

Fine structure of *in situ* *Pteruchus* pollen from the Upper Permian of the Dead Sea region, Jordan

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The pollen organ *Pteruchus* is a member of Umkomasiales (Corystospermales), an extinct group of seed ferns. Other taxa of this group include those established for leaves (e.g., *Dicroidium*), wood (e.g., *Rhexoxylon*, *Kykloxylon*), and ovuliferous organs (e.g., *Umkomasia*, *Fanerotheca*). We present a detailed study of *in situ* pollen from *P. lepidus*, one of the oldest records of *Pteruchus* worldwide and also part of one of the most completely reassembled Umkomasiaceae plants, with *Dicroidium robustum* leaves and *Umkomasia aequatorialis* ovuliferous organs (Blumenkemper et al. 2020). The material comes from the upper part of the late Permian (Lopingian) Umm Irna Formation exposed at the Dyke Plateau locality, Dead Sea region, Jordan; it was treated following standard protocols for transmitted light (LM), scanning electron (SEM), and transmission electron (TEM) microscopy.

Pollen grains are monosulcate and bisaccate with crescent-shaped, laterally attached sacci, and measure on average 61 (52.4-70) μm from saccus to saccus. Sacci are eusaccate and have distinct endoreticulations. The proximal and saccus surface is psilate to scabrate, the aperture membrane is rugulate. The ectexine in the cappus region consists of a relatively thick tectum, an infratectum with one row of 'alveoli' and a thin foot layer. The endexine is more electron-dense, lamellate, and of uniform thickness throughout the pollen except for the saccus region where it is considerably thickened and multi-lamellated. The aperture region is represented by an endexine and a very thin ectexine layer.

Dispersed pollen grains compared to those from *Pteruchus* pollen organs are *Pteruchipollenites* and *Alisporites*. Electron microscopy studies on these dispersed genera are scarce and the few pollen types studied thus far do not show much similarity to *P. lepidus* pollen in the exine ultrastructure. *In situ* pollen of several *Pteruchus* species was previously studied with SEM and TEM from the Triassic of Argentina, South Africa, and Antarctica; namely *P. dubius*, *P. africanus*, *P. papillatus*, and *P. fremouwensis*. The pollen size is similar or somewhat larger in the studied *Pteruchus* pollen except for *P. dubius* from Argentina which is characterized by significantly larger pollen. Further differences can be observed in the aperture membrane ornamentation and in the structure of the cappus region. The aperture membrane is rugulate in *P. lepidus*, but smooth (or unknown) in other *Pteruchus* species. The cappus region is described as homogeneous or nearly so in earlier studied *Pteruchus* pollen, whereas in *P. lepidus* the exine shows a one-row 'alveolate' or "honeycomb" layer. Small lacunae along the outer saccus wall together with long pending ectexine elements create a characteristic saccus ultrastructure in the studied pollen. Another unusual feature is the multi-lamellated and significantly thickened endexine under the saccus regions observed for pollen of *P. lepidus*. The same multi-lamellated endexine thickened under the sacci was reported for *Caytonanthus arberi*. The ultrastructure of the saccus and cappus regions in *Caytonanthus arberi* also resemble those of *P. lepidus*, but *Caytonanthus* pollen is considerably smaller. Based on the still limited evidence available to date, the studied material appears most similar to *Caytonanthus* pollen grains. Such similarity, however, might reflect functional aspects rather than close phylogenetic relationship.



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ABSTRACT BOOKLET

HOSTED ONLINE BY THE NATURAL HISTORY MUSEUM, LONDON

9 – 13TH AUGUST 2021

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