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duced by early members of plant groups whose heyday happened in the Mesozoic or by some their precursors? Alternatively, do we deal with cases of convergence or repeated independent appearance of the same characters in unrelated plant groups? One more aspect should not be forgotten: early members of a particular plant group did not necessarily have the same pollen as later members. Data on in situ pollen grains from Permian male fructifications can shed light on the problem. However, the amount of dispersed pollen types of unknown botanical affinities exceeds many times the amount of pollen types whose affinities are defined with certainty by in situ finds. This is true both for the Mesozoic and Permian, but for the latter even more so. The situation will become better with time, but we fear that many pollen variants will probably never be discovered in situ because of the incompleteness of the palaeontological record. A good remedy is to collect all possible information about such dispersed pollen grains not only by means of conventional light

## The Permian through the eyes of pollen morphologists

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Dispersed pollen grains and spores are a useful stratigraphic tool, and that is particularly true for the Permian, with its abundant terrestrial deposits. For pollen morphologists, the Permian is unique because of the first appearance of several morphological types which became prominent later, during the Mesozoic. What might be the relation between such pollen taxa from the Permian and those found in the Mesozoic? Were the former pro-

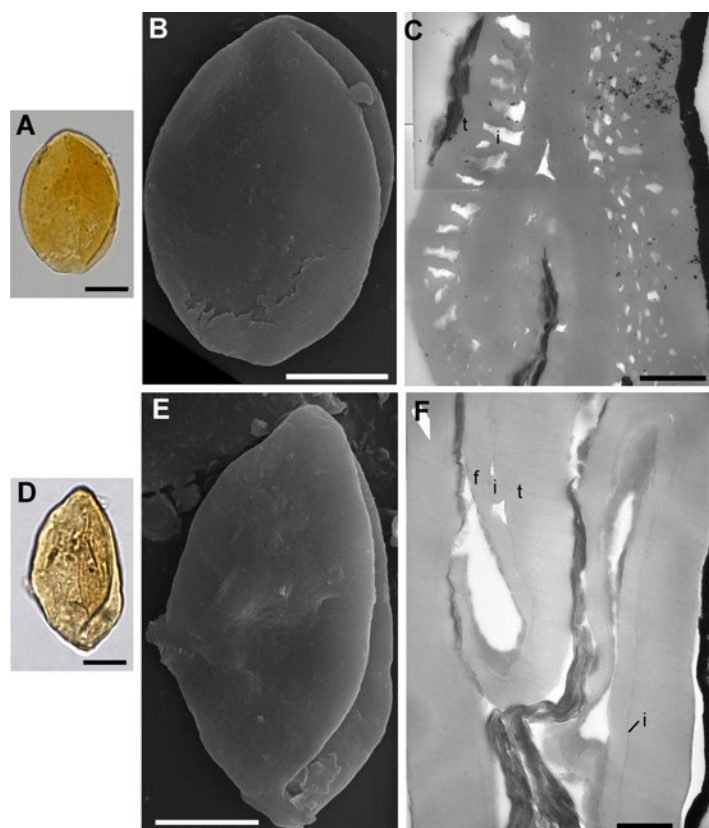


Fig. 1. A-C. Cycad in situ pollen grains from cones of *Androstrobis manis*, Jurassic of Yorkshire (reproduced from Zaviolova, van Konijnenburg-van Cittert, 2016 and raw materials to this paper). D-F. Dispersed pollen grains of the hypothesized ginkgoalean affinity from the Cretaceous of the Russian Far East (reproduced from Zaviolova et al., 2011). A, D. Light microscopical images. B, E. SEM images. C, F. TEM images. C. Note a thin tectum (t) and a typically cycadalean infratectum (i) with regular perpendicular alveolae, visible to the left of the image. F. A co-occurrence of a thick solid tectum, a thin infratectum, and a thin foot layer is typical of a ginkgoalean exine ultrastructure. Compare with Osborn and Taylor (1995, fig. 1, 9 for the morphology and ultrastructure of bennettite pollen). Scale bar (A, B, D, E) 10  $\mu$ m, (C, F) 0.5  $\mu$ m.

