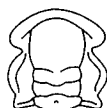


# Pollen in the guts of Permian insects: first evidence of pollinivory and its evolutionary significance

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## LETHAIA



Krassilov, V.A. & Rasnitsyn, A.P. 1997 03 03: Pollen in the guts of Permian insects: first evidence of pollinivory and its evolutionary significance. *Lethaia*, Vol. 29, pp. 369–372. Oslo. ISSN 0024-1164.

Uniquely preserved pollen was extracted from intestines of fossil insects from the Lower Permian of the Urals. A species of Hypoperlidae, an extinct family ancestral to bark-lice, bugs and plant-hoppers, and two species of Grylloblattida, a predominantly Permian group with a few extant representatives related to stoneflies, contain protosaccate taeniate grains of several pollen genera well known as dispersed microfossils and occasionally found in sporangia of conifers, peltasperms and glossopterids. This is so far the earliest direct evidence of pollinivory, a major factor of plant–insect coevolution. The partly digested pollen grains reveal infratectal reticulum and other structural details of evolutionary significance. It is suggested that the peculiar taeniate pollen of worldwide distribution in the Permian might simultaneously evolve in several groups of Paleozoic seed plants in relation to pollinivory that, by altering the micropyle load and thereby the pollen/ovule ratio, could also affect ovuliferous structures. Thus pollinivory might impel rapid diversification of gymnosperms in the Permian. The pollinivorous Hypoperlidae, which have evolved in the direction of ovulivory, might initiate insect pollination in the process. □ *Co-evolution, gymnosperms, insects, Permian, pollination, pollinivory, taeniate pollen.*

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Of all evidence of the plant–insect interaction in the past (Taylor & Scott 1983; Scott *et al.* 1992), fossil insect gut contents are the most direct and instructive. Pollen preserved in the intestines was first discovered in 1982 in a few species of Xyelidae from the Lower Cretaceous of the Trans-Baikal area (Krassilov & Rasnitsyn 1982). Further records came from the Cretaceous of Brazil (Caldas *et al.* 1989) and the Eocene of Germany (Lutz 1993), while Paleozoic insects have yielded lycopod spores (Taylor & Scott 1983). Our new findings result from a survey of a comprehensive collection of fossil insects from the Lower Permian Tchekarda locality in the Urals and are related to a critical period of both seed plant and insect evolution.

The Tchekarda locality has been known since the 1920s (Martynov 1928). It occurs on the Sylva River in the historical type area of the Permian System in the southern part of the Ufa–Solikamsk Basin, the Middle Urals. Insects occur in a shale–sandstone sequence of Kungurian (late Early Permian) age also containing a marine fauna of foraminifers, bryozoans, brachiopods and cephalopods as well as a Bardinian-type flora dominated by conifers and callipterids (Stepanov 1966; Meyen 1987).

Of the three species with pollen in the guts, one belongs to the Hypoperlidae, an extinct family supposedly ancestral to bark-lice, bugs, plant-hoppers and related groups of extant insects. Two other species are assigned to the order Grylloblattida, an essentially Permian group with a few living descendants related to stoneflies (Rohdendorf & Rasnitsyn 1980).

The most abundant pollen came from the pollen lump at the hind end of the rectum (arrow in Fig. 1A) in a well-preserved specimen of *Idelopsocus diradiatus* Rasnitsyn (Hypoperlidae). The lump consists of about thirty tightly clumped (but separable under acid and alkali treatment) and partly digested pollen grains (Fig. 1B), most of which belong in the Striatiti group (Infraturma) of the formal classification developed for dispersed pollen. Such pollen grains are peculiar for the Late Paleozoic and Triassic assemblages and are dominant in the Permian all over the world and locally, e.g., in the Urals and Tien-Shan, since the Late Carboniferous (Zhou 1994). The extracted pollen grains are further classifiable into two dispersed pollen genera, *Lunatisporites* and *Protohaploxypinus*, both including dissaccate haploxytonoid pollen in which the

