

# First Find of Pollen Grains in the Gut of Permian Insects

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**Abstract**—Pollen grains are found for the first time in the gut of *Idelopsocus diradiatus* A. Rasnitsyn, sp. nov. (Hypoperlida, Hypoperlidae) and *Tshekardaenigma pollinivorum* A. Rasnitsyn, sp. nov. (Insecta incertae sedis) from the Kungurian of the Urals. Striate pollen grains of two formal genera, *Lunatisporites* and *Protohaploxypinus* predominate in the mass of extracted pollen. These morphotypes belong to conifers and/or peltasperms and are widespread as dispersed grains in the Permian deposits of both the Northern and Southern hemispheres. Both genera are protosaccate suggesting an initial development of protosacci in relation to plant—pollinivorous insect coevolution.

## INTRODUCTION

Recently, direct paleontological evidence of insects feeding on the pollen of extinct plants was obtained. Well preserved pollen grains, eaten perhaps not long before death and deposition, were found in the gut of lower hymenopteran insects assigned to the family Xyelidae (Krassilov and Rasnitsyn, 1982). Analysis of the gut contents indicated the pollen sources for each of the insect species and assessment of morphological variation in pollen grains of a single plant. Later, similar finds were reported from the Lower Cretaceous of Brazil (Caldas *et al.*, 1989) and Eocene of Germany (Lutz, 1990, 1993).

At present pollen grains are obtained from the gut of Paleozoic insects from the well-known Kungurian locality Tshekarda in the Urals. A single specimen received from Professor S.V. Meyen shortly before his untimely death in 1986, was not properly studied till recently. A search for appropriately preserved material was made by V.A. Krassilov and D.E. Shcherbakov in the collections of the Arthropod Laboratory of the Paleontological Institute of the Russian Academy of Sciences. This paper reports the first results of studies on the newly found material and that of S.V. Meyen.

## SYSTEMATIC PALEONTOLOGY

Insecta

Order Hypoperlida

Family Hypoperlidae Martynov, 1928

Genus *Idelopsocus* G. Zalesky, 1929

*Dinopsocus*: Martynov, 1928: 40 (type species, *D. arcuatus* Martynov, 1928) (not Banks, 1920)

*Idelopsocus*: Zalesky, 1929: 17 (type species, *I. tartaricus* G. Zalesky, 1929).

*Martynopsocus*: Karny, 1930: 446 (new name for *Dinopsocus*).

*Hypoperlopsis*: Zalesky, 1948: 1042 (type species, *H. splendens* G. Zalesky, 1948).

Synonymy after Shcherbakov (1995). In addition to the type species and a new species described below, the genus also includes the recently described *Martinopsocus levis* Novokshonov, 1995.

