intermediate and last stage wood. (B) Petrographic thin section with brownish wood stage illuminated. (C) Cathode luminescence spectrum for different wood types in (A, B).

Palynofacies

The seven samples taken for palynofacies analysis (Table 6.4; Figs 6.3, 6.13) are typified by an important ratio of opaque particles. Samples (44, 45) (Locality 1) hardly differ and contain chiefly equidimensional opaque particles. Sample (46) contains relatively more blade-like particles, indicating higher buoyancy, with some admixture of brown particles, indicating transport at normal temperatures. Sample (49) is typified by structure-less organic matter particles (SOM) and some brown particles (BOM). Palynofacies (organic matter) at the mouth of the Karing River (Locality 2; sample 132) consists of numerous

Table 6.4: Palynofacies composition from point counts

	Opaque				Brown						
Number	**Equidimensional POM**	**BOM**	**SOM**	**TOM**	**Equidimensional POM**	**BOM**	**TOM**	**DOM**	**P&S**	**ALGEN**	**EXO**
45	64.0	9.0	14.0	2.0	4.0	2.0	1.0	0.0	3.0	0.0	1.0
44	44.0	10.0	22.0	4.0	1.0	5.0	2.0	0.0	4.0	0.0	8.0
110	42.0	7.0	15.0	12.0	1.0	0.0	1.0	1.0	16.0	0.0	5.0
46	24.0	23.0	18.0	13.0	0.0	2.0	1.0	0.0	1.0	0.0	18.0
132	23.0	28.0	23.0	0.0	1.0	4.0	2.0	4.0	3.0	0.0	12.0
112	1.0	0.0	4.0	2.0	2.0	1.0	2.0	67.0	19.0	1.0	0.0
49	1.0	9.0	76.0	2.0	1.0	1.0	1.0	3.0	6.0	0.0	0.0

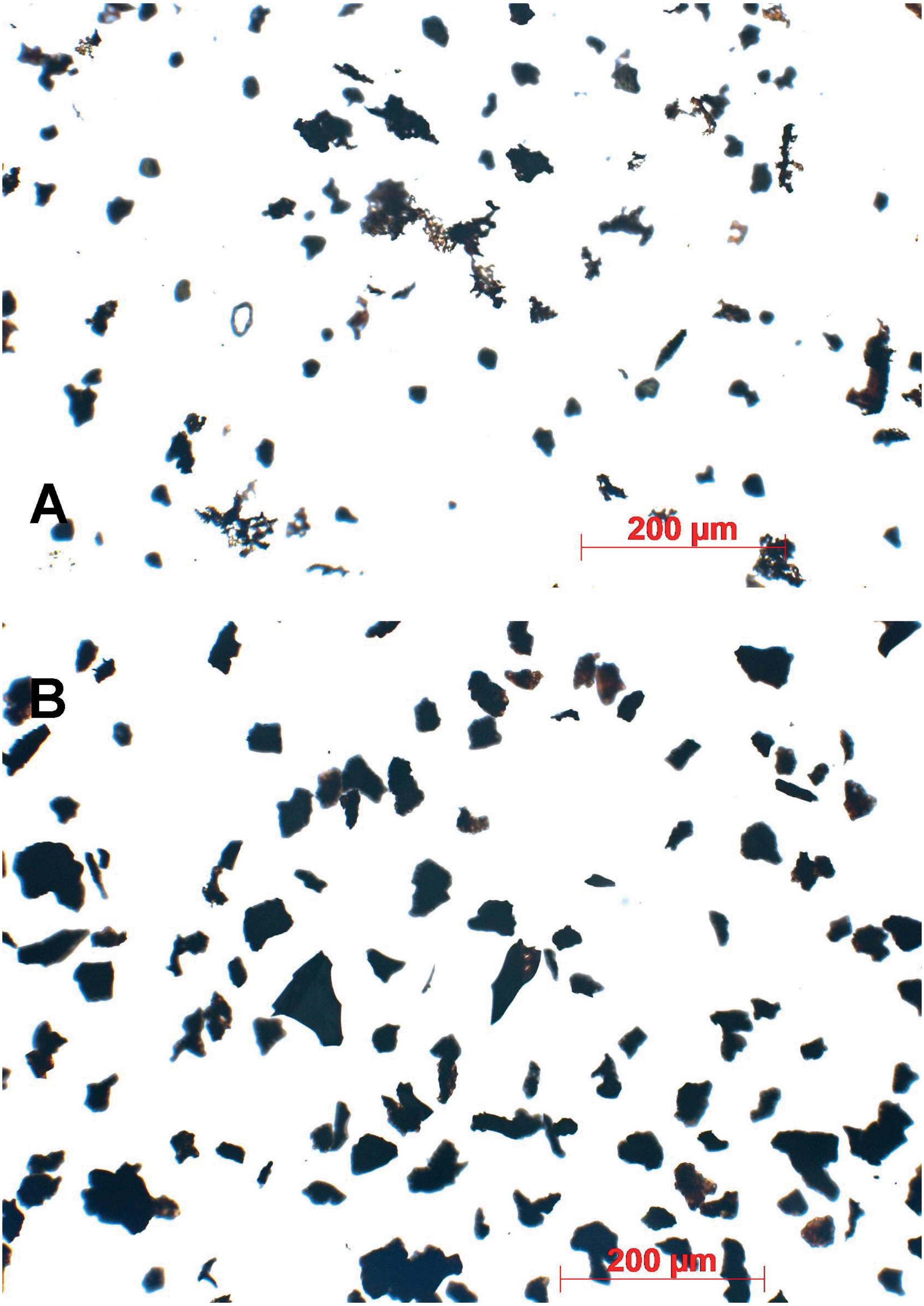


Figure 6.13: Examples of contrasting palynofacies. (A) Specimen rich in SOM (structureless organic matter). (B) Specimen rich in BOM (blade-like organic matter).

