Paleontological Journal, Vol. 38, Suppl. 2, 2004, pp. S80–S145.

Dedicated to the honored memory of V.G. Novokshonov

The Fauna of Grylloblattid Insects (Grylloblattida) of the Lower Permian Locality of Tshekarda

D. S. Aristov

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: danil_aristov@mail.ru

Received July 25, 2003

Abstract—Twenty new genera and 50 new species classified in the families Pinideliidae, Euryptilonidae, Lemmatophoridae, Tillyardembiidae, Tshekardominidae, Sylvaphlebiidae, Euremiscidae, Probnidae, Sheimiidae, Visheriferidae, Aliculidae, Ideliidae, Idelinellidae, Megakhosaridae, and Liomopteridae are described from the localities of Tshekarda, Barda, and Kishert'. The family Pinideliidae is transferred to the suborder Lemmatophorina, the families Sylvaphlebiidae and Euremiscidae are transferred to the suborder Protoperlina, and the family Phenopteridae is synonymized under Sylvaphlebiidae. The genera *Sylvaella* Martynov, 1940, *Parasylviodes* Martynov, 1940, and *Khosarophlebia* Martynov, 1940 are transferred to the family Liomopteridae. The genera *Sylviodes* Martynov, 1940, *Permostriga* Novokshonov, 1999, *Bardapteron* G. Zalessky, 1944, *Paratillyardembia* Aristov, 2000, and *Neraphidia* Novokshonov et Novokshonova, 1997 are transferred to the families Ideliidae, Idelinellidae, Atactophlebiidae, Sylvardembiidae, and Aliculidae, respectively. The genera *Gurianovella* G. Zalessky, 1939 and *Sylvanympha* Novokshonov et Pan'kov, 1999 are transferred to Grylloblattida incertae sedis. The genus *Kirkorella* G. Zalessky, 1939 is reinstated from junior synonyms of the genus *Gurianovella*. Representatives of the families Pinideliidae, Probnidae, Sheimiidae, Visheriferidae, Aliculidae, and Idelinellidae are described from Tshekarda for the first time. An annotated list of grylloblattids from Tshekarda is provided. Other Permian localities of grylloblattids are characterized. The similarity of Tshekarda to the largest Permian localities, first of all Obora (Czech Republic), Elmo (United States), and Soyana (Arkhangel'sk region, Russia), is analyzed. The morphological characterization of grylloblattids is improved on the basis of new material.

Key words: Grylloblattida, Permian, Kungurian, Tshekarda, Urals, new taxa, new synonymy, local faunas, nymphs.

INTRODUCTION

The era of the flourishing of the order Grylloblattida coincides with the Permian Period and, especially, with the end of the Early Permian and the beginning of the Late Permian. Grylloblattids were extremely diverse at that time (among the 44 families of the order, 35 are either Permian or occur in the Permian) and are common among insects in fossil assemblages. Among all Permian insect localities, Tshekarda possesses the largest taxonomic diversity (representatives of 24 insect orders having been described) and the largest number of insect specimens (nearly 8000) in the accumulated collections. There are two reasons why grylloblattids of this locality are interesting.

The first is their exceptional diversity: the number of taxa described from Tshekarda (19 families, 61 genera, and 90 species) is larger than that from any other Permian locality (the second largest locality, Soyana, has yielded 14 families, no more than 25 genera, and no more than 40 species); thus, they constitute a large proportion of all Permian taxa, at least at the familial level. The second reason is the size of the collection and their state of preservation: Insects are usually preserved as wings or their fragments, whereas material from Tshekarda is commonly represented by complete insects with folded or expanded wings. Given the large size of the collection, this allows for accurate morphological reconstruction of fossils. Both reasons combined provide an important basis for understanding the morphology and phylogeny of the entire order.

Most of this work is devoted to describing new taxa. Known species are redescribed only if their systematic position changes. In total, 20 new genera and 50 new species are described. The family Pinideliidae is transferred to the suborder Lemmatophorina, the families Sylvaphlebiidae and Euremiscidae are transferred to the suborder Protoperlina, and Phenopteridae are synonymized under Sylvaphlebiidae. The genera *Sylvaella, Parasylviodes*, and *Khosarophlebia* are transferred to the family Liomopteridae. The genera *Sylviodes, Permostriga, Bardapteron, Paratillyardembia*, and *Neraphidia* are transferred to the families Ideliidae, Idelinellidae, Atactophlebiidae, Sylvardem-

biidae, and Aliculidae, respectively. The genera *Gurianovella* and *Sylvanympha* are placed in Grylloblattida incertae sedis, and the genus *Kirkorella* is reinstated within the family Atactophlebiidae. Representatives of the families Pinideliidae, Probnidae, Sheimiidae, Visheriferidae, Aliculidae, and Idelinellidae are described from Tshekarda for the first time. Because of this increase in the number of taxa in Tshekarda, Liomopteridae has become a taxonomically dominating family, and the number of families of the suborder Protoperlina exceeds that of the suborders Lemmatophorina and Grylloblattina combined.

MATERIAL

The present work is based on collections nos. 99, 118, 168, 212, 514, and 1700 (about 1250 specimens) stored at the Paleontological Institute of the Russian Academy of Sciences (PIN) and gathered in various years by E.V. Permyakova, Z.I. Dzyu, and expeditions headed by A.G. Sharov in 1959–1961; collections of the Vernadskii State Geological Museum (SGM) nos. VI-198 and KP-769 (about 50 specimens) gathered in various years by T.G. Mauer, E.V. Permyakova, M.D. Zalessky, and G.M. Zalessky; and collection PIN, no. 4987 (about 200 specimens) gathered by V.G. Novokshonov in 1989–2000.

PERMIAN GRYLLOBLATTID FAUNAS

The current review is based on the published literature (Storozhenko, 1998; Storozhenko, 2002, Hörnschemeyer, 1999; Aristov, 2000a, 2000b, 2002, 2003, 2004a, 2004b, 2004c; Rasnitsyn, Aristov, 2004; Aristov, in press) and unpublished data of the author.

The first members of the order Grylloblattida appeared in the Upper Carboniferous. They were represented by two scarce and rather conservative families, Protoperlidae and Daldubidae, from the Stephanian of France (Commentry) and from the upper part of the Kata Formation in eastern Siberia (Chunya), respectively. Grylloblattid fauna changed abruptly at the Carboniferous–Permian border, and neither of these two families continued into the Permian.

Asselian grylloblattid fauna had a typical Permian habitus. Both families and genera are typical of the Permian even in the fauna of the Carboniferous–Permian boundary beds in the locality of Carrizo Arroio (United States). This fauna is not rich and is represented by two families: Liomopteridae, which predominates in the majority of Permian localities, and, more rarely, Probnidae. An unusual fauna of another Asselian locality, Nierdermoschel, is represented by the single genus *Artinska* (Lemmatophoridae), to which nearly half of all insect impressions collected there belong. In general, Asselian grylloblattids are very similar to Artinskian forms; all the genera are known from Artinskian or even later beds.

Later, the order began to flourish. Diversity increased abruptly, and grylloblattids became one of the common insect orders. Liomopteridae are a dominant family in the Early Artinskian (Sakmarian, according to other data; see Shcherbakov, 2000) locality of Obora (Czech Republic). New families—widely distributed Euryptilonidae, Aliculidae, Sylvaphlebiidae and endemic Jablonidae, Havlatidae, and Scaliciidae—appeared (seven families altogether). A younger Artinskian locality, Elmo (United States), contains even more diverse fauna (nine families). In addition to Lemmatophoridae, Probnidae, Liomopteridae, Euryptilonidae, and Sylvaphlebiidae, which had appeared earlier, new families appeared in the record; these are the widely distributed Permembiidae and Protembiidae and endemic Chelopteridae and Demopteridae. The lemmatophorids dominated both taxonomically and in numbers, whereas the probnids dominated only in numbers. The Liomopteridae are important, but are not as diverse as the lemmatophorids. Another Artinskian locality, Vil'va (Perm region), contains a single representative of the Sylvaphlebiidae. Thus, members of 13 grylloblattid families are known from all Sakmarian?–Artinskian localities.

Liomopteridae and Aliculidae are known from the Lower Permian of Germany (Upper Rhine), Megakhosaridae are known from the Lower Permian of Texas, and Grylloblattidae incertae sedis have been recorded in the Lower Permian of China (Xiashihezi Formation, Meidigou of Hejin, Shanxi).

Diversity continues to increase during the Kungurian, in which the order's growth reaches its highest point. It should be taken into account that all the data on Kungurian grylloblattids come from a collection gathered at the largest Permian locality of Tshekarda in the Perm region. Tshekarda, as well as other geographically close localities of Sylva and Barda, are considered in detail below. Additionally, Kungurian grylloblattids are represented by occasional specimens of the families Pinideliidae and Kortshakoliidae from the localities of Prokop'evsk and Korchakol, both in the Kemerovo region. Grylloblattid diversity reached its maximum in the Kungurian; to date, members of 21 families are known from this stage.

Ufimian grylloblattid diversity is less than that of Kungurian and Lower Kazanian grylloblattids: only ten families have been recorded. This is most probably due to the poor state of knowledge of Ufimian localities rather than to an actual decrease in their abundance and diversity (12 families and 6 genera passed from the Kungurian to the Kazanian). Insect-bearing deposits of the Kuznetsk Subgroup of the Kuznetsk Coal Basin are usually classified in the Ufimian Stage (Betekhtina, *et al.*, 1988); according to other data, they are Kazanian (Shcherbakov, 2000). More than 600 grylloblattid impressions have been collected from the localities of Starokuznetsk, Kaltan (the majority of specimens), and Sorbala. These localities are dominated by Liomop-

teridae, Ideliidae and Megakhosaridae are considerably less abundant, and Archiprobnidae, Euryptilonidae, Kortshakoliidae, and Geinitziidae (this last first having appeared at that time) are rare.

The deposits of the Vorkuta Group in the Vorkuta Coal Basin, i.e., the Lek-Vorkuta and Inta formations, are also assignable to the Ufimian Stage. On the basis of macroflora, the lower part of the Lek-Vorkuta Formation is assignable to the Kungurian. On the basis of brachiopods, bivalves, and miospores, however, all parts of this formation, along with the overlying Inta Formation, have been assigned to the Ufimian (Kalashnikov *et al.*, 1990). Since the lower part of the Lek-Vorkuta Formation cannot be separated with confidence from other deposits of the Vorkuta Group on the basis of either grylloblattid fauna or other insects (Rasnitsyn and Sukacheva, pers. comm.), we are inclined to treat the entire locality of Vorkuta as Ufimian. Several tens of grylloblattid impressions are known from the Lek-Vorkuta Formation, and the fauna is typical of the Upper Permian: dominating Liomopteridae and occasional Ideliidae and Megakhosaridae. The scarce fauna of the Inta Formation is represented by dominating Liomopteridae; rare Megakhosaridae, Permotermopsidae, and Geinitziidae; and undescribed Lemmatophoridae. Occasional representatives of the families Ideliidae, Pinideliidae, and Visheriferidae and an undescribed representative of the Liomopteridae are known from several geographically close localities of the Solikamsk Horizon in the Perm region (Pokcha, Mogil'nikovo, Tyul'kino, and Shchugor).

