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Pollen morphotypes from the intestine of a Permian booklouse

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Abstract

Two morphotypes of disaccate taeniate pollen grains *Lunatisporites* and *Protohaploxypinus*, and two types of monosaccate pollen grains, *Florinites* and *Potonieisporites* are recognized in the organic gut content of a primitive booklouse *Parapsocidium uralicum* G. Zalessky (Psocidiidae, Psocida) from the Tshekarda locality in the Urals. Details of infrastructure are described for *Lunatisporites*. Lamellate nexine was not observed in sectioned pollen grain of *Protohaploxypinus perfecta*. Pollen grains with several to many taeniae are abundant in the gut, whereas other morphotypes are represented by a single grain each. Such proportions are typical for pollinivorous insects from Tshekarda. *Parapsocidium* has shared its foraging habitat with another pollinivorous insect, *Idelopsocus diradiatus* Rasnitsyn (Hypoperlida). The latter is considered as a representative of an extinct group ancestral to booklice.

Keywords: Permian; pollen morphology; pollinivory; palaeoecology

1. Introduction

A collection of fossil insects from the Tshekarda locality in the Middle Urals contains well preserved specimens with definable pollen grains in the organic gut contents. Previously we found several morphotypes of taeniate pollen grains in the guts of three species belonging to Hypoperlida and Grylloblattida (Krassilov and Rasnitsyn, 1997). Here we report on the gut contents of a pollinivorous booklouse that proved to be especially versatile in its dietary requirements. Four morphotypes of pollen grains were recognized in the pollen mass filling the intestine. Their preservation occasionally allows one to observe structural features that are not normally seen in dispersed pollen grains.

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2. Material

The Tshekarda locality is located at the Sylva River in the historical type area of the Permian System in the southern part of the Ufa–Solikamsk Basin, Middle Urals. The fossil insects came from a sequence of alternating shales and sandstones also containing a typically Kungurian (late Early Permian) marine fauna of foraminifers, bryozoans, brachiopods and cephalopods (Stepanov, 1966). A specimen under study (Fig. 1; Plate I, 1) is assigned to *Parapsocidium uralicum* G. Zalessky (family Psocidiidae Tillyard, 1926 = Dichentomidae Carpenter, 1932) previously described from the same strata (Zalessky, 1939).

The pollen mass is contained in the fore part of intestine. It consists of about 50 compressed pollen grains. Parts of the pollen mass were removed from the specimen, cleansed in nitric acid and studied with SEM. After taking micrographs from both sides

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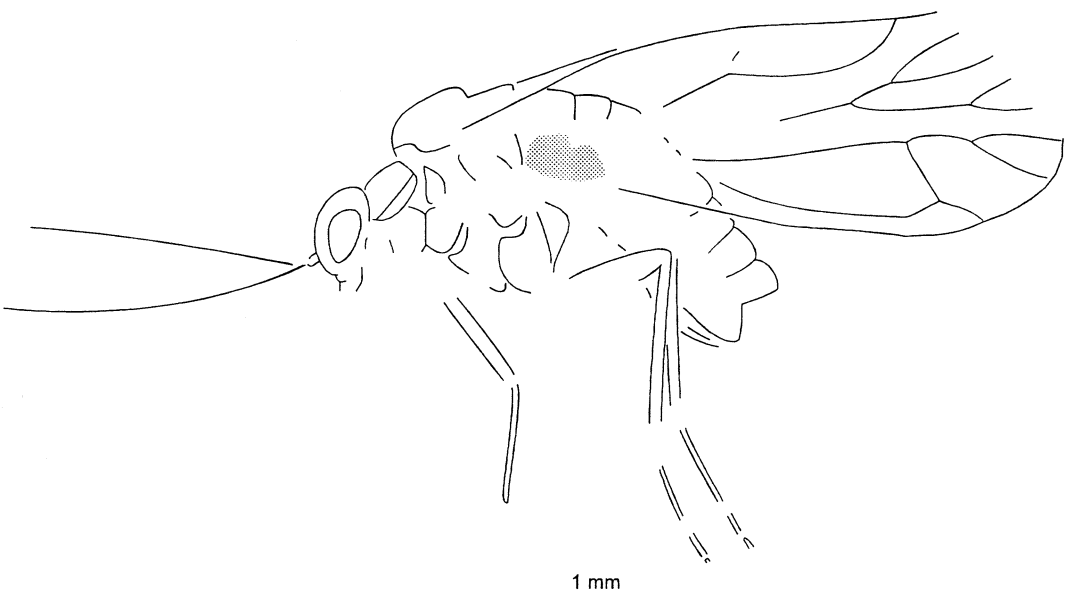