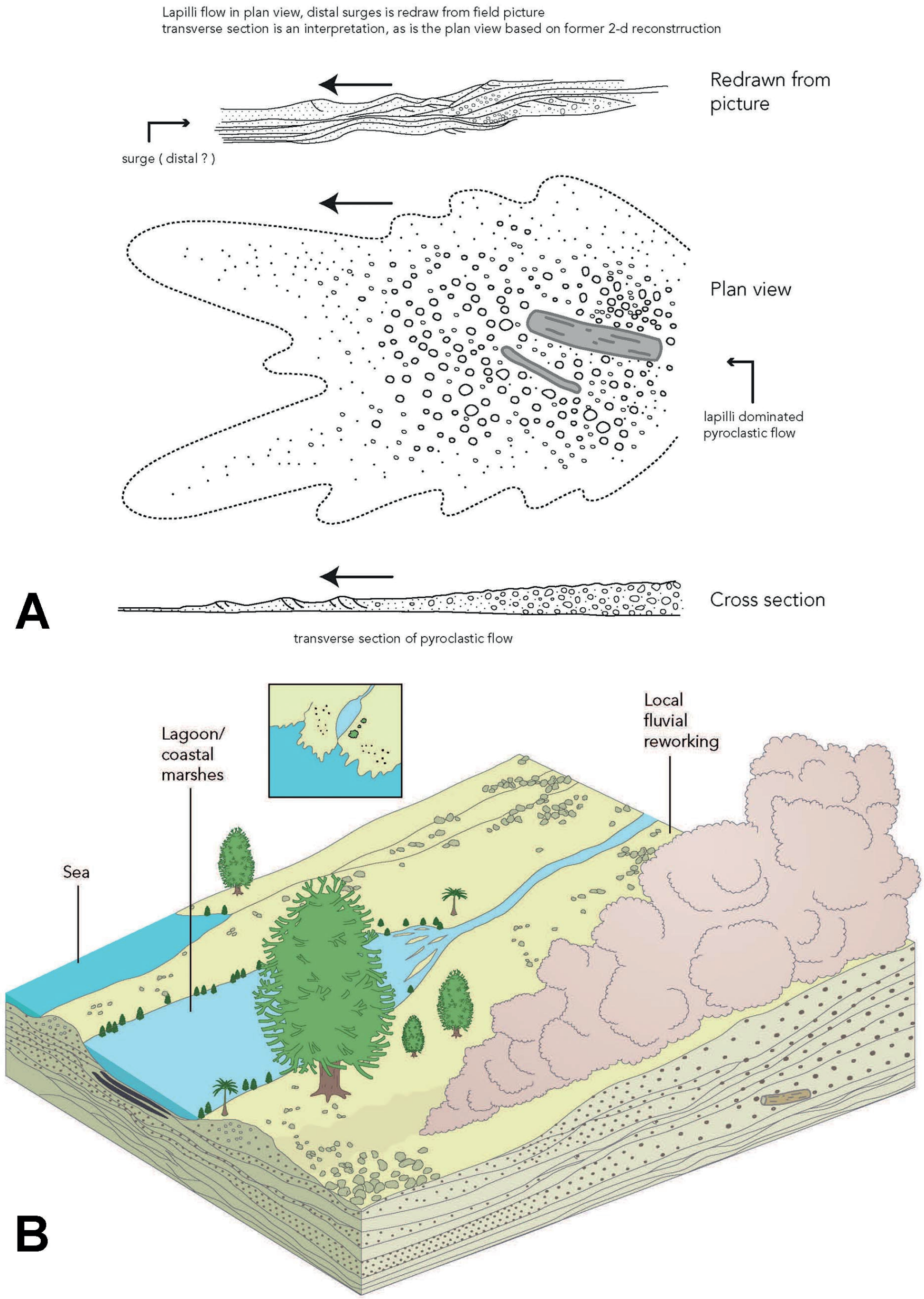
blade-like organic particles reminiscent of sample 46. At the Gurami beds (Locality 3), two samples were collected close to the preserved roots. Sample (110) resembles samples (44, 45), and is dominated by equidimensional particles. Sample (112) is chiefly composed of diffuse, brown aggregates, and a high ratio of pollen and spores. All seven palynofacies samples display a dominance of opaque particles, except for sample (112).

Discussion

The typically positive relief of the second accretion wedge (Locality 1), its inverted foresets (pointing backwards from the obvious flow direction) and the convolute dark grey pillows are all typical of pyroclastic flows. The coarse-grained, pebbly tuffs thinning distally into the darker coloured, finer-grained beds represent pyroclastic flows with ground surges shooting ahead of them (Cas and Wright, 1987; Fig. 14A herein), and this interpretation is supported by the petrography of samples 35 and 37 with high ratios of vitric groundmass.

The first accretion wedge composed of pebbly beds, based on the petrography of the pebbles (samples 30, 31) and the structure in comparison to the above, is a typical pyroclastic flow, but is possibly more proximal. This flow carried down small trees, similarly to modern volcanoes like the Merapi where the coarser-grained pyroclastic flows transport trees (Takahashi and Tsujimoto, 2000). The third flow, characterized by two samples with a strong percentage of vitric groundmass proximally (sample 40) and half way down the outcrop (sample 41), also constitutes a typical pyroclastic flow.

The last accretion wedge, of which the proximal component (sample 43) is also typified by a vitric groundmass, is overgrown by a small forest holding the giant *in situ Agathoxylon* which was described in detail by Booi *et al*. (2014). It is rooted half way up the thickness of the flow. The distal shoot of the flow was typified by sample (42) with a high matrix ratio. Half way up the wedge, the samples are typified by a matrix instead of a vitric groundmass. The bed at the foot of the tree and thickening against it (Fig. 6.5A) is considered to be a lahar or a gravity flow, either indirectly or directly induced by the volcanic activity. Basal pyroclastic flows (surges) cool down as they flow, and pick up clasts and other particles from the ground they cover. It is consequently not possible, based on the petrography, to establish if such deposits are alluvial or volcanic, yet they are distal to beds typified by a true vitric mass. Just above these distal surges, shallow, concave, channel-like structures are observed. No pyroclastic flows are observed directly above this level and these shallow channels follow from alluvial reworking processes at the foot of the volcanic slope.



Lapilli flow in plan view, distal surges is redraw from field picture
transverse section is an interpretation, as is the plan view based on former 2-d reconstrruction

Figure 6.14: (A) Interpretation and model of the pyroclastic accretion wedge. (B) Reconstruction of the *in situ Agathoxylon* site (Locality 1) at the time of a distal surge (right foreground).

The palynofacies just below and next to the giant *in situ* tree gives some insight into its palaeoecology. Generally, the ratio of opaque to brown particles is a bit high, but not dramatically so, indicating that the hot volcanic setting did not affect the palynofacies spectrum significantly. Recognizing that a tree with a diameter of 2.5 m requires about 350 years to grow (Stephenson and Demetry, 1995), there was sufficient time for the vegetation to come back. That is, models based on palynofacies analysis in alluvial systems are applicable to the present setting. Van der Laar and van der Zwan (1996) suggested that a palynofacies dominated by opaque equidimensional particles fits in their low energy fluvial deposit; samples (44, 45) are dominated by this palynomaceral category. Dominance of blade-like particles, such as in sample (46) in which the tree initially rooted, represents a swamp. Structureless particle associations (SOM), dominant in sample (49), represent high energy fluvial deposits, and are considered herein to indicate shallow channels on alluvial fans from the reworked tuffs and ashes of the growing volcano. As the diameter of the roots on top of the accretion wedge (above sample 43), neighbouring the *Agathoxylon*, is smaller than that of the giant *in situ* tree, the trees slightly higher up on the accretion wedge are expected to have been smaller.

