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# Permian Insects of the Vorkuta Group in the Pechora Basin, and Their Stratigraphic Implications

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**Abstract**—Insect distribution over the formations and rock units of the Vorkuta Group in northeastern European Russia is considered based on 342 identifiable and properly dated insect fossils. The fossils are found to form a distinctly impoverished assemblage, which is further indivisible in terms of evolutionary level and stratigraphic affinities along the whole characterized part of the Vorkuta Group, except for the lower half of the Ayach'yaga Subformation and the very top of the Inta Fm. The assemblage represents a stratigraphically unresolved mixture, consisting mainly of Kungurian and Early Kazanian elements, with a considerable admixture of Carboniferous relicts. A number of insect species are recorded, each in remote members of the section explored, including those belonging to different formations. The results are inconsistent with the hypothesis of considerable age difference between parts of the Vorkuta Group section, although they do not help with dating the deposits within the Kungurian through Kazanian interval. The impoverished character of the assemblage is ascribed to its supposed northern origin. New taxa of the order Grylloblattida are described: *Sylvaprisca alba* Aristov, sp. nov., *Artinska vorkutensis* Aristov, sp. nov. (Lemmatophoridae), *Neprotembia complicata* Aristov, sp. nov. (Aliculidae), *Permopectina vorkutensis* Aristov, gen. et sp. nov. (Permopectinidae Aristov, fam. nov.), *Khosaridelia rigida* Aristov, sp. nov. (Permotermopsidae), *Parapermula circummaculosa* Aristov, sp. nov., *Vorkutopterum monstruosum* Aristov, gen. et sp. nov., *Liomopterella parakitiakensis* Aristov, sp. nov., *L. tota* Aristov, sp. nov., *Liomopterum minor* Aristov, sp. nov. (Liomopteridae) from the mid-Permian of the Pechora Basin in north European Russia, and *Permopectina tshekardensis* Aristov, sp. nov. (Permopectinidae) from the Kungurian of the Middle Urals.

*Key words*: Permian insects, Pechora coal basin, stratigraphy.

## INTRODUCTION

Permian deposits of the Pechora Coal Basin were studied in detail for many years due to their economic importance, and they are thoroughly subdivided and correlated over the large area of the basin (see, for example, *Geology* …, 1965; Pukhonto, 1998). However, correlation to the international scale and especially position of the Lower/Upper Permian boundary are still disputable (*The Coal-Bearing*…, 1990, pp. 11–13, 65). Forty years ago Pogorevich and Makedonov (1965) wrote: "The Kungurian age of the [Vorkuta] Group can be considered to be reliably proven only for the Lower Vorkuta [Lek-Vorkuta] Formation …" (p. 41), and further: "Most probably, though still tentatively, the Upper Vorkuta [Inta] Formation can be correlated to the Solikamsk and (at least partly) Sheshma horizons of the 'Ufimian' Stage" (p. 61). Thirty years later the authors of *Biotas*… (1998) drew this boundary somewhat lower. Some of them correlate it to the boundary between the Ayach'yaga and Rudnik subformations of the Lek-Vorkuta Formation (Grunt, p. 145; Grunt, Kalashnikov, and Gizatulin, pp. 133–134; less certainly, Naugolnykh, p. 212), others draw the boundary within the Rudnik Subformation, between Members M and N (Esaulova, p. 216; this hypothesis is substantiated in detail by Pukhonto (1998)), and still others assign the entire Vorkuta Group to the Upper Permian (Igonin and Sukhov, pp. 94, 99, text-fig. 29; Kanev, p. 168; Koloda, text-fig. 47). In a recent paper arguing that the Ufimian Stage should be abandoned (Kotlyar *et al.*, 2004), the Vorkuta Group is entirely included in the Kungurian.

In this context the data on fossil insects received by the Arthropoda Laboratory, Paleontological Institute, Russian Academy of Sciences (PIN), from several generations of geologists that worked in the Pechora Basin, are quite interesting. These fossils were collected from various levels within the Lek-Vorkuta and Inta formations, chiefly from core samples. There are more than 550 insects altogether. after excluding those which are not identifiable to order level, or lack proper stratigraphic attribution, we used 342 specimens for further analysis.

Deposits of the Inta and Lek-Vorkuta formations, constituting the Vorkuta Group, are divided into rock units (members) labeled from top to bottom with the letters "E" to "T" (*The Coal-Bearing* …, 1990; Pukhonto, 1998). The interval from I to R yielded the most insect specimens: 173 from the Inta Formation (Members E–L); 113 from the Rudnik Subformation of the Lek-Vorkuta Formation (Members M–O), including 18 from Member M, specially discussed below; 43 from the Ayach'yaga Subformation (Members P–T); 11 from the undivided Lek-Vorkuta Formation, and 2 from an interval embracing more than one formation. The material was identified by D.S. Aristov (Grylloblattida), V.N. Vishnyakova (Blattida), A.P. Rasnitsyn (Blattinopseida, Hypoperlida, Palaeomanteida), N.D. Sinitshenkova (Dictyoneurida, Mischopterida, Diaphanopterida, Perlida), I.D. Sukacheva (Panorpida), and D.E. Shcherbakov (Homoptera, Forficulida), all at PIN.

In this paper, typified names are used for the higher taxa of insects (*History* …, 2002); namely, Blattida for Blattodea, Diaphanopterida for Diaphanopterodea, Dictyoneurida for Palaeodictyoptera, Grylloblattida for Grylloblattodea, Mischopterida for Megasecoptera, Palaeomanteida for Miomoptera, Panorpida for Mecoptera, Perlida for Plecoptera, and Forficulida for Dermaptera.

The distribution of insect finds over the section is represented in the table.

Taking into account only stratigraphically meaningful taxa, i.e., those occurring only in part of the disputable interval, or above or below it, the insects are distributed over the section as follows.

The Inta Formation contains *Glaphyrophlebia subcostalis* (described from the Lower Kazanian; Martynov, 1928), *Baeoneura* sp. (Carboniferous genus; Sharov and Sinichenkova, 1977), *Vorkutoneura variabilis* (endemic genus; other Spilapteridae in the Carboniferous and Lower Permian; Sharov and Sinichenkova, 1977), *Vorkutia tschernovi* (second species of *Vorkutia* in the Kungurian of Chekarda, Urals; Novokshonov, 1998), Prosbolopseidae Ivaiinae (Kungurian–Tatarian), *Kunguroblattina elongata, K. latimarginata, K. minima* (the genus also in the Kungurian; Vishnyakova, 1965), *Sojanidelia vorkutensis* (most species of *Sojanidelia* in the Lower Kazanian, one in the Kungurian (Chekarda, Urals), one from Kaltan; Storozhenko, 1998), *Sylvaprisca alba* sp. nov. (the genus since the Kungurian, Aristov, 2001; the species in Members K, E–L, M), *Artinska vorkutensis* sp. nov. (other species in the Asselian, Artinskian (Leonardian), Kungurian (Novokshonov, 1999) and Lower Kazanian), *Liomopterella* sp. (other species from the Kungurian up to the Upper Kazanian; Aristov, 2004a, b), *Liomopterum minor* sp. nov. (the genus from the Artinskian onward; Storozhenko, 1998, the species in Members K, M, and, presumably, N).

In the Rudnik Subformation, Member M contains *V. variabilis, Cyclocelis* sp. (Carboniferous genus; Carpenter, 1992), *K. minima, S. alba* sp. nov., *Parakhosara incommoda* (most species of *Parakhosara* in the Lower Kazanian; Storozhenko, 1998, one in the Kungurian), *Khozaridelia martynovi* (endemic genus, all other species of Permotermopsidae in the Lower Kazanian; Storozhenko, 1998), and *L. minor* sp. nov.