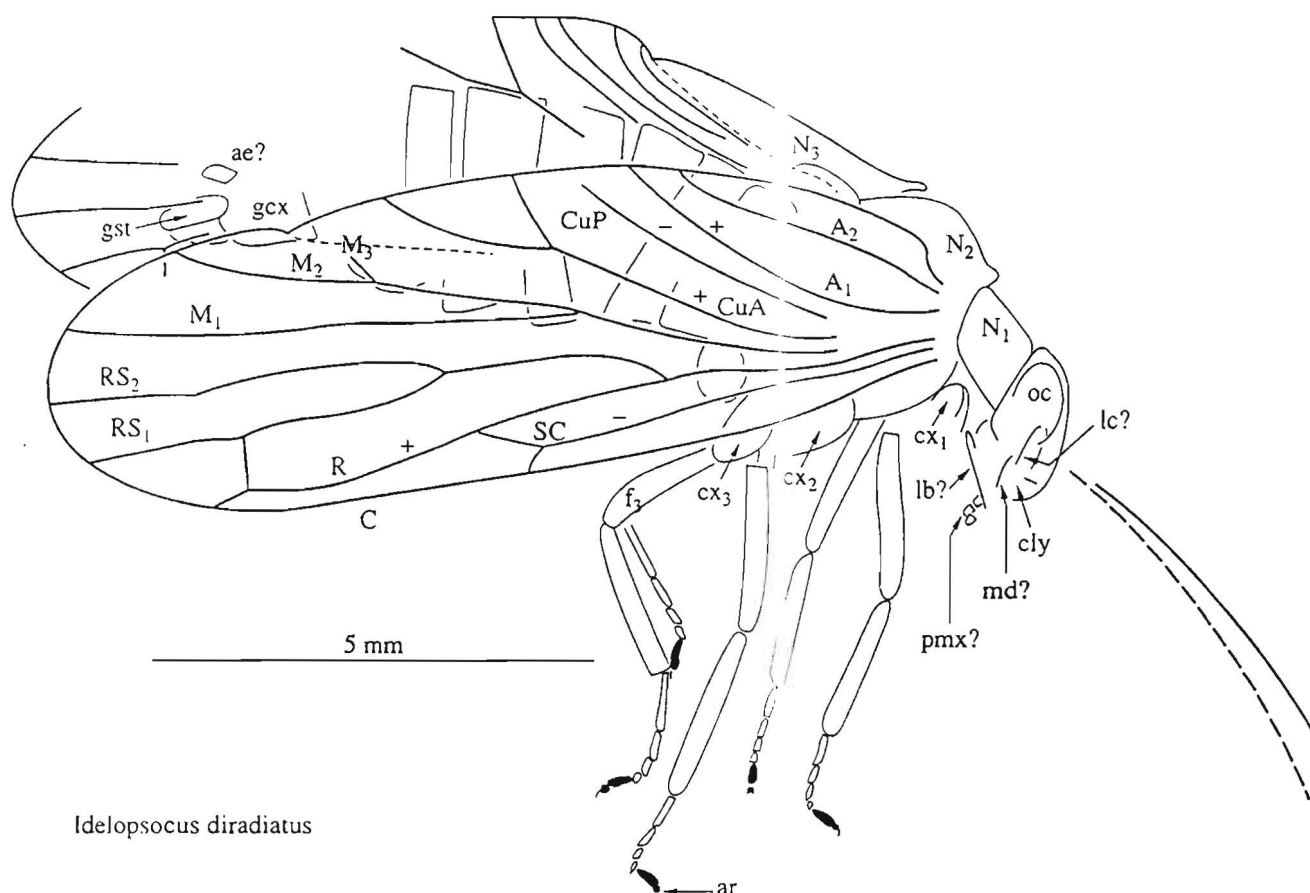
*Idelopsocus diradiatus* A. Rasnitsyn, sp. nov.

Plate 13, fig. 1

**Etymology.** From Latin *diradiatus* (diradiate, alluding to the two-branched RS).

**Holotype.** PIN 1700/3296; Russia, Perm Region, Suksun District, left bank of the Sylva River near Tshekarda Village; Lower Permian, Kungurian Stage, Koshelevka Formation.

**Description** (Fig. 1). Antenna 16-segmented, bristle-shaped, moderately short, with flagellar segments strongly elongate. Eyes large, clypeus short, convex, mandibles short, labial(?) palp short, with apical segment scarcely elongate, not incrassate relative to the penultimate one. Pronotum moderately short (about half as long as the head). Legs moderately short, femora and tibia subcylindrical, of nearly equal width, tibiae lacking strong spurs. Tarsi thin, short (anterior and middle shorter, and, the posterior, subequal in length to the respective tibia), segments I–IV subcylindrical, elongate (segment IV scarcely elongate), with oblique apex due to the intersegmental articulation displaced dorsally and a little basally. Ultimate segment inflated, longer than two penultimate segments combined or in the hind legs, subequal to them with large arolium and thin, gently curved claws. Fore wing RS with single, long fork,  $M_{2+3}$  fork wide, A3 may be lost. Male genitalia with gonocoxa large, somewhat rounded apically, gonostylus parallel-sided, rounded both basally and apically, almost as long as gonocoxa, but less than half its width, attached near the dorsal margin of gonocoxa. Ground color of body and antennae dark (lighter in



*Idelopsocus diradiatus*

Fig. 1. *Idelopsocus diradiatus* sp. nov.; holotype, PIN 1700/3296. Abbreviations: ae—aedeagus, ar—arolium, cly—clypeus, cx—coxa, f—femur, gcx—gonocoxa, gsty—gonostyle, lb—labium, lc—lacinia, md—mandible, N—thoracic notum, pmx—maxillary palp. Venational symbols are standard. Dashed lines indicate crumpled wing parts.

paratype, in particular the pronotum, head, and antennae), legs light except coxae and apical tarsomere.

Length of holotype: body 10.0 mm, antenna ca. 5 mm, fore wing 10.0 mm, fore femur 1.7 mm, fore tibia 1.6 mm, fore tarsus 1.1 mm, hind tibia 1.7 mm, hind tarsus 1.5 mm.

**Comparison.** New species differs from all others in 2-branched RS, additionally differs from *I. arcuatus* (Mart.) and *I. splendens* (G. Zal.) in wide  $M_2 + 3$  fork, and from *I. levis* (Novokshonov, 1995, comb. nov.) in larger size, short, thick legs, and long flagellar segments (if Novokshonov, 1995, describes these characters correctly).