An *in situ Psaronius* (Locality 1), with internal pyrite and carbonate diagenetic deposition, is also considered to relate to alluvial preservation and some pedogenesis. The *Psaronius* sample of the root mantle differs in mineralogy from other silicified *Psaronius* samples of Permian age, such as from Chemnitz in Germany, Tocantins in Brazil or Nová Paka in the Czech Republic, particularly by its poor preservation, its petrographic appearance and the presence of abundant fromboidal pyrite. Only sclerenchymatic cortex tissue of roots is recognizable, albeit not well preserved, and the central parts such as the vascular stele are completely missing. The material is commonly silicified and its matrix is formed mainly by microquartz, but, because of the heterogenous structure of the adventitious roots and their mantle, it enclosed many other mineral phases/sedimentary grains. Cathode luminescence is impossible to use because the mineral mass is rich in CL quenchers. Overall, it points to more reducing condition of formation, probably an anoxic anaerobic environment of bacterial decay of the organic matter.

At the mouth of the Karing River (Locality 2), the petrographic analysis indicates a tight alternation of epi- and pyroclastic deposits. Tree rooting appears to be independent of the substrate, yet the trees are badly preserved. All deposits are dark grey, suggesting that mostly the distal parts of flows are observed. The palynofacies analysis of sample (132), with numerous buoyant, blade-like particles just below the forested levels, indicates a swamp-like environment by comparison to Van der Laar and Van der Zwan (1996).

At the Gurami beds (Locality 3), petrographic samples are typified by basalts and epiclastic deposits, but pyroclastic flow deposits were not observed. Either the basalts have encapsulated the roots or they grew into the basalt. Considering the remarkable composition of the roots (a natural coke), the absence of any hint of a soil, and the absence of fossil fissures and, indeed, of any rock that could have aided the growth of the 10 cm diameter root, transport in basalt is the preferred interpretation. Coke is formed under hot, oxygen-free circumstances, so embedding in or covering by the basalt is considered most probable. The palynofacies analysis indicates that sample (110) resembles (44, 45) in composition, which fits it in the low energy alluvial system, while sample (112), rich in pollen and with little opaque organic matter, fits in the lake facies.

Silicification

The silica in woody macrofossils is amorphous and follows the morphology of the plants perfectly. In some specimens they even display some cell material which was pushed to the cell sides by the amorphous silica that is considered to have impregnated the *in situ* tree. Solubility of SiO_2 is strongly Ph and temperature dependant, and precipitation is expected either at dropping temperatures and/or a low Ph (Utami *et al*., 2014). Larger crystals forming from the centre of the cells and destroying the secondary wood structure are considered to result either from a different process following burial and increased pressure, or recrystallization related to regional metamorphism associated with the Tantan Granite being reactivated in the Triassic (Crow and Van Waveren, 2010). The poor preservation of root and *Psaronius* is considered here to relate to long subareal exposure and soil processes.

The transition from a low stand to climbing sea level conditions is considered to have affected the dramatic preservation in the Chinle Formation (Gastaldo and Demko, 2011). Marine deposits have been described from beds directly below the *in situ* tree at Locality 1 (Donovan *et al*., 2013). At a rise in sea level, the sea water either invades the coastal zone or is floated over by the freshwater bag. Thus, a sea level rise would have affected the groundwater table and exposed the trees to sedimentary salts in dissolution. In the present case, dacitic tuffs composed chiefly of plagioclase ($NaAlSi_3O_8$-$CaAl_2Si_2O_8$) and quartz (SiO_2) form the bulk of the minerals in the sedimentary rocks (Crow and Van Waveren, 2010). A scenario whereby the freshwater lens affected the sediments seems most probable as it would have caused a more dramatic drop in Ph, but both may be the case. Similarly, it is hypothesized that what was the case for the *in situ* tree, was less so for the mouth of the Karing River (Locality 2) where only faint, round mounds testify to the existence of a palaeoforest. Such minimal preservation can be explained by a reduced sediment supply and/or a slower rise in sea level.

Hot cathode luminescence

Application of the interpretation of Goétze *et al*. (2001) to the significance of the hot cathode luminescence data indicates an interesting gradient within the tree from base to top. This suggests different circumstances at the tree base than at its top. The red spectrum dominates in all slides which indicates a matrix of quartz and phenocrysts of volcanic origin only (Goétze *et al*., 2001). But the tree base is different in that it has a strong blue green and blue component, indicating hydrothermal circumstances, while the slow decrease in luminescence at the red brown tail of the spectrum suggests some metamorphic influences.

This blue green hydrothermal element is present, but weak, in the silicified wood samples on the other side of the river and the red peak also tails off slowly, indicating regional metamorphism. As suggested above, the metamorphism can be explained from the activity of the intrusive Tan Tan Granite in the Triassic (Crow and Van Waveren, 2010).

Hydrothermal vents and lakes are common in many volcanic settings. For example, trees in Yellowstone National Park grow within a short distance of such an ephemeral lake with a hydrothermal source (Evans *et al*., 2010, fig. 2) which produces 'white socks' of silica to trees. In the present example, it is expected that a hydrothermal lake, with a high Ph, did affect the base of the tree which also explains the surprising absence of the skeletal remains and tracks of tetrapods.

