Gondwanan Palaeozoic Plant spores: a review

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The earliest plant spores are called cryptospores because they are devoid of haptotypic features such as trilete or monolete mark. They were presumably produced by bryophytes. The earliest unambiguous cryptospores known to date appear during the Dapingian on the Western Gondwana. It has however to be noted that some authors consider that some Cambrian palynomorphs are also cryptospores.

The Dapingian and Darriwilian cryptospores are poorly diversified. During the Sandbian, new morphologies evolve, including specimens enclosed in a membrane. The assemblages remain stable up to the Aeronian, which suggests that plants had a low evolutionary rate during more than 22 Myr. Surprisingly, the Hirnantian glaciation did not affect the cryptospore biodiversity. This putative climatic tolerance may explain why cryptospore-producing plants survived in latitudes ranging from the palaeoequator up to the palaeopole. The earliest trilete spores are known from the Katian and the Hirnantian of Saudi Arabia. They were presumably produced by tracheophytes. They remain very rare up to the Wenlock. Few elements may be used for biostratigraphy. The main element allowing an estimation of the age is the abundance (i) of trilete spores and (ii) of cryptospores enclosed in a membrane. The first appearance of the trilete spore *Archaeozonotriletes chulus* in the Telychian is the first reliable biostratigraphic event.

From Wenlock times onwards, the palynostratigraphic scheme is better resolved. Palaeogeographic interpretations become possible. For example, *Emphanisporites splendens* is only known in the Ludlow/Pridoli of Gondwana and Spain; *Streelispora newportensis* is only known in the Lochkovian of Laurussia and Spain. This strongly suggests that the Iberian plate was located between Gondwana and Laurussia, and favours plate reconstructions showing a short distance between the two palaeocontinents.

We described a phylogenetic succession of trilete spores from a Lochkovian to Pragian locality on the ORSC. Those trilete spores are unknown on the Gondwana, except on the small Moesian peri-Gondwanian terrane. This terrane has supposedly moved northwards during the Devonian and collided with Laurussia during Carboniferous times. Our results suggest that the terrane was already close to the ORSC during Early Devonian times.

The acquisition of the heterospory is the next important step in the evolution of the vegetation. Heterospory is marked by the development of spores larger than ca. 150 µm. They are called megaspores and develop into female gametophytes. The microspores are the smaller spores that develop into male gametophytes. The joint presence of both types of spores is necessary to allow heterosporous plants to reproduce. A rich, exquisitely preserved assemblage of megaspores has been described from the Eifelian and the Givetian from Gondwana. Among 20 different taxa of megaspores, 6 are also known from the Laurussia continent. Their presence on both continents suggests that they could be transported from one

palaeocontinent to the other. In addition, because (i) large megaspores cannot be transported over long distances, and (ii) megaspores and microspores need to fall down close to each other, palaeogeographic reconstructions showing a pre-Pangea during the second half of Devonian are again preferred to reconstructions showing a large ocean between Laurussia and Gondwana.