Fig. 1. *Parapsocidium uralicum* G. Zalessky, a booklouse from the Lower Permian (Kungurian) of Tshekarda, the Urals; PIN no. 1700/44386, with pollen mass in the gut shaded.

of the lump, a few grains were separated, studied with light microscope and sectioned. It was found that most of the pollen mass consists of relatively small *Lunatisporites*-type grains. Mixed with them are several larger grains of *Protohaploxypinus perfecta* (Plate I, 3). Two other morphotypes, *Florinites luberae* and *Potonieisporites* sp. are represented by a single grain each.

The collection is deposited in the Palaeontological Institute, Moscow, No. 1700.

3. Description of pollen grains

Subturma MONOSACCITES (Chitaley) Potonié et Kremp, 1954

Genus ***Florinites*** Schopf, Wilson et Bentall, 1944

Florinites luberae Samoilovich (Plate II, 5)

1953: *Florinites luberae* Samoilovich, p. 42, pl. 8, 2a, b.
1971: *Florinites luberae*, Waryuchina, pl. IV, 10, pl. XIV, 1, pl. XIX, 7.
1994: *Florinites luberae*, Utting, p. 46, pl. IV, 22, 23, Pl. V, 1.

Description: A single monosaccate pollen grain, discoid, with saccus 53 μm broad, 23 μm high, slightly laterally constricted in median plane and likewise slightly distally depressed, with broad radial folds. The contact area is convex, nearly circular, 22 μm in diameter, divided from the saccus by a narrow con-

PLATE I

Pollen grains from the gut content of *Parapsocidium uralicum* G. Zalessky, a primitive booklouse from the Lower Permian of the Tshekarda locality, the Urals.

1. *Parapsocidium uralicum* G. Zalessky, PIN no. 1700/44386, lumps of pollen grains are seen as light spots (arrow). ×20.
2. Lump of pollen grains with *Lunatisporites* sp. (smaller grains) and *Protohaploxypinus perfecta* (Naumova) Samoilovich (top grain), SEM. ×800.
3. Lump of pollen grains with *Lunatisporites* sp., distal view (bottom) and *Potonieisporites* sp. (top grain), SEM. ×630.
4. *Lunatisporites* sp, proximal view, SEM. ×1500.
5. *Lunatisporites* sp., saccus infrastructure, lateral view, SEM. ×4000.