**Remarks.** Pollinivory of Hypoperlidae has been predicted on the basis of their book-lice-like strong, rod-like, detached, maxillar lacinia (Rasnitsyn, 1980a, b). Moreover, this character allowed a reasonable taxonomic assignment of the family that previously had been considered enigmatic (cf. Carpenter, 1992). The Hypoperlidae (s.l., or Hypoperlidae s.str. and Ampelipetridae, as defined by Shcherbakov, 1995) were conceived of as an ancestral group of all the higher Cimiciformes (the former group Paraneoptera covering Cimi-

cida and Psocoptera s.l., including thrips), with their mode of pollen-feeding by using detached lacinia, taken as an intermediate ecological stage toward the specialized sporo- and pollinivory in the primitive book-lice, and toward the sucking mode of feeding in the Cimicida (=Rhynchota). Additionally, an ecological transition was postulated from the hypoperlid manner of eating, through the feeding adaptations of Synmalloptilidae and Strephocladidae, whose features indicate the gnawing of gymnosperm ovules, and eventually to the feeding adaptations of palaeodictyopteroids (Dictyonereidae). This group reportedly sucks unripe gymnosperm seeds with their thick beaks (Sharov, 1973). The key position of Hypoperlidae and their new, previously unexpected, relatives in insect classification necessitated the establishment of a new order, the Hypoperlida, to comprise the Hypoperlidae, Synmalloptilidae, and Strephocladidae, as well as a little known family the Perilytridae (Rasnitsyn, 1980a, 1980b). Our data on the gut contents of *I. diradiatus* provides additional evidence in favor of the above hypothesis.

