

Plant remains from the guts of fossil insects: Evolutionary and Paleoecological inferences

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KRASSILOV, V.A. & RASNITSYN, A.P. 1999. Plant remains from the guts of fossil insects: Evolutionary and Paleoecological inferences. In: AMBA/AM/PFICM98/1.99: 65-72. The plant remains from the guts of fossil insects has provided new data on folivory and pollinivory in the Permian, Jurassic and Cretaceous insects. The Jurassic folivorous species of the Phassmatoptera and another group related to the Embioptera consumed fleshy scale leaves of hymnerellids, an extinct gymnosperm group with certain angiospermoid characters. The Jurassic katedids *Aboilus* fed on *Classopollis*, pollen grains of the same plants. The early Cretaceous xyelid pollinivory involved several proangiosperm groups. A widespread pollinivory was found in the Early Permian entomofauna involving the Hypoperlida, Psocida, Palaeomanteida, and Grylloblattida. The presently confirmed pollinivory adds significantly to our understanding of ecological evolution and functional morphology of phylogenetically important insect groups as well as providing insight in the plant community structure and seed plant evolution. The similarity of feeding habits in *Parapsocidium* (Hypoperlida) and *Idelopsocus* (Psocida) sharing a common pollen source, is of particular importance, for their phylogenetic affinity has been previously postulated on morphological grounds. In the Kungurian of Urals the conifer - petridosperm - rufloriacean plant community was a major source of edible pollen for all the hitherto studied pollinivorous insects. Phylladoderms (*Vittatina*) might represent a subordinate or marginal component of this community, while a remote cordaitalean - walchian *Florinites-Potonieisporites* community was occasionally visited by pollinivores with a wider foraging area. It is concluded that pollinivory played a role in the basic diversification of the Permian gymnosperms as well as the Cretaceous proangiosperms. The pollen loads contain the most advanced contemporaneous pollen grain morphotypes. In particular, the taeniate pollen morphology might simultaneously evolve in several groups of Paleozoic seed plants in relation to pollinivory.

Introduction

The palaeoecology and evolution of plant - insect systems are presently studied from many points of view using traces of insect herbivory left on fossil plants or as coprolites (reviewed in LABANDEIRA, 1998). The approach used, starting with a find of pollen grains consumed by Cretaceous xyelids (KRASSILOV and RASNITSYN, 1982), is based on structurally preserved plant material extracted from organic matter remaining in intestines of fossil insects. It has an advantage of direct evidence on identifiable insects interacting with identifiable plants. The survey of entomological collections have shown that material of this kind is actually not so rare as previously expected. Here is reviewed the results concerning folivory and pollinivory in the Permian, Jurassic and Cretaceous insects.

Folivory in Jurassic insects

Leaf-cutting is known since the Late Carboniferous, but the traces could be left by myriapods or crustaceans rather than insects. We found identifiable leaf remains in the guts of three insect

species, one belonging to the Phassmatoptera and other two of a questionable systematic position, but probably related to the Embioptera, from the well-known fossil plant and insect locality Karatau in Southern Kazakhstan (KRASSILOV, RASNITSYN, 1999, in press). The plant remains preserved in the guts are fragments of scale leaves about 0.25 sq. mm of which the cuticles were macerated and studied with SEM. The cuticles show thick-walled epidermal cells, with the stomata either scattered or arranged in distinct stomatal bands, forming either indistinct stomatal bands (Plate I, 6, 7). The cell pattern and stomatal morphology is typical of the widespread Mesozoic plant family Hirmerellaceae the foliar shoots of which are assigned to the formal genera *Brachyphyllum* and *Pagiophyllum* having thick scale-leaves with durable cuticles. In addition, *Classopollis*-type pollen grains produced by the hirmerellids, are found stuck to the cuticles.

The hirmerellids are usually described as conifers, but their reproductive morphology indicate gnetalean affinities with certain angiospermoid features (KRASSILOV, 1982). Their remains are most abundant in deltaic to estuarine facies suggesting a dominant group of coastal to riparian vegetation.

