

Pollen in the Gut Contents of Fossil Insects as Evidence of Coevolution

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Abstract—In addition to the recently published *Idelopsocus diradiatus* A. Rasnitsyn (Hypoperlida) and *Tschekardaenigma pollinivorum* A. Rasnitsyn (Grylloblattida?) containing striate pollen of the form-genera *Lunatisporites* and *Protohaploxypinus*, a new species *Sojanidelia florea* A. Rasnitsyn yielding *Lunatisporites* and *Vittatina* pollen grains is presently described from the same locality Chekarda in the Permian of the Fore-Urals. Dispersed pollen grains of these genera are widespread in the Permian of both northern and southern continents. Our data suggest entomophily as a factor of origin and parallel evolution of striate pollen morphotypes in different groups of Paleozoic plants inhabiting littoral environments. At the same time, interaction with insects might promote a rapid diversification of Permian gymnosperms.

Pollen preserved in the gastro-intestinal system of fossil insects provides direct evidence of their feeding habits and, in a wider sense, of the plant–insect interaction and coevolution. The first finds of well preserved pollen in the intestines of Early Cretaceous Xyelidae (Krassilov and Rasnitsyn, 1982) indicated a good prospect of studying plant–insect interactions by this method. We then scanned the extensive entomological collections deposited in the Paleontological Institute, Moscow, in search of suitable material. Our first good fortune was with the Permian insects from the well-known Chekarda locality, upper Lower Permian of the Fore-Urals (Rasnitsyn and Krassilov, 1996). Striate pollen grains of two form-genera, *Lunatisporites* and *Protohaploxypinus* were found in the gut compressions of *Idelopsocus diradiatus* A. Rasnitsyn and *Tschekardaenigma pollinivorum* A. Rasnitsyn, the first species belonging to the extinct order Hypoperlida, the other described as *incertae sedis* with possible affinities in the Grylloblattida, an order having a relict extant species but mostly Permian. It is one of the dominant groups of Permian entomofauna and the ancestor of stoneflies, as well as supposedly some other orders of the infraclass Gryllones (Rohdendorf and Rasnitsyn, 1980).

Here we describe a definite representative of the latter order, *Sojanidelia florea* A. Rasnitsyn, sp. nov., from the same locality and also yielding striate pollen of *Lunatisporites* and *Vittatina* morphotypes. These data suggest that pollinivory was common in Paleozoic insects (previously only spores were found: Taylor and Scott, 1983). They also seem relevant to the problem of striate pollen being produced by different groups of gymnosperms and having parallel successions of morphotypes in different parts of the world.

The type material is deposited in the Paleontological Institute (PIN), Russian Academy of Sciences.

SYSTEMATIC PALEONTOLOGY

Order Grylloblattida

Family Ideliidae

Genus *Sojanidelia* Storozhenko, 1992

Sojanidelia florea A. Rasnitsyn, sp. nov.

Figs. 1–4

Holotype. PIN, no. 1700/3538, a part and counterpart fossil of the almost complete insect.

Etymology. From Latin *florens* (blossom) referring to the feeding habits of the insect.

Diagnosis. Unlike other species described, venation is impoverished, with only 2 or 3 M branches, and with the only branch leaving CuA bending and reaching the wing hind margin. In the key (Storozhenko, 1992) it converges toward *S. makarkini* Storozhenko, but differs, in addition to the above features, in the more sloping Sc branches, and in the shorter RS stalk.

Description. Size average for genus: length of body 25.6 mm, of forewing 27.6 (holotype)—29.7 mm. Ground color light. Head small, triangular (in holotype fossil mouthparts directed backward), with eyes large, somewhat protruding, one eye diameter apart. Antennae thin (segmentation not discernible, full length unknown). Pronotum much wider than head, narrowing backward, with straight fore margin and widely rounded fore angles (inner margins of paranota not discernible). Legs short, not especially thick, fore legs shorter than hind legs. Wings probably with weak (hardly seen on the fossils) but comparatively dense archidictyon. In forewing costal space moderately wide, SC branches simple, oblique, comparatively long, somewhat more than 10 in number. RS leaving R near 0.4 wing length, with short stalk and probably 4–5 branches. M with 2 or 3 branches (in the last case M1 branches), with basal fork placed far basally and