Lower and Upper Kazanian faunas are essentially different and will be considered separately. In the Lower Kazanian, the diversity and abundance of grylloblattids were still high. The richest locality (with more than 500 specimens) is Soyana in the Arkhangel'sk region, which contributes a great deal to the Lower Kazanian grylloblattid fauna. In this locality, the dominating families are Liomopteridae and Ideliidae, and ideliids surpass liomopterids in number of taxa (taxonomic and quantitative dominance of ideliids are both unique to the Permian). The Megakhosaridae and Lemmatophoridae also hold an important place. Representatives of the families Atactophlebiidae, Permotermopsidae, Sojanoraphidiidae, Sylvaphlebiidae, Aliculidae, Sheimiidae, Sylvardembiidae, and Idelinellidae and undescribed members of the Euremiscidae and Tshekardominidae are scarce. Surprisingly, there are no endemics in Soyana, and, among the families named above, only Permotermopsidae are unknown in Tshekarda. The locality of Tikhie Gory in Tatarstan is poorer, with about 100 impressions having been collected. This locality is unusual in the absolute dominance of Atactophlebiidae, which constitute more than two-thirds of the impressions. The situation is otherwise quite typical: the Liomopteridae subdominate, the Ideliidae are rarer, and the Permotermopsidae and endemic Camptoneuridae are represented by isolated specimens. Owing to these two localities, there are 16 grylloblattid families recorded from the Lower Kazanian in total; one, Geinitziidae, is known from the Ufimian through the Jurassic, but has not been found in Lower Kazanian deposits. It is noteworthy that only one family, Camptoneuridae, appeared, whereas 11 families out of 16 (Atactophlebiidae, Lemmatophoridae, Euryptilonidae, Sojanoraphidiidae, Aliculidae, Sylvardembiidae, Euremiscidae, Camptoneuridae, Idelinellidae, Kortshakoliidae, and Permotermopsidae) died out by the beginning of the Upper Kazanian, i.e., this was one of the largest extinctions in the entire history of grylloblattids.

Upper Kazanian and Lower Tatarian faunas are similar to each other and are considered together. At that time, after an abrupt extinction in the middle Kazanian, the diversity remained low (representatives of six families having been found), but their abundance decreased insignificantly. In fact, the fauna consisted of three families, dominating Liomopteridae and scarce Ideliidae and Megakhosaridae. The Geinitziidae are probably added to the above families in the Upper Kazanian localities of the Kuznetsk Basin (Zelenyi Lug, Mitina, Suriekova 1, and Abasheva), where only about a dozen specimens have been collected, and in the richer eastern European locality of Kityak, with approximately 200 specimens having been collected. The family Chaulioditidae (= Tomiidae; Aristov, 2003) appears for the first time in a fairly rich (86 specimens) Lower Tatarian locality of Kargala in the Orenburg region, in addition to the dominating Liomopteridae and scarce Ideliidae and Megakhosaridae. The scanty fauna of the Early Tatarian (Kazanian, according to other data) locality of Bor-Tolgoy in Mongolia includes dominating Liomopteridae and scarce Tshekardominidae. In the localities of Galevo and Chepanikha in Udmurtiya, only rare liomopterids have been collected.

The situation changed markedly in the second half of the Tatarian. Diversity increased to ten families due to the appearance of new families as well as the reappearance of the families Sheimiidae and Geinitziidae, which appeared in the Lower Kazanian and Ufimian, respectively; however, abundance decreased appreciably. Liomopteridae continued to dominate, but families characteristic of the Triassic had already appeared.

Liomopteridae dominate in the largest (about 50 specimens) Upper Tatarian locality of Karaungir in eastern Kazakhstan, while Ideliidae, Megakhosaridae, and Blattogryllidae are scarce. Isolated Liomopteridae and Chaulioditidae are known from the locality of Aristovo in the Vologda region. The still undescribed fauna of the locality of Novo-Aleksandrovka in the Orenburg region includes dominating Liomopteridae and scarce Ideliidae, Geinitziidae, and Sheimiidae. Isolated Tunguskapteridae and an undescribed Mesorthopteridae member are recorded in the localities of Nizhnyaya Tunguska (Krasnoyarsk territory) and Isady (Vologda region), respectively. Several grylloblattids of uncertain position have been found in the Upper Tatarian localities of the Kuznetsk Basin, Salagaevo, and Sokolova 2.

Liomopteridae and Megakhosaridae are known from Upper Tatarian localities in Natal province, South Africa. A single representative of the Sylvaphlebiidae is known from the locality of Belmont in Australia.

In spite of dominating Liomopteridae and the presence of Sheimiidae and Sylvaphlebiidae, Upper Tatarian fauna is nearly Triassic in its nature, being more similar to Middle Triassic than to Permian faunas. An abrupt decrease in diversity occurred at the end of the Tatarian; thus, the grylloblattids are represented by few Chaulioditidae species and isolated Geinitziidae during the first half of the Triassic. Amazingly, the actual decrease in taxonomic diversity was not so sharp: six of the ten Upper Tatarian families survived into the Middle or Upper Triassic of Madygen in Kyrgyzstan.

After the reduction in numbers during the first half of the Triassic, the order showed its last increase in diversity and abundance in the middle of the Triassic. Later, the process of the extinction of the order began. Grylloblattids are very rare in the Jurassic, and the last winged forms became extinct by the middle of the Cretaceous. The only modern family of the order, Grylloblattidae, is uncommon and is represented by wingless cryptozoic forms.

GRYLLOBLATTID LOCALITIES OF THE KOSHELEVKA FORMATION, KUNGURIAN, LOWER PERMIAN

Locality of Tshekarda

The locality of Tshekarda was discovered in 1928 by a student of local lore, T.G. Mauer, who gathered a small collection of fossil insects from there. In the 1930s and 1940s, this locality was frequented by Permyakova, Dzyu, Zalessky, and Zalessky, who collected substantial material. The largest insect collection from Tshekarda was made by Sharov's expeditions in 1959–1961. Abundant material was collected by Novokshonov and his students in 1989–2000.

The first descriptions of grylloblattid insects from Tshekarda appeared in works by Zalessky (1937, 1939, 1951, 1952, 1955a, 1955b) and Martynov (1940). Their taxonomic treatment has now recommenced after a nearly 40-year break (Storozhenko, 1993). An immense contribution to the study of grylloblattids of Tshekarda was made by Novokshonov, who described many taxa from this locality (Vilesov and Novokshonov, 1993; Novokshonov, 1995, 1997, 1998a, 1998c, 1999a, 1999b, 2000; Novokshonov and Novokshonova, 1997; Novokshonov and Aristov, 1999, 2002; Storozhenko and Novokshonov, 1995, Novokshonov and Storozhenko, 1996; Novokshonov and Pan'kov, 1999).

The locality of Tshekarda is situated on the northeastern slope of the Krasnaya Gora mountain on the left bank of the Sylva River near the Tshekarda River mouth near the village of Tshekarda, Suksun district, Perm region.

The Tshekarda section is composed of fine clastic sediments of the Koshelevka Formation, Iren' Horizon, Kungurian, Lower Permian. Tshekarda belongs to the structure-facies zone of the Cis-Urals foredeep in its eastern coarse-grained variety and is represented by sediments of submontane marine molasse association. It was formed during the early stage of arid lithogenesis under coastal marine conditions and is represented by underwater and above-water alluvial cones of a mountain river in the Urals (Ponomareva, 1998).

The Tshekarda section consists of three outcrops. The first outcrop is situated 160 m upstream of the Tshekarda River mouth, and its length is 50 m; the second outcrop is situated immediately beyond the Tshekarda River mouth, and its length is 550 m; and the third outcrop is situated 850 m downstream of the Tshekarda River mouth, and its length is 120 m. The first two outcrops partially overlap each other, and the third overlies them. The majority of insects were collected from marl beds of the second outcrop and from the Sylva River bottom opposite the outcrop. From the first outcrop, several tens of grylloblattids have been collected, mainly by Mauer, Zalessky, and Zalessky. No grylloblattids have been recorded from the third outcrop. In general, the occurrence of grylloblattids varies at different outcrops. It constitutes 10–15, 25–30, and 30–35 impressions per square meter of the insect-bearing beds located in the first and second outcrops and on the Sylva River bottom, respectively. The third outcrop has been poorly explored (Sharov, 1999).

The contemporaneous locality of Yulaevo is situated on the left bank of the Sylva River 2 km downstream of the Tshekarda River mouth near the village of Yulaevo. This locality was discovered by T.G. Mauer in 1935; only one grylloblattid nymph has been recorded from there to date.

To the present, Tshekarda has yielded mainly numerous insect and plant impressions. In addition, only isolated impressions of fishes and arachnids (Sharov, 1999) and single impressions of Diplopoda and Symphyla have been recorded. Other animals have not been found.

The flora is extremely diverse and includes more than 200 species of higher plants. The Tshekarda flora has been described in detail by S.V. Naugolnykh (1998).

The insect fauna of Tshekarda is unique in both its diversity (representatives of 23 orders, more than 70 families, more than 150 genera, and 200 species having been described) and state of preservation (the majority of the impressions being of complete insects). To date, members of the orders Ephemerida, Odonata, Orthoptera, Grylloblattida, Perlida, Forficulida, Blattida, Caloneurida, Blattinopseida, Hypoperlida, Thripida, Dictyoneurida, Mischopterida, Diaphanopterida, Psocida, Hemiptera, Palaeomanteida, Coleoptera, Corydalida, Neuroptera, Jurinida, Panorpida, and Trichoptera have been recorded. Among these, the most

diverse orders are Grylloblattida (19 families, 60 genera, and 89 species), Hypoperlida (8 families, 12 genera, and 16 species), and Gryllida (5 families, 14 genera, and 17 species). The insect collection from Tshekarda consists of nearly 8000 specimens, about 20 percent of which belong to the grylloblattids, and next in abundance are the orders Panorpida, Palaeomanteida, and Hemiptera. Thus, the grylloblattids dominate the locality of Tshekarda both taxonomically and numerically.

To date, the grylloblattid collections from Tshekarda (PIN and SGM) comprise approximately 1500 specimens, 1300 of which have been identified down to the familial level. Below, we give their relative proportions in different families.

In terms of the number of impressions, the families Tillyardembiidae (Figs. 1, 18–21) (about 24%), Atactophlebiidae (Figs. 2b, 3) (about 15%), Lemmatophoridae (about 14%), Ideliidae (about 11%), and Liomopteridae (about 10%) dominate; Sylvaphlebiidae (about 5%), Euryptilonidae (about 3%), and Sheimiidae (about 1.5%) are less abundant. The families Sylvardembiidae, Sojanoraphidiidae, Sylvabestiidae, Euremiscidae, Probnidae, Visheriferidae, Permembiidae, Aliculidae, Megakhosaridae, Idelinellidae, and Kortshakoliidae constitute less than 2% each.

To date, representatives of 19 families, 61 genera, and 90 species, of which 21 genera and 51 species are described below, are known from Tshekarda. The suborder Lemmatophorina (Figs. 2–8) comprises 3 families, 9 genera, and 14 species, with 2 genera and 6 species being newly described. The suborder Protoperlina (Figs. 1, 9–24) includes 12 families, 24 genera, and 37 species, of which 8 genera and 21 species are described below. The suborder Grylloblattina (Figs. 25–34) incorporates members of 4 families, 21 genera, and 28 species, with 6 genera and 14 species being described below. Eleven species in seven genera, of which ten species in five genera are new, have been assigned to Grylloblattida incertae sedis (Figs. 2a, 35–38). The complete list of taxa is given below.

In terms of number of species, the family Liomopteridae, which constitutes about 20%, dominates; the family Lemmatophoridae (more than 10%) holds the second place. The relative proportions of the families Euryptilonidae, Tillyardembiidae, Sylvardembiidae, Sylvaphlebiidae, Aliculidae, Sheimiidae, Tshekardominidae, Ideliidae, and Megakhosaridae are 5–10%. Each of the families Atactophlebiidae, Sojanoraphidiidae, Sylvabestiidae, Euremiscidae, Probnidae, Visheriferidae, Permembiidae, and Idelinellidae constitutes less than 5%.

Order Grylloblattida Walker, 1914

Suborder Lemmatophorina Storozhenko, 1997

Family Atactophlebiidae Martynov, 1930

This is one of dominating families in Tshekarda; it is represented by one monotypic genus *Kirkorella*.