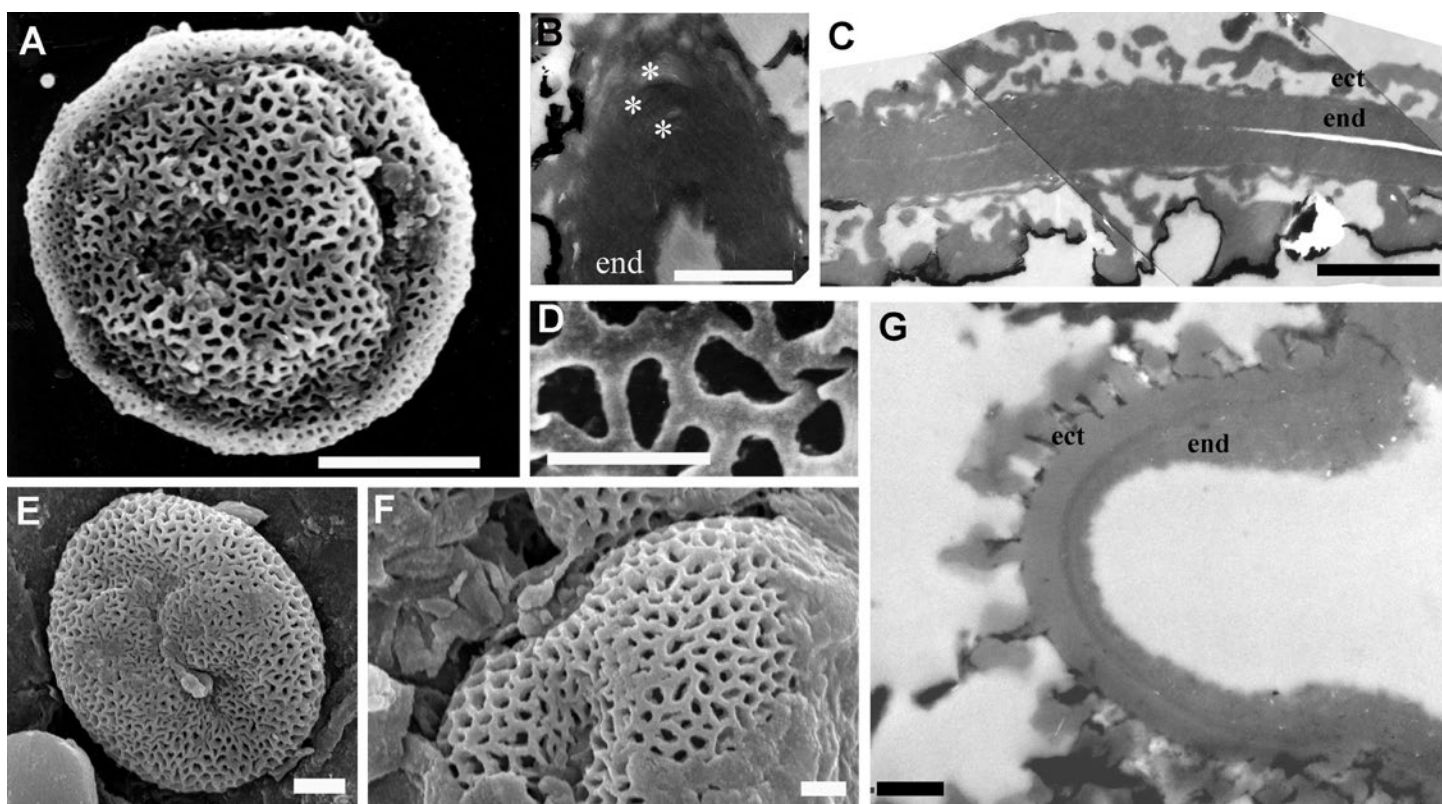


Fig. 2. A-D. Dispersed pollen grains of *Reticulatina microreticulata* from the Permian of the Russian Platform (reproduced from Zavialova and Gomankov, 2009). A. Reticulate surface is evident. B. Enlargement of a section showing lamellae (asterisks) in the endexine (end), typical of a gymnospermous exine. C. Flattened exine of the pollen grain, note the endexine of a constant thickness. D. Enlargement of A. E-G. Pollen grains adhered to infructescences of *Frisicarpus kubaensis* from the Cretaceous of the Kemerovo region, Russia. E. Pollen grain with a reticulate surface. F. Enlargement of pollen surface. G. Area of the exine, note columellate ectexine (ect) and non-lamellate endexine (end), which becomes thicker towards the aperture; both features are typical of an angiospermous exine. A, D, E, F. SEM images. B, C, G. TEM images. Scale bar (A) 20  $\mu\text{m}$ , (B, F) 1  $\mu\text{m}$ , (C, E) 2  $\mu\text{m}$ , (D) 4  $\mu\text{m}$ , (G) 0.5  $\mu\text{m}$ .

microscope, but also by electron microscopes (scanning electron microscopy, SEM, and especially transmission electron microscopy, TEM), to hypothesize about their affinity.

For example, boat-shaped monosulcate pollen ascribed to the genus *Cycadopites* are common in Mesozoic deposits, where they are known to have been produced by bennettites, cycads, ginkgoaleans, as well as several other gymnosperm groups (Balme, 1995). This Mesozoic trio of gymnosperm groups is known from the Palaeozoic as well, but the majority of records are represented by fossil leaves, and the information about in situ pollen has been so far lacking (Taylor et al., 2009). On the other hand, *Cycadopites* sporadically occurs also in the Permian (e.g., Zavialova et al., 2001), but unlike in the Mesozoic it has never been found in plant macrofossils. Available data on in situ *Cycadopites* from pollen organs of different Mesozoic gymnosperms show that such pollen grains though being very uniform in general morphology discernible in transmitted light, are different in the ultrastructure of their exines, and TEM data allows us to differentiate between *Cycadopites* pollen grains of different botanical affinities (Fig. 1; Zavialova and Nosova, submitted). While waiting for in situ Permian *Cycadopites* to be found, a TEM study of dispersed *Cycadopites* from the Permian seems desirable.

