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
Title: Innovation and stasis : gymnosperms from the early Permian Jambi flora
Date: 2017-11-15

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).