bending slightly distad of CuA compared with RS base. M5 discernible among basal m-cu crossveins due to its thickness. CuA S-like curve, basally with weak, irregular, blind branchlets, and single branch leaving stalk at its curve and reaching hind wing margin. Distal to that branch, CuA with ca. 5 rearward directed branches. Anal veins simple, almost straight, 4 in number. Hind wing with at least 7 RS branches (the two hindmost ones are in fact possibly M branches). Undoubted M branches not more than 2. CuA concave, almost straight, forking far distad. Abdomen comparatively narrow, without wide paranota, with cerci thin, short (about half as long as head width). Intestine filled with food from mesothorax almost to abdominal apex.

Material. Holotype and paratype PIN, no. 1700/3411, isolated fore wing; Russia, Perm Region, Suksun District, left bank of the Sylva River near Tsherkarda Village; Lower Permian, Kungurian Stage, Koshelevka Formation.

Remarks. This species is assigned to the genus *Sojanidelia* on the basis of the strongly S-like curve CuA in combination with having very few M branches: the latter character distinguishes *Sojanidelia* from *Sylvidelia* and *Idelinella* which also have an S-like CuA.

Sojanidelia florea is possibly the only Lower Permian representative of the genus, for the two species described by Storozhenko (1992) as from the Lower Permian of the Vorkuta Basin, come, in fact, from the Ayachyaginskaya Subsuite of the Lekvorkutskaya Suit, whose stratigraphic position is not yet specified in the broad interval from the upper part of the Kungurian Stage of the Lower Permian to the lower part of the Ufimian Stage of the Upper Permian (Dedelev, 1990). Despite its greater geological age, the new species has a more specialized wing venation than even its continued congeners from the Late Permian.

POLLEN

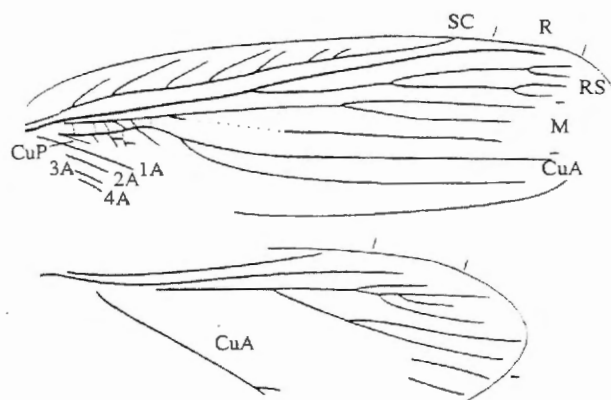
The gut content of this large insect is preserved as a coal-like organic material yielding upon maceration clumps of pollen grains, most of which belong to the form-genus *Lunatisporites* (Fig. 5) These are striate bisaccate grains with a broad lateral connection of the sacchi transitional to the monosaccate structure, haploxylonoid, elliptical in equatorial outline, with a long axis about 50–56 μm . The scutum is broadly elliptical to almost circular, with four to five main taenia and with approximately the same but more variable number of wedge-shaped taeniae fragments. Occasionally the taeniae are transversely dissected into short rectangular blocks. The scutum is traversed along its entire width by a gently arching median slit, slightly gaping in the middle, constricted to the ends. In one case two grains are bound by sexinal strands emerging from the proximal slits (Fig. 5d). The scutellum is a narrow depression between the sacchi lacking distinct apertural features, occasionally showing a pore-like hole, but this



Fig. 1. *Sojanidelia florea* sp. nov.: holotype PIN, no. 1700/3538, general appearance of the fossil from below. Gut contents shaded.

feature can be preservational. The sacchi are narrower than the corpus, crescent-shaped. Occasional fractured sacchi show infrastructural network of partitions joined to the corpus.

These grains are similar to *Lunatisporites multiplex* (Visscher) Scheuring (Scheuring, 1970) in the irregular pattern of their taeniae, but they are considerably larger.