In the Rudnik Subformation, Members N and O contain *G. subcostalis, Dunbaria borealis* (the genus also occurs in the Artinskian (Leonardian) and Kungurian; Sharov and Sinichenkova, 1977), *D. quinquefasciata* (the species described from the Kungurian; Martynov, 1940), *Homaloneura* sp. (Carboniferous genus; Carpenter, 1992), *V. variabilis, Epimastax sojanensis* (the species described from the Lower Kazanian; Rasnitsyn, 1977), *Artinska* sp., *Khosaridelia rigida* sp. nov., *Liomopterella tota* (distribution of the genus, see above), and *L. ?minor* sp. nov.

The Ayach'yaga Subformation contains *D. quinquefasciata, Homaloneura* sp., *Vorkutia* sp., *K. latimarginata, S. multimediana, S. vorkutensis, Liomopterella* sp., *Permopectina vorkutensis* sp. nov. (the genus also occurs in the Kungurian), *Parapermula circummaculosa* sp. nov. (the genus also occurs in the Upper and Lower Kazanian, Storozhenko, 1998; Aristov, 2004b).

The undivided Lek-Vorkuta Formation contains *D. quinquefasciata, E. sojanensis, Petromantis* sp. (of 18 species of the genus, only one comes from the Kungurian, all or nearly all others from the Upper Permian; Novokshonov, 1997).

Therefore, one can see a mixture of taxa characteristic of the Upper Permian (especially of the Lower Kazanian; insects of undoubtedly Ufimian age are poorly known), of the Lower Permian, and of the Carboniferous. Among these are even species described from the Lower Kazanian (*G. subcostalis, E. sojanensis*) and Kungurian (*D. quinquefasciata*). A number of species are fixed as persisting through a considerable part of the section, that is important due to high evolutionary rates at the species level characteristic of insects (Rasnitsyn, 1987, 2002). So, the species *S. vorkutensis* is recorded in Member Ia of the Inta Formation and Member P of the Ayach'yaga Subformation, *S. alba* sp. nov. in Member K of the Inta Formation and Member M of the Rudnik Subformation, *K. minima* in Member I of the Inta Formation and Member M of the Rudnik Subformation, *G. subcostalis* in the Inta Formation and Rudnik Subformation below Member M, *V. variabilis* and *L. minor* sp. nov. in the Inta Formation and Rudnik Subformation (including Member M), *K. latimarginata* in the Inta Formation and Ayach'yaga Subformation, *D. quinquefasciata* and *Homaloneura* sp. in the Rudnik and Ayach'yaga Subformations.

The general composition of the insect assemblage (absence of dragonflies, rarity of Homoptera, nearly complete absence of holometabolans other than Palaeomanteida and scorpionflies, including the complete absence of beetles and neuropteroids, combined with the abundance of palaeodictyopteroids, cockroaches, and Grylloblattida) resembles only that of the Carrizo Arroyo locality near the Permian–Carboniferous boundary, New Mexico, United States (Rasnitsyn *et al.*, 2004). The presence of some groups characteristic of

Distribution of identifiable insect remains over the rock units of the Inta and Lek-Vorkuta formations, Pechora Basin. In the column "Member," lettering like E–F, G–H, etc. means the finds dated only up to the interval specified (E–L and M–T, Inta and Lek-Vorkuta formations undivided, M–O, Rudnik and P–T, Ayach'yaga subformations undivided). In the column "n" the number of found representatives of the order given is indicated

| Member | Order | *n* | Including identified |
|---|---|---|---|
| E–F | Blattida | 1 | |
| F | Blattida | 1 | |
| G | Blattida | 3 | *Phyloblatta* sp. |
| G | Grylloblattida | 3 | Liomopteridae |
| G–H | Blattida | 1 | |
| H | Homoptera | 1 | Archescytinidae |
| H | Blattida | 5 | |
| H | Grylloblattida | 2 | |
| H–I | Blattida? | 1 | |
| I | Blattinopseida | 6 | *Glaphyrophlebia subcostalis* Mart. |
| I | Dictyoneurida | 1 | |
| I | Palaeomanteida | 1 | |
| I | Blattida | 16 | *Kunguroblattina elongata* Vishn., *K. minima* Vishn. |
| I | Grylloblattida | 13 | *Liomopterella* sp. |
| I | Mischopterida | 1 | *Vorkutia* sp. |
| Ia | Blattinopseida | 19 | *Glaphyrophlebia subcostalis* Mart. |
| Ia | Blattida | 12 | *Kunguroblattina* sp. |
| Ia | Grylloblattida | 22 | *Sojanidelia vorkutensis* Storozh., *Liomopterella* sp. |
| F–I | Blattida | 1 | |
| I–K | Blattida | 1 | |
| K | Homoptera | 1 | Prosbolopseidae Ivaiinae |
| K | Blattida | 6 | |
| K | Grylloblattida | 3 | *Sylvaprisca alba* sp. nov., *Liomopterum minor* sp. nov. |
| L | Diaphanopterida | 3 | |
| L | Dictyoneurida | 3 | *Vorkutoneura* sp. |
| L | Mischopterida | 1 | *Vorkutia tschernovi* Rohd. |
| L | Homoptera | 1 | Archescytinidae |
| L | Blattida | 1 | *Kunguroblattina latimarginata* Vishn. |
| L | Grylloblattida | 5 | Liomopteridae |
| E–L | Mischopterida | 1 | Vorkutiidae gen. sp. |
| E–L | Dictyoneurida | 3 | *Baeoneura* sp., *Vorkutoneura variabilis* Shar. et Sinitsh. |
| E–L | Homoptera | 1 | Archescytinidae |
| E–L | Panorpida | 1 | gen. sp. nov. aff. Lithopanorpa Carpenter |
| E–L | Blattida | 16 | |
| E–L | Grylloblattida | 15 | *Sylvaprisca alba* sp. nov., *Artinska vorkutensis* sp. nov. |
| E–L | Orthoptera | 1 | |
| M | Dictyoneurida | 1 | *Vorkutoneura variabilis* Shar. et Sinitsh. |
| M | Mischopterida | 1 | *Cyclocelis* sp. |
| M | Blattida | 7 | *Kunguroblattina minima* Vishn. |
| M | Grylloblattida | 9 | *Sylvaprisca alba* sp. nov., *Parakhosara incommoda* Storozh., *Khozaridelia martynovi* Storozh., *Liomopterum minor* sp. nov., Liomopteridae indet. |
| L–M | Grylloblattida | 1 | Lemmatophoridae gen. sp. |
| M–N | Blattida | 2 | |
| M–N | Perlida | 1 | *Uralonympha vorkutica* Sinitsh. |

