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Unique sets of exine features in morphology and ultrastructure of oculata and triprojectate pollen from Zeya-Bureya Basin

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Dispersed pollen grains from oculata and triprojectate (unica) groups were studied using transmitted light (LM), scanning (SEM) and transmission (TEM) electron microscopy. The material comes from the Amur River Region, Far East, and is dated to the Maastrichtian (Markevich et al., 2011). Pollen grains of these groups are similar in their distinct and short-time stratigraphic distribution, unusual morphology and so far unknown botanical affinity.

From oculata group we studied pollen grains of the most common species, *Wodehouseia spinata* Stanley, with LM, SEM, and TEM. From triprojectate group, seven species were studied with LM and SEM, and four of them were studied with TEM.

In all studied species the unusual and complex exine, both in morphology and ultrastructure, implies a high degree of specialization of the parent plants and their adaptation to the environment. The pattern of the pollen shape, exine sculpture (fig. 1A-D; fig. 2A-C) and sporoderm ultrastructure (fig. 2D-G) suggest that insects contributed to pollination.

Species of the both groups show highly specific features facilitating harmomegathy (changing the volume of partly hydrated/dehydrated pollen without damaging its living content). In *Wodehouseia*, these are a flange and unevenly thickened endexine (fig. 1A; fig. 2A, D). In the studied triprojectate pollen, these are differences in the thickness of the foot layer and endexine in the polar and equatorial regions (fig. 1 B-D; fig. 2E, G). In *Pseudointegricorpus reticulata* (one of the studied triprojectates) furrows additionally might have played a role in the harmomegathy (fig. 1C). Other features possibly concerning harmomegathy in this and some other triprojectate species are a non-extended region with a cavity in the ectexine or an increased ectexine thickness with a loosely arranged infratectum which is located near the endexinous thickenings (fig. 2F, G; Tekleva et al., 2015).

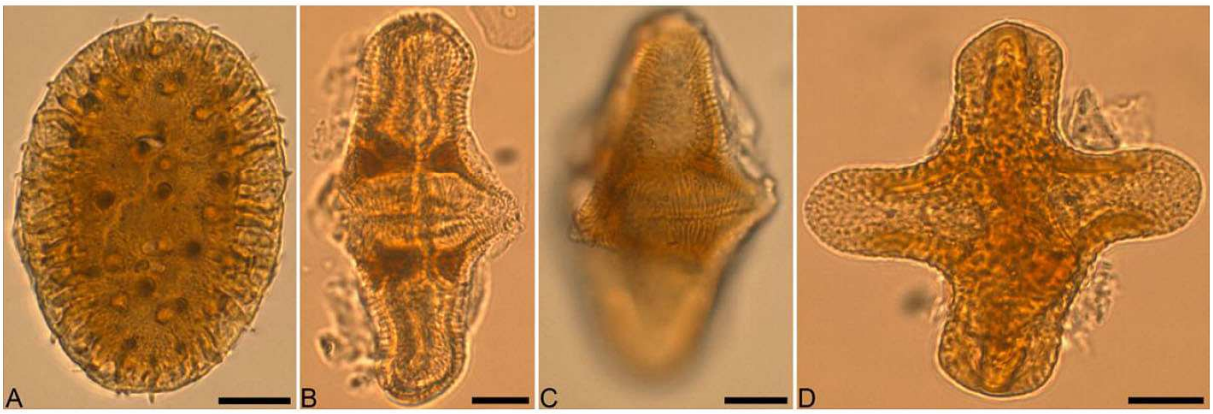

Fig. 1. *Wodehouseia* (A), *Pseudointegricorpus* (B, C), and *Aquilapollenites* (D) pollen, LM. Scale 10 µm.

Until now, pollen grains of these groups have been found only in a dispersed state and, thus, the possible systematic affinity and ecology of the parent plant can be judged only on the basis of sporoderm morphology and ultrastructure data, the character of the host rock and the accompanying plants. The only exception is an article on in situ triprojectate pollen by McIver et al. (1991) but it does not mention possible botanical relationships of the plant. Our analysis has shown that the pollen was probably produced by wetland or aquatic plants, adapted to a sudden change in the water regime during the vegetation season. The infratectum structure suggests that *Wodehouseia* should be placed within an advanced group of eudicots (Tekleva et al., 2019). The triprojectate taxa are so far difficult to relate even at such distant degree, though the aperture type and infratectum structure indicate their affinity to dicots.

The full functional significance of these features and their relationship to the overall ecology of the parent plants have remained unresolved. However, it is now becoming clearer that the set of characters present in pollen of the triprojectate group, and especially in the species studied here, is quite distinct from any modern plant lineage.

Additional information is needed for resolving the taxonomic affinities of the plants that produced pollen grains grouped in the triprojectate and oculata types. The existence of such pollen types for more than 20 million years over a vast territory of Asia and North America may indicate that the pollen producing plants had a good adaptive potential, which was realized in their adaptation to a certain ecological niche. It is possible that it was a narrow specialization that contributed to the complete extinction of this lineage.

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