In 1939, on the basis of nymphs, Zalessky described three new monotypic genera with the type species *Gurianovella silphidoides* (Fig. 2a) and *Kirkorella mira* (Fig. 2b, Pl. 1, Fig. 1) from Tshekarda and *Peremella ambigua* from the Barda 3 locality (Zalessky, 1939). Nearly simultaneously, Martynov (1940) described another nymph, *Czekardia blattoides*, from Tshekarda. All these species, as well as *Mariella gracilis* G. Zalessky, 1955 (Zalessky, 1955a), were subsequently synonymized under *G. silphidoides* and transferred to grylloblattids of unclear systematic position (Sharov, 1962). Later, these nymphs were shown to belong to atactophlebiids on the basis of an examination of a large series of impressions (Storozhenko, 1998).

The reexamination of the type material has shown that the holotype of *G. silphidoides* (Fig. 2a) differs essentially from holotypes of other species. The anterior margin of the pronotum having a deep incision, robust fore femora, forwardly directed middle tibiae, and unarmed tibiae are the most distinctive features. This is enough to justify separating the nymphs under consideration into two groups, rare representatives of *G. silphidoides* (two impressions) and numerous (more than 200 specimens) representatives of *K. mira*, the synonyms of which are *P. ambigua, Cz. blattoides*, and *M. gracilis.* Since the commonly occurring nymphs have been recognized as atactophlebiids, the treatment of *Gurianovella* as a separate genus puts a question about its taxonomic placement. Despite a certain resemblance, there are no grounds for considering it a member of the atactophlebiids or any other grylloblattid family; therefore, *Gurianovella* has been transferred to Grylloblattida incertae sedis and redescribed.

Genus *Kirkorella* G. Zalessky, 1939

K. mira G. Zalessky, 1939

Family Euryptilonidae Martynov, 1940

This is an uncommon family. *E. blattoides* is a dominating species.

Genus *Euryptilon* Martynov, 1940

E. blattoides Martynov, 1940

E. cuculiophoris Aristov, 2002

Genus *Stereosylva* Aristov, 2002

S. singularis Aristov, 2002

Genus *Euryptilodes* Sharov, 1961

E. commatulus sp. nov.

Family Lemmatophoridae Sellards, 1909

This is one of the dominating families in Tshekarda.

Subfamily Parapriscinae Carpenter, 1935

This is a diverse but infrequent family. *M. vernacula* was originally placed in neither of the two subfamilies. Elongated wings and slender legs fit the diagnosis of Parapriscinae (Storozhenko, 1998), and *Megorkhosa* is treated here as a representative of this subfamily.

Genus *Sylvaprisca* Aristov, 2001

S. gravis Aristov, 2001
S. focaleata sp. nov.
S. forta sp. nov.

Genus *Culiciforma* gen. nov.

C. formosa sp. nov.

Genus *Paraprisca* Handlirsch, 1909

P. uralica G. Zalessky, 1939
P. fragilis Novokshonov, 2000

Genus *Megorkhosa* Novokshonov, 2000

M. vernacula Novokshonov, 2000

Subfamily Lemmatophorinae Sellards, 1909

This is an abundant subfamily, 90% of which is represented by *A. larisae.*

Genus *Artinska* Sellards, 1909

A. larisae Novokshonov, 1999
A. infigurabilis sp. nov.

Suborder Protoperlina Storozhenko, 1997

Family Tillyardembiidae G. Zalessky, 1938

This is the most abundant family in Tshekarda, almost entirely restricted to representatives of *T. antennaeplana. K. brevicervix* sp. nov. is much less numerous. Other species are rare.

Genus *Tillyardembia* G. Zalessky, 1938

T. antennaeplana G. Zalessky, 1938
T. ravisedorum Vilesov et Novokshonov, 1993

Genus *Tshekardembia* Novokshonov, 1995

Tsh. sharovi Novokshonov, 1995

Genus *Kungurembia* gen. nov.

K. brevicervix sp. nov.
K. pallida sp. nov.

Family Sylvardembiidae Novokshonov, 2000

This family is known from isolated impressions. *P. sepicolorata* has been described as Grylloblattida incertae sedis (Aristov, 2000b); however, the wide head, triangular pronotum, and short legs show that it should be classed in the sylvardembiids.

Genus *Sylvardembia* Novokshonov, 1997

S. tamaena Novokshonov, 1997
S. matura Aristov, 2000
S. pectinata Novokshonov, 2000

Genus *Barmaleus* Novokshonov, 1997

B. dentatus Novokshonov, 1997

Genus *Paratillyardembia* Aristov, 2000

P. sepicolorata Aristov, 2000

Family Sojanoraphidiidae O. Martynova, 1952

This is an uncommon family. *S. martynovae* is dominating.

Genus *Sojanoraphidia* O. Martynova, 1952

S. martynovae Storozhenko et Novokshonov, 1995

Genus *Aibolitus* Novokshonov et Storozhenko, 1996

A. medicinus Novokshonov et Storozhenko, 1996

Family Sylvabestiidae Aristov, 2000

This family is known from isolated impressions.

Genus *Sylvabestia* Aristov, 2000

S. tenuis Aristov, 2000

Family Tshekardominidae Novokshonov et Aristov, 2002

This is an uncommon family. *Tsh. maculosa* is dominating.

Genus *Tshekardomina* Novokshonov et Aristov, 2002

Tsh. maculosa Novokshonov et Aristov, 2002
Tsh. imbicilla sp. nov.
Tsh. imbicillisima sp. nov.
Tsh. subincurvata sp. nov.

Family Sylvaphlebiidae Martynov, 1940

Phenopteridae: Carpenter, 1950, p. 204. (syn. nov.)

This is one of the abundant and rather taxonomically diverse families. *S. tuberculata* is dominating. Other members—*S. fucata* sp. nov., *S. perlongata* sp. nov., *S. fimbriata* sp. nov., and *K. spinosa* sp. nov.—are known from isolated impressions.

Martynov (1940) described three new families from Tshekarda: The Sylvaphlebiidae, which include only one member, *S. tuberculata*; Sylviodidae, which con-

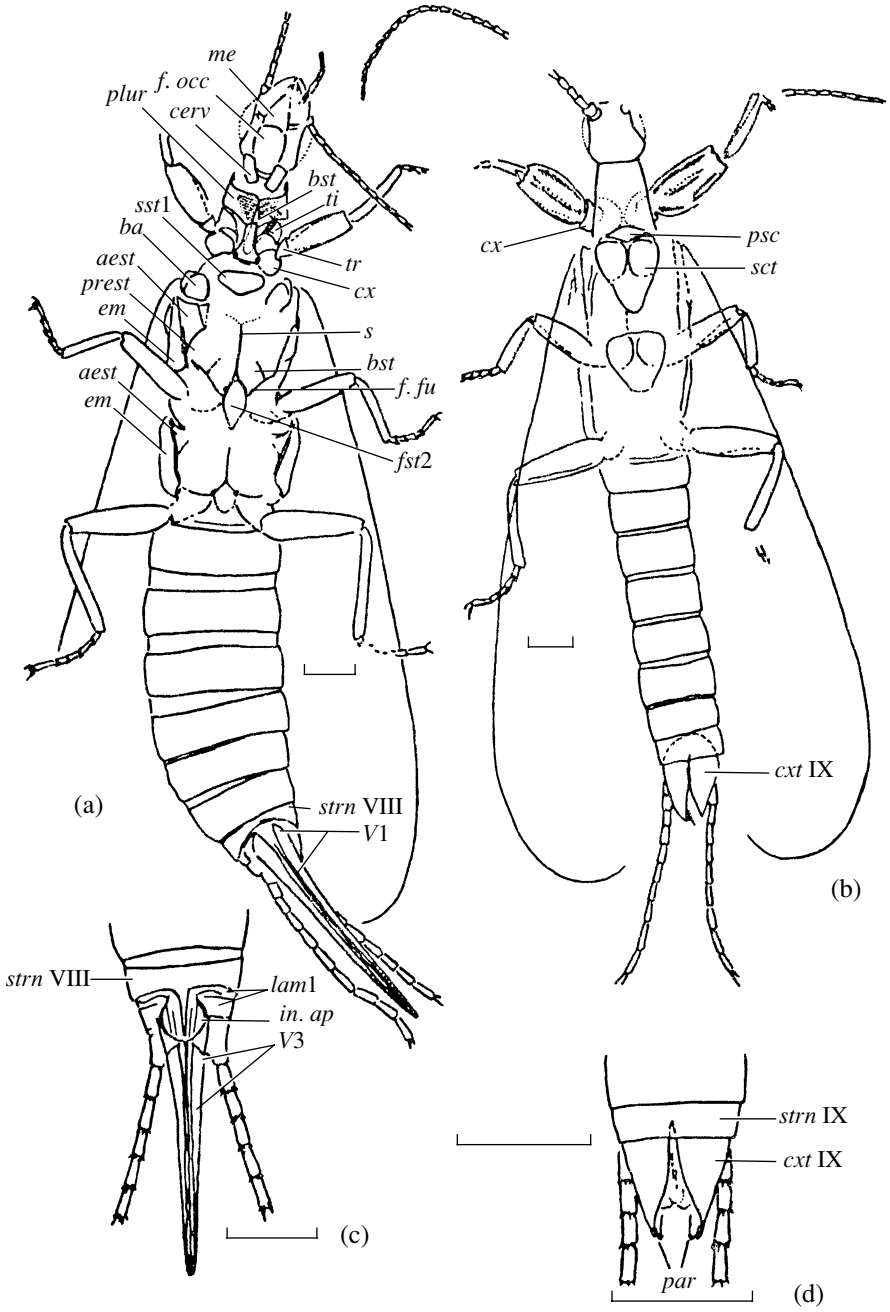

Fig. 1. Representatives of the genus *Tillyardembia* (from Vilesov and Novokshonov, 1995): (a–c) *T. antennaeplana* G. Zalessky, 1937; (a) specimen PIN, no. 1700/4020, female from below; (b) specimen PIN, no. 4987/54, male from above, (c) ovipositor reconstruction based on specimens PIN, nos. 1700/3739, 3838, and 4285; (d) *T. ravasedorum* Vilesov et Novokshonov, 1995, holotype PIN, no. 4987/55, male genitalia from below. Abbreviations: (*aest*) anepistern, (*ba*) basal sclerite, (*bst*) basistern, (*cerv*) cervical sclerites, (*cx*) coxae, (*cxt* IX) gonocoxites, (*em*) epimeron, (*f. fu*) furcal foramens, (*f. occ*) occipital foramen, (*fst*2) mesothoracic furcasternum, (*in. ap*) lower apophyses of ovipositor, (*lam*1) first valvifers, (*me*) mentum, (*par*) paramers of phallic base, (*plur*) pleurite, (*prest*) preepistern, (*psc*) prescutum, (*s*) longitudinal suture in pterothoracic basistern, (*sct*) scutum, (*sst* 1) pterothoracic spinistern, (*strn* VIII) eighth abdominal sternite, (*strn* IX) ninth abdominal sternite, (*ti*) trochantine, (*tr*) trochanter, (*V*1) first valves of ovipositor, (*V*3) third valves of ovipositor. Scale bar 1 mm.

tain *Sylviodes perloides* and *Parasylviodes tetracladus*; and Sylvaellidae, which are restricted to *Sylvaella paurovenosa.* Subsequently, the latter two families were synonymized by Sharov (1962) under Sylvaphlebiidae.