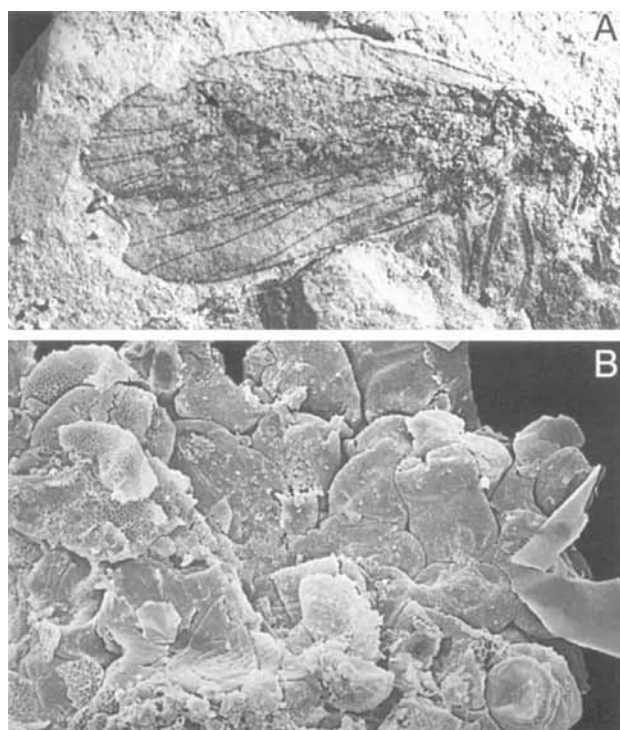


Fig. 1. Fossil insect from the Permian of Tschekarda locality, the Urals, containing identifiable pollen in the guts. □A. *Idelopsocus diradiatus* Rasnitsyn, a representative of the extinct family Hypoperlidae, with pollen lump preserved at the hind end of the rectum (arrow),  $\times 6$ . □B. Pollen lump from A, showing saccate pollen grains, SEM,  $\times 300$ .

proximal shield of the corpus is typically divided into four (in the former) or more (in the latter) stripes, or taeniae (Scheuring 1970; Foster 1979).

Preservation in the guts is unique in showing not only external morphological details but also the inner structures of the pollen wall, which are sometimes more distinct than in the standard SEM/TEM studies. In *Lunatisporites* the clefts between taeniae are deep and broad, the central one forming a furrow in the inner layer of exine (Fig. 2A). The partly digested grains lacking the outermost exinal layer, or tectum, show a reticulate infratectal structure with different patterns in the corpus and sacci (Fig. 2B). Moreover, the sacci reveal a honeycomb network of partitions attached to the corpus (Fig. 2C), thus forming a protosaccate inner structure. Notably, the infrateculum is similar to the surface reticulum of semitectate angiosperm pollen which stores the pollen/stigma recognition substances (we leave the possibility of the surface reticulum in angiosperm pollen grains evolving from reticulate infrastructure as well as the development of a self-incompatibility syndrome in the Permian pollen for further studies).

The *Lunatisporites*-type pollen grains have been found in sporangia of the Permian conifer *Ulmannia* (Clement-