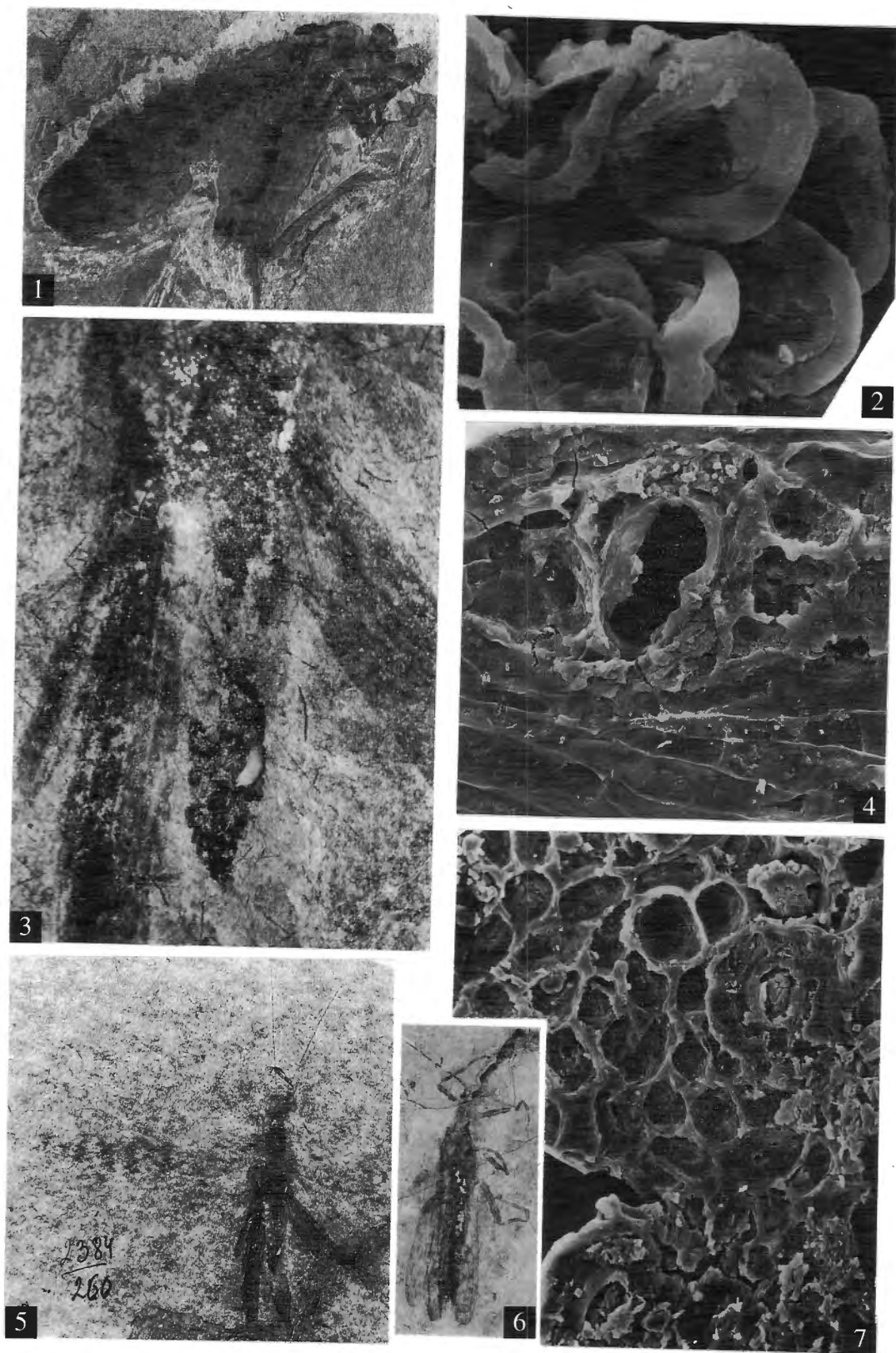


Plate I Folivory and pollinivory in the Late Jurassic insects from Karatau, southern Kazakhstan: 1, 2. *Aboilus* cf. *dilutus* GOROCHOV, a katedid insect (1, x1) with pollen load of *Classopollis* (2, SEM, x 1600); 3-5. *Brachyphyllophagus phantasus* A. RASN., a folivorous insect (5, x1) with *Brachyphyllum*-type scale-leaves in the lower part of abdomen (3, x 5), the leaf cuticle showing cell files and a transversely orientated stoma of stomatal band (4, SEM, x 550); 6, 7. *Phasmomimoides minutus* GOROCHOV, a folivorous insect with *Brachyphyllum*-type scale leaves in the gut (6, x1), the leaf cuticle showing scattered stomata (7, SEM, x 330).