Figs. 2-3. *Sojanidelia florea* sp. nov., holotype PIN, no. 1700/3538, fore and hind wings. Venational symbols common.

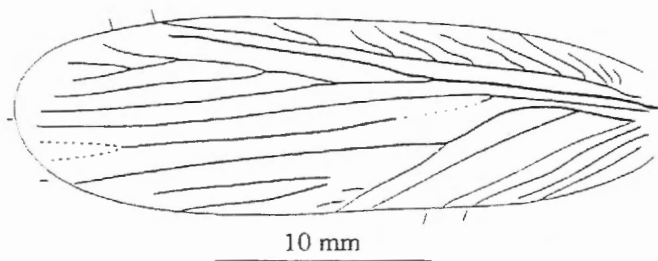


Fig. 4. *Sojanidelia florea* sp. nov., paratype PIN, no. 1700/3411, fore wing.

The less common pollen morphotypes admixed to *Lunatisporites* clumps belong to the form-genus *Vittatina* including asaccate or rudimentary saccate multi-taeniate grains. The better preserved *Vittatina* grains are ellipsoid, about 50 μ m long, with up to 14 parallel-sided proximal taeniae of uniform width (Figs. 6c, 6d). They are similar to the widespread dispersed grains *V. fasciolata* (Balme et Henedy) Bharadwaj. A few grains with less regular taeniae and rudimentary sacchi (Figs. 6a, 6b) might belong to a different species.

DISCUSSION

The finds of striate pollen grains in the gut compressions of Permian insects is of considerable palynological interest, as this morphological group constituted a dominant element of the world-wide Permian spore-pollen assemblages. The pollen grains appearing striate under the light microscope are universally characterised by the external layer of their exine being divided, or only proximally so, into parallel or subparallel bands, or taeniae, the number and the pattern of which are diagnostic of the numerous form-genera also differing from each other in the presence or absence of sacchi and their configuration (Foster, 1979). The most frequent bisaccate forms may have incompletely differentiated sacchi forming a morphological continuum with

monosaccate forms. On the other hand, the normally asaccate morphotypes occasionally show rudimentary sacchi indicating their origin from saccate forms. They typically differ from the modern saccate pollen of pinaceous conifers in having protosaccate, rather than eusaccate infrastructure with the inner partitions filling all the space inside the sacchi and attached to the corpus.

The world-wide occurrence of striate pollen stands in sharp contrast with the macrofossil evidence of differentiation of the late Paleozoic floras into the northern Laurasian and southern Gondwanaland realms (in turn divisible into distinct provinces) having few floristic elements in common. It has been shown that striate pollen was produced by at least three different groups of gymnosperms: glossopterids, peltasperms and conifers (Clement-Westerhof, 1974; Zavada, 1991), the former group being dominant in Gondwanaland and the two latter being common to dominant in the Euroamerican, Subangarian and Cathaysian provinces of Laurasia. Thus, the global spread of striate pollen resulted from parallel development of palynological characters in different gymnosperm lineages dominating separate phytogeographical realms. Nevertheless, even the narrowly defined pollen morphotypes not only occur in different realms but also can be used as intercontinental or inter-provincial stratigraphic markers.

The first appearance of striate pollen in the Late Carboniferous was nearly synchronous in Gondwana and northern realms. Initially it was subordinate to non-striate types, although in the Urals and Tian-Shan its rapid rise to dominance took place before the end of the Carboniferous (Zhou, 1994). The diversity and numerical representation of striate morphotypes had steadily increased through the Permian and was still considerable in the Triassic. Among them, the asaccate *Vittatina* group was most prominent in the so called Tatarina Province of the Fore-Urals, East European Plain and northern China extending to North America as far North as Greenland. Meyen (1987) has suggested parallel successions of non-striate to striate protosaccate to striate asaccate morphotypes in both the northern and southern continents.