PLATE I

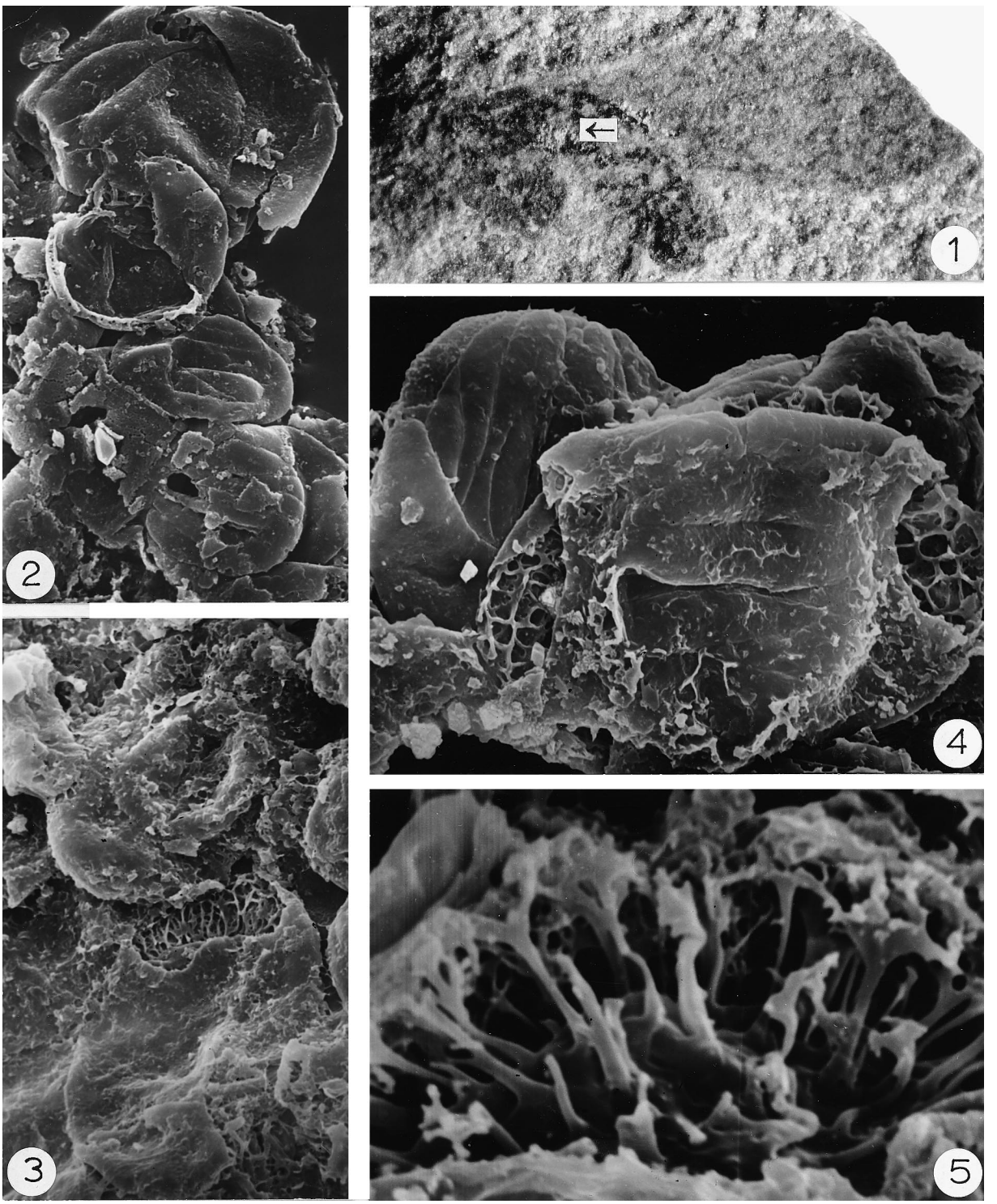
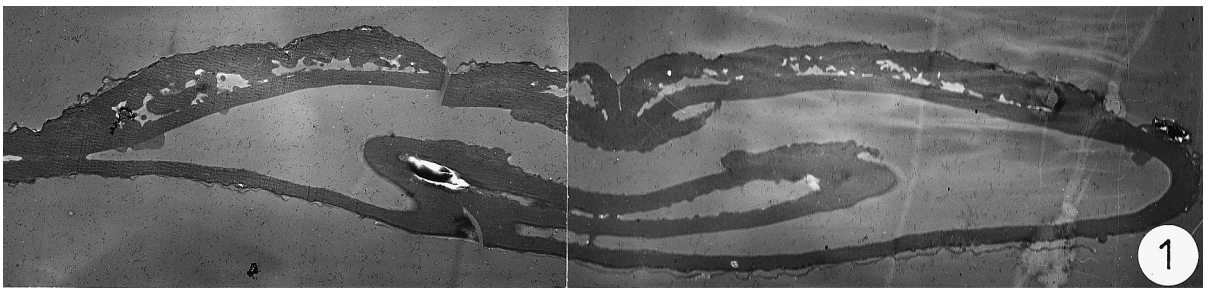
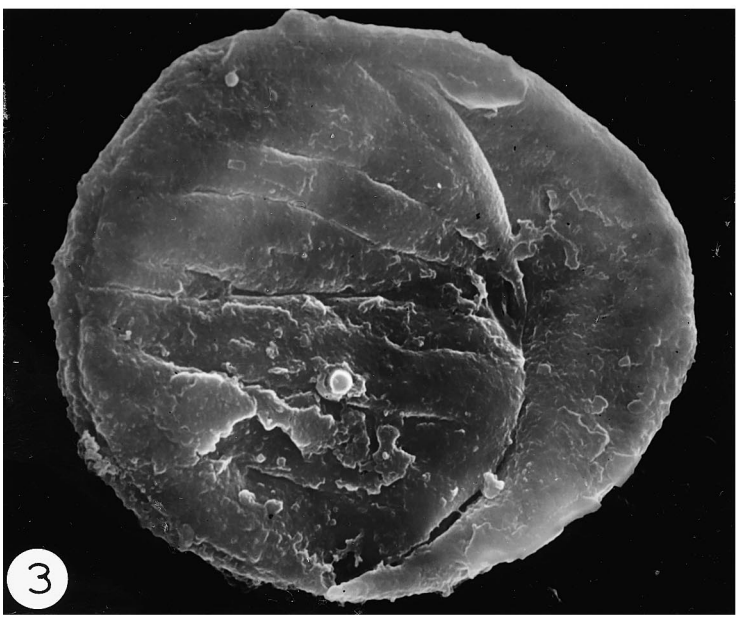
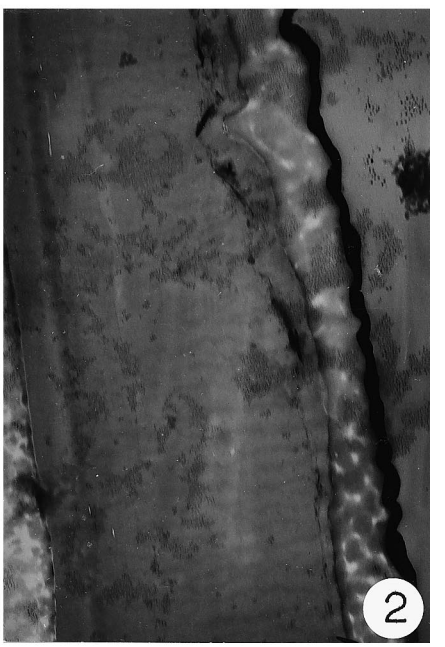
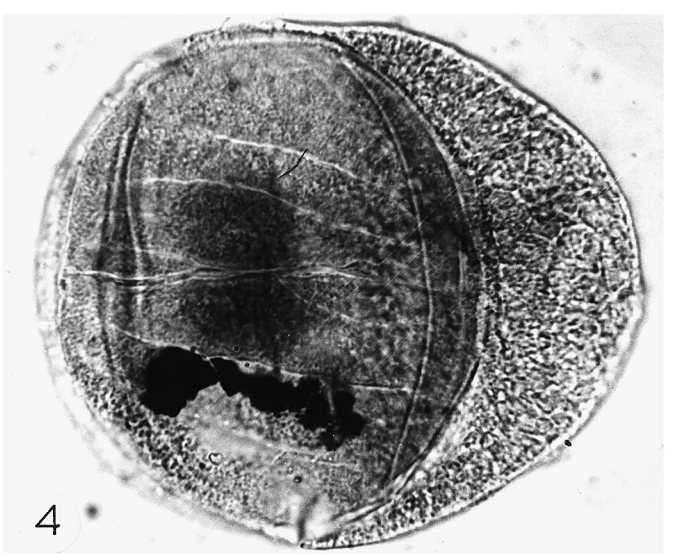