Taphonomy

The large *in situ Agathoxylon* (Locality 1) was not preserved by catastrophic entombment as was the case for the trees of the Joggins section of eastern Canada (Calder *et al*., 2006), nor was it directly buried into wet pyroclastic flows (Brea *et al*., 2009). Ash clouds certainly must have been part of the pyroclastic events whose products are preserved in the Merangin River section, but nothing kept the ashes from flowing off the volcanic slope. The shales may well represent reworked ashes, but they did not specifically entomb the various forested levels. The approximately coeval ecological setting approaches the Merangin forest is the Permian volcaniclastic deposits at Valdeviar, Spain, which contains a rich assemblage of mixed mesic and hygrophytic plants that were transported into a lacustrine environment through mass movement (Wagner and Mayoral, 2007). However, it is closer to Darwin's (1846) palaeo-forest that developed on volcaniclastic floodplain deposits (Brea *et al*., 2009). Such mixed assemblages have been found along the Merangin section, but require a detailed description (Van Waveren *et al*., research in progress). Further, comparison can be made with the Buckley Formation of Antarctica, which have been described as fluvio-volcanic (Matysova *et al*., 2010) and proved to have a similar type of cathode luminescence to that observed herein. The palaeoecological setting of the tree and the surrounding forested areas at Merangin consists of alluvial reworked volcanic deposits on the shores of a (short-lived) volcanic lake (Fig. 6.14B), with rapid burial following from the accreting volcanic slope. High volcanic burial rate, possibly rapid volcanic collapse as depicted by Ramalho *et al*. (2013) and rapid (relative) sea level rise at the section base is considered. Overall, it is similar to the evolution of the Chinle Formation (Gastaldo and Demko, 2011) and certainly influenced the quality of preservation. The petrography of the volcanic deposits showing vitric tuffs at the base of the section and basalts at the top, indicating that the volcano changed in character during the history of the section. Preservation is less spectacular at the top of the section, either through slower rates of volcanic burial or due to slower (relative) rise in sea level. Donovan *et al*. (2013) demonstrated the base of the section was marine and Fontaine and Gafoer (1989) described fusulines from the central part of the section, so one should rather consider the interference of both sea level and burial to explain preservation along this volcanic section, where high burial and sea level rise characterize the base section while slower rise and slower burial typify its top.

Conclusions

The Merangin River section (Figs 6.1B, 6.2) preserves abundant evidence of a Permian forest which grew at the foot of an active volcano. Pyroclastic flows often made way and destroyed the vegetation (Fig. 6.14), and epiclastic reworked pyroclastics rapidly entombed it. The *in situ Agathoxylon* (Figs 6.4E, 6.5A) was near enough to the volcanic slope to be buried rapidly, shallow enough to avoid extreme crystallisation in the lumina and far enough from the metamorphic centre not to get recrystallized. All these combined contingencies make this a most unique find that provides significant insights into a rarely studied palaeoecological setting from the Early Permian.

7

Conclusions

The Jambi Flora is a fossil flora found within the Early Permian Mengkarang Formation that outcrops along several rivers in the vicinity of the town of Bangko (Merangin Regency, Jambi) in Middle Sumatra. A sizable collection of over 1800 compression specimens from this flora, collected in 1925, is part of the Jongmans collection as housed in the Naturalis Biodiversity Center in Leiden. This was the collection described by Jongmans and Gothan in 1935. A revision of the original descriptions (Van Waveren et al., 2007) gave an insight into the potential of this palaeoflora, but also led to many questions that could not be answered with the available data. This resulted in a number of expeditions to the area and a full reinvestigation of the original localities in terms of geographical and sedimentological data, as well as a reassessment of the combined old and newly collected material. In this research particular emphasis was lain on various gymnosperm groups that are found in this flora. The result has been a substantial enrichment of the original collection, in terms of new material, as well as added and much needed geological and taphonomical context. This has brought these collections to new life and has made it relevant again for current palaeobotanical, palaeoecological and palaeogeographical research.

Whereas the previously known material of *Macralethopteris hallei* gave little information about its overall morphology, the far more numerous newly collected specimens give more insight. It has now become likely that *M. hallei*'s fronds were simple pinnate only, which, in turn, suggests a monopodial (or even cormous) habit. Based on these features, as well as on its dense venation and sometimes almost detached pinnules, it is sufficiently different from other alethopterids to warrant upholding its genus and not to include it in *Alethopteris*. The morphology of the fronds of *M. hallei* gives every indication of rather xeric growth conditions, with the remarkably dense venation possibly pointing to an ecology with high irradiation.

In the newly collected material, *Macralethopteris hallei* is found as part of a mesophytic association of which *Gothanopteris bosschana* is also a member. *Gothanopteris*, along with *Palaeogoniopteris mengkarangensis* represents one of the two endemic gigantopterid genera of the Jambi flora. Although the specific reticulate leaf morphology of these alone is already sufficient for them to be marked as clear members of the gigantopterids (as separate from *Gigantopteris* sensu stricto), a 'deconstruction' of the leaf morphologies of the various gigantopterid genera found worldwide makes it clear that the Jambi gigantopterids can also be deconstructed along similar lines. These deconstructions all lead to recognizable but distinct, possible original morphologies, strongly supporting the idea of the gigantopterids as a very polyphyletic group, in concordance with suggestions by previous authors (Mamay, 1988, Glasspool et al., 2004a).

Another way in which the renewed exploration of the old localities has enriched the existing collection is the addition of a large amount of material with peltasperm affinity. Of these, *Comia variformis* is both the most interesting find, as well as the most abundantly represented one. Although clearly comioid in general leaf morphology, with simple pinnate fronds and fasciculated venation, its morphological variability is beyond any other species of *Comia*. The additional finds of material attributable to *Rhachiphyllum* and *Supaia*, as well as a peltasperm fructification, conclusively confirm the similarity of this flora to contemporary floras throughout the amerosinian paleotropics. This also means that, unless what we see here is a similar level of evolutionary convergence as seen in the gigantopterids, the occurrence of these peltasperm genera puts constraints on the possible plate configurations of the Cathaysian region in general and the paleogeographic position of the West Sumatra region in particular. It necessitates a configuration, which, for the early Permian, would allow migration of plants with constrained dispersal strategies (such as seed ferns) either to or from West Sumatra.

A feature left insufficiently explored in the previous century was the large amount of fossilized wood collected from the Mengkarang formation. Although Kramer (1974) had reviewed part of the material available, a comprehensive treatment of all the collected specimens was never performed. The size of this part of the collection, consisting of more than 150 specimens, offered the opportunity to go beyond an ordinary taxonomic description, and perform an exploration and analysis of the morphological variability of the pycnoxylic wood of the Mengkarang Formation. Since at least 250 (and probably many more) fossil species have been described worldwide based on this pycnoxylic wood type, it was expected that this analysis would result in at least several clearly morphologically delineated species. However, it turned out that it was impossible to make such a distinction on any particular character or set of characters. Moreover, virtually all characters turned out to be normally distributed, with none exhibiting a multimodal distribution. Since this variability is large enough to encompass a large number of the species of this wood type, which have been described in the past, it becomes questionable whether pycnoxylic wood, so poor in diagnostic characters really lends itself to a strictly Linnean approach to classification.