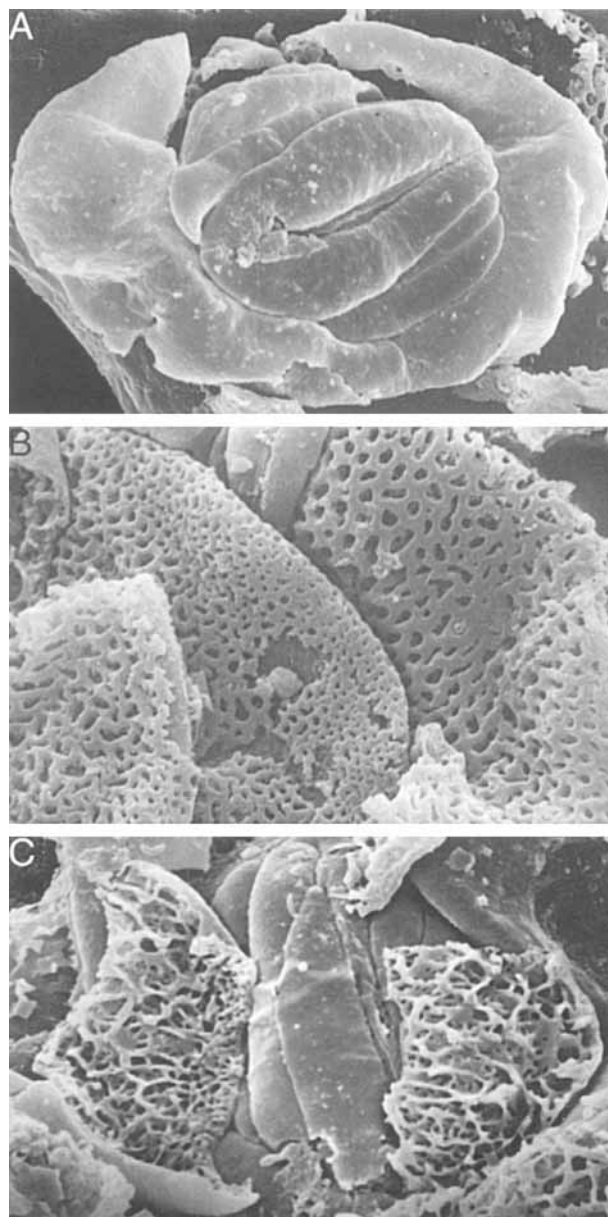


Fig. 2. Pollen extracted from the guts of fossil insect shown in Fig. 1A; *Lunatisporites*-type pollen grains, SEM micrographs. □A. Proximal aspect with four main taeniae, shorter additional taeniae and a furrow in the middle of the shield,  $\times 1500$ . □B. Infratectal reticulum exposed from beneath the digested tectum, with different lumina patterns on the body (middle) and sacci,  $\times 2000$ . □C. Inner protosaccate structure of sacci with partitions arising from their roots,  $\times 1700$ .

Westerhof 1974), while *Protohaploxylinus* occurs in glossopterids (Zavada 1991) and perhaps some phylogenetically related or convergent groups of northern gymnosperms (for it is abundant in the northern localities lacking any glossopterid macrofossils). In the guts of *Idelopsocus* there are also diploxytonoid taeniate and ephedroid costate pollen types represented by a single