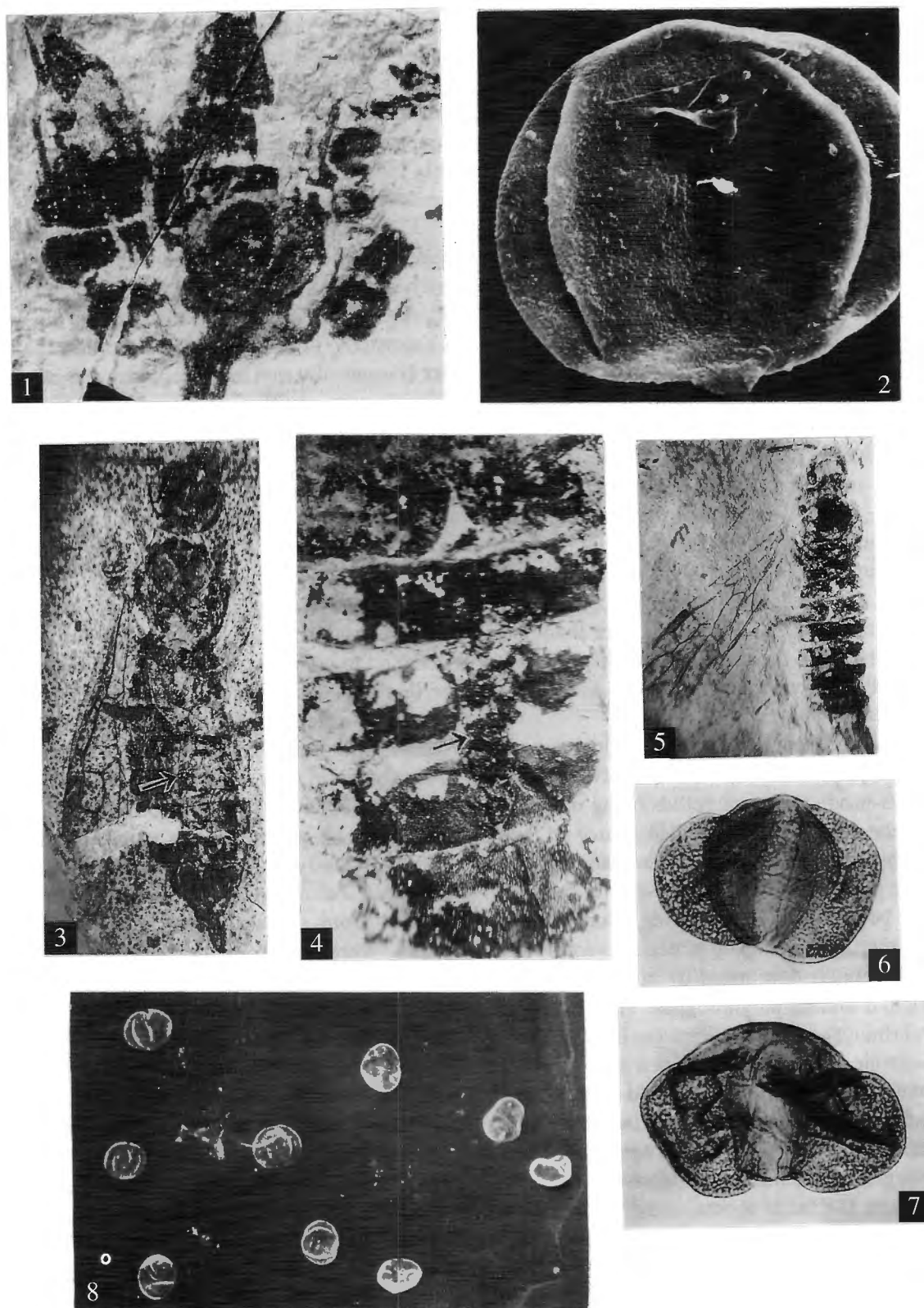


Plate II Early Cretaceous insect pollinivory: Baisa locality, Transbaikalia: 1. Flower-like reproductive structure producing saccate pollen grains of the type found in the guts of contemporaneous xyelids, x 6; 2, 3, 8. *Ceroxyella dolichocera* A. RASN., a xyelid insect with pollen load (arrow) of saccate pollen grains *Vitimipollis edulis* KRASSIL. (2, SEM, x 1400; 8, SEM, x 150); 4 - 7. *Anthoxyella anthophaga* A. RASN., a xyelid insect (5, x 2.5) with pollen load in the rectum (4, arrow, x 10); of bisaccate pollen grains *Alicosporites alimentosus* KRASSIL. (6, 7, x 500)

Various groups of Mesozoic insects might inhabit hirmereid plant communities consuming not only leaves, but also pollen grains (see below).

Mesozoic pollen-eaters

In addition to the cases of folivory, the Late Jurassic Karatau material provided evidence of pollinivory in an archaic katydid genus *Aboilus* of the extinct subfamily Aboilinae widespread in the Jurassic and Early Cretaceous (KRASSILOV, ZHERIKHIN, RASNITSYN, 1997a, b). In two species of *Aboilus* the organic matter in the intestines contained large masses of pollen grains (Plate I, 2) readily identifiable as *Classopollis*, a widespread Mesozoic pollen morphotype produced by hirmereids (see above). The Aboilinae are considered as ancestral to modern katydids, the Tettigoniodea (GOROCHOV 1995) first appearing in the early Cretaceous but rare until the Palaeogene. GRINFELD (1962) has suggested that pollinivorous adaptations are primary for the group, already appearing in ancestral forms, and that Ensifera, rather than beetles, could have been the most ancient unspecialized pollinators. Presently these suggestions are receiving some factual support.