**Material.** Two specimens, holotype and paratype PIN 1700/3280 from the Tshekarda locality.

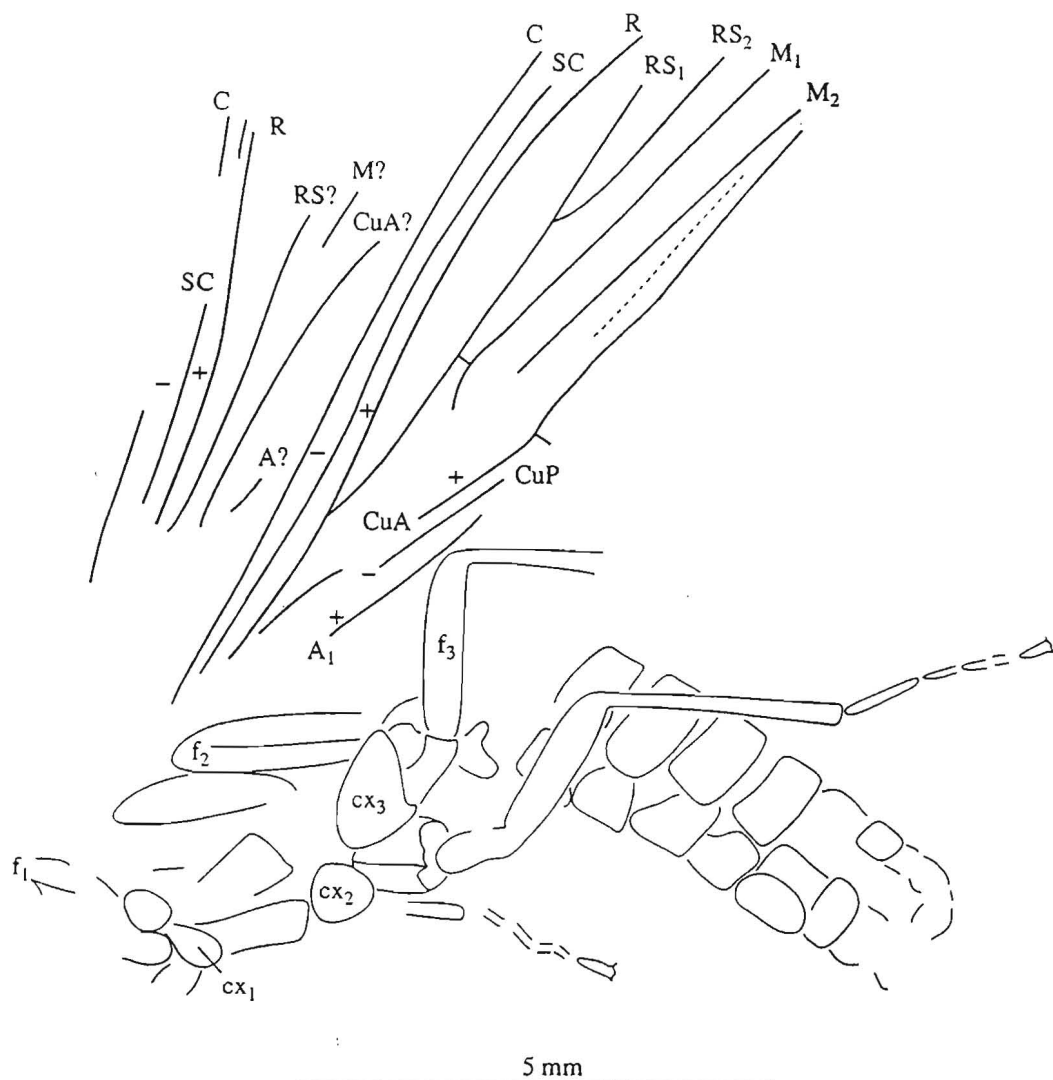


Fig. 2. *Tshekardaenigma plinivorum* sp. nov.; holotype, PIN 1700/4915. Abbreviations as in Fig. 1.

#### Insecta insertae sedis

#### Genus *Tshekardaenigma* A. Rasnitsyn, gen. nov.

**Etymology.** From the type locality (Tshekarda Village) and Greek *aenigma* (mystery).

**Type species.** *T. plinivorum* A. Rasnitsyn, sp. nov., Lower Permian (Kungurian); Perm Region.

**Diagnosis.** Size moderately small: body and wing length about 1 cm. Wing venation not rich, without alternating convex and concave veins between convex R and CuA, probably with numerous, though weak and not preserved, crossveins indicated by a zigzag course of longitudinal veins. Fore wing with costal space moderately narrow, RS leaving R well before wing midlength. Hind wing with the costal space narrow, wider subapically, SC entering the enlarged section of costal space. RS leaving R in about basal 1/4 of the wing length, with 3 or 4 (possibly only 2) branches at most. *M* probably with 2 branches, *M*<sub>1</sub> subbasally

connected with RS by short crossvein (or may be fused with the basal RS branch). CuA forking beyond the wing midlength, with CuA1 very long, almost aligned with CuA base, CuA2 short, vertical. Anal lobe, if defined, small. Mid and hind legs thin, moderately long, with hind coxa large and mid coxa small, tarsi long, 5-segmented, claws and arolium small. Abdomen subcylindrical, with 9 segments visible and with no appendages preserved.

**Composition.** Type species only.

**Remarks.** Poor preservation of the only specimen, with the features of the head, thoracic dorsum, most part of the hind wing, part of fore wing, and abdominal appendages not preserved for study, hinders taxonomic assignment of the fossil genus. Some of the characters (the fore wing with RS leaving R more basally than in the hind wing, and the costal space of the latter apically enlarged, with SC entering at this



Fig. 3. Pollen clump from the gut of *Idelopsocus diradiatus*, SEM ( $\times 700$ ).

point) are uncommon among the Permian insects, though hardly diagnostic of higher taxa. By the more standard characters, *Tshekardaenigma* cannot be assigned either to the dragonflies (infraclass Libellulones), or to the mayflies (Ephemeroformes). The Paleodictyopteroids (superorder Dictyoneuridea) are also excluded on account of the alternate convex and concave veins between R and CuA lacking in the fossil genus. As for the infraclass Gryllones (former Polyneoptera), *Tshekardaenigma* differs from all the constituent orders, except for Grylloblattida, in either the 5-segmented tarsus (from the majority of the orders), or the subcylindrical body (roaches), or non-saltatory hind legs (Gryllida), or in poor wing venation (Eoblattida). Most members of Grylloblattida differ also in having their hind wing CuA concave, and the anal lobe large. Within the cohorts Cimiciformes, all the higher taxa (Cimicida = Rhynchota, and the superorder Psocidea) can be excluded from consideration because of their 4-segmented tarsi. The known representatives of the superorder Caloneuridea (orders Caloneurida and Blattinopseida) have a different general appearance as well as specialized wing venation. The last order of Cimiciformes, Hypoperlida, is diverse morphologically and not easily discounted. However, among its three suborders, Hypoperlina differs in having the hind wing with concave CuA and with RS leaving R near the wing base. Strephocladina are dissimilar because of their large size, rich wing venation, and strong, climbing legs. Perilytrina differs in fore wings that are somewhat elytrized. As for the holometabolous insects (cohorts Scarabaeiformes), the beetles (Scarabaeida) differ in the elytrized fore wings, the hymenopterans

(Vespida) and glosselytrideans (order Jurinida) have a differently specialized wing venation and the miomopters (Palaeomanteida) are characterized by the hind wing with short SC and concave CuA. The Permian representatives of neuropteroid (superorder Myrmeconeontidea) and mecopteroid insects (superorder Panorpidia) usually have a richer wing venation, particularly in the combined radial and medial region. Certainly, *Tshekardaenigma* could be an aberrant representative of any of the above mentioned orders. Thus, the problem of its taxonomic position remains unresolved, awaiting better preserved material.