Examination of the holotypes of *Sylvaella* (Novokshonov and Aristov, 1999) and *Parasylviodes* has shown that both are representatives of the family Liomopteridae (see below for details). Study and comparison of

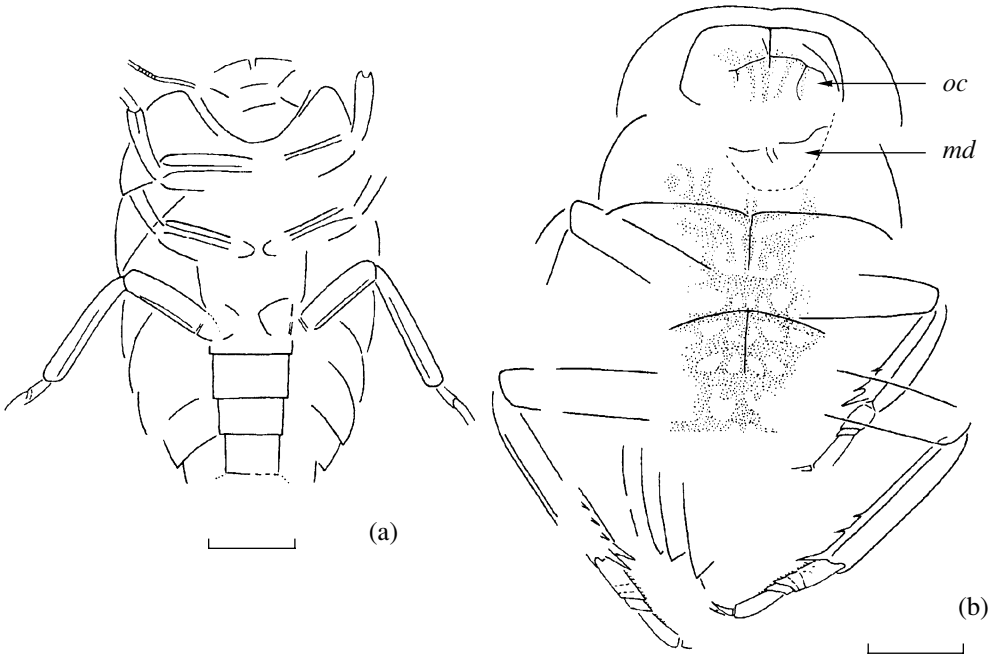

Fig. 2. Grylloblattid nymphs: (a) *Gurianovella sylphidoides* G. Zal., holotype SGM, no. VI 196/15; (b) *Kirkorella mira* G. Zal., holotype SGM, no. VI 196/15. Abbreviations: (*oc*) eye, (*md*) mandible. Scale bar 3 mm.

the venation in the type material of *Sylvaphlebia* and in other grylloblattids show that its venation resembles that of the family Phenopteridae. The difference between the wings of *Sylvaphlebia* (Fig. 13b) and *Phenopterum* (Carpenter, 1950) is so insignificant (*Sylvaphlebia* has not three- but two-branched RS, not simple but two-branched MP, and earlier fork of CuA) that it prevents placing these insects not only in different suborders but in different families as well. Thus, the family Phenopteridae is a junior synonym of the family Sylvaphlebiidae, and the sylvaphlebiids are transferred into the suborder Protoperlina. *S. perloides* is transferred to the family Ideliidae on the basis of its similarity to *Tsh. media* Aristov, 2002.

Currently, the family Sylvaphlebiidae includes nine genera: *Sylvaphlebia*, *Sylvophenoptera* gen. nov., *Kungurocauda* gen. nov. and *Tshekardophlebia* gen. nov. from the Lower Permian of Russia (Tshekarda locality); *Phenopterum* Carpenter, 1950 from the Lower Permian of the United States (Elmo locality); *Brnia* Kukalová, 1964 and *Chlumia* Kukalová, 1964 from the Lower Permian of the Czech Republic (Obora locality); *Paraphenopterum* Storozhenko, 1992 from the Upper Permian of Russia (Soyana locality); and *Belmontophenopterum* Rasnitsyn et Aristov, 2004 from the Upper Permian of Australia (Belmont locality).

Genus *Sylvaphlebia* Martynov, 1940

S. tuberculata Martynov, 1940
S. fucata sp. nov.

Genus *Kungurocauda* gen. nov.

K. spinosa sp. nov.

Genus *Sylvophenoptera* gen. nov.

S. fimbriata sp. nov.
S. perlongata sp. nov.

Genus *Tshekardophlebia* gen. nov.

Tsh. capitata sp. nov.

Family Euremiscidae G. Zalessky, 1951

The family is of low abundance. *E. splendens* has been considered a member of the suborder Grylloblattina (Storozhenko, 1998); however, the elongated anterior legs, straight CuA that has no bend at the point of separation of CuA_1 and CuA_2, and its general venation pattern (Novokshonov and Aristov, in press) make this family more similar to the Sylvaphlebiidae (e.g., to the genus *Sylvophenoptera*) than to any other family of the suborder Grylloblattina.

Genus *Euremisca* G. Zalessky, 1951

E. splendens G. Zalessky, 1951
E. elegans sp. nov.

Family Probnidae Sellards, 1909

In Tshekarda, this family is known from a single impression.

Genus *Sylvafossor* gen. nov.

S. forcipatus sp. nov.

Family Sheimiidae O. Martynova, 1958

In Tshekarda, this family is known from a single impression.

Genus *Sheimia* O. Martynova, 1958

Sh. tshekardensis sp. nov.

Genus *Parasheimia* gen. nov.

P. truncata sp. nov.
P. rotundata sp. nov.

Genus *Pseudosheimia* gen. nov.

P. caudata sp. nov.

Family Visheriferidae Novokshonov, Ivanov, Aristov, 2002

In Tshekarda, this family is known from a single impression.

Genus *Visherifera* Novokshonov, Ivanov, Aristov, 2002

V. sylvaensis sp. nov.

Family Permembiidae Tillyard, 1937

This family is known from isolated impressions.

Genus *Kungurmica* Novokshonov, 1998

K. tshekardensis Novokshonov, 1998

Family Aliculidae Storozhenko, 1997

This is a quite diverse family; however, it is represented by rare specimens.

Genus *Neprotembia* gen. nov.

N. truncata sp. nov.

Genus *Neraphidia* Novokshonov et Novokshonova, 1997

N. mitis Novokshonov et Novokshonova, 1997
N. rigida sp. nov.

Genus *Sojanopermula* Storozhenko, 1992

S. tshekardensis sp. nov.
S. minor sp. nov.

Suborder Grylloblattina Walker, 1914

Family Ideliidae M. Zalessky, 1929

This is an uncommon family. *S. perloides* dominates.

In spite of some similarity to sylvaphlebiids, the genus *Sylviodes* has not been included in the Sylvaphlebiidae and has not been transferred into the suborder Protoperlina. This is due to the absence in *Sylviodes* of a long pectinate distal branch of CuA, which is characteristic of other sylvaphlebiids. Additionally, in a number of features (the greater than average size, archedyction, the presence of blind posterior branches on CuA, and the pattern of its branching), *S. perloides* (Fig. 25) is more similar to a member of the family Ideliidae, *Tsh. media*, than to *Sylvaphlebia* and, thus, is moved to the family Ideliidae.

Genus *Rachimentomon* G. Zalessky, 1939

R. reticulatum G. Zalessky, 1939

Genus *Sylvidelia* Martynov, 1940

S. latipennis Martynov, 1940

Genus *Sylviodes* Martynov, 1940

S. perloides Martynov, 1940

Genus *Sojanidelia* Storozhenko, 1992

S. floralis A. Rasnitsyn, 1996

Genus *Tshekardelia* Aristov, 2002

Tsh. media Aristov, 2002

Genus *Micaidelia* gen. nov.

M. minutissima sp. nov.

Family Idelinellidae Storozhenko, 1997

The species *P. augustata* has been described as a member of the family Kortshakoliidae (Novokshonov, 1999); however, a very broad costal area with straight and nearly vertical anterior branches of SC, CuA possessing short forks in both its branches and the archedyction are more characteristic of the family Idelinellidae than of kortshakoliids. The genus *Permostriga* differs from the type genus *Idelinella* Storozhenko, 1992 (Storozhenko, 1998) in its smaller size, broad intercubital field, and larger archedyction cells.

Genus *Permostriga* Novokshonov, 1999

P. augustata Novokshonov, 1999

Genus *Sylvastriga* gen. nov.

S. miranda sp. nov.

Family Megakhosaridae Sharov, 1961

This is an infrequent family, with the genus *Parakhosara* dominating. *P. martynovi* has been described

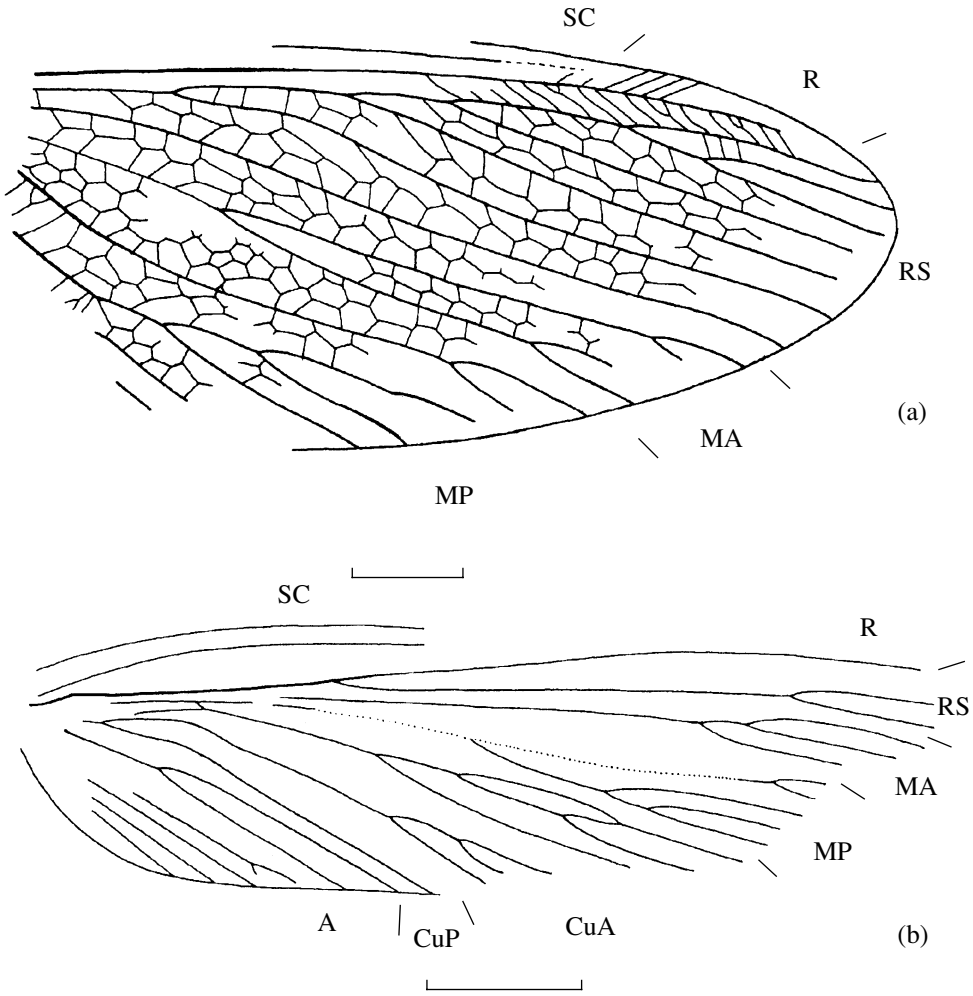

Fig. 3. Representatives of the families Atactophlebiidae and Pinideliidae: (a) *Bardapteron ovale* G. Zal., holotype SGM, no. VI 198/1; (b) *Kishertia tricubitalis* gen. et sp. nov., holotype SGM, KP-769-1. Vein abbreviations standard in all figures. Scale bar 5 mm.

as a separate genus *Sylvakhosara* (Storozhenko, 1993), which was subsequently synonymized under the genus *Parakhosara* (Aristov, 2000a).