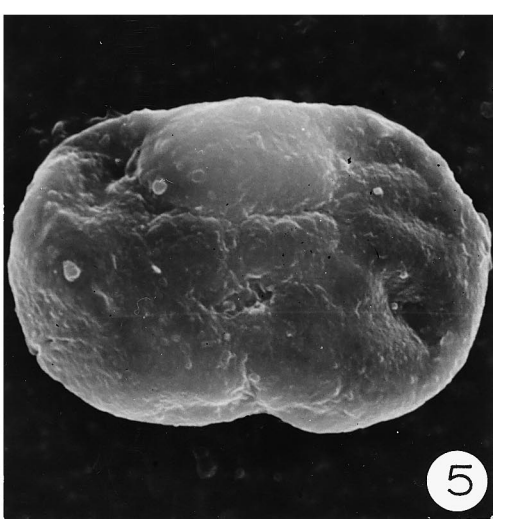
PLATE II











centric groove. No haptotypic features are observed except faint folds that can be preservational.
Remarks: This pollen grain falls in the dimension range of *F. luberae*, a common Kungurian to Late Permian species in the Uralian and Arctic localities. For this species the type material was not yet studied with SEM, but the diagnostic features seem to match the material found in the guts.

Genus ***Potonieisporites*** Bharadwaj, 1954

Potonieisporites sp. (Plate I, 3)
Description: Monosaccate pollen grain with elliptical amb 51 × 30 μm. The saccus is bilobed, with a broad lateral connection, indistinctly rugulate, showing radially elongate lumina transparent through the tectum. The body is rounded-elliptical, 26 × 21 μm, bordered by a thick sexinal fold forming an encircling ridge. The laesura is slightly bent in the middle, reaching to the encircling ridge.
Remarks: This grain is comparable with *Potonieisporites methoris* (Foster, 1979) and *P. bharadwajii* (e.g., specimens figured in Broutin et al., 1990), but is much smaller and differs also in the prominent ridge encircling contact area of the corpus. The latter feature is characteristic of Mesozoic morphotypes *Illinites* (*Angustisulcites*), *Parillinites* and *Ovalipollis* some forms of which, in particular *O. notabilis* Scheuring, show broad lateral connections of sacci approaching a bilobed monosaccate structure (Scheuring, 1970).