**Table.** (Contd.)

| Member | Order | *n* | Including identified |
|---|---|---|---|
| N | Blattinopseida | 2 | *Glaphyrophlebia subcostalis* Mart. |
| N | Dictyoneurida | 5 | *Dunbaria borealis* Shar. et Sinitsh., *Dunbaria quinquefasciata* Mart., Homaloneura sp. |
| N | Homoptera | 1 | Scytinopteridae |
| N | Palaeomanteida | 1 | |
| N | Panorpida | 1 | |
| N | Blattida | 24 | *Syscioblatta vorkutensis* Vishn., *Phyloblatta* sp. |
| N | Grylloblattida | 20 | *Artinska* sp., *Khosaridelia rigida* sp. nov., *Liomopterum ?minor* sp. nov., *Liomopterella tota* sp. nov., *Liomopterella* sp., Megakhosaridae |
| N | Perlida | 1 | |
| N–O | Dictyoneurida | 1 | *Vorkutoneura variabilis* Shar. et Sinitsh. |
| N–O | Palaeomanteida | 1 | *Epimastax sojanensis* (Rasn.) |
| F–O | Dictyoneurida | 1 | |
| O | Dictyoneurida | 1 | *Vorkutoneura* sp. |
| O | Blattida | 6 | *Phyloblatta* sp. |
| O | Grylloblattida | 2 | Lemmatophoridae, *Liomopterella* sp. |
| M–O | Hypoperlida | 2 | *Tshekardobia* sp. |
| M–O | Dictyoneurida | 4 | *Vorkutoneura variabilis* Shar. et Sinitsh. |
| M–O | Homoptera | 1 | Archescytinidae |
| M–O | Blattida | 10 | |
| M–O | Grylloblattida | 7 | *Neprotembia complicata* sp. nov., *Liomopterum* sp. |
| M–O | Orthoptera | 2 | |
| P | Dictyoneurida | 1 | |
| P | Blattida | 3 | *Kunguroblattina* sp., *Phyloblatta* sp. |
| P | Grylloblattida | 8 | *Sojanidelia vorkutensis* Storozh., *Liomopterum* sp., *Liomopterella* sp. |
| P–R | Palaeomanteida | 1 | *Delopterum* sp. |
| P–R | Grylloblattida | 1 | *Sojanidelia vorkutensis* Storozh. |
| R | Dictyoneurida | 2 | |
| R | Blattida | 3 | |
| R | Grylloblattida | 4 | *Permopectina vorkutensis* sp. nov., *Vorkutopterum monstruosum* sp. nov., *Parapermula circummaculosa* sp. nov., *Kaltanympha vorkutensis* Aristov |
| S–T | Dictyoneurida | 1 | *Dunbaria* sp. |
| T | Blattida | 3 | *Phyloblatta* sp. |
| P–T | Dictyoneurida | 3 | *Homaloneura* sp. nov., *Dunbaria quinquefasciata* (Mart.) |
| P–T | Mischopterida | 1 | *Vorkutia* sp. |
| P–T | Blattida | 4 | *Kunguroblattina latimarginata* Vishn. |
| P–T | Grylloblattida | 7 | *Sojanidelia vorkutensis* Storozh., *Sojanidelia multimediana* Storozh., Liomopteridae |
| P–T | Forficulida | 1 | Protelytrina gen. sp. |
| M–T | Dictyoneurida | 2 | *Dunbaria quinquefasciata* (Mart.) |
| M–T | Palaeomanteida | 1 | *Epimastax sojanensis* (Rasn.) |
| M–T | Panorpida | 2 | *Agetopanorpa* sp., *Petromantis* sp. |
| M–T | Blattida | 1 | |
| M–T | Grylloblattida | 5 | Liomopteridae |

the Carboniferous rather than the beginning of the Permian (*Baeoneura, Cyclocelis*, and *Homaloneura*), strengthens this impression. However, there are some basic differences, including the occurrence of many taxa characteristic either of the Kungurian (or broader, of Lower Permian), or of the Upper Permian and, especially, of the Lower Kazanian. As already mentioned, there are even species (sometimes abundant) described from the Kungurian and Lower Kazanian. The older forms show no preference for the lower, or the younger ones for the upper part of the section (as shown above, the same is true of species widespread within the section). Therefore, assignment of the insects from the Vorkuta Group to the lowermost Permian is excluded.

It is also not yet possible to identify the age of insect-bearing deposits within the interval of the Kungurian through the Kazanian (and even the Lower Tatarian): from the entomological point of view, the Vorkuta Group may occupy any level in this interval. Independent of the dating chosen, one should assume that the assemblage was enriched with unusually long-lived insect species, recorded as such nowhere else, and with the higher taxa, which occur elsewhere only much earlier or (if the Kungurian level is selected) also much later.

In any case, the insects do not support the hypothesis of a considerable age difference between parts of the Vorkuta Group section. The distribution of transient species shows that assemblages of different parts of this section are much more similar to each other than to those of the Kungurian (Chekarda) and the Lower Kazanian (Soyana, Tikhie Gory). Indeed, the Inta assemblage shares four species with the Rudnik assemblage, two with the Ayach'yaga assemblage, one with the Lower Kazanian assemblage, and none of the species with the Kungurian assemblage. The Rudnik assemblage shares two species with the Ayach'yaga assemblage, one with the Lower Kazanian assemblage, and one with the Kungurian assemblage. Finally, the poorly studied Ayach'yaga assemblage shares one species with the Kungurian assemblage and none of the species with the Lower Kazanian assemblage. As mentioned above, there are no species common to the Vorkuta Group and the remaining Permian assemblages.

The overall composition of the assemblage differs between the formations, subformations, and sometimes even between members of the Vorkuta Group, but these differences do not significantly affect the evolutionary level of the assemblage. So, of 173 specimens collected in the Inta Formation, 63 belong to Grylloblattida (22 in Member Ia); 65 to Blattida (12 in Ia); 25 to Blattinopseida (19 in Ia), 7 to Dictyoneurida, 4 to Homoptera, 3 to Mischopterida, 3 to Diaphanopterida, 1 to Palaeomanteida, 1 to Panorpida, and 1 to Orthoptera. The dominants are Grylloblattida (38% specimens), Blattida (37%), and Blattinopseida (*G. subcostalis*, 14%). In Member Ia (53 specimens), the order of dominance is different: 41% belong to Grylloblattida, 36% to Blattinopseida, and 23% to Blattida.

The Rudnik Subformation of the Lek-Vorkuta Formation contains 115 specimens, of which 49 belong to Blattida; 39 to Grylloblattida; 12 to Dictyoneurida; two to Blattinopseida, Hypoperlida, Homoptera, Palaeomanteida, Perlida, and Orthoptera; and one to Mischopterida and Panorpida. The orders that dominate here differ only slightly from those in the Inta Formation: Blattida, 44%; Grylloblattida, 43%; and Dictyoneurida, 10%. Member M yielded only 18 insects and shows no significant differences from the Rudnik assemblage: Grylloblattida, about 50%; Blattida, 39%; and Dictyoneurida, 5%.

The Ayach'yaga Subformation is also insufficiently studied: only 43 identifiable insect specimens have been collected, including 20 Grylloblattida, 13 Blattida, 7 Dictyoneurida, 1 Mischopterida, 1 Palaeomanteida, and 1 Forficulida. The dominating orders are the same as in the Rudnik Subformation: Grylloblattida (46%), Blattida (30%), and Dictyoneurida (16%), but their relative abundances are somewhat different.

Therefore, the insect composition is not identical in all the formations and subformations. However, excluding marker Horizon Ia with aberrant composition, we find out that in the remaining part of the Inta Formation the relative abundances are as follows: Grylloblattida, 37%; Blattida, 43%; and Dictyoneurida 6%; i.e., virtually as in the Rudnik Subformation. The differences of the Ayach'yaga Subformation (about 10% more palaeodictyopterans and less cockroaches) are so slight that should not be interpreted without a deeper knowledge on changes in ecology and paleogeography. As for the insect composition of Horizon Ia (of 53 specimens, 22 Grylloblattida, 19 Blattinopseida and 12 Blattida), it is clearly unusual, first of all in the abundance of Blattinopseida. The only known analogy is the Niedermoschel locality (basal Permian in southeastern Germany; Hörnschemeyer, 1999), but even there Blattinopseidae constitute only 11% of the assemblage, Grylloblattida are absolute dominants (40%), and subdominants (15%) are miomopterans instead of cockroaches. Moreover, there are seven species of Blattinopseida instead of only one in the Vorkuta Group (Hörnschemeyer and Stapf, 2001). The reasons for the peculiarity of the assemblage in Horizon Ia (and in Niedermoschel) are uncertain, but in the case of Ia it is clearly not attributable to an age difference.

So, the relative abundances are quite similar in all the Vorkuta assemblages: Blattida and Grylloblattida each comprise about 30–45% of specimens, and Dictyoneurida a much lower percentage (6–16%). Nothing similar is found in other sufficiently rich Permian assemblages of comparable age. In Chekarda (Kungurian, Middle Urals), Kaltan (Kazanian, Kuznetsk Basin), and Soyana (Lower Kazanian, Arkhangelsk Region), Grylloblattida retain a similar level of dominance (40, 35, and 32%, respectively). However, they are followed closely by scorpionflies (15, 25, and 17%) and Homoptera (13, 25, and 21%, respectively), both of which are very rare in the Pechora Basin. Conversely, cockroaches and palaeodictyopterans constitute at most a few percent in Chekarda and Soyana, and are absent in Kaltan.