With the morphological variation of the older and newer collections completely overlapping, we can now state with certainty that all the gymnosperm wood in the Jambi collection is of an early Permian age. The evidence coming from several *in situ* specimens of fossilized tree trunks and logs, and one large specimen in particular, supports this. Analysis of this specimen and the circumstances of its burial confirm the Mengkarang Formation (as exposed along the Merangin River) as bearing witness to a system of major volcanic activity, on or near the volcanic slope, in which pyroclastic flows frequently destroyed and entombed the vegetation. This would result in volcanic activity frequently creating barren plots of ground in which all the vegetation had been raised and where the soil would have a high acidity. Such an environment would give opportunities for ruderal plant groups or species to rapidly colonize this newly barren ground. Moreover, an ancestry of these plants in the acidic conditions of forest mires, would give an advantage to growing in the similarly acidic volcanic ash deposits.

One of the more remarkable revelations brought about by the renewed investigation of the Jambi flora localities is the insight into the distinct floral associations found in the Mengkarang Formation. Where previously gymnosperm groups like the gigantopterids and *Macralethopteris* were known from the Jambi flora, it was unclear what their relation was to the forest mire flora, consisting of lycopsids, calamites and marattialean (pecopterid) ferns. In addition to rendering several remarkable new finds of gymnosperm species, renewed investigation of the localities made clear that, on the whole, the associations in which the gymnosperm elements are found are very distinct from those floras consisting of more classic Late Paleozoic ever-wet elements. Moreover, in several instances we find these gymnosperm-dominated associations in deposits that are interpreted as resulting from a pyroclastic- or gravity flow. This suggests that these associations, under normal circumstances, were not growing in conditions with high preservation potential, but, on occasion, were washed into the ‘basin’ by such a gravity flow.

Ongoing research demonstrates that two of these associations come from particularly abundant localities discovered during the recent expeditions. One can be described as dominated by (mainly) *Macralethopteris* and *Gothanopteris* (next to *Cordaites*). The other can be accurately called the peltasperm-association, since it mainly consists of *Comia*, *Rhachiphyllum* and *Supaia* (next to the sphenophytes *Sphenophyllum*, *Parasphenophyllum* and the fern *Sphenopteris*). The latter association, based particularly on the combined presence of *Sphenophyllum* and *Rhachiphyllum,* appears to represent a more mesic, though still well-drained, environment (DiMichele et al., 2006a, Bashforth & Zodrow, 2007). This differs from early- and middle Permian Euramerican finds for *Comia*, which usually grew in more xeric and often seasonally dry circumstances. The *Macralethopteris-Gothanopteris* association on the other hand, based on the morphology of *Macralethopteris*, but also on the virtual absence of elements indicating more humid conditions, seems to suggest a more xeric habitat. For the first time, this gives a perspective on the variety of associations and ecologies present in the Jambi flora.

With the present new data on gymnosperms from the Jambi flora, this flora can now be ranked with the other Cathaysian early Permian floras, and used for comparisons with contemporaneous floras from the amerosinean region, with regard to palaeoecology and palaeogeography. In so doing, this research illustrates the value of re-studying old collections as well as of visiting the original localities. This offers both a new perspective on an existing collection through a more detailed view on its geological-, paleogeographical- and taphonomical context, as well as an enrichment through new discoveries.

In the preceding work, one of the aspects that seems to demand further investigation is the question whether pycnoxylic wood in general can be described as morphologically circumscribed groups (*i.e.* distinct species), or whether it can more accurately characterized as a morphological continuum. If similarly large collections of fossil wood allow, it would be interesting to find whether a similarly continuous morphospace could be described from the pycnoxylic wood of these collections, as that found for the Jambi specimens. If this would be the case, the next question that presents itself is what determines the constraints on this morphospace.

One of the major problems in macro-paleobotanic research in general, is the difficulty in bridging the gap between taxonomy based on morphological descriptions on the one hand, and concrete phylogeny based on genetic similarities on the other hand. This comes to the fore in the preceding work especially in the research on peltasperms and gigantopterids. Here it is particularly difficult to determine whether the morphological similarities are caused by morphological convergence or by shared ancestry for species that are geographically often quite remote.

The problem is that what is deemed similar and what different in morphological comparisons, and on which features to base that distinction, is arbitrary and based on personal preference. In other words, what is hindering a more objective approach to morphological comparisons is the human factor. A completely different method might be called for to judge similarity of morphological features independently from the researcher’s preferences or bias. Harnessing the power of object- or image recognition through machine learning, starting with active learning on unambiguous specimens, could provide a more objective approach towards classifying plant fossil organ morphologies. Although this would require a significant time investment for both the development of software and for sufficient ‘training’ (through active learning) to arrive at a sufficiently advanced decision model, an basic proof of concept should still be possible within the scope of a PhD research project (for example).

8

Summary and future research

Chapter 1 describes the Jambi flora, an approximately 290 million year old flora found as part of the geological Mengkarang Formation in the province of Jambi, Sumatra, Indonesia. This flora was originally discovered by the Swiss geologist Tobler, and was subsequently first extensively described by the Dutch paleobotanist Jongmans and his German colleague Gothan. Jongmans grew so intrigued with this flora that he organized a dedicated expedition to the area. This expedition resulted in the main body of the current collection of plant fossils from the Jambi province that is now housed in the Naturalis Biodiversity Center in Leiden. After nearly a century of neglect, a reinvestigation of this collection and the taxonomic work based on it by Van Waveren and others renewed interest to such an extent that it led to the organisation of four expeditions to find and investigate the original localities.

What is so special about the Jambi flora that induced two researchers to independently go to considerable lengths in organizing expeditions to the remote localities in the tropical forest of Sumatra?

The Jambi flora represents an intriguing mix of on the one hand plant groups known from earlier forest mire floras of the middle and late Carboniferous (330 to 300 million years ago) and on the other hand plant groups, most of which are seed ferns, that would play important roles in the time to come and are making their first appearance. One of the things that was not clear from the old collection, was whether these plants all grew as part of the same vegetation, or whether they grew separately in different ecological circumstances. This is something that the recent expeditions have clarified. We now know that the newly appearing groups are part of a different vegetation (or vegetations) than those of the older plant groups. The latter also represent a typical peat-forming swamp ecology, while the first occur in drier conditions.