Subturma DISACCITES Cookson, 1947

Genus ***Lunatisporites*** Leschik emend. Scheuring, 1970

Lunatisporites sp. (Plate I, 2–5)
Description: Pollen grains haploxylonoid, amb elliptical about 50 × 40 μm, corpus spherical, diameter about 30 μm, with 4 to 5 taeniae. Median cleft gaping or split at the ends or at one end only. Sacci sparsely verrucate. Reticulum of sacci with a proximal series of radially elongate, tangentially rectanguloid brochi, distally rapidly divided at short intervals to form a network of small secondary lumina less than 1 μm broad.

The haploxylonoid transversely elliptical grains are about 48–56 μm long, with spherical corpus and nearly hemispherical sacci 17–20 μm broad offlapping about one fifth of the corpus, and with the cappa typically divided by three to four clefts of which the median one is laesural. A pollen grain in proximal view (Plate I, 4) shows a narrow lateral connection of sacci that are slightly less than hemispherical. The sexinal clefts traverse the entire length of the cappa. The lateral clefts are occasionally divided in the middle, the median cleft is sometimes shortly forked at the ends. Surface of the taeniae is microscabrate, that of sacci is irregularly radially folded and sparsely verrucate. The verrucae are rounded, about 1 μm broad, of varying height, occasionally confluent, denser along the margin of cappa than distally on the bladders.

In a number of grains the tectum of the sacci is partly eroded. In a few grains the infrastructure is also exposed on the corpus. Windows in the tectum expose infrastructure of sacci in surface view, with lumina rounded elliptical to rectanguloid or polygonal, about 4 μm wide, the smaller lumina are indistinct at the level of exposure (Plate I, 4), but can be seen closer to the surface, each larger lumen enclosing 5–6 smaller ones.

The distal aspect of a slightly smaller grain in Plate I, 3 shows an elongate cappula 18 μm broad, bordered by the nearly straight bases of sacci. The cappula is slightly concave, unsculptured. This and another distally orientated grain in Plate I, 5 show infrastructure of sacci in lateral view, with endosexinal elements spreading from the corpus and expanded at

PLATE II

Pollen grains from the gut content of *Parapsocidium uralicum* G. Zalessky, a primitive booklouse from the Lower Permian of the Tshekarda locality, the Urals.

1. *Protohaploxypinus perfecta* (Naumova) Samoilovich, median longitudinal section of pollen grain shown in 3–5, TEM. ×4000.
2. Part of 1 showing infrastructure (right) and non-lamellate nexine, TEM. ×100,000.
3. *Protohaploxypinus perfecta* (Naumova) Samoilovich, proximal view, SEM. ×1400.
4. Same grain, light microscopy. ×940.
5. *Florinites luberae* Samoilovich, monosaccate pollen grain, proximo-lateral view, SEM. ×1200.

base, forming elongate brochi 5–6 μm long, distally repeatedly divided at short distance from the outer wall to form a palmate pattern of inclusive brochi the smallest of which are less than 0.5 μm broad.

Remarks: These grains are similar to *Lunatisporites noviaulensis* (Leschik) Foster, a heterogeneous species divisible into distinct varieties perhaps deserving morphospecies rank (Scheuring, 1970). The Uralian species is typically smaller and differs from this and other congeneric pollen grains in having verrucate sacci and radially strongly elongate, distally minutely divided brochi. Significance of infrastructural characters for species definition has yet to be studied, but at least *L. acutus* Leschik and *L. noviaulensis* var. *mollis* Scheuring as illustrated in Scheuring (1970) seem different, with the brochi divided at a shorter distance from the roots of sacci.

Genus ***Protohaploxypinus*** Samoilovich, 1953

Protohaploxypinus perfecta (Naumova) Samoilovich, 1953 (Plate I, 2; Plate II, 1–4)

1953: *Protohaploxypinus perfectus* Samoilovich, pl. XII, 1a, 1b.
1971: *Striatohaploxypinites perfectus* Waryuchina, pl. XVII, 1a–1c.
1964: *Striatopinites perfectus* Abramova et Marchenko, pl. III, 4, 5.
1964: *Striatopinites prolixus* Abramova et Marchenko, pl. III, 6, 7.
1994: *Protohaploxypinus perfectus*, Utting, p. 55, pl. VII, 4–6.