That these large insects fed exclusively on *Classopollis* pollen can be taken as evidence of *Classopollis*-producing hirmereids being if not the only then the most abundant pollen source in their habitats. There is little doubt that these habitats were close to the site of deposition for insects of this size can hardly be transported intact over a considerable distance either by wind or by water. Previously the idea of dry habitats dominated by hirmereids was rather popular among palynologists. The equatorial girdle and rimula of *Classopollis* were interpreted as harmomegathic structures developed in respect to arid climate. Alternatively they could mitigate the effects of long exposure of pollen transferred by slow fliers such as *Aboilus*. We suggest that xeromorphic vegetative characters in *Brachyphyllum* and *Pagiophyllum*, the foliar shoots of the hirmereids, are due to littoral adaptations rather than to arid regional climate.

Although pollinivory does not necessarily associate with entomophily, it may strengthen the idea of an animal pollen vector which has been previously suggested in respect to the peculiar *Classopollis* morphology and persistent tetrads. At the first glance, abundance of dispersed *Classopollis* grains may seem more consistent with wind-pollination

than entomophily. However entomophilous plants pollinated by pollen-eating insects are known to produce extra pollen for attraction. Since the foliar shoots of hirmereids were also eaten by several species of relatively large insects, the overall insect impact on these plants should be significant, probably inducing such angiospermous adaptations as the inclosure of ovules.