Chapter 2 concerns a detailed description of both the older and the newly found material from the alethopterid seed fern *Macralethopteris hallei*. Alethopterid seed ferns are already known from the middle Carboniferous onwards, but this particular species is exceptional both in the size of the pinnules (leaflets) as well as in the density of its venation. The recent expeditions have provided much more and better material that, for the first time, gives an impression of what the fronds of *Macralethopteris* look like. Some authors have questioned whether *Macralethopteris* is sufficiently different from other alethopterids (of the genus *Alethopteris)*, to include it in a separate genus. Particularly the new material allows confirmation of *Macralethopteris* as sufficiently different in its morphology, primarily in the attachment of its thick pinnules and the extremely dense venation, to keep it in a separate genus. This typical morphology of *Macralethopteris* suggests growth conditions that are drier than those of the majority of known late Carboniferous plant groups.

Three species attributable to the newly emerging Late Paleozoic seed fern group of the Peltaspermales are the subject of **Chapter 3**. The most remarkable of these is a new species belonging to the genus *Comia*, called *Comia variformis*. As the name suggests, this species is characterized by its variable morphology that far exceeds any seen in other species belonging to that genus. If less material had been found for this species the material would probably have been described as two or three distinct species, because it would not have been clear that all the variations in leaf morphology were part of a continuum. In the same vegetational association we also find material attributable to the peltasperm genera *Rhachiphyllum* and *Supaia*, as well as a peltasperm fructification. Given the age of the deposits, these genera make a rather early appearance in Jambi compared to their occurrence in the rest of the world. In the case of *Comia*, it is even the earliest currently known. The fact that these genera are also found in the early and middle Permian throughout Asia, Europe and America, suggests that the position of West Sumatra at that time must have allowed migration to and/or from there to the rest of the world.

Chapter 4 treats two early representatives (*Palaeogoniopteris mengkarangensis* and *Gothanopteris bosschana*) of the gigantopterids, one of the more enigmatic Permian plant groups, which is characterized by a particular form of net venation (involving multiple orders of veins). For both of these taxa, new material found during the recent expeditions allows more accurate descriptions and more insight into the unique morphology of these species. Taking the morphology of these Jambi species as a starting point, an attempt is made to reconstruct possible evolutionary trends that might have led to the gigantopterid leaf morphology through a visual analysis of all species found in the gigantopterids (excluding the genera *Gigantopteris* and *Gigantonoclea*). These 'deconstructions' show that virtually all these gigantopterid leaf morphologies are reducible to patterns commonly found among late Carboniferous plant groups. This not only hints at the physiological process that enabled the development of the gigantopterid leaf morphologies, but also allowed speculation as to possible ancestors. What becomes apparent, is that the original morphologies must have been rather diverse, indicating that the gigantopterids are not a phylogenetically coherent group, but rather consist of plants deriving from various ancestors.

Whereas the previous chapters primarily dealt with fossilized leaves of various gymnosperms, **Chapter 5** concerns the fossilized wood of the Mengkarang Formation. Fossilized wood in various forms, ranging from enclosed fragments to big *in situ* tree stumps, is common in the Mengkarang Formation and the existing collection contains a large number of specimens. The gymnosperm wood (found as dispersed fragments) has been described by Kramer, who ascribed a handful of specimens to a new species, *Dammaroxylon kaurioides.* He designated all of the Jambi gymnosperm fossil wood as Tertiary in age, because they were collected as loose-lying fragments from streams together with specimens of angiosperm wood that clearly were Tertiary in age. The size of the collection allowed for a novel approach in describing and analysing the morphology. By creating a large dataset of all the measurements for the specimens and subsequently performing a Principal Components Analysis (PCA) on this dataset an attempt was made to objectively determine what morphologically coherent groups (*i.e.* species) could be discerned. It was surprising to find that no separate groups could actually be discovered and that the dataset formed one morphologically coherent whole. While it is conceivable that all the wood in the collection was derived from a single species, both the range of ecologies from which it was collected and the timespan of the Mengkarang Formation make this rather unlikely. If the Jambi gymnosperm wood is representative for late Paleozoic fossil wood in general, the implications could be significant. Even a comparison with wood from modern-day species from the Araucariaceae, shows that the Permian wood differs from it in only a few quantitative characteristics. Could it be that the 250+ species that have up till now been described from this wood type are not truly distinct species at all, but just small samples from a morphologically continuous whole as well? If that is the case, perhaps a vegetative organ that is so little subject to evolutionary change is not suitable for Linnean taxonomy. In addition, a comparison with several *in situ* specimens of fossil tree trunks in particular and the old and newly collected fossil wood in general, has made it clear that all the gymnosperm fossil wood in the Jambi collection is of early Permian, rather than Tertiary age.

Chapter 6 explores the preservational conditions, taphonomy and ecology of a particularly large fossil tree stump, preserved *in situ*. What emerges is a picture of an environment that is very dynamic with regular disruptions from volcanic activity in the form of pyroclastic flows. The tree itself is encased in layers of reworked volcanic ash. Volcanic deposits like these are common throughout the Jambi outcrops of the Mengkarang Formation. Such disruptions of (reworked) pyroclastic deposits would make this environment ideal for those plant groups that specialize in the rapid colonization of barren ground (ruderals).

Future research

The research presented here has provided a significant broadening of our knowledge of this early Permian flora, as well as providing an intriguing point of reference for research on the Late Paleozoic paleo-tropics. Revisiting the original localities has rooted the collection firmly in a geological and ecological framework that was previously lacking.

One of the aspects that seems to demand further investigation is the question whether this type of gymnosperm wood in general can be described as morphologically circumscribed groups (*i.e.* distinct species), or whether it can more accurately be characterized as a morphological continuum. If similarly large collections of fossil wood are available, it would be interesting to find whether a similarly continuous morphospace could be described from the wood of these collections, as that found for the Jambi specimens.

This research has also repeatedly highlighted one of the more frustrating problems in paleobotany, namely that of the difficulty of establishing the relationship between morphology of (parts of) plants on the one hand and true phylogeny on the other. This is exacerbated by the fact that much of the distinctions made in paleobotanical taxonomy are somewhat arbitrary and for a large part based on preferences of the individual researchers. Although statistical processing of large datasets of morphological measurements provides a means of a more objective approach, it might be that an equally promising avenue would be the harnessing of machine learning in objectively discerning morphological patterns. Using object- or image-recognition, perhaps starting with active learning on unambiguous specimens, could provide a more objective approach towards classifying plant fossil organ morphologies.