Genus *Parakhosara* Storozhenko, 1993

P. martynovi (Storozhenko, 1993)

P. coalita sp. nov.

Genus *Tshekhosara* Novokshonov, 1998

Tsh. improvida Novokshonov, 1998

Genus *Pectinokhosara* gen. nov.

P. sylvardembioides sp. nov.

Family Liomopteridae Sellards, 1909

This most diverse family is uncommon. Representatives of the genera *Sylvaella* and *Parasylviodes* prevail.

As previously mentioned, the genera *Sylvaella* and *Parasylviodes* have up to the present been included in the family Sylvaphlebiidae. However, the former genus differs from the type genus of this family in its quadrangular pronotum, simple anterior branch of CuA (a pectinate anterior branch is typical for all sylvaphlebiids), dominance of simple crossveins, and longer ovipositor (Fig. 28a). *P. tetracladus* also differs from *S. tuberculata* in the small pronotum with wide paranoralia, long hind legs, broad costal field with numerous and occasionally ramifying anterior branches of SC, pectinate RS, and long ovipositor. The same characters make this genus differ from *Sylviodes*, which was earlier included in Sylvaphlebiidae. The above-listed distinguishing features of both *Sylvaella* and *Parasylviodes* are characteristic of Liomopteridae. *Kh. sylvaensis* has been described on the basis of an isolated hindwing as a grylloblattid of unclear systematic position (Martynov, 1940). Later, a better-preserved hindwing and a complete insect (Figs. 28b–28e) were found, thus allowing

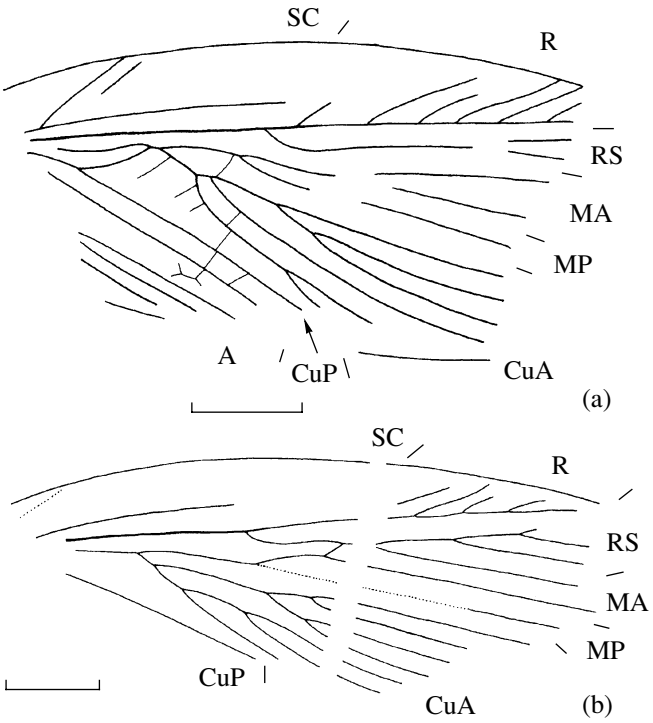

Fig. 4. Forewings of *Euryptilodes commatulus* sp. nov.: (a) holotype PIN, no. 111/168; (b) paratype SGM, KP-769-4. Scale bar 3 mm.

placement of this genus into liomopterids on the basis of the same characters as *P. tetracladus.*

Genus *Sylvaella* Martynov, 1940

S. paurovenosa Martynov, 1940
S. affinis (G. Zalessky, 1939)
S. vitiosa Novokshonov et Aristov, 1999

Genus *Parasylviodes* Martynov, 1940

P. tetracladus Martynov, 1940

Genus *Khosarophlebia* Martynov, 1940

K. sylvaensis Martynov, 1940

Genus *Uralioma* Storozhenko et Aristov, 1999

U. variabilis Storozhenko et Aristov, 1999
U. maxima sp. nov.

Genus *Ornaticosta* Sharov, 1961

O. tshekardensis Aristov, 1999
O. novokshonovi sp. nov.

Genus *Sylvictor* gen. nov.

S. major sp. nov.

Genus *Parasylvaella* gen. nov.

P. umbra sp. nov.
P. minor sp. nov.

Genus *Liomopterella* Sharov, 1961

L. kungurica sp. nov.

Genus *Kungurolioma* gen. nov.

K. cancellata sp. nov.

Genus *Cerasopterum* Kukalová, 1964

C. megakhosaroides sp. nov.
C. impurum sp. nov.

Grylloblattida incertae sedis

The genus *Termoides* has been left within the grylloblattids of unclear taxonomic position because of the lack of an opportunity to reexamine the holotype.

The genus *Sylvanympha* has been described on the basis of a nymph in the superorder Plecopteroidea as an insect of unclear taxonomic position (Novokshonov and Pan'kov, 1999). Strange as this nymph might seem, only two of its characters are still unknown in grylloblattid nymphs: laterally directed hindwing sheaths and forwardly pointed hind tibiae. In other characters, *Sylvanympha* resembles *G. silphidoides* very much, differing from the latter mainly in the shape of its abdomen. For these reasons, *Sylvanympha* has been transferred into Grylloblattida incertae sedis.

Genus *Termoides* G. Zalessky, 1955

T. productus G. Zalessky, 1955

Genus *Gurianovella* G. Zalessky, 1939

G. silphidoides G. Zalessky, 1939

Genus *Sylvanympha* Novokshonov et Pan'kov, 1999

S. tshekardensis Novokshonov et Pan'kov, 1999

Genus *Tshekardites* gen. nov.

Tsh. comitialis sp. nov.
Tsh. lientericus sp. nov.
Tsh. calcomessor sp. nov.
Tsh. curculianticus sp. nov.
Tsh. gracilis sp. nov.

Genus *Sylvaclinicus* gen. nov.

S. echinatus sp. nov.

Genus *Permedax* gen. nov.

P. effertus sp. nov.

Locality of Barda

The locality of Barda is situated on the right and left banks of the Barda River (Sylva River basin) near the village of Matveevo, Kishert' district, Perm region, 60 km north of the locality of Tshekarda. This locality includes three geographically close outcrops—Krasnaya Glinka = Barda 1 (right bank of the Barda River), Barda 2 (left bank of the Barda River downstream of the village of Matveevo), and Krutaya Katushka = Barda 3 (left bank of the Barda River upstream of the village of Matveevo)—which belong to the Koshelevka Formation, Iren' Horizon.

At this point, the grylloblattid collection from this locality that was gathered in various years by Mauer, Permyakova, Zalessky, and Zalessky includes several tens of impressions. There are representatives of four families, eight genera, and nine species in the collection; among them, one genus *Bardapteron* and three species, two of which are described below (*B. ovale, D. bardum* sp. nov., and *Tsh. bardensis* sp. nov.), are endemic.

Family Atactophlebiidae Martynov, 1930

Genus *Bardapteron* G. Zalessky, 1944

B. ovale G. Zalessky, 1944

Genus *Kirkorella* G. Zalessky, 1939

K. mira G. Zalessky, 1939

Family Euryptilonidae Martynov, 1940

Genus *Euryptilodes* Sharov, 1961

E. commatulus sp. nov.

Family Tillyardembiidae G. Zalessky, 1938

Genus *Tillyardembia* G. Zalessky, 1938

T. antennaeplana G. Zalessky, 1938

T. ravisedorum Vilesov et Novokshonov, 1993

Family Liomopteridae Sellards, 1909

Genus *Uralioma* Storozhenko et Aristov, 1999

U. variabilis Storozhenko et Aristov, 1999

Genus *Depressopterum* Kukalová, 1964

D. bardum sp. nov.

Grylloblattida incertae sedis

Genus *Gurianovella* G. Zalessky, 1939

G. silphidoides G. Zalessky, 1939

Genus *Tshekardites* gen. nov.

Tsh. bardensis sp. nov.

Locality of Kishert'

The locality of Kishert' is situated in the Sylva River basin not far from the Barda River mouth, near the village of Ust'-Kishert', Kishert' district, Perm region, 40 km north of the locality of Tshekarda. This locality is represented by three geographically close outcrops: Sylva 1 = Spas-Barda (left bank of the Sylva River upstream of Zapolinskii Log near the village of Spas-Barda), Ust'-Kishert' (Sylva River Basin, Zuevskii Log outcrop near the village of Ust'-Kishert'), and Salamatskii Log (Sylva River Basin, near the village of Ust'-Kishert'), which belong to the Koshelevka Formation, Iren' Horizon.

The grylloblattid collection from this locality that was gathered in various years by Mauer, Zalessky, and Zalessky consists of only a few tens of impressions and includes representatives of three families, five genera, and five species, of which two monotypic genera, *Uralotermes* and *Kishertia* gen. nov., are endemic.

Family Pinideliidae Storozhenko, 1997

This family is represented by a single member of the genus *Kishertia* gen. nov. from the outcrop of Salamatskii Log.

The genus *Pinidelia* has been described in the family Ideliidae and subsequently given family rank in the suborder Grylloblattina (Storozhenko, 1994, 1997). The morphology of *Kishertia* shows that, in its wing shape, structure of the costal field, and general pattern of venation, *Pinideliidae* are closer to Atactophlebiidae, especially to the genus *Kirkorella*, of which both nymphs and subimagoes are known, than to any other family of Grylloblattina. Pinideliidae differ from Atactophlebiidae in MP that ramifies not at the wing base but at wing midlength and M_5 that enters CuA after the latter divides into CuA_1 and CuA_2, whereas it enters CuA before its bifurcation in *Kirkorella*. In the present work, the family Pinideliidae is treated as a member of the suborder Lemmatophorina.

Genus *Kishertia* gen. nov.

K. tricubitalis sp. nov.

Family Tillyardembiidae G. Zalessky, 1938

Genus *Tillyardembia* G. Zalessky, 1938

T. antennaeplana G. Zalessky, 1938

Family Ideliidae M. Zalessky, 1929

Genus *Rachimentomon* G. Zalessky, 1939

R. reticulatum G. Zalessky, 1939

Grylloblattida incertae sedis

The genus *Uralotermes* has been retained among grylloblattids of unclear taxonomic position because of the lack of an opportunity for reexamining the holotype.