That pollinivory had some bearing on the origins of angiospermy is further suggested by a diversity of pollen-eating insects in the famous Early Cretaceous locality Baisa in Transbaikalia (KRASSILOV, RASNITSYN, 1982, in press). This locality is especially rich in gnetophytes and other proangiospermous plants (KRASSILOV, 1997) showing parallel evolution of angiospermy. Pollen masses were found in the gut contents of four Hymenopteran species of the archaic family Xyelidae. One species of *Spathoxyella* fed on non-saccate pollen grains of a recently found gnetophyte plant *Baisianthus*. Three other xyelid species of the genera *Anthoxyella*, *Ceroxyella* and *Chaetoxycella* yielded saccate pollen grains that had been previously assigned to conifers. A recent find showed, however, that such grains were also produced by plants that might have been closer to angiosperm ancestry. A saccate morphotype described from the guts was then found in situ in a flower-like reproductive structure (Plate II, 1) showing sporangia in peltate clusters as in peltaspermous pteridosperms. It has been previously suggested that some pollen morphotypes of angiosperms might have actually derived from saccate pollen grains. Such pollen grains were involved in pollinivory since the Permian.

Permian pollen-eaters and plant communities

A widespread pollinivory was found in the Early Permian entomofauna. In the Kungurian of the Urals, the pollen gut load is recorded in a number of insect orders, including the Hypoperlida, Psocida, Palaeomanteida, and Grylloblattida (RASNITSYN, KRASSILOV, 1996a, b, and in press). There is evidence of both indiscriminate and species-specific pollen foraging in the Permian insects. The indiscriminate pollinivores visited plants that grew at flight distance from one another, thereby providing an insight into the Permian plant community structure. The specific pollinivory might lead to obligatory plant species - to - insect species interaction impelling diversification of both plants and insects.

Most Permian (Tschekarda) insects with preserved gut contents fed on saccate taeniate pollen grains. Non-taeniate pollen grains are rare in the consumed pollen mass. The following pollen morphotypes were found:

(1) *Lunatisporites*, supposedly produced by *Ullmannia*-like conifers (BALME, 1995). This morphotype prevails in the guts of *Idelopsocus diradiatus* RASNITSYN (RASNITSYN and KRASSILOV, 1996) and *Parapsocidium uralicum* ZALESSKY. Notably, *Lunatisporites* is relatively rare as dispersed pollen morphotype in the Lower Permian of the Urals.

(2) *Protohaploxypinus*, produced by glossopterids and some related or convergent northern groups (BALME, 1995). Dispersed pollen grains of this type are abundant in the Permian of the Urals and elsewhere. In both *Idelopsocus* and *Parapsocidium* this type associates with *Lunatisporites* perhaps indicating a proximity of their producing plants.

(3) *Vittatina* group, produced by phylladoderm peltasperms (MEYEN, 1987), prominent in the gut content of *Sojanidelia floralis* (RASNITSYN and KRASSILOV, 1996) in association with *Lunatisporites* - *Protohaploxypinus* group.

(4) *Florinites* - *Potonieisporites* group, produced by cordaites or walchiacean coniferoids, found as occasional pollen grains in the gut of *Parapsocidium uralicum*.

(5) *Cladaitina*, produced by the rufloracean gymnosperms, forming the pollen load of *Tillyardembia* (AFONIN, in press).

These data might have some ecological meaning perhaps indicating the ullmanniacean - petridosperm - rufloriacean community as a major source of edible pollen for all hitherto studied pollinivorous insects. Phylladoderms (*Vittatina*) might represent a subordinate or marginal component of this community, while a remote cordaitalean - walchian *Florinites* - *Potonieisporites* community was occasionally visited by pollinivores with a wider foraging area.

Most prominent in the pollen loads are taeniate grains of worldwide distribution produced by several groups of the Permian gymnosperms. Since they simultaneously appeared in a number of lineages, it was suggested (KRASSILOV, 1997) that pollinivory might play a role as a factor of parallel evolution, perhaps by spreading microorganisms that were capable of transducing genetic material. New developments in the pollen grain morphology might affect the ovuliferous structures by altering the micropyle

pollen load and, consequently, the pollen/ovule ratio. Thus pollinivory might impell rapid diversification of gymnosperms in the Permian.