Interesting results are obtained from more detailed analysis of the dominant and better studied order Grylloblattida. Compared to Chekarda, Soyana, and Kaltan, the Vorkuta grylloblattid assemblage stands out for its low diversity. It cannot be explained by a real decrease in global faunal diversity, because in addition to those seven families which are found in the Vorkuta Group, six more should exist at that time, as they have been recorded from both older and younger deposits. The apparently diminished diversity of the Vorkuta assemblage may be associated with a small amount of material collected there (some 130 specimens compared to 1500 from Chekarda, 500 from Soyana, and 250 from Kaltan). Assemblages of similar volume (about 100 specimens) from Tikhie Gory (Lower Kazanian, Tatarstan), Kityak (Upper Kazanian, Kirov Region), and Kargala (Lower Tatarian, Orenburg Region) contain even fewer families: five, three, and four, respectively.

In family composition the Vorkuta assemblage is most similar to Chekarda and Soyana, being distinct from the former in the presence of Permotermopsidae and from the latter in the presence of Permopectinidae. Differences from Kaltan are more significant. In Kaltan there are no Lemmatophoridae characteristic of Vorkuta, whereas Euryptilonidae, Kortshakoliidae, and Archiprobnidae, unknown from Vorkuta, are present, and only three genera in common are recorded.

The Vorkuta Grylloblattida are dominated by Liomopteridae, constituting more than 70%, and subdominated by Lemmatophoridae and Ideliidae (about 10% each). Chekarda differs in the dominance of Tillyardembiidae (about 24%), Atactophlebiidae and Lemmatophoridae (15% and 14%, respectively), and infrequent Liomopteridae (some 10%). Soyana differs in the subequal share of Liomopteridae and Ideliidae (about 30% each, Lemmatophoridae about 10%). Kaltan is similar to the Vorkuta Group in the absolute dominance of Liomopteridae (about 80%) and abundance of Ideliidae (some 13%; next subdominant Megakhosaridae constitute 5%), but distinct in the absence of Lemmatophoridae, being one of the dominants in Vorkuta.

Therefore, the Vorkuta Grylloblattida are most similar to those of Chekarda in the family composition and taxonomic dominance of Liomopteridae and Lemmatophoridae. The generic composition of the Vorkuta assemblage (of 13 genera two are endemic, four transient, four Lower Permian, and only one Upper Permian) confirms this similarity. Kaltan appears the least similar, first of all in the family and generic composition.

Comparison of Grylloblattida from the Lek-Vorkuta and Inta formations shows a considerable diversity decrease in the latter. Despite nearly equal amounts of material, seven families and 12 genera are recorded in the Lek-Vorkuta Formation, and only two families and five genera in the Inta Formation. The reason is not an extinction of Grylloblattida at the boundary between the formations (all the Lek-Vorkuta families, except for Permopectinidae, survived into the Lower Kazanian, including those not recorded in the Inta Formation), but probably environmental change. At the Lek-Vorkuta/Inta transition, mostly rare and poorly known groups became extinct, so it is difficult to analyze the causes of these changes. One can only note that the fauna of the Lek-Vorkuta Formation is more similar to Chekarda, which was situated in the warm semiarid zone, nearer to the equator than Vorkuta. The Inta fauna is more similar to Kaltan, which was situated further north, in the temperate humid zone. So these differences are presumably of climatic nature, the more so that a small shift of the zonal climatic boundary, which ran near Vorkuta, is sufficient for climatic changes (Chumakov and Zharkov, 2002; Eskov, 2002).

It remains to discuss the ecology of insects from the Vorkuta Group. Generally insects of the mid-Permian (Kungurian–Kazanian) are quite diverse, but here their composition is markedly impoverished, at least at the ordinal level. On the mobilistic map for the mid-Permian (Eskov, 2002, text-fig. 498), the Pechora Basin occupies one of the northernmost positions among all more or less studied Permian entomofaunas (only Kaltan is further to the north). It is known that high-latitude insect assemblages were strongly impoverished in the Paleozoic (Chunya in the Upper Carboniferous of the Tunguska Basin; *History* …, 2002). Similarity to Chunya is stressed by the presence of the genus *Baeoneura*, formerly known only from there. Therefore, one cannot exclude that the Vorkuta entomofauna was impoverished due to climatic factors, but the degree of this impoverishment is incomparable to that in Chunya: there are very few cockroaches, and palaeodictyopterans, though abundant, are represented by few species. Kaltan, in those times still closer to the pole than Pechora, is even richer than the latter in the number of families, but may be just due to the fact that it is better studied. Indeed, in the unusual order of dominance (80% of Grylloblattida belong to a single family) the Kaltan assemblage apparently has no Permian analogues.

Another peculiarity of the Vorkuta assemblage is the rarity of aquatic insect remains. In the Permian they are generally not numerous compared to the Mesozoic and Cenozoic, in both coal-bearing (Vorkuta, Kuznetsk Basin) and coal-less environments (Chekarda, Soyana, Tikhie Gory). However, in the Vorkuta Group they are extremely few: only two stoneflies (Perlida) for more than 340 insect specimens: that is too few even for the Permian. Deposits of the Vorkuta Group are considered to be chiefly lagoon-marine, lagoon-lake, and lagoon-swamp (*The Coal-Bearing* …, 1990, p. 7), with the marine influence markedly decreasing from the Ayach'yaga Subformation to the Inta Formation (Makedonov, 1965; Pukhonto, 1998). On account of predominantly inorganic composition of the insect-bearing rock, these were lakes (or lagoons) but not swamps. However, strong influence of swamp and maybe sea water on the water bodies where the insects were buried is quite possible, and may explain the scarcity of aquatic insects.

So, the analysis of the Vorkuta entomofauna demonstrated that the insect assemblage is essentially indivisible at least in the interval of Members I–R, which is inconsistent with the hypothesis of considerable age differences between parts of the Vorkuta Group section. Characteristic of the Vorkuta assemblage are an impoverished character, supposedly due to its northern origin, mixed composition including Kungurian, Lower Kazanian and sometimes even Upper Carboniferous elements, and extreme paucity of aquatic insects.

## SYSTEMATIC PALEONTOLOGY

Order Grylloblattida

Suborder Lemmatophorina

**Family Lemmatophoridae Sellards, 1909**

**Subfamily Parapriscinae Carpenter, 1935**

**Genus *Sylvaprisca* Aristov, 2001**

***Sylvaprisca alba* Aristov, sp. nov.**

E t y m o l o g y. From the Latin *alba* (white).

H o l o t y p e. PIN, no. 1206/16, well preserved forewing (positive impression); Vorkuta locality, Khal'mer-Yu, Vodorazdel'nyi Creek, Outcrop 10, 5-427/54; Inta Formation.

D e s c r i p t i o n (Fig. 1a). Medium-sized insect. The anterior margin of the forewing is nearly straight, its apex is slightly acuminate, and the posterior margin convex. The costal area is somewhat broader than the subcostal one; SC bears straight anterior branches and terminates about the wing midlength. R bears two anterior branches, basal one being long with five endings, distal one simple. The medial vein is basally fused with CuA, MA bearing three to five branches, MP simple or two-branched. $CuA_1$ bears two endings; $CuA_2$ in apical part runs parallel to the posterior wing margin. Crossveins are simple or form a double cell row in the medial area.

M e a s u r e m e n t s (mm): forewing length, 16.

C o m p a r i s o n. This species differs from the most similar species, *S. gravis* from the Kungurian Chekarda locality, Middle Urals (Aristov, 2001), in the shorter SC, longer anterior branches of R, and the presence of the anastomosis M + CuA.

M a t e r i a l. Besides the holotype, paratypes PIN, nos. 1206/5 (borehole K-438, depth 52.2 m; Rudnik Subformation, Member M) and 1631/370 (Vorkuta coalfield, borehole K-1011, depth 340.5 m; Inta Formation, Member K).