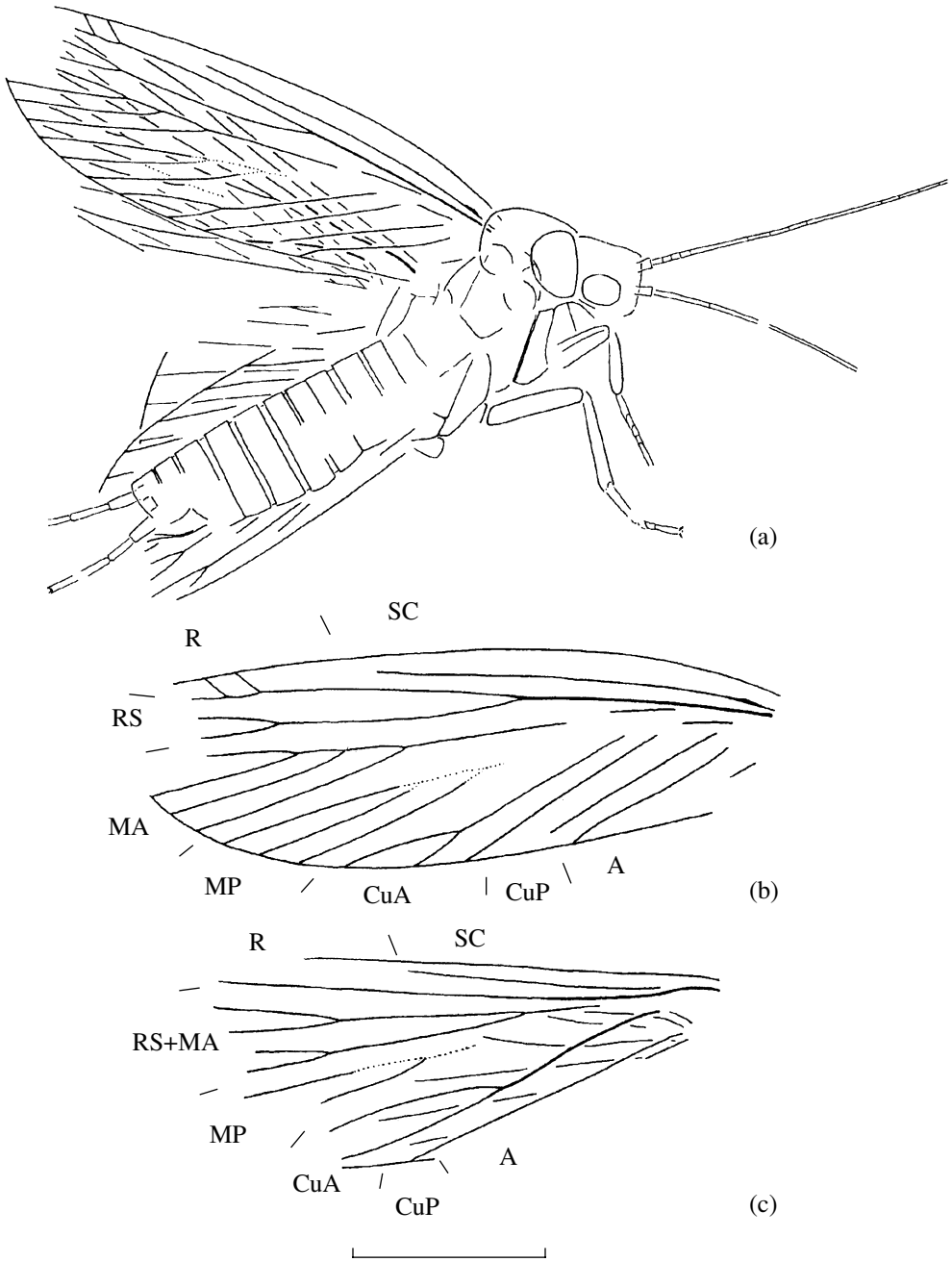

Fig. 5. *Culiciforma formosa* sp. nov., holotype PIN, no. 1700/782: (a) general appearance, (b) forewing, (c) hindwing. Scale bar 3 mm.

Genus *Uralotermes* G. Zalessky, 1937

U. permianus G. Zalessky, 1937

Thus, the fauna of the contemporaneous localities of Tshekarda, Barda, and Kishert' includes 20 families, 63 genera, and 94 species, of which 20 genera and 50 species are described for the first time.

The suborder Protoperlina (12 families) clearly predominates over the suborders Lemmatophorina and Grylloblattina (three and four families, respectively). However, Grylloblattina differs little from Protoperlina in the generic and species diversity because of the high diversity of the family Liomopteridae, whereas the majority of the families of Protoperlina are less diverse.

The Liomopteridae dominate taxonomically and comprise 20% of the grylloblattid species in Tshekarda; however, they account for only 10% of the specimens.

Lemmatophoridae are one of the families dominating in the number of both species (more than 10%) and specimens (14%).

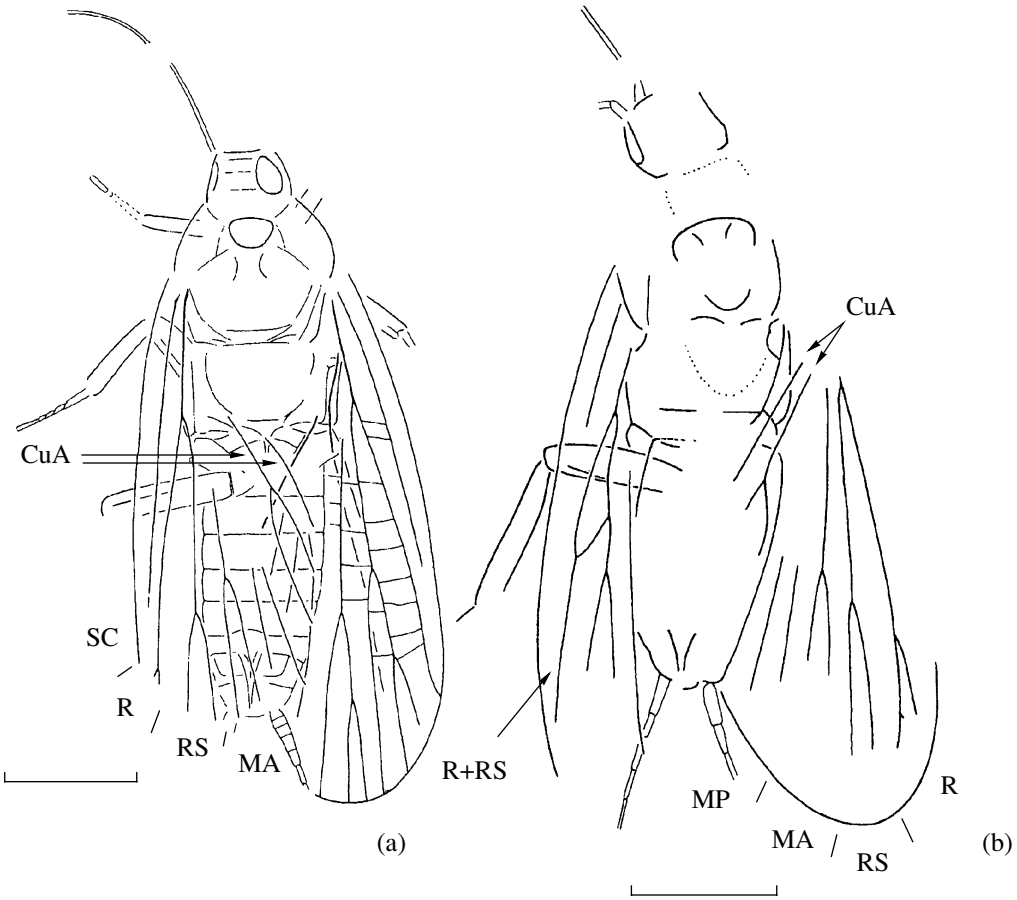

Fig. 6. Representatives of the genus *Sylvaprisca*: (a) *S. focaleata* sp. nov., holotype PIN, no. 4987/2, general appearance; (b) *S. forta* sp. nov., holotype PIN, no. 1700/3491, general appearance. Scale bar 3 mm.

The low-diversity families Tillyardembiidae, Atactophlebiidae, and Ideliidae also dominate in terms of number of specimens (24, 15, and 11%, respectively).

The taxonomic dominance of the Liomopteridae is typical (with rare exceptions) for Permian localities, but liomopterids usually dominate numerically as well, which has not been observed in Tshekarda.

The combination of dominating Lemmatophoridae, which are characteristic of the Lower Permian, and Atactophlebiidae and Ideliidae, which are typical for the beginning of the Upper Permian, are unusual also.

Another distinctive feature of Tshekarda is a large number of families of the suborder Protoperlina, which is three times larger than the number of Grylloblattina families and four times larger than the number of Lemmatophorina families; this feature is characteristic of Artinskian localities. Although the majority of these families are known from single impressions, the suborder also dominates quantitatively owing to the family Tillyardembiidae and makes up a quarter of all grylloblattid specimens. Among Permian localities, this feature is unique to Tshekarda.

Below, a comparison of the Tshekarda grylloblattid fauna with large Permian faunas from the Artinskian through Kazanian is given.

The Early Artinskian (Sakmarian?) locality of Obora (Czech Republic) is similar to Tshekarda in the taxonomic dominance of the Liomopteridae, prevalence of families of the suborder Protoperlina, and four shared families (among seven families known from Obora). Tshekarda differs in the quantitative dominance of the family Lemmatophoridae, which appeared in the Asselian but is not known in Obora, and in the low abundance of Euryptilonidae.

The younger Artinskian locality of Elmo (United States) has nine families in common with Tshekarda. The similarity is even greater because of the prevalence of families of the suborder Protoperlina and the quantitative dominance of the Lemmatophorina and Protoperlina (owing to the families Lemmatophoridae and Probnidae, respectively). Tshekarda differs in the taxonomic dominance of Liomopteridae and in the absence of quantitative dominance of the family Probnidae.

The Ufimian faunas of Vorkuta and Kaltan are far less similar to Tshekarda, although they are close to the

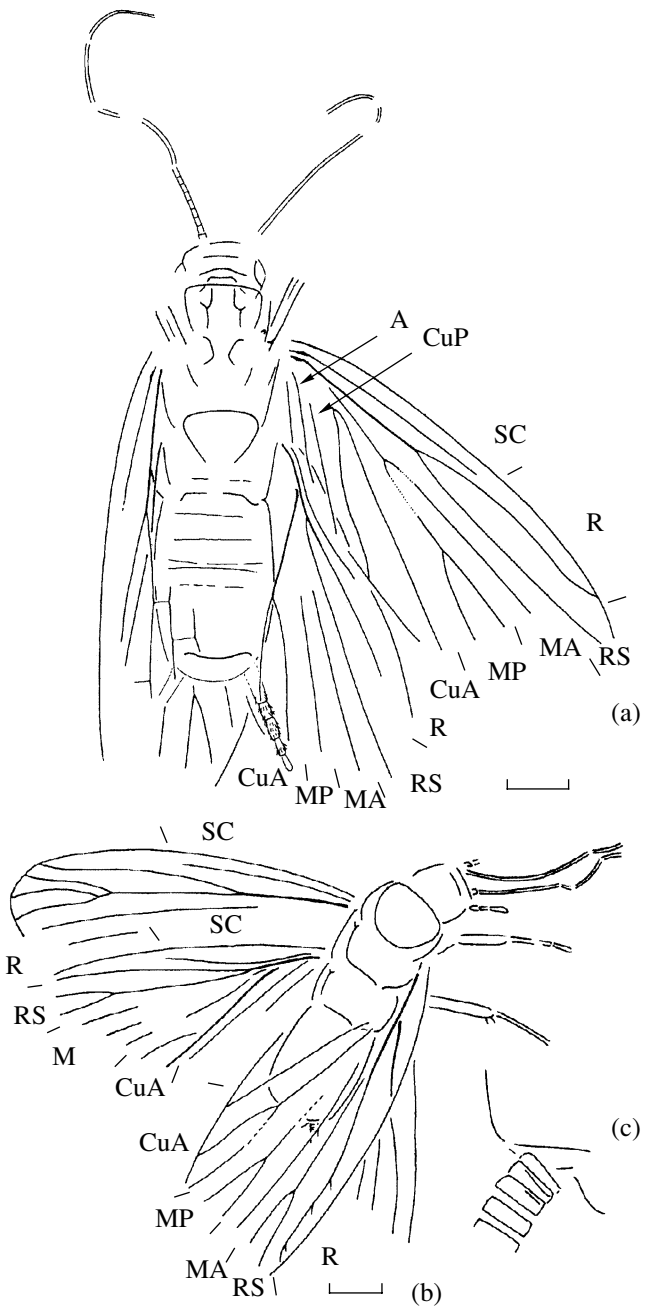

Fig. 7. *Artinska infigurabilis* sp. nov., males: (a) holotype PIN, no. 4987/3, general appearance; (b) paratype PIN, no. 4987/5, general appearance; (c) paratype PIN, no. 4987/5, tip of abdomen. Scale bar 1 mm in Figs. 7 and 8.

latter in age. The only shared feature is, probably, the taxonomic domination of the liomopterids. Both Vorkuta and Kaltan differ in the absolute numerical domination of the Liomopteridae and in the complete absence of representatives of the suborder Protoperlina.