The presently confirmed pollinivory adds significantly to our understanding of ecological evolution and functional morphology of phylogenetically important insect groups. Pollinivory is a predicted feature of the orders Hypoperlida, Psocida and Palaeomanteida (RASNITSYN, 1980; ROHDENDORF and RASNITSYN, 1980). The similarity of feeding habits in *Parapsocidium* and *Idelopsocus* sharing a common pollen source, is of particular importance, for their phylogenetic affinity has been previously postulated on morphological grounds (RASNITSYN, 1980; ROHDENDORF and RASNITSYN, 1980). *Idelopsocus* supposedly represents a line of extinct order Hypoperlida leading to primitive book-lice (order Psocida, suborder Permopsocina). *Parapsocidium* belongs to the Permian book-louse family Psocidiidae which is considered as a stem group of all living Cimiciformes. Palaeomanteida are hypothesised to be the stem group of the entire cohort Scarabaeiformes, the insects with complete metamorphosis. The very origin of this developmental type is supposed to result from pollinivory of an immature ancestor. The ancestral pollinivorous Hypoperlida might initiate insect pollination in the process of evolving into the ovulivorous Strephocladina (and further to the palaeodictyopteran assemblage: RASNITSYN, 1980).

In contrast to the above cases, the grylloblattid pollinivory is unexpected, the more so that different unrelated groups of this order fed on pollen grains (*Sojanidelia* STOROZHENKO: Ideliidae, and *Tillyardembia* ZALESSKY: Tillyardembiidae). Since the living Grylloblattidae are zoonecrophagous, a similar feeding habit has been previously postulated for the extinct representatives also.

Conclusion

We conclude that the data on structurally preserved plant remains from the guts of fossil insects not only document folivory and pollinivory in a number of extinct pollen groups, but also provide an insight into the plant - insect coevolution and palaeoecology. As in the case of *Parapsocidium* and *Idelopsocus*, similarity of feeding habits gives a functional dimension to phylogenetic reconstructions based on morphological comparisons. We recorded both the conservative trophic adaptations, as in the Hypoperlida and their derived forms, and

