Innovation and stasis : gymnosperms from the early Permian Jambi flora

Booi, M.

Citation

Booi, M. (2017, November 15). *Innovation and stasis : gymnosperms from the early Permian Jambi flora*. Retrieved from https://hdl.handle.net/1887/57351

Author: Booi, Menno
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Date: 2017-11-15

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.

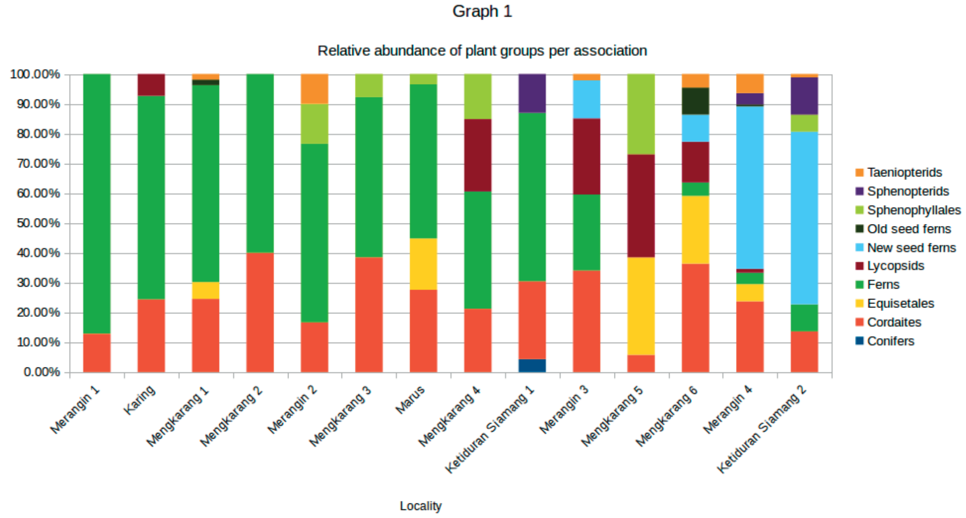

Figure 1.1: Relative abundances of phylogenetic groups for the more abundant localities from the Mengkarang Formation (as collected during the recent expeditions). Order of localities is determined by a DCA (Detrended Correspondence Analysis).

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.