Samenvatting en toekomstig onderzoek

Hoofdstuk 1 beschrijft de ‘Jambi-flora’, een bij benadering 290 miljoen jaar oude flora die wordt gevonden als onderdeel van de Mengkarang Formatie in de provincie Jambi in Sumatra, Indonesië. Deze flora werd ontdekt door de Zwitserse geoloog Tobler en is vervolgens voor het eerst uitgebreid beschreven door de Nederlandse paleobotanicus Jongmans en zijn Duitse collega Gothan. Jongmans raakte zo geïntrigeerd door deze flora dat hij een speciale expeditie naar het gebied organiseerde. Deze expeditie resulteerde in het grootste deel van de huidige collectie van plantenfossielen uit de provincie Jambi, die zich op dit moment bevindt in de collecties van het Centrum voor Biodiversiteit Naturalis. Pas bijna een eeuw later volgde een herevaluatie van de collectie en het taxonomisch werk dat er op is gebaseerd door van Waveren en collega’s. Dit leidde tot een dermate grote interesse dat het resulteerde in vier nieuwe expedities met als doel de oorspronkelijk vindplaatsen terug te vinden en te onderzoeken.

Wat is er nu zo speciaal aan de Jambi flora dat het twee onderzoekers onafhankelijk van elkaar er toe aanzette om de niet geringe moeite te ondernemen expedities naar de moeilijk bereikbare vindplaatsen in het oerwoud van Sumatra te organiseren?

De planten van de Jambi flora zijn een intrigerende mix van plantengroepen. Aan de ene kant zijn er die groepen die al bekend zijn van de veenmoerassen uit het midden- en laat Carboon (330-300 miljoen jaar geleden), aan de andere kant groepen die hun eerste opwachting maken (vooral zaadvarens) en die in de daaropvolgende tijd een belangrijke rol zouden spelen. Uit de gegevens van de oude collectie kon niet worden opgemaakt of al deze planten onderdeel uitmaakten van dezelfde vegetatie, of dat ze gescheiden waren door verschillende ecologische omstandigheden. Dankzij de recente expedities weten we nu dat de ‘modernere’ plantgroepen onderdeel waren van een andere vegetatie dan die van de oudere groepen. Deze laatste vormen een typische veen-vormende moerasvegetatie, terwijl de eerste in drogere omstandigheden groeiden.

Hoofdstuk 2 geeft een uitgebreide beschrijving van zowel het oudere als het nieuw verzamelde materiaal van de alethopteridische zaadvaren *Macralethopteris hallei*. Alethopteridische zaadvarens zijn al bekend vanaf het midden Carboon, maar deze specifieke soort is in zowel de grootte van de pinnulen (deelblaadjes) als in de dichtheid van de nervatuur uitzonderlijk. De recente expedities hebben veel meer en beter materiaal opgeleverd wat voor de eerste keer een indruk geeft van hoe de bladeren van *Macralethopteris* er uit moeten hebben gezien. Sommige auteurs hebben in twijfel getrokken of *Macralethopteris* wel voldoende afwijkt van andere alethopteriden (in het genus *Alethopteris*) om toegewezen te worden aan een apart genus. Het nieuwe materiaal in het bijzonder bevestigt de unieke en afwijkende morfologie van *Macralethopteris*, vooral waar het de aanhechting van de opvallende dikke pinnulen en de zeer dichte nervatuur betreft, en daarmee de validiteit van het aparte genus. De typerende morfologie van *Macraletopteris* suggereert dat deze plant in drogere omstandigheden voorkwam dan die van de meeste plantgroepen die uit het laat Carboon bekend zijn.

Drie soorten die alle tot de dan recent ontstane plantengroep van de Peltaspermales behoren, zijn het onderwerp van **Hoofdstuk 3.** De meest opmerkelijke van deze drie is een nieuwe soort van het genus *Comia*, *Comia variformis*. Zoals de naam al suggereert, wordt deze soort gekarakteriseerd door een meer variabele morfologie dan bekend is van enige andere soort in dit genus. Als er minder materiaal gevonden was van deze soort, zodat niet duidelijk was geworden dat alle variaties in bladmorfologie onderdeel waren van hetzelfde continuüm, waren er waarschijnlijk drie aparte soorten beschreven. In dezelfde associatie vinden we ook materiaal van de peltasperm genera *Rhachiphyllum* en *Supaia*, naast een peltasperm fructificatie. Gezien de ouderdom van de afzetting, is het een zeer vroeg voorkomen van deze genera vergeleken met hun verschijnen elders in de wereld. In het geval van *Comia* is het zelfs het tot nu toe vroegst bekende voorkomen. Aangezien deze genera ook gevonden worden in afzettingen uit het vroeg- en midden Perm in heel Azië, Europa en Amerika, zou de toenmalige positie van West Sumatra het mogelijk gemaakt moeten hebben dat er migratie tussen dit gebied en de rest van de wereld plaats vond.

Hoofdstuk 4 behandelt met *Palaeogoniopteris mengkarangensis* en *Gothanopteris bosschana* twee vroege vertegenwoordigers van de gigantopteriden, een raadselachtige Permische plantgroep. Deze groep wordt gekarakteriseerd door een specifieke vorm van netnervatuur, die meerdere niveaus van nervatuur omvat. Voor beide taxa geldt dat nieuw materiaal, verzameld bij de recente expedities, nauwkeurigere beschrijvingen en nieuwe inzichten in deze unieke soorten mogelijk heeft gemaakt. Met de morfologie van deze Jambi soorten als beginpunt, is een poging gedaan om de mogelijke evolutionaire patronen die hebben geleid tot het ontstaan van de unieke bladmorfologie en nervatuur van de gigantopteriden te achterhalen via een visuele analyse van alle gigantopteriden (met uitzondering van de genera *Gigantopteris* en *Gigantonoclea*). Deze 'deconstructies' laten zien dat vrijwel al deze bladmorfologieën in de gigantopteriden te reduceren zijn tot patronen die veelvuldig gevonden worden bij plantgroepen uit het laat Carboon. Dit geeft niet alleen een idee van het fysiologische proces dat de ontwikkeling van de bladmorfologie van de gigantopteriden mogelijk heeft gemaakt, maar geeft ook voer voor speculatie over de mogelijke voorouders. Wat duidelijk naar voren komt, is dat de oorspronkelijke morfologieën vrij divers moeten zijn geweest. Dit geeft aan dat de gigantopteriden geen fylogenetisch coherente groep is, maar waarschijnlijk bestaat uit soorten met uiteenlopende voorouders.