Reticulate pollen grains are a reliable marker of the advent of flowering (angiosperm) plants, if one finds such pollen in Cretaceous palynological assemblages. However, reticulate pollen grains are known from much older deposits, including the Permian, where they are a challenge for interpretation rather than a proof of the presence of this plant group a hundred million years earlier than all other indices suggest. A dispersed reticulate pollen *Reticulatina* was studied from the Permian of the Russian Platform with TEM and a typically gymnospermous lamellate endexine was found in its exine (Zavialova and Gomankov, 2009). Earlier, pollen grains of this type were discovered in male cones of a Permian primitive conifer *Kungurodendron* (Meyer-Melikian et al., 1998). Both studies proved the gymnospermous affinity of this angiosperm-like pollen, whatever was the reason for the appearance of an angiosperm-like character much earlier than angiosperms appeared (Fig. 2).

Recently, we have studied the morphology and ultrastructure of another peculiar pollen, *Pretricolpipollenites bharadwaji*, from the Permian of Jordan (Tekleva et al., submitted). This is thought to be the earliest pollen grain with three sulci. Later, in the Mesozoic, similar pollen grains are incorporated in *Eucommiidites* (Tekleva et al., 2006). Much is still to be understood about this Mesozoic genus as well, which is

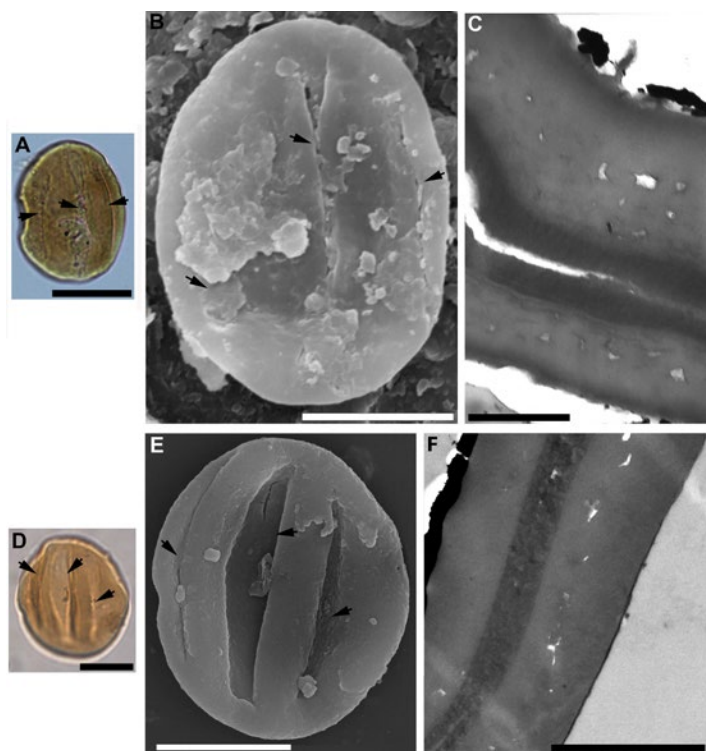


Fig. 3. A-C. *Eucommiidites* type pollen grains from pollen organs of *Hastystrobus muirii*, Jurassic of Yorkshire (B, C reproduced from Tekleva, 2012). D-F. Dispersed pollen grains of *Pretricolpipollenites bharadwaji*, Permian of Jordan. A, D. Light microscopical images. B, E. SEM images. C, F. TEM images. C. Note a difference in the ectexine thickness of proximal and distal pollen sides, with infratectal granules in several rows. F. The infratectal structure is not always discernable on proximal pollen side, the infratectal granules are disposed in one row. Arrowheads indicate the apertures. Scale bar (A) 20  $\mu\text{m}$ , (B, D, E) 10  $\mu\text{m}$ , (C) 0.5  $\mu\text{m}$ , (F) 1  $\mu\text{m}$ .

supposedly related to several groups within gnetophytes. As to *Pretricolpipollenites*, our study provides the first data on the exine ultrastructure of a member of this genus. The present state of knowledge of *Pretricolpipollenites* pollen does not allow any definite conclusion on its relationship with other similar taxa. Most probably, *Pretricolpipollenites* species are related to some *Eucommiidites* species, so these two genera might require taxonomic reconsideration (Fig. 3).

This note is to stress the importance of deeper knowledge of members of palynological assemblages. Their potential for stratigraphy is a consequence of the evolutionary fate of the parent plants. The more information about the plant-producers we are able to draw from pollen grains, the more substantiated their usage in stratigraphic and other reconstructions will be. A prospective method for this is an electron-microscopical study, particularly with help of TEM. Unfortunately, the number of studies on fossil pollen made with application of TEM constantly decreases. About twenty years ago, Hesse et al. (2003) wrote that “pollen morphologists are an endangered species and their field of work should be put on a Red data list”. The situation has not been much improved since their appeal.

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