**Subfamily Lemmatophorinae Sellards, 1909**

**Genus *Artinska* Sellards, 1909**

***Artinska vorkutensis* Aristov, sp. nov.**

E t y m o l o g y. From the Vorkuta locality.

H o l o t y p e. PIN, no. 1631/249, well preserved forewing fragment (positive impression); Upper Syr'yaga coalfield, borehole VSK-352, depth 123.4 m; Inta Formation.

D e s c r i p t i o n (Fig. 1b). Small insect. The anterior margin of the forewing is nearly straight. SC is extended beyond wing midlength. R distal to the origin of RS is S-shaped; the interradial area is narrow; RS originates in the basal wing third, straight and unbranched. MA is simple, MP and $CuA_1$ are two-branched, $CuA_2$ is simple. Crossveins are simple.

M e a s u r e m e n t s (mm): forewing length about 8.

C o m p a r i s o n. The new species is most similar to *A. larisae* from the Chekarda locality (Novokshonov, 1999), being distinct in the narrow interradial area and straight simple RS.

R e m a r k s. A forewing fragment collected in Member N and belonging to the genus *Artinska* (Fig. 1c) differs from the holotype of *A. vorkutensis* sp. nov. in the broader interradial area; however, in the absence of the distal wing half, it is impossible to decide if this fossil represents a new species or just an aberrant specimen of *A. vorkutensis* sp. nov.

M a t e r i a l. Holotype.

Suborder Protoperlina

**Family Aliculidae Storozhenko, 1997**

**Genus *Neprotembia* Aristov, 2004**

***Neprotembia complicata* Aristov, sp. nov.**

E t y m o l o g y. From the Latin *complicata* (folded).

H o l o t y p e. PIN, no. 1631/314, well preserved, folded forewing (positive impression); Khal'mer-Yu coalfield, borehole KhK-371, depth 88 m; Lek-Vorkuta Formation, Rudnik Subformation.

D e s c r i p t i o n (Figs. 1d, 1e). Small insect. The basal part of the forewing is narrow, its anterior margin is weakly convex; the costal area in the basal wing half is much wider than, and in the distal half as wide as, the subcostal one. SC almost reaches the wing tip; anterior branches of SC form a double cell row. RS is two-branched, originates in the basal wing third. The medial vein is for some distance fused with CuA; MA and possibly MP are simple. CuA bifurcates about its midlength, $CuA_1$ bears a long distal branch. CuP is straight, $A_1$ and $A_2$ are simple and slightly curved. Crossveins are simple or form a double cell row.

M e a s u r e m e n t s (mm): forewing length, 13.

C o m p a r i s o n. This species differs from the type species *N. truncata* from the Chekarda locality (Aristov, 2004a) in the narrower basal wing part, less convex anterior wing margin, and narrow costal area in the distal wing half.

M a t e r i a l. Holotype.

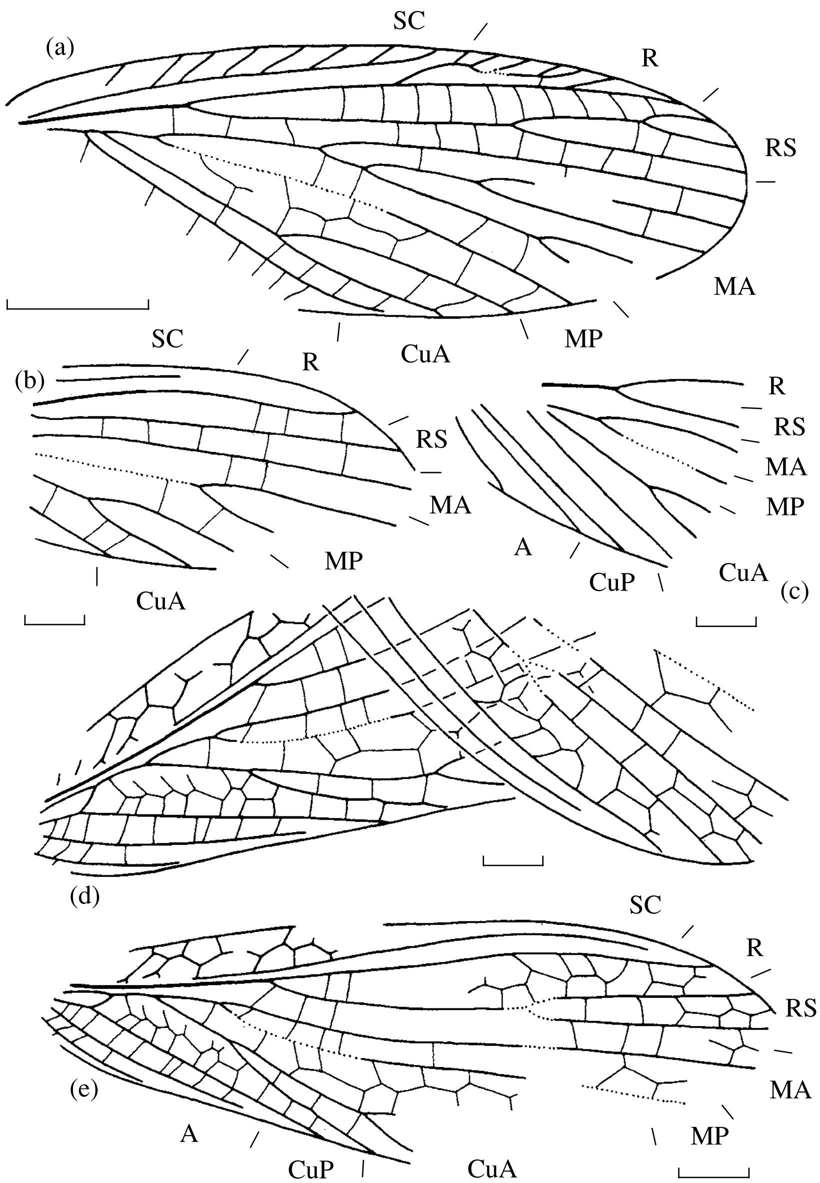


**Fig. 1.** Members of the order Grylloblattida: (a) *Sylvaprisca alba* sp. nov., holotype PIN, no. 1206/16; (b) *Artinska vorkutensis* sp. nov., holotype PIN, no. 1631/249; (c) *Artinska* sp., specimen PIN, no. 1631/219; (d, e) *Neprotembia complicata* sp. nov., holotype PIN, no. 1631/314, (d) as preserved and (e) reconstruction. Scale bar in all figures 2 mm.

Suborder Grylloblattina

**Family Permopectinidae fam. nov.**

Type genus. *Permopectina* gen. nov.

Diagnosis. Small insect. In the forewings costal area moderately wide, near wing base wider than, and at wing midlength as wide as, subcostal one. RS and MA with few branches, MP pectinately multibranched. CuA extended into distal wing third, pectinate, its branches bent at junctions with crossveins and ending blindly between them. Intercubital area wide, filled with network of crossveins; anal area very small, anal veins as thin as crossveins.

Composition. Type genus.

Remarks. The new family is assigned to the suborder Grylloblattina on account of similarity to the family Idelinellidae Storozhenko, 1997. Characteristic of the smaller representatives of the latter family (Novokshonov, 1999; Aristov, 2004a) are the wide intercubital area filled with the network of crossveins and reduced anal area, unknown in the other families. However, the moderately wide costal area, multibranched pectinate MP combined to few branches on both MA and RS, and pectinate CuA with blind branches allow us to consider Permopectinidae as a new family.

**Genus *Permopectina* Aristov, gen. nov.**

Etymology. From the Permian and the Latin *pecten* (comb). Gender feminine.

