

Initiation of eusaccatism in Late Permian : A key to the origin of true saccus in modern gymnosperms

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SACCUS is the sexinal extension of the pollen exine, as explained by Erdtman, 1952; p. 468 : air sac is the sexine loosened from nexine where bacula or baculoid elements usually sticking to the under surface of the tegillum. According to Potonié & Kremp, 1955; p. 19 : "In the development of sacci the bases of the columellae detach from intexine, and the air space between the intexine and exoexine expands". In such a process the sexine expands and may form pouch-like lobes; it is an essential organ for wind dispersal. In the extant families of coniferales, i.e., Pinaceae, Abietineae and Podocarpaceae, there are few genera in which the pollen are saccate, viz., *Pinus*, *Abies*, *Cedrus*, *Podocarpus*.

The modern saccate pollen are exclusively eusaccate, i.e., they possess true sacci having a cavity which occupies most of the inner space lined by one or two layers of alveoli (Scheuring, 1978; Klaus, 1977). On the other hand, most of the pollen taxa found in Palaeozoic and Mesozoic sediments are predominantly protosaccates where there is no cavity within the saccus and the whole inner space is filled with endoreticulum or alveoli. However, trend of eusaccatism was introduced at different times in the geological past, but it appears that the fossil non-striate disaccate pollen group (e.g. species of *Podocarpidites*, *Pinuspollenites*, *Abietinaepollenites*, etc.) began to attain eusaccatism in Jurassic. And this trend continued in the saccate pollen of a few modern conifer taxa.

The origin and relationship of *Teichertospora*, a trilete-bearing cavate miospore (analogous to eusaccate pollen) from Devonian are uncertain (Balme, 1988). Recently, Foster and Balme (1994) have interpreted, on the basis of TEM studies, that *Teichertospora* is protosaccate; however, all their illustrations show that eusaccatism

was initiated in this genus. Most of the mono- and bisaccate pollen from Permian Gondwana possess filled sacci (Tiwari, 1981). However, definite eusaccate morphos appeared at the Upper Permian level as it has been recently re-assessed by Vijaya (in press) in the case of *Playfordiaspora* Maheshwari & Banerji (1975). The nature of saccus structure in various species of this genus has been found to be eusaccate, enclosing an empty space, i.e., cavity which is internally lined by a single layer of regular endoreticulum. Thus, the saccus in *Playfordiaspora* is typically eusaccus which covers the central body on to the contact region proximally and complete body surface distally. This genus also bears a trilete mark (a pre-pollen character). *Playfordiaspora* appeared at the latest Permian level and continued to occur through Triassic. Its morpho-evolutionary relationships are yet obscure as no detailed study has been done on the saccus structure of other pollen taxa.

The discovery of another pollen genus *Protoeusaccites* by Tiwari, Vijaya and Ram-Awatar (in press), a non-striate disaccate, having a partial cavity within the sacci, records a transitional stage of evolution in saccus structure – from Protosaccate to Eusaccate. Although the stratigraphic level of the occurrence of this protoeusaccate pollen is Late Permian (Middle Member of the Pali Formation) in South Rewa Gondwana Basin, India, its total range of distribution is not yet known. In any case, no such forms are on record from the strata older than the Upper Permian. In the saccus of *Protoeusaccites* Tiwari, Vijaya and Ram-Awatar (in press), most of the inner space is filled with endoreticulum from all sides except for an elongated narrow cavity in the central region of the saccus which is left as an empty space without any filling. This stage is a step towards achieving eusaccatism from protosaccatism.

In the strata younger to Late Permian, there are definite records of eusaccatism in the Mesozoic saccate pollen (Couper, 1958; Scheuring, 1978). It is certain that the eusaccatism is the Advanced (derived) Character State as it is the mode of organization in the modern saccate pollen, while protosaccatism is the Primitive Character State that had occurred in most of the Palaeozoic and Mesozoic pollen. The initiation of eusaccatism by having a partial cavity in saccus chamber is the attainment of the Transitional Character State, recorded at the Late Permian level. This trend of evolution further achieved the eusaccatism in Late Mesozoic which culminated in the modern conifers. The progressive non-development of endoreticulum within the saccus could lead to the origin of partial cavity and ultimately a full cavity. The conservation of building material and perfection in buoyancy are the probable aims of such lines of evolution. A process which was initiated in the Upper Permian in disaccate pollen, ultimately prevailed upon in the modern gymnospermous taxa.

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