Aridity is generally considered as a leading factor in floristic evolution in the Permian. In particular, the scale-leaved conifers and peltasperms with thick leaf cuticles are considered to represent a xeric type of Permian vegetation palynologically distinguishable by the prevalence of striate pollen grains. However their frequent association with coal-bearing facies makes this interpretation improbable, whereas the even more obvious association with marginal marine facies suggests littoral environments as their main habitats (not precluding their progradation inland). Our discovery of striate pollen in the gut compressions of relatively large insects that were neither long-distance fliers, nor resistant enough to withstanding long-distance transportation, gives additional evidence of the proximity of their producers to the site of deposition.

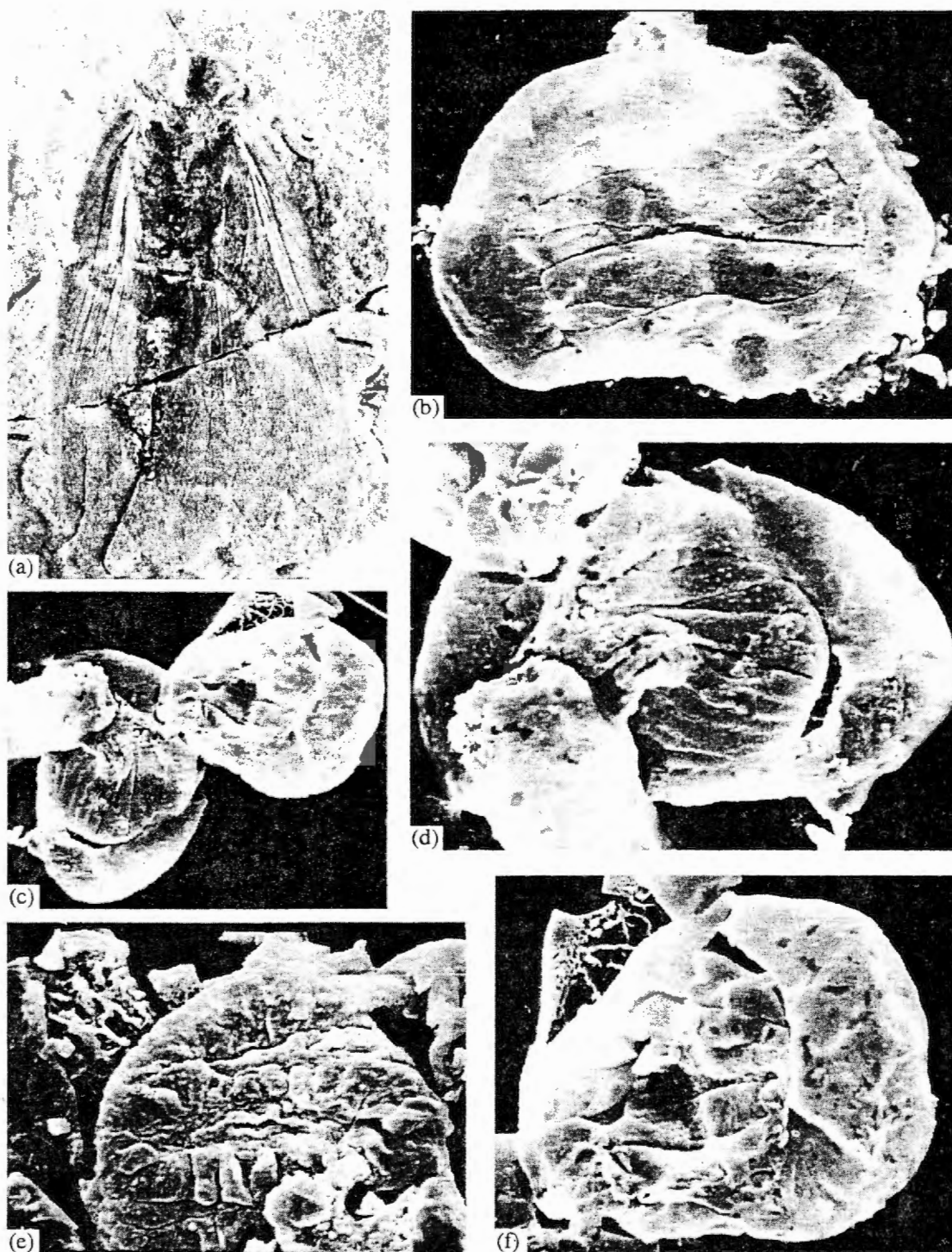


Fig. 5. *Lunaisporites* pollen grains from the gut compression of *Sojanidelia florea* sp. nov.: (a) holotype PIN, no. 1700/3538, $\times 3$, (b) pollen grain, distal aspect, SEM, $\times 1500$, (c) two adhering pollen grains, SEM, $\times 800$, (d) pollen grain showing sexinal strands emerging from the proximal slit, SEM, $\times 1500$, (e, f) pollen grains showing infrastructure of sacci, SEM $\times 2000$ and 1500 .

Insofar as xeromorphism is a characteristic feature of extant littoral plant communities, the xeromorphic vegetative morphology of the Permian conifers and peltasperms can be accounted for by littoral habitats without invoking global aridity. Their southern counterparts, glossopterid-dominated communities, are known

to develop *Vertebraria*-type aerenchymatous underground organs indicating a peat bog or mangrove swamp type habitat.

Thus, helophyte adaptations prevailed among the producers of striate pollen grains. Since helophytes are