The fauna of the Lower Kazanian locality of Tikhie Gory noticeably differs from that of Tshekarda in the presence of the low-diversity but relatively abundant Liomopteridae and in the small number of Protoperlina families (one out of five). The resemblance lies in the domination of the Atactophlebiidae, although there, in contrast to Tshekarda, they dominate entirely.

Lower Kazanian Soyana is very similar to Tshekarda in taxonomic composition. Of the 14 families known from the latter locality, only the Permotermopsidae have not been found in Tshekarda. Additionally, six common genera are known, *Sojanoraphidia* (Sojanoraphidiidae), *Sheimia* (Sheimiidae), *Sojanopermula* (Aliculidae), *Barmaleus* (Sylvardembiidae), *Sojanidelia* (Ideliidae), and *Parakhosara* (Megakhosaridae). Similar also are the taxonomic domination of the Liomopteridae (20% in Tshekarda and 30% in Soyana) and a relatively large number of Lemmatophoridae and Sylvaphlebiidae impressions (10% of each family in both localities). However, Soyana differs from Tshekarda in the domination of Liomopteridae (20% of species and 30% of impressions of Soyana grylloblattids) and Ideliidae (30% of species and 30% of impressions). In general, members of the suborder Grylloblattina constitute 60% of species and 70% of grylloblattid impressions. in addition, there are a few families of the suborder Protoperlina (7 of 14).

The fauna of the only large Upper Kazanian locality, Kityak, differs from that of Tshekarda in consisting of representatives of only three families, the dominating Liomopteridae and infrequent Ideliidae and Megakhosaridae.

Thus, despite the taxonomic resemblance to Soyana, Tshekarda is most similar to the locality of Elmo in the domination of families of the suborder Protoperlina, taxonomic and numerical domination of the Lemmatophorina and Protoperlina, and presence of seven common families.

MORPHOLOGY OF REPRESENTATIVES OF THE ORDER GRYLLOBLATTIDA

The size varies from very small (in some Permembiidae, the forewing is 2.5 mm long) to large (the forewing of some Atactophlebiidae is 90 mm long).

The head is most often hypognathous, but, more rarely, it is prognathous, as in the families Tillyardembiidae (Fig. 1), Megakhosaridae, and some others. The head capsule is an elongated oval that is almost always smooth (finely tubercular in the Megakhosaridae and Sylvaphlebiidae). The compound eyes are usually large, and the ocelli are often reduced. The frontoclypeal and clypeolabral sutures are developed. The frontal sutures are fused with the epicranial suture; these sutures may not be expressed in many families, e.g., in the Tillyardembiidae. The parietal sutures are long, and the occipital foramen is large. The antennae are filiform, the scape is large, and the antennomeres are usually elongated.

The mouthparts are chewing. The labrum is oval-shaped or trapezoidal. The mandibles are stocky with three or four teeth, one of which may be larger, or are

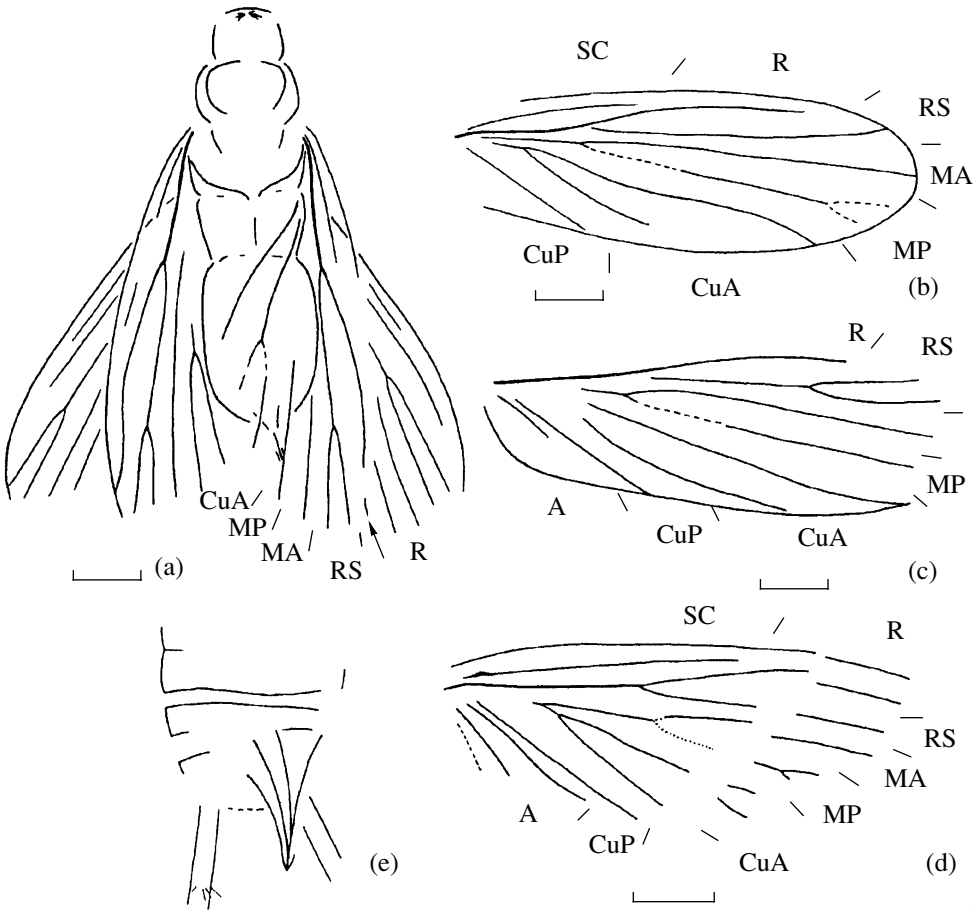

Fig. 8. *Artinska infigurabilis* sp. nov.: (a) paratype PIN, no. 4987/6, general appearance; (b–d) forewings: (b) paratype PIN, no. 4987/8; (c) paratype PIN, no. 4987/6; (d) paratype PIN, no. 4987/4; (e) paratype PIN, no. 1700/2046, tip of female abdomen.

rather narrow with acuminate tips. The maxillary palps are three- or five-segmented. Other mouthparts are known in *T. antennaeplana* only (Vilesov and Novokshonov, 1993). The lateral cervicalia are known in a few species and are large and rectangular, triangular, or rhomboidal.

The pronotum varies from heavily elongated and narrow in Tshekardominidae to transverse in Sylvaphlebiidae, but more often it is approximately as long as it is wide. The prothorax may have a ring of the paranotalia, which is usually rather narrow and narrowing anteriorly. The paranotalia may be narrow or very wide, as in Idelinellidae (Pl. 5, Fig. 4). The sternal region of the prothorax is narrow, and the pleural suture runs vertically. The mesonotum is elongated and subdivided into a notum and postnotum. The scutum is elongated, triangular or rhomboidal, with a longitudinal suture. The prescutum is separated from the scutum by parapsidal sutures and has more or less convex anterior and posterior margins. The scutellar lobes have tergal fissures and are usually not contiguous, and the scutellum is not large. The scutum varies from almost flat (Euryptilonidae) to strongly convex (Euremiscidae). The pleural part is divided by a pleural suture, the epimerons are elongated, the anepisterna and preepisterna are trapezoidal, and the basalars are large. The basisternum is not large and is divided by a longitudinal suture (discrimen) that ends with elongated or rhomboidal furcasternum. The metathorax is similar in structure; however, it differs in the scutum being transverse and having smaller lobes and in the smaller basalars.

The legs are cursorial, usually medium-long; the forelegs are the shortest, and the hind legs are the longest. Leg length may vary from very short (Sylvardembiidae) to very long and slender (Lemmatophoridae). In members of the order Protoperlina, the fore femora are often modified. They may be enlarged in males (Tillyardembiidae), strongly elongated (Sylvabestiidae), highly shortened alongside the normal tibiae (Sylvardembiidae), or transformed into digging femora (Probnidae). The coxae are not large and are widely separated or closely approximate; the trochanters are not large. The femora are usually stocky, each bears a longitudinal ridge, and they may have spinules as well; the tibiae are usually slender and may have spurs. The tarsus is five-segmented; the first and fifth tarsomeres

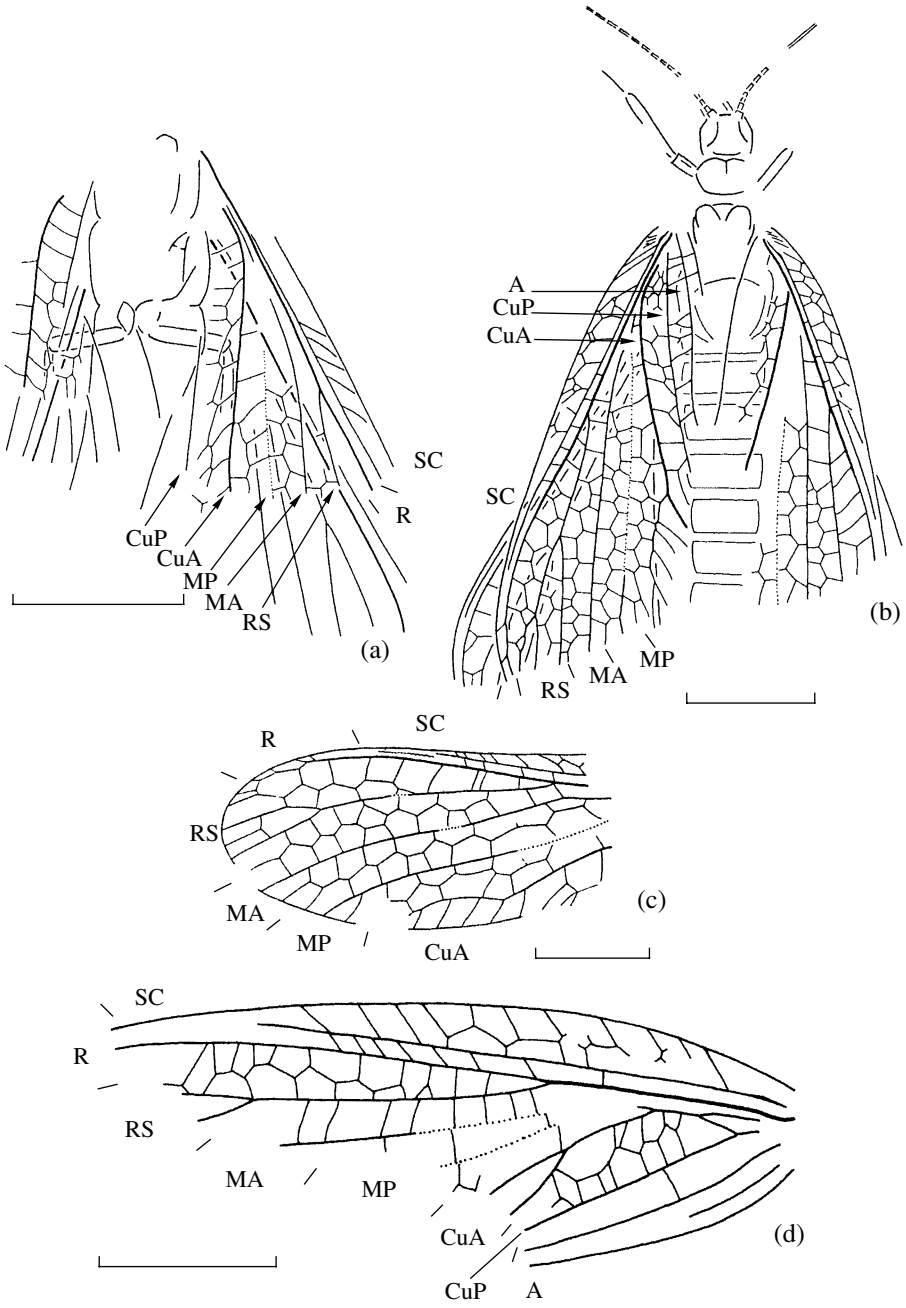

Fig. 9. Representatives of the family Aliculidae: (a) *Neraphidia rigida* sp. nov., holotype PIN, no. 1700/940, general appearance; (b, c) *Neraphidia mitis* Novokshonov et Novokshonova, 1997: (b) specimen PIN, no. 4987/10, general appearance; (c) holotype PIN, no. 1700/643, forewing fragment; (d) *Neprotembia truncata* sp. nov., holotype PIN, no. 1700/1026, forewing. Scale bar 5 mm in Figs. 9a and 9b, and 3 mm in Figs. 9c and 9d.

are the longest, the fourth tarsomere is the shortest, and the terminal tarsomere has a pair of claws and the arolium. In members of the families Probnidae and Tshekardominidae, the tarsus is three-segmented, and the second tarsomere is the shortest.