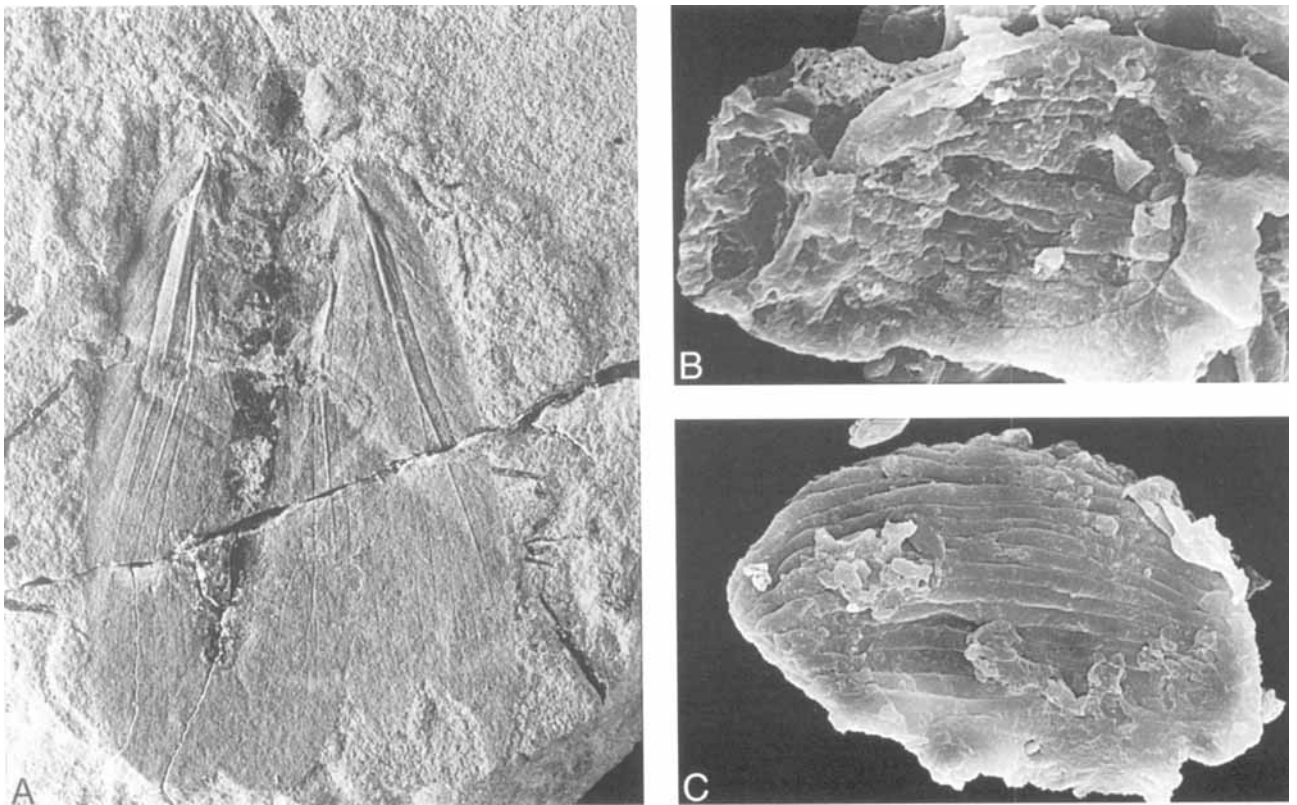


Fig. 3. □A. *Sojanidelia floralis* (Grylloblattida) containing two types of pollen grains in the guts. □B. *Protohaploxypinus*-type dissacate grain, proximal aspect, SEM,  $\times 1500$ . □C. *Vittatina*-type pollen grain with dense taeniae, SEM,  $\times 1150$ .

grain each. *Sojanidelia floralis* Rasnitsyn (Grylloblattida) contains abundant taeniate pollen of *Lunatisporites*-type mixed with a subordinate number of *Protohaploxypinus*- and *Vittatina*-type grains (Fig. 3), the latter also associated with the dominant Permian peltaspermid complex (Meyen 1987). *Tschekardaenigma pollinivorum* Rasnitsyn, another species of Grylloblattida, contains tightly appressed striate grains of one morphological type only.

Pollinivory has been suggested for Hypoperlidae on the basis of mandible morphology (Rasnitsyn 1980). This is now confirmed by direct evidence. Their descendant families Synomaloptilidae and Strephocladidae seem to evolve in the direction of ovulivory giving rise to the ovule-sucking Dictyoneuridae with their strong proboscises. Some intermediate species feeding on both pollen and ovules might have played a crucial role in the origin of insect pollination.

Saccate pollen in the insect guts may seem contrary to the latter suggestion, for sacchi are traditionally associated with wind pollination. However, since the extracted pollen grains are protosaccate and insofar as all the suggested functions of protosacchi (reviewed in Foster 1979) are secondary rather than primary, a new hypothesis relating these structures to pollinivory is advanced here. Pollini-

vory creates a selection pressure for increased pollen output (terminology after Inouye *et al.* 1994) in terms of pollen number and/or size of pollen grains (Faegri & van der Pijl 1966), the latter often inflated by various appendages. With the development of pollinivory presently confirmed for the Permian but perhaps arising as early as the Late Carboniferous, a tendency for increased pollen output has been conferred to conifers and other major pollen producers. It was reinforced by the large body size of Paleozoic insects and their proportional pollen consumption. The protosacchi and perhaps also the taeniae might initially appear in response to the pollinivory selection pressure as the pollen mass increasing structures later acquiring additional harmomegathy – particularly important in seasonally arid environments – and other functions. This would explain parallel acquisition of protosaccate taeniate pollen in the dominant groups of Paleozoic gymnosperms inhabiting wide ranges of physical environments. Whatever the pollination methods, the pollen size increase would change the micropyle pollen load, thereby affecting the pollen/ovule ratio and, consequently, the morphology of ovulate structures. The lesser pollen load of the larger grains would impel the development of pollen recognition and discrimination functions to a certain

extent reflected in the morphology of pollen and pollen receptive structures. Pollinivory thus might induce a concerted modification of the seed plant reproductive sphere. It is hardly incidental that major evolutionary events in gymnosperms coincided with the onset of specialized pollinivory and the ensuing specific plant–insect interaction.

There is evidence of both indiscriminate and species-specific pollen foraging in the Permian insects, the former visiting plants which grew at flight distance from one another and, potentially, with accumulation of evidence, providing an insight into Permian plant community structure; the latter leading to obligatory plant species-to-insect species interaction impelling diversification of both plants and insects.

*Acknowledgements.* – This work was supported by the Russian Foundation for Fundamental Research, grant No. 95-04-11105, and the International Science Foundation, grant No. N6V000.

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