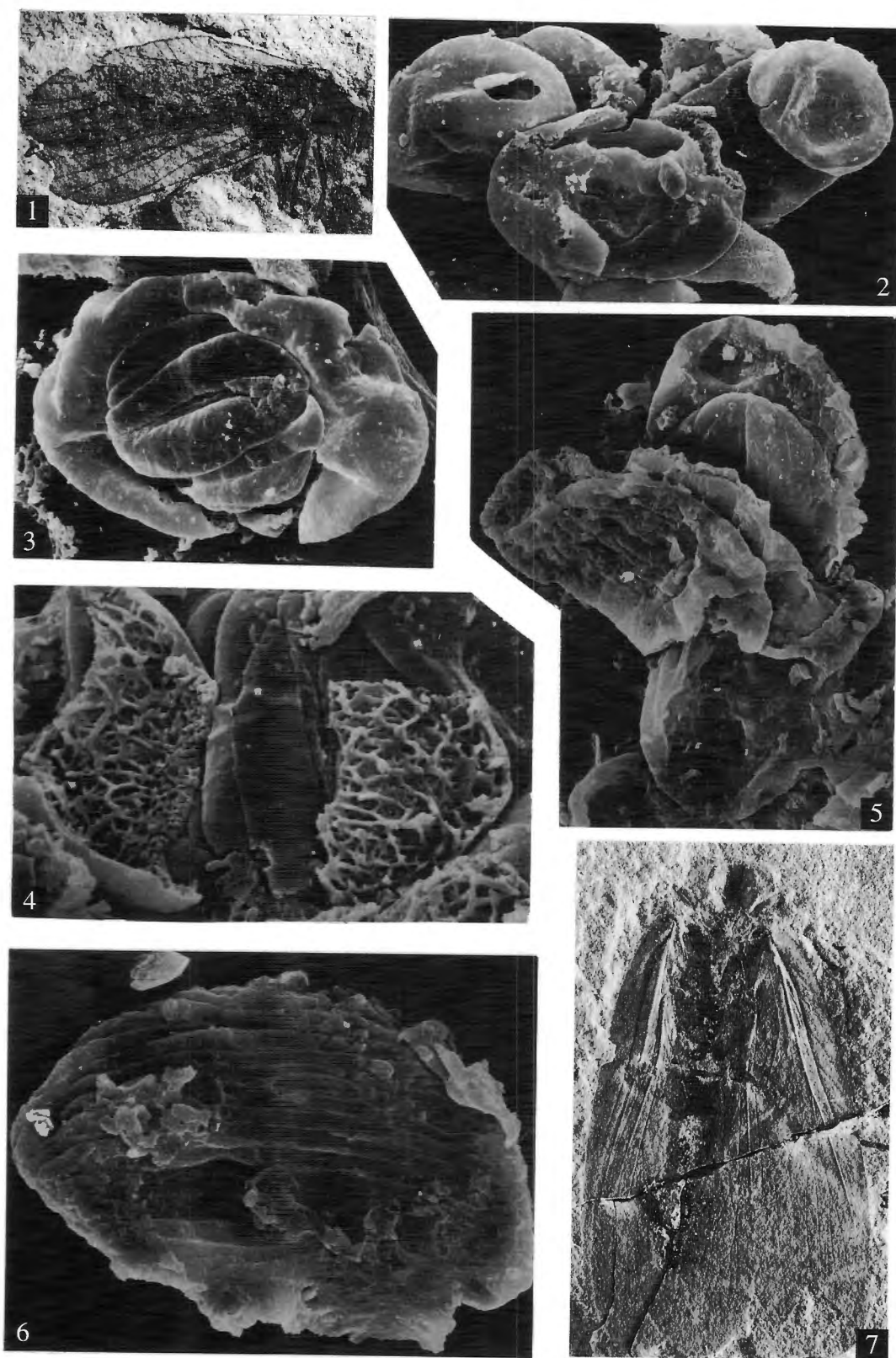


Plate III Pollinivory in the Early Permian insects: Tchekarda locality 1 - 4. *Idelopsocus diradiatus* RASN., a hypoperlid insect (1, x 6) with pollen load at hind end of the rectum containing *Lunatisporites* pollen grains (2, lump of several grains, SEM, x; 1000; 3, proximal aspect of a taeniate grain, SEM, x 1500; 4, split grain showing protosaccate infrastructure, SEM, x 2000). 5 - 7. *Sojanidelia floralis* RASN., a grylloblatid insect with pollen load of taeniate grains *Lunatisporites*, *Protohaploxypinus* (5, SEM, 800) and *Vittatina* 6, SEM, 1800).