The wings are normally developed or shortened (Fig. 38) and are elongated, membranous, and may have a color pattern and be hirsute. Venation may be polymerized (Ideliidae) as well as highly simplified (Visheriferidae). In the forewing, the subcosta (SC) is often thickened near its base, neutral basally and neutral apically. The radius (R) and radius-sector (RS) are convex, the anterior branch of the media (MA) is convex or neutral, and the posterior branch of the media (MP) is neutral and desclerotized along its middle part. The anterior branch of the cubitus (CuA) is neutral

before meeting the convex M_5, if the latter is present, then it is convex (it is especially noticeable in members of the family Megakhosaridae), the posterior branch (CuP) is concave, the anal veins are convex. In many families, the position of the RS, MA, and MP stems and the distal branch of CuA with respect to the wing membrane is inverted. Places of inversion are often marked by desclerotized sections, which are arranged along the nodal line. The change of the sign is reported for the entire CuA in the family Chaulioditidae (Aristov, 2004b), and all veins, except for SC, are convex in Euryptilonidae and Atactophlebiidae. Wing fields are named after the veins anteriorly bordering the fields, i.e., the costal field between C and SC, the subcostal field between Sc and R, the interradial between R and RS, the radial field between the basal part of R and MA, the intermedial field between the branches of the media, the medial field between MP and CuA, and the intercubital field between the branches of the cubitus. Crossveins may be simple or form double rows of cells or an archedictyon. The hindwing is similar to the forewing, differing from the latter in the concave CuA and in the large anal lobe formed by A_2 branches. This lobe is folded under the wing at rest.

The abdomen is fusiform, consists of ten segments, and only occasionally reaches the apices of the folded wings. There are ten tergites and nine sternites in males and eight sternites in females. The cerci may be segmented and long (Lemmatophoridae) or shortened (Probnidae) and may be one-segmented (Liomopteridae). The males of some families, e.g., Sylvaphlebiidae, have one-segmented heavily sclerotized cerci. The ovipositor consists of three pairs of valves; the lower pair is the shortest, the second pair is not externally visible, and the upper part is the longest. The ovipositor may be very slender and very long (Sojanoraphidiidae) or, in contrast, much shortened (Lemmatophoridae). In males, the gonocoxae are large and narrowed apically, while the gonostyli are small.

A body color pattern in the form of bands and spots is known in Sylviodidae and Tshekardominidae.

Individual variability in size and venation pattern changes from family to family and is best expressed in such families as Tillyardembiidae and Liomopteridae and less expressed in Tshekardominidae and Euremiscidae.

There are only two examples of sexual dimorphism among grylloblattids; these are the thickened femora in Tillyardembiidae males and the size difference between the sexes in Sojanoraphidiidae.

Individual development may follow two paths; namely, prometaboly in the suborder Lemmatophorina and hemometaboly in the suborders Protoperlina and Grylloblattina (Storozhenko, 1998; Aristov, 1999).

The eggs of fossil grylloblattids are rather large and oval-shaped, bearing longitudinal ridges in Triassic Costatooviblatta (Blattogryllidae).

To date, only one nymph, *Kirkorella mira* (Atactophlebiidae), can be said to unambiguously belong to the grylloblattids, because all the instars have been traced for it (Storozhenko, 1998). Other nymphs that are thought to belong to grylloblattids differ from stonefly-like nymphs in having spurred tibiae that are directed backward—not forward as in stoneflies—five-segmented tarsi, and in the posterior corners of abdominal tergites being drawn out backward (Novokshonov and Pan'kov, 1999; Novokshonov *et al.*, 2000).

SYSTEMATIC PALEONTOLOGY

Order Grylloblattida Walker, 1914

Suborder Lemmatophorina Storozhenko, 1997

Family Atactophlebiidae Martynov, 1930

Genus *Bardapteron* G. Zalessky, 1944

Bardapteron ovale G. Zalessky, 1944

Holotype. SGM, no. VI 198/1, well-preserved fragment of forewing; Barda 3 locality; Kungurian, Koshelevka Formation.

Redescription (Fig. 3a). Large insects. The wing apex is acuminate, and the distal part of the posterior margin of the wing is weakly convex. The costal field is narrow, and the SC nearly reaches the wing apex. R is straight and has simple and straight anterior branches, the RS base is situated in the basal half of the wing, RS has seven branches, and the bases of the basal branches are sinuous. MA has four outruns and more than ten branches. The crossveins form double or triple rows of cells. The simple or Y-shaped crossveins are inclined backward.

Measurements, mm: Forewing fragment length, 41; length of complete wing, about 60.

Remarks. *B. ovale* had been described by G.M. Zalessky (1944) as a representative of a new order, Permodictyoptera, which was synonymized under Palaeodictyoptera. *Bardapteron* was subsequently transferred from palaeodictyopterans to Insecta incertae sedis (Sinitshenkova, 2002). In spite of an incomplete state of preservation, comparison of this insect with the grylloblattids demonstrates its affinity with the family Atactophlebiidae, within which *Bardapteron* is the closest to the genus *Olgaephilus* (Storozhenko, 1994) because of its size, wing shape, and general pattern of venation. *B. ovale* differs from the type species *O. emendatus* in its crossveins being inclined backward, four-branched MA, and greater number of MP branches.

Material. Holotype.

Family Pinideliidae Storozhenko, 1997

Genus *Kishertia* Aristov, gen. nov.

Etymology. From the village of Kishert'.

Type species. *K. tricubitalis* sp. nov.

Diagnosis. Large insects. Forewing strongly elongated, SC parallel to anterior margin of wing, costal field narrower than subcostal field. MA free, total

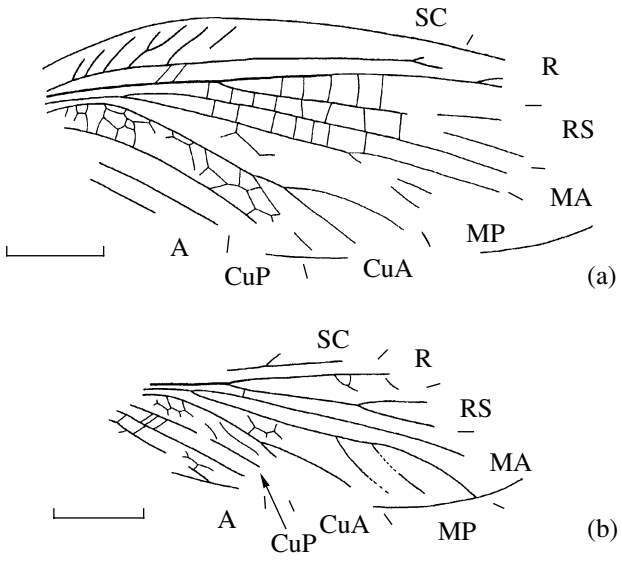

Fig. 10. Representatives of the genus *Sojanopermula*: (a) *S. tshekardensis* sp. nov., holotype PIN, no. 1700/1151, forewing; (b) *S. minor* sp. nov., holotype PIN, no. 1700/4934, forewing fragment. Scale bar 5 mm.

number of RS, MA, and MP branches not less than ten. Media straight before it branches. CuA ramifies very early, prior to its fusion with M_5, and has six to seven branches. A_1 two-branched.

Species composition. Type species.

Comparison. Differs from the type genus *Pinidelia* in its larger size, free MA, greater number of RS, MA, MP, and CuA, and very early branching CuA.

***Kishertia tricubitalis* Aristov, sp. nov.**

Plate 1, fig. 3

Etymology. From Latin *tres* (three) and the cubital vein.

Holotype. SGM, KP-769-1, well-preserved part and counterpart of forewing; Kishert' locality; Kungurian, Koshelevka Formation.

Description (Fig. 3b). The anterior margin of the wing is weakly convex in the basal third; the posterior margin is straight. The costal field is 0.5 times as broad as the broadest part of the subcostal field. R is straight and angled near its base and has two to three branches. MA has three branches; MP stem is slightly arched backward. For the first time, MP ramifies near the wing midlength and has five to six branches. CuA_1 branches for the first time near its midlength, curved at the connection with M_5, and having four branches. CuA_2 is sinuous basally and having three branches. CuP is also bent basally. A_1 bifurcates rather early. A_2 has five branches.

Measurements, mm: Forewing length, about 43.

Material. Holotype.

Family Eurypilonidae Martynov, 1940

Genus *Euryptilodes* Sharov, 1961

***Euryptilodes commatulus* Aristov, sp. nov.**

Plate 1, fig. 2

Etymology. From Latin *commatulus* (neatly brushed).

Holotype. PIN, no. 168/111, moderately preserved positive impression of forewing without apex; Tshekarda locality; Kungurian, Koshelevka Formation.

Description (Fig. 4). Medium-sized insects. The anterior margin of the wing is convex. The costal field is twice as broad as the subcostal one, SC does not reach the distal third of the wing, preserved anterior branches of SC are simple and straight. R is straight and having simple, straight or slightly curved anterior branches. The radial field is narrow, RS is starting just before the wing midlength and having two to three outruns. The media is fused with CuA for a short distance, MA is free or forming a short anastomosis with RS and branches prior to MP, MA has two to three branches, MP is simple or dichotomizing near the wing margin. CuA is pectinate, with six to seven branches. The field between CuA and CuP is strongly widened basally and lacking a net of fine cells. CuP and A_1 are straight, approximate branches of A_2 terminate at the posterior margin of the wing. Crossveins are simple and H-like, the wing membrane is dark.

Measurements, mm: Forewing length, about 23.

Comparison. This new species has a typical for *Euryptilodes* convex anterior margin of the wing, broad costal margin, and polymerized CuA, which is fused with the media for a short distance. *E. commatulus* sp. nov. differs from a single species *E. cascus* Sharov, 1961 from the Upper Permian of the Kuznetsk Basin in its larger size, straight R, field between CuA and CuP without a net of fine cells, and A_2 branches terminating at the posterior margin of the wing.

Remarks. To date, the nymph exuviae are assigned to the species *E. cascus* in addition to the imaginal forewing. Sharov (1961) described it as *E. horridus* placed in this genus with a reservation. This species was subsequently synonymized under *E. cascus* (Storozhenko, 1998). The discussed nymph possesses two characters that are atypical for grylloblattids: legs that are short and hidden under the body (this cannot be explained by incomplete preservation, since both the antennae and the cerci are preserved) and massive and short cerci with transverse striation. These characters are more typical for Palaeodictyoptera nymphs, and the comparison of *E. cascus* with *Rochdalia parkeri* Woodw. (Sinichenkova, 1980) suggests that we are dealing with a palaeodictyopteran nymph.

Material. In addition to the holotype, paratypes PIN, no. 1700/846 from the same locality and SGM, KP-769-4 from the Barda locality.