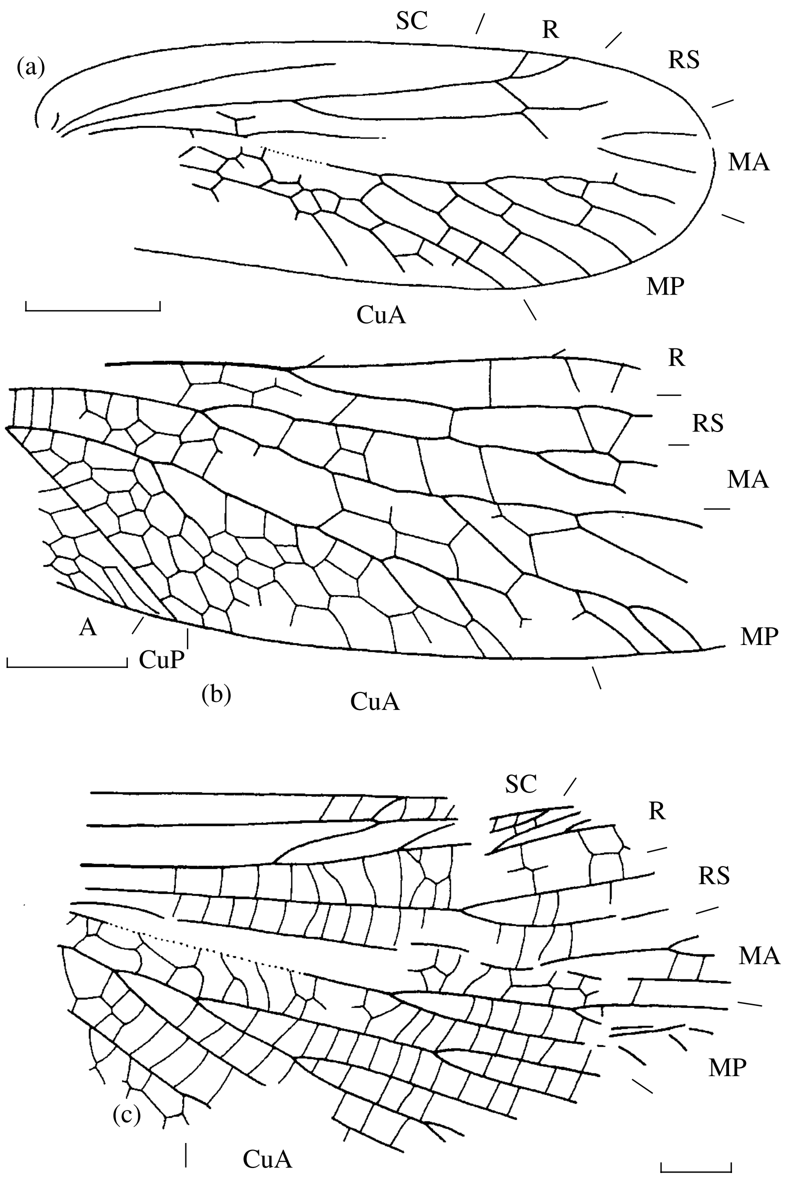


**Fig. 2.** Members of the suborder Grylloblattina: (a) *Permopectina tshekardensis* gen. et sp. nov., holotype PIN, no. 1700/4930; (b) *Permopectina vorkutensis* gen. et sp. nov., holotype PIN, no. 1206/34; and (c) *Khosaridelia rigida* sp. nov., holotype PIN, no. 1631/407.

T y p e s p e c i e s. *P. tshekardensis* sp. nov.

D i a g n o s i s. Anterior margin of forewing straight, apex rounded, posterior margin straight. RS simple, originating before wing midlength; MA with two or three branches; CuA and CuP straight. Crossveins form network of small cells in basal wing half, a double cell row about midwing, simple in distal part.

C o m p o s i t i o n. Besides the type species, *P. vorkutensis* sp. nov. from the Vorkuta locality.

##### *Permopectina tshekardensis* Aristov, sp. nov.

E t y m o l o g y. From the Chekarda locality.

H o l o t y p e. PIN, no. 1700/4930, well preserved forewing (part and counterpart); Perm Region, left bank of the Sylva River near the mouth of the Chekarda River, Chekarda locality; Kungurian, Koshelevka Formation.

D e s c r i p t i o n (Fig. 2a). R joins the anterior wing margin. MP is desclerotized near midlength, with five branches. CuA bears four branches.

M e a s u r e m e n t s (mm): forewing length, 9.

M a t e r i a l. Holotype.

##### *Permopectina vorkutensis* Aristov, sp. nov.

E t y m o l o g y. From the Vorkuta locality.

H o l o t y p e. PIN, no. 1206/34, moderately preserved forewing fragment; Vorkuta locality, Outcrop 49, Bed 13b; Lek-Vorkuta Formation, Ayach'yaga Subformation, Member R.

Description (Fig. 2b). R is directed to the wing apex. MP shows no desclerotization, with three branches, CuA bears five branches.

Measurements (mm): forewing length about 8.

Comparison. This species differs from the type species in R directed apically and in the smaller number of branches on MP.

Material. Holotype.

### Family Permotermopsidae Martynov, 1937

### Genus *Khosaridelia* Storozhenko, 1992

#### *Khosaridelia rigida* Aristov, sp. nov.

Etymology. From the Latin *rigida* (stiff).

Holotype. PIN, no. 1631/407, moderately preserved forewing (part and counterpart); Upper Syr'yaga coalfield, borehole VSK-608, depth 1446.7 m; Rudnik Subformation, Member N.

Description (Fig. 2c). Medium-sized insect. The anterior margin of the forewing is straight; the costal area about wing midlength is narrower that the subcostal one. SC bears short anterior branches, terminates in the distal wing third; the subcostal area is crossed with long crossveins. RS originates in the basal wing third, bifurcates in the distal wing third, with no less than two branches. MA and MP bear three or four branches each, CuA bears seven branches. Crossveins are simple or form a double cell row.

Measurements (mm): forewing length, about 30.

Comparison. This species differs from the type species *Kh. martynovi* from the Rudnik Subformation (Member M) of the Vorkuta Group, Pechora Basin (Storozhenko, 1998), in the narrow costal area and in the earlier origin and later bifurcation of RS.

Material. Holotype.

### Family Liomopteridae Sellards, 1909

### Genus *Vorkutopterum* Aristov, gen. nov.

Etymology. From the Vorkuta locality and the genus *Liomopterum.* Gender neutral.

Type species. *V. monstruosum* sp. nov.

Diagnosis. Medium-sized insect. Costal area twice as wide as subcostal one; basal branch of MA not reaching wing margin, ending among crossveins. MP fused with CuA, bearing eight branches altogether; the basal branch of CuA fused with CuP.

Composition. Type species.

Comparison. This species differs from all genera of the family in the anastomosis MP + CuA.

#### *Vorkutopterum monstruosum* Aristov, sp. nov.

Etymology. Latin *monstruosum* (abnormal).

Holotype. PIN, no. 1631/239, well preserved forewing fragment; Yun'yaga coalfield, borehole YuK-1, depth 247.6 m; Lek-Vorkuta Formation, Ayach'yaga Subformation, Member R.

Description (Fig. 3b). The anterior branches of SC are simple and dichotomous, connected with crossveins. MA bears more than three branches; two branches of CuA + MP form an anastomosis. CuP is S-shaped; anal veins are straight.

Measurements (mm): forewing length, about 25.

Material. Holotype.

### Genus *Parapermula* Sharov, 1961

#### *Parapermula circummaculosa* Aristov, sp. nov.

Etymology. From the Latin *circummaculosa* (circled with spots).

Holotype. PIN, no. 1631/414, well preserved forewing fragment; Khal'mer-Yu coalfield, borehole KhK-997, depth 717.7 m; Lek-Vorkuta Formation, Ayach'yaga Subformation, Member R (upper part).

Description (Fig. 3a). Medium-sized insect. The anterior margin of the forewing is convex; the apex is acuminate. The costal area is twice as wide as the subcostal one, crossed with simple anterior branches of SC, the latter are connected by crossveins. R bears five simple anterior branches; RS originates beyond the wing midlength, pectinate, with four branches. MA bears five endings, its distal branch running close to RS; MP is simple; CuA bears four or five branches. Crossveins are simple. The color pattern consists of small rounded spots and dark streaks along the anterior and apical margins and along the distal branch of CuA.