Description: The pollen grains assigned to this species are haploxylonoid with elliptical amb, 72–77 μm long. The sacci are crescent-shaped to hemispherical, 17–22 μm broad, narrowly laterally connected, infrareticulate with small lumina. The body is elliptical, either transversely or longitudinally elongate, 40–43 μm broad. The cappa is well defined, with 8–10 taeniae divided by narrow clefts. Haptotypic marks are lacking. The taeniae are of fluctuating width about 6–8 μm, commonly wedging to the margins or interfingering, irregularly branched. The cappula is nearly parallel-sided and extends full length of corpus. It is about 25 μm broad, scabrate, with the bordering roots of sacci traversed by short striae.

A median longitudinal section (Plate I, 1) shows taeniae as lense-shaped exosexinal thickenings with clefts of varying depth. The infrastructure is alveolate, with small irregular lumina. The nexine appears to consist of a single non-lamellate layer (foot layer) of a nearly uniform thickness, infolded at the base of sacci.

Remarks: *P. perfecta* (previously spelled '*perfectus*', here corrected to conform to the grammatical gender of generic name) is a polymorphic species in which the body can be either transversely or longitudinally elliptical and the number of taeniae vary from 6–8 to 10–12. In contrast to *Protohaploxypinus*-type grains from the sporangia of *Arberiella* (Zavada, 1991), our material does not show lamellation of nexine.

4. Discussion

Our data indicate widespread pollinivory among the Permian insects. Most 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 are found:

(1) *Lunatisporites*, supposedly produced by *Ullmannia*-like conifers (Clement-Westerhof, 1974). This morphotype prevails in the guts of *Idelopsocus diradiatus* Rasnitsyn (Krassilov and Rasnitsyn, 1997) 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 (Zavada, 1991) and probably by some related or convergent northern groups (for dispersed pollen grains of this type are abundant in the Permian of the Urals and elsewhere). In both *Idelopsocus* and *Parapsocidium* this type is associated with *Lunatisporites* perhaps indicating proximity of their producing plants.

(3) *Vittatina* group, produced by phylladoderm peltasperms (Meyen, 1987), prominent in the gut content of *Sojanidelia floralis* (Krassilov and Rasnitsyn, 1997) in association with the *Lunatisporites–Protohaploxypinus* group.

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

These data might have some ecological meaning perhaps indicating the ullmanniaceous–pteridosperm 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.

From an entomological point of view, the similarity of feeding habits in *Parapsocidium* and *Idelopsocus* sharing a common pollen source, is of some interest, for their phylogenetic affinity has been previously postulated on morphological grounds (Rasnitsyn, 1980; Rohdendorf and Rasnitsyn, 1980). *Idelopsocus* supposedly represents a line of the extinct order Hypoperlida leading to primitive booklouse (order Psocida, suborder Permopsocina). *Parapsocidium* belongs to the Permian booklice family Psocidiidae which is considered as a stem group of all living Cimiciformes. The presently confirmed pollinivory adds significantly to our understanding of functional morphology of this phylogenetically important group.

5. Conclusion

The gut content of an Early Permian (Kungurian) insect *Parapsocidium* (booklouse) yielded four morphotypes of pollen grains: *Florinites luberae* Samoilovich, *Potonieisporites* sp., *Lunatisporites* sp., and *Protohaploxypinus perfecta* (Naumova) Samoilovich. The partly digested pollen grains of *Lunatisporites* show details of protosaccate infrastructure with long proximal brochi that are repeatedly divided close to the wall forming a hierarchial pattern in surface view. Infrastructure of the corpus is similar, but with smaller brochi that may resemble columellae. Both *Lunatisporites* sp. and *Protohaploxypinus perfecta* have non-laminate nexine.

These data confirm that a plant community producing *Lunatisporites* and *Protohaploxypinus* pollen grains might serve as a major foraging ground for pollinivorous insects. Incidentally, *Idelopsocus* (Hypoperlidae) and *Parapsocidium* (Psocidiidae) were restricted to this type of habitat, their similar feeding habits perhaps confirming their phylogenetic relations as representatives of a stock group of diverse cimiciform insects. Other pollinivores might occasionally visit adjacent phylladoderm and cordaitalean communities as possible sources of *Vittatina* and *Florinites–Potonieisporites* pollen grains, respectively.

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