*Tshekardaenigma pollinivorum* A. Rasnitsyn, sp. nov.

Plate 13, fig. 2

**Etymology.** From Latin *pollinivorus* (pollen-eating).

**Holotype.** PIN 1700/4915; Russia, Perm Region, Suksun District, left bank of the Sylva River near Tshekarda Village; Lower Permian, Kungurian Stage, Koshelevka Formation.

**Description** (Fig. 2). Ground colour more or less uniform. Lengths: body without head ca. 10 mm, hind wing minimum 11 mm, hind femur 2.0 mm, hind tibia 2.6 mm, hind tarsus 2.4 mm.

**Material.** Holotype.

## POLLEN GRAINS

The holotype of *Idelopsocus diradiatus* contains a large clump of adpressed pollen at the hind end of the rectum. Maceration revealed well preserved striate





## Plate 13

Fig. 1. *Idelopsocus diradiatus* sp. nov.; holotype, PIN 1700/326,  $\times 9.8$ .

Fig. 2. *Tshekardaenigma pollinivorum* sp. nov.; holotype, PIN 1700/4915,  $\times 8.2$ .

Fig. 3. *Lunatisporites* sp., pollen grain from the gut of *Idelopsocus diradiatus*, SEM,  $\times 1700$ .

Fig. 4. *Protohaploxylinus* sp., pollen grain from the gut of *Idelopsocus diradiatus*, SEM,  $\times 1450$ .

bisaccate pollen grains forming the main mass of the clump. The pollen grains are assigned to the palynological form-genera *Lunatisporites* Leschick emend. Madler and *Protohaploxylinus* Samoilovich emend. Morbey (Pl. 13, figs. 3, 4, Text-fig. 3). *Lunatisporites* includes the haploxylonoid or weakly diploxylonoid grains, with the amb elliptical, the corpus outline rounded-elliptical, transversely elongated, sharply delimited from the sacchi. The latter embrace most of the corpus and are sometimes laterally connected by a narrow stripe of exine. The split sacchi show a protosaccate structure, with the endoreticulum connected to the corpus. The cappa is divided into four main taeniae and two short wedge-shaped taeniae fragments. The clefts between taeniae are deep and the middle one gaping, exposing a narrow strip of exine. In distinction, *Protohaploxylinus* has more numerous taeniae (Foster, 1979), about 6–8, parallel-sided and divided by narrow clefts. The grains with the exine partly digested show a reticulate infrastructure.

The pollen grains extracted from the gut of *Tshekardaenigma pollinivorum* are likewise striate and with narrow taeniae as in *Protohaploxylinus*, but poorly preserved and difficult to separate.

The following is presently known of the systematic assignment of the plants producing striate pollen grains. *Lunatisporites*-type grains have been found in the pollen cones of *Ulmannia*, a Permian conifer widespread in the Northern Hemisphere (Clement-Westerhof, 1974). At the same time they abundantly occur in the Permian deposits of the southern continents from which *Ulmannia* is not reported at present. The pollen grains of *Arberiella*, a pollen organ associated with glossopterids, are of the *Protohaploxylinus* type (Zavada, 1991) that is certainly not restricted to this southern group of gymnosperms.

In addition to the abundant striate grains, the pollen clumps in the gut of Permian insects contained a few costate grains supposedly produced by gymnosperms of gnetalean affinities.

The association of two or more pollen types in the gut suggest that the insect visited different plants growing not far from each other and perhaps coexisting in a single community. Such data are potentially useful for reconstruction of extinct plant communities. Conifers and peltasperms provided the most abundant pollen source that confirms their status as ecological dominants of the Permian plant communities inhabited by pollinivorous insects.

Insofar as protosacci are hardly useful in wind-dispersal, their appearance in Paleozoic gymnosperms

was perhaps because of some other, not yet fully understood, factors. Although pollinivory does not necessarily correlate with insect pollination, the latter seems likely in plants that increased their cumulative pollen offer by developing protosacci and taeniae. Their significance in relation to plant–insect coevolution deserves further study.

## ACKNOWLEDGMENTS

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