Measurements (mm): forewing length, about 35.

Comparison. The new species is most similar to *P. sibirica* from the Kaltan locality, Kuznetsk Basin (Upper Permian, Kuznetsk Formation) (Sharov, 1961), differing from it in the larger size, late origin of RS, simple MP, and in the absence of the double cell row formed by crossveins.

Material. Holotype.

### Genus *Liomopterella* Sharov, 1961

#### *Liomopterella parakitiakensis* Aristov, sp. nov.

Etymology. From the Greek *para* (near) and the species *L. kitiakensis.*

Holotype. PIN, no. 1631/408, well preserved forewing fragment; Upper Syr'yaga coalfield, borehole VSK-607, depth 1015.5 m; stratigraphical assignment uncertain.

Description (Fig. 3c). Medium-sized insect. The costal area near the base is somewhat wider, in the basal third twice as wide as the subcostal one, and crossed by simple and bifurcating anterior branches of SC. RS originates in the basal wing third; MP bifurcates about wing midlength. The first bifurcation of $CuA_1$ is not far from its base; $CuA_2$ is extended almost

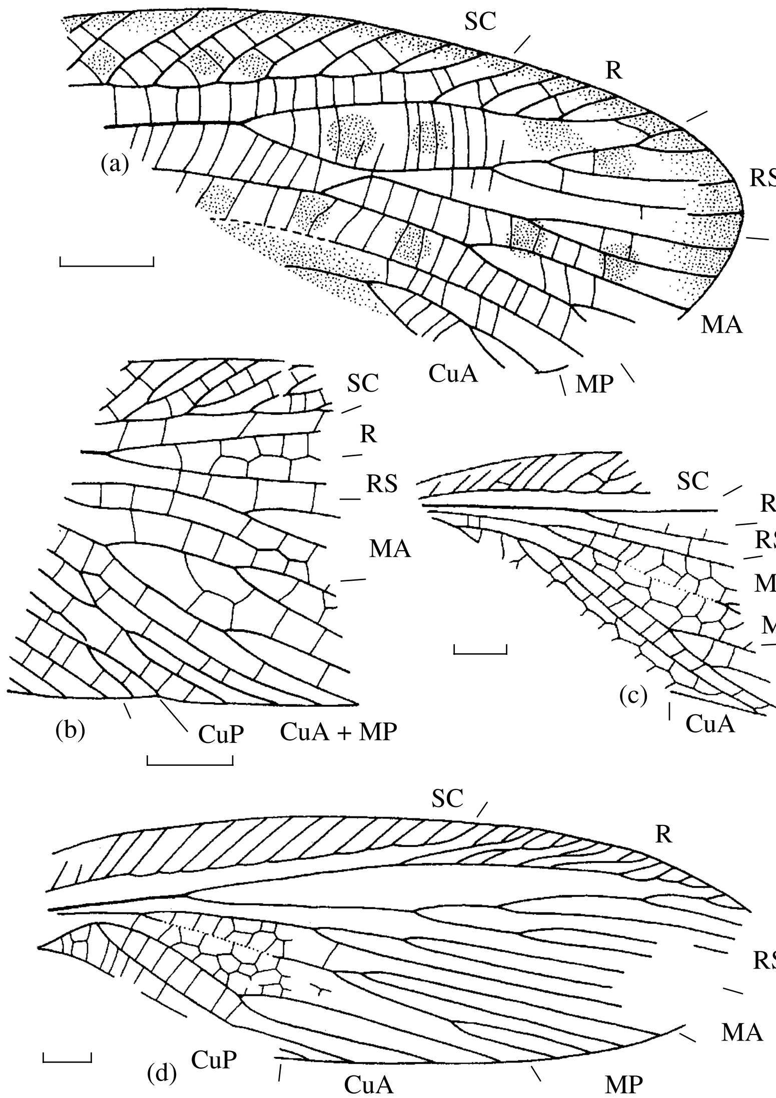


**Fig. 3.** Members of the family Liomopteridae: (a) *Parapermula circummaculosa* sp. nov., holotype PIN, no. 1631/414; (b) *Vorkutopterum monstruosum* gen. et sp. nov., holotype PIN, no. 1631/239; (c) *Liomopterella parakitiakensis* sp. nov., holotype PIN, no. 1631/408; and (d) *Liomopterella tota* sp. nov., holotype PIN, no. 1631/429.

to the posterior wing margin, bent at junctions to crossveins. Crossveins are simple or form a double cell row.

M e a s u r e m e n t s (mm): forewing length, about 20.

C o m p a r i s o n. The new species is most similar to *L. kitiakensis* from the Kityak locality, Kirov Region (Upper Kazanian, Upper Permian) (Aristov, 2004b), differing from it in the narrow costal area (about as wide as the subcostal area near the wing base) and $CuA_2$ bent at crossvein junctions.

M a t e r i a l. Holotype.

#### *Liomopterella tota* Aristov, sp. nov.

E t y m o l o g y. From the Latin *tota* (complete).

H o l o t y p e. PIN, no. 1631/429, forewing (part and counterpart); Khal'mer-Yu coalfield, borehole KhK-972, depth 346.5 m; Lek-Vorkuta Formation, Rudnik Subformation, Member N.

D e s c r i p t i o n (Fig. 3d). Medium-sized insect. The anterior and posterior wing margins are weakly convex, the apex is acuminate. The costal area is twice as wide as the subcostal one, crossed with simple, straight anterior branches of SC, the latter ending at two-thirds of the wing length. R bears long, simple or bifurcating anterior branches; RS originates in the basal wing quarter, bears six branches. MA is three-branched, MP bears four endings. The medial area with a triple cell row. $CuA_1$ and $CuA_2$ are two-branched; CuP is curved basally. Crossveins are simple or forming a double to triple cell row.

M e a s u r e m e n t s (mm): forewing length, 32.

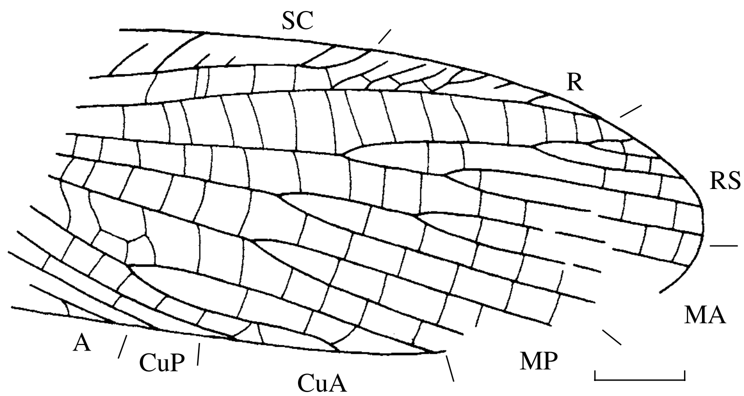


**Fig. 4.** Forewing of *Liomopterum minor* sp. nov. (Liomopteridae), holotype PIN, no. 1631/409.

C o m p a r i s o n. The new species is most similar to *L. bella* from the Kaltan locality (Sharov, 1961), differing from it in the greater number of medial branches, two-branched $CuA_1$, and the triple cell row in the medial area.

M a t e r i a l. Holotype.

### Genus *Liomopterum* Sellards, 1909

#### *Liomopterum minor* Aristov, sp. nov.

E t y m o l o g y. From the Latin *minor* (lesser).

H o l o t y p e. PIN, no. 1631/409, well preserved forewing; Khal'mer-Yu coalfield, borehole KhK-993, depth 328 m; Inta Formation, Member K.