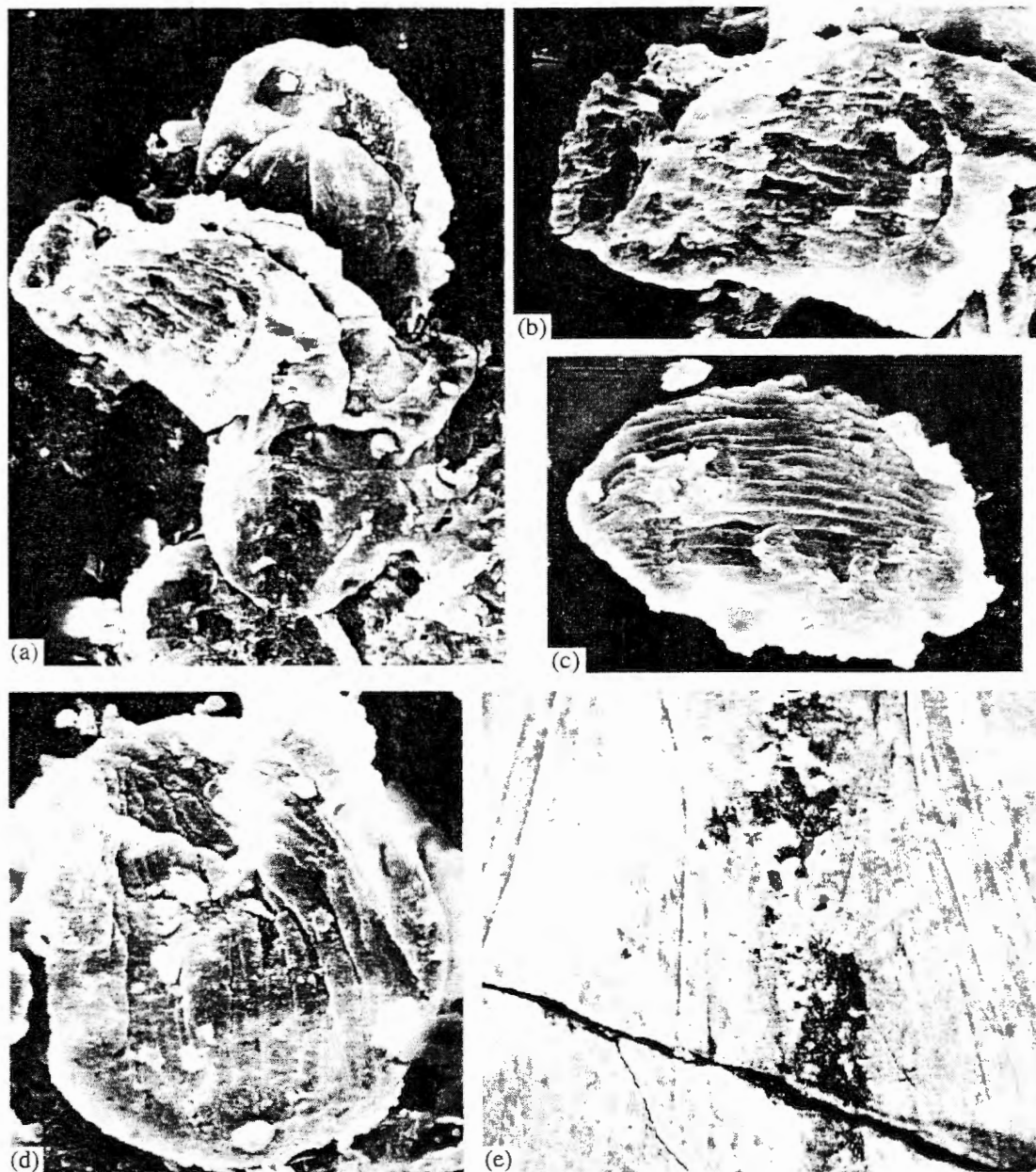


Fig. 6. *Vittatina*-type pollen from the gut compression of *Sojanidelia florea* sp. nov.: (a) clumped pollen grains of different morphotypes, *Vittatina* in the center, SEM, $\times 1000$, (b) the same grain enlarged, $\times 1500$, (c, d) another species with more regular taeniae, SEM, $\times 1200$ and 1400 , (e) part of paratype PIN, no. 1700/3411 showing intestine compression, $\times 6$.

the least sensitive to general climatic change, it does not seem plausible to us that synchronous appearance of striate pollen morphotypes and their parallel evolution in different parts of the world were driven by any long-term directional climate changes.

On the other hand, the evolutionary parallelism of palynological characters in the Permian gymnosperms can be more realistically explained by the plant-insect interaction. We found that striate pollen constituted a major food supply for three species representing at least two orders of Permian entomofauna. *Tscekardaenigma* contained adpressed grains of what

was apparently a single morphotype. In the gut compression of *Idelopsocus*, there were two types of striate pollen, *Lunatisporites* and *Protohaploxypinus*, while *Sojanidelia* fed on *Lunatisporites* mixed with *Vittatina* grains of two types. These Permian pollinivorous insects obviously associated with a conifer-peltasperm xeromorphous littoral community feeding either on a single plant species or on different species. In the latter case, the occurrence of two or more different pollen types in the insects intestines suggest that the respective plants grew in close proximity to each other. The gut