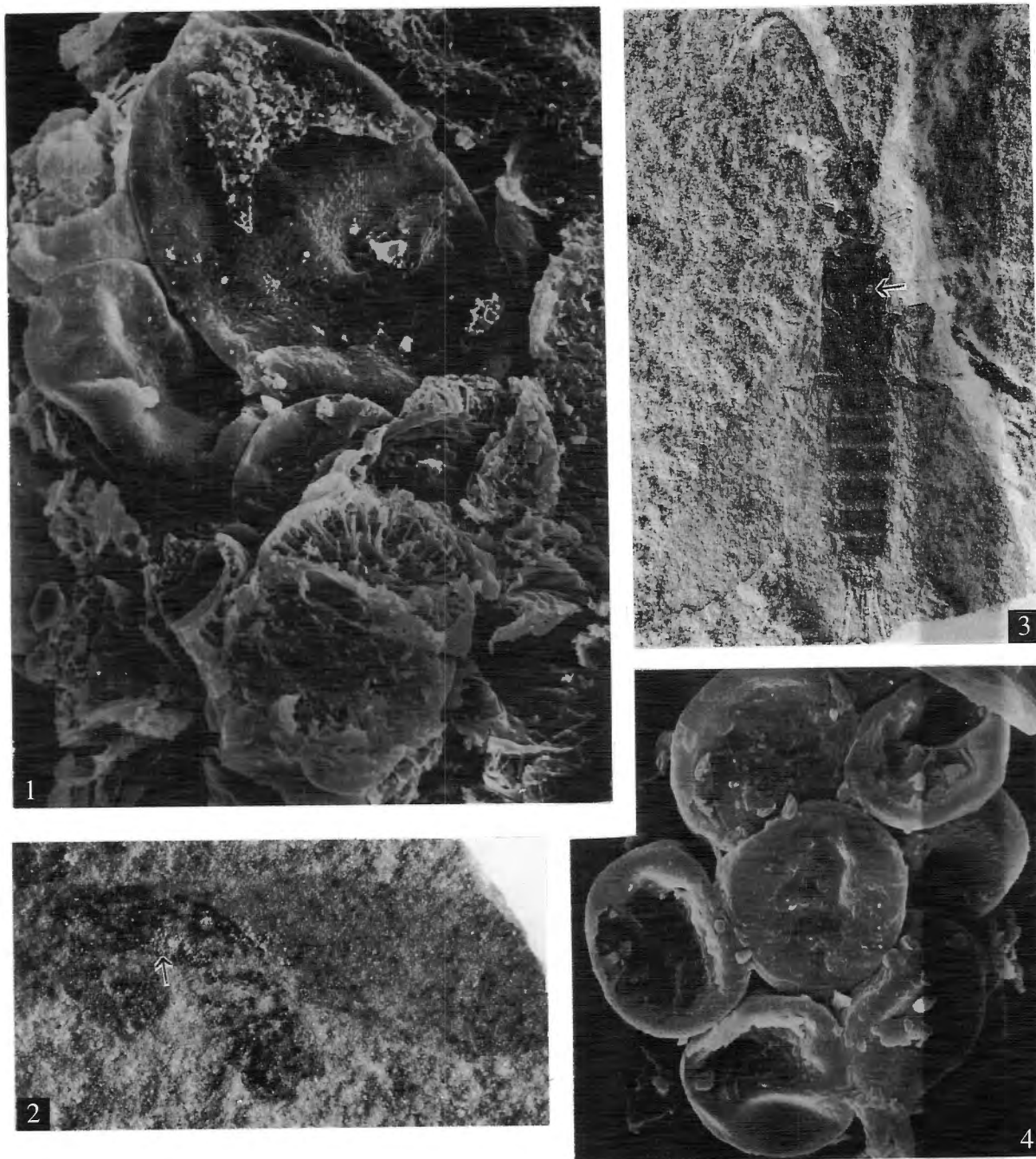


Plate IV Pollinivory in the Early Permian insects: Tchekarda locality 1, 2. *Parapsocidium uralicum* G. ZALESKY, a psocid insect (2, x 20) with pollen load (arrow) of taeniate grains *Lunatisporites* (smaller grains) and *Protohaploxypinus* (1, SEM, x 800). 3, 4. *Tillyardembia antennaeplana* G. ZALESKY, a grylloblatid insect (3, x 5) with pollen load of Cladaitina (4, SEM, x1180), after Afonin (1999, in press).

switches to a totally different diet, as in the Grylloblattidae. Pollen morphologies of the dominant Permian to Mesozoic groups of gymnosperms and proangiosperms have developed under the impact of pollinivory that partly explains their parallel evolution in different seed plant lineages.

Summarily our data on folivory and pollinivory are factual evidence of plant -insect interaction in the critical periods of seed plant evolution. The pollen loads of fossil insects also suggest associations of the foraged plants in the contemporaneous plant communities.

Acknowledgements

This work is supported by the Russian Foundation of Basic Research, grants no. 96-04-11105 and 98-04-48518.

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