D e s c r i p t i o n (Fig. 4). Medium-sized insect. The anterior and posterior wing margins are convex, the apex is acuminate. The costal area in the basal wing third is twice as wide as the subcostal one; anterior branches of SC are simple; anterior branches of R are simple or bifurcating. RS bears five branches, originates in the basal wing third; MA is three-branched; MP and CuA bear two endings each; the basal branch of $CuA_1$ is S-shaped. CuP and anal veins are straight. Crossveins are simple or form a double cell row.

M e a s u r e m e n t s (mm): forewing length, about 18.

C o m p a r i s o n. The new species is most similar to *L. ornatum* Carpenter, 1950 from the Elmo locality (Storozhenko, 1998), differing from it in the earlier origin of RS and S-shaped basal branch of $CuA_1$.

M a t e r i a l. Besides the holotype, paratype PIN, no. 1631/248 (borehole VSK-14, depth 128.3 m, Rudnik Subformation, Member M), and also tentatively assigned to the species and not included in the type series specimens 1631/420 (borehole K-1297, depth 884.4–884.8 m, Rudnik Subformation, Member N) and 1631/425 (borehole VSK-195, depth 129.0–129.2 m, stratigraphical assignment uncertain).

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## REFERENCES

1. D. S. Aristov, "A New Representative of the Lemmatophoridae (Insecta, Grylloblattida) from the Lower Permian of Urals (Russia)," N. Jb. Geol. Paläontol. Mh. **5**, 257–264 (2001).
2. D. S. Aristov, "The Fauna of Grylloblattid Insects (Grylloblattida) of the Lower Permian Locality of Tshekarda," Paleontol. Zh. (2004a) [Paleontol. J. **38** (Suppl. 2), S80–S145 (2004a)].
3. D. S. Aristov, "Grylloblattids of the Family Liomopteridae (Insecta: Grylloblattida) of the Upper Half of the Upper Permian," Paleontol. Zh. (2004b) [Paleontol. J. **38** (Suppl. 2), S150–S157 (2004b)].
4. *Biotas of Eastern European Russia at the Early–Late Permian Boundary* (GEOS, Moscow, 1998) [in Russian].
5. F. M. Carpenter, *Treatise on Invertebrate Paleontology: Part R (Arthropoda 4): Superclass Hexapoda* (Kansas Univ., Lawrence, 1992).
6. N. M. Chumakov and M. A. Zharkov, "Climate during the Permian–Triassic Biosphere Reorganizations: Article 2. Climate of the Late Permian and Early Triassic: General Inferences," Stratigr. Geol. Korrelyatsiya **10** (6), 62–81 (2002) [Stratigr. Geol. Correlation **10** (6), 361–375 (2002)].
7. K.Yu. Eskov, "Geographic History of Insects," in *History of Insects* (Kluwer Acad. Publ., Dordrecht, 2002), pp. 427–435.
8. *Geology of Coal and Oil Shale Deposits of the USSR*, Vol. 3: *The Pechora Coal Basin and Other Coal Deposits of the Komi ASSR and Nenets Autonomous Area* (Nedra, Moscow, 1965) [in Russian].

9. *History of Insects*, Ed. by A. P. Rasnitsyn and D. L. J. Quicke (Kluwer Acad. Publ., Dodrecht, 2002).
10. T. Hörnschemeier, "Fossil Insects from the Lower Permian of Niedermoschel (Germany)," *Proceedings of the First Palaeoentomological Conference, Moscow, 1998* (AMBA Projects Int., Bratislava, 1999), pp. 57–59.
11. T. Hörnschemeier and H. Stapf, "Review of Blattinopsidae (Protorthoptera) with Description of New Species from the Lower Permian of Niedermoschel (Germany)," N. Jb. Geol. Paläontol. Abhandl. **221**, 81–109 (2001).
12. G. V. Kotlyar, O. L. Kossovaya, S. B. Shishlov, *et al.*, "Boundary between Permian Series in Diverse Sedimentary Facies of North European Russia: Constraints of Event Stratigraphy," Stratigr. Geol. Korreltsiya **12** (5), 29–54 (2004) [Stratigr. Geol. Correlation **12** (5), 460–484 (2004)].
13. A. V. Makedonov, "Lithology and Facies of Permian Coal-Bearing Deposits," in *Geology of Coal and Oil Shale Deposits of the USSR*, Vol. 3: *The Pechora Coal Basin and Other Coal Deposits of the Komi ASSR and Nenets Autonomous Area* (Nedra, Moscow, 1965), pp. 83–96 [in Russian].
14. A. V. Martynov, "Permian Fossil Insects of North-East Europe," Tr. Geol. Muz. Akad. Nauk SSSR **4**, 1–118 (1928).
15. A. V. Martynov, "Permian Fossil Insects of Chekarda," Tr. Paleontol. Inst. **11** (1), 5–62 (1940).
16. V. G. Novokshonov, *The Early Evolution of Scorpionflies* (Nauka, Moscow, 1997) [in Russian].
17. V. G. Novokshonov, "New Insects (Insecta: Hypoperlida, Mischopterida, Jurinida) from the Lower Permian of the Middle Urals," Paleontol. Zh., No. 1, 50–57 (1998) [Paleontol. J. **32** (1), 46–53 (1998)].
18. V. G. Novokshonov, "Eine neue Notoptere aus dem unteren Perm des Urals (Insecta, Grylloblattida, Lematophoridae)," N. Jb. Geol. Paläontol. Mh. **11**, 641–646 (1999a).
19. V. G. Novokshonov, "A New Genus of the Family Kortshakoliidae (Insecta: Grylloblattida) from Lower Permian of the Urals," in *Proceedings of the Regional Scientific Conference on Geology of the Western Urals at the Threshold of the 21st Century* (Permsk. Gos. Univ., Perm, 1999b), pp. 166–168 [in Russian].
20. V. V. Pogorevich and A. V. Makedonov, "Permian System," in *Geology of Coal and Oil Shale Deposits of the USSR*, Vol. 3: *The Pechora Coal Basin and Other Coal Deposits of the Komi ASSR and Nenets Autonomous Area* (Nedra, Moscow, 1965), pp. 27–70 [in Russian].
21. S. K. Pukhonto, *Stratigraphy and Floristic Characterization of the Permian Coal Deposits of the Pechora Basin* (Nauchnyi Mir, Moscow, 1998) [in Russian].
22. A. P. Rasnitsyn, "New Paleozoic and Mesozoic Insects," Paleontol. Zh., No. 1, 64–77 (1977).
23. A. P. Rasnitsyn, "The Rate of Evolution and Evolutionary Theory (Hypothesis of Adaptive Compromise)," in *Evolution and Crises of Biocenoses* (Nauka, Moscow, 1987), pp. 46–64 [in Russian].
24. A. P. Rasnitsyn, "The Process of Evolution and Methodology of Systematics," Tr. Russk. Entomol. O–va **73**, 1–107 (2002).
25. A. P. Rasnitsyn, D. S. Aristov, A. V. Gorochov, *et al.*, "Important New Insect Fossils from Carrizo Arroyo and the Permo-Carboniferous Faunal Boundary," New Mexico Museum Nat. History Bull. **25**, 215–246 (2004).
26. A. G. Sharov, "The Order Protoblattodea, Paraplecoptera," in *Paleozoic Insects of the Kuznetsk Basin* (Akad. Nauk SSSR, Moscow, 1961), pp. 157–234 [in Russian].
27. A. G. Sharov and N. D. Sinitchenkova, "New Palaeodictyoptera from the USSR," Paleontol. Zh., No. 1, 48–63 (1977).
28. S. Yu. Storozhenko, "Systematics, Phylogeny, and Evolution of Grylloblattid Insects (Insecta: Grylloblattida)," (Dal'nauka, Vladivostok, 1998) [in Russian].
29. *The Coal-Bearing Formation of the Pechora Basin* (Nauka, Leningrad, 1990) [in Russian].
30. V. N. Vishnyakova, "New Species of the Genus *Kunguroblattina* from the Lower Permian of the Urals Region," Paleontol. Zh., No. 4, 50–59 (1965).