Terwijl de voorgaande hoofdstukken vooral gefossiliseerde bladeren van verschillende gymnospermen behandelden, gaat **Hoofdstuk 5** over het versteend hout uit de Mengkarang formatie. Gefossiliseerd hout in verschillende vormen komt algemeen voor in de Mengkarang formatie; van ingesloten fragmenten tot grote boomstronken die in situ bewaard zijn gebleven. De huidige collectie bevat dan ook een grote hoeveelheid stukken hiervan. Het hout van gymnospermen (verzameld als fragmenten uit de verschillende rivieren en beken) is beschreven door Kramer, die een handvol stukken toeschreef aan een nieuwe soort *Dammaroxylon kaurioides*. Daarnaast bestemde hij al het hout van gymnospermen uit Jambi als Tertiair in ouderdom, omdat het als losse fragmenten samen gevonden was met fragmenten van angiospermenhout dat overduidelijk uit het Tertiair afkomstig was. De omvang van de collectie bood gelegenheid tot een nieuwe benadering in het beschrijven en analyseren van de morfologie van dit fossiel hout. Nadat een grote dataset met meetgegevens was gecreëerd, werd met een Principal Components Analysis (PCA) geprobeerd op een objectieve manier te achterhalen welke morfologisch coherente groepen (*c.q.* soorten) in de dataset te onderscheiden zouden zijn. Het was verrassend om te ontdekken dat het niet mogelijk bleek om individuele groepen in de dataset te onderscheiden en dat het één morfologisch coherent geheel bleek te vormen. Hoewel het voorstelbaar is dat al het hout in de collectie afkomstig is van één enkele soort, is dit op zijn minst onwaarschijnlijk, gezien de verschillende ecologische omstandigheden van de vindplaatsen en het tijdsbestek van de Permische afzettingen van de Mengkarang formatie. Als het hout van de Jambi gymnospermen representatief is voor laat Paleozoïsch hout in het algemeen, kan dit belangrijke implicaties hebben. Zelfs een vergelijking met hout van recente soorten uit de Araucariaceae laat slechts relatief klein, kwantitatieve verschillen zien. Is het denkbaar dat de meer dan 250 soorten die tot nu toe zijn beschreven op basis van dit type hout in werkelijkheid geen verschillende soorten zijn, maar slechts kleine steekproeven uit een groot morfologisch continuüm? In dat geval is een plantenorgaan dat zo weinig onderhevig is aan evolutionaire verandering misschien niet geschikt voor Linneaanse taxonomie. Hiernaast heeft een vergelijking tussen het oude en het nieuw verzamelde materiaal, in het bijzonder met de verschillende *in situ* boomstronken, duidelijk gemaakt dat al het fossiele gymnospermenhout van de Jambi collectie niet Tertiair is, maar uit het vroege Perm stamt.

Hoofdstuk 6 verkent de ecologie en de omstandigheden waaronder een zeer grote fossiele boomstronk *in situ* bewaard is gebleven. Dit geeft een beeld van een zeer dynamisch ecosysteem, met regelmatige verstoring door vulkanische activiteit in de vorm van pyroclastische stromen. De boomstronk zelf is omsloten met door water getransporteerde lagen van geërodeerde vulkanische as. Zulke vulkanische afzettingen zijn algemeen in alle Permische ontsluitingen van de Mengkarang formatie in Jambi. Deze verstoringen maken dit ecosysteem bijzonder geschikt voor plantgroepen die gespecialiseerd zijn in het snel koloniseren van braakliggende grond (zogenaamde ruderalen).

Toekomstig onderzoek

Het bovenstaande onderzoek heeft voor een belangrijke verdieping gezorgd van de kennis over deze flora uit het vroege Perm. Daarnaast heeft het mogelijk gemaakt dat de Jambi flora nu als een intrigerende referentie kan gelden voor onderzoek naar de laat Paleozoïsche paleo-tropen. Het opnieuw bezoeken van de oude vindplaatsen heeft de collectie een grondige referentie gegeven in de vorm van een geologisch en ecologisch raamwerk dat voorheen ontbrak.

Eén van de onderdelen die om verder onderzoek vraagt is de vraag of dit type gymnospermenhout in het algemeen beschreven kan worden als morfologisch duidelijk afgebakende groepen (*c.q.* soorten) of dat het ook hier in werkelijkheid altijd een morfologisch continuüm betreft. Gegeven collecties van fossiel hout van een vergelijkbare omvang, zou het interessant zijn om uit te vinden of dezelfde continue morfologische ruimtes, zoals bij de Jambi collectie gevonden wordt, ook op basis van deze collecties te vinden zijn.

Dit onderzoek heeft ook bij herhaling één van de meer frustrerende problemen in de paleobotanie naar voren gebracht. Namelijk, dat het moeilijk blijft om de morfologie van (onderdelen van) planten te koppelen aan concrete evolutionaire fylogenie. Dit wordt verergerd door het feit dat veel van de grenzen die getrokken worden in de paleobotanische taxonomie vrij willekeurig zijn en voor een aanzienlijk deel gebaseerd op de voorkeuren van individuele onderzoekers. Statistische analyse van grote datasets van morfologische meetgegevens zijn een manier om een meer objectieve benadering mogelijk te maken. Maar een minstens zo veelbelovende richting zou het inzetten van machine-learning voor het objectief onderscheiden van morfologische patronen kunnen zijn. Het gebruik van object- or beeldherkenning, waarbij eventueel begonnen kan worden met actief leren op basis van onomstreden classificeerbare stukken, zou kunnen zorgen voor een meer objectieve benadering in het indelen van de morfologie van fossiele plantorganen.

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Curriculum Vitae

Menno Booi was born on september 15th 1976 in Uithoorn. In 1995 he graduated (VWO) from Geert Groote School in Amsterdam. At the University of Utrecht he specialised in Late Paleozoic paleobotany and pollen morphology of the recent Lythraceae. In 2003 he graduated with an MSc in Biology on a thesis about the life and work to Dutch paleobotanist W. A. Jongmans. In the same year, he started with his studies on the Early Permian flora of Jambi, Sumatra at the Naturalis Biodiversity Center (formerly the National Natural History Museum Naturalis), initially enabled by a grant from the Stichting Fundatie van de Vrijvrouwe van Renswoude. As a part of these studies, he took part in expeditions to the area (in 2003, 2004 and 2006) which aimed at a greater understanding of the geological setting as well as the collection of new material. During 2007 and 2008, a combined effort from Naturalis and Leiden branch of the National Herbarium allowed him to pursue his PhD work on a full-time basis for two years. From 2010 onwards he has decided to pursue a career in software development, but has continued to work on his PhD in his spare time.

Publications

Booi, M., Punt, W., Hoen, P.P. 2005. The Northwest European Pollen Flora, 68 Lythraceae. Review of Palaeobotany and Palynologie 123: 163-180.

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