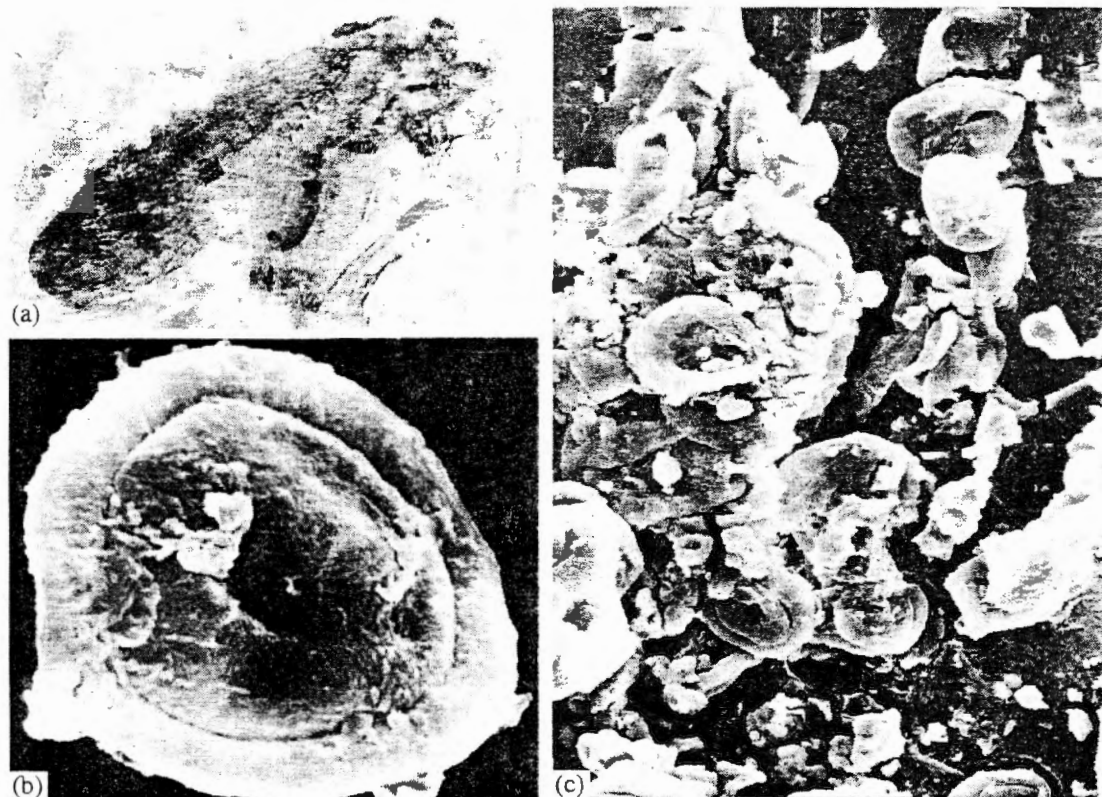


Fig. 7. *Aboilus* cf. *dilutus* Gorochoy, PIN, no. 2904/1675, katydid insect with organically preserved gut contents from the Middle Jurassic of Karatau Range, Kazakhstan. $\times 1$ and *Classopollis* grains from the gut, SEM, $\times 1700$ and 3000 .

contents thus give some indication of the composition of plant communities.

Although bladders are traditionally considered anemophilous adaptations, this may not be true in the case of protosaccate pollen grains with the endoreticulum of sacchi attached to the corpus. Such sacchi could hardly facilitate wind dispersal. However, a volume-regulating (harmomegathy) function of protosacchi and taeniae could be important in pollen transferred by large slow flying insects. Moreover, these structures might provoke pollinivory by increasing pollen mass thus making it more attractive to insects. Naturally, pollinivory could be advantageous to plants only in combination with entomophilous dispersal.

If insect visits gave any advantage to the pollen producers, then the respective morphological adaptations would rapidly spread among them. Incidentally, mutations responsible for the taeniate structure of the exine could be fixed in different plant populations in the course of transition from anemophily to entomophily. This would explain parallel evolution of striate pollen morphotypes in separate gymnosperm lineages. In addition, insects are known to transfer various gene-transducing microorganisms that can confer parallel genetic changes to the target plants. This mechanism might already have been in action in the Permian pro-

moting a rapid spread of such peculiar morphological features as taeniae.

The effects of plant-insect interaction could scarcely be restricted to the pollen organs alone. The larger the pollen grains, the fewer of them could compete for space in the target pollen chamber, thus creating a selection pressure in favour of larger or densely aggregated ovules, as well as stimulating adaptive modifications of their receptive structures. These processes might have brought about the burst of gymnosperm diversity in the Permian.

These conclusions may be valid also for other prominent episodes of plant diversification beyond the Permian. In the Mesozoic, the conifer-peltasperm littoral communities were replaced by the likewise xeromorphous brachyphyll-bennettite communities including, among brachyphylls, both conifers and gnetaleans (hirmerelleans). These communities are, in a coenogenic sense, direct descendants of the littoral Permian vegetation. They are not only the most diverse of their time, but also of great evolutionary potential as a cradle of proangiospermous and early angiospermous plants. Our recent finding of angiospermoid *Classopollis* pollen grains in the intestines of Jurassic grasshopper-like katydid insects (Fig. 7) testifies to the most advanced pollen type of the epoch being involved in plant-insect interactions. It further suggests that insects have been

likewise involved in the innovation of reproductive morphology occurring in the Mesozoic plant lineages that evolved